Nature reserves as a bioeconomic management tool – a simplified modeling approach

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December 2005

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Abstract

This paper demonstrates analytically how a nature reserve may protect the total population, realize maximum sustainable yield (MSY), maximum economic yield (MEY) and consumer surplus (CS) and how this depends on biological growth, migration, reserve size and economic parameters. The pre-reserve population is assumed to follow the logistic growth law and two post-reserve growth models are discussed. For Model A, the post-reserve growth has a common carrying capacity as in the pre-reserve case. In Model B, each sub-population has its own carrying capacity proportionate to its distribution area. Population protection against extinction is assured against low cost harvesting, including zero cost, when relative reserve size is greater than relative migration. Reserve size may be tuned to realize MSY in Model A, but not in Model B. MEY can not be realized in any of the two models, but generally economic yield is greater in Model A than B. CS is greater with a reserve than without.

1. Introduction

For many harvested marine and terrestrial populations, parts of their habitat area have been reserved against exploitation. A nature reserve is a tract of land or sea created as a management instrument usually serving several objectives, including the preservation of its populations and physical features, and increased biological and economic yields. This paper focuses on economic issues related to partitioning of the habitat area of a single population into two sub-areas, (i) a nature reserve (NR) where the animals are completely protected from harvesting, and (ii) a harvest zone (HZ) where harvesting may take place. The modeling approach is kept simple, to investigate analytically to what extent reserve size may be tuned to achieve economic and biological objectives by use of fish or wildlife in a homogeneous habitat. We will investigate to what extent reserve size should be chosen relative to biological and economic parameters and how this depends on management objectives. The analysis is limited to a single population, questions related to i.a. multi-species, by-catch and ecosystem management are not directly discussed.

Human activities and expansion have contributed to overuse of several terrestrial and marine populations and ecosystems around the world [1], [2] and [3], and some populations have even become extinct [4], [5] and [6]. Economic and legal instruments to mitigate such problems have been designed and implemented, including input control (hunting licenses, fishing effort and capacity control, etc.) and output control (fish and game quotas – both tradeable and non-tradeable, etc.), as well as zoning with harvest bans, or restrictions on resource use in one or more zones of the population habitat areas. The economic efficiency of different management tools, including reserves have been questioned [7], [8] and [9], even though natural scientists lately seem to have favored the use of reserves to achieve management objectives [10], at least, conditionally [11]. In fact, natural scientists discussed the use of reserves decades before economists did so [12] and [13].

Economic analyses of terrestrial and marine reserves have largely been developed during the last two decades [14], [15] and [16]. There are numerous studies of reserve effects on population size and biological and economic yield, and the importance of population growth, density dependence, migration, effort and reserve size and shape, including [7], [17], [18], [19], [20], [21], [22], [23], [24], [25] and [26]. Economic and biological assessments of nature reserves and other management tools found in these and other papers cover a wide range of models and scientific methods. Assumptions made, explicitly or implicitly, mirror both the complexity of ecosystems and the complex multifaceted management systems in use. Marine and terrestrial ecosystems often differ in the way humans utilize their resources, partly because they differ in scale and variability. Humans harvest mostly carnivore organisms, in particular fish, from marine ecosystems, whereas on land, in addition to carnivore organisms, plants, trees and herbivore animals are harvested. The openness of the sea has made it more difficult and costly to "fence" marine resources than natural resources on land. In addition, in marine systems, sea currents may influence dispersal of pollutants and organisms to a greater extent than air does for terrestrial systems, requiring other mechanisms for environmental protection and management. Despite such differences between living marine resources and terrestrial resources, we think our analysis may contribute to the reserve analysis of both types. This is also because natural resources displaying common property characteristics, such as the difficulties of establishing individual ownership, require the same type of basic institutions.

The bioeconomic modeling approach of this paper is of the "simplistic" type, following the tradition of Clark [27]. We seek to understand complex resource issues by developing and analyzing simple models. Simple, but not too simple - we still manage to include in the analysis major economic, biological and management characteristics, such as revenue and cost, population growth, migration, harvest effort and reserve size. Questions analyzed include, first, how does the post-reserve open-access equilibrium depend on biological and economic model characteristics, and how does this compare with the pre-reserve equilibrium? Second, will a reserve protect a low cost - high value population against extinction even in the zero cost case? Third, can a reserve and open-access harvest

zone assure a greater total population level than the pre-reserve? Fourth, can a reserve and open-access harvesting in HZ realize maximum sustainable yield (MSY)? Fifth, how does the post-reserve resource economic rent (EY) and consumer surplus (CS) depend on biological characteristics and reserve size? We choose to use and analyze simple logistic growth models to produce analytic results regarding the effects of the division of a population's habitat area into the two sub-areas, NR and HZ. This modeling approach allows some analytical findings regarding the explicit relationship between resource rent and population yield and protection on the one hand, and, on the other hand, reserve size and economic and biological parameters, including price of harvest and cost of effort, as well as population growth and migration. Despite widespread use of simple logistic growth models for bioeconomic analysis purposes, other researchers have not, to the best of our knowledge, analyzed and compared the two bio-economic nature reserve sub-models in the Gordon-Schaefer-like form set out in this paper[1].

The next section presents and discusses the two models, while MSY, EY and CS are discussed in a separate section. The results are discussed and summarized in the concluding section.

2. Growth and migration

We shall assume that the pre-reserve population is uniformly distributed across its habitat area, with no distinction between patches for e.g. mating, spawning, growth, maturation and protection. Thus the model does not account for spatial heterogeneity of populations other than the differences between reserve and non-reserve populations. The pre-reserve population is assumed to follow the logistic growth law, and this growth pattern may be kept or changed after partitioning into two administratively different sub-areas. Two models for post-reserve population dynamics are formulated and discussed, and for both models net migration moves in the direction from the high-

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[1] Non-economic issues related to reserve size and effort control within this modelling approach are discussed in [28]. Sanchirico [26] nests multiple metapopulation models, whereas our analysis commences with a homogenous population to be disaggregated into two sub-populations.

density sub-area to the low-density area. The two sub-populations are assumed homogeneously distributed across their sub-areas. For Model A, the post-reserve growth of the total population continues following the pre-reserve logistic growth, independent of the relative distribution between the two sub-populations. In Model B, we assume that each sub-population has its own carrying capacity proportionate to its distribution area. Thus in Model A, the overall population is implicitly able to exploit its total carrying capacity for growth, whereas in Model B, the creation of a nature reserve puts some restrictions to aggregate population growth. We use the two post-reserve models with different population growth characteristics to compare similarities and differences in the implied economic and biological yield effects of reserve creation and expansion. This enables us to explore how different assumptions regarding post-reserve growth may lead to different predictions for the benefits of nature reserve creation.

2.1. Pre-reserve population dynamics

The pre-reserve growth of a population in a given area is assumed to follow the logistic path described by the growth equation[2]

(1) $\dot{S} = rS(1 - S),$

with S as the population size, normalized such that the carrying capacity equals unity, and r the intrinsic growth rate ($r > 0$). Thus, if W and K are actual population and carrying capacity, respectively, measured in e.g. tonnes or number of animals, $S = W / K$.

Now, imagine that the population is divided into two sub-populations with the same homogeneous characteristics and that $S = S_1 + S_2$. Growth equation (1) can now be written

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[2] At this stage we could have simplified notation by normalizing time, with $r = 1$. However, the intrinsic growth rate is kept to explicitly demonstrate below its importance relative to the migration rate.

(2) $\qquad \dot{S} = rS_1\left(1 - S_1 - S_2\right) + rS_2\left(1 - S_1 - S_2\right).$

If we also assume that $\dot{S}_1$ and $\dot{S}_2$ equal the first and second term, respectively, on the right hand side

of equation (2), equilibrium requires $\dot{S}_1 = \dot{S}_2 = 0$.

2.1.1. Model A

In Model A, we assume that equation (2) describes the post-reserve growth of the total population in

the absence of harvesting. Sub-area 1 is the nature reserve (NR) and Sub-area 2 is the harvest zone

(HZ), with sub-populations S_1 and S_2, respectively. The total population distribution area equals unity

and Sub-areas 1 and 2 equal m and $1-m$, respectively ($0 < m < 1$).[3] We assume that the two sub-

areas are delineated only on paper and animals are free to migrate between the two and inside each of

them. Net migration between the two areas is assumed proportional to the differences in sub-

population densities, i.e. on S_1/m and $S_2/(1-m)$. Assuming net migration is proportional to the

difference in sub-population densities, net emigration from Area 1, which equals immigration to Area

2, is $M = \sigma(S_1/m - S_2/(1-m))$, $\sigma > 0$ being the migration coefficient. By assumption, harvest in

HZ gives catch per unit effort (CPUE) proportional to the population density. This implies the

Schaefer harvest function $Y = q\hat{E}S_2/(1-m)$, where $\hat{E}$ is harvest effort and q is the catchability

constant. To simplify the notation below, we shall use $Y = rES_2/(1-m)$ where E is normalized effort

when the catchability constant equals r, the intrinsic growth rate; thus $E = q\hat{E}/r$. Note that Y is

normalized harvest, just as S is normalized population. The growth equation for each of the sub-

populations $S_{1,2}$, adjusted for migration between the sub-areas and harvesting, can now be written

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[3] If $m = 0$ or $m = 1$ we are back to a single area model with the basic equations (1) and (2) to be used for further analysis.

$$(3) \qquad \dot{S}_1 = r\left[S_1(1 - S_1 - S_2) - \gamma\left(\frac{S_1}{m} - \frac{S_2}{1-m}\right)\right]$$

and

$$(4) \qquad \dot{S}_2 = r\left[S_2(1 - S_1 - S_2) + \gamma\left(\frac{S_1}{m} - \frac{S_2}{1-m}\right) - E\frac{S_2}{1-m}\right],$$

where $\gamma = \sigma/r$ is the relative migration rate. This turns out to be the natural parameter in what

follows, where r by assumption is constant. Note that in the absence of harvesting, i.e. $E = 0$,

equations (3) and (4) and $\dot{S} = \dot{S}_1 + \dot{S}_2$ is reduced to that of equation (2) as well as to equation (1).

Model A fits a population where any resource available for growth throughout the total area is being

utilized. It may seem paradoxical that individuals from the NR should be able to utilize resources in

the HZ without experiencing harvest mortality. However, in a virtual ecosystem this may happen if

e.g. there is a flow or migration of non-modeled surplus forage species from the HZ to the NR or

undersized non-harvestable individuals utilize the total habitat for foraging. In other words, the feed

will always find the population, or vice a versa. In discrete time models this paradox may be solved

by allowing harvesting, population growth and redistribution of the total population to take place

sequentially.[4]

The growth of the total population of Model A depends on total population level and harvesting,

given by

$$(5) \qquad \dot{S} = r\left[S(1 - S) - E\frac{S_2}{1-m}\right].$$

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[4] In [29] (p. S78), the total stock remaining after fishing "… is well mixed over the combined reserve and fishing area in order to determine the stock size in the next year. That is, the reserve boundaries are set for harvesting but the stock moves smoothly across the boundary and fills the entire fishing ground." In the Mangel model "… reproduction takes place after fishing and stock from fished and unfished portions of the habitat are mixed at the time of reproduction." [30] (p. 16).

At any point in time yield is a function of effort and HZ stock density, as given by the Schaefer harvest function. Sustainable yield depends on total stock level and may be found from equation (5) for $\dot{S} = 0$. However, for comparison to Model B yield below, sustainable yield of Model A may be written

(6) $Y_A = F_A(S_1, S_2) = r(S_1 + S_2)\big(1 - (S_1 + S_2)\big).$

In this case yield contour lines are straight lines, illustrated as downward sloping broken lines in Figure 1. Point Q_0 represents the unharvested equilibrium point $(S_1, S_2) = (m, 1 - m)$, for $m = 0.25$ with total population equal to unity (see [28]). Any other value of m would of course put Q_0 another place on the zero yield contour line in the unharvested case. Issues related to the Maximum sustainable yield (MSY) line P_1P_2 will be discussed below.

2.1.2 Model B

In papers studying the effects of nature reserves, it is often assumed that each sub-population has its own carrying capacity (see e.g. [7], [31] and [32]). In this paper, we assume for Model B that the carrying capacity of each sub-population is in proportion to the size of the sub-area. Sub-population growth is described by the equations:

(7) $\dot{S}_1 = r\left[S_1\left(1 - \dfrac{S_1}{m}\right) - \gamma\left(\dfrac{S_1}{m} - \dfrac{S_2}{1-m}\right) \right]$

(8) $\dot{S}_2 = r\left[S_2\left(1 - \dfrac{S_2}{1-m}\right) + \gamma\left(\dfrac{S_1}{m} - \dfrac{S_2}{1-m}\right) - E\dfrac{S_2}{1-m} \right],$

assuming migration and harvesting, as in Model A.

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For $S = S_1 + S_2$ we have

$$(9) \qquad \overset{\bullet}{S} = r\left[S_1\left(1 - \frac{S_1}{m}\right) + S_2\left(1 - \frac{S_2}{1-m}\right)\right]$$

In the case of harvesting, the growth of the total population, $S = S_1 + S_2$, is given by

$$(10) \qquad \overset{\bullet}{S} = r\left[S_1\left(1 - \frac{S_1}{m}\right) + S_2\left(1 - \frac{S_2}{1-m}\right) - E\left(\frac{S_2}{1-m}\right)\right].$$

This equation predicts somewhat different growth compared to that of Model A, as given by equation (5).[5]

Sustainable yield, derived from (10) for $\overset{\bullet}{S} = 0$, is

$$(11) \qquad Y_B = F_B(S_1, S_2) = rS_1\left(1 - \frac{S_1}{m}\right) + rS_2\left(1 - \frac{S_2}{1-m}\right).$$

Note that sustainable yield in this model depends on not only the total stock level, but also the distribution of the stock between S_1 and S_2. In this case yield contour lines are ellipses, with vertical and horizontal axes, as illustrated in Figure 1. The zero yield straight contour line of Model A is tangent to the zero yield ellipsis of Model B, at the point Q_0. It will be demonstrated below, in Subsection 3.6, that in general the MSY can not be attained for Model B.

(Figure 1 here)

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[5] Details of growth characteristics of Model B are found in [28].

3. Bioeconomic equilibrium and yield analysis

3.1. Effort dynamics and equilibrium

To model an open access harvest industry in a simple way [33] we assume that E changes in proportion to profit, or resource rent:

$$(12) \qquad \frac{dE}{dt} = \mu(R - C)$$

where $R = pY$ is total revenue, $C = aE$ is total cost, p is price per unit catch and a is cost per unit effort. Using (12), and the defined harvest function, this gives

$$(13) \qquad \frac{dE}{dt} = \mu \left(pr \frac{S_2}{1-m} - a \right) E \ .$$

Equation (13) defines an equilibrium HZ population

$$(14) \qquad S_2 = c(1-m), \qquad c = \frac{a}{pr} \ ,$$

with relative cost c equal to the pre-reserve population density at open-access equilibrium. Thus at equilibrium, the HZ sub-population density equals the pre-reserve density. This pre-reserve density plays an important role in the analysis of reserve implications for population size and yield that follows.

3.2. Stationary state and protection – Model A

We now investigate whether a nature reserve can protect the population against extinction at low, including zero, harvest costs. For stationary state, or equilibrium, we have, in addition to (14):

(15) $S_1(1 - S_1 - S_2) + \gamma \left(\dfrac{S_2}{1 - m} - \dfrac{S_1}{m} \right) = 0$

(16) $S_2(1 - S_1 - S_2) + \gamma \left(\dfrac{S_1}{m} - \dfrac{S_2}{1 - m} \right) - E \dfrac{S_2}{1 - m} = 0$

Eqs. (14) and (15) determine S_1, S_2 at equilibrium, while (16) then determines E for a given m. From (15) and (16) we can also deduce

(17) $Y = rS(1 - S)$

where $S = S_1 + S_2$, for the sustainable yield Y. The HZ open-access sub-population equilibrium level can be derived graphically the following way. At equilibrium it follows from (15) that the isocline of the NR sub-population may be written

(18) $S_2 = \dfrac{S_1(A - S_1)}{S_1 - \alpha} = \phi(S_1).$

where

(19a) $\alpha = \gamma / (1 - m)$,

(19b) $A = 1 - (\gamma / m)$.

Equation (18) together with the equilibrium HZ sub-population S_2, given by (14), determines the

equilibrium NR sub-population S_1. The curve (18), which expresses the isocline $\dot{S}_1 = 0$, we shall

denote C. Figure 2 shows C as a hyperbola, which enters the positive quadrant at $(S_1, S_2) = (A, 0)$ if

$A > 0$ and at (0,0) when $A < 0$,[6] and a horizontal $\hat{S}_2$ curve.[7] The vertical asymptote of C, for

$S_1 = \alpha$, is omitted in Figure 2.

(Figure 2 here)

Let us now use Figure 2 to investigate the problem of extinction which would occur for the pre-

reserve open-access regime if $c \to 0$. For this cost structure, Figure 2 demonstrates that a nature

reserve would save the population when $A > 0$, since $S \to A$ for $c \to 0$. This is the case only when

migration is less than intrinsic growth ($\gamma < 1$) and reserve size is chosen such that $\gamma < m$, recalling

(18) and (19b). However, when $1 < \gamma$, implying $A < 0$, a nature reserve would not be sufficient to

save the population for zero cost and HZ open-access harvesting. Thus when relative migration is

greater than intrinsic growth additional management tools, such as quotas, effort control or taxes,

would be necessary to avoid extinction, in the zero cost case.

3.3. Stationary state and protection – Model B

For stationary state we have, in addition to (14), from (7) and (8):

$$(20) \qquad S_1\left(1 - \frac{S_1}{m}\right) + \gamma\left(\frac{S_2}{1-m} - \frac{S_1}{m}\right) = 0$$

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[6] Other forms of this and the other isocline are discussed in [28]. Note that $\gamma > 1$, i.e. $\sigma > r$, always implies $A < 0$. Highly migratory species, such as tuna and caribou, may belong to this category.

[7] The isocline $\dot{S}_2 = 0$ could be derived the same way for a given value of E.

(21) $\qquad S_2\left(1-\dfrac{S_2}{1-m}\right)+\gamma\left(\dfrac{S_1}{m}-\dfrac{S_2}{1-m}\right)-E\dfrac{S_2}{1-m}=0$

Equations (14) and (20) determine the equilibrium values $(\hat{S}_1,\hat{S}_2)$ at equilibrium, while (21) then

determines the equilibrium value $\hat{E}$ for a given reserve size and parameter values.

The HZ open-access sub-population equilibrium level can be derived graphically the same way as for

Model A. At equilibrium it follows from (20) that

(22) $\qquad S_2=\psi(S_1)=\beta S_1(S_1-F)$,

where

(23a) $\quad \beta=(1-m)/\gamma\, m$

(23b) $\quad F=m-\gamma$.

The curve (22), which expresses the isocline $\dot{S}_1=0$, is a parabola with its axis parallel to the S_2 axis.

This parabola is similar to C in Figure 2. It would enter the positive quadrant at $(S_1,S_2)=(F,0)$ when

$F>0$ and through the origin when $F<0$. Also for Model B, a nature reserve of sufficient size, i.e. for

$F>0$, which is the case when $\gamma<m$, assures survival of the population for any value of c, including

$c\to 0$. However, a nature reserve would not be sufficient to save the population when $F<0$, i.e. for

$m<\gamma$ according to (22) and (23b), for zero cost and HZ open-access harvesting. Thus, also for

Model B, when relative migration is greater than unity, additional management tools, such as quotas,

effort control or taxes, would be necessary to avoid extinction, unless the total habitat area is made a

reserve.

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3.4. Population size with reserve

The objective of just avoiding extinction can hardly be called a precautionary objective. It would be better to secure a minimum target level for the total population. This target level could be derived from any biological or economic objective, such as maximizing sustainable yield (MSY), maximizing economic yield (MEY) or maximizing present value of all future resource rent (PV). We now investigate if a nature reserve of size m and open-access harvest in a harvest zone may raise total population level above its pre-reserve open-access level. The pre-reserve open-access level, $S = S_2 = c$ for $m = 0$, is a key parameter in this analysis.

In the absence of harvesting, both Model A and Model B has the equilibrium point $Q_0 : (S_1, S_2) = (m, 1 - m)$. This represents a state with the same population density in the Reserve (NR) and the Harvest Zone (HZ). When harvesting is applied in HZ, one expects intuitively that the density becomes larger in NR than in HZ. A simple proof of this follows:

The line of equal densities can be represented as $L : S_1 = mc$, $S_2 = (1 - m)c$, $c \in [0,1]$. In Figure 2, it is marked by a dotted line. All points to the right of L are states with larger density in NR than in HZ, while the points to the left of L are states with higher density in HZ than in NR. Note that the actual state space is $\Sigma : S_1, S_2 \geq 0$, $S_1 + S_2 \leq 1$.

The locus of equilibrium is represented by $C : S_2 = \chi(S_1)$, where the function $\chi = \phi$ (Model A), or $\chi = \psi$ (Model B). Note that the harvest parameters do not enter this function, which stems from the S_1-component of the governing equations. Our aim is to show that C is located to the right of L in the interior of Σ. This follows from the following observations: (i) The point Q_0 is on C. (ii) The origin is on or to the left of C. (iii) C has positive curvature. We do not go into details about the latter; it follows from the properties of C, noticed in [28], being a parabola (Model B) or a hyperbola

(Model A). It could be mentioned that in Model A, there may be cases where C does not connect Q_0 and the origin. This happens when $\alpha < m$ and $A > m$. However, in those cases, C is even to the right of the vertical $S_1 = m$, which in turn is to the right of L .[8]

Corollary: In the model of open access harvest, a reserve acts to increase the total equilibrium population.

Proof: Refer to Figure 2. Let $S_2 = (1-m)c$ be the break-even population determined by open access harvesting, recalling the total break-even population without reserve, c. The state $Q:(S_1, S_2) = (mc, (1-m)c)$ corresponds to this situation. The actual equilibrium state P lies to the right of Q, and therefore corresponds to a larger total population.

Thus, any reserve size, $0 < m < 1$, would increase the total equilibrium population level compared to the pre-reserve open-access level, even if the open-access harvest regime prevails in the harvest zone.

3.5. Tuning reserve size for maximum yield – Model A

As is well known [27], the largest yield that can be sustained, is, according to (5):

$$(24) \qquad \text{MSY} = Y_{\max} = \frac{r}{4} .$$

This maximum sustainable yield (MSY) is achieved if and only if

$$(25) \qquad S = \frac{1}{2} .$$

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[8] The situation $m < A, \alpha$ cannot occur. The two inequalities imply $\gamma > m(1 - m)$ and $\gamma < m(1 - m)$ respectively.

We now investigate whether (25) can actually be achieved by tuning m while allowing open-access harvest in HZ. To this end, we determine S_1 from (25):

(26) $\qquad S_1 = \dfrac{1}{2} - S_2$

where S_2 is given by (14). With S_1 and S_2 given, eq. (15) becomes an equation for m, with γ and c as parameters. Inserting (14) and (26) into (15), yields:

(27) $\qquad cm^2 + \left(\dfrac{1}{2} - c\right)m + 2\gamma\left(c - \dfrac{1}{2}\right) = 0$.

An acceptable solution must have

(28) $\qquad 0 \le m \le 1$

and $S_1 \ge 0$, which implies, by use of (14) and (26),

(29) $\qquad \dfrac{1}{2} \ge (1 - m)c$

From (27)-(29) we can deduce:

Theorem: For c in the interval

(30) $\qquad c_{\min} \le c \le \dfrac{1}{2}$,

for Model A, with

$$c_{\min} = \max(0, g(\gamma))$$

where

(31) $g(\gamma) = \dfrac{1}{2} - \dfrac{1}{4\gamma}$

there is a unique reserve size m^* that realizes MSY,

(32) $m^* = M(c; \gamma)$

which has the following properties:

(i) $\lim\limits_{c \to 1/2} m^* = 0$

(ii) $\lim\limits_{c \to c_{\min}} m^* = 1$, for $c_{\min} > 0$, i.e., $\gamma > \tfrac{1}{2}$

while

$\lim\limits_{c \to c_{\min}} m^* = 2\gamma$, for $c_{\min} = 0$, i.e., $\gamma < \tfrac{1}{2}$.

(iii) m^* is monotonically decreasing with c in the interval $c_{\min} < c < 1/2$.

(iv) The graph of m^* as a function of c has vertical tangent at $c = 1/2$.

Figure 3 gives a graphical presentation of this theorem, showing m^* as a function of the pre-reserve open-access population level, which equals relative cost c, for two cases of the relative migration rate, $\gamma < 1/2$ and $\gamma > 1/2$. The proof of the theorem is given in the appendix.

(Figure 3)

Our result suggests that it is only in a certain parameter range that the reserve size m can be tuned for maximum sustainable yield. There is a need to understand the reasons for this. The parameter c represents cost of effort relative to price of harvest. Large c requires large fish density for a profitable fishery. When introducing reserve, the equilibrium total stock density increases with m, as demonstrated above. However, for $c > \frac{1}{2}$, the total equilibrium stock density, for $m = 0$, is already above the MSY density, which will not be achieved when introducing a reserve m. On the other hand, with low c, $(c < \frac{1}{2})$, the open-access fishery leads to a low density in the absence of reserve. If a reserve is introduced, the equilibrium total stock density is increased. But if the relative mobility γ is also high ($\gamma > \frac{1}{2}$), the effect of a reserve is less pronounced. Then, when $c < c_{min}$, the total stock density stays below the level at which MSY is achieved for all values of m.

It will be demonstrated below that to generate economic rent it may be necessary to control harvest effort in addition to reserve creation. Related to this is the question whether effort control can be used to achieve MSY.

In Figure 4, Panel A and Panel B demonstrate, for Model A, cases where MSY may and may not be achieved, respectively. In the former γ equals that of the uppermost curve in Figure 3. In this case MSY may be achieved by increasing effort such that the equilibrium point is moved below the MSY line. However, Figure 4 Panel B demonstrates that even though γ is low enough that MSY could have been achieved, m in this case is too great for any E to realize MSY. Thus using effort control in

combination with a nature reserve to achieve MSY can be effective, but only for some values of *m.* In fact, when $2\gamma < m$ MSY cannot be attained by tuning of effort (see (19) and Figure 3).

(Figure 4)

3.6. Tuning reserve size for maximum yield - Model B

We now show that the sustainable yield of Model A, derived from equation (6) is greater or equal to the sustainable yield of Model B, derived from equation (11), for the same equilibrium point (S_1^*, S_2^*). In fact, the equality sign is valid only in a limiting case. Initially, let us assume that harvesting takes place at a sustainable basis at equilibrium sub-population levels, and then perform a comparative static analysis. Recall that the law of net migration by assumption is the same for Model A and B, and that they differ in the migration excluded population growth. Equation (6) gives sustainable yield for Model A, that is $Y_A = F_A(S_1, S_2)$ for $\overset{\bullet}{S} = 0$. Note that migration does not matter for the sustainable yield level of equation (6), neither does the relative distribution of the population on the two sub-populations. It is the total population level that matters for equilibrium yield in Model A, in addition to the carrying capacity and the intrinsic growth rate; the former does not explicitly appear in equation (6) due to the use of normalized populations.

From equation (11) the sustainable yield for Model B is $Y_B = F_B(S_1, S_2)$. The result for Model B also indicates that migration does not matter for the sustainable yield level, but in this model, the relative distribution of the population on the two sub-populations matters.

Let us now compare the sustainable yield rates of Model A and B, respectively in (6) and (11). We have[9]

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[9] This result, demonstrated in [28], is used below for comparing resource rent of Model A and Model B.

$$(33) \quad \Delta Y = Y_A - Y_B = r\left[-\left(S_1 + S_2\right)^2 + \frac{S_1^2}{m} + \frac{S_2^2}{1-m} \right]$$

$$= r\left(\sqrt{\frac{1-\mathrm{m}}{\mathrm{m}}}\, S_1 - \sqrt{\frac{m}{1-m}}\, S_2 \right)^2 \geq 0.$$

From (33) we conclude that the sustainable yield of Model A is greater or equal to the sustainable yield of Model B, for the same equilibrium point (S_1^*, S_2^*), with the equality sign valid only when the densities are equal, $S_1 / m = S_2 /(1-m)$. Since harvesting implies that the sub-population density of HZ becomes smaller than that of NR, the inequality sign of equation (33) is always strict when sustainable harvesting takes place.

The expressions $Y_{A,B}$ say something about the possible yields for the two models. For example, varying E from 0 up to E_C, the level that effort cannot exceed on a permanent basis if extinction is to be avoided, the equilibrium point traces out a curve starting at the point $(S_1,S_2) = (m,1\text{-}m)$ at $E = 0$. For Model A, it has to pass the line $S = \frac{1}{2}$ of MSY, shown as the MSY-level line in Figure 4, provided $A < \frac{1}{2}$. According to (19b) $A < \frac{1}{2}$ corresponds to $m < 2\gamma$, as noted above. Thus, in this case, according to Model A, the MSY of $Y_A = r/4$ is always possible for some E. Equivalently, it may be obtained by tuning m. For Model B, however, equation (33) shows that MSY of $r/4$ will not be obtainable. The equilibrium points as E varies upward from zero, are, in Figure 4 Panels C and D, on the whole curve, the S_1-isocline, amanating at Q_0. The closer this isocline comes to a straight line $L : (ms, (1-m)s, s \in [0,1]$, the closer does the maximum yield of Model B come to the MSY (see also Figure 1). This is the case when γ is large (see (18)).

Sustainable harvest means harvesting of the natural growth at constant population levels. A given set

of parameters $(\gamma^*, m^*, E^*)^{10}$ does not, in general, imply the same equilibrium point (S_1^*, S_2^*) for

Model A and Model B. For this reason it is of interest to investigate how sustainable harvest differs

between the two models. We start by investigating how growth in the two sub-areas differ in Model

A and B. Assume that sub-population densities differ in the following way

$$(34) \qquad \frac{S_1}{m} > \frac{S_2}{1-m} \; ,$$

due to harvest. By use of (34), (3)-(4) and (7)-(8), it follows that

$$(35) \qquad \dot{S}_1^{\,A} > \dot{S}_1^{\,B} \; .$$

By use of (35), (3)-(4) and (7)-(8), it also follows that

$$(36) \qquad \dot{S}_2^{\,A} < \dot{S}_2^{\,B} \; .$$

Thus if the sub-stock density is greater in NR than in HZ, the NR sub-stock growth will be greater in

Model A than in B, as demonstrated in (35). However, the HZ sub-stock growth will be greatest in

Model B, as shown in (36). The former is a result of the Model A stock's ability to always utilize the

total distribution area. Any available resources for growth left over in HZ are implicitly used for

growth by the NR sub-stock in Model A. On the other hand, (36) demonstrates that growth in the HZ

is higher in Model B than in A. However, these two results combined do not give a definite answer

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[10] Alternatively (γ^*, m^*, c^*) for the HZ open-access harvesting.

regarding differences and similarities of the harvest potential in the two models, since the sub-stocks are linked through net migration in addition to growth.

(Figure 5)

Figure 5 shows equilibrium yield as a function of reserve size, assuming HZ open-access harvesting for Model A and Model B. The greatest yield difference is found when relative migration is "small" (Panels A and C). Note that $Y_B > Y_A$ for a wide range of reserve size in Figure 5 Panel C. This is a case where relative cost, c, is at 40% of what is needed to a pre-reserve commercial harvest to take place. This implies a population size below but close to the MSY level. However, above the m^* level that realizes MSY in Model A both Y_B and Y_A decrease with m (Figure 5 panel c). Thus, if achieving MSY is a management objective, reserve size should not be too large, in particular for less mobile living resources.

3.7. Economic yield

Having demonstrated that the sustainable yield of Model B is smaller than that of Model A, for any pair of sub-populations, we now investigate whether this is the case also for economic yield, the resource rent. First, we review some characteristics of the pre-reserve resource rent

(37) $\quad \pi = pY - aE$,

where harvest $Y = rES$ and total cost $TC = aE$. The sustainable resource rent may be written

(38) $\quad \pi(S) = prS(1-S) - a(1-S) = pr(S-c)(1-S)$,

recalling relative cost $c = a/pr$. Thus at open-access harvesting, both pre-reserve and post-reserve, no economic benefits are achieved due to the infinitely elastic demand for harvest and supply of effort. We will, however, return to the case of finite elasticity of demand in the following subsection to see what difference this makes.

It may be argued that if management instruments such as effort control (licences), harvest quotas and input or output taxes were used, a nature reserve would be redundant, in particular if realization of resource rent is a main policy objective. In the economic reserve literature, focus is often on combined effects of a nature reserve and an open-access harvest zone versus overall open-access (e.g. [7] and [34]). However, investigating the resource rent potential of different reserve models, as well as actual reserves, may be of interest, in particular when extensions are made to include e.g. multi-species, by-catch, non-use, management cost and enforcement issues. The necessary condition for pre-reserve maximum resource rent, derived from equation (38), implies population level

$$(39) \qquad S_{MEY} = S_{MSY} + \frac{c}{2},$$

with $S_{MSY} = 1/2$, which is a well-known result of the Gordon-Schaefer model. Substituting for S_{MEY} from (39) into (38) gives the maximum economic yield (MEY)

$$(40) \qquad \pi_{MEY} = \frac{pr}{4}(1-c)^2 \ .$$

It will be demonstrated graphically that the unconstrained MEY in (40) can not be realized in the reserve case.

The Model A resource rent is

(41) $\pi^A(S_1, S_2) = pr\left(1 - \dfrac{(1-m)c}{S_2}\right)(S_1 + S_2)(1 - (S_1 + S_2))$,

with $S_2 = (1-m)c$ as the open-access HZ sub-population level.

Figure 6 shows a Model A set of iso-resource-rent curves and isocline of the NR sub-population. The latter is the graphical representation of the constraint given by equation (18). To maximize π^A, the long-term sub-population constraint given by $S_2 = \phi(S_1)$ in (18), must be observed. In Figure 6 the isocline is positively sloped and enters the positive quadrant at $(S_1, S_2) = (0,0)$ since $A < 0$ (see [28] for a discussion). Note that the iso-resource-rent curves are independent of the migration coefficient σ, as seen from equation (41). However, the location of the MEY point will depend on biological, economic, migration and reserve parameters. The constrained maximum of $\pi^A(S_1, S_2)$, subject to (18), may in principle be found by use of Lagrange's method, but it has not been possible to derive an explicit solution of the MEY point (S_{1MEY}^A, S_{2MEY}^A).

Based on this discussion and graphical analysis of Figure 6 we derive the following properties of π_A.

1. The absolute maximum is always on the vertical axis $S_1 = 0$. It is taken at $S_2 = \frac{1}{2}(1 - S_2^*)$, with

    $S_2^* = c$, and has the value

    $$\pi_{MEY}^A = pr\frac{1}{4}\left(1 - S_2^*\right)^2.$$

2. The actual maximum along the isocline $S_2 = \phi(S_1)$ always exists in the interior of $(S_2^*, 1 - m)$, and is always unique, but smaller than the absolute maximum.

3. This maximum is larger the smaller m is.

(Figure 6 here)

The Model B resource rent is

(42) $\quad \pi^B(S_1, S_2) = pr\left(1 - \frac{(1-m)c}{S_2}\right)\left[S_1\left(1 - \frac{S_1}{m}\right) + S_2\left(1 - \frac{S_2}{1-m}\right)\right]$.

To maximize π^B, again the long-term sub-population constraint for Model B given by equation (22), must be observed. The constrained maximum of π^B, subject to (22), may be found the same way as for π^A above.

Figure 7 shows a Model B set of iso-resource-rent curves and isocline of the NR sub-population. Note, from (42), that the iso-rent curves of Model B also are independent of the migration coefficient σ. However, the location of the MEY point depends on all biological, economic, migratory and reserve parameters, as indicated by Figure 7.

(Figure 7 here)

Let us now return to the introductory question of this subsection. Does Model B generate less economic rent than Model A? It follows from (41) and (42) that $\pi^A, \pi^B > 0$ if $c < S_2/(1-m)$. We have, recalling Y_A in (6) and Y_B in (11),

(43) $\quad \Delta\pi_{AB} = \pi^A - \pi^B = p\left(1 - \frac{(1-m)c}{S_2}\right)(Y_A - Y_B) \geq 0$,

due to (33). From (43) we conclude that the economic yield of Model B is smaller or equal to that of

Model A for the same equilibrium point (S_1^*, S_2^*), with the equality sign valid only when the

densities are equal, $S_1 / m = S_2 / (1 - m)$. The inequality sign of (43) is always valid when sustainable

harvesting takes place, since harvesting implies that the sub-population density of HZ becomes

smaller than that of NR.

3.8. Consumer surplus

From an economic point of view, why bother with establishing nature reserves if no economic rent is

generated? With constant price of harvest and cost of effort, no economic benefits such as consumer

surplus (CS) or producer surplus are generated in the analyses above. However, increased harvest

following a reserve creation could actually give an economic gain for consumers if demand is

downward sloping. In addition, upward sloping marginal cost of effort could realize producer surplus

for the harvesters or hunters. Pezzey et al. [34] mention additionally, in the case of marine reserves,

the possibility of shift in demand caused by "more desirable fish" and in supply, caused by "more

easily catchable fish". Let us now investigate the case of consumer surplus to see how this changes

the previous conclusions.

(Figure 8 here)

In Figure 8, the backward bending long-run open-access supply curve is S [35]. In this case, S is

based on HZ open-access harvesting, which implies $S_2 = (1-m) = a/pr = c$. Substituting for S_2 into

(5), recalling (37), we have at equilibrium

(44) $Y^A = r(S_1 + (1 - m)c)(1 - (S_1 + (1 - m)c))$

where S_1 is implicitly given by (18). Thus Y^A is now implicitly a function of reserve, biological and economic parameters, including price of harvest, and is shown as the S curve in Figure 8.

For a downward sloping demand curve for harvest we assume that there is a unique stable equilibrium at overall open-access with price of harvest p_0 and harvest Y_0.[11] Imagine that this price enters the formula of the pre-reserve population density at open-access equilibrium, $c_0 = a / p_0 r$ (see also Figure 2). Demand and supply conditions in Figure 8 are such that HZ open-access is close to realizing MSY for reserve size $m = 0.75$. In this case, the CS equals the triangle Mpp_m, which is significantly greater than the pre-reserve CS triangle Opp_m.

For Model B, we can use (11), otherwise as for Model A to derive the backward bending supply curve, given by

$$(45) \qquad Y^B = rS_1(1 - \frac{S_1}{m}) + r(1-m)c(1-c).$$

where S_1 implicitly is given by (22). Based on this and (33) we conclude that a reserve combined with an open-access HZ create CS, but this is smaller (or equal) to that of Model A.

As demonstrated above, tuning reserve size to realize MSY, under HZ open-access, may or may not be possible, depending on biological and economic parameters. This is the case for both Model A and B (even though complete MSY is never possible in Model B). In case of biological over-harvesting pre-reserve, reserve creation and HZ open-access harvesting imply increased harvest, as well as increased consumer surplus when demand is downward sloping.[12]

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[11] For a discussion of multiple equilibria, see [36].
[12] This discussion on consumer surplus effects can easily be applied to producer surplus via cost of effort, a, in $c = a/pr$.

4. Discussion and conclusions

This paper demonstrates within a simple modeling approach, how a nature reserve as the only management instrument may serve to realize important biological and economic objectives, both for Model A and B. Further, we have demonstrated analytically how reserve size depends on management objectives and key biological, migratory and economic parameters. In general, nature reserves created in a natural environment described by Model A are more effective than if described by Model B. In brief, this is due to the fact that in Model A total biological productivity is kept the same post-reserve as pre-reserve, whereas total productivity is reduced post-reserve in Model B. Model A and Model B resemble the additivity and subadditivity cases, respectively, discussed in [26]. Yield isoclines in the sub-population plane prove to be straight lines for Model A and ellipses for Model B. This difference tells that for a given total population the relative distribution on reserve and harvest zone sub-populations does not matter for yield of Model A, whereas it does for Model B. This basic biological difference has implications also for nature reserve effectiveness with respect to economic objectives, which is an issue closely related to that of [26]. Sanchirico discusses implications for the assessment of marine reserves of the relationship of aggregate biological production to the production of each patch. A major feature of our study is reserve size as a flexible management instrument, whereas other papers, including [25] and [26], treat reserve size as given for biological, institutional or other reasons.

We have seen that post-reserve open-access equilibrium depends on biological and economic model characteristics. Of particular importance is the pre-reserve population density at open-access equilibrium. This, as usual, depends on economic and harvest technical parameters only, not on biological factors when using the Schaefer- harvest function. Other papers (e.g. [7] and [34]) have also acknowledged the importance of the pre-reserve population density at open-access equilibrium for analysis of nature reserve efficiency.

This paper demonstrates that a reserve may protect the population against extinction in case of low cost of effort – high priced harvest, including zero cost. However, this result hinges on relative migration - the ratio of migration to intrinsic growth. When relative migration, γ, is greater than the (relative) reserve size, m, a reserve as the only management tool is not sufficient to protect against extinction in the zero cost case. Of course, this will always be the case when $\gamma > 1$. Thus in such cases, additional management tools such as quotas, and effort control and taxes would be necessary to avoid extinction in the zero cost case. This result is valid for both Model A and B and have some resemblance to the issues discussed in [25]. They show that a critical factor for the results is whether the wildlife flows from the reserve to the outside area or the opposite. In our modeling context wildlife or fish always flow in the direction from the high density to the low density area, that is, in the direction from the reserve when harvesting takes place outside.

A nature reserve and open-access in a harvest zone can assure a greater total population than pre-reserve open access. The effectiveness of a reserve in realizing this objective depends on the pre-reserve population density at open-access equilibrium, which, as usual, depends on economic and harvest technical parameters. The relative increase in total population is greater the lower the pre-reserve level is (see Figure 2). In other words, a nature reserve is most efficient in increasing total population the more overused it is.

It has been demonstrated that MSY can be reached with a reserve and open-access in the harvest zone by tuning reserve size, provided the economic conditions have contributed to biological overuse of the pre-reserve population. However, this is the case only for Model A. For Model B the inherent lower productivity post-reserve prevent MSY to be achieved, even though sustainable yield may increase compared to post-reserve open-access. This may be one of the reasons why studies assuming Model B form of biology post-reserve (e.g. [7]) do not find nature reserves as efficient with respect to conservation and biological and economic yield, as demonstrated for Model A in this paper. For both models, the pre-reserve population is assumed to follow the logistic growth law. For Model A,

the post-reserve growth of the total population continues following the pre-reserve logistic growth. Thus in Model A, the population is implicitly able to exploit for growth its total carrying capacity. In Model B, where each sub-population has its own carrying capacity proportionate to its distribution area, the population has some restrictions to aggregate growth due to the creation of a nature reserve. It may seem paradoxical that individuals from the NR should be able to utilize resources in the HZ without experiencing harvest mortality. However, in a virtual ecosystem this may happen if e.g. there is a flow or migration of non-modeled surplus forage species from the HZ to the NR, or undersized non-harvestable individuals utilize the total habitat for foraging. In other words, the feed will always find the population, or vice a versa. This includes the marine case with two sub-populations, eggs and larvae, which are dispersed evenly throughout the reserve and fishing ground, and adults, which do not migrate at all [34] and [37]. In discrete time models, this paradox may be solved by allowing harvesting, population growth and redistribution of the total population to take place sequentially.

It is an established modeling truth that resource rent is fully wasted in open access equilibrium with Schaefer harvest technology, in addition to infinitely elastic supply of effort and demand for harvest. This also holds for post-reserve open-access to a harvest zone. To generate resource rent in this case it is necessary with some kind of effort and quota control in addition to the reserve. However, with downward sloping demand for harvest or upward sloping supply of effort, consumer surplus or producer surplus may be generated. It is demonstrated that a nature reserve increases CS, and further, how the magnitude of this depends on economic, biological and reserve parameters. CS increases with reserve creation, for both Model A and B, but the increase is less for Model B than for Model A, since reserve tuning as the only management instrument can not realize MSY in the case of Model B. Thus within this modeling approach, integrating catch dependent price in reserve analysis is no longer "intractable", to use a word from [34].

Management of living natural resources comes with a price. Cost of monitoring, control and enforcement (MCE), accruing to both public institutions and private stakeholders may be significant

(see e.g. [38] and [39]). For nature reserves such costs may vary with reserve shape, in addition to size. In particular, high population density in a reserve may attract poachers, making reserve geometry of importance. For future economic research, reserve design should act as an additional or joint management tool to reserve size; such issues have been discussed in several natural science papers, including [40] and [41], but seldom in economic literature (see [42]). For simple geometric forms of the population distribution area the migration coefficient, contained in γ, may be directly related to reserve size and shape in both models discussed in this paper. For example, for a rectangular-shaped total distribution area, m is determined by the location of the NR/HZ border of constant length l. For other geometric forms, such as those for a circular total population distribution area, the border line length l varies with reserve size m. NRs of size m may be created in most regular-shaped areas by use of straight border lines of different length. Of all the possible NRs of size m, it is likely that the one with the shortest border length l has the lowest MCE cost. If, for example, the population distribution area is a river (like a very narrow rectangle) the migration coefficient is smaller with the two sub-areas down-stream and up-stream rather than along the left-bank and right-bank. This paper demonstrates that reserve efficiency is higher the lower γ is, in both models. Thus reserve shape and size should, within this modeling approach, be determined simultaneously to minimize net migration between the two sub-areas.

Uniform distribution of homogeneous populations is mainly a theoretical artifact. But even so the two models discussed in this paper may be used for comparison with more realistic, detailed models that stress spatial distribution, heterogeneity, different forms of migration between patches, and effort adaption to reserve creation and other management tools. The way sub-elements differ for heterogeneous areas and populations may have implications for the impacts of a nature reserve. For example, effects of reserve growth assumptions, location, reserve geometry and place in time may be difficult to disentangle from proper reserve size effects. In this paper, we have examined homogeneous populations and areas, in order to emphasize bioeconomic implications of a nature reserve. This modeling approach has managed to produce simple analytic results regarding the

explicit relationship between population size, yield, resource rent, and consumer surplus on the one hand, and reserve size, migration characteristics, and economic parameters on the other.

Appendix

Proof of the Theorem

Proof: We seek a solution to (27) satisfying (28) and (29). We first note that

(A1) $(c,m) = \left(\dfrac{1}{2},0\right) \overset{\text{def}}{=} P_1$

satisfies (27)-(29). For $\gamma < 1/2$,

(A2) $(c,m) = (0, 2\gamma) \overset{\text{def}}{=} P_2$

satisfies (28)-(30), while for $\gamma > 1/2$,

(A3) $(c,m) = \left(\dfrac{1}{2} - \dfrac{1}{4\gamma}, 1\right) \overset{\text{def}}{=} P_2$

satisfies (27)-(29). We next prove that P_1 and P_2 are connected by a smooth and monotonic curve $m^* = M(c\,;\gamma)$. To this end, we solve (27) for c :

(A4a) $c = D(m;\gamma)$

(A4b) $D(m;\gamma) = \dfrac{\gamma - \frac{1}{2}m}{P(m;\gamma)}$

33

(A4c) $P(m;\gamma) = \left(m - \dfrac{1}{2}\right)^2 + 2\left(\gamma - \dfrac{1}{8}\right)$

For $\gamma > 1/8$, $P(m;\gamma) > 0$ for all m. Consequently (A4) defines c as a smooth function of m in the interval $0 < m < \min(1, 2\gamma)$. Therefore, the points P_1 and P_2 are connected by a smooth curve in the (c,m) plane satisfying (27) and (28). It remains to treat the monotony condition (29), and the case $\gamma < 1/8$. To these ends, consider

(A5) $\dfrac{\partial D}{\partial m} = \dfrac{\frac{1}{2}m(m - 4\gamma)}{P^2}$

Eq. (A5) shows that the relationship between c and m is monotonically decreasing in the interval $0 < m < 4\gamma$, which contains the interval $0 < m < \min(1, 2\gamma)$, which is the interval connecting the points P_1 and P_2. Moreover, the boundary points of condition (29) have $c \geq \tfrac{1}{2}$ (see Figure 3).

It remains to treat the case $0 < \gamma < 1/8$, for which $P(m;\gamma)$ has zeroes. Thus, we can write

(A6) $D(m;\gamma) = \dfrac{\frac{1}{2}m - \gamma}{(m_2 - m)(m - m_1)}$

where

$$m_1 = \dfrac{1}{2} - \sqrt{\dfrac{1}{4} - 2\gamma}$$

(A7)

$$m_2 = \dfrac{1}{2} + \sqrt{\dfrac{1}{4} - 2\gamma}$$

First, it is noted that

Lemma: $2\gamma < m_1$ for $0 < \gamma < 1/8$.

Proof: Consider $r(\gamma) = 2\gamma - m_1 = 2\gamma - 1/2 + \sqrt{\frac{1}{4} - 2\gamma}$. We have $r(0) = 0$, $r(1/8) = -1/4$.

Moreover,

$$\frac{dr(\gamma)}{d\gamma} = 2 - \frac{2}{\sqrt{1 - 8\gamma}} < 0 \quad \text{for} \quad 0 < \gamma < \frac{1}{8}$$

so that $r(\gamma)$ is non-increasing in $0 < \gamma < 1/8$. QED.

As a consequence of this, all the conclusions above relating to connecting P_1 and P_2 remain valid, since the connection is not interrupted by the singularities at m_1 and m_2.

However, $D(m;\gamma)$ is positive for $m_1 < m < m_2$; moreover, $m_2 < 1$ for $0 < \gamma < 1/8$. It remains to show that the points $c = D(m;\gamma)$ obtained for $m_1 < m < m_2$ break condition (29). This follows by considering

$$\Delta = D(m;\gamma) - \frac{1}{2}\frac{1}{1-m}$$
$$= \frac{\gamma\, m}{(m - m_1)(m_2 - m)(1 - m)} > 0 \quad \text{for} \quad m_1 < m < m_2 < 1$$

Thus, the only acceptable solutions of (27) are those connecting points P_1 and P_2. QED.

Acknowledgments

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Figure captions

Figure 1. Yield contour lines; downward sloping straight broken lines are for Model A and solid ellipses are for Model B, representing yields 0.0, 0.05, 0.10, 0.15, 0.20 and MSY = 0.25. The broken MSY line is for Model A.

Figure 2. Model A loci of equilibrium. L: The line of equal densities. C: The locus of equilibrium. Horizontal broken line: Open-access HZ sub-population equilibrium. Q: Equilibrium for equal densities. Q_0: Equilibrium with no harvest. P: Actual equilibrium.

Figure 3. Reserve size tuned to realize MSY of Model A; Downward sloping curves show m^* as a function of c, for two cases, $\gamma = 0.3 < 1/2$ and $\gamma = 0.7 > 1/2$. Such tuning is not possible when $c > 1/2$.

Figure 4. Examples of loci of equilibrium relative to maximum yield. Panel a and b: Model A, where whole line and broken line represent loci of equilibrium as given in (18) and (16), respectively. Panel c and d: Model B, where loci of equilibrium are given by (22) and (23) and iso-contours of yield Y_B is given by (11). Values $Y_B = 0$, 0.05, 0.10, 0.15, 0.20, and 0.248. In case a, MSY can be attained by tuning E, while in cases b, c and d this cannot be achieved.

Figure 5. Equilibrium yield as a function of reserve size for low and intermediate values of relative migration, γ, and relative cost, c. Whole lines and broken lines represent yield of Model A and Model B, respectively. Horizontal dotted lines represent MSY.

Figure 6. Model A sustainable resource rent iso-curves and isocline. Horizontal line at $S_2 = (1-m)c$ is the reserve case open-access (zero rent) harvest zone sub-population level. Parameter values are γ

= 0.5, c = 0.3, m = 0.2. The four positive resource rent curves shown are for 0.03, 0.06, 0.09 and 0.12.

Figure 7. Model B sustainable resource rent iso-curves and isocline. Horizontal line at $S_2 = (1-m)c$ is the reserve case open-access (zero rent) harvest zone sub-population level. Parameter values are γ = 0.5, c = 0.3, m = 0.2. The seven iso-rent curves shown are for 0.0, 03, 0.06, 0.09 and 0.12.

Figure 8. Backward bending open-access yield curves and consumer surplus (CS). The triangle Opp_0 is CS for overall open-access and the triangle Mpp_M is CS for a nature reserve tuned to give nearly MSY, allowing open-access in the harvest zone.

Figure 1

Parameters:
$m=0.40$
$\gamma=0.30$
Contours:
Y=0.00, 0.05, 0.10, 0.15, 0.20
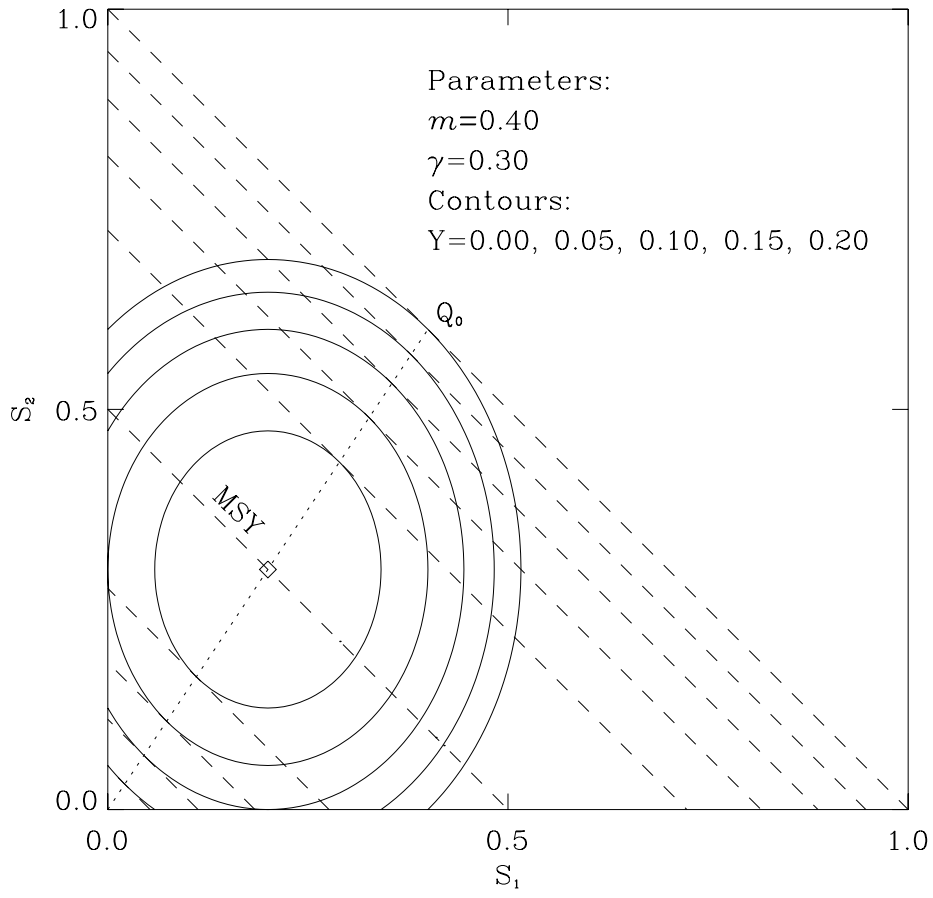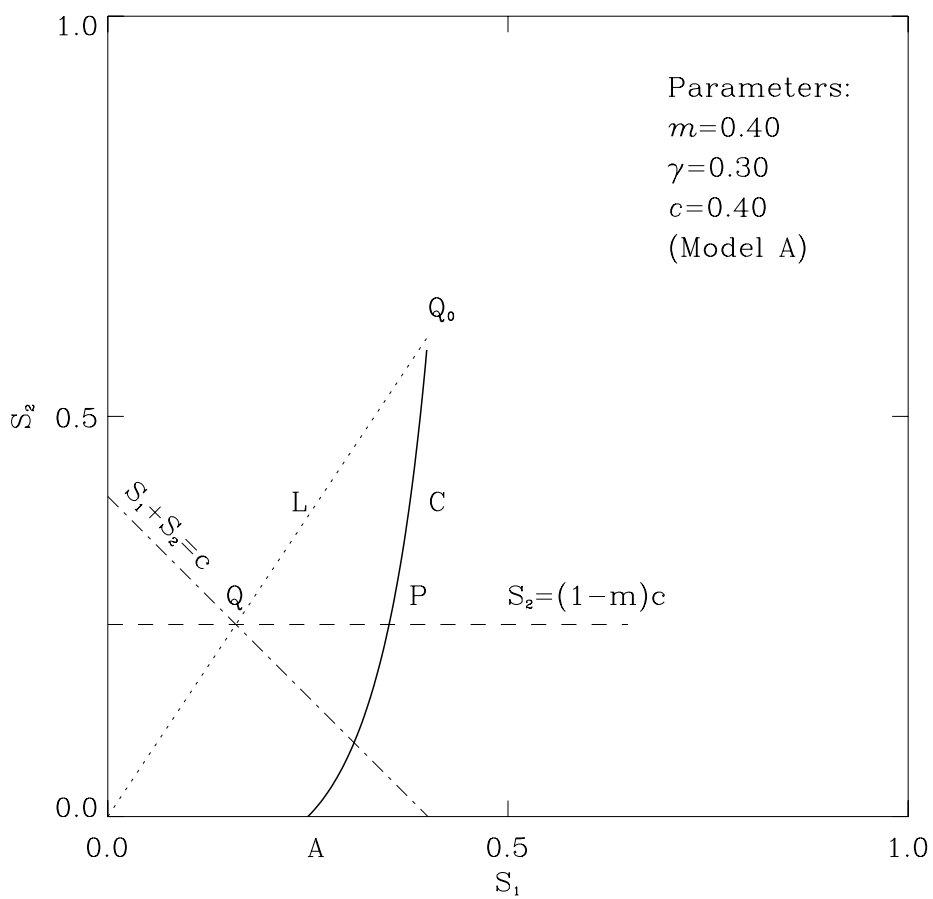
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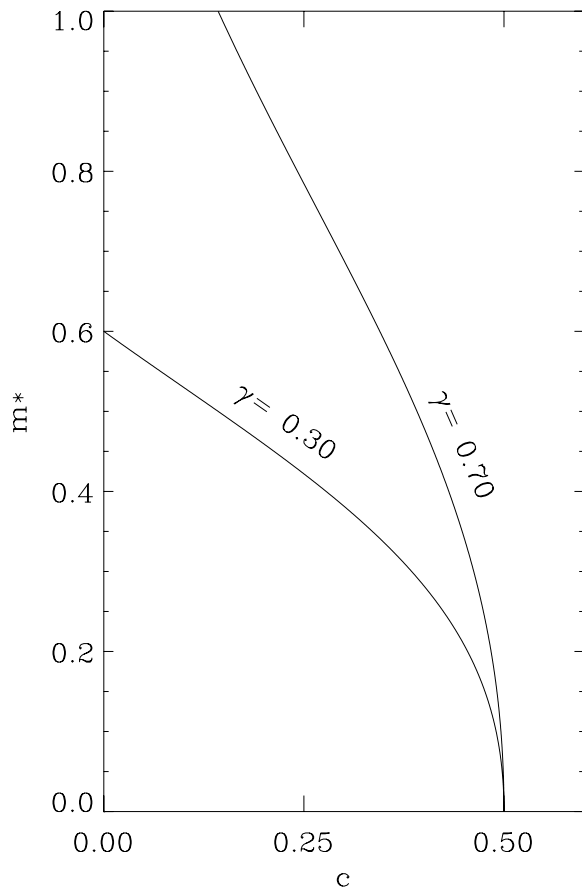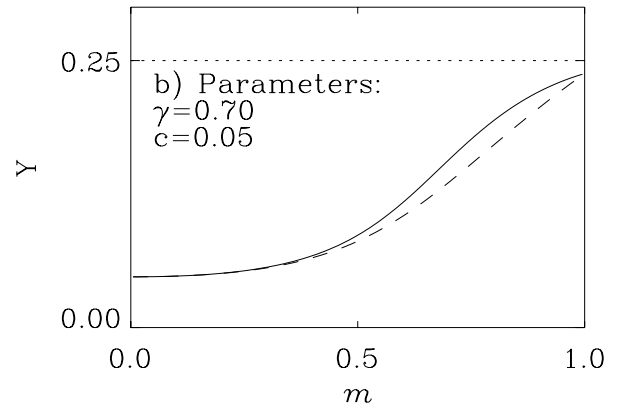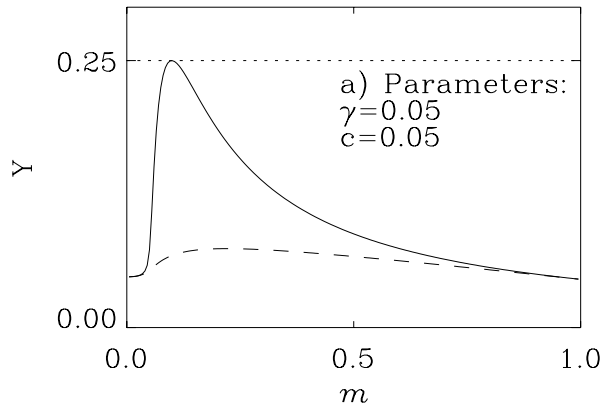

Figure 2

Figure 3

Figure 4
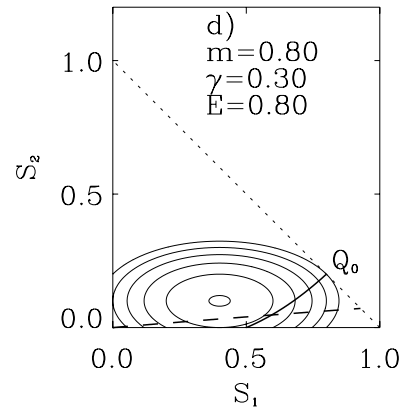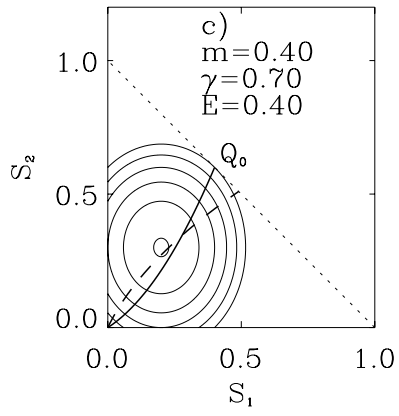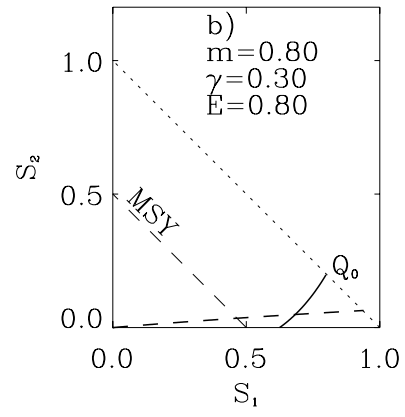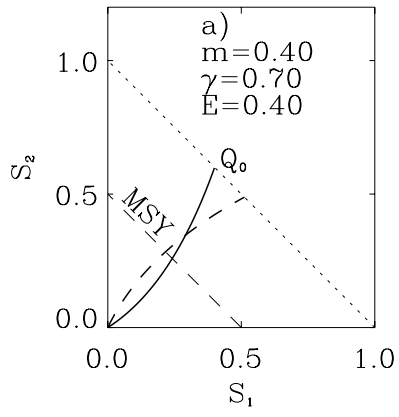
Figure 5

Figure 6

Figure 7

Parameters:
$m=0.20$
$\gamma=0.50$
$c=0.30$
Contours:
$\pi_B=$ 0.00, 0.03, 0.06, 0.09, 0.12

Q_0

$S_2=(1-m)c$

S_2

S_1

Figure 8