

7. To construct a targeting vector, we used 3.5- and 5.2-kb fragments from a murine genomic ES BAC clone for the 5' and 3' regions of homology, respectively. Culture, selection, and screening of targeted clones were as described [D. Y. Li *et al.*, *Nature* **393**, 276 (1998)]. There was no evidence of random integration in the homologous recombinant clones used for chimera generation. Resulting chimeric animals were crossed to C57BL/6J mice and germ line transmission was confirmed. Genotypes were assigned on the basis of Southern blot analysis of DNA extracted from tails, embryos, or yolk sacs.
8. L. Sorensen and D. Li, unpublished data.
9. D. Wendel and D. Li, unpublished data. Reverse transcriptase-polymerase chain reactions for these molecular markers were done as described [F. Shalaby *et al.*, *Nature* **376**, 62 (1995)].
10. Immunoperoxidase staining of mouse embryos was done with monoclonal antibodies to PECAM (Pharmingen, San Diego, CA), endoglin (Pharmingen), FLK-1 (Santa Cruz Biotechnology, Santa Cruz, CA), or  $\alpha$ -smc actin (clone 1A4, 1:500; Sigma, St. Louis, MO). Staining was developed in 3,3'-diaminobenzidine chromagen (Vector Laboratories, Burlingame, CA). Sections of stained tissue were counterstained with eosin B.
11. L. Sorensen, L. Urness, D. Li, unpublished data.
12. Hybridization was performed at 70°C with an RNA probe described by Li *et al.* [L. Li, J. M. Miano, P. Cserjesi, E. N. Olson, *Circulation* **78**, 188 (1996)]. Sense RNA probes showed no hybridization.
13. Tissue was fixed in 3% glutaraldehyde and sequentially stained with osmium tetroxide, tannic acid, and uranyl acetate. After dehydration, tissue was embedded in Epon. Thin sections (60 nm) were counterstained with uranyl acetate and lead citrate and examined on a JEOL 1200 electron microscope.
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# Equivalence in Yield from Marine Reserves and Traditional Fisheries Management

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Marine reserves have been proposed as a remedy for overfishing and declining marine biodiversity, but concern that reserves would inherently reduce yields has impeded their implementation. It was found that management of fisheries through reserves and management through effort control produce identical yields under a reasonable set of simplifying assumptions corresponding to a broad range of biological conditions. Indeed, for populations with sedentary adults (invertebrates and reef fishes), reserves have important advantages for sustainability, making marine reserves the preferred management approach.

Marine reserves have been recommended as an alternative to existing fisheries management and as a means of conserving declining biodiversity. Where fisheries are concerned, reserves have been proposed to provide greater fishery yields when effort is high (1, 2), to prevent overfishing in the presence of parameter uncertainty (3), and to reduce variability in catch (2). However, the implementation of reserves has been slowed by concerns that they would reduce fishery yields substantially. In our study, we examined whether reserves can produce a yield equivalent to harvesting a fixed fraction or a fixed number of the population and determined a simple formula for the optimal fraction of area in reserves.

To assess this complex multifaceted problem, we made a number of simplifying, but robust, assumptions (4) that allowed us to focus on the essential issues. The most important assumptions are that adults are stationary, that larvae are distributed so broadly that the density of settling juveniles along the coastline is independent of location, and that

all density dependence occurs at the time of settling and depends only on the density of settling juveniles. For the reserve case, we present the details of the analysis for the case in which all adults outside the reserves are caught in the fishery—there is no reproduction outside the reserves. We also describe results for the case of a mixed strategy employing reserves and managed harvests.

We set up simple optimization models describing the yield in each case of interest. There are a number of parameters and functions common to both models. The number of settling juveniles produced per year by each adult is assumed to be  $m$ , adults reach maturity at age  $j$ , and annual adult survival is  $a$ . In the case of reserves, we assume that a fraction  $c$  of the coastline is set aside in reserves. We denote the density of adults in year  $t$  by  $n_t$ . We normalize the length of the coastline we are considering to be 1, so that if the density of organisms is constant over space, then the number (density multiplied by length of coastline) of adult organisms is also  $n_t$ .

Although a complete assessment of marine reserves requires an explicit consideration of the potential density dependence (5) in predispersal, larval, and postdispersal components of recruitment, this has not been done to date. Including these features would require a model of such complexity that no

simple conclusions could be drawn. To establish an initial benchmark for reasonably common conditions, we first analyzed a model in which we only allow postdispersal density dependence and only consider the effect of settling juveniles on density dependence. Thus, if the density of larvae attempting to settle is  $l$ , then the density successfully reaching the adult, reproductive class (perhaps years later) is  $f(l)$ . Our results do not depend on the form of density dependence,  $f$ .

Traditional fishery models are often phrased in terms of removing a fraction, or a fixed amount, of the available resource each year, producing the same yield in each case. When a fixed fraction  $H$  is harvested, the number of adults the following year is the sum of those reaching maturity and those surviving from the previous year multiplied by the probability of escape from harvest

$$n_{t+1} = (1 - H)[f(mn_{t-j}) + an_t] \quad (1)$$

At equilibrium, the population size  $n$  satisfies

$$n = (1 - H)[f(mn) + an] \quad (2)$$

The maximum sustainable yield in this model is

$$Y_h = \max\{H[f(mn) + an]\} \quad (3)$$

which is subject to Eq. 2. By solving Eq. 2 for the expression on the right-hand side of Eq. 3, one can rewrite the equation for the maximum sustainable yield for traditional harvesting as

$$Y_h = \max\{[f(mn) + an] - n\} \quad (4)$$

where  $n$  is the variable that can be chosen to maximize yield.

In the case of reserves, we assume that the density of organisms in the reserves is  $n'_r$ , so the number (not density) of juveniles produced is thus  $cmn'_r$ . Because we make the simplifying assumption that the larvae are widely dispersed, we posit that the density of settling juveniles is once again independent of location. Therefore, the density of postdispersal juveniles is equal to  $cmn'_r$ , both inside reserves and in the fished areas outside reserves. Thus, inside the reserves, the dynam-

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ics of the population is given by

$$n'_{t+1} = f(cmn'_{t-j}) + an'_t \quad (5)$$

and the maximum sustainable yield can be found by choosing the fraction of coastline in reserves,  $c$ , to maximize the number of larvae that settle outside the reserves

$$Y_r = \max[(1-c)f(cmn'_r)] \quad (6)$$

which is subject to the equilibrium condition

$$n' = f(cmn'_r) + an' \quad (7)$$

A simple change of variables can be used to show that the yield is the same as the yield with harvesting. Letting  $u = cn'_r$  and  $p = 1 - c$ , from Eq. 6 the maximum yield is found to be

$$Y_r = \max[pf(mu)] \quad (8)$$

where, from Eq. 7, we see that  $u$  satisfies

$$u = (1-p)f(mu) + au \quad (9)$$

Solving Eq. 9 for the right-hand side of Eq. 8, one sees that

$$Y_r = \max\{[f(mu) + au] - u\} \quad (10)$$

where  $u$  is the variable that can be chosen to maximize yield, which is the same maximum sustainable yield as that in the traditional management models (with  $u$  and  $n$  chosen to be the same).

We can also use our formulation to find a relation between the optimal fraction of the coastline in reserves and the optimal fraction of the adult population allowed to escape harvesting under traditional management approaches. Setting the yields in Eqs. 3 and 8 as equal and noting that the equality of Eqs. 4 and 10 implies that  $u = n$ , one obtains the relation

$$c = (1-H) - H \left[ \frac{an}{f(mn)} \right] \quad (11)$$

where the density  $n$  is the density at the optimal harvest level. Thus, the optimal fraction of the coastline in reserves is always less than the fraction of adults allowed to escape harvest under traditional management techniques, unless the species is semelparous ( $a$  is zero) and the two fractions are equal. This makes sense because the adults in reserves can reproduce until they die, so if the population is iteroparous, the fraction of the adult population set aside can be lower than that under traditional management. This relation is also important because it can be used as an initial guideline for the area set aside in reserves, based on earlier management approaches and life histories of species.

A similar analysis could be used to study a combination approach to management, in which the fraction of coastline set aside for reserves is smaller than the one producing the optimal yield and traditional management is

used outside reserves to maximize yield. Once again, exactly the same maximum sustainable yield is obtained as that in the case of only reserves or only traditional management.

With the simplifying assumptions used here, the maximum yield under a system of reserves is identical to the maximum yield under traditional management. Because reserves have other advantages over traditional fisheries management in terms of reduced variability and sustainability under uncertainty, they would be the preferred alternative in this case. Thus, reserves can do more than just provide higher yields in situations that would otherwise result in overfishing (1, 2), they can also provide the same yield as traditional management. Furthermore, the fraction of area in reserves can be less than the optimal escapement fraction.

Given this result, the question of the global efficacy of reserves then depends on the frequency of postdispersal density-dependent recruitment, without a dependence on local adults, and the consequences of other types of density dependence. Postdispersal density-dependent recruitment depending only on settling individuals is certainly common (6). A simple modification of the above approach would show that, with predispersal density dependence (7), yield in the case of reserves would be less than the yield from traditional harvesting. Postdispersal density dependence in which local adult or subadult abundance plays a role (8) can also be shown to reduce the yield under a system of reserves, relative to that of traditional management approaches.

The factors considered in this simple model allow us to include the essential trade-offs necessary to compare reserve management to traditional management; however, we have not explicitly incorporated all relevant factors (9). We have not specifically accounted for uncertainty in parameter values (2) but rather have shown that, even without considering precautionary measures to reduce the chance of overfishing, reserves are a reasonable alternative to effort management. Although we have ignored many important features of biological importance, by showing a simple case in which yield is the same with reserves as with more traditional management approaches and determining the relation between optimal reserve area and optimal harvest fraction, we have set the benchmark for the future study of the trade-offs that will favor different management strategies.

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4. We do not address relations between dispersal and spatial configuration of reserves here [M. H. Carr and D. C. Reed, *Can. J. Fish. Aquat. Sci.* **50**, 2019 (1993); G. W. Allison, J. Lubchenco, M. H. Carr, *Ecol. Appl.* **8**, S79 (1998)]. We assume that the fecundity of all mature individuals is the same. In the case of traditional fisheries management, we assume that the age of maturity and the age of first catch are the same.
5. Before dispersal, the number of larvae produced may be density dependent. After dispersal, the number of juveniles successfully metamorphosing and surviving to the adult stage will, in general, depend on the density of larvae attempting to metamorphose and on the density of individuals, both adults and subadults, that are already present.
6. Postdispersal density-dependent recruitment without a dependence on local adults occurs typically when postmetamorphosis density is limited by available habitat, as is the case for reef fishes [M. A. Hixon and M. H. Carr, *Science* **277**, 946 (1997); M. J. Caley *et al.*, *Annu. Rev. Ecol. Syst.* **27**, 477 (1996)] and structure-dwelling benthic invertebrates [J. F. Caddy, *Can. J. Fish. Aquat. Sci.* **43**, 2330 (1986); R. A. Wahle and R. S. Steneck, *Mar. Ecol. Prog. Ser.* **69**, 231 (1991)], but may not be the case for macroinvertebrates in soft sediments [E. B. Olafsson, C. H. Peterson, W. G. Ambrose Jr., *Oceanogr. Mar. Biol. Annu. Rev.* **32**, 65 (1994)]. Postdispersal density dependence without a dependence on local adult density would result in a Beverton-Holt type of stock-recruitment relationship [R. J. H. Beverton and S. J. Holt, *U.K. Minist. Agric. Fish. Fish. Invest. Ser.* **2**, 19, 1 (1957)], which is the type most commonly observed in compendia of stock-recruitment relationships of commercially fished species [R. A. Meyers, J. Bridson, N. J. Barrowman, *Can. Tech. Rep. Fish. Aquat. Sci.* **2024**, 1 (1995)].
7. Predispersal density dependence would most commonly be some form of density-dependent fecundity, which certainly exists in the case of marine fish and invertebrates [E. A. Trippel, O. S. Kjesbu, P. Solemdal, in *Early Life History and Recruitment in Fish Populations*, R. C. Chambers and E. A. Trippel, Eds. (Chapman & Hall, New York, 1997), pp. 31–62], but is rarely specifically demonstrated in stock-recruitment relationships.
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9. Increased fecundity of older individuals, which we ignored, could increase the maximum yield under a system of reserves relative to that obtained with traditional management techniques, depending on the nature of predispersal density dependence. We also ignore the role of dispersal distance and reserve configuration. We have assumed that settlement in the reserve area declines linearly with the amount of area placed in reserves. Presumably, reserves can be placed close enough so that this assumption holds. Adult migration could have a great effect on the results here if it is large [T. Polacheck, *Nat. Res. Model.* **4**, 327 (1990); E. E. DeMartini, *Fish. Bull.* **91**, 414 (1993); C. G. Attwood and B. A. Bennett, *S. Afr. J. Mar. Sci.* **16**, 227 (1995)], but highly migratory species are not under serious consideration for management by reserves. We have not considered growth/mortality trade-offs made in classical yield-per-recruit analyses, but presumably, size limits could be chosen and the same results would hold.
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