

When do marine reserves increase fishery yield?

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Abstract: An age-structured model is developed for analyzing the effects of marine reserves and other long-term closures on fishery yield, assuming larvae are well-mixed and that exchange of adults between the open and closed areas is negligible. A number of analytic results are derived, including a formula for the gradient of yield with respect to fishing mortality and closure fraction. Increasing the closure fraction at equilibrium spawning stock biomass (SSB), B , will increase yield if and only if $s'(B) > 1/b_0(0)$, where $s'(B)$ is the slope of the stock–recruitment curve at B and $b_0(0)$ is SSB per recruit at zero fishing mortality. Conditions for the level of closure required to prevent stock collapse are also derived. Applications of the theory to canary rockfish (*Sebastes pinniger*) and Georges Bank sea scallop (*Placopecten magellanicus*) illustrate that long-term closures increase yield only at low SSB associated with fishing mortalities greater than F_{MSY} and with low closure fractions. The theory presented here gives simple analytic and graphical techniques for predicting the effects of long-term closures on yield and stock persistence.

Résumé : Un nouveau modèle structuré d'après l'âge permet d'analyser les effets des réserves marines et des autres fermetures de longue durée de la récolte sur le rendement de la pêche, si l'on présume que les larves sont bien réparties et que les échanges d'adultes entre les zones ouvertes et fermées sont négligeables. Il en dérive plusieurs résultats analytiques, dont une formule pour déterminer le gradient du rendement en fonction de la mortalité due à la pêche et la fraction représentée par les zones fermées. L'accroissement de la proportion des zones fermées lorsque la biomasse du stock reproducteur (SSB) est à l'équilibre B va faire augmenter le rendement seulement si $s'(B) > 1/b_0(0)$, où $s'(B)$ est la pente de la courbe stock–recrutement au point B et $b_0(0)$ est la SSB par recrue lorsque la mortalité due à la pêche est nulle. On peut aussi obtenir les conditions du niveau de fermeture nécessaire pour prévenir l'effondrement du stock. Des exemples utilisant le sébaste canari (*Sebastes pinniger*) et le pétoncle marin (*Placopecten magellanicus*) du banc Georges montrent que les fermetures de longue durée de la pêche augmentent le rendement seulement lorsque des SSB basses sont associées à des mortalités dues à la pêche supérieures à F_{MSY} et que les fractions des zones fermées sont petites. La théorie présentée ici fournit des techniques analytiques et graphiques simples pour prédire les effets de fermetures de longue durée sur le rendement et la persistance des stocks.

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Introduction

There has been enormous interest in recent years in long-term fishery closures, often termed “marine reserves”, as a management tool. Although there is little question that such closures can be part of a precautionary approach to fisheries management, their effect on fishery yields is more controversial. Although increases in biomass within closures and (somewhat less commonly) “spillover” of adults or larvae into adjacent areas has often been observed, these phenomena do not necessarily imply enhanced yields because the additional yield from spillover must be balanced against the direct loss of yield from the closures. The natural variability

of recruitment and yield, together with the lack of true controls or replication, make it difficult to empirically determine the effect of long-term closures on yield.

For this reason, models, most of them simulations, have often been used to understand the effects of closures (reviewed in Gerber et al. 2003). It is difficult to infer general principles from simulations, and results can be sensitive to parameter choices. Previous analytic modeling of the effects of closures has typically involved neglecting age structure or some other unrealistic oversimplification. For example, Hastings and Botsford (1999) demonstrated that maximal sustainable yield (MSY) from a conventional effort-based strategy can also be obtained using closures with infinite fishing mortality in the open areas. However, yield was measured in numbers caught, rather than weight. Because the mean age of the catch is greater in the conventional MSY policy, the catch in weight will usually be greater with the effort-based strategy than with their marine reserve approach.

The purpose of this article is to develop an analytical age-structured approach for analyzing the effects of long-term closures. It is an extension of the ideas from Beverton and

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Fig. 1. Yield as a function of fishing mortality and closure fraction for (a, c, e, g) canary rockfish (*Sebastes pinniger*) and (b, d, f, h) Georges Bank sea scallop (*Placopecten magellanicus*). (a–b) Equilibrium yield as a function of fishing mortality for closure fractions 0 (solid line), 0.1 (broken line), 0.4 (dashed–dotted line), and 0.7 (dotted line). (c–d) Yields as a function of closure fraction for various fishing mortalities (for canary rockfish, $F = 0.05$ (solid line), 0.15 (broken line), 0.3 (dashed–dotted line), 0.5 (dotted line); for sea scallop, $F = 0.24$ (solid line), 0.6 (broken line), 1.2 (dashed–dotted line), 2.0 (dotted line)). (e–f) Surface plots of yield. (g–h) Yield gradient fields (arrows, fifth root transformed) and yield isopleths (solid lines); the shaded area indicates the portion of the (F, C) plane where an increase in the closure fraction increases yields, according to eq. 15. The two arrows on the abscissa indicate (left to right) F_{MSY} and F_{max} , the fishing mortalities that maximize sustainable yield and yield per recruit, respectively. Note that the fishing mortality that produces maximal yield at a given closure fraction C increases for canary rockfish and approaches F_{max} at high closure fractions. This optimal fishing mortality for sea scallop is nearly constant with C because the stock–recruitment function is almost completely saturated at F_{max} , so that $F_{max} \approx F_{MSY}$.

Holt (1957) and Shepherd (1982), who combined per recruit and stock–recruitment curves to calculate yield.

Model development and results

Yield can be expressed as

$$(1) \quad Y = yR$$

where y is yield per recruit and R is recruitment (Beverton and Holt 1957; Shepherd 1982; Quinn and Deriso 1999). Recruitment at spawning stock biomass (SSB), B , is determined through a stock–recruitment relationship $R = s(B)$. At equilibrium, recruitment is implicitly defined by the equation

$$(2) \quad R = s(B) = s(bR)$$

where b is SSB per recruit. Here, egg production, perhaps adjusted for the viability of the eggs, could be substituted for SSB, in which case b would represent eggs per recruit. It will be assumed through eq. 15 that recruitment is positive at the equilibrium of interest (i.e., the R satisfying eq. 2 is positive), and that at this equilibrium,

$$(3) \quad |bs'(bR)| < 1$$

where s' represents the derivative of s with respect to B . This condition (eq. 3) will assure that in the dynamical system defined by

$$(4) \quad R_{n+1} = s(bR_n)$$

the equilibrium solution (eq. 2) is attracting (i.e., asymptotically stable; Hale and Koçak 1991); it will be satisfied by nonzero equilibria under most realistic conditions. Of course, the system is never exactly in equilibrium, but it will tend to return towards an attracting equilibrium after a perturbation, so that an equilibrium analysis will give insights into the dynamics of the system.

It will be assumed that adults are sufficiently sedentary so that exchange of adults between open and closed areas is negligible, but that larvae are well mixed between the open and closed areas. Let C be the fraction of recruitment that occurs in areas closed to fishing. Because recruits in the closures produce no yield, the mean yield per recruit (y) and SSB per recruit (b) with closures at fully recruited fishing mortality F are given by

$$(5) \quad y = (1 - C)y_0(F)$$

and

$$(6) \quad b = Cb_0(0) + (1 - C)b_0(F)$$

where y_0 and b_0 are yield per recruit and SSB per recruit without closures. To simplify notation, y and b will represent yield and SSB per recruit at fishing mortality F and closure fraction C , i.e., $y = y(F, C) = (1 - C)y_0(F)$ and $b = b(F, C) = Cb_0(0) + (1 - C)b_0(F)$. Fishing mortality rates will always be calculated with respect to the fished area only.

Equations 1 and 2 implicitly define yield Y as a function of fishing mortality F and the fraction closed C . The partial derivatives of Y with respect to these quantities are

$$(7) \quad \frac{\partial Y}{\partial F} = \frac{\partial y}{\partial F} R + y \frac{\partial R}{\partial F} = (1 - C) \left[y'_0(F)R + y_0(F) \frac{\partial R}{\partial F} \right]$$

and

$$(8) \quad \frac{\partial Y}{\partial C} = \frac{\partial y}{\partial C} R + y \frac{\partial R}{\partial C} = \frac{d(1 - C)}{dC} y_0(F)R + (1 - C)y_0(F) \frac{\partial R}{\partial C} \\ = y_0(F) \left[(1 - C) \frac{\partial R}{\partial C} - R \right]$$

The partial derivatives of R can be computed from eq. 2 by implicit differentiation, i.e., by differentiating both sides of eq. 2 and then solving for the derivative of R :

$$(9) \quad \frac{\partial R}{\partial F} = \frac{s'(bR) \frac{\partial b}{\partial F} R}{1 - s'(bR)b} = (1 - C) \frac{s'(bR)b'_0(F)R}{1 - s'(bR)b}$$

and

$$(10) \quad \frac{\partial R}{\partial C} = \frac{s'(bR) \frac{\partial b}{\partial C} R}{1 - s'(bR)b} = \frac{s'(bR)[b_0(0) - b_0(F)]R}{1 - s'(bR)b}$$

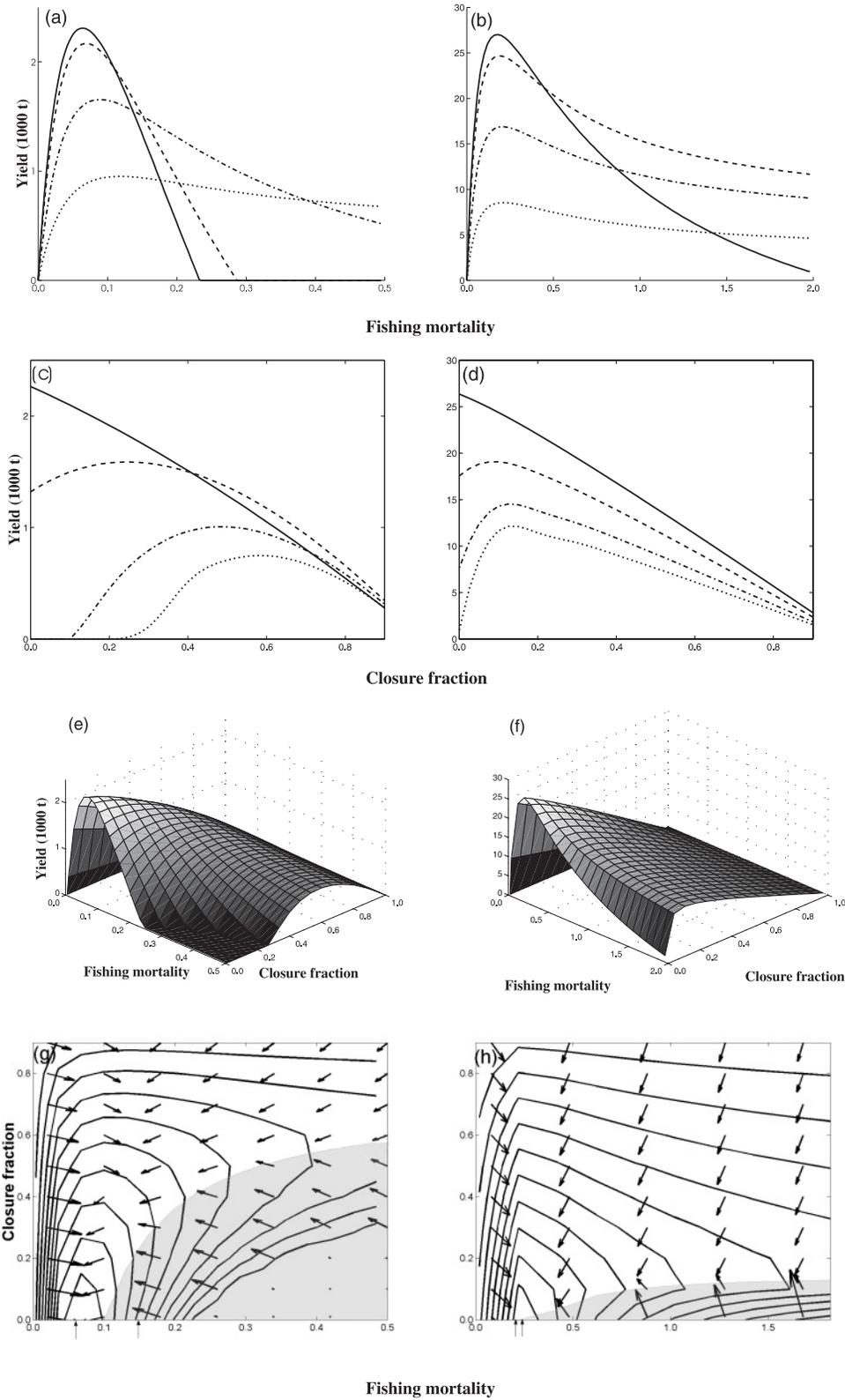
Setting $B = bR$ and substituting eqs. 9 and 10 back into eqs. 7 and 8 gives

$$(11) \quad \frac{\partial Y}{\partial F} = (1 - C)R \left[y'_0(F) + y_0(F) \frac{s'(B)(1 - C)b'_0(F)}{1 - s'(B)b} \right]$$

and

$$(12) \quad \frac{\partial Y}{\partial C} = y_0(F)R \left[\frac{(1 - C)s'(B)[b_0(0) - b_0(F)]}{1 - s'(B)b} - 1 \right]$$

Equations 11 and 12 allow computation of the gradient of Y , $\nabla Y = \left(\frac{\partial Y}{\partial F}, \frac{\partial Y}{\partial C} \right)$, that points in the direction of the steepest ascent of yield on the (F, C) plane.



As example applications, the theory is applied here to canary rockfish (*Sebastes pinniger*) and Georges Bank sea scallop (*Placopecten magellanicus*) (Fig. 1; Table 1). Both of these cases are given for the purposes of illustration; the stock–recruitment relationship for Georges Bank sea scallops is uncertain, and movement of adult canary rockfish is

neglected in this analysis. These examples nonetheless illustrate and contrast a low productivity species (canary rockfish) that is prone to recruitment overfishing with a highly productive and fecund species (sea scallops) that has a stock–recruitment function that is nearly saturated at F_{max} , the fishing mortality that maximizes yield per recruit. In

Table 1. Parameter estimates and other key quantities for canary rockfish (*Sebastes pinniger*) and Georges Bank sea scallop (*Placopecten magellanicus*).

Stock	α	β , kg	F_{MSY}	F_{max}	$b_0(0)$, kg/recruit	$s'(0)$, recruits/kg	B_c , kg	C_{crit}		
								No exchange	10% exchange	20% exchange
Canary rockfish	9.6×10^6	6.7×10^6	0.06	0.15	1.37	1.4	2.7×10^6	0.51	0.70	0.91
Sea scallop	1.6×10^9	1.4×10^7	0.18	0.22	0.245	112	5.9×10^7	0.036	N/A	N/A

Note: Stock–recruitment functions were specified by the Beverton–Holt parameters α and β , where $s(B) = \alpha B / (\beta + B)$. The stock–recruitment parameters and per recruit calculations for canary rockfish were based on Methot and Stewart (2005), assuming that most of the catch is taken by commercial trawlers; the sea scallop per recruit estimates are from Hart (2003). An attempt to fit a Beverton–Holt curve to scallop stock–recruitment data from 1982–2005 gave a reliable estimate of the asymptote α but could not accurately estimate β because of high recruitment variability together with limited increases in mean recruitment as SSB has increased. Because the Georges Bank sea scallop stock–recruitment relationship appears to be at least partially saturated during the entire observed period, β was estimated as the lowest observed spawning stock biomass (SSB) in the time series. F_{max} and F_{MSY} are the fishing mortalities (with no closures) that maximize yield per recruit and equilibrium yield, respectively. B_c is the SSB for which $s'(B_c) = 1/b_0(0)$, so that closures increase yield below, but not above, this biomass at equilibrium. C_{crit} is the fraction of closure required to prevent stock collapse regardless of fishing mortality or selectivity. For canary rockfish, this quantity is computed assuming that adult exchange between closed and open areas is 0%, 10%, and 20%. N/A, not applicable.

both cases, closures increase yield (indicated by the shaded area and upward slants of the gradients in Figs. 1g–1h) only at low biomasses corresponding to overfished conditions, and MSY over all F and C occurs at the conventional F_{MSY} with no closures.

It is of particular interest to determine under what conditions $\frac{\partial Y}{\partial C} > 0$, so that yield increases with greater closure.

According to eq. 12, this occurs when

$$(13) \quad 1 < \frac{(1-C)s'(B)[b_0(0) - b_0(F)]}{1 - s'(B)b}$$

Multiplying both sides of eq. 13 by $1 - s'(B)b$ (note that by eq. 3, this quantity is positive) and then adding $s'(B)b$ to both sides gives

$$(14) \quad \begin{aligned} 1 < s'(B)\{(1-C)[b_0(0) - b_0(F)] + b\} \\ &= s'(B)[(1-C)b_0(0) - (1-C)b_0(F) \\ &\quad + Cb_0(0) + (1-C)b_0(F)] \\ &= s'(B)b_0(0) \end{aligned}$$

Thus, $\frac{\partial Y}{\partial C} > 0$ if and only if

$$(15) \quad s'(B) > \frac{1}{b_0(0)}$$

Intuitively, the increase in recruitment from a marginal increase in the closure fraction, which depends on the slope $s'(B)$ and on SSB per recruit at the origin, must be great enough to compensate for that lost to the additional closure. For typical stock–recruitment curves, an incremental increase in the fraction closed is more likely to increase yield at high fishing mortalities and at low closure fractions, as these factors imply a small B and hence a relatively large $s'(B)$. Moreover, for any stock that will not go extinct at zero fishing mortality, $s'(0) > 1/b_0(0)$ (Shepherd 1982), so that eq. 15 must be satisfied at sufficiently low biomass. Thus, eq. 15 gives theoretical insights into the results of numerous simulations that indicate that closures will typically increase yield under overfished conditions, but not when fishing mortality is small.

The formulism described here can answer another important question considered by Mangel (1998) using an aggregate biomass dynamics model: how much closure is necessary to prevent extinction (at equilibrium) at a given fishing mortality F ? To assure population persistence, the $R = 0$ solution to eq. 2 must be repelling (unstable) in the dynamical system defined by eq. 4. This will occur when

$$(16) \quad b|s'(0)| > 1$$

(Hale and Koçak 1991).

Solving for $s'(0)$ and assuming that $s'(0) > 0$ (which is always true in any realistic case), the population is assured of not going extinct when

$$(17) \quad s'(0) > \frac{1}{Cb_0(0) + (1-C)b_0(F)}$$

Solving eq. 17 for C shows that the closure fraction C will be sufficient to prevent stock collapse if $C > C_{crit}(F)$, where

$$(18) \quad C_{crit}(F) = \frac{1/s'(0) - b_0(F)}{b_0(0) - b_0(F)}$$

If $b_0(F)$ is negligible, as is likely the case at very high fishing mortalities, this simplifies to $C_{crit} = \frac{1}{b_0(0)s'(0)}$.

These ideas can be generalized to allow for some types of adult movement. If adults are emigrating out of the closed area at a rate E and they do not contribute to spawning after emigrating, then E represents a loss to the closed area population entirely analogous to fishing mortality. Thus, closed area SSB per recruit under these assumptions is given by $Cb_0(E)$, and the population will not go extinct if

$$(19) \quad s'(0) > \frac{1}{Cb_0(E) + (1-C)b_0(F)}$$

Discussion

The analytic and graphic techniques derived here give simple methods for predicting the effects of closures on yield and stock persistence. They explicitly show the tradeoff between the direct loss of yield from the closures and the increase in yield obtained by recruitment spillover. Although

the former is simply a fixed fraction of the total yield, the latter depends on the increase in SSB per recruit from the closures and the slope of the stock–recruitment relationship (see eq. 15).

It has been assumed that density dependence occurs only in the early life history of the target species and so is reflected in the stock–recruitment function only. The predicted yields with closures may be overestimated if there was a reduction of growth or increase in natural mortality of adults due to density dependence in the closures (Gårdmark et al. 2006). On the other hand, an Allee effect, such as density-dependent fertilization success that often occurs in broadcast spawners, could cause the calculated benefits of closures to be underestimated. The assumption of a “well-mixed” larval pool would cause the model with closures to overestimate yield if larvae released in the closed area were more likely to stay in the closed area but it would underestimate yields if the larvae spawned in closed areas tended to be transported to open areas (Gaines et al. 2003; Gårdmark et al. 2006).

Although the criterion for increased yield (eq. 15) was derived under the assumption of no adult mixing between closed and open areas, moderate adult movement should produce qualitatively similar results. The effect of closures in this case would be to create more variability in fishing mortality among individuals in the stock, with some animals remaining in the closed area (and thus subject to zero fishing mortality), others always in the open areas (subject to full fishing mortality), and the remainder spending some time in both open and closed areas (with reduced, but not zero, fishing mortality). Similar to the effect of closures on sedentary stocks, the net effect is to increase SSB per recruit and, except possibly at high fishing mortalities, reduce yield per recruit (Hart 2001). Thus, the effect on SSB and yield per recruit for stocks of moderate mobility is qualitatively similar to that computed here for sedentary stocks, though the effects should be less than those predicted by eqs. 5 and 6.

The evidence presented here and in most other models indicates that long-term closures are unlikely to increase yield when open area fishing mortality is at or less than that which produces MSY (Gerber et al. 2003; Gårdmark et al. 2006). On the other hand, closures can increase yield at high fishing mortalities, prevent stock collapse, and have other conservation benefits (e.g., for biodiversity). They also can serve as useful controls for scientific research purposes. Expectations of marine reserves and other long-term closed areas

should focus on these benefits, rather than a hope that they can contribute to optimal yield.

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