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Permalink

<https://escholarship.org/uc/item/0zb446n6>

Journal

Ecological Applications, 15(3)

ISSN

1051-0761

Authors

Baskett, Marissa L
Levin, Simon A
Gaines, Steven D
[et al.](#)

Publication Date

2005-06-01

DOI

10.1890/04-0723

Peer reviewed

MARINE RESERVE DESIGN AND THE EVOLUTION OF SIZE AT MATURATION IN HARVESTED FISH

MARISSA L. BASKETT,^{1,3} SIMON A. LEVIN,¹ STEVEN D. GAINES,² AND JONATHAN DUSHOFF¹

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA

²Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106 USA

Abstract. By significantly changing size-dependent mortality, fisheries can cause rapid evolution toward earlier maturation in harvested species. Because earlier maturation negatively affects biomass yield and sustainability, ignoring evolutionary changes could significantly reduce the success of fisheries management policy. With a quantitative genetic model of size at maturation that incorporates phenotype plasticity, we examine the impact of different management strategies including traditional effort control and Marine Protected Areas (MPAs). After verifying the model's accuracy, using historical trajectories for size at maturation in cod (*Gadus morhua*), we test model predictions under different management schemes with life history parameters for red snapper (*Lutjanus campechanus*) and two rockfish species (*Sebastes paucispinis* and *S. ruberrimus*). The model results show that no-take MPAs can protect against strong fisheries-based selection for earlier maturation. The potential to protect against anthropogenic selection declines with increasing fragmentation of reserves to networks of small reserves. Accounting for the evolution of size at maturation increases the predicted biomass contribution from MPA populations to harvested populations. Traditional management approaches, such as adjustments to harvest rate and maximum size limits, can lead to equivalent protection against anthropogenic selection and equivalent or greater long-term biomass yield than establishing MPAs; however, the protection and yield from establishing no-take MPAs appears more robust to uncertainty.

Key words: fisheries; *Gadus morhua*; life history evolution; *Lutjanus campechanus*; marine protected areas; marine reserves; quantitative genetic model; rapid evolution; *Sebastes paucispinis*; *Sebastes ruberrimus*; size at maturation; size-dependent mortality.

INTRODUCTION

Anthropogenic disturbance can cause rapid evolutionary changes that impact ecological processes and conservation management decisions (Ashley et al. 2003, Neuhauser et al. 2003). For example, biased harvesting changes the selection acting on the life history strategies of exploited species (Palumbi 2001, Stockwell et al. 2003). Rapid evolution resulting from selective harvesting occurs in both terrestrial ecosystems, such as the evolution of smaller body mass and horn size in bighorn trophy rams (Coltman et al. 2003), and marine ecosystems, where size-selective fishing is common. By significantly altering size-specific mortality, size-selective fishing alters selection on growth rate, timing of maturation, and reproductive investment in targeted species (Pitcher and Hart 1982; reviewed by Heino and Godø 2002).

For fishing to cause evolutionary changes in life history strategies, variation in the trait(s) must cause differential survival and reproductive success as well as have a heritable basis (Policansky 1993). An array of theoretical models show that changes in survival and reproductive success associated with fishing mortality

can select for earlier age at maturation (Rowell 1993, Stokes and Blythe 1993, Kaitala and Getz 1995, Heino 1998), smaller size at maturation (Rijnsdorp 1993b, Ratner and Lande 2001), and smaller size, which serves as an indicator for growth rate (Kirkpatrick 1993, Witting 2002); results depend on the size selectivity of the fishing gear (Miller and Kapuscinski 1994) and presence of predation (Gårdmark et al. 2003). Quantitative model predictions, limited by a lack of accurate knowledge of parameter values (Law 1991), vary from slow (Law and Rowell 1993, Martínez-Garmendia 1998) to rapid (Kirkpatrick 1993) evolutionary responses to fishing.

Although growth and maturation traits have low heritabilities (additive genetic components ~0.2–0.3; Stokes and Law 2000), selection in heavily exploited natural populations is likely to be strong (Law 2000) and may cause genetically based changes in body size within decades (Stokes and Law 2000). In addition, accounting for environmental (nonheritable) influences in models yields theoretical predictions similar to those described in the previous paragraph (Hutchings 1993, Ernande et al. 2004). Empirically, aquaculture (reviewed by Law 2000) and experiments (Edley and Law 1988, Conover and Munch 2002) support theoretical predictions that size-selective harvesting causes rapid genetic and phenotypic changes in growth rate and tim-

Manuscript received 4 April 2004; revised 2 September 2004; accepted 17 September 2004. Corresponding Editor: P. S. Levin.

³ E-mail: mbaskett@princeton.edu

ing of maturation. Also, the predicted changes in maturation and growth rates have occurred in many exploited natural populations, such as salmon, cod, sole, plaice, and haddock (e.g., Ricker 1981, Rijnsdorp 1993a, Haugen and Vøllestad 2001, Olsen et al. 2004, reviewed by Sheridan 1995, Trippel 1995, Law 2000); evidence that the phenotypic changes involve genetic changes includes shifts in maturation reaction norms (e.g., Barot et al. 2004).

Evolution toward earlier maturation threatens the long-term sustainability of fishery yields. Because earlier maturation results in earlier investment of resources in reproduction rather than growth (assuming a life history trade-off with reduced growth after maturation), selection for earlier maturation may result in smaller fish of a given age, which in turn reduces biomass yield (Law 2000). Furthermore, the combined effect of reduced size and size-dependent fecundity may cause lower reproductive output (Kirkpatrick 1993) and reduced ability to recover from large anthropogenic or natural disturbances (Ratner and Lande 2001). In support of these hypotheses, theoretical models indicate that adjusting size limits and harvest rates to account for evolutionary changes can increase sustainable fisheries yield (first demonstrated by Law and Grey [1989], and further supported or generalized by Blythe and Stokes [1993], Brown and Parman [1993], Grey [1993], and Stokes and Blythe [1993]).

With the frequent occurrence of overharvesting in marine systems under traditional fisheries management (Botsford et al. 1997), alternatives to decreasing the harvest rate and/or increasing the minimum size limit, such as introducing a maximum size limit or establishing marine protected areas (Conover and Munch 2002), may prove more effective at reducing selection for earlier maturation. Marine protected areas (MPAs) reduce anthropogenic disturbance by closing regions to some or all fishing activity (Pauly et al. 2002). Generally, MPAs in coastal ecosystems may provide benefits both to fisheries, by supplying source populations and reducing uncertainty (especially when overfishing occurs), and to conservation, by protecting self-sustaining populations, ecosystem structure, and vital habitats (Fogarty 1999, Murray et al. 1999).

MPAs may further benefit fisheries and conservation by reducing the selection caused by anthropogenic harvesting and the associated negative effects on fisheries yield and population persistence (Plan Development Team 1990, Bohnsack 1998). In a terrestrial parallel, Tenhumberg et al. (2004) show that harvest refuges theoretically can protect against evolutionary effects of size-selective kangaroo harvesting. For marine systems, Trexler and Travis (2000) suggest that one no-take reserve protecting several square kilometers can lead to increased average optimum age at maturation, under the assumption that protected and harvested populations are panmictic; however, their approach does not account for differences in selection strength inside

and outside reserves. Weak selection in reserves compared to strong selection in harvested areas may delay or impede recovery from, and protection against, fisheries-based selection.

Here we present a dynamical, spatially structured, quantitative genetic model of the evolution of size at maturation in harvested species. We use this model to assess qualitatively: (1) how well MPAs can protect against selection for earlier maturation both in and out of reserves; (2) how MPA network design, in terms of network size (total area protected), number and spacing of individual reserves, and level of protection (no-take vs. partial-take MPAs), affects the potential for MPAs to protect against selection for earlier maturation; and (3) how establishing MPAs compares to using traditional fisheries management approaches, such as changing harvest rate as well as minimum and maximum size limits, in terms of size-at-maturation evolution and evolutionarily stable fisheries yield.

We explore the model in the context of the evolution of size at maturation in several species of fish. First, in order to verify the accuracy of our model, we compare our model predictions to the observed decline in size at maturation in Atlantic cod (*Gadus morhua*) over multiple decades. Then we test the robustness of model predictions across varying life histories using red snapper (*Lutjanus campechanus*), the species that Trexler and Travis (2000) investigated, as well as two rockfish species, bocaccio (*Sebastes paucispinis*) and yelloweye rockfish (*S. ruberrimus*), that have experienced recent overfishing (Methot et al. 2002, MacCall 2003). A comparison of these tropical and temperate species with differing life histories allows us to make general, qualitative predictions of how MPA network design and traditional fisheries management affect size-at-maturation evolution and fisheries yield.

METHODS

This section contains an intuitive description of our size-at-maturation model, followed by detailed mathematical formulation. Although age, size, and growth rate all influence the timing of maturation, the evolving trait in the model proposed here is size at maturation, the trait that size-selective harvesting most directly impacts. Even though size at maturation may initially (within years) increase in an exploited population if lower densities enhance performance (e.g., through decreased competition for food and increased growth), the long-term (within decades) evolutionary effect of harvesting is generally reduced size at maturation (Rochet 1998). For mathematical simplicity, we focus on long-term dynamics and ignore density-dependent somatic growth, where individual size depends on size at maturation and age such that a change in size at maturation directly corresponds to a change in age at maturation. An individual-based simulation analogous to the main population model compares the outcome

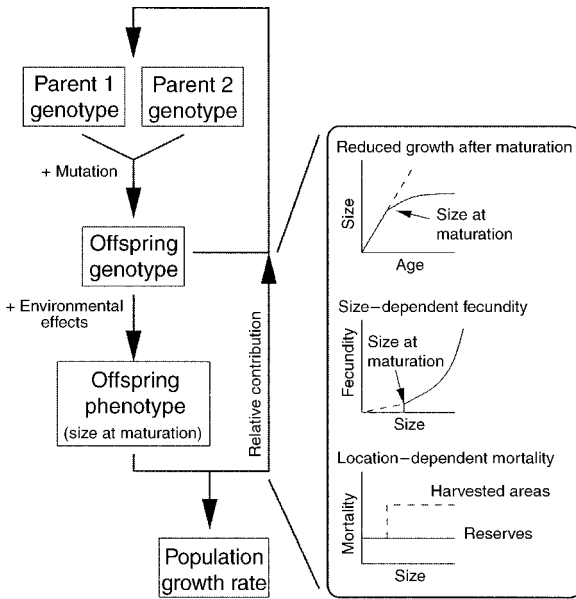


FIG. 1. Schematic of genetic and population dynamics in the size-at-maturation model.

with and without density-dependent somatic growth to test the importance of this assumption.

The model assumes that size at maturation evolves as a quantitative genetic trait. Evidence that timing of maturation in fish is a quantitative genetic trait includes experimental measurements of heritability (Conover and Munch 2002), indirect measurement of heritability in natural populations (Trexler and Travis 2000), and variation in timing of maturation unexplained by phenotype plasticity (Rijnsdorp 1993a). To account for both genetic and environmental effects on size at maturation, the model separates each individual's size-at-maturation genotype, or genetic predisposition to mature at a particular size, from its size-at-maturation phenotype, or actual size at which the individual matures; the joint distribution of size-at-maturation genotypes and phenotypes describes the population. At each generation, individuals inherit a genotype based on their parental genotypes, under the assumption that a large number of unlinked loci each contribute a small amount to the overall genotype (the infinitesimal model; e.g., Cavalli-Sforza and Feldman 1976, Bulmer 1980, Turelli and Barton 1994).

Both the genotype and the environment (protected or harvested area) determine the individual's phenotype, and both the environment and the phenotype determine the individual's fitness. An individual's fitness is its relative contribution to the subsequent generation, taking survivorship, growth, and fecundity into account. As a function of size at maturation, the fitness represents the life history trade-off of resource investment in growth vs. reproduction by incorporating reduced growth after maturation, size-dependent fecundity, and location-dependent (protected or harvested

area) mortality. The growth, fecundity, and mortality rates, along with the population's size-at-maturation distribution, control the population size dynamics over time (Fig. 1).

To model gene flow and population movement between protected and harvested areas in an MPA network, we allow exchange rates between the pool of protected populations and the pool of harvested populations to vary with the total reserve network size, the number of reserves, and the species' dispersal rates. The exchange rates reflect random movement due to larval dispersal and adult movement (Fig. 2). Distinguishing the protected and harvested pools, we let the constant-effort harvest mortality impact the fitness of each size-at-maturation phenotype, thus influencing genetic and population dynamics. To test the importance of the assumptions behind the exchange between the protected and harvested pools for different MPA networks (see *Linking protected and harvested areas* section), we compare the dynamics of this two-pool model to a spatially explicit diffusion model.

The final output of a numerical simulation of the model is the size-at-maturation distribution, population size, size distribution, and biomass yield, all separately calculated in protected and harvested areas once the dynamics reach an equilibrium. Changes in the harvest and exchange rates over multiple simulation runs indicate how yield, population size, organism size, and size at maturation depend on size of reserves, number of reserves (i.e., single large or several small reserves), and harvest mortality inside reserves (i.e., no-take or partial-take reserves). In addition, we compare the results that include reserves to results that only use traditional fisheries management approaches such as de-

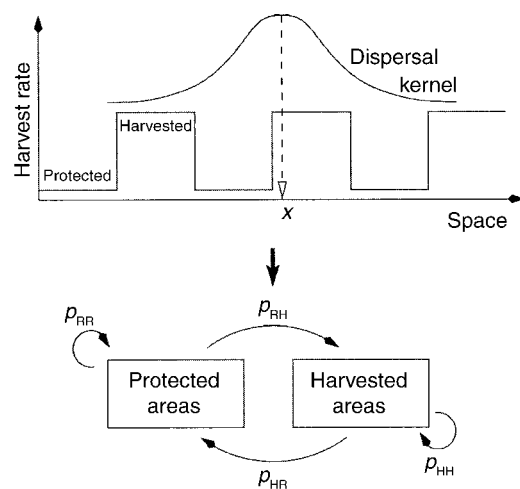


FIG. 2. The dispersal kernel determines the probability of moving between protected and harvested areas, which are distinguished by the harvest mortality. Integrating the dispersal kernel yields exchange rates between protected and harvested areas: p_{RR} , p_{RH} , p_{HH} , and p_{HR} .

creasing the harvest mortality, increasing the minimum size limit, or implementing a maximum size limit.

Population and genetic dynamics

In the model, an individual's size-at-maturation genotype, g , is its genetic predisposition to mature at a particular size. Given the distribution of parental genotypes $\psi_i(g)$, the probability that two parents with genotypes g_1 and g_2 mate and the probability that such a mating produces offspring with each genotype g summed over all mating pairs give the distribution of offspring genotypes $\psi_{t+1}(g)$. Under the assumption of random mating, the probability that two parents mate is the product of the proportions of the two parental genotypes after fitness is taken into account, $\psi_t^*(g_1) \times \psi_t^*(g_2)$. Based on the infinitesimal model of quantitative genetics, the genotype of an offspring is a random normal variable with mean $(g_1 + g_2)/2$, the average parental genotype, and variance $G_t/2 + M$, half the genetic variance in the parental generation (G_t) plus additional variance due to mutation (e.g., see Cavalli-Sforza and Feldman 1976). Let $\mathcal{G}(x, \mu, V)$ represent the normal density function of variable x with mean μ and variance V , $\mathcal{G}(x, \mu, V) = \exp[-(x - \mu)^2/(2V)]/\sqrt{2\pi V}$. Then the offspring genotype distribution is given by the recursion (e.g., see Cavalli-Sforza and Feldman 1976, Karlin 1979, Bulmer 1980, Turelli and Barton 1994):

$$\begin{aligned} \psi_{t+1}(g) &= \iint \psi_t^*(g_1)\psi_t^*(g_2)\mathcal{G}\left(g, \frac{g_1 + g_2}{2}, \frac{G_t}{2} + M\right) dg_1 dg_2. \end{aligned} \tag{1}$$

The assumption of unlinked loci in the infinitesimal model may cause inaccurate predictions of the genetic variance (for debate on this assumption, see Felsenstein [1981] and Feldman and Cavalli-Sforza [1981]). Ignoring linkage disequilibrium is one of several simplifying assumptions in this model, as our aim is to assess qualitative trends rather than exact quantitative outcomes.

Phenotype-genotype distribution.—In addition to its genotype, each individual has a size-at-maturation phenotype, f , which is the actual size at which the individual matures, and the joint phenotype-genotype distribution $\psi_i(f, g)$ describes the population. Each individual's phenotype is a random variable based on its genotype g , the environmental variance E , the degree of plasticity ρ_f , and the optimum phenotype v_f , according to

$$\frac{1}{\sqrt{2\pi E}} \exp\left[-\frac{\{f - [(1 - \rho_f)g + \rho_f v_f]\}^2}{2E}\right]. \tag{2}$$

If $\rho_f = 0$, the phenotype depends only on the genotype and is independent of the specific environment; thus the environmental contribution to the phenotype is random (as in Cavalli-Sforza and Feldman 1976). If $\rho_f =$

1, then the phenotype depends only on the environment, with random variance E , and is not genetically determined. If $\rho_f = 1 - h^2$, where h^2 is the heritability, then individuals exhibit plasticity and adjust their response dependent on their environment such that heritable proportion (h^2) of the phenotype depends on the genotype and the remainder ($1 - h^2$) depends on the optimum phenotype v_f in the individual's environment (analogous to the approach in Slatkin and Lande 1976). Underlying this approach to phenotype plasticity is the assumption that environmental cues, such as encounter rates with social dominants, bias the norm of reaction toward the optimum phenotype (described in more detail in the *Discussion*). We test the two extreme (0, 1) and one intermediate ($1 - h^2$) values for ρ_f against historical data to determine which is most accurate (see *Analysis: Parameterization*).

The phenotype determines the fitness of an individual, or its relative contribution to the next generation. The fitness is defined by expected lifetime reproductive output $R_0(f)$, where an individual's size-at-maturation phenotype f changes R_0 by changing the size at which growth declines due to investment of resources in reproduction, and how R_0 changes with f depends on an individual's location in a protected or harvested area through the mortality rate (see Appendix A). The phenotype f that maximizes $R_0(f)$ is the optimum phenotype v_f in Eq. 2.

Adding phenotype dynamics to Eq. 1 gives

$$\begin{aligned} \psi_{t+1}(f, g) &= \mathcal{G}[f, (1 - \rho_f)g + \rho_f v_f, E] \\ &\times \iint \psi_t^*(g_1)\psi_t^*(g_2)\mathcal{G}\left(g, \frac{g_1 + g_2}{2}, \frac{G_t}{2} + M\right) dg_1 dg_2 \end{aligned} \tag{3}$$

where

$$\psi_t^*(g) = \frac{\int R_0(f)\psi_t(f, g) df}{\iint R_0(f)\psi_t(f, g) df dg}. \tag{4}$$

Because size-selective harvesting is likely to incur strong selection for earlier maturation (Law 2000), the mathematically complex approach to modeling the genetic dynamics used here is necessary to avoid the assumption of weak selection (Barton 1999). Furthermore, this formulation separates genotype and phenotype dynamics, which allows a more realistic representation of the evolution of timing of maturation with its significant environmental component (Trippel 1995).

Coupled genetic and population dynamics.—To model overlapping generations, we assume that the time scale is generations, with $\psi(t, f, g)$ as the continuous-time equivalent of $\psi_i(f, g)$, and we use the fol-

lowing continuous-time approximation of Eq. 3 (analogous to Barton 1999), coupled with population dynamics:

$$\begin{aligned} \frac{d\psi}{dt} = & \mathcal{G}[f, (1 - \rho_f)g + \rho_f v_f, E] \\ & \times \iint \psi^*(t, g_1) \psi^*(t, g_2) \\ & \times \mathcal{G}\left[g, \frac{g_1 + g_2}{2}, \frac{G(t)}{2} + M\right] dg_1 dg_2 \\ & - \psi(t, f, g) \end{aligned} \quad (5)$$

$$\frac{dN}{dt} = r(\psi)N \left(1 - \frac{N}{K}\right) \quad (6)$$

where

$$\psi^*(t, g) = \frac{\int R_0(f) \psi(t, f, g) df}{\iint R_0(f) \psi(t, f, g) df dg} \quad (7)$$

Here $G(t)$ is the genetic variance based on $\psi(t, f, g)$, and $r(\psi)$ is the intrinsic growth rate for a population with genotype-phenotype distribution $\psi(t, f, g)$, defined in Appendix B (Eq. B.7). For the population dynamics, we use logistic growth rather than a more traditional stock-recruitment relationship because the logistic model (specifically, the parameter r) more easily allows us to mechanistically model how the size-at-maturation distribution influences population dynamics through somatic growth, size-dependent mortality, and size-dependent fecundity (see Appendix B).

Eq. 6 includes density-dependent mortality (with carrying capacity K) in order to limit population growth; this density dependence does not impact the genetic dynamics. Density-dependent mortality in marine fish often occurs at larval settlement, based on competition for space as a refuge from predation (Myers and Cagigan 1993), in which case it effectively reduces the proportionality constant for birth rate (and therefore fitness) by the same factor, regardless of the size-at-maturation phenotype (see Eq. A.2 in Appendix A). Thus density-dependent mortality does not affect the normalized fitness values and this assumption holds. Accordingly, Heino and Kaitala (1999) suggest that R_0 is the appropriate fitness measure for ESS models in the case of density-dependent larval survival. Another important regulatory factor in fish populations is density-dependent growth due to competition for food (Lorenzen and Enberg 2002). When incorporating density-dependent growth, Heino and Kaitala (1997) found that R_0 is an appropriate measure of fitness for ESS models in the absence of size-dependent mortality. Therefore, R_0 is a good measure of fitness in no-take reserves, and an individual-based model verifies that R_0 is also a good measure of fitness with density-de-

pendent growth and size-selective harvest mortality. In addition to the treatment of density dependence, the individual-based model, described in Appendix C, tests the impact of separating the size structure dynamics and genetic dynamics (see Appendices A and B).

Linking protected and harvested areas

To model population and gene flow between protected and harvested areas in a reserve network, the model separately tracks the pooled population size and genotype-phenotype distribution in reserves, N_R and ψ_R , and harvested areas, N_H and ψ_H , of an MPA network. Individuals in protected area(s) move to unprotected area(s) at the rate p_{RH} and from unprotected to protected area(s) at the rate p_{HR} . Additionally, individuals may disperse beyond the boundary of the region modeled, and the proportion of individuals retained within protected area(s) is p_{RR} and harvested area(s) is p_{HH} (Fig. 2). Then the following system extends Eqs. 5–6 to include exchange between the two pools (analogous to Polacheck 1990, Tuck and Possingham 2000):

$$\frac{dN_R}{dt} = r_R(\psi_R)N_R \left(1 - \frac{N_R}{K_R}\right) - (1 - p_{RR})N_R + p_{HR}N_H \quad (8)$$

$$\frac{dN_H}{dt} = r_H(\psi_H)N_H \left(1 - \frac{N_H}{K_H}\right) - (1 - p_{HH})N_H + p_{RH}N_R \quad (9)$$

$$\frac{d\psi_R}{dt} = \frac{p_{RR}N_R \mathcal{F}(\psi_R) + p_{HR}N_H \mathcal{F}(\psi_H)}{p_{RR}N_R + p_{HR}N_H} - \psi_R \quad (10)$$

$$\frac{d\psi_H}{dt} = \frac{p_{HH}N_H \mathcal{F}(\psi_H) + p_{RH}N_R \mathcal{F}(\psi_R)}{p_{HH}N_H + p_{RH}N_R} - \psi_H \quad (11)$$

where

$$\begin{aligned} \mathcal{F}(\psi_X) = & \mathcal{G}[f, (1 - \rho_f)g + \rho_f v_{fX}, E] \\ & \times \iint \psi_X^*(t, g_1) \psi_X^*(t, g_2) \\ & \times \mathcal{G}\left[g, \frac{g_1 + g_2}{2}, \frac{G}{2} + M\right] dg_1 dg_2 \end{aligned} \quad (12)$$

$$\psi_X^*(t, g) = \frac{\int R_{0X}(f) \psi_X(t, f, g) df}{\iint R_{0X}(f) \psi_X(t, f, g) df dg} \quad (13)$$

and the pool X (protected R or harvested H) determines $r_X(\psi)$, $R_{0X}(f)$, and v_{fX} by dictating the harvest mortality (constant effort harvest within size limits; see Eqs. A.4–A.7, B.6 in Appendices A and B).

To calculate how the migration rates p_{RR} , p_{RH} , p_{HH} , and p_{HR} depend on reserve size and number of reserves, we assume that individuals disperse along an idealized linear coast with a network of reserves (Fig. 2). Each migration parameter is the probability that an individual starts at some point x of the initial pool (the inverse of the area of the protected or unprotected area, as-

suming even density throughout each area) multiplied by the probability that an individual disperses to some point y in the destination pool, and is summed over all of the points in the initial and destination pools.

Note that in calculating the exchange parameters, we assume uniform population density in each protected or harvested area; however, population densities generally decline within protected areas and increase within harvested areas near boundaries between the two (Kramer and Chapman 1999). To show that the assumption of uniform density does not significantly impact qualitative model predictions, we use a spatially explicit model, described in Appendix D. For comparison with the spatially explicit model, we use a normal dispersal kernel to calculate the migration parameters in the two-pool model:

$$k(x, y) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left[-\frac{(x-y)^2}{2\sigma^2}\right]. \quad (14)$$

Here the variance σ^2 represents random diffusion due to larval dispersal and adult movement. Although movement rates vary across life history stages, we use averaged, unstructured dispersal dynamics rather than a stage- or size-structured model to greatly simplify the mathematics (for additional assumptions underlying our unstructured approach, see Appendices A and B).

Furthermore, we tested the importance of including advection, which models a bias in dispersal due to oceanic currents, along with random diffusion. In general, the inclusion of advection in spatial dynamics can significantly alter the predictions from MPA models (Gaines et al. 2003). For a quick, simple test of the impact of including advection to and from MPAs, we shifted the mean of the previous kernel by $\pm\alpha$. Although incorporating advection (with $\alpha = \sigma/2$; results not shown) did not alter the qualitative trends described in the *Results* section, this may not hold for stronger or more realistic (e.g., Possingham and Roughgarden 1990) advection dynamics.

Analysis

Analysis of this model with different MPA network sizes, number of reserves, and harvest mortalities determines how MPA design affects size at maturation and yield inside and outside reserves. Because the model is analytically intractable, we analyze it with numerical simulations of Eqs. 8–11. Once the population and genetic dynamics in each simulation reach an equilibrium, the simulation calculates size structure (Eq. B.5 in Appendix B). Based on the equilibrium size structure \hat{n}_x , equilibrium population size \hat{N}_x , harvest mortality h_x , and minimum and maximum size limits S_h and S_m , the simulation calculates the equilibrium yield in biomass Y_b by numerically integrating the following:

$$Y_b = h_x \hat{N}_x \int_{S_h}^{S_m} W(s) \hat{n}_x(s) ds \quad (15)$$

where $W(s)$ represents the conversion of the size metric, length, into body mass ($W(s) = \alpha s^b$). Therefore, the final output of the numerical simulation is the equilibrium size-at-maturation distribution, population size, size distribution, and biomass yield. For the details of the simulations, see Appendix E.

Varying the proportion of coastline with no harvesting determines how no-take MPA size affects the simulation outputs. As the proportion A_R/A_T of the coast designated as protected increases (where A_R is area of reserve and A_T is total area), the harvest mortality outside reserves h_H also increases, to account for the displaced fishing effort, according to Guénette and Pitcher (1999) and Apostolaki et al. (2002):

$$h_H = \frac{h_{H_{\text{standard}}}}{1 - A_R/A_T}. \quad (16)$$

We compare results using this method (compensatory harvest) to those using a constant harvest mortality with changing MPA network size. Then, holding the proportion of coastline in reserves constant and changing the exchange rates determines the effect of changing the number of reserves. Next, increasing the harvest mortality inside protected areas (h_R) determines how establishing partial-take MPAs compares to no-take MPAs. Finally, eliminating the reserve pool and changing the harvest mortality (h_H), minimum size limit (S_h), or maximum size limit (S_m) allows us to compare the use of traditional fisheries management to establishing MPA networks.

Parameterization.—A preliminary test of the genetic dynamics (Eq. 5) is whether model predictions, given life history parameters and past harvest rate and size limits, match historic trajectories of size at maturation over time in harvested populations. For this test, Atlantic cod (*Gadus morhua*, from Northwest Atlantic Fisheries Organization Subarea 4) provide a relatively complete long-term data set (historical data on size-at-maturation trajectories are from Beacham [1983]; historical data on effort and size limits are from Pinhorn and Halliday [1990]; and life history parameters are from Pauly [1978] and Martin [1953], as reported by Froese and Pauly [2003]). Next, parameterizing the model based on various species allows testing of the effect of establishing MPA networks and changing traditional fisheries management across different life histories.

We parameterize the model with two rockfish species from the Northeast Pacific rocky subtidal. The extensive diversity in rockfish species provides a large variety of possible life histories with which to test the model's results. This array of life histories includes many long-lived, late-maturing species (Leaman and Beamish 1984) particularly susceptible to anthropo-

genic selection for earlier maturation, and overfishing of some species has led to relevant management and conservation concerns (Love et al. 2002). Specifically, we use bocaccio (*Sebastes paucispinis*) and yelloweye rockfish (*S. ruberrimus*); Love et al. (2002) and Haldorson et al. (1991) provide life history parameters for both species. These two species are important in U.S. commercial and recreational fisheries where overfishing has recently occurred: in 2003, bocaccio spawning output was estimated to be 7.4% of the unfished level (MacCall 2003), and in 2002, yelloweye rockfish spawning biomass was estimated to be 24.1% of the unfished level (Methot et al. 2002). Yelloweye rockfish, which are particularly long lived (maximum age ~ 118 years) and slow growing, occur in coastal areas from northern Baja California to the Aleutian Islands, most frequently at 91–180 m deep. Bocaccio, shorter lived (maximum age ~ 40 –50+ years) and faster growing than yelloweye rockfish, span from coastal central Baja California to the Alaskan peninsula, most frequently at 50–200 m deep; the two species co-occur in central California (Love et al. 2002).

To compare the results from these two temperate species to a tropical species, we use red snapper (*Lutjanus campechanus*; life history parameters from Nelson and Manooch [1982]), which is an important commercial and recreational fishery ranging from the Yucatan to North Carolina, and the model species that Plan Development Team (1990) and Trexler and Travis (2000) used to address similar questions. We choose red snapper, bocaccio, and yelloweye rockfish to compare our model results across differing life histories using commercially important species that occur in regions where MPAs are being implemented and that have experienced intensive harvesting and, hence, possibly selection for earlier maturation.

In addition, we estimate heritability and the relative contributions of mutation, environmental, and genetic variance to the total phenotypic variance in size at maturation from Mackay et al. (1992), Garcia-Dorado and Marin (1998), Vassilieva and Lynch (1999), and Conover and Munch (2002). Finally, we choose general estimates for dispersal potential from the taxonomic predictions in Kinlan and Gaines (2003) and the correlation between planktonic larval duration and distance in Shanks et al. (2003).

RESULTS

We test the accuracy of our size-at-maturation model by comparing simulation predictions to historical data as well as comparing simulation trajectories using the primary model just described to an individual-based model (results in Appendix C) and a spatially explicit model (results in Appendix D). After reporting the results from these comparisons, we report our simulation predictions of how changes in fisheries management, using protected areas or traditional approaches, affect equilibrium mean size-at-maturation phenotype and

biomass yield in four different scenarios: each combination of long-distance or short-distance dispersal and strong or weak selection.

This dichotomy in selection strength reflects how constant-effort harvesting with a minimum size limit, our standard scenario, generally selects for either earlier or later maturation, depending on harvest mortality, with little variation within each size at maturation (e.g., see Fig. 12). Within the range of harvest mortalities that select for earlier maturation, we choose an annual fishing mortality for “strong selection” simulations that is just below the predicted harvest rate that would maximize long-term biomass yield if evolution were ignored. Similarly, for “weak selection” simulations, we choose a lower annual fishing mortality that is just below the predicted harvest rate that would maximize long-term biomass yield when accounting for evolution.

The interpretation of dispersal distance in the simulations depends on the size of the region being managed. Because the model dynamics are closed, the region should contain a closed population, such as an isolated subpopulation, biogeographic region, or species range. The length of the region in question determines the actual average distance between parent and offspring for “long-distance dispersal” (scaled $\sigma = 0.2$; average parent–offspring distance is 20% of the region’s length) or “short-distance dispersal” (scaled $\sigma = 0.02$; average parent–offspring distance is 2% of the region’s length) simulations.

Similarly, we express MPA size as the proportion of the region protected. When increasing MPA size, we term the simulations where fishing mortality increases outside the MPA due to displaced effort “compensatory harvest,” and those with no changes in harvest mortality outside the MPA “constant harvest.” In the simulations where the number of reserves varies (with total area protected held constant) or where harvest mortality rate varies within the reserve, we use an MPA network size of 50% of the coast to demonstrate the influence of anthropogenic selection in the largest protected areas considered. Unless otherwise specified, harvested populations have a minimum size limit equal to the initial mean size at maturation, as reported by the parameter sources previously mentioned.

Simulation results compared to historical data

We compare the model’s predictions to historical trajectories of size at maturation in Atlantic cod to test the model’s accuracy. Of the four Northwest Atlantic Fisheries Organization (NAFO) regions (4Vn, 4Vs, 4W, 4X) where long-term trajectories of size at maturation are available for Atlantic cod (from Beacham 1983), we compare the model predictions in each of the three adjacent regions with identical fishing effort and size limits over the time frame simulated (4Vn, 4Vs, and 4W; based on Pinhorn and Halliday 1990). We do not compare model predictions to the fourth region (4X),

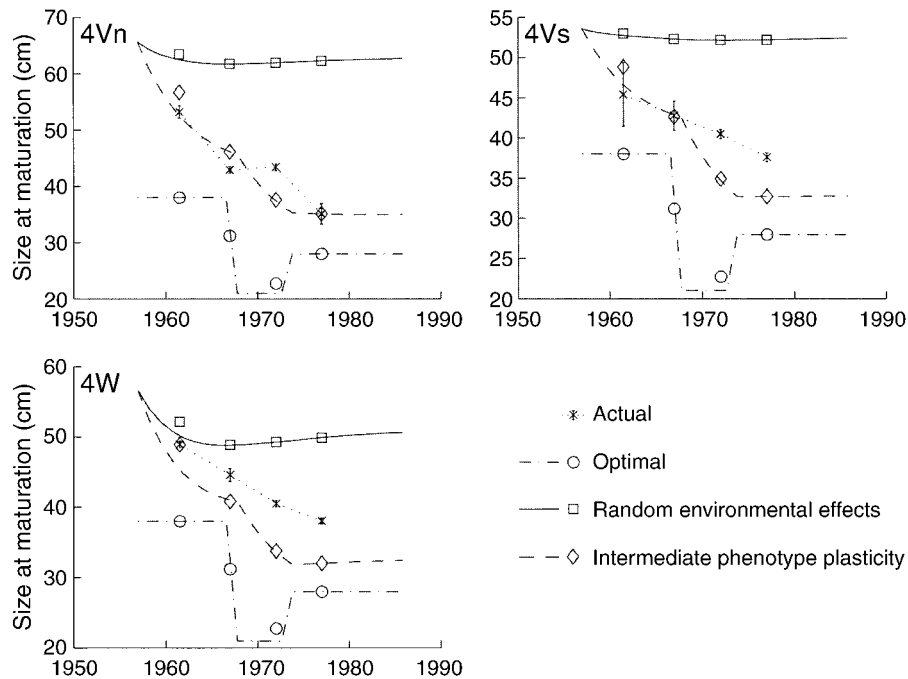


FIG. 3. Time trajectories for mean size at maturation of cod, from historical data and from simulations where the phenotype varies around the genotype based on random environmental effects (degree of plasticity $\rho_f = 0$), intermediate phenotype plasticity ($\rho_f = 1 - h^2$, where h^2 is the heritability), or optimal values ($\rho_f = 1$). For historical data, cross symbols represent mean size at maturation during each of 1959–1964, 1965–1969, 1970–1974, and 1975–1979, and error bars represent 95% confidence intervals. For simulated data, lines represent simulated time trajectories, and marker symbols (circles, squares, and diamonds) represent mean size at maturation during the same time segments as the historical data. Each of the three plots represents different Northwest Atlantic Fisheries Organization (NAFO) regions (4Vn, 4Vs, 4W).

because it has a different pattern of fishing effort from the adjacent regions and exchange rates between these regions are not readily available. Comparisons of the simulation results to the historical data indicate that the intermediate phenotype plasticity approach ($\rho_f = 1 - h^2$ in Eq. 2) matches the actual trajectories better than the random environmental effects approach ($\rho_f = 0$) or a purely plastic approach that would assume that individuals adopt the optimal phenotype ($\rho_f = 1$; Fig. 3). To estimate the degree of plasticity, we select the heritability based on the references mentioned in the *Parameterization* section ($h^2 = 0.2$) rather than the heritability that gives the best fit to the historical data (in terms of least sum of square differences; $h^2 = 0.33$); the heritability commonly reported in empirical, experimental, and aquaculture studies of a variety of species is more generally representative than the best fit for one species and still yields relatively accurate model predictions for that one species.

Because the comparison of the simulation results to cod historical data indicates that the intermediate phenotype plasticity approach is more realistic than the other two approaches, we present results using this approach for the remainder of this paper. However, we first compare this approach to the random environmental effects approach in terms of equilibrium pre-

dictions for different MPA network designs. Equilibrium size at maturation and the difference between protected and unprotected areas in strong-selection simulations are generally greater in simulations with intermediate phenotype plasticity than those with random environmental effects. In addition, equilibrium biomass yield in simulations with intermediate phenotype plasticity is generally greater than or equal to yield in those with random environmental effects (sample results in Fig. 4).

MPA networks and traditional fisheries management

Using the intermediate phenotype plasticity approach, we explore the effect of MPA network design and changes in traditional fisheries management on size-at-maturation evolution and long-term biomass yield with multiple life histories (bocaccio, yelloweye rockfish, and red snapper). Generally, all life histories result in qualitatively similar patterns of equilibrium mean size at maturation and biomass yield under different management approaches (sample results in Fig. 5), with the exception that MPAs offer less protection against fisheries yield collapse for the longest lived species, yelloweye rockfish, when assuming long-distance dispersal and strong selection. For simplicity, we primarily present the results using bocaccio because it

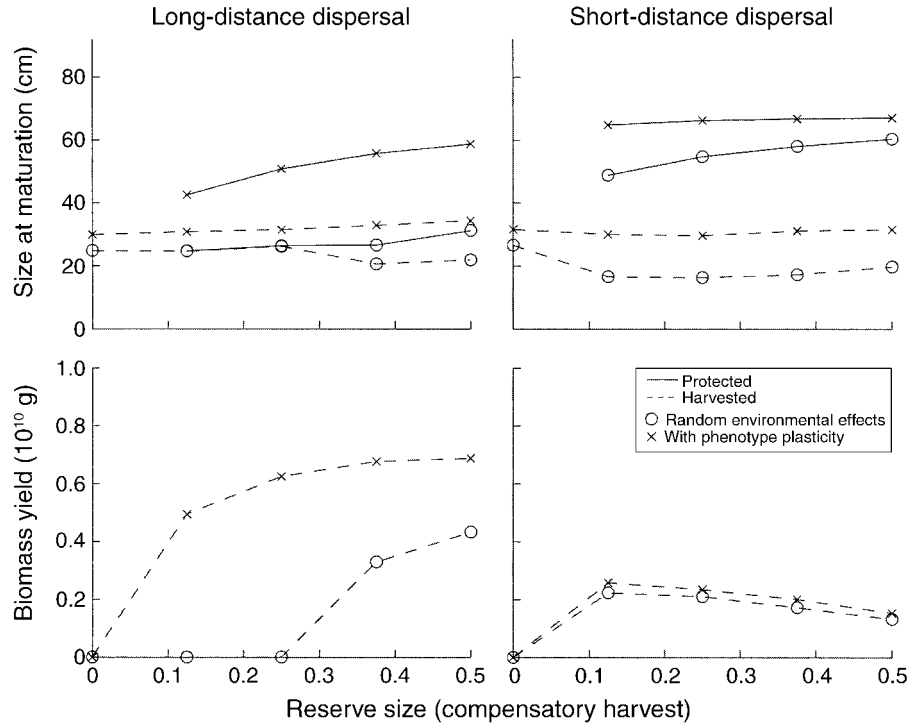


FIG. 4. Results, under long- and short-distance dispersal, for equilibrium mean size at maturation and biomass yield of bocaccio with strong selection (harvest mortality of 0.4, with minimum size limit of 48 cm) and varying size of a single no-take MPA, where the phenotype varies around the genotype based on random environmental effects or intermediate phenotype plasticity. MPA size is expressed as the proportion of the region protected. Biomass scale numbers must be multiplied by 10^{10} to obtain actual values.

has the intermediate life history (intermediate growth and fecundity).

No-take MPAs have greater equilibrium size at maturation inside reserves compared to harvested areas in strong-selection simulations. For long-distance dispersers, this effect increases with reserve size and can lead to small increases in size at maturation outside reserves (Fig. 6). Because MPAs only impact equilibrium size at maturation in strong-selection simulations, we only present results on MPA network design and size limit changes from strong-selection simulations. Holding the total protected area constant and increasing the number of reserves causes equilibrium size at maturation in protected and harvested areas to approach a similar, intermediate value; this effect occurs more rapidly for long-distance dispersers (Fig. 7, first row). Equilibrium size at maturation in partial-take MPAs decreases with increasing take allowed (Fig. 7, second row), and the rate of this decrease is greatest for longer lived, later maturing life histories (results not shown).

For the simulations that investigate changing traditional fisheries management limits without MPAs, we do not present results with different dispersal distances, because exchange between protected and unprotected populations is not under consideration. In these simulations, decreasing fishing effort (harvest mortality)

leads to increased equilibrium size at maturation (Fig. 8). Increasing the minimum size limit or decreasing a maximum size limit, both of which decrease the overall (lifelong) harvest rate as well as change the pattern of size-based mortality, can lead to increased equilibrium size at maturation in strong-selection simulations (Fig. 8).

To examine the influence of evolutionary changes in size at maturation, we compare the equilibrium biomass yield in simulations of this model to simulations without evolution. In the simulations without evolution, only population size changes over time, according to Eqs. 8–9, and the size-at-maturation distribution remains constant over time at the initial state estimated from the references listed in the *Parameterization* section. In the simulations with evolving size at maturation and strong selection, establishing no-take MPAs leads to increases in equilibrium biomass yield, particularly for long-distance dispersers. Analogous strong-selection simulations that do not incorporate the evolution of size at maturation predict higher equilibrium biomass yield without MPAs and decreases in equilibrium biomass yield with MPA establishment (Fig. 9).

Similarly, when we account for the evolution of size at maturation, predicted equilibrium biomass yield for populations under strong selection increases with the

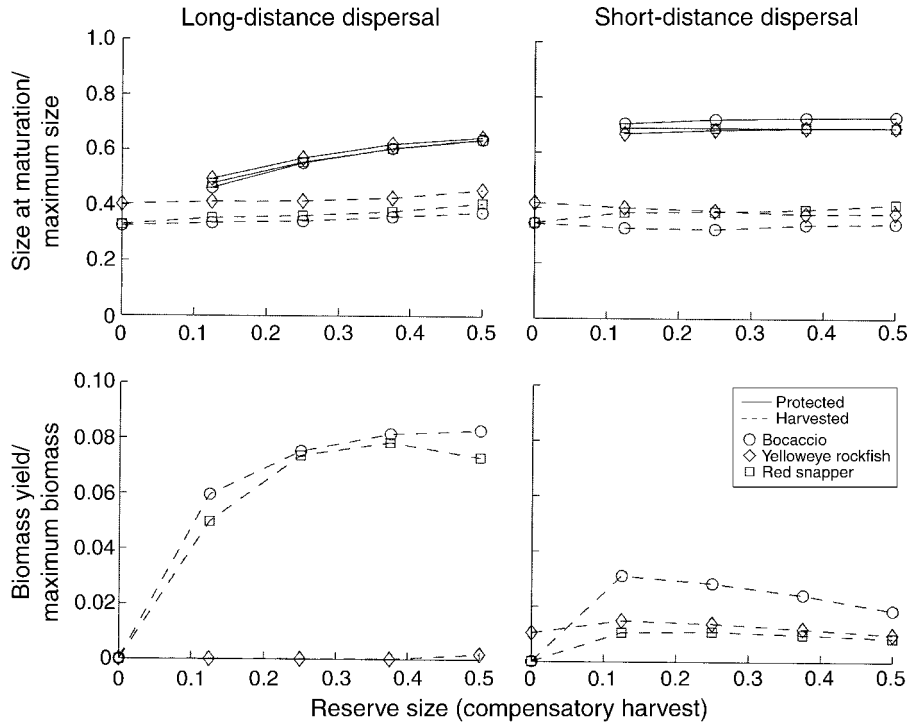


FIG. 5. Results, under long- and short-distance dispersal, for equilibrium size at maturation and yield of bocaccio, yelloweye rockfish, and red snapper with strong selection parameters (harvest mortality is about $2\times$ natural mortality; minimum size limit is the initial mean size at maturation) and varying size of a single no-take MPA (proportion of the region that is protected).

number of reserves in a no-take MPA network (with total area protected held constant), particularly for short-distance dispersers; not accounting for evolutionary effects leads to substantial underestimation of this increase (Fig. 10, first row). In simulations with evolution, implementing partial-take MPAs leads to increases in equilibrium biomass yield for populations experiencing strong selection outside MPAs only if the fishing effort in reserves is moderate enough; at higher

harvest mortalities, the population collapses and the long-term biomass yield declines. Alternatively, simulations without evolution do not predict a collapse in equilibrium biomass yield at higher MPA harvest mortalities (Fig. 10, second row).

In simulations without MPAs, but with size-at-maturation evolution, decreasing the maximum size limit in strong-selection simulations or decreasing fishing effort prevents population collapse and leads to in-

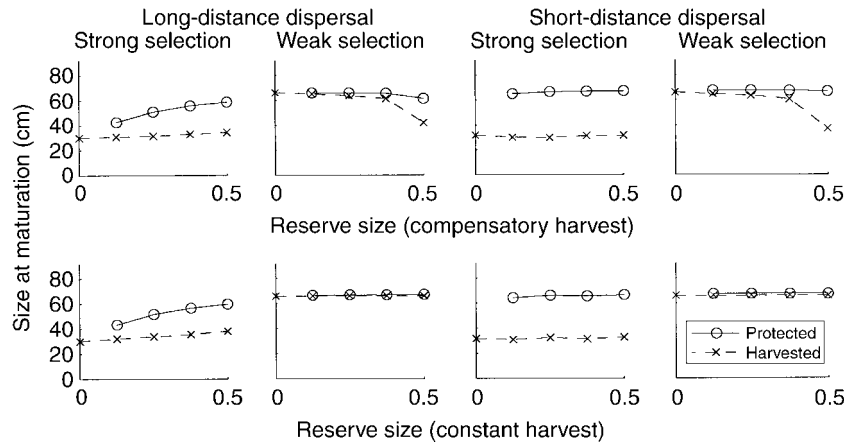


FIG. 6. Results for equilibrium mean size at maturation of bocaccio with one no-take reserve of varying size, depending on dispersal distance and selection pressure.

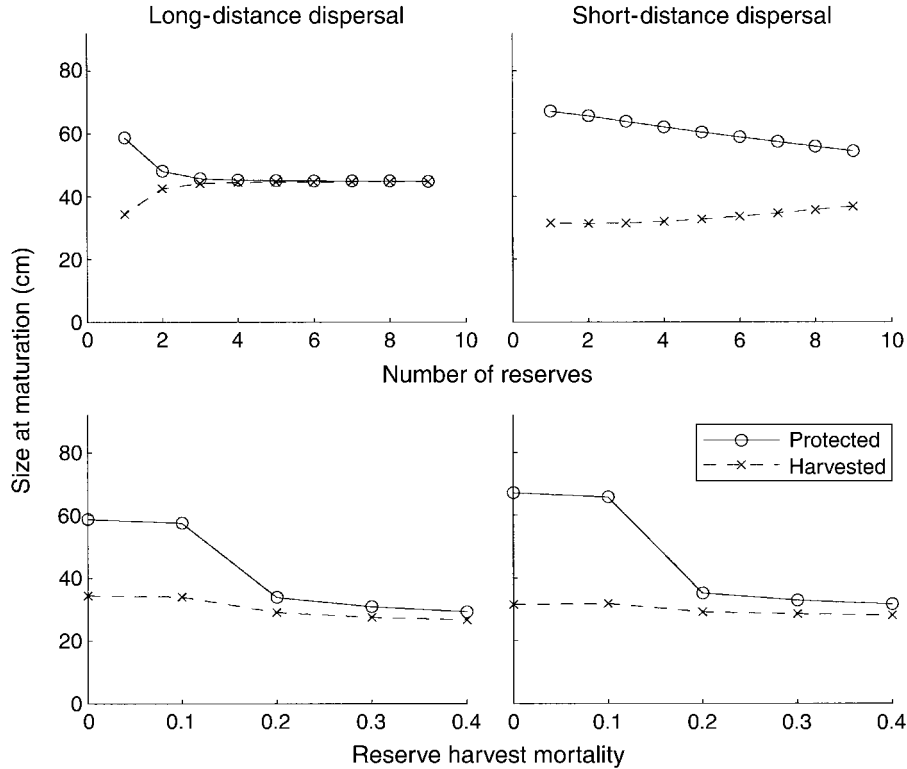


FIG. 7. Results for equilibrium mean size at maturation of bocaccio with strong selection harvest mortality of 0.4, with minimum size limit of 48 cm and varying MPA network design (in terms of the number of reserves for a no-take MPA network that covers a total of 50% of the region, or reserve harvest mortality for a single partial-take MPA that covers 50% of the region).

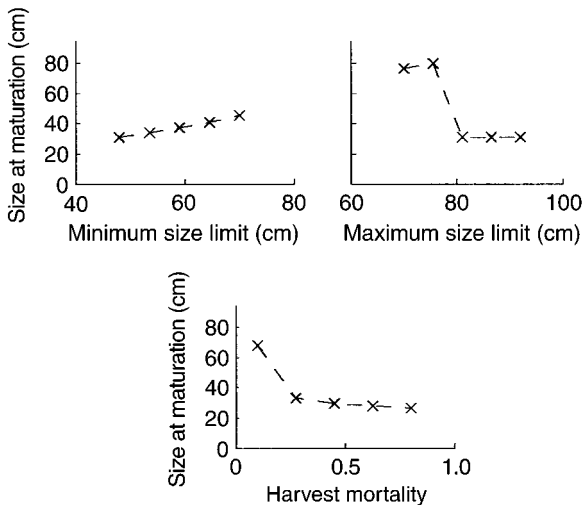


FIG. 8. Results for equilibrium mean size at maturation of bocaccio with varying traditional fisheries management limits (minimum size limit with harvest mortality of 0.4, maximum size limit with harvest mortality of 0.4 and minimum size limit of 48 cm, or harvest mortality with minimum size limit of 48 cm; no protected areas).

creases in equilibrium biomass yield. Although fisheries yield declines and strong selection for earlier maturation occur at the same harvest mortalities with the parameters tested, we do not have the analytic or computational power to determine whether they occur at precisely the same point; fisheries collapse can occur without evolution toward earlier maturation if fishing mortality is sufficiently high. Ignoring evolution in simulations without MPAs leads to significantly increased optimum harvest mortality, overestimation of the effectiveness of minimum size limits, and underestimation of the effectiveness of maximum size limits in terms of protecting long-term biomass yield (Fig. 11).

Because changing the minimum size limit is less effective at protecting size-at-maturation evolution and biomass yield (Figs. 8 and 11), and changing the maximum size limit is not a broadly applicable management tool (see *Discussion*), we only present changes in harvest mortality for simulations that explore combining traditional fisheries management and MPAs. The decrease in equilibrium size at maturation with increasing harvest mortality outside one no-take MPA decreases with MPA size for long-distance dispersers, but is independent of MPA size for short-distance dispersers. For long-distance dispersers, the addition of MPAs

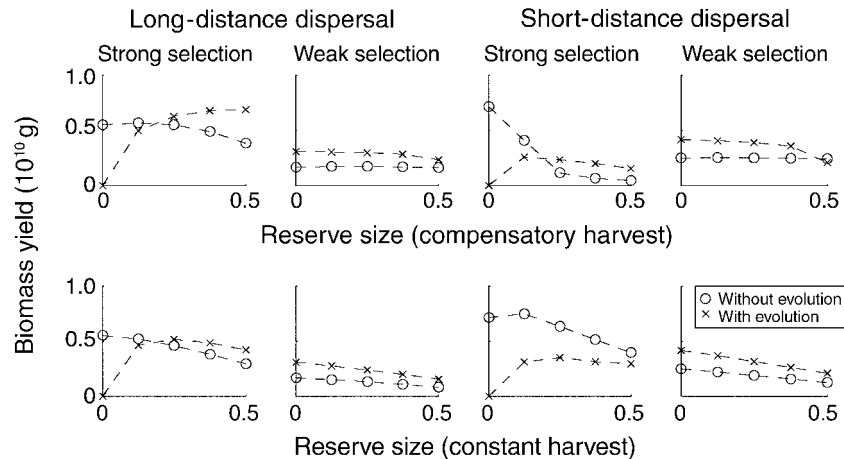


FIG. 9. Results for equilibrium biomass yield of bocaccio with one no-take reserve of varying size, in both simulations that incorporate the evolution of size at maturation and simulations that assume size at maturation remains at its initial value over time. Note that here and in Figs. 10–12, biomass scale numbers must be multiplied by 10^{10} to obtain actual values.

leads to increased biomass yield, beyond that possible without MPAs, at high harvest mortalities outside MPAs. For short-distance dispersers, a greater equilibrium biomass yield is possible without MPAs, but the collapse of biomass yield at high harvest mortalities does not occur in simulations with MPAs (Fig. 12).

DISCUSSION

Empirical (reviewed by Sheridan 1995, Trippel 1995, and Law 2000), experimental (Edley and Law 1988, Conover and Munch 2002), and theoretical (e.g., Rijnsdorp 1993b, Rowell 1993, Stokes and Blythe 1993, Kaitala and Getz 1995, Heino 1998, Ratner and Lande 2001) evidence show that size-selective fishing mortality results in rapid evolution toward earlier maturation in harvested species. Because earlier maturation means earlier investment of resources in reproduction rather than growth, the resulting smaller fish with their typically reduced reproductive output lead to reduced biomass yield and sustainability for fisheries (Kirkpatrick 1993, Law 2000, Ratner and Lande 2001). Possible approaches to protect against anthropogenic selection for earlier maturation include adjusting traditional fisheries management tools such as effort and size limits to attain an evolutionarily stable optimal harvest strategy (Law and Grey 1989, Blythe and Stokes 1993, Brown and Parman 1993, Grey 1993, Stokes and Blythe 1993) and establishing marine protected areas (MPAs; Plan Development Team 1990, Bohnsack 1998, Trexler and Travis 2000). In order to explore the potential for MPA networks and traditional fisheries management to reduce anthropogenic selection, we have developed a quantitative genetic model of size at maturation in harvested fish.

Model assumptions and accuracy

In our model of size at maturation, we make several simplifying assumptions. For example, the model as-

sumes that changes in size structure occur on a much more rapid time scale than size-at-maturation evolution, and that density-dependent mortality and somatic growth do not affect the size-at-maturation evolution. Comparison to an individual-based model verifies that the time scale and density dependence assumptions in the population model do not significantly alter equilibrium predictions for size at maturation, but they do affect population size predictions (Appendix C). In addition, in forming the spatially implicit model, we ignore edge effects: decreasing densities at the edges of protected areas and increasing densities at the edges of harvested areas. Comparison to a spatially explicit model verifies that ignoring edge effects does not alter qualitative trends for equilibrium predictions of size at maturation and biomass yield (Appendix D). Although these assumptions, particularly the lack of density-dependent somatic growth, prevent our model from being accurate enough for quantitative predictions, these tests indicate that our model can provide reasonable qualitative trends in size at maturation and biomass yield under different management schemes.

Furthermore, we use the infinitesimal model of quantitative genetics with the assumption that many unlinked loci each contribute a small amount to the overall size-at-maturation genotype. Then we explore three approaches for how genotype and environment combine to determine the phenotype: with random environmental effects, with intermediate phenotype plasticity, and without genetic determination. The intermediate phenotype plasticity approach yields more accurate predictions of historical size-at-maturation trajectories in Atlantic cod populations than both the random environmental effects and the nongenetic approaches (Fig. 3). The relative accuracy of the intermediate phenotype plasticity model without any parameter calibration to match the historical data supports

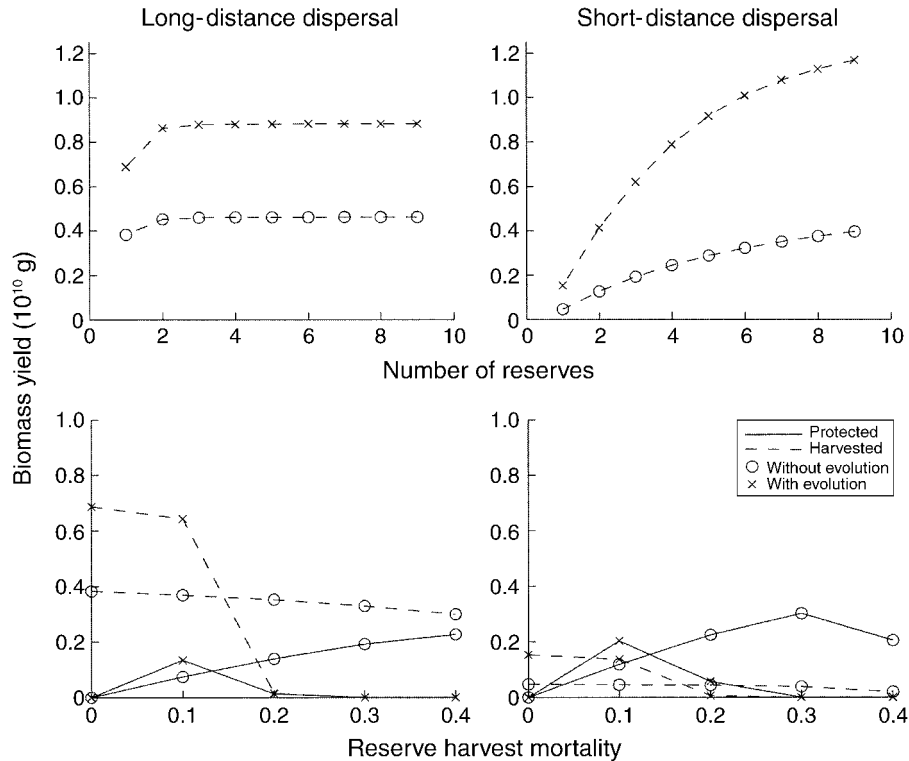


FIG. 10. Results for equilibrium biomass yield of bocaccio with strong selection (harvest mortality of 0.4, with minimum size limit of 48 cm) and varying MPA network design (in terms of number of reserves for a no-take MPA network that covers a total of 50% of the region, or reserve harvest mortality for a single partial-take MPA that covers 50% of the region), in both simulations that incorporate the evolution of size at maturation and simulations that assume size at maturation remains at its initial value over time.

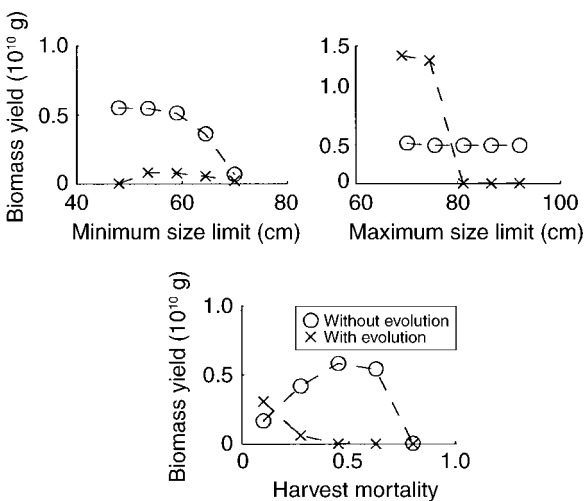


FIG. 11. Results for equilibrium biomass yield of bocaccio with varying traditional fisheries management limits (minimum size limit with harvest mortality of 0.4, maximum size limit with harvest mortality of 0.4 and with minimum size limit of 48, or harvest mortality with minimum size limit of 48; no protected areas), in both simulations that incorporate the evolution of size at maturation and simulations that assume size at maturation remains at its initial value over time. Note the change in y-axis for the maximum size limit panel.

the potential for our model to predict qualitative changes in size at maturation with changes in harvest mortalities and size limits.

These results suggest that both genetics and environment are critical to a realistic model of size-at-maturation determination, where the environment alters how the phenotype varies around the genotype to bias the reaction norm toward the optimum phenotype. One possible mechanism for such plasticity is through social cues: the presence of social dominants (larger individuals) could delay maturation, whereas the absence of social dominants could hasten maturation. Providing experimental support for this mechanism, Sohn (1977) found that platyfish (*Xiphophorus maculatus*) delay age at maturation, a genetically based trait, in the presence of social dominants. Furthermore, Rodd et al. (1997) found, in two populations of guppies that experience different size-based predation patterns, that size at maturation depends on both the population of origin (i.e., genetic inheritance) and the resident population in which they were reared (i.e., social environment). With the biased environmental influence on size at maturation in the intermediate phenotype plasticity approach, smaller MPAs are necessary to protect against anthropogenic selection (Fig. 4), and harvested fish respond

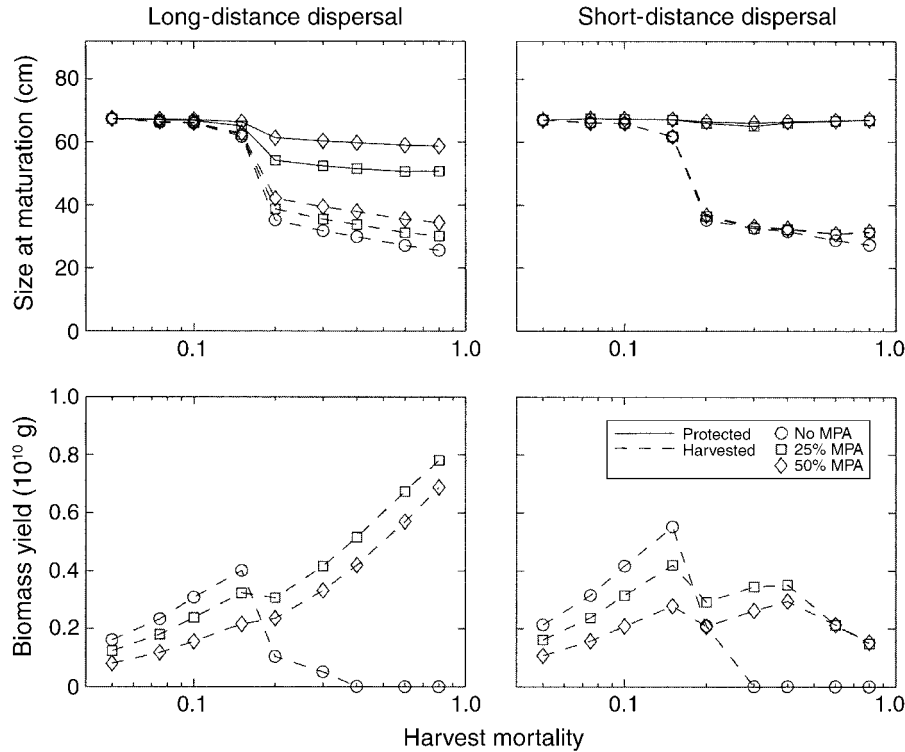


FIG. 12. Results for equilibrium size at maturation (solid lines, protected area; dashed lines, harvested area) and biomass yield of bocaccio with varying no-take MPA size (no MPA, 25% of the region protected, or 50% of the region protected) and harvest mortality outside the MPA (plotted on a log scale; minimum size limit of 48 cm).

more rapidly to MPA establishment (within a few generations; Fig. D1 in Appendix D) than would be expected if environmental effects were random.

Model predictions

We formed our size-at-maturation model to address three central questions. (1) Can MPAs protect against selection for earlier maturation, given exchange between protected and harvested regions? (2) How does MPA network design affect the potential for MPAs to protect against anthropogenic selection? (3) How does establishing MPAs compare to using traditional fisheries management in terms of protecting against anthropogenic selection? We test the model predictions for MPA networks and traditional fisheries management approaches across the varying life histories of bocaccio, yelloweye rockfish, and red snapper under four different scenarios: each combination of long-distance or short-distance dispersal and strong or weak selection.

MPAs and network design

MPA establishment and size.—Theoretical models of larval supply and/or adult spillover from reserves into harvested areas yield differing predictions as to whether establishing MPAs results in increased (e.g., Apostolaki et al. 2002, Gaines et al. 2003, Neubert 2003),

decreased (e.g., Die and Watson 1992, Mangel 2000a, Tuck and Possingham 2000), or equivalent (e.g., Polacheck 1990, Hastings and Botsford 1999) yield compared to using traditional fisheries management. In such models of population dynamics in MPAs, one common result is that MPAs are more likely to minimize loss in yield or to supply fisheries if they protect heavily fished species (e.g., Man et al. 1995, Holland and Brazeal 1996, Sladek Nowlis and Roberts 1999, Gerber et al. 2002; reviewed by Gerber et al. 2003). Similarly, our results suggest that MPAs have the greatest potential to benefit biomass yield, as well as protect against anthropogenic selection, in heavily exploited populations.

Specifically, our model predicts that no-take MPAs can protect against strong fisheries-based selection for earlier maturation, regardless of whether harvest mortality outside MPAs remains constant or increases to account for displaced effort (Fig. 6). This result applies across varying life histories, whereas the MPA size necessary for protection depends on the dispersal distance (exchange between protected and unprotected areas; Fig. 5). Because the greater equilibrium size at maturation within MPAs usually represents an increase from initial conditions, MPA establishment also has the potential to allow recovery from previous anthropogenic selection. In addition, no-take MPAs protect

source populations that enhance biomass yield in heavily fished populations outside protected areas (Fig. 9), depending on life history and dispersal distance (Fig. 5). At lower harvest mortalities, selection is weak and MPA establishment is not necessary to protect against anthropogenic selection (Fig. 6); in such cases, MPA establishment may not benefit or may detract from biomass yield (Fig. 9). Therefore, in terms of both yield and size-at-maturation evolution, MPAs are effective as protection against intensive fishing.

SLOSS.—The debate over whether to construct a network of single large or several small (SLOSS) reserves, extensively explored in terrestrial systems, has received renewed attention in marine systems because of the existence of greater dispersal scales (Carr et al. 2003) and because proponents of MPAs include supplying fisheries outside reserves (along with protecting species within reserves) among potential MPA benefits (Plan Development Team 1990, Bohnsack 1998, Fogarty 1999, Murray et al. 1999, Dayton et al. 2000). Although several small reserves would increase transfer rates to fisheries due to increased perimeter-to-area ratio (Gaines et al. 2003, Hastings and Bostford 2003, Neubert 2003), individual reserve sizes must be large enough to protect entire home ranges when possible (Polacheck 1990, Kramer and Chapman 1999). However, the increased exchange with increased perimeter-to-area ratio also reduces protection and therefore potential for population growth, which may cause decreased potential for supplying fisheries beyond the increased gain in transfer rate (DeMartini 1993). Accordingly, single-species models and complex ecosystem simulations both suggest that single large, rather than several small, reserves better achieve the MPA goal of creating refuges from overfishing by minimizing the loss of individuals through reserve boundaries (Walters 2000, Acosta 2002), especially given intensified harvesting at reserve boundaries based on such spillover (Fogarty 1999). Therefore, the optimal MPA network design, in terms of transfer rate between protected and harvested areas, here explored under the framework of the SLOSS debate, depends on the goals of the MPA and the movement rates of the protected species.

Our results further emphasize the importance of MPA goals and dispersal rate in determining the impact of increasing the number of reserves in an MPA network with constant total area protected. As a result of increased transfer, protection against strong fisheries-based selection for earlier maturation can decrease within MPAs and increase outside MPAs with an increased number of reserves (particularly for long-distance dispersers; Fig. 7, first row); therefore, a single large reserve is better than several small reserves in terms of protection within MPAs. Also, because increasing the number of reserves results in increased biomass yield outside the MPA network (particularly for short-distance dispersers; Fig. 10, first row), several

small reserves are better than a single large reserve in terms of fisheries yield. Thus the balance between protection and yield as well as the scale of dispersal determine the optimum design of an MPA network.

Level of protection.—Debate over the amount of protection MPAs should offer (i.e., no-take reserves, recreational-take reserves, restricted-gear reserves, etc.) remains a contentious political issue among scientists, conservationists, commercial fishermen, and recreational fishermen (for example, see Suman et al. 1999, Roberts et al. 2002, Tupper et al. 2002). The current focus among conservationists on no-take MPAs may risk oversimplifying scientific uncertainties and overstating MPA benefits, with politically costly unfulfilled expectations (Agardy et al. 2003). However, although it is a simplified representation of a complicated process, our model's results suggest that establishing partial-take MPAs risks eliminating MPA benefits for heavily fished populations in terms of both yield and size-at-maturation evolution.

In particular, shifting from no-take MPAs to partial-take MPAs can quickly remove the protection against strong fisheries-based selection for earlier maturation (Fig. 7, second row) as well as the ability for MPAs to protect source populations that enhance fisheries yield (Fig. 10, second row). With partial-take MPAs, the reduced potential to protect source populations and to protect against selection for earlier maturation together negatively impact both commercial and recreational fisheries by reducing protection of long-term biomass yield, organism size (given growth–reproduction trade-offs), and sustainability (given size-dependent fecundity) against the scientific and management uncertainties that may lead to overfishing.

MPAs and traditional fisheries management

Harvest rate and size limits without MPAs.—Previous models have explored using changes in fisheries effort and size limits to reduce selection for earlier maturation (Law and Grey 1989, Blythe and Stokes 1993, Brown and Parman 1993, Grey 1993, Stokes and Blythe 1993); here, we compare our model predictions when implementing such traditional fisheries management approaches to establishing MPAs. In our model, decreasing the harvest mortality to sustainable levels can eliminate selection for earlier maturation (Fig. 8) as well as avert population collapse, and can lead to increased biomass yield (Fig. 11). The harvest mortalities that maximize long-term biomass yield and the harvest mortalities that protect against anthropogenic selection are similar for each species. These results reinforce our conclusion that MPAs are most likely to benefit fisheries, in terms of both enhancing yield and protecting against anthropogenic selection, when there is intensive harvesting leading to strong selection.

Increasing the minimum size limit can provide some protection against strong fisheries-based selection for earlier maturation (Fig. 8), and can increase long-term

biomass yield by preventing population collapse from intensive fishing (Fig. 11), although to a lesser extent than establishing MPAs can. Thus, changing the minimum size limit is a less effective tool than establishing MPAs, in terms of protecting against anthropogenic selection and protecting long-term biomass yield in heavily exploited populations. Establishing a low maximum size limit results in similar protection against strong fisheries-based selection for earlier maturation compared to establishing MPAs (Fig. 8), and prevents population collapse from intensive fishing and increases biomass yield beyond the level of establishing MPAs (Fig. 11). Therefore, when feasible, a maximum size limit may be a useful tool to reduce anthropogenic selection and protect long-term biomass yield in heavily exploited populations. However, an effective maximum size limit is probably not possible in many species, dependent on the fisheries gear and ability of the target species to sustain catch-and-release; the catch-and-release mortality used here, 10% of the harvest mortality, is less than that which many species experience (Bohnsack 2000).

Combined management.—MPA establishment occurs in the context of traditional fisheries management (Allison et al. 1998), and the balance between reducing uncertainty and maximizing yield dictates the optimal management scheme that incorporates both traditional fisheries management and MPAs (Mangel 1998). Here, increasing the harvest mortality outside a no-take MPA decreases protection against fisheries-based selection for earlier maturation and increases biomass yield for long-distance dispersers; whether a greater biomass yield is possible with MPAs than without MPAs depends on dispersal distance. Regardless of dispersal distance, the addition of MPAs prevents the collapse of fisheries yield at high harvest mortalities (Fig. 12). In general, a no-take MPA of intermediate size is most effective at enhancing biomass yield for long-distance dispersers and protecting against fisheries collapse for short-distance dispersers. The optimal combination of effort limits and MPAs depends on both the dispersal distance of the target species and the management goals in terms of increasing yield and reducing uncertainty.

The importance of incorporating evolution

Comparison between simulations with and without the evolution of size at maturation demonstrates the importance of incorporating evolution to determining the optimal management strategy for maximizing long-term biomass yield. In simulations without MPAs, ignoring evolutionary effects results in optimal harvest mortality and size limits that cause population and biomass yield collapse in simulations with size-at-maturation evolution (Fig. 11). While overestimating the yield in populations without MPAs, simulations without size-at-maturation evolution predict declines in long-term biomass yield with MPA establishment, whereas simulations with size-at-maturation evolution

predict increases in strong-selection simulations (Fig. 9). Furthermore, simulations without evolution do not predict the decreased potential for partial-take MPAs to protect source populations that occurs in the simulations with evolution (Fig. 10). Overall, ignoring evolution leads to overestimation of the amount of take that populations can sustain and underestimation of the potential for no-take MPAs to enhance biomass yield through spillover.

MPAs and uncertainty

Our model indicates that no-take MPAs protect against anthropogenic selection and enhance fisheries yield in heavily exploited populations. Heavy exploitation in marine systems occurs frequently and has lasting effects (Botsford et al. 1997, Hutchings 2000, Myers and Worm 2003). Although environmental, management, and scientific uncertainty have often prevented traditional fisheries management from effectively preventing overfishing in the past, MPAs provide an alternative form of management to reduce the chance of overfishing (Pauly et al. 2002). Specifically, MPAs may reduce fisheries uncertainty on two levels (Roberts 2000): they may reduce variability in catch caused by the environmental uncertainty inherent to marine species with open population dynamics (Sladek Nowlis and Roberts 1999, Mangel 2000*a, b*), and they may reduce the scientific and management uncertainty in assessing and enforcing sustainable harvest rates (Quinn et al. 1993, Guénette et al. 1998, Lauck et al. 1998, Guénette and Pitcher 1999, Mangel 2000*c*, Apostolaki et al. 2002).

Our results suggest that no-take MPAs can reduce the uncertainty in fisheries beyond previous predictions. By protecting against anthropogenic selection for earlier maturation, MPAs will harbor more large, highly fecund fish. Therefore, MPAs can have a greater potential to supply adjacent harvested areas in the event of population declines due to stochastic environmental fluctuations or accidental overfishing. However, for long-lived species, the effectiveness of MPAs at supplying adjacent harvested areas depends on dispersal distance, a relatively poorly known parameter in marine systems. Furthermore, as Botsford et al. (2001) propose, the greater potential for MPAs to protect short-distance dispersers may introduce a new anthropogenic selective pressure on dispersal distance.

MPAs and traditional fisheries management appear similarly vulnerable to uncertainty in enforcement, as the decreasing protection in partial-take MPAs parallels that without MPAs and with increasing harvest mortality. To compare vulnerability to uncertainty in assessing sustainable policy, the protection against selection for earlier maturation and of long-term biomass yield is fairly constant across different MPA sizes. Although changing harvest rate and maximum size limits can result in similar evolutionary and yield protection as in MPAs, the protection declines sharply as limits

move away from sustainable levels. Thus the protection offered by MPAs appears to be more robust to scientific and management uncertainty than that offered by traditional fisheries management alone.

ACKNOWLEDGMENTS

Discussions with B. Rosemary Grant, Stephen Pacala, Brian Gaylord, Yoh Iwasa, Russell Lande, and Ellen Pikitch were extremely helpful to the development of the ideas and model presented here. Nick Barton generously provided *Mathematica* code relevant to our simulations. This paper benefited greatly from comments on an earlier manuscript by Phillip Levin, Hugh Possingham, and two anonymous reviewers. Funding from the National Science Foundation Graduate Research Fellowship Program to M. L. Baskett, and the Burroughs Wellcome Fund Training Program in Biological Dynamics (Number 1001781) and the Andrew W. Mellon Foundation to S. A. Levin supported this research.

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APPENDIX A

The derivation of fitness is available in ESA's Electronic Data Archive: *Ecological Archives* A015-024-A1.

APPENDIX B

A calculation of size structure is available in ESA's Electronic Data Archive: *Ecological Archives* A015-024-A2.

APPENDIX C

Details and results for the individual-based model are available in ESA's Electronic Data Archive: *Ecological Archives* A015-024-A3.

APPENDIX D

Details and results for the spatially explicit model are available in ESA's Electronic Data Archive: *Ecological Archives* A015-024-A4.

APPENDIX E

Details of the numerical simulation are available in ESA's Electronic Data Archive: *Ecological Archives* A015-024-A5.