No-take areas for sustainability of harvested species and a conservation invariant for marine reserves

Abstract
Various kinds of no-take areas (refuges, reserves) are gaining attention as conservation tools. The efficacy of reserves can be considered from the perspectives of providing baseline data sets, protecting the stock, maximizing yield to the fishery, or some combination of these. Regardless of the measure of effectiveness of a reserve, practical application requires the development of techniques for settling operational and policy questions such as how large a reserve should be. A simple model, involving population growth and harvest, is used to explore how the fraction of habitat assigned to a reserve affects the sustainability of a take and to frame the tradeoff between control of harvest outside of the reserve and the size of the reserve. This exploration also leads to the discovery of a robust conservation invariant for reserves.

Keywords
Invariants, marine protected areas, marine reserves, sustainable fisheries.

INTRODUCTION
No-take areas (refuges, reserves) are increasing in visibility as conservation and management tools (e.g. Carr & Reed 1993; Gubbsary 1995; Shackell & Willison 1995; Bohnsack & Ault 1996). Sound scientific advice to those involved with legislation and decision-making concerning reserves must include information on the size of the reserve and often must be provided in the face of considerable biological and operational uncertainty. In such circumstances, a tool for policy analysis should be robust to alternative assumptions. Consistent with a precautionary approach (Bodansky 1991; Costanza & Cornwell 1992; Dovers & Handmer 1995), a conservative estimate of reserve size is most likely to be appropriate. Finally, because recent legislation in the US focuses on the sustainability of fisheries (104th Congress of the United States of America 1996), it is important to know if reserves or no-take areas can improve the prospects for sustainability.

MATERIALS, METHODS, AND RESULTS
Envision a population that grows according to logistic stock dynamics,

\[ N(t+1) = N(t) + rN(t)\left[1 - \frac{N(t)}{K}\right] \]  

(1)

where \( N(t) \) is the size of the population at the start of year \( t \), before either take or reproduction, \( r \) is the maximum per capita reproductive rate, and \( K \) is the carrying capacity of the habitat. The choice of growth dynamics in eqn 1 is not crucial for the development that follows, but allows some analytical simplification. Logistic dynamics or their generalization fit a wide variety of species, from barnacles (Roughgarden et al. 1994) to whales (Clark 1985), and do so because of the logical simplicity: when population size is small [so that \( N(t)/K \ll 1 \)] the population grows proportional to its size; when the population is larger growth slows. Although eqn 1 is based on the assumption of a closed population, this is not crucial for the analysis that follows.

Creating a no-take reserve means that some fraction \( A \) of the habitat is set aside and that harvest does not occur in the reserve. In the remaining part of the habitat, harvest (take) occurs and a fraction \( u \) of the population there is removed. In most harvesting operations, the precise value of the harvest fraction is not known; the sources of this uncertainty include lack of controllability of effort, natural fluctuations, incidental mortality, and/or illegal take (Milner-Gulland & Leader-Williams 1992; Leader-Williams & Milner-Gulland 1993; Mangel 1993; Alverson et al. 1994; Gillis et al. 1995a, b; Hart 1997). Regardless of the source of uncertainty, one can assume that the take can be bounded by a maximum value \( u_{\max} \), which in the extreme case could be as large as 1 (Nowliss & Roberts 1998). A specific alternative in which the harvest fraction is targeted but varies stochastically is considered by Lauck et al. (1998); their results could be combined with the
approach described here. By working with the maximum value of take, one implicitly accepts that some kinds of harvest mortality, such as incidental by-catch and discard, will never really be known (Gillis et al. 1995a, b; Gunderson 1997), and that effective management should not only recognize this lack of certainty, but embrace it as part of the planning (Mangel et al. 1996).

If reproduction follows take, the population size after take, but before reproduction is \( AN(t) + (1-A)(1-u)N(t) = (1-u + Au)N(t) \). Consequently, in a year in which the take is \( u \), the population dynamics are

\[
N(t+1) = (1-u + Au)N(t) + (1-u + Au)N(t) \times \\
\frac{1 - [(1-u + Au)N(t)]}{K}
\]

The steady state population size, found by setting \( N(\infty) = N(t+1) = N(u) \), is given by

\[
N(u) = \frac{K}{1 - u + Au} \left[ 1 - \frac{u(1-A)}{r(1-u + Au)} \right]
\]

and the steady state yield is \( Y(u) = u(1-A)N(u) \).

Since \( u \) is bounded by \( u_{\text{max}} \), the minimum reserve fraction needed to ensure sustainability of the population at a fraction \( f \) of the carrying capacity is the value of \( A \) that makes \( N(u)/K = f \) when \( u = u_{\text{max}} \). This value is the larger of 0 or

\[
A_{\text{r}}(f) = 1 + \\
\frac{1 + r - 2rf - \sqrt{(1 + r - 2rf)^2 - 4rf(f - 1)}}{2rf_{\text{max}}}
\]

When \( f = 0 \), eqn 4 simplifies and gives the minimum value of the reserve fraction to ensure that the population persists

\[
A_{\text{r}}(0) = \frac{u_{\text{max}}(r+1)-r}{u_{\text{max}}(r+1)}
\]

If \( u_{\text{max}} < r(r+1) \) then the minimum reserve size required to guarantee persistence is 0; otherwise it is greater than 0 (Fig. 1).

The steady population level given by eqn 3 and steady state yield \( Y = u_{\text{max}}(1-A)N \) involves the combination of parameters \( I = u_{\text{max}}(1-A) \). This combination is thus a no-take invariant, in the sense that similar results are obtained regardless of the individual values of \( u_{\text{max}} \) and \( A \), as long as \( I \) is constant. Invariant values have a long and rich contribution to fishery science (Beverton 1992; Charnov 1993; Mangel 1996), so it is not completely remarkable that another one arises here. In terms of this invariant, the steady state population size is

\[
Y(I) = I N(I) = \frac{IK}{1-I} \left[ 1 - \frac{I}{r(1-I)} \right]
\]

Because the steady state yield is

\[
Y(I) = I N(I) = \frac{IK}{1-I} \left[ 1 - \frac{I}{r(1-I)} \right]
\]

it is possible to find the value of the invariant that maximizes yield, for each value of \( r \), consistent with the population being sustained at a level \( fK \) (Fig. 2). This figure demonstrates that commercial fisheries and stock conservation may be able to operate positively together. That is, if per capita growth rate is sufficiently high, the optimal level of yield for stock protection occurs at a reserve size that is larger than that for stock persistence at a specified fraction of carrying capacity.

**DISCUSSION**

No-take areas have been proposed for ground fish, reef fish, mollusks, crustaceans, and echinoderms (Bohnscck 1992; Dugan & Davis 1993; Auster & Shackell 1997), but design considerations for marine reserves are still developing. Although some ideas from terrestrial reserve design may be helpful in the determination of marine reserves, the primary concern to fishery management is
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REFERENCES


**BIOGRAPHY**

Marc Mangel is Professor in the Department of Environmental Studies and the Institute of Marine Sciences at the University of California, Santa Cruz. His research interests are focused on the ecological implications of life history variation. He has written *Decision and Control in Uncertain Resource Systems*, *Dynamic Modelling in Behavioural Ecology* (with Colin Clark) and *The Ecological Detective: Confronting Models with Data* (with Ray Hilborn).

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