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A reassessment of equivalence in yield from marine reserves and traditional fisheries management

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Lively debate continues over whether marine reserves can lead to increased fishery yields when compared to conventional, quota-based management, apparently driven by differences in the complexity and biological richness of the models being used. In an influential article, Hastings and Botsford used an analytically tractable, spatially implicit, non-age-structured model to assert that reserves are typically incapable of increasing yields relative to conventional management, regardless of the type (pre- or post-dispersal, involving adults and/or larvae) or functional form (Ricker or Beverton-Holt) of density dependence present. A recent numerical (simulation) model by Gaylord et al. concludes that reserves can enhance yield compared to conventional management, a result the authors attribute to their spatially-explicit evaluation of stage-structured adult growth, survivability and fecundity; and intercohort (adult-on-larvae) post-dispersal density dependent population dynamics. Here we demonstrate that the increased model complexity is not responsible for the different conclusions. We analyze a spatially-implicit model without stage structure that incorporates intercohort post-dispersal density dependence. In this simple model we still find annual extirpation of adult populations outside reserves due to fishing to enhance larval recruitment there, allowing for increased yields compared to those achieved when harvest is evenly spread across the entire domain under conventional management. Consideration of neither spatially-explicit dispersal dynamics nor stage-structure in adult demographics is required for reserves to substantially improve yield beyond that attainable under conventional management. In contrast, consideration of within cohort post-dispersal density dependence among larva during settlement in an otherwise identical model generates equivalence in yield between the two management strategies. These results recast a common message characterizing the relative benefit of reserve versus non-reserve management from “equivalence at best” to “potentially improved”.

The use of marine reserves as a tool in fisheries management is relatively new in most regions, and their ultimate influence on fish stocks and fishery yield is only just beginning to be resolved empirically (Halpern and Warner 2002). In the absence of long-term studies, models can offer assistance in predicting such effects; however, any error in model conclusions may be especially consequential to fishery welfare due to the large spatial scale over which fishery management operates. In a highly influential paper, Hastings and Botsford (1999) claimed that reserves could at best provide equivalent yields to conventional fishery management. This claim was based on an extremely simple

model that abstracted away most of the richness of fish life histories and the spatial complexities of the environment; the gain from this simplicity was an analytical result that seemed applicable for a variety of fishery species.

Recently, Gaylord et al. (2005) analyzed a numerical model that incorporated stage-structured growth, survivability and fecundity, as well as explicit larval dispersal in space; they found circumstances where marine reserves could enhance yield relative to conventional management. The authors credit this contrast with the earlier result to their model's spatially-explicit, stage-structured evaluation of post-dispersal density

dependent fish population dynamics (Hastings and Botsford (1999) claimed – but did not show – that their results extended to this life history). This follows a general trend in theoretical research on fisheries, where numerically-derived results elaborate upon or sometimes contradict past conclusions based on less complex, analytical models (Gerber et al. 2003). Evaluation of alternative management strategies incorporating no-take marine reserves has become commonplace, and novel results describing population dynamics of marine and terrestrial (e.g. plant) species characterized by long-distance dispersal are often attributed to complex life history characteristics being evaluated in a spatially-explicit manner for the first time (Nathan 2006).

There are actually two ways in which post-dispersal density dependence can act. First, the recruitment success of settling larvae may depend negatively on the total number of settling larvae if they are competing with one another for space (e.g. refugia) or food (Shima and Osenberg 2003, Hixon and Jones 2005). Second, the recruitment success of settling larvae may depend negatively on the number of conspecific adults already at the site if the adults are controlling space or if they cannibalize the larvae. The latter form of post-dispersal density dependence is common among nearshore fish (Myers and Cadigan 1993, Caley et al. 1996, Hixon and Webster 2002, Webster 2003), especially among predatory fish and invertebrates (Botsford and Hobbs 1995, Folkvord 1997, Skajaa et al. 2003), which also happen to be priority target species for many fisheries (CDFG 2005). Gaylord et al. (2005) used the second form; we suspect that Hastings and Botsford (1999) had the first form in mind. Here, we revisit Hastings and Botsford's model, and show that with the second type of post-dispersal density dependence, the model does predict higher yields from reserves than from conventional management. In our model, annual extirpation of adult populations in between reserves due to fishing enhances larval recruitment there, allowing for increased yields. In contrast, consideration of the first type of density dependence in an otherwise identical model recovers Hastings and Botsford's "equivalence" result. As a result, neither stage structure nor explicit space is required for Gaylord et al.'s qualitative result.

Methods and results

We constructed a model similar in framework and identical in assumptions to that built by Hastings and Botsford. In the model adults are stationary and affected by a constant mortality probability, and larvae are distributed so widely that the density of settling individuals is independent of location along the coastline. Hastings and Botsford's technique did not require

that the functional form of density dependence be specified. Their technique cannot be applied to adult-on-larvae density dependence, so we illustrate the analysis using a Ricker function to represent this process (Ricker 1954). Given conventional, non-reserve management along a coastline of length = 1, fish population dynamics are given as

$$N_{t+1} = N_t + \lambda_0 N_t e^{-gN_t} - mN_t - Y_t \quad (1)$$

where N equals both the total number of adults as well as the adult density at any location along the coast, Y equals harvest, m equals the adult natural mortality probability, λ_0 equals the density independent per capita production of larvae by adult fish, and g is the density dependence coefficient. The latter parameter only affects the scale at which N is expressed, and so is set equal to one. At a fixed harvest rate, the population reaches equilibrium, with surplus growth (yield to the fishery) being

$$Y^* = \lambda_0 N^* e^{-N^*} - mN^* \quad (2)$$

Maximum sustainable yield (MSY) is achieved when N^* is maintained at the level where the derivative of yield with respect to population density equals zero:

$$\frac{\partial Y^*}{\partial N^*} = \lambda_0 e^{-N^*} - \lambda_0 N^* e^{-N^*} - m = 0 \quad (3)$$

$$N_{msy}^* = 1 - W(em/\lambda_0) \quad (4)$$

where $W()$ is the Lambert W -function: $W(z)$ is the value of w that solves $z = we^w$ (Corless et al. 1996). Substituting N_{MSY}^* from Eq. 4 into Eq. 2 and solving for $Y^*(\lambda_0, m)$ produces an ugly equation that offers no insights. As a more practical approach, we determine MSY by solving Eq. 3 numerically, then placing the corresponding N_{MSY}^* -values into Eq. 2.

With reserves, a fraction c of the coastline is protected from fishing. Production outside the reserves, thus import of larvae into reserves from fishable areas, is zero because all adults in fishable areas are immediately caught by the fishery. Although we recognize this zero-escapement fishery management policy to be problematic in practice (Discussion), our model offers a best case scenario for reserves: only if reserves outperform conventional management in this scenario do they have a chance of performing competitively in more reasonable fishing scenarios. This also parallels the assumptions made by Hastings and Botsford (1999) and Gaylord et al. (2005). As a result, the equilibrium population size for a given reserve size is

$$N_r^* = N_r + c\lambda_0 N_r^* e^{-gN_r^*} - mN_r^* \quad (5)$$

where N_r^* equals the adult density in the reserves. (Note that c/c has been factored out of Eq. 5). Once again g is set to one. The fishery catches all individuals that recruit outside the reserves:

$$Y_r^* = c\lambda_0 N_r^* (1 - c)e^{-N_r^*} \quad (6)$$

where N_0^* is the adult density outside the reserve before recruitment. Assuming that $N_0^* = 0$, solving Eq. 5 for N_r^* ,

$$N_r^* = \log\left(\frac{c\lambda_0}{m}\right) \quad (7)$$

and substituting the solution into Eq. 6 generates

$$Y_r^* = \lambda_0 c (1 - c) \log(\lambda_0 c / m) \quad (8)$$

Maximum sustainable yield with reserves, MSY_r , is achieved at $Y_r^*(c)$ when the derivative of yield with respect to c is zero:

$$\frac{\partial Y_r^*}{\partial c} = \lambda_0 \log\left[\frac{c\lambda_0}{m}\right] + \lambda_0 - 2c\lambda_0 \log\left[\frac{c\lambda_0}{m}\right] - c\lambda_0 = 0 \quad (9)$$

We determine MSY_r by solving Eq. 9 numerically, then placing the corresponding c_{MSY_r} -values into Eq. 8.

Maximum sustainable yield under conventional versus reserve-based management is compared in Fig. 1, and optimal proportion of the coast in reserves corresponding to MSY_r is presented in Fig. 2. Yield is always greater with reserves for all values $\lambda_0 > 1$ and/or $m < 1$, and this benefit of reserves over conventional management increases with increased per capita larval production and/or reduced adult mortality probability. Optimal proportion of the coast in reserves is highest when per capita production of larva is low and mortality probability is high, and it plateaus to approximately 50–60% as λ_0 becomes large (e.g. 1000+) and/or m approaches zero.

Reconfiguration of the above models to instead contain within cohort post-dispersal density dependence among larva at their settlement location generates equivalence in yield between conventional and reserve-based management strategies.

Discussion

Agreement between our analytical model and Gaylord et al.'s numerical model results removes any ambiguity about the potentially positive effect of marine reserves on yield for fisheries targeting species exhibiting post-dispersal density dependence where recruitment success of settling larvae depends negatively on the number of conspecific adults at the settlement site. In light of this concurrence, we recommend that referencing of Hastings and Botsford's high-profile "equivalence at best" results (Gårdmark et al. 2006, Hilborn et al. 2006, Holland and Schnier 2006, Ojeda-Martinez et al. 2007) be limited to discussions of species exhibiting pre-dispersal density dependence, or intracohort ("larvae-on-larvae") post-dispersal density dependence. Note that we do not compare fishery management strategies under sub-optimal conditions, where, for example, reserves may increase yield compared to over-fished conditions under conventional management (Hart 2006).

In our analysis reserve-based management outperforms conventional management because only under reserves does the optimal harvest strategy call for zero escapement (i.e. local extirpation) in the fishing area. This strategy incapacitates the density dependence equation outside reserves, allowing all larvae that settle

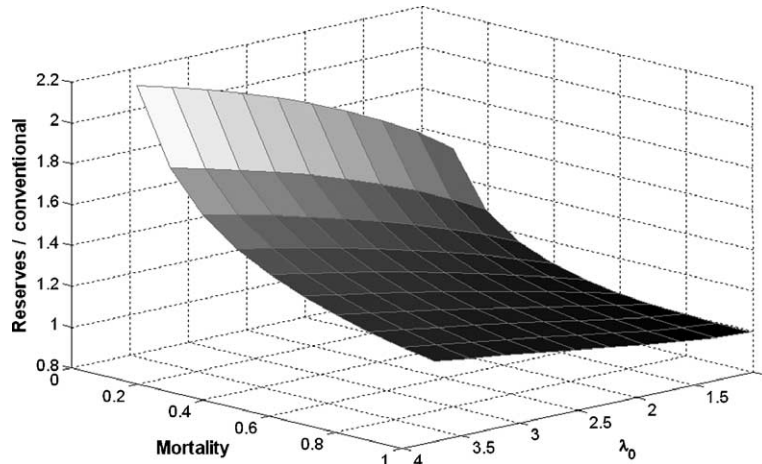


Fig. 1. Maximum sustainable yield (MSY) with reserves relative to that without reserves ("conventional"), evaluated across per capita larva production (λ_0) and adult mortality (m) parameter values. MSY with reserves is equivalent to that without reserves for semelparous fish with $\lambda_0 = 1$, and is increasingly larger than MSY without reserves for all other, more realistic, demographic parameter values.

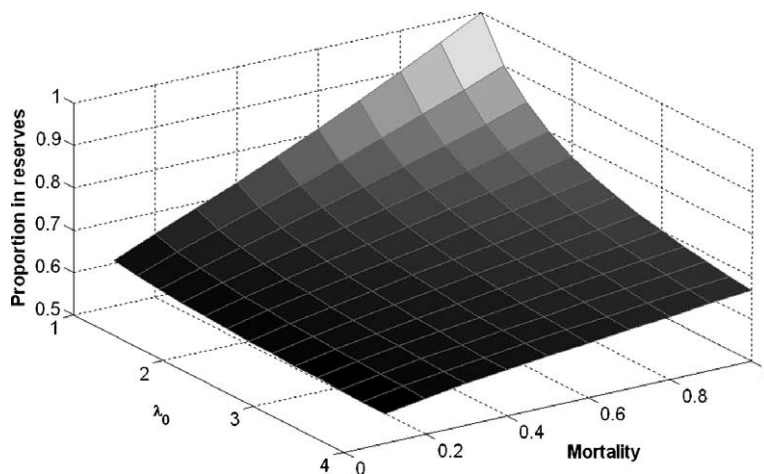


Fig. 2. Optimal proportion of coast protected from fishing that maximizes MSY_r , evaluated across per-capita production and annual mortality parameter values. Optimal proportion in reserves ranged from 0.57 to 1.0, where $MSY_r = 0$. Optimal proportion in reserves plateaus at 50–60% as λ_0 becomes very large (e.g. 1000+).

there to recruit into the population and be harvested at the next time step. Qualitatively identical results are also expected from using a Beverton-Holt density dependence equation, because it too would allow all settling larvae to recruit into an area experiencing zero escapement. Under conventional management, however, density dependence still operates across the fishing area because maximum yield requires a positive, non-zero escapement management policy. As a result, mortality of settling larvae due to density dependence reduces the recruit population available for harvest.

A zero escapement management strategy, even if limited to between no-take marine reserves, remains problematic. Annual extirpation of local fish populations by fisheries may be impossible and undesirable due to inadequate efficiency and unacceptably high economic costs associated with trying to harvest so comprehensively (Clark 1990). Moreover, such a strategy may result in substantial destruction or deterioration of nearshore fishery grounds habitat important for recruitment processes (Parrish 1999, Fromentin et al. 2001, Campbell and Pardede 2006). Some level of escapement is required for practical, if not economic and conservation, reasons; prompting the need for further evaluation of the relative costs and benefits to fisheries exhibiting non-zero escapement in a reserve-based management program. In our model, this would enter as a positive value of N_o^* . As this value increases, the maximum sustainable yield decreases by a factor of $e^{-gN_o^*}$. Thus, if g and/or N_o^* is sufficiently small, overall yield may still be larger under reserve management.

Optimal proportion in reserves corresponding to MSY_r remains above 50% for all reasonable parameter values, a remarkably high figure compared that im-

plemented in practice (McNeill 1994, CDFG 2007). Although reserves may need to constitute large proportions of the coast for conservation goals to be met (Halpern 2003), our simplified results should not be used for guiding reserve design or as evidence that large proportions are essential for maximizing benefits to fisheries. High optimal proportions of the coast in reserves are sometimes associated with optimal management (Botsford et al. 2003, Gaylord et al. 2005, Neubert 2003); however, such results are also associated with high or infinite harvest rates in between reserves. With increased escapement levels in between reserves, thus less reliance by fisheries on exportation of larvae from source populations in reserves, optimal proportion of the coast under protection from fishing will likely decrease.

Gaylord et al. (2005) highlight “three interconnected factors [that are] particularly fundamental to reserve function” (p. 2188). They attribute a dramatic increase in yield (up to 60%) under reserve management compared to conventional management to their (1) spatially-explicit evaluation of fish population and fishery dynamics coupled with (2) post-dispersal density dependence of fishery species acting in concert with (3) stage-structured adult growth, survivability and fecundity. Hastings and Botsford (1999) also discuss the potential for reserves to enhance yield when evaluated with a model having stage-structured adult fecundity. However, our model’s simple construct illustrates the solitary effect of post-dispersal density dependence in substantially enhancing yield under reserve management. MSY_r is at least 60% greater than that under conventional management for nearly all species with $\lambda_0 > 1$, given moderately low adult mortality probabilities (Fig. 1). While stage-age structured demographics

and explicit consideration of spatial dynamics may further increase yield, their exclusion does nothing to diminish the qualitative result that reserves can substantially benefit fisheries targeting species exhibiting post-dispersal density dependence.

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