

POACHING, ENFORCEMENT, AND THE EFFICACY OF MARINE RESERVES

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Abstract. Marine reserves are promoted as an effective supplement to traditional fishery management techniques of harvest quotas and effort limitation. However, quantitative fishery models have ignored the impact of noncompliance (poaching). Here we link a model of a harvested fish population to a game-theoretic representation of fisherman behavior to quantify the effect of poaching on fishery yield and the enforcement effort required to maintain any desired level of reserve effectiveness. Although higher fish densities inside reserves will typically entice fishermen to poach, we show that the initial investment in enforcement efforts provides the greatest return on maintaining the benefits of the reserve to the fishery. Furthermore, we find that poaching eliminates the positive effect of fish dispersal on yield that is predicted by traditional models that ignore fisherman behavior. Our results broaden a fundamental insight from previous models of marine reserves, the effective equivalence of the harvest quota and reserve fraction, to the more realistic scenario in which fishermen attempt to maximize their economic payoffs.

Key words: *deterrence; dispersal; fisheries; fishing mortality; game theory; illegal harvest; marine protected areas; maximum sustainable yield; population dynamics; source-sink dynamics; tragedy of the commons.*

INTRODUCTION

The implementation of marine reserves to protect overexploited fisheries has received considerable attention in the last decade (e.g., Halpern 2003, Halpern and Warner 2003, Palumbi 2004, Cicin-Sain and Belfiore 2005, Sale et al. 2005, Stefansson and Rosenberg 2005). Marine reserves protect a portion of a harvested population and provide dispersing recruits to the open fishery. Marine reserves also offer many advantages over the traditional management methods of catch quotas and effort limitation, such as reducing both habitat degradation by fishing gear and bycatch of nontarget species (Allison et al. 1998, Lauck et al. 1998, Gell and Roberts 2003, Stobutzki et al. 2003). However, any benefits depend on the degree to which the reserve is respected by fishermen. Illegal take (poaching) has been acknowledged and measured in the sociological literature (Kuperan and Sutinen 1998, Hønneland 1999, Gezelius 2002, Wilen et al. 2002) and promoted as a factor to consider in reserve design (Kritzer 2004). Furthermore, economists have developed general mod-

els to predict the effect of penalties on fisherman compliance (Sutinen and Andersen 1985, Furlong 1991, Hatcher et al. 2000). However, illegal take from marine reserves has not been treated explicitly in quantitative models of fish population dynamics and fishery yield.

Two related factors make poaching from reserves attractive: higher fish density inside the reserve, and reduced catch per unit effort (CPUE) outside the reserve. Most models of reserve management assume not only control of reserve size, but also that all or a fixed fraction of fish outside the reserve are harvested before reproduction (Mangel 1998, Hastings and Botsford 1999, Botsford et al. 2001, Gerber et al. 2002). However, imposition of a reserve may simply transfer effort from inside to outside the reserve area, because the capacity of the fishing fleet does not necessarily decrease when managers reduce the area open to fishing (Halpern et al. 2004, Hicks et al. 2004, Hilborn et al. 2004). Hence, even in the absence of any change in fish population size, a reserve forces more fishermen to compete for a smaller fraction of the fish population.

We formulate a game-theoretic model of fisherman behavior under the assumption that individual fishermen maximize profit from a fixed amount of fishing effort but compete with one another in the harvest. We incorpo-

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rate fish population dynamics in the model such that fishermen behavior (including poaching) responds to the impact of harvesting on fish density inside and outside a year-round spatial reserve. We address two questions: (1) How does poaching in a marine reserve negate the expected benefit of reduced mortality in the entire fish population? (2) What level of enforcement and penalization for poaching is necessary to achieve a desired level of fishermen compliance with reserve regulations? Furthermore, we explore the effects of fish dispersal and total fishing pressure on the outcome of reserve implementation.

MODEL AND DISCUSSION

We denote the total area of the fishery A_T , and a is the fraction of the total area that is inside the reserve. If the abundances of fish inside and outside the reserve are N_R and N_O , respectively, fish density is $N_R/(aA_T)$ and $N_O/[(1-a)A_T]$. We assume a fixed total fishing effort, E , measured in units of, e.g., hours. Compliance, c , is the fraction of effort spent outside the reserve.

We first derive the relationship between fishermen compliance and the effect of the reserve, before developing the model to predict fishermen behavior. The fraction of the fish population that is harvested is an increasing function $u(\epsilon)$ of effort per unit area, ϵ , and $0 \leq u(\epsilon) \leq 1$. Effort per unit area inside the reserve is

$$\epsilon_R = \frac{(1-c)E}{aA_T}. \tag{1}$$

Similarly, outside the reserve,

$$\epsilon_O = \frac{cE}{(1-a)A_T}. \tag{2}$$

The fishery yield, Y , is the sum of legal and illegal harvest, which we calculate at equilibrium fish abundance (N_i^*):

$$Y = u(\epsilon_O)N_O^* + u(\epsilon_R)N_R^*. \tag{3}$$

For instance, with complete compliance ($c=1$) there is no poaching so $\epsilon_R = 0$, $u(\epsilon_R) = 0$, and $Y = u(\epsilon_O)N_O^*$.

A reserve potentially influences fish demographic rates as well as the yield from the fishery, and it is the effect on demography that is of interest from a conservation perspective. The simplest and most direct benefit of a reserve is the reduction in fish mortality (Botsford et al. 2003). We quantify the benefit of a reserve as the reduction in average harvest mortality, F , of the fish population at equilibrium:

$$F = \frac{N_O^*}{N_O^* + N_R^*} u(\epsilon_O) + \frac{N_R^*}{N_O^* + N_R^*} u(\epsilon_R) = \frac{Y}{N_O^* + N_R^*}. \tag{4}$$

In addition to buffering the population from overharvesting, reducing mortality also increases the expected life span and therefore potentially the size of individual fish. Because fecundity typically increases with size,

reducing mortality may have benefits beyond the direct increase in fish abundance that we model.

The quantitative effects of a given level of compliance depend on the particular form of the harvest function and the fish population dynamics. Our primary goal is to develop a general theoretical model of poaching; however, specific functions may be substituted to approximate particular systems. In order to make the outcome of the game-theoretic model of fisherman behavior as transparent as possible while illustrating the general effects of poaching, we employ a basic representation of the fishery dynamics. We assume a simple harvest function for the fraction of the fish population caught during a season:

$$u(\epsilon_i) = u_{\max}(1 - e^{-\alpha\epsilon_i}) \tag{5}$$

where u_{\max} is the maximum harvest fraction and α determines the rate at which harvest decelerates with increasing effort per unit area. The index $i = R, O$ denotes effort inside and outside the reserve, respectively. Eq. 5 implies that the fraction of the fish population that is harvested increases with effort per unit area, but catch per unit effort (CPUE) decreases with increasing ϵ_i . This is equivalent to harvesting in proportion to fish density, as in the Schaefer (1957) model, but with reproduction occurring at discrete intervals.

We model fish population dynamics inside and outside the reserve with dispersal between the two populations. We assume density dependence acts on the post-harvest population, and a fixed fraction of the remaining fish disperse. If the abundance of fish at time t is $N_i(t)$, then

$$\begin{aligned} N_R(t+1) &= (1-d_R)f_R\{[1-u(\epsilon_R)]N_R(t)\} \\ &\quad + d_O f_O\{[1-u(\epsilon_O)]N_O(t)\} \\ N_O(t+1) &= (1-d_O)f_O\{[1-u(\epsilon_O)]N_O(t)\} \\ &\quad + d_R f_R\{[1-u(\epsilon_R)]N_R(t)\} \end{aligned} \tag{6}$$

where the function $f_i\{[1-u(\epsilon_i)]N_i(t)\}$ is the number of new recruits and adults that survive to $t+1$, and d_i is the fraction of population i that moves to the other population. We assume simple Beverton-Holt dynamics:

$$f_i\{[1-u(\epsilon_i)]N_i(t)\} = \frac{r_i[1-u(\epsilon_i)]N_i(t)}{1+b_i[1-u(\epsilon_i)]N_i(t)} \tag{7}$$

in which r_i and b_i are maximum per capita recruitment and effect of density on recruitment, respectively.

In general, habitat inside and outside the reserve might differ in quality, e.g., if the reserve were created around the most productive habitat. In this case (all else being equal) the reserve would support a higher density of fish, and this would increase the payoff from poaching. For the sake of comparison, we would like the equilibrium fish density in the absence of harvesting to be equal inside and outside the reserve, which implies that total fish abundance (N_i^*) is proportional to area. With no larval dispersal and no harvesting the equilibrium fish abundance is as follows:

$$N_i^* = \frac{r_i - 1}{b_i} \tag{8}$$

The parameter b_i is in effect an inverse measure of the carrying capacity of each area. To make equilibrium abundance proportional to area, we let

$$b_O = 1/[(1 - a)A_T K]$$

$$b_R = 1/aA_T K$$

where K is simply a scaling factor for the density dependence, e.g., doubling K doubles the carrying capacity per unit area. The parameter K is constant inside and outside the reserve and A_T is the total area of the fishery.

We can use Eq. 4 (with compliance in Eqs. 1 and 2) to predict the reduction in average harvest mortality (F) as a function of compliance (Fig. 1a). The minimum compliance is $1 - a$, i.e., at equilibrium fishing effort inside the reserve should not be greater than effort in the same area before it was designated a reserve. With $c = 1 - a$, the distribution of fishing effort is evenly spread across the entire habitat and average mortality is identical to the pre-reserve mortality. As c increases, average mortality decreases relative to this baseline value. In the absence of any assumption that total fishing effort (E) is optimal, the total yield (Y) of the fishery is greater with a reserve than without (Fig. 1a); however, increasing compliance improves the yield up to a maximum when c is slightly less than 1.

We now ask, if each fisherman allocates his effort between fishing inside and outside the reserve so as to maximize his economic return, what do we expect the overall fisherman compliance to be? Because the payoff to an individual fisherman depends on the behavior of all other fishermen, the problem can be readily addressed with game theory. For instance, if most fishermen stay outside the reserve, the fish population inside the reserve will increase and the individual payoff from noncompliance will therefore increase.

The game-theoretic equilibrium compliance is the value $c = \hat{c}$ that, when adopted by the entire fishing fleet, results in a payoff per unit effort that can not be surpassed by an individual fisherman who adopts a compliance $c \neq \hat{c}$ (see, e.g., Maynard Smith [1982], and a detailed derivation of our game-theoretic model in the Appendix). If overall compliance of the fishing fleet is \hat{c} with reserve fraction a , we can calculate the equilibrium fish population densities from Eq. 6, given fleet effort per unit area inside and outside the reserve (Eq. 1 and Eq. 2, with $c = \hat{c}$). The payoff per unit effort to fishermen is proportional to the catch, $u(\epsilon_i)N_i^*$, divided by the effort spent. We define v to be the market value of fish after fishing costs (e.g., boat fuel, payment of crew) are subtracted. Hence, the payoff per unit effort outside the reserve is

$$w_O = \frac{vu(\epsilon_O)N_O^*}{\hat{c}E} \tag{9}$$

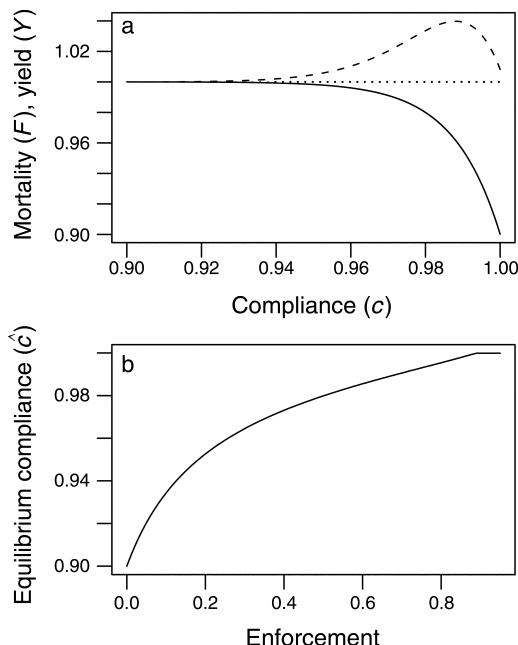


FIG. 1. (a) Average harvest mortality (F , solid line) and fishery yield (Y , dashed line) expressed relative to their pre-reserve values (dotted line). (b) Equilibrium compliance (\hat{c}) increases with enforcement, which is scaled so that the value on the horizontal axis is the probability of catching a poacher who fishes without regard to the reserve regulations. For example, in order to obtain the level of enforcement corresponding to 0.5 on the horizontal axis, reserve managers must allocate sufficient resources to have $\text{Pr}\{\text{caught}\} = 0.5$ for an individual with $c = 1 - a$, or $p = -\ln(0.5)/(aE_1)$ (see Eq. 10). Given the other parameters ($E = 800$, $r_R = r_O = 10$, $K = 100$, $A_T = 1$, $u_{\max} = 0.8$, $\alpha = 0.01$, $v = 1$, $E_1 = 4$) we obtain $\epsilon_O = 800$ (Eq. 2 with $c = 1$ and $a = 0$), $u(\epsilon_O) = 0.79$ (Eq. 5), $N_O^* = 524$ (Eq. 6 with $N_R = d_R = d_O = 0$), and the pre-reserve harvest value for an individual $w_O E_1 = 2.07$ (Eq. 9 with $\hat{c} = 1$). The fine is set to 35% of the pre-reserve harvest value for an individual fisherman: $L = 0.72$. In both panels the reserve fraction is $a = 0.1$, and all fish disperse and settle in proportion to area ($d_R = a$, $d_O = 1 - a$).

The payoff from fishing inside the reserve includes additional costs associated with penalties and the probability of being detected while inside the reserve. We consider two types of penalties levied against individual fishermen: confiscation of the individual's catch from inside the reserve, and a monetary fine. We assume the probability of a fisherman getting caught poaching increases asymptotically with the effort an individual spends inside the reserve:

$$\text{Pr}\{\text{caught}\} = 1 - e^{-p(1-c)E_1} \tag{10}$$

where E_1 is the total effort of an individual fisherman, and c is the fraction of time that the individual spends outside the reserve (distinct from the total fleet compliance, \hat{c}). The parameter p , which we call "enforcement," is the rate at which the probability of detection and prosecution increases with effort that a poacher spends in the reserve. Enforcement effort is proportional to the time and money allocated to protecting the reserve as

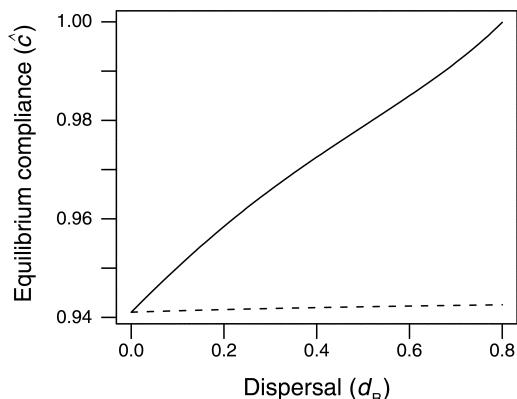


FIG. 2. Game-theoretic equilibrium compliance (\hat{c}) increases with dispersal (d), but the strength of the effect depends on the relative movement of fish between reserve and non-reserve areas. Solid line: “spillover” from reserve to non-reserve areas. ($d_O \approx 0$, $d_R =$ value on horizontal axis; equilibrium fish abundance, $N_R^* = 0$ for $d_R > 0.9$). Dashed line: random settlement of recruits in proportion to reserve and non-reserve areas ($d_R =$ value on horizontal axis, $d_O = (a/[1 - a])d_R$). Enforcement effort is $p = 0.375$. Other parameters are as in Fig. 1.

well as the effectiveness of enforcement measures. If a fisherman is caught poaching, the illegal harvest is confiscated. Hence, the expected payoff per unit effort inside the reserve to an individual with compliance c when fleet compliance is \hat{c} , is

$$w_R = \frac{vu(\epsilon_R)N_R^*}{(1 - \hat{c})E} e^{-p(1-c)E_1} - \frac{L}{(1 - c)E_1} [1 - e^{-p(1-c)E_1}] \tag{11}$$

where L is the monetary fine for poaching. The first term in Eq. 11 is the value of the CPUE in the reserve multiplied by the probability of avoiding capture while poaching. The second term is the value of the fine multiplied by the probability of being caught poaching per unit fishing effort spent inside the reserve. The total expected payoff to an individual fisherman who adopts strategy c is therefore

$$W(c, \hat{c}) = E_1 cw_O + E_1(1 - c)w_R. \tag{12}$$

The game-theoretic equilibrium is the value of \hat{c} such that the maximum individual payoff, $W(c, \hat{c})$, occurs at $c = \hat{c}$. The condition is

$$\left. \frac{dW(c, \hat{c})}{dc} \right|_{c=\hat{c}} = 0. \tag{13}$$

Inserting Eqs. 9 and 11 into Eq. 13, we obtain

$$\frac{vu(\epsilon_O)N_O^*}{\hat{c}E} - \left\{ \frac{vu(\epsilon_R)N_R^*}{(1 - \hat{c})E} [1 - p(1 - \hat{c})E_1] - pL \right\} e^{-p(1-\hat{c})E_1} = 0 \tag{14}$$

which can be solved numerically for the equilibrium, \hat{c} . (For this model, the solution is always a maximum; see Appendix.)

The influence of increasing enforcement effort (p) for a given value of the fine for poaching (L) on equilibrium compliance is displayed in Fig. 1b. We set the fine (L) to 35% of the pre-reserve harvest value for an individual fisherman. Setting L as a percentage of the fish harvest value serves to couple the fine to fish dynamics. The initial increase in p from zero has a strong positive effect on compliance; however, the potential CPUE inside the reserve increases with compliance because equilibrium fish abundance inside the reserve increases. Hence, further increases in enforcement effort have diminishing influence on fisherman behavior, and a large p is required to achieve complete compliance with the reserve.

In practice, if a manager desires a given reduction in fish mortality, he or she can find the degree of compliance that is necessary to achieve this goal in Fig. 1a. Given the required compliance, he or she can find the combination of regulations (enforcement, confiscation, fines) that must be imposed to motivate that degree of compliance (Fig. 1b and, more generally, Eq. 14). Note that if the reserve is not enforced ($p = 0$), fishermen have no incentive to stay outside the reserve and predicted compliance is equal to the pre-reserve fraction fishing outside the reserve, $\hat{c} = 1 - a$. (This prediction is an outcome of the assumption that fishermen simply maximize their economic payoffs. A more realistic sociological model could include “willingness” to comply. In our model framework, this might involve decomposing the enforcement effort (p) into policing and self-regulation, and decomposing the penalty (L) into a monetary fine and a social-stigma component.)

In Fig. 1 we simulated a population in which all fish disperse and individuals settle into reserve and non-reserve habitats in proportion to their area. One or both of these assumptions have been adopted in many mathematical models of marine reserves for fish with pelagic larvae or mobile adults (Mangel 1998, Hastings and Botsford 1999, Gerber et al. 2002). We can examine the effect of fish mobility on compliance by varying the fraction of fish that disperse each year across the entire continuum of fully sedentary to fully mobile fish, while maintaining the assumption that settlement of dispersers is proportional to the area of reserve and non-reserve. Without strong enforcement, dispersal has only a weak effect on predicted compliance (Fig. 2, dashed line) because fish move in both directions—emigration from the reserve is partially offset by immigration to the reserve. An alternative assumption in some arguments for marine reserves is that fish will “spill-over” the reserve boundary as the population inside the reserve increases (Halpern and Warner 2003). This assumption implies that movement is primarily unidirectional: $d_O \approx 0$ and $d_R > 0$. Our model demonstrates that under these

conditions, the predicted compliance increases rapidly with increasing dispersal (Fig. 2, solid line) because the incentive to poach is lessened as fish move out of the reserve with increasing frequency.

Compliance is always difficult with sedentary species because they build up inside a reserve, motivating poaching. However our model demonstrates that for mobile fish (and larvae) the relationship of fish mobility to compliance is sensitive to the form of dispersal. Unidirectional “spill-over” movement of fish from a reserve provides a direct subsidy to the legal fishery and more mobile species support greater compliance. However, if dispersal is random with respect to the reserve (settlement is proportional to area), our model predicts little effect of mobility on compliance (Fig. 2). Highly mobile species move in and out of the reserve and, because the total population is well mixed, the subpopulations in both areas are depressed by the legal harvest. Hence increasing dispersal provides little additional subsidization to the population outside the reserve and only a slight incentive to reduce fishing inside the reserve.

We compare our predictions for yield with the case in which compliance is assumed to be complete (fixed $c = 1$). This case is similar to many previous models (e.g., Hastings and Botsford 1999, Lundberg and Jonzen 1999, Mangel 2000, Gerber et al. 2002) but we vary total effort in the fishery as well as dispersal. With complete compliance, dispersal has a strong effect on yield (Fig. 3a). This influence is particularly large when total effort is high, because fishermen maintain a low equilibrium fish abundance outside the reserve and rely on dispersal from inside the reserve. When fishermen adopt the game-theoretic equilibrium compliance (under low enforcement), the effect of dispersal on yield is much weaker because fishermen move inside the reserve when the yield is low outside (Fig. 3b). Hence, by ignoring poaching, previous models overestimate the differential effect of reserves on the yield of highly mobile relative to sedentary species.

Our simple model predicts that a reserve increases fishery yield relative to the same fishery without a reserve, even if compliance is not perfect. Furthermore, perfect compliance ($c = 1$) does not produce the maximum yield. Instead, yield increases with compliance up to a maximum at $c < 1$, then drops with further increases in compliance (Fig. 1). Increasing compliance protects fish, but fishermen must forgo harvesting a greater proportion of the population. Reserve benefits are frequently assessed in terms of greater fishery yield, but if the primary goal of a reserve is maximum protection of the stock, then yield will not necessarily be maximized.

Reserves help restore exploited fish stocks by placing a portion of the fish population off-limits to harvest. Hence, mathematical models have predicted that setting aside a reserve is similar to limiting fishermen catch (quotas) or any similar management strategy to decrease mortality

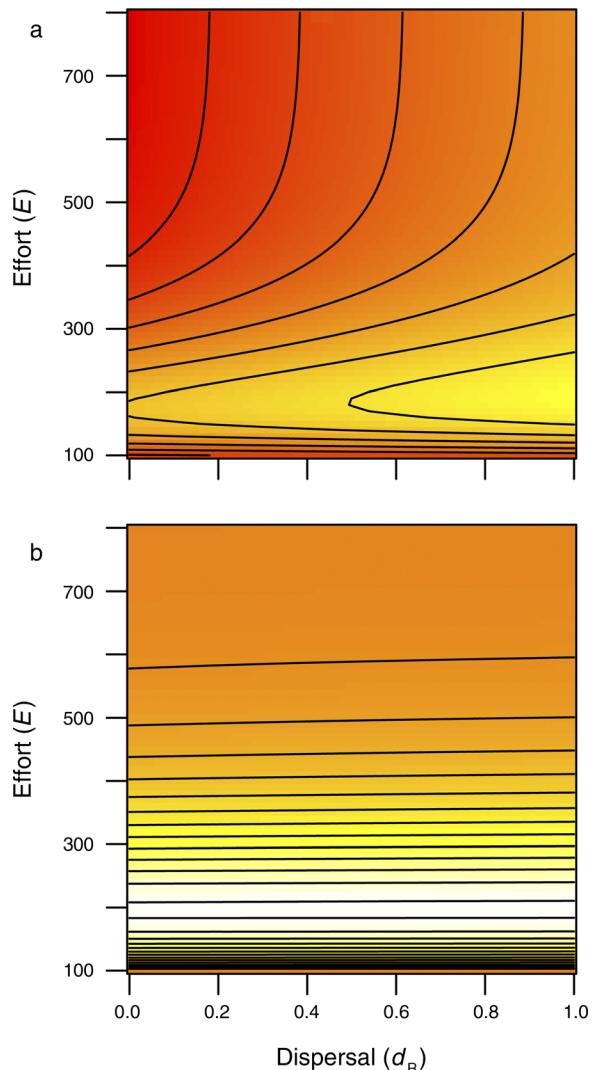


FIG. 3. Equilibrium fishery yield as a function of fishing effort (E) and dispersal of fish between reserve and non-reserve areas (d_R and d_O , with proportional settlement; see Fig. 2 legend) if (a) complete compliance ($c = 1$) is assumed, and (b) fishermen adopt the game-theoretic equilibrium compliance ($c = \hat{c}$). Colors indicate equilibrium yield from low (red) to high (white) on the same scale in both plots. Although dispersal has a larger influence on yield with complete compliance, yield is typically greater when poaching occurs because some harvest occurs in the reserve. This level of poaching is generally low [$(1 - c) < a$] and decreases with decreasing total effort. We have not subtracted penalties and illegally harvested fish from poachers' yield (consistent with the definition of yield in Eq. 3). Enforcement effort in (b) is low ($p = 0.375$); as enforcement is increased, compliance approaches 1, and the output of scenario (b) converges on (a). Other parameters are as in Fig. 2.

(Mangel 1998, Hastings and Botsford 1999). Indeed, Mangel (1998) suggested that the product of the fraction of fish outside the reserve that is harvested and the fraction of habitat that is open to fishermen ($(1 - a)u(\epsilon_O)$ in our notation) is an “invariant,” i.e., a proportional change in either quantity has an equal effect on equilibrium fish

abundance. Because setting quotas requires an estimate of fish abundance, reserves offer a simpler mechanism to protect the stock against stochastic population fluctuations. However, poaching may undermine the reliability of predicted consequences of a reserve on the fish population. Without perfect compliance, a and $u(\epsilon_O)$ can have different effects on fish abundance via the fraction harvested inside the reserve, $u(\epsilon_R)$. To maximize fisheries benefits, the influence of poaching and the cost of enforcement must be included in quantitative assessments of management with reserves.

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LITERATURE CITED

- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8:S79–S92.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144–150.
- Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. *Ecological Applications* 13: S25–S31.
- Cicin-Sain, B., and S. Belfiore. 2005. Linking marine protected areas to integrated coastal and ocean management: A review of theory and practice. *Ocean and Coastal Management* 48: 847–868.
- Furlong, W. J. 1991. The deterrent effect of regulatory enforcement in the fishery. *Land Economics* 67:116–129.
- Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution* 18:448–455.
- Gerber, L. R., P. M. Kareiva, and J. Bascompte. 2002. The influence of life history attributes and fishing pressure on the efficacy of marine reserves. *Biological Conservation* 106:11–18.
- Gezelius, S. S. 2002. Do norms count? State regulation and compliance in a Norwegian fishing community. *Acta Sociologica* 45:305–314.
- Halpern, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* 13:S117–S137.
- Halpern, B. S., S. D. Gaines, and R. R. Warner. 2004. Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications* 14:1248–1256.
- Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London B* 270:1871–1878.
- Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. *Science* 284:1537–1538.
- Hatcher, A., S. Jaffry, O. Thebaud, and E. Bennett. 2000. Normative and social influences affecting compliance with fishery regulations. *Land Economics* 76:448–461.
- Hicks, R. L., J. Kirkley, and I. E. J. Strand. 2004. Short-run welfare losses from essential fish habitat designations for the surfclam and ocean quahog fisheries. *Marine Resource Economics* 19:113–129.
- Hilborn, R., et al. 2004. When can marine reserves improve fisheries management? *Ocean and Coastal Management* 47: 197–205.
- Hønneland, G. 1999. A model of compliance in fisheries: theoretical foundations and practical application. *Ocean and Coastal Management* 42:699–716.
- Kritzer, J. P. 2004. Effects of noncompliance on the success of alternative designs of marine protected-area networks for conservation and fisheries management. *Conservation Biology* 18:1021–1031.
- Kuperan, K., and J. G. Sutinen. 1998. Blue water crime: deterrence, legitimacy, and compliance in fisheries. *Law and Society Review* 32:309–337.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications* 8: S72–S78.
- Lundberg, P., and N. Jonzen. 1999. Spatial population dynamics and the design of marine reserves. *Ecology Letters* 2:129–134.
- Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* 1:87–90.
- Mangel, M. 2000. On the fraction of habitat allocated to marine reserves. *Ecology Letters* 3:15–22.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge, UK.
- Palumbi, S. R. 2004. Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources* 29:31–68.
- Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* 20:74–80.
- Schaefer, M. B. 1957. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Journal of the Fisheries Research Board of Canada* 14:669–681.
- Stefansson, G., and A. A. Rosenberg. 2005. Combining control measures for more effective management of fisheries under uncertainty: quotas, effort limitation and protected areas. *Philosophical Transactions of the Royal Society of London B* 360:133–146.
- Stobutzki, I., P. Jones, and M. Miller. 2003. A comparison of fish bycatch communities between areas open and closed to prawn trawling in an Australian tropical fishery. *ICES Journal of Marine Science* 60:951–966.
- Sutinen, J. G., and P. Andersen. 1985. The economics of fisheries law enforcement. *Land Economics* 61:387–397.
- Wilen, J. E., M. D. Smith, D. Lockwood, and L. W. Botsford. 2002. Avoiding surprises: incorporating fisherman behavior into management models. *Bulletin of Marine Science* 70:553–575.

APPENDIX

Detailed derivation of the game-theoretic model and a table summarizing the variables and parameters of the game-theory model (*Ecological Applications* A017-074-A1).