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Irreducible uncertainties, sustainable fisheries and marine reserves

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ABSTRACT

Marine reserves are increasingly proposed as a management tool. Models can play a valuable role in the evaluation of the possible benefits of reserves because they allow us to conduct many more investigations than could ever be done empirically. In this paper, I develop a model for a marine reserve for an open population subject to environmental uncertainty.

Keywords: environmental uncertainty, marine reserves, mean–variance trade-off, open systems.

IRREDUCIBLE UNCERTAINTY IS A FACT OF LIFE

The work of Dan Cohen stands out in evolutionary ecology because of his early and consistent recognition that irreducible uncertainty is a fact of life (e.g. Cohen, 1966, 1967, 1971, 1976; Lewontin and Cohen, 1969). These are still beautiful papers, and I encourage the young ones to read them. Part of their brilliance lies in Cohen's recognition that there exist in nature stochastic effects that no amount of sampling (scientific or otherwise) will remove and that natural selection (and human intervention in ecosystems; Mangel *et al.*, 1996) must operate within this stochastic framework, rather than ignore it. Of course, today the general response to uncertainty or stochasticity is 'simulate', and another brilliant aspect of Cohen's work was the significant progress that he made by thinking about problems deeply and carefully and by using simple models.

Marine reserves and marine protected areas are increasingly proposed as a means to protect various stocks of fish and invertebrates, as well as a major rehabilitation tool for depleted stocks (Carr and Reed, 1993; Gubbay, 1995; Shackell and Willison, 1995; Bohnsack and Ault, 1996; Lauck *et al.*, 1998). Although there is strong evidence that marine protected areas achieve benefits within their geographic region, there is weaker demonstration of benefits (e.g. to fisheries) outside of these protected areas (e.g. Russ and Alcala, 1996). Models can be used to evaluate the benefits of marine reserves, to deal with management under uncertainty, and to help move our foci from yield to stock and from maximum sustainable yield as a target to maximum sustainable yield as a constraint (cf. Mace, 1999).

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The methods are somewhat more complicated than those used by Dan Cohen 30 years ago, but his influence pervades the work.

Irreducible uncertainties arise, for example, in the mechanics of coin tossing (Keller, 1986), river management (Dovers and Handmer, 1995) and earthquake prediction (Geller *et al.*, 1997). In fisheries management, for example, although a harvest fraction can be targeted, fishing mortality is fundamentally unknowable. Indeed, recognizing that incidental catch rates are very difficult to estimate, or the difficulty of either gathering accurate information about or predicting discard behaviour (e.g. Gillis *et al.*, 1995a,b; Hart, 1997a,b), makes the assumption of fundamentally unknowable fishing mortality mandatory. At best, it will be possible to provide probability distributions for fishing mortality (e.g. Anonymous, 1998, 1999; Patterson, 1999), but precise values will not be obtained. Nonetheless, we usually have to act to decide on fishery quotas and on how to sustain takes in the face of such uncertainties. Rice (1999) noted in a discussion about coping with uncertainty in fisheries management that, 'By making "knowing with certainty" our standard for success, we have taught our constituencies to expect THE answer and thus set ourselves up for failure . . . We would do well to learn from meteorologists, who make it clear that their predictions aren't exact and present their judgments in terms of percentages and probabilities. We don't like that uncertainty, but we accept it and make our plans accordingly, weighing the risks and various outcomes against their likelihood'.

In this situation, models can play a valuable role because they allow us to conduct many more investigations than could ever be done empirically. They allow us to examine the consequences of our assumptions, determine sensitivities of outputs to inputs, and identify the quantity and the nature of the data to be collected (Starfield, 1997). For the evaluation of marine reserves, models can use a suite of transfer functions realistically based in biology, including information on dispersal rates and interception rates, recruitment and the population dynamics of adults, and a careful articulation of various objectives. Here I provide one such example.

A TAXONOMY OF LIFE HISTORIES FOR THINKING ABOUT MARINE RESERVES

One of the great attractions of biology is variation, and marine organisms use many different life strategies to achieve successful reproduction (Potts and Wootton, 1984). When thinking about models for reserves, it is helpful to classify life histories in the following manner (Fig. 1). First, we ask if the population is open or closed, in the sense that recruitment to the population (birth-class individuals) depends strongly on the current population size (closed) or only weakly on the current population size (open). Second, we ask if adults and juveniles share the same habitat. Examples of each kind of life history are shown in Fig. 1 and examples of previous models are described in Table 1.

Elsewhere (Lauck *et al.*, 1998; Mangel, 1998, in press), colleagues of mine and I considered reserves for closed populations where the stock grows logistically and the harvest fraction of the stock in the fished region is targeted at a specified mean value, but fluctuates. Our results show that a no-take reserve can improve chances for the sustainability of a fish stock but need not disadvantage the fishery; catch in the presence of a reserve may be higher than catch without reserve. Here I describe a model that captures many features of an open population, in particular a pelagic juvenile phase (e.g. Miller and Geibel, 1973; Figurski, 1997; Gunderson, 1997), episodic recruitment (Dixon *et al.*, 1999) and, in the spirit of honouring Dan Cohen, considerable environmental uncertainty.

Table 1. Some previous models of marine reserves, classified according to the number of species, the number of locations and the type of population dynamics modelled

- Polacheck (1990): single species, one location, deterministic age structure
- DeMartini (1993): application of Polacheck's model to hypothetical damselfish, surgeonfish and jack
- Man *et al.* (1995): metapopulation (single species), deterministic
- Roberts (1997; see also Bellwood *et al.*, 1998; Sale and Cowen, 1998; Roberts, 1998): multispecies, many locations, geographic information on current patterns
- Horwood *et al.* (1998): multispecies, many locations, deterministic age structure
- Lauck *et al.* (1998): single species, one location, stochastic
- Mangel (1998): single species, one location, deterministic
- Hastings and Botsford (1999): single species, one location, deterministic
- Mangel (in press): single species, two locations, stochastic population dynamics (juveniles and adults) with spatially segregated locations

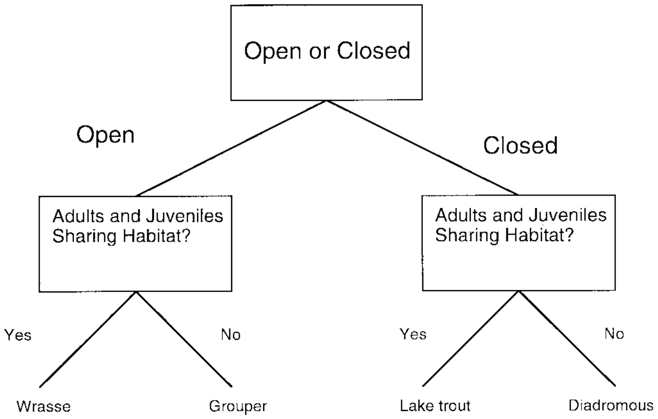

Fig. 1. A taxonomy of life histories as they relate to reserves.

TOWARDS AN OPEN POPULATION WITH ENVIRONMENTAL UNCERTAINTY

The biology, which is motivated by rockfish *Sebastes* spp. (Love, 1996; Helfman *et al.*, 1997), goes as follows: A key component of the habitat is the breeding ground on which adults establish territories. Adults with territories (reproductives) are sedentary, whereas those without territories (floaters) are mobile, moving around looking for territories. Consequently, this is a model based on site-dependent regulation of population size (cf. Rodenhouse *et al.*, 1997). Larvae have a pelagic juvenile phase, with potentially large excursions from the breeding ground and potentially high mortality, so that only a fraction of offspring return to the breeding ground as juveniles; this fraction is environmentally determined (cf. Dixon *et al.*, 1999). Once they return, juveniles are also mobile, until they become adults and settle when a territory becomes available. Maturation from juvenile to adult phases occurs at a fixed rate. Reproduction by mature individuals is environmentally cued but also irregular. Environmental variables are correlated from one year to the next, natural mortality varies according to a correlated random process driven by environmental variables, and fishing mortality is targeted but fluctuating. For simplicity, I lump all juvenile age classes into one category and all adults into another; this makes the analysis simpler without changing the qualitative conclusions. Parameters were chosen so that the results are representative of the general features of the model. The qualitative results are consistent over a wide range of parameters.

Suppose that part of the breeding ground (indexed by 1) is protected as a no-take zone and that on the rest (indexed by 2) harvest is allowed. Let A denote the fraction of the breeding ground that is protected. The number of breeding sites in portion i (= 1 or 2) in year t is

$$\begin{aligned} K(1,t) &= AK_0 \exp(\mathfrak{E}_1(t)) \\ K(2,t) &= (1-A)K_0 \exp(\mathfrak{E}_1(t)) \end{aligned} \tag{1}$$

where K_0 (= 300) is a parameter and $\mathfrak{E}_1$ is an environmental variable; it has zero mean, fixed standard deviation and serial correlation.

Let $N_a(i,t)$ denote the number of adults on habitat part i at the start of season t. Then, the number of breeders will be

$$\begin{aligned} B(1,t) &= \min\{K(1,t),\ N_a(1,t)\} \\ B(2,t) &= \min\{K(2,t),\ N_a(2,t)\} \end{aligned} \tag{2}$$

Floaters are the adults remaining after breeders are determined by equation (2), so that (using W to denote wandering; cf. Trout, 1974).

$$W_a(i,t) = N_a(i,t) - B(i,t) \qquad i = 1, 2 \tag{3}$$

If $M_a(t)$ and $M_j(t)$ denote natural adult and juvenile mortality in year t, $F_a(t)$ and $F_j(t)$ denote fishing mortality on adults and juveniles in year t, and f_j denotes the fraction of juveniles who become adults in a year, the adult population dynamics are

$$\begin{aligned} N_a(1,t+1) = {} & B(1,t)\exp(-M_a(t)) \\ & + A\{W_a(1,t)\exp(-M_a(\mathrm{t})) + W_a(2,t)\exp(-M_a(t) - F_a(t))\} \\ & + Af_j\{(N_j(1,t)\exp(-M_j(t)) + N_j(2,t)\exp(-M_j(t) - F_j(t))\} \end{aligned} \tag{4}$$

$$\begin{aligned} N_a(2,t+1) = {} & B(2,t)\exp(-M_a(t) - F_a) \\ & + (1-A)\{W_a(1,t)\exp(-M_a(t)) + W_a(2,t)\exp(-M_a(t) - F_a(t))\} \\ & + (1-A)f_j\{(N_j(1,t)\exp(-M_j(t)) + N_j(2,t)\exp(-M_j(t) - F_j(t))\} \end{aligned} \tag{5}$$

The first term on the right-hand side of equation (4) represents the number of breeders that survive natural mortality; the expression $W_a(1,t)\exp(-M_a(t)) + W_a(2,t)\exp(-M_a(t) - F_a(t))$ represents the total number of floaters surviving natural and fishing mortality, a fraction A of which end up on the reserve. Finally, the expression $N_j(1,t)\exp(-M_j(t)) + N_j(2,t)\exp(-M_j(t) - F_j(t))$ is the number of juveniles surviving natural and fishing mortality, a fraction Af_j of which mature to adults in year t and end up on the reserve.

Reproduction occurs with probability z_r (= 10% for computations); if it does occur, total production is $\varphi\{B(1,t) + B(2,t)\}$, where φ (= 5 for computations) is the adult per capita reproduction. However, the recruitment $\Re(t)$ coming back to the habitat is driven by an environmental variable $\mathfrak{E}_2(t)$, so that

$$\Re(t) = \varphi\{B(1,t) + B(2,t)\}\ \min\{1, \zeta \exp(\mathfrak{E}_2(t))\} \tag{6}$$

(with $\zeta = 0.45$ for computations); in essence, the random component in equation (6) can be envisioned as another source of mortality. The population dynamics for juveniles are

$$\begin{aligned} N_{\mathrm{j}}(1,t+1) &= A\{(1-f_{\mathrm{j}})[N_{\mathrm{j}}(1,t)\exp(-M_{\mathrm{j}}(t)) + N_{\mathrm{j}}(2,t)\exp(-M_{\mathrm{j}}(t) - F_{\mathrm{j}}(t))] + \Re(t)\} \\ N_{\mathrm{j}}(2,t+1) &= (1-A)\{(1-f_{\mathrm{j}})[N_{\mathrm{j}}(1,t)\exp(-M_{\mathrm{j}}(t)) + N_{\mathrm{j}}(2,t)\exp(-M_{\mathrm{j}}(t) - F_{\mathrm{j}}(t))] + \Re(t)\} \end{aligned} \tag{7}$$

The environmental variables are correlated and normally distributed. In particular,

$$\mathfrak{E}_i(t+1) = \rho_i \mathfrak{E}_i(t) + (1-\rho_i)\, Z_i(t) \tag{8}$$

where ρ_i (= 0.5 for computations) is a measure of correlation and $Z_i(t)$ is normally distributed with zero mean and standard deviation σ_i (= 0.5 for computations).

Fishing mortality is assumed to be targeted but fluctuating, so that

$$\begin{aligned} F_{\mathrm{a}}(t) &= \bar{F}_{\mathrm{a}} \exp(Z_{\mathrm{a}} - \tfrac{1}{2}\sigma_{\mathrm{a}}^2) \\ F_{\mathrm{j}}(t) &= \bar{F}_{\mathrm{j}} \exp(Z_{\mathrm{j}} - \tfrac{1}{2}\sigma_{\mathrm{j}}^2) \end{aligned} \tag{9}$$

where $\bar{F}_{\mathrm{a}}$ and $\bar{F}_{\mathrm{j}}$ are the targeted fishing mortalities on adults and juveniles respectively (= 0.1 and 0.05 for computations; these are typical values for fisheries management; see Quinn and Deriso, 1999), and Z_{a} and Z_{j} are normally distributed random variables with zero mean and standard deviations 50% of the mean values. Note that this assumption allows fishing mortality to be less sometimes than the targeted level; an alternative would be to assume that fishing mortality is always at least the targeted level (cf. Hightower and Lenarz, 1989).

Natural mortality also fluctuates over time with

$$\begin{aligned} M_{\mathrm{a}}(t) &= \bar{M}_{\mathrm{a}} + Y_{\mathrm{a}}(t) \\ M_{\mathrm{j}}(t) &= \bar{M}_{\mathrm{j}} + Y_{\mathrm{j}}(t) \end{aligned} \tag{10}$$

where $\bar{M}_{\mathrm{a}}$ and $\bar{M}_{\mathrm{j}}$ are the mean values of adult and juvenile natural mortalities respectively (= 0.02 and 0.2 for computations, so that I am considering a long-lived species), and $Y_{\mathrm{a}}(t)$ and $Y_{\mathrm{j}}(t)$ are normally distributed with zero mean and standard deviations of 0.02 and 0.1 respectively.

Catch is computed according to the standard methods in fisheries science (Quinn and Deriso, 1999), by attributing a fraction of the fish that disappear in year t to fishing mortality (the rest to natural mortality), so that the catch in year t is

$$\begin{aligned} C(t) = (B(2,t) + W_{\mathrm{a}}(2,t))(1 - \exp(-M_{\mathrm{a}}(t) - F_{\mathrm{a}}(t)))\frac{F_{\mathrm{a}}(t)}{F_{\mathrm{a}}(t) + M_{\mathrm{a}}(t)} + \\ N_{\mathrm{j}}(2,t)(1 - \exp(-M_{\mathrm{j}}(t) - F_{\mathrm{j}}(t)))\frac{F_{\mathrm{j}}(t)}{F_{\mathrm{j}}(t) + M_{\mathrm{j}}(t)} \end{aligned} \tag{11}$$

For simplicity, I weight adults and juveniles equally, but one could weight them differently (e.g. adults might be weighted 3–100 times more than juveniles); the qualitative results presented here change very little or not at all with different weightings.

The model generates trajectories of adult (Fig. 2) and juvenile (Fig. 3) population sizes that show large variations over time. This raises the question of how a reserve can be evaluated when the population fluctuates widely for natural reasons. I adopted the following procedure:

1. Run the model for 500 years with $A = 1$ (no fishing) and track the total population size in each year during this run.
2. Re-run the model, using the same sequence of random variables as in step 1, but with $A < 1$. This generates a second set of population sizes for each year.
3. Randomly pick 300 'windows' of length 20 years and calculate the number of years in which the population with $A < 1$ (step 2) exceeds a fixed fraction ($= 0.35$ for computations reported here; elsewhere I've used 60%, rather than 35%, each of which has a history in fisheries management; see Quinn and Deriso, 1999) of the population with $A = 1$ (step 1). The fraction of years determined in this manner is a measure of the probability of success of maintaining the population at a sustainable level.

This procedure thus generates an average and standard deviation for the probability of success (Fig. 4), from which one can select the fraction of habitat for protection according to the desired chance for success. Maintaining the population at or above 35% of the level in the absence of fishing and the acceptable probability for achieving that goal are social decisions. Once they are agreed upon, however, the model allows computation of the requisite probabilities as a function of the fraction of habitat protected.

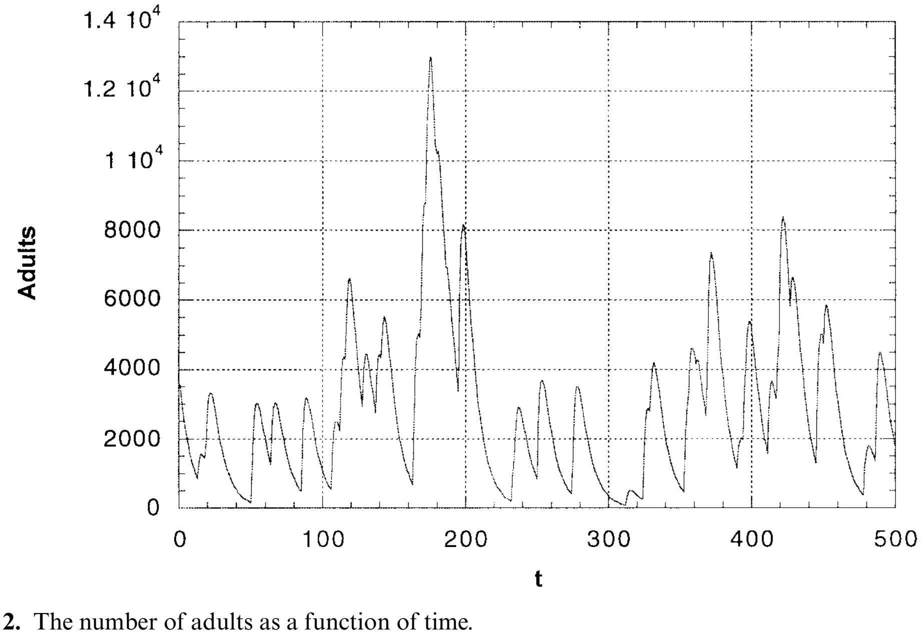

Fig. 2. The number of adults as a function of time.

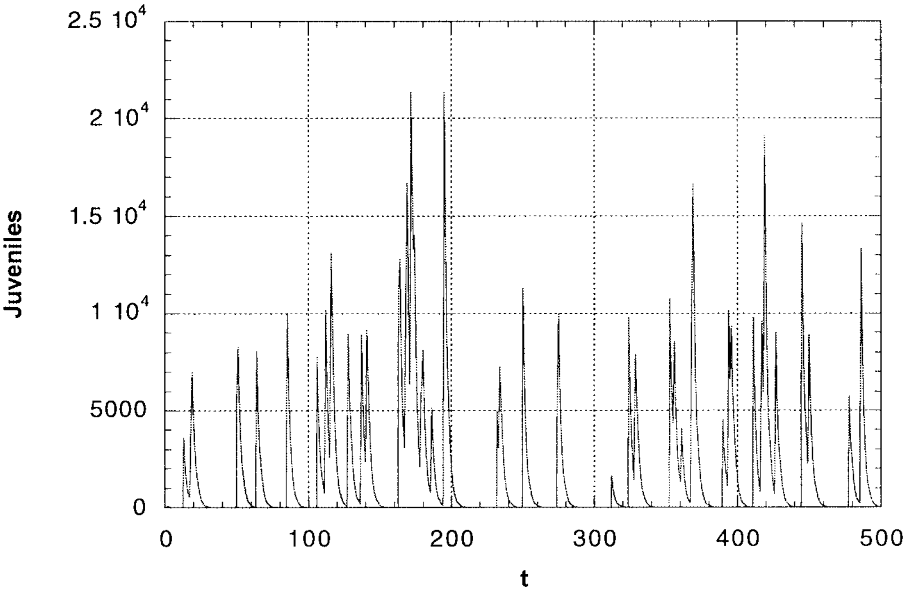

Fig. 3. The number of juveniles as a function of time.

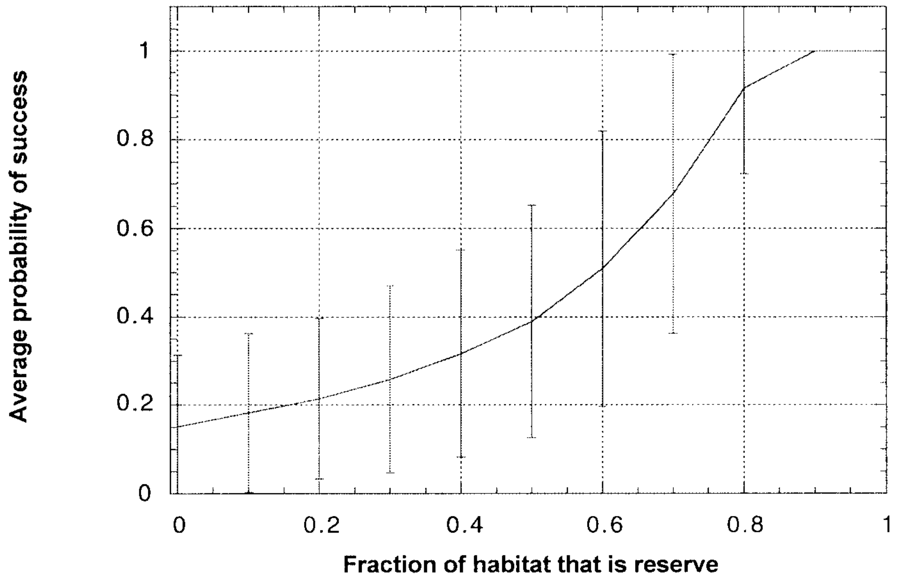

Fig. 4. The average and standard deviation of the probability of success as a function of the fraction of habitat that is reserve.

Now, consider catch. It is a general property of this model (unlike some of the others that I have considered) that catch is a declining function of reserve size (Fig. 5a). Note from Fig. 5a, however, that smaller reserves lead to larger but more variable catches. Thus, mean–variance trade-offs (e.g. Dixit and Pindyck, 1994) – another topic of lifelong interest

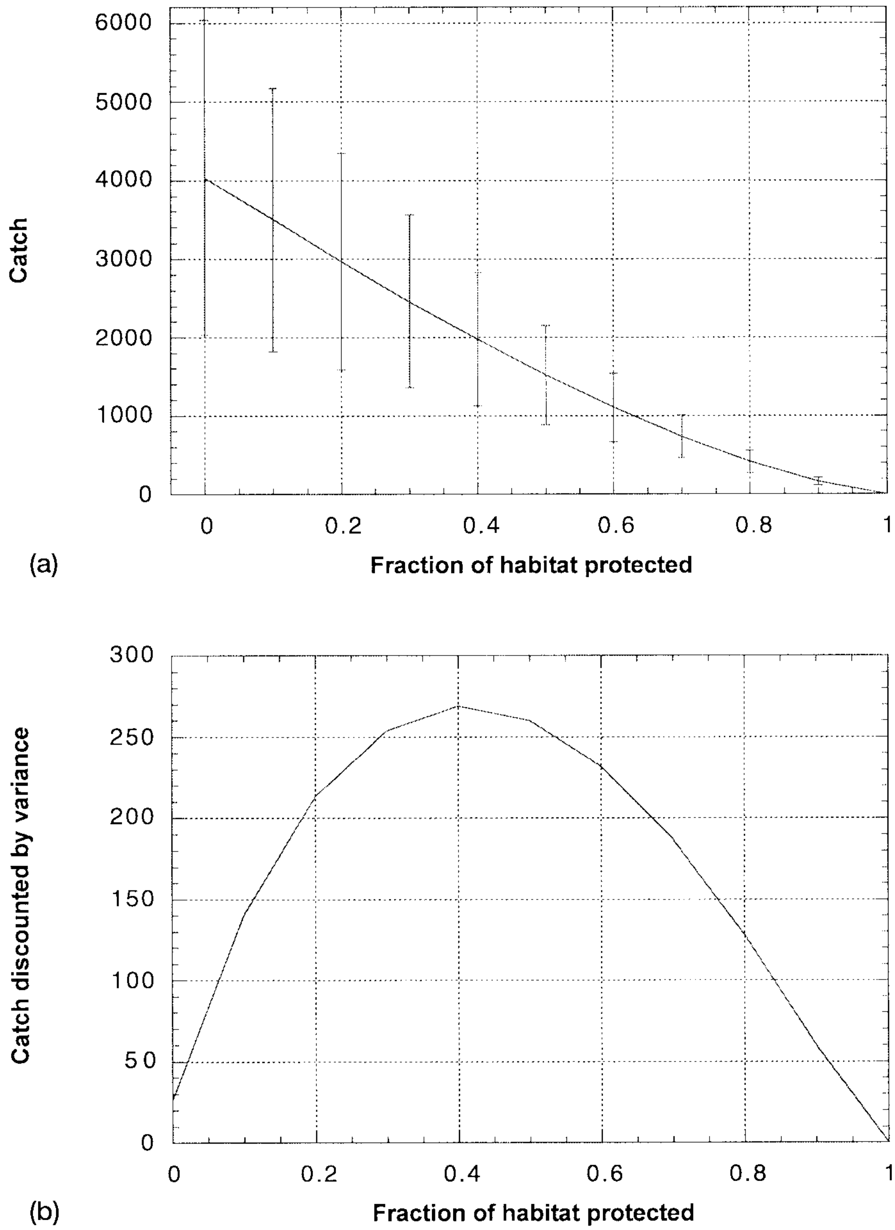

Fig. 5. (a) The average and standard deviation of catch as a function of the fraction of habitat that is reserve. (b) The average catch discounted by twice the standard deviation in catch (i.e. $<C> - 2\mathrm{SD}(C)$).

to Dan Cohen – can be conducted. For example, Fig. 5b shows the average catch discounted by twice the standard deviation; if catch were normally distributed, then this would roughly be the lower 95% confidence interval. The discounted catch is small when a small fraction of the habitat is protected because there is so much variability in catch, and small when most of the habitat is protected because there is so little catch. In summary, the predictions are that implementing a reserve in this case will not increase catch, but it will decrease variability in catch and, consequently, will be advantageous in avoiding boom-and-bust cycles (e.g. Clark, 1990).

THE NEED FOR THEORETICAL APPLIED ECOLOGY

Finding means to conserve fish populations and achieve sustainable fisheries is an important challenge in applied ecology. Here, and elsewhere, I have used theoretical models (Mangel *et al.*, in press) to provide intuition about the roles that marine reserves can make in achieving these goals. This is an example of 'theoretical applied ecology', a phrase coined by the National Center for Ecological Analysis and Synthesis Working Group on Managing Variability (members H. Possingham, T. Coulson, E.-J. Milner Gulland, K. Shea and C. Wilcox) in spring 1999. They observed that in science we tend to think about one axis that runs between basic and applied and another axis that runs between theoretical and empirical/observational. The notion of theoretical applied ecology is most appropriate for those individuals who are interested in using models to solve important environmental problems.

Dan Cohen has not worked on many applied problems, but I trust that he will find great joy in seeing many of the theoretical ideas that he has pioneered and championed used in the solution of the pressing environmental questions of the next century.

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