USING RESERVES TO PROTECT FISH AND WILDLIFE – SIMPLIFIED MODELING APPROACHES

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ABSTRACT. This paper investigates theoretically to what extent a nature reserve may protect a uniformly distributed population of fish or wildlife against negative effects of harvesting. Two objectives of this protection are considered: avoidance of population extinction and maintenance of population, at or above a given precautionary population level. The pre-reserve population is assumed to follow the logistic growth law and two models for post-reserve population dynamics are formulated and discussed. For Model A by assumption the logistic growth law with a common carrying capacity is valid also for the post-reserve population growth. In Model B, it is assumed that each sub-population has its own carrying capacity proportionate to its distribution area. For both models, migration from the high-density area to the low-density area is proportional to the density difference. For both models there are two possible outcomes, either a unique globally stable equilibrium, or extinction. The latter may occur when the exploitation effort is above a threshold that is derived explicitly for both models. However, when the migration rate is less than the growth rate both models imply that the reserve can be chosen so that extinction cannot occur. For the opposite case, when migration is large compared to natural growth, a reserve as the only management tool cannot assure survival of the population, but the specific way it increases critical effort is discussed.

KEY WORDS: Nature reserve, marine reserve, modeling, population protection, precautionary population level, renewable resources, extinction.

Introduction. A nature reserve is a tract of land or sea usually managed to serve several objectives, including the preservation of its flora, fauna and physical features, and yield increases. This paper

focuses on the effects of dividing the habitat area of a single population into two sub-areas, (i) a nature reserve (NR) where the animals are fully protected from harvesting, and (ii) a harvest zone (HZ) where harvesting may take place, in terms of protection and yield. Within a simple modeling approach, we will investigate theoretically, to what extent a nature reserve may protect a population of fish or wildlife in a homogeneous habitat against negative effects of harvesting. The aim of the protection may be either to protect against extinction or to protect against harvesting the population below a given threshold, the precautionary population level. In this paper we are not concerned about questions of how to determine the precautionary population level or any other optimization level. Since the analysis is limited to a single population, questions related to multi-species and ecosystem management are not directly discussed.

Several terrestrial and marine populations and ecosystems around the world have been overused (Pauly et al. [1998], FAO [2002], Roman and Palumbi [2003], Oldfield et al. [2004]) and some populations have even become extinct (Norton-Griffiths [2000], Ceballos and Ehrlich [2002]). Methods to mitigate such problems have been designed and implemented, including input control (fishing effort and capacity control, hunting licenses, etc.) and output control (fish quotas, game quotas, etc.), as well as zoning with harvest bans, or restrictions on resource use in one or more zones of the population habitat areas. Questions have been asked about the efficiency of different management tools including reserves (Mangel [2000], Skonhoft et al. [2002]). Increased emphasis on nature reserves over the last decades (Gerber et al. [2003], Halpern [2003]) may have come as a result of failures to achieve policy objectives (Hilborn et al. [2004]). Important as they may be, policy questions related to the use of nature reserves are outside the scope of this paper.

Scientific analyses of terrestrial and marine reserves have largely been developed independently of each other. Terrestrial reserves seem to have attracted most attention over the last few decades (see, e.g., Pickett and Thompson [1978], Meffe and Carroll [1994], Prendergast et al. [1999]), even though marine reserves were discussed relatively early, in Beverton and Holt [1957], and extensively elaborated and discussed in i.a. Polacheck [1990] and Guénette et al. [1998]. There are numerous studies on reserve effects on population size and yield, and

the importance of population growth, density dependence, migration, effort and reserve size and shape, including Buechner [1987], DeMartini [1993], Sladek Novlis and Roberts [1999], Paddock and Estes [2000], Apostolaki et al. [2002] and Rodwell et al. [2003]. 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 differ in scale and variability, and they differ in the way humans have utilized their resources. For example, in marine systems, sea currents may influence dispersal of pollutants and organisms to a greater extent than air does for terrestrial systems. Further, 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.

Following the tradition of Clark [1985], the modeling approach of this paper is of the "simplistic" type. We try to understand complex management issues by developing and analyzing simple models. Despite the simplifying assumptions being used, we still manage to include in the analysis major biological and management characteristics, such as population growth, migration, harvest effort and reserve size. To produce analytic results regarding the effects on population level and yield of the division of a population's habitat area into two sub-areas, a nature reserve (NR) and a harvesting zone (HZ), we choose to use and analyze simple logistic growth models. These modeling approaches allow some simple analytical findings regarding the explicit relationship between population protection, yield, reserve size, critical harvest effort and biological parameters, including population growth and migration. Despite widespread use of simple logistic growth models for analytic purposes, other researchers have not, to the best of our knowledge, analyzed and compared the two nature reserve sub-models in the form set out in this paper.[1] The next section presents and discusses the two models, while equilibrium and stability issues are discussed in a separate section. Following this are sections on how to hedge against extinction and overuse, and yield issues. The results are discussed and summarized in the concluding section.

The models.   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. The pre-reserve population is assumed to follow the logistic growth law and two models for post-reserve population dynamics are formulated and discussed. This growth pattern may be kept or changed after partitioning into two administratively different sub-areas. Net migration moves in the direction from the high-density sub-area to the low-density area, and the two sub-populations are homogeneously distributed across their sub-areas. For Model A, the post-reserve growth of the total population continues following the pre-reserve logistic growth. In Model B, we assume that each sub-population has its own carrying capacity proportionate to its distribution area. Thus in Model A, the population is implicitly able to exploit its total carrying capacity for growth, whereas in Model B, the population has some restrictions to aggregate growth due to the creation of a nature reserve. We use the two post-reserve models with different population growth characteristics to compare similarities and differences in the implied effects of reserve creation and expansion. Differences and similarities of the growth assumptions are discussed further in the concluding section.

Pre-reserve population dynamics. The pre-reserve growth of a population in a given area is assumed to follow the logistic path described by

$$(1) \qquad \dot{W} = \frac{dW(t)}{dt} = rW\left(1 - \frac{W}{K}\right)$$

with W as the population size, K the carrying capacity and r the intrinsic growth rate, $(r > 0, \ K > 0)$. Normalizing population by dividing population level with carrying capacity gives the growth equation[2]

$$(2) \qquad \dot{S} = rS(1 - S), \qquad S = \frac{W}{K}.$$

Now, imagine that the population is divided into two sub-populations with the same homogeneous characteristics and that $S = S_1 + S_2$, where $S_1 = W_1/K$, $S_2 = W_2/K$ and $W = W_1 + W_2$. Growth equation (2) can now be written

$$(3) \qquad \dot{S} = rS_1(1 - S_1 - S_2) + rS_2(1 - S_1 - S_2).$$

If we also assume that $\dot{S}_1$ and $\dot{S}_2$ equal the first and second term, respectively, on the righthand side of equation (3), equilibrium requires $\dot{S}_1 = \dot{S}_2 = 0$.

Model A. In Model A, we also assume that equation (3) 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 depends on the differences in sub-population densities, i.e., on $S_1/m = W_1/mK$ and $S_2/(1-m) = W_2/(1-m)K$. 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

$$(4) \quad \dot{S}_1 = r\left[S_1(1 - S_1 - S_2) - \gamma\left(\frac{S_1}{m} - \frac{S_2}{1-m}\right)\right]$$

and

$$(5) \quad \dot{S}_2 = r\left[S_2(1 - S_1 - S_2) + \gamma\left(\frac{S_1}{m} - \frac{S_2}{1-m} - E\frac{S_2}{1-m}\right)\right]$$

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 (4) and (5) and $\dot{S} = \dot{S}_1 + \dot{S}_2$ is reduced to that of equation (3) as well as to equation (2). 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 now depends on total population level and harvesting, given by

$$(6) \qquad \dot{S} = r\left[S(1-S) - E\,\frac{S_2}{1-m}\right].$$

Sustainable yield may be found from equation (6) for $\dot{S} = 0$.

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., Hannesson [1998], Sanchirico and Wilen [2002]. 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:

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

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

assuming migration and harvesting, as in Model A. This model can be shown to be equivalent to the model in Hannesson [1998].

For $S = S_1 + S_2$ we have

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

Note that, in this case, post-reserve total population growth does not follow the pre-reserve growth law in equation (2). Rather, logistic

growth is in this model incorporated in the following way: With no harvesting, the logistic growth law is followed in the case of equal densities $S_1/m = S_2/(1 - m)$; if this is so initially, it remains so for all time, since both (7) and (8) reduce to

(10)
$$\frac{ds}{dt} = rs(1 - s)$$

with $s = S_1/m = S_2/(1 - m)$. Still, with no harvest, regardless of initial densities, as will be shown below, the two sub-populations will approach the globally stable equilibrium $S_1^* = m$, $S_2^* = 1 - m$ of equal density, yielding total population $S^* = S_1^* + S_2^* = 1$, the carrying capacity.

In the case of harvesting, the growth of the total population is given by

(11)
$$\dot{S} = r\left[S_1\left(1 - \frac{S_1}{m}\right) + S_2\left(1 - \frac{S_2}{1 - m}\right) - E\left(\frac{S_2}{1 - m}\right)\right].$$

This equation predicts somewhat different growth compared to that of Model A, as given by equation (6), which is demonstrated in detail below, following the discussion on equilibrium and stability. Sustainable yield may be found from equation (11) for $\dot{S} = 0$.

Equilibrium and stability. Let us now check if each of the models has an equilibrium point with positive sub-populations and whether this is a stable equilibrium. Equilibrium for each of the sub-populations requires $\dot{S}_1 = \dot{S}_2 = 0$, and this obviously implies $\dot{S} = 0$.

Model A. At equilibrium it follows from (4) and (5) that

(12)
$$\alpha S_2 + (A - S_2)S_1 - S_1^2 = 0,$$

and

(13)
$$\beta S_1 + (\beta - S_1)S_2 - S_2^2 = 0,$$

where

(14a) $$\alpha = \frac{\gamma}{1-m},$$

(14b) $$\beta = \frac{\gamma}{m},$$

(14c) $$A = 1 - \frac{\gamma}{m},$$

(14d) $$B = 1 - \frac{\gamma}{1-m} - \frac{E}{1-m}.$$

Note that α and β both are positive, whereas A and B can be positive or negative. When $m < \gamma$, i.e., when the reserve size is less than the relative migration rate, A is negative. It will be demonstrated below that this case poses a threat of overuse, or extinction of the population.

The isoclines[5] of the sub-populations are found from equations (12) and (13) and may be written

(15) $$S_2 = \frac{S_1(A - S_1)}{S_1 - \alpha} = \phi(S_1),$$

(16) $$S_1 = \frac{S_2(B - S_2)}{S_2 - \beta} = \psi(S_2).$$

The curve (15), which expresses the isocline $\dot{S}_1 = 0$, we shall denote C1, and the curve (16), which expresses the isocline $\dot{S}_2 = 0$, we shall call C2, to be used in Figures 1–3. The shape of C1 and C2 is discussed below.

The equilibrium populations, S_1^* and S_2^*, can, in principle, be found from equations (15) and (16). We first discuss the case $E = 0$. In this case, it is straightforward to demonstrate that each sub-population of Model A is simply proportional to its own area:

(17) $$S_1^* = \frac{\alpha}{\alpha + \beta} = m$$

and

(18) $$S_2^* = \frac{\beta}{\alpha + \beta} = 1 - m$$

for $E = 0$. The total population equals the carrying capacity, and the density is uniform.

In the case of non-vanishing harvesting, $E > 0$, we make the following graphical analysis, assuming S_1 along the horizontal axis and S_2 along the vertical axis. We have:

(i) C1 is a hyperbola with a vertical asymptote $S_1 = \alpha$, which enters the positive quadrant at $(S_1, S_2) = (A, 0)$ if $A > 0$, and at the origin when $A < 0$. This gives the three cases $i = 1$: $A > \alpha$, $i = 2 : 0 < A < \alpha$ and $i = 3$: $A < 0$.

(ii) Likewise, C2 is a hyperbola with a horizontal asymptote $S_2 = \beta$, entering the positive quadrant at $(S_1, S_2) = (0, B)$ when $B > 0$, or at the origin when $B < 0$. This gives the three cases $j = 1$: $B > \beta$, $j = 2$: $0 < B < \beta$ and $j = 3$: $B < 0$.

This gives altogether nine cases that we represent as (i, j), where $i, j = 1, 2, 3$. For $i = 1$, $\alpha < S_1^* < A$, while for $i = 2$, $A < S_1^* < \alpha$. Likewise, for $j = 1$, $\beta < S_2^* < B$, while for $j = 2$, $B < S_2^* < \beta$. In all eight cases with either $i \neq 3$ or $j \neq 3$, there is a unique positive equilibrium; we show two examples in Figures 1 and 2. This equilibrium is globally stable, attracting the entire positive quadrant; as indicated by arrows in the figures, schematically representing the direction field in the four separate regions that the positive quadrant is divided into by C1 and C2. In fact, $\dot{S}_1 > 0$ (< 0) to the left (right) of C1, and $\dot{S}_2 > 0$ (< 0) below (above) C2; from this, the indicated arrows follow. Figure 2 differs from Figure 1 in two ways. Firstly, the larger γ shifts the vertical asymptote $S_1 = \alpha$ to the right and the isocline C1 to the left side of this asymptote. Secondly, $E > 0$ shifts the horizontal asymptote $S_2 = \beta$ upwards and the isocline C2 downwards.

Equations (15)–(16) may be used to analyze the impact on the equilibrium sub-populations from changes in the reserve size, m, the relative migration rate γ and harvest effort, E. For example, the effect of increased effort on the HZ sub-population will be negative, whereas the effect on the NR sub-population may be negative or positive, depending on parameters. An increase in harvest effort, E, decreases B but leaves the parameters A, α and β unchanged. In case $i = 1$, e.g., Figure 1, this implies a decrease in the HZ equilibrium sub-population S_2^*, but an increase in the NR sub-population S_1^*. However, in case $i = 2$, Figure 2, the slope of C1 is such that increased harvest effort E implies a reduction in both the NR and HZ sub-populations. The C1 slope in Figure 1, or cases $i = 1$, require $A > a$, which is equivalent to $\gamma < m(1 - m)$. Thus the positive effect on the reserve
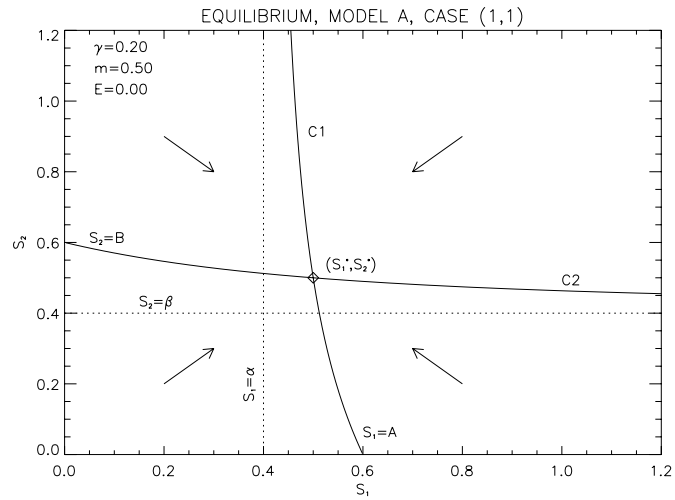
FIGURE 1. Isoclines C1 and C2, equilibrium (S_1^*, S_1^*) and direction field, Model A, for a case of the type (1,1). Parameter values are indicated.
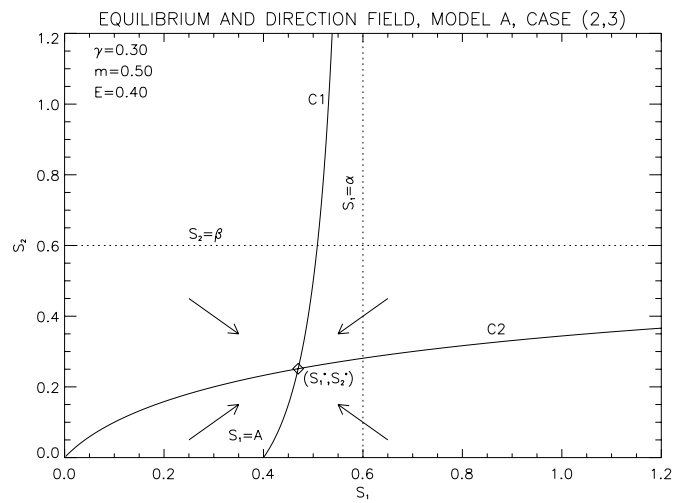

FIGURE 2. Isoclines C1 and C2, equilibrium (S_1^*, S_1^*) and direction field, Model A, for a case of the type (2,3). Parameter values are indicated.

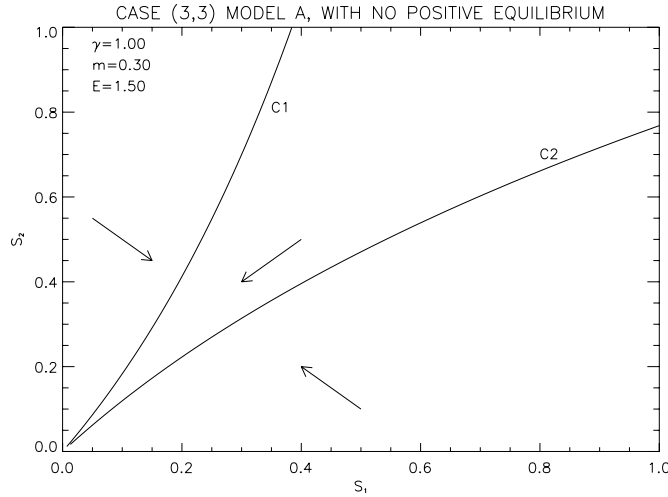CASE (3,3) MODEL A, WITH NO POSITIVE EQUILIBRIUM

FIGURE 3. Isoclines C1 and C2, and direction field, Model A, for a case of
the type (3,3) with no positive equilibrium. Parameter values are indicated.

sub-population from an increase in harvest effort is possible in this model only if the relative migration rate, γ, is smaller than the product of the two sub-population areas. This may happen if the population is rather sedentary (γ is small) and the reserve occupies about half of the total population area. In this case, reduction of the harvestable sub-population implicitly leaves more resources, prey, to allow the NR sub-population to grow slightly. Since the maximum value of $m(1-m)$ is $1/4$, for $m = 1/2$, this implies that for $\gamma > 1/4$ we know for sure that C1 will have a slope as shown in Figure 2. Thus for $\gamma > 1/4$ an increase in the harvest effort will definitely reduce the equilibrium levels of both sub-populations.

Threat of extinction may arise in the (3,3) case where there are two sub-cases, of which one is illustrated in Figure 3. In this case the origin is globally attracting the whole positive quadrant, i.e., parameter values and harvest effort combined threatens to extinguish the population. We shall return to this issue below, particularly to see if and how reserve size and effort control may be used to hedge against extinction and overuse of the resource.

Model B. At equilibrium in Model B, one has from equations (7) and (8)

(19) $$S_2 = \phi_1(S_1) = r_1 S_1 (S_1 - F),$$

and

(20) $$S_1 = \psi_1(S_2) = r_2 S_2 (S_2 - G),$$

where the parameters are

(21a) $$F = m - \gamma$$

(21b) $$G = 1 - m - \gamma - E$$

(21c) $$r_1 = \frac{1 - m}{\gamma m}$$

(21d) $$r_2 = \frac{m}{1 - m}\gamma.$$

We have the cases (i, j) where $i, j = 1, 2$, where $i = 1$ for $F > 0$, $i = 2$ for $F < 0$, $j = 1$ for $G > 0$ and $j = 2$ for $G < 0$.

The curve (19), which expresses the isocline $\dot{S}_1 = 0$ is denoted C1 and the curve (20), which expresses the isocline $\dot{S}_2 = 0$ is denoted C2. Both curves are parabolas. Curve C1 has its axis parallel to the S_2 axis, and curve C2 has its axis parallel to the S_1 axis. C1 enters the positive quadrant at $(S_1, S_2) = (F, 0)$ when $F > 0$ and through the origin when $F < 0$. These two cases are $i = 1$ and $i = 2$, respectively. Likewise, C2 is entering the positive quadrant at $(S_1, S_2) = (0, G)$ when $G > 0$ (case $j = 1$) and $(S_1, S_2) = (0, 0)$ when $G < 0$ (case $j = 2$). This gives altogether five cases, when we count that the case (2,2) has two sub-cases, analogous to Model A. Two of the cases are shown in Figures 4 and 5. For each of the cases (i, j) with either i or $j \neq 2$, there is a stable equilibrium with positive sub-populations S_1 and S_2. In the sub-case (2,2)b the curves C1 and C2 are such that both sub-populations are extinct, similar to what is demonstrated above for Model A in Figure 3, implying extinction of the total population. The conditions for extinction and the question of how to avoid such an irreversible solution are discussed below, following the discussion on yield potentials.
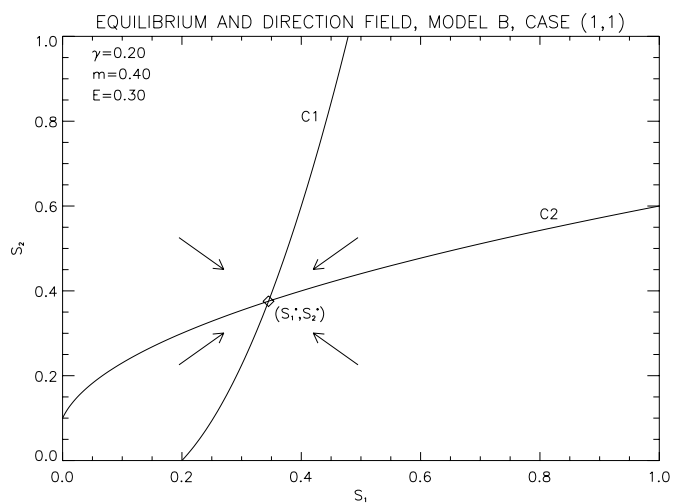
EQUILIBRIUM AND DIRECTION FIELD, MODEL B, CASE (1,1)

$\gamma = 0.20$
$m = 0.40$
$E = 0.30$

FIGURE 4. Isoclines C1 and C2, equilibrium (S_1^*, S_1^*), and direction field for Model B, for a case of the type (1,1). Parameter values are indicated.

EQUILIBRIUM AND DIRECTION FIELD, MODEL B, CASE (2,2)
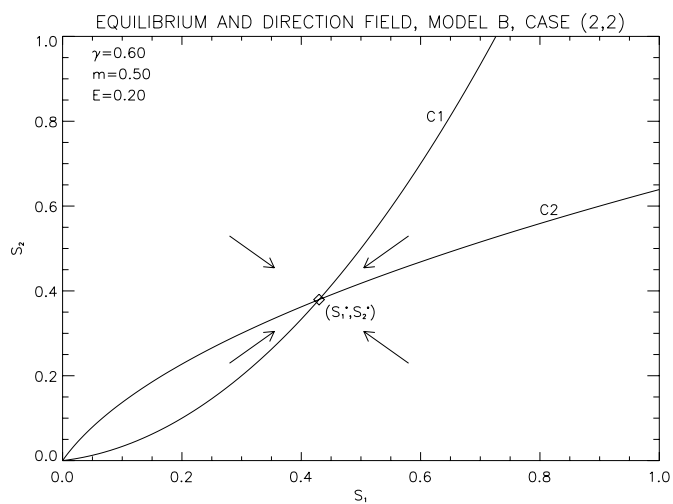
$\gamma = 0.60$
$m = 0.50$
$E = 0.20$

FIGURE 5. Isoclines C1 and C2, equilibrium (S_1^*, S_1^*), and direction field for Model B, for a case of the type (2,2). Parameter values are indicated.

Comparing yield potentials. 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). Initially, assume that harvesting takes place at a sustainable basis at constant sub-population levels, and 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. From equation (6) sustainable yield for Model A, that is, for $\dot{S} = 0$, is

$$(22) \qquad Y_A = F_A(S_1, S_2) = r(S_1 + S_2)(1 - (S_1 + S_2)).$$

Note that migration does not matter for the sustainable yield level derived in (22), 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 that do not appear in equation (22) due to the use of normalized populations and time scale.

From equation (11) the sustainable yield for Model B is

$$(23) \qquad Y_B = F_B(S_1, S_2) = rS_1\left(1 - \frac{S_1}{m}\right) + rS_2\left(1 - \frac{S_2}{1 - m}\right).$$

From (23) 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 Models A and B, respectively, in (22) and (23). We have

$$(24) \qquad \begin{aligned} \Delta Y = Y_A - Y_B &= r\left[-(S_1 + S_2)^2 + \frac{S_1^2}{m} + \frac{S_2^2}{1 - m}\right] \\ &= r\left(\sqrt{\frac{1 - m}{m}}\, S_1 - \sqrt{\frac{m}{1 - m}}\, S_2\right)^2 \geq 0. \end{aligned}$$

From (20) 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 (24) is always valid when sustainable harvesting takes place.

Hedging against extinction. The question about how to avoid overuse of the resource may be divided into two sub-questions. First, can a reserve protect the population against extinction threatened by harvesting? Secondly, can a reserve act as a hedge against biological overuse? In this section we shall elaborate on the conditions of E leading to extinction.

Model A. Referring to Figure 3, consider the slopes of C1 and C2 at the origin. If

$$(25) \qquad \frac{dS_2}{dS_1}(0)\Big|_{C1} < \frac{dS_2}{dS_1}(0)\Big|_{C2},$$

then there is a positive equilibrium,[6] while the opposite inequality, there is no positive equilibrium. Since, by (15), $(dS_2/dS_1)(0)|_{C_1} = (-A)/\alpha$ and, by (16), $(dS_2/dS_1)(0)\Big|_{C_2} = \beta/(-B)$, (25) implies $AB < \alpha\beta$ (recall that in the case (3,3) demonstrated in Figure 3 we have $A < 0$ and $B < 0$). By (14) this in turn gives the condition

$$(26) \qquad E < E_c = (1 - m)\frac{\alpha + \beta - 1}{\beta - 1}$$

for the existence of a positive equilibrium in the (3,3) case. We may rewrite E_c to show its dependence on the reserve size and the relative migration rate:

$$(27) \qquad E_c = 1 + \frac{m}{(\gamma/m) - 1}.$$

Thus E_c is the critical normalized effort level that the effort cannot exceed on a permanent basis if extinction is to be avoided.[7] Note that (27) should only be used when $A < 0$, i.e., $\beta > 1$, implying a positive value of E_c. Extinction in Model A is possible only if $m < \gamma = \sigma/r$, i.e., for $\beta > 1$, recalling the parameter definitions in (14). For $m > \gamma$ ($\beta < 1$) extinction is avoided for any level of E. It is important to

CRITICAL EFFORT
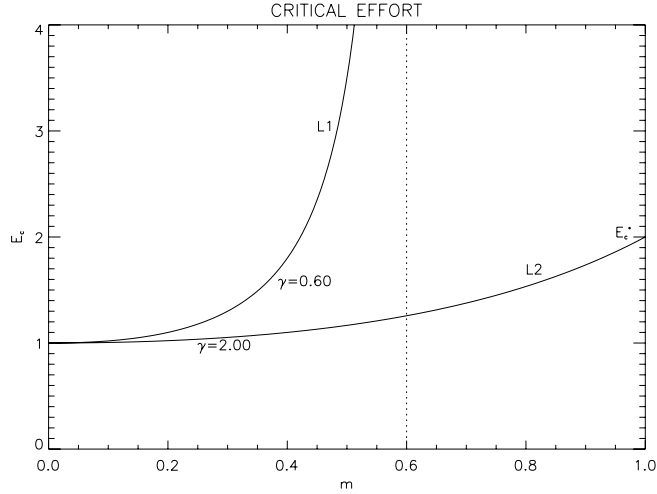

FIGURE 6. Critical effort E_c as a function of reserve size m, for two values of γ. Vertical dotted line indicates asymptote for the case $\gamma = 0.6$. For $\gamma < 1$, L1 has an asymptote at $m = \gamma$ and extinction is avoided for any level of E for $m > \gamma$. For $\gamma > 1$, there is an upper limit to the critical effort level, E_c^*.

distinguish between the cases $\gamma < 1$ and $\gamma > 1$ since we always have $m < 1$.

Figure 6 shows two critical effort level curves L1 and L2 as a function of the reserve size, m, for a given relative migration rate, γ . The L1 curve is for a case with $\gamma < 1$, while the L2 curve is for a case with $\gamma > 1$. The L1 curve originates at $E_c \approx 1$ for a small nature reserve with m close to zero. A nature reserve of size $m < \gamma$ combined with restrictions on harvest effort, such that effort is below the L1 curve in Figure 6, protects the population against extinction. On the other hand, choosing a nature reserve large enough that $\gamma < m < 1$ in Figure 6 fully protects the population against extinction for any effort level.

For $\gamma > 1$ there is an upper limit to the critical effort level, equal to $E_c^* = \gamma/(\gamma - 1)$ for $m = 1$, indicated in Figure 6 by the terminal point of the L2 curve. The equilibrium population is[8] $S = 1 - E$ in the case of no reserve ($m = 0$), with harvesting taking place throughout the population's distribution area. Thus the critical limit to normalized

effort is unity in the case of no reserve, whereas a reserve expands this critical limit along the L1 and L2 curves, as illustrated in Figure 6.

Model B. Using equations (19) and (20) we find that to avoid extinction, in the case of $F < 0$ and $G < 0$, it is again necessary that (25) is satisfied. In this case, $(dS_2/dS_1)_{C1}(0,0) = -r_1F$ while $(dS_2/dS_1)_{C2}(0,0) = 1/(-r_2G)$. This leads to

$$(28) \qquad\qquad (-r_1F) < \frac{1}{(-r_2G)}$$

which in turn gives $E < E_c$, where E_c is again given by (27).

In other words, we find exactly the same formula for the critical effort level for Model B as for Model A, and Figure 6 is valid for both models. This indicates that the two models become similar at very low population levels, despite differences in growth conditions at other levels, as seen in equations (4)–(5) and (7)–(8).

For both Model A and B the population is saved from extinction for any effort level if $\gamma < m < 1$. This may happen when net migration is "small" compared to natural growth, recalling $\gamma = \sigma/r$, and the fraction of the total area set aside for the nature reserve, m, is sufficiently "large." Thus a reserve can assure survival of the population both in Model A and B, if the migration coefficient σ is less than the intrinsic growth rate r, since the upper limit to m is one. On the other hand for $m < \gamma < 1$ the critical value of effort, E_c, is given by (27). Thus, management of a nature reserve could save the population from extinction if combined with sufficient restrictions on harvest effort in the case of a slowly growing (small r) and fast net migrating (large σ) species.

It is noted above for Model A that the critical effort is one in case of no reserve ($m = 0$) and that a reserve expands this limit, as demonstrated by the L-curves in Figure 6. This is valid also for Model B. Also note that the critical effort level $E_c^* = \gamma/(\gamma - 1)$ in Figure 6 is approaching one if $\gamma \to \infty$. A very high net migration would seriously erode the advantages of a nature reserve as a hedge against extinction for both Model A and B. Similar results have been shown by use of other types of models, e.g., for the Beverton-Holt type of cohort models used in Polacheck [1990] and DeMartini [1993], even

though these two papers mainly are concerned with yield and spawning stock issues. The threat of model population extinction by harvesting depends to a great extent on the specification of the model for low population levels (Clark [1990, Chapter 2] discusses this, in relation to economic and harvest efficiency issues). Model A and B have proved the same characteristics in relation to nature reserve creation and critical effort against extinction. Whether this will hold for a positive target population will be discussed below.

Hedging against overuse. From a precautionary point of view, a more conservative objective than simply avoiding extinction would be to secure a minimum target level for the population. We now investigate if a nature reserve may prevent the total population, S, to fall below a precautionary or target population level, ε. More generally, one may investigate whether there is a precautionary effort level E_ε such that as long as $E < E_\varepsilon$, the total population does not fall below ε, where $0 < \varepsilon < 1$.

A few general statements are valid for both models:

(i) For the logistic model, Model A, without a marine reserve, $E_\varepsilon = 1 - \varepsilon$. It is therefore to be expected that with a marine reserve, $E_\varepsilon \rightarrow (1 - \varepsilon)$ when the mobility goes to infinity, expressed by $\gamma \rightarrow \infty$, and that this limit is approached faster the smaller m is.

(ii) One will of course have $E_\varepsilon < E_c$, i.e. the critical effort to ensure that the population remains above a security threshold is smaller than the critical effort of extinction. Also, $E_{\varepsilon_1} < E_{\varepsilon_2}$ if $\varepsilon_1 > \varepsilon_2$.

(iii) In the case of $i = 1$ or 2 for Model A, or $i = 1$ for Model B, the equilibrium value of S_1 approaches a finite value ($S_1 \rightarrow 1 - (\gamma/m)$ in case of Model A and $S_1 \rightarrow m - \gamma$ in case of Model B). Now, if this value is also greater than ε, no effort can bring the population below the threshold ε. This gives the conditions:

$m > \gamma/(1 - \varepsilon)$ for Model A, and

$m > \varepsilon + \gamma$ for Model B.

Of course, since $m < 1$, these conditions cannot be achieved when $\gamma > 1 - \varepsilon$; this is true for both models.

This gives the general features of $E_\varepsilon(m)$:

$E_\varepsilon(m) \to \infty$ when $m \to \gamma/(1-\varepsilon)$ (for $\gamma < 1-\varepsilon$, Model A), or

$m \to \gamma + \varepsilon$ (for $\gamma < 1-\varepsilon$, Model B) from below, and

$E_\varepsilon(\gamma) \to 1-\varepsilon$ when $\gamma \to \infty$,

and, finally, $E_\varepsilon \to 1-\varepsilon$ when $m \to 0$.

We can determine E_ε in the following way. In Figure 7, which refers to Model A, but is representative of both models, the line L_ε defined by $S_1 + S_2 = \varepsilon$ is shown as a broken line. Let S_1^1 be the value of S_1 at the intersection between L_ε and the curve C1 defined by (15), and let S_1^2 be the value of S_1 at the intersection between L_ε and the curve C2 defined by (16). Then the condition for the equilibrium point to be outside L_ε is

(29)
$$S_1^2 < S_1^1.$$

On L_ε,

(30)
$$S_2 = \varepsilon - S_1.$$

For Model A, we can find a simple expression for E_ε as follows: Substituting (30) into (15) gives

(31)
$$S_1^1 = \frac{\varepsilon\alpha}{\alpha - \bar{A}}$$

where $\bar{A} = A - \varepsilon$, and α, A were defined in (14). Likewise, substituting (30) into (16), gives

(32)
$$S_1^2 = \frac{\varepsilon\overline{B}}{\overline{B} - \beta}$$

where $\overline{B} = B - \varepsilon$ and B, β were defined in (14). From (29) we now derive

(33)
$$\overline{A}\,\overline{B} < \alpha\beta$$

from which this condition follows:

(34a)
$$E < E_\varepsilon$$

(34b)
$$E_\varepsilon = 1 - \varepsilon + \frac{m(1-\varepsilon)}{(\gamma/m(1-\varepsilon)) - 1}.$$
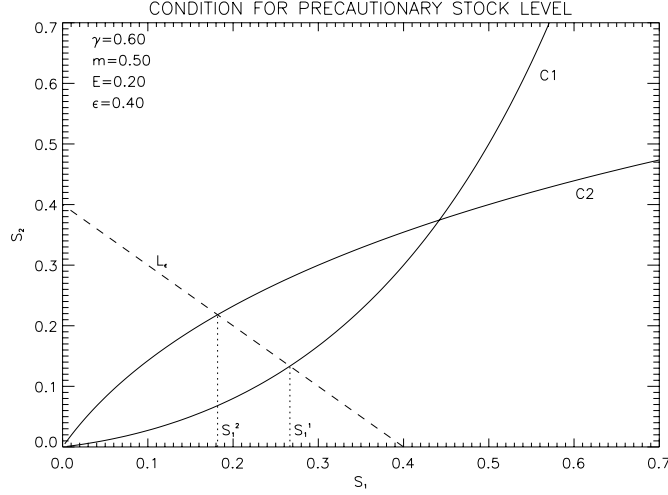
CONDITION FOR PRECAUTIONARY STOCK LEVEL

FIGURE 7. Illustration of the condition $S_1^2 < S_1^1$ for the computation of precautionary population level. Broken line $L_\varepsilon : S_1 + S_2 = \varepsilon$. Solid lines: isoclines.

In the case of Model B, the equations for S_1^1 and S_1^2 are quadratic. Consequently, we have not obtained a simple explicit expression for E_ε.

Figure 8 shows for Model A the two solid curves for the precautionary effort level as a function of the reserve size, m, for a given relative migration rate. The L1 curve is for a case $\gamma < 1 - \varepsilon$ and L2 is for a case $\gamma > 1 - \varepsilon$. L1 has a minimum value of $E_\varepsilon = 1 - \varepsilon$, for $m = 0$, and an asymptote at $m = \gamma/(1 - \varepsilon)$. A nature reserve of size $m < \gamma/(1 - \varepsilon)$, combined with restrictions on harvest effort such that effort is below the L1 curve in Figure 8, protects the population against falling below the precautionary level ε. On the other hand, by choosing a nature reserve, in Model A, large enough that $\gamma/(1 - \varepsilon) < m < 1$ in Figure 8, keeps the population above the precautionary population level for any effort level.

For $\gamma > 1 - \varepsilon$ there is an upper limit to the precautionary effort level, to be found by substituting $m = 1$ in (34),

$$(35) \qquad E_\varepsilon^* = \frac{\gamma(1 - \varepsilon)}{\gamma - (1 - \varepsilon)}.$$
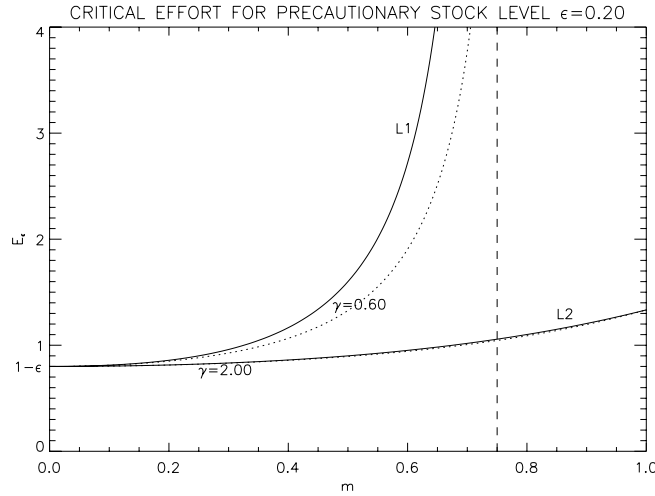
FIGURE 8. Critical effort for precautionary population level, E_ε, as a function of reserve size m, for two values of γ and one value of ε. Solid lines: Model A. Dotted lines: Model B (for L2 the dotted line virtually overlaps the solid line). Vertical broken line: Asymptote $\gamma/(1-\varepsilon)$ for curve of Model A, in case $\gamma = 0.6$ and $\varepsilon = 0.2$.

As demonstrated in Figure 8 with the L2 curve, for $\gamma > 1-\varepsilon$, a nature reserve as the only management tool can not assure the precautionary population level, but combined with a limitation on harvest effort, a reserve may contribute to fulfilling this objective. Thus Figure 8 demonstrates, for Model A, that a reserve raises the limit of effort and may contribute to the assurance of the precautionary population level even if $\gamma > 1 - \varepsilon$. For Model B we have included numerical results in Figure 8, demonstrated by the dotted lines, and this confirms the traits described above.

Reserve shape design may act as an additional or joint management tool to reserve size, as discussed in several papers, including Diamond and May [1981], Buechner [1987], Guénette et al. [1998], Acosta [2002] and Neubert [2003]. In cases of 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 total population areas by use of straight border lines of different length. Thus of all possible NRs of size m, we should choose the one with the shortest border length l.[9] 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.[10] Figures 6 and 8 illustrate that reserve efficiency is higher the lower γ is, for both models. Thus reserve shape and size should, within this modeling approach, be determined simultaneously to minimize net migration between the two sub-areas.

Conclusion. This paper demonstrates that a nature reserve as the only management tool may serve as a hedge against extinction for both Model A and B. Dividing the total distribution area of a uniformly distributed homogenous population into two sub-areas, a nature reserve, NR, and a harvest zone, HZ, the former may protect the population against negative implications of harvesting. The effectiveness of a reserve is greatest if mobility is small compared to population growth, as demonstrated in several other papers for other models and specific populations, e.g., Polacheck [1990], Guenette et al. [1998], Skonhoft et al. [2002]. For the two models discussed in this paper, the explicit relationship between critical effort, population growth, migration and reserve size has been demonstrated analytically. When the migration rate is less than the growth rate both models imply that the reserve can be chosen so that extinction cannot occur. For the opposite case, a reserve as the only management tool cannot assure survival of the population, but the specific way it increases critical effort is demonstrated. Also, for a given precautionary population level a reserve contributes to keeping the population at or above this level. This is the case for low values of the relative migration rate. However, for greater values of the relative migration rate, a reserve may be an effective hedge only if combined with a limitation on harvest effort. Based on the analytical solutions, Figure 8 illustrates, for Model A, that a reserve raises the limit of effort and may contribute to the assurance of the precautionary

population level. For numerical parameter values Model B produces a picture comparable to that of Model A.

It has been demonstrated that the sustainable yield of Model A is always greater than that of Model B, for the same reserve size and equilibrium levels of the sub-populations. However, in general it is difficult to compare in a precise way the effectiveness of reserves in different models due to differences in model structure, migration and other characteristics, see, e.g., the discussion in Apostolaki et al. [2002].

Reserve shape matters, through the effect on net migration between NR and HZ. For a given reserve size the shape of it should be chosen to minimize net migration by minimizing the length of the border between NR and HZ. In the case of great net migration, it is well known from the literature cited above that the effectiveness of a nature reserve is reduced. However, even in this case a reserve contributes to increasing the critical effort to avoid extinction and the precautionary effort to avoid biological overuse of the population.

Even though uniform distribution of homogeneous populations is a theoretical artifact, the two models discussed in this paper may be used for comparison with more realistic, detailed models that stress patchiness, heterogeneity and different forms of interconnections between patches. The way sub-elements differ for heterogeneous areas and populations may have implications for the impacts of a nature reserve. For example, effects of location, reserve geometry and place in time may have effects that are difficult to disentangle from reserve size effects. In this paper we have chosen to examine homogeneous populations and areas, in order to emphasize the implications for population protection of a nature reserve. This modeling approach has managed to produce simple analytic results regarding the explicit relationship between population protection and yield on the one hand, and reserve size and critical harvest effort on the other.[11]

ENDNOTES

1. Despite the critical discussion of maximum sustainable yield analysis, originating from Larkin [1977], this paper is aligned with numerous others when continuing doing this type of analysis.

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.

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.

4. In Lauck et al. [1998, 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." (Mangel [2000, p. 16]).

5. The graph of an equation $aS_1^2 + bS_1S_2 + cS_2^2 + dS_1 + eS_2 + f = 0$ is a hyperbola or two intersecting lines in the cases of equations (4) and (5), since $4ac < b^2$ in this case, see Berck and Sydsaeter [1991].

6. In this case the isoclines would be similar to what is demonstrated for Model B in Figure 5, with both sub-populations being positive.

7. Recall that the connection between normalized effort and harvest effort is given by $E = q\hat{E}/r$. Since r is constant, by assumption, the results demonstrated in equation (27), illustrated in Figure 6, may easily be re-scaled from E to $\hat{E}$.

8. This follows from equation (6) in the case of $m = 0$ and $S_2 = S$ in the case of equilibrium harvesting, $\dot{S} = 0$.

9. For more complicated or irregular-shaped population distribution areas simulation models may be used to find optimal reserve size, see, e.g., Buechner [1987], Pelletier [2002].

10. Also for monitoring, control and enforcement reasons a short border may be preferable to a long one due to management costs and law enforcement reasons. In addition, the high population density in a reserve may attract poachers, making reserve geometry of importance. However, these issues require further research (Sumaila and Charles [2002], Hilborn et al. [2004]).

11. The authors have studied additional management and bioeconomic issues related to this modeling approach, to be published elsewhere.

REFERENCES

C.A. Acosta [2002], *Spatially Explicit Dispersal Dynamics and Equilibrium Population Sizes in Marine Harvest Refuges*, ICES J. Marine Sci. **59**, 458–468.

P. Apostolaki, E.J. Milner-Gulland, M.K. McAllister and G.P. Kirkwood [2002], *Modelling the Effects of Establishing a Marine Reserve for Mobile Fish Species*, Can. J. Fish. Aq. Sci. **59**, 405–415.

P. Berck and K. Sydsaeter [1991], *Economist's Mathematical Manual*, Springer, Berlin.

R.J.H. Beverton and S.J. Holt [1957], *On the Dynamics of Exploited Fish Populations*, Chapman & Hall, London (Facsimile reprint, 1993).

M. Buechner [1987], *Conservation in Insular Parks*: *Simulation Models of Factors Affecting the Movement of Animals across Park Boundaries*, Biol. Conserv. **41**, 57–76.

G. Ceballos and P.R. Ehrlich [2002], *Mammal Population Losses and the Extinction Crisis*, Science **296**, 904–907.

C.W. Clark [1985], *Bioeconomic Modelling and Fisheries Management*, John Wiley, New York.

Clark [1990], *Mathematical Bioeconomics–The Optimal Management of Renewable Resources*, 2nd ed., John Wiley, New York.

E.E. DeMartini [1993], *Modelling the Potential of Fishery Reserves for Managing Pacific Coral Reef Fishes*, Fish. Bull. **91**, 414–427.

J.M. Diamond and R.M. May [1981], *Island Biogeography and the Design of Natural Reserves*, in *Theoretical Ecology–Principles and Applications* (R.M. May, ed.), 2nd ed., Blackwell, Oxford.

FAO [2002], *The State of World Fisheries and Aquaculture* 2002, The United Nation's Food and Agricultural Organization, Rome.

L.R. Gerber, L.W. Botsford, A. Hastings, H.P. Possingham, S.D. Gaines, S.R. Palumb and S. Andelman [2003], *Population Models for Marine Reserve Design*: *A Retrospective and Prospective Synthesis*, Ecol. Appl. **13**, Supplement, S47–S64.

S. Guénette, T. Lauck and C.W. Clark [1998], *Marine Reserves*: *From Beverton and Holt to the Present*, Reviews in Fish Biol. Fish. **8**, 251–272.

B.S. Halpern [2003], *The Impact of Marine Reserves*: *Do Reserves Work and Does Reserve Size Matter?* Ecol. Appl. **13**, Supplement, S117–S137.

R. Hannesson [1998], *Marine Reserves*: *What Would They Accomplish?* Mar. Res. Econ. **13**, 159–170.

R. Hilborn, K. Stoke, J.-J. Maguire, T. Smith, L.W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, K.L. Cochrane, S. Garcia, S.J. Hall, G.P. Kirkwood, K. Sainsbury, G. Stefansson and C. Walters [2004], *When Can Marine Reserves Improve Fisheries Management?* Ocean Coastal Manage. **47**, 197–205.

P.A. Larkin [1977], *An Epitaph for the Concept of Maximum Sustainable Yield*, Trans. Amer. Fish. Soc. **106**, 1–11.

T. Lauck, C.W. Clark, M. Mangel and G.R. Munro [1998], *Implementing the Precautionary Principle in Fisheries Management through Marine Reserves*, Ecol. Appl. **8** Supplement, S72–S78.

M. Mangel [2000], *On the Fraction of Habitat Allocated to Marine Reserves*, Ecol. Lett. **3**, 15–22.

G.K. Meffe and R.C. Caroll [1994], *Principles of Conservation Biology*, Sinauer, Sunderland, Massachusetts.

M.G. Neubert [2003], *Marine Reserves and Optimal Harvesting*, Ecol. Lett. **6**, 843–849.

M. Norton-Griffiths [2000], *Wildlife Losses in Kenya: An Analysis of Conservation Policy*, Natur. Resource Modeling **13**, 13–34.

T.E.E. Oldfield, R.J. Smith, S.R. Harrop and N. Leader-Williams [2004], *A Gap Analysis of Terrestrial Protected Areas in England and Its Implications for Conservation Policy*, Bio. Conserv. **120**, 303–309.

M.J. Paddack and J.A. Estes [2000], *Kelp Forest Fish Populations in Marine Reserves and in Adjacent Exploited Areas of Central California*, Ecol. Appl. **10**, 855–870.

D. Pauly, V. Christensen, J. Dalsgaard, R. Froese and F. Torres Jr. [1998], *Fishing Down Marine Food Webs*, Science **279**, 860–863.

J.D. Pelletier [2002], *Model Assessments of the Optimal Design of Nature Reserves for Maximizing Species Longevity*, J. Theoret. Biol. **202**, 25–32.

S.T.A. Pickett and J.N. Thompson [1978], *Patch Dynamics and Design of Nature Reserves*, Biol. Conserv. **13**, 27–37.

T. Polacheck [1990], *Year Around Closed Areas as a Management Tool*, Natur. Resource Modeling **4**, 327–354.

J.R. Prendergast, R.M. Quinn and J.H. Lawton [1999], *The Gaps between Theory and Practice in Selecting Nature Reserves*, Conserv. Biol. **13**, 484–492.

L.D. Rodwell, E.B. Barbier, C.M. Roberts and T.R. McClanahan [2003], *The Importance of Habitat Quality for Marine Reserve–Fishery Linkages*, Can. J. Fish. Aq. Sci. **60**, 171–181.

J. Roman and S.R. Palumbi [2003], *Whales before Whaling in the North Atlantic*, Science **301**, 508–510.

J.N. Sanchirico and J.E. Wilen [2002], *The Impacts of Marine Reserves on Limited-Entry Fisheries*, Natur. Resource Modeling **15**, 291–309.

A. Skonhoft, N.G. Yoccoz, N.C. Stenseth, J.M. Gaillard and A. Loison [2002], *Management of Chamois* (Rupicapra Rupicapra) *Moving between a Protected Core Area and a Hunting Area*, Ecol. Appl. **12**, 1199–1211.

J. Sladek Nowlis and C.M. Roberts [1999], *Predicted Fisheries Benefits and Optimal Marine Fishery Reserves Design*, Fish. Bull. **97**, 604–616.

U.R. Sumaila and A.T. Charles [2002], *Economic Models of Marine Protected Areas: An Introduction*, Natur. Resource Modeling **15**, 261–272.