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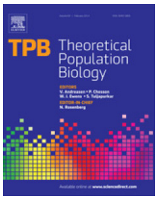

The effectiveness of marine protected areas for predator and prey with varying mobility

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ABSTRACT

Marine protected areas (MPAs) are regions in the ocean where fishing is restricted or prohibited. Although several measures for MPA performance exist, here we focus on a specific one, namely the ratio of the steady state fish densities inside and outside the MPA. Several 2 patch models are proposed and analyzed mathematically. One patch represents the MPA, whereas the second patch represents the fishing ground. Fish move freely between both regions in a diffusive manner. Our main objective is to understand how fish mobility affects MPA performance. We show that MPA effectiveness decreases with fish mobility for single species models with logistic growth, and that densities inside and outside the MPA tend to equalize. This suggests that MPA performance is highest for the least mobile species. We then consider a 2 patch Lotka–Volterra predator–prey system. When one of the species moves, and the other does not, the ratio of the moving species first remains constant, and ultimately decreases with increased fish mobility, again with a tendency of equalization of the density in both regions. This suggests that MPA performance is not only highest for slow, but also for moderately mobile species. The discrepancy in MPA performance for single species models and for predator–prey models, confirms that MPA design requires an integrated, ecosystem-based approach. The mathematical approaches advocated here complement and enhance the numerical and theoretical approaches that are commonly applied to more complex models in the context of MPA design.

1. Introduction

Marine protected areas (MPAs) are regions in the ocean where fishing is restricted or prohibited. They have been used to manage fisheries for conservation and for habitat restoration, while taking the economic interests of the fishing fleet into account, both at local as well as regional scales. For example, MPAs have been shown to increase the densities of harvested species inside of MPAs (Halpern, 2003; Claudet et al., 2010), and MPAs may also increase fish densities outside of the MPA via spillover and/or larval export (Roberts et al., 2001; Sale, 2005; Goñi et al., 2008). Spillover is the net movement of adult fish from the reserve into the fishing grounds. To increase yield from the fishery, the density of fish in the fishing grounds must increase enough to more than compensate for creation of the MPAs and the associated reduction in the area of the fishing grounds (Roberts et al., 2001; Kellner et al., 2007; Abesamis and Russ, 2005). Spillover and larval export are essential to successfully increase fisheries yield, highlighting the importance of explicitly incorporating movement into models of MPA function and design (Botsford et al., 2001; Moffitt et al., 2009; Langebrake et al., 2012). Although some early mathematical models of MPAs did not explicitly include spatial movement (Mangel, 1998; Hastings and Botsford, 1999), there has also been an extensive numerical modeling literature where models do include fish mobility dating back to the work (Beverton and Holt, 1957) by Beverton and Holt, see for instance Polacheck (1990) for single species models, and (Walters et al., 1999; Walters, 2000; Micheli et al., 2004; White, 2008; White and Samhouri, 2011; Takashina et al., 2012) for numerical models that include predators and prey, or (Baskett et al., 2007; Kellner and Hastings, 2009; Kellner et al., 2010; Barnett and Baskett, 2015) for numerical models with multiple trophic levels and structure.

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A prevailing conclusion of these numerical investigations is that MPAs are believed to be effective for slow species, but far less so for more mobile species. This aligns with most field assessments of MPAs that show that densities of fish inside MPAs are much greater than densities outside of MPAs (Halpern, 2003; Claudet et al., 2008, 2010), but that increased species mobility diminishes this effect. In Moffitt et al. (2009) it is shown that in a model with both larval and adult movement, species persistence may decrease sharply when the home range of the adults increases, and is less dependent on larval dispersal distances. This suggest that the adult dispersal rates and distances are important features in MPA design. However, recent studies have suggested that some of the putative beneficial effects of MPAs have alternative explanations, e.g. due to biases in siting of MPAs (Osenberg et al., 2011) or differential movement of fishes inside vs. outside of MPAs (Eggleston and Parsons, 2008; Langebrake et al., 2012). In the recent review Baskett and Barnett (2015), it is shown that alternative hypotheses may lead to opposing effects of MPAs on disease prevalence, on density-dependent fish movement, and on the strength of trophic cascades within MPAs. On the other hand, the same review Baskett and Barnett (2015) indicates that MPAs tend to increase species diversity, and tend to decrease the variability of several measures, including fish biomass.

These findings indicate that there is currently not always a consensus about the factors that promote MPA effectiveness, and therefore a continued (re-)evaluation is necessary. We propose to contribute to this effort by using a more rigorous analytical approach, instead of the more traditional numerical and simulation-based methods. One of our findings is that MPAs can also be effective for species with intermediate movement rates, especially in the context of predator–prey systems. This agrees with the more recent empirical findings, and would enlarge the class of species that would benefit from protected areas.

The purpose of this paper in particular, is to mathematically investigate how differences in species impact MPA performance. We considered two kinds of variations in species ecology. First, species have variable mobility, which is represented by diffusivity parameters in our mathematical models. Second, species interact through a simple predator–prey relation, rather than considering isolated species.

Throughout the paper we will use a traditional measure of MPA effectiveness, namely the ratio of the densities of each species inside versus outside the MPA. Our analysis is guided by two specific questions which are part of the folklore in ecological modeling:

- **Is increased mobility always stabilizing**? That is, if species mobility is increased, will the system display a higher degree of stability, both locally as well as globally?
- **Is increased mobility always equalizing**? That is, if species mobility is increased, will the density ratio get closer to 1?

There are several other measures for MPA effectiveness that are commonly used in the theoretical and empirical literature, such as the fisheries yield, and the ratio of total biomass inside versus outside, or before versus after MPA implementation. For a similar mathematical analysis of the behavior of these other MPA measures with respect to fish mobility for a related single-species, spatially-explicit model, see Langebrake et al. (2012). As discussed in White et al. (2011), the interpretation of the numerical values of all these MPA efficiency measures should always be considered in the appropriate context by MPA designers and managers. This is accomplished by incorporating as many features as possible about size and scale of the MPA, as well as the life-histories of the species that the MPA is intended to protect.

Empirical data (Claudet et al., 2010) shows that the ratio of the density of fish inside versus outside an MPA increase as mobility of the fish increase. Specifically, among commercially exploited fishes, the least mobile species showed an approximately 2-fold increase and the most mobile species showed a 2.64-fold increase in abundance in response to protection. We first show that a simple model with only a single fish species contradicts this empirical result. However, as already mentioned, many fish species are part of a foodweb or of trophic cascades. Here we consider a predator–prey system with one predator and one prey. In some cases, this additional feature in the model does allow the ratios of both predator and prey to increase when the mobilities of either the predator or the prey is increased. For example, we will show that the prey steady state ratio increases with prey mobility, provided that the predator mobility is low.

2. One-species MPA-FG model

We considered an environment that consists of two patches. One is the MPA, and the other is the Fishing Ground (abbreviated to FG henceforth). The variable $u_1(t)$ is the fish density in the MPA at time t and $u_2(t)$ is the fish density in the FG. Inside each patch, fish densities follow the logistic differential equation (Kot, 2001), with per-capita growth rates $r(1-u/K)$. In the FG, there is removal of fish at the per-capita harvesting rate f. Fish migrate between the two patches according to Fick's law: the migration rate is proportional to the difference of the fish densities in both patches, in the direction of the patch with lower density. These assumptions yield the system of equations:

$$\begin{aligned}\frac{du_1}{dt} &= ru_1(1-u_1/K)+D(u_2-u_1),\\ \frac{du_2}{dt} &= ru_2(1-u_2/K)-fu_2+D(u_1-u_2)\\ &= \tilde{r}u_2(1-u_2/\tilde{K})+D(u_1-u_2),\end{aligned} \tag{1}$$

where

$$\tilde{r} := r-f \quad \text{and} \quad \tilde{K} := K\frac{\tilde{r}}{r}, \tag{2}$$

where the sign of $\tilde{r}$, or equivalently of $\tilde{K}$, may or may not be positive. We cannot directly solve for the non-extinction equilibrium of (1), but we can characterize this equilibrium. It satisfies

$$\begin{aligned}u_1 &= \frac{K}{r}\left[r-D\left(1-\frac{u_2}{u_1}\right)\right]=\frac{K}{r}\left[r-D\left(1-\frac{1}{\rho}\right)\right],\\ u_2 &= \frac{\tilde{K}}{\tilde{r}}\left[\tilde{r}+D\left(\frac{u_1}{u_2}-1\right)\right]=\frac{\tilde{K}}{\tilde{r}}\left[\tilde{r}+D\left(\rho-1\right)\right],\end{aligned} \tag{3}$$

where $\rho := \frac{u_1}{u_2}$ is the ratio of the fish densities. Dividing the first by the second, noting that $\frac{K}{r}=\frac{\tilde{K}}{\tilde{r}}$, and rearranging gives the cubic equation for the equilibrium ratio

$$F(\rho,D) := \rho^3+\left(\frac{\tilde{r}}{D}-1\right)\rho^2-\left(\frac{r}{D}-1\right)\rho-1=0. \tag{4}$$

For a fixed value of the diffusivity parameter D, any solution ρ of (4) such that the corresponding values of u_1 and u_2 in (3) are positive, yields a positive steady state. It is shown in Theorem 1 in the Appendix A that such a positive steady state is always unique, that it is globally stable, and that the corresponding ratio ρ is always larger than 1. More precisely, if $f \leq 2r$, then there is a positive steady state for every positive value of D. If $f > 2r$ on the other hand, a positive steady state exists only if $D < r\tilde{r}/(r+\tilde{r}) =: D_{\max}$. Furthermore, it can be shown by implicit differentiation of (4) that the ratio ρ is a decreasing function of D in all cases. If $f \leq 2r$, then $\rho \to 1$ as $D \to \infty$. But if $f > 2r$, then $\rho \to (f-r)/r > 1$ as $D \to D_{\max}$. The expressions (3), and the fact that $\rho > 1$ for