

ISSN 1503-299X


WORKING PAPER SERIES

No. 3/2005

MARINE RESERVES. A BIO-ECONOMIC MODEL WITH ASYMMETRIC DENSITY DEPENDENT MIGRATION

Claire W. Armstrong
Anders Skonhoft

Department of Economics

 Norwegian University of Science and Technology

N-7491 Trondheim, Norway

www.svt.ntnu.no/iso/wp/wp.htm

Marine reserves.

A bio-economic model with

asymmetric density dependent migration

by

Claire W. ARMSTRONG
Associate Professor
Department of Economics and Management
Norwegian College of Fishery Science
University of Tromsø
N-9037 Tromsø
Norway
clairea@nfh.uit.no

and

Anders Skonhoft
Professor
Department of Economics
Norwegian University of Science and Technology
N-7491 Dragvoll-Trondheim
Norway
Anders.Skonhoft@SVT.NTNU.NO

Claire Armstrong gratefully acknowledges support from the Norwegian Research Council, and excellent working conditions at the Coastal Marine Resources Centre at University College Cork, Ireland.

Abstract

A static bioeconomic model of a marine reserve allowing asymmetric density dependent migration between the reserve and the fishable area is introduced. This opens for habitat or ecosystem differences allowing different fish densities within and outside a reserve, not described in earlier studies. Four management scenarios are studied; a) maximum harvest, b) maximum current profit, c) open access and d) maximum sustainable yield (MSY) in the reserve. These are all analysed within the Induced Sustainable Yield Function (ISYF), giving the relationship between the fish abundance inside the reserve and the harvesting taking place outside. A numerical analysis shows that management focused on ensuring MSY within the reserve under the assumption of symmetric migration may be negative from an economic point of view, when the area outside the reserve is detrimental compared to the reserve. Furthermore, choice of management option may also have negative consequences for long run resource use if it is incorrectly assumed that density dependent migration is symmetric. The analysis also shows that the optimal area to close, either a more or a less attractive ecosystem for the resource in question, may differ depending on the management goal.

Key Words: bioeconomics, marine reserves, migration, management

Introduction

In most biological studies the main goal of the implementation of marine reserves is stock or ecosystem conservation. The political motivation behind the introduction of marine reserves has also mainly had this focus. Recently, however, economic studies of marine reserves have shifted focus towards taking into account the economics of the fisheries as well (Holland and Brazee, 1996; Hannesson, 1998; Sanchirico and Wilen, 1999, 2001, 2002 and Smith and Wilen, 2004). Hence the possibility of using marine reserves as a fisheries management tool has emerged. In the aftermath of the failures first of input controls, and then also to some degree of output controls in fisheries, the attention has now reverted back to a more complete form of input control, in the shape of closed areas. This article studies a general bioeconomic model allowing asymmetric density dependent dispersal of resources between a marine reserve of a given size, and its adjacent area, presenting how a set of different management goals and standard equilibrium results are affected by this new management tool.

The ecological conditions within a reserve can be expected to differ from conditions outside a reserve, depending on exploitation and habitat effects. This may be the case both regarding the relationship between species and within single species. Inside a reserve no species are subjected to harvesting pressure, and their relative densities may be very different to that found outside the reserve. For instance, in lieu of intense fishing upon a predator species outside a reserve, the density of prey may be higher outside the reserve than inside, due to greater predatory pressures within the reserve. On the other hand, intense fishing upon a prey species may lead to lower concentration of the predator outside the reserve due the competition with the harvesters. One would here expect there to be lower concentrations of

prey outside the reserve, due to this competition. Furthermore, some exploitation may cause habitat degradation outside the reserve, leading to greater concentrations of species within the reserve. However, increased numbers or predation within the reserve may for instance reduce space or success for breeding and the like, that is decrease the attractiveness of the habitat within the reserve, thereby increasing the density outside the reserve. Hence depending on these density effects, we may expect migration between the reserve and the outside area to be affected in such a way that density dependent migration may be asymmetric. That is, there may be migration in or out of the reserve despite the densities being the same in both areas and the equilibrium densities may differ in the two areas.

In this article we model a marine reserve with asymmetric dispersal between the reserve and the outside area. This type of dispersal process has been discussed in biological research (see below), but was first modeled in a bio-economic context by Skonhøft and Armstrong (2005), in a purely terrestrial context¹. In the bio-economic literature a simpler version of this type of dispersion function is used by amongst others, Conrad (1999) and Sanchirico and Wilen (2001), who both assume symmetric dispersion². Though many models presented in the literature allow for differing habitat conditions (see Schnier, 2005, for a broad analysis of this), it is assumed that the densities of fish in these different habitats are equal, via the assumption of symmetric density dependence. The contribution of this paper is therefore to allow for differing fish densities, an occurrence which has been observed in nature in many instances (see Attwood *et al.*, 1997, for an overview), but not formally allowed for in the literature. This article expands the model in Skonhøft and Armstrong (2005) to a marine analysis, and studies how the dispersal asymmetry affects the management of the outside area. Another contribution of

the paper is the introduction of the Induced Sustainable Yield Function (*ISYF*), giving the relationship between fish abundance in the reserve and harvesting taking place outside, offering a novel way of comparing interests with regard to preservation within the reserve and harvest opportunities outside the reserve.

We formulate a set of different management options; a) maximum harvesting, or MSY in the non-reserve area, b) maximum profit, or MEY in the non-reserve area, c) open access in the non-reserve area, and d) MSY within the reserve, or equivalently maximum dispersal out of the reserve. The first management option is the most usual biological management goal, commonly found in fisheries management around the world. The two next options describe optimal management and open access, or zero management outside the reserve in the latter case. Armstrong and Reithe (2001) discuss the issue of management cost reduction with the introduction of marine reserves combined with open access, alluding to the attractiveness of this management option in some fisheries. Managing the fishery outside the reserve is however in most cases a superior vehicle for rent maximisation, hence speaking for management option b). Nonetheless, most bioeconomic models of marine reserves do not study optimal management in the sense of maximizing economic rent outside the reserve area (for an exception see Reithe, 2002)³. The final management option focuses on physical output maximisation within the reserve. The actual implementation of marine reserves has so far had a clear motivation directed towards conservation, the focus often being specific habitats, but also species. In this context, and due to the increasing worry over serious stock depletion the last century (Botsford *et al.*, 1997; Myers and Worm, 2003; and Jackson, *et. al.*, 2003), the issue of maximising biomass output holds many attractions.

The analysis of the four management options is done analytically when possible, with numerical comparisons where necessary. Focus is upon how this general density dependent dispersal model affects results described for more specific models given in the literature, and opens for new insight in possibilities and limitations in the implementation of marine reserves. The evaluation of the various regimes concentrates on efficiency; that is, economic rent in the fishing area, and the degree of conservation measured as fish density in the reserve. The analysis is static, leaving issues of transitional dynamics, and discounting the future, as discussed by Holland and Brazee (1996), for future analysis.

The article is organised as follows. In the next section the ecological model is presented. Here we also introduce the Induced Sustainable Yield Function (*ISYF*), In section three we study the different management goals presented above. A numerical analysis is done for the North East Atlantic cod stock in section four, followed by a discussion of the results in section five.

The ecological model

We consider a marine reserve and an outside area of fixed sizes⁴, and a fish population that disperses between the two areas. The areas are governed by some state authority, and fishing is allowed only outside the marine reserve. It is assumed that this property rights structure is perfectly enforced meaning that *de jure* and *de facto* property rights coincide. In the outside area harvesting takes place by commercial agents, and, as already indicated, there may be different management goals. We let one fish stock represent the populations of economic

interest, though one could also imagine this one stock being an aggregation of many commercial species present⁵.

The population growth of the stock in the two areas is described as follows:

$$\begin{aligned} dX_1/dt &= F(X_1) - M(X_1, X_2) & (1) \\ &= r_1 X_1 (1 - X_1/K_1) - m(\beta X_1/K_1 - X_2/K_2) \end{aligned}$$

and

$$\begin{aligned} dX_2/dt &= G(X_2) + M(X_1, X_2) - h & (2) \\ &= r_2 X_2 (1 - X_2/K_2) + m(\beta X_1/K_1 - X_2/K_2) - h \end{aligned}$$

where X_1 is the population size in the reserve at a given point of time (the time index is omitted) and X_2 is the population size in the fishable area at the same time. $F(X_1)$ and $G(X_2)$ are the accompanying logistic natural growth functions, with r_i ($i = 1, 2$) defining the maximum specific growth rates and K_i the carrying capacities, inside and outside the reserve, respectively. h is the harvesting, taking place only outside the reserve.

In addition to natural growth and harvesting, the two sub-populations are interconnected by dispersion as given by the term $M(X_1, X_2)$ assumed to depend on the *relative* stock densities in the two areas. $m > 0$ is a parameter reflecting the general degree of dispersion; that is, the size of the areas, the actual fish species, and so forth. Hence, a high dispersion parameter m corresponds to a fish stock with large spatial movement. The parameter $\beta > 0$ takes care of the fact that the dispersion may be due to, say, different predator-prey relations and

competition within the two sub-populations as the reserve causes change in the inter and intra species composition (see DeLong and Lamberson, 1999, for modeling of such species relationships)⁶. For equal $X_i / K_i, i = 1, 2$, and when there is no harvesting, $\beta > 1$ results in an outflow from the reserve and could be expected in a situation with greater predatory pressure here, for instance due to there being no harvesting in the reserve. Hence, when mobile prey species choose specific habitats for enhanced feeding possibilities, hiding places and/or nursery areas (Fosså *et al.*, 2002 and Mortensen, 2000, describe this for deep water coral habitats), there can be an outflow surpassing that of when the relative densities do not involve β . On the other hand, when $0 < \beta < 1$, the circumstances outside the reserve are detrimental, creating less potential migration out of the reserve. Hence, as opposed to the simpler sink-source models found in the literature (cf. the sink-source concept of the metapopulation theory, see, e.g., Pulliam (1988), but also see the density dependent dispersion growth models analysed in the biological literature by Hastings (1982), Holt (1985) and Tuck and Possingham (1994)), this model incorporates possible intra-stock or inter-species relations that may result in different concentrations in the two areas; that is, the dispersal may be *asymmetric*. As indicated above, Conrad (1999) and Sanchirico and Wilen (2001) assume symmetric dispersion in their analysis. Hence, $\beta = 1$ in their models.

The above system is studied only in ecological equilibrium, and hence, $dX_1 / dt = 0$ and $dX_2 / dt = 0$ are assumed to hold all the time⁷. The X_1 -isocline of equation (1) may be expressed as:

$$X_2 = K_2 X_1 (\beta / K_1 - (r_1 / m)(1 - X_1 / K_1)) = R(X_1), \quad (3)$$

and generally has two roots; $X_1 = 0$, and $X_1 = K_1 - m\beta / r_1$ which may be either positive or negative. When negative, typically reflecting a situation with large spatial movement, $R(X_1)$ will first slope downwards and intersect with the X_1 -axis for this negative value, reach a minimum and then run through the origin and slope upwards for all positive X_1 . When $K_1 - m\beta / r_1 > 0$, $R(X_1)$ will slope downwards for all negative X_1 -values and reach a minimum in the interval $[0, K_1 - m\beta / r_1]$. It then slopes upwards. The isocline is therefore not defined for X_1 -values within this interval in the situation of modest spatial movement. Accordingly, whenever defined, $R(X_1)$ will slope upwards, $R'(X_1) > 0$.

Adding together equations (1) and (2) when $dX_i / dt = 0$ ($i = 1, 2$), and combined with (3) yields:

$$h = F(X_1) + G(X_2) = F(X_1) + G(R(X_1)) = h(X_1). \quad (4)$$

In what follows this will be referred to as the *Induced Sustainable Yield Function (ISYF)*, and gives the relationship between the fish abundance in the reserve and the harvesting taking place outside. This function represents therefore the harvesting ‘spill-over’ from the fishing zone to the reserve. $h(X_1) \geq 0$ is defined for all $X_1 > 0$ that ensures a positive X_2 through equation (3).

ISYF will be the basic building block in the subsequent analysis. In the Appendix it is demonstrated that it will be upward sloping for small positive values of X_1 , reach a peak value and then slope downwards. If $K_1 - m\beta / r_1 < 0$, so that $X_2 = R(X_1)$ is defined for all $X_1 \geq 0$, we have $h(0) = 0$ as $X_2 = X_2(0) = 0$ and accordingly $F(0) + G(0) = 0$. Thus, the *ISYF* intersects the origin. When $X_1 = K_1$, we have $X_2 = K_2\beta$ from the X_1 -isocline (3), and hence $h(K_1) = 0 + G(K_2\beta)$. The harvesting is then nil when $\beta = 1$, $h(K_1) = 0$. In models with symmetric dispersal, the *ISYF* therefore intersects K_1 . Moreover, $h(K_1) > 0$ if $\beta < 1$. When $\beta > 1$, $h(K_1) < 0$, and the *ISYF* is therefore not defined. On the other hand, if $K_1 - m\beta / r_1 > 0$ and the spatial movement is modest, $h(X_1)$ is not defined over the interval $[0, K_1 - m\beta / r_1]$, and $h(K_1 - m\beta / r_1) = 0$. However, also in this situation $h(K_1) = G(K_2\beta)$.

Fig. 1 about here

Fig. 1a depicts the *ISYF* for $0 < \beta < 1$ (and $K_1 - m\beta / r_1 < 0$), which, as mentioned, is the situation when the circumstances outside the reserve are detrimental, hence creating less potential dispersal out of the reserve. In addition, the natural growth in the reserve is plotted. As equation (1) yields $F(X_1) = M(X_1, X_2)$ in ecological equilibrium, the figure gives information about the size and direction of the dispersal between the two areas as well. Moreover, the natural growth in the outer area $G(R(X_1))$ is seen in the figure as the difference between these two curves. The reserve may be either a source or a sink for the same amount of harvesting. However, when the harvest pressure is sufficiently high, the reserve becomes a source and fish flows out of the reserve. On the other hand, when the reserve stock is high,

the harvest is more modest and the reserve serves as a sink. This is seen in Fig. 1a where the natural growth in the reserve $F(X_1)$, and hence the migration M , is negative. With no harvesting, as already noted, fish flows to the reserve when $0 < \beta < 1$. Hence, if the outside area is detrimental as compared to the reserve, the reserve becomes a sink when there is no fishing or quite heavy fishing, depending on the relative sub-stock sizes.

Fig. 1b depicts the *ISYF* when $\beta > 1$, i.e. the conditions within the reserve are detrimental. We observe that as long as the *ISYF* is defined, migration out of the reserve is positive, and the reserve is a source. Similarly for the symmetric case of $\beta = 1$, as portrayed in Fig. 1c.

The various harvesting scenarios

Based on the *ISYF*, various harvesting scenarios are analysed. Altogether we will study four regimes, with the evaluation of the regimes basically following two axes; the rent or profitability of the fishery, and ‘sustainability’ as measured by the fish abundance in the reserve. In all cases, the influence of the dispersal parameter β will be of main concern. As mentioned, the four scenarios or regimes, to be studied are: a) Maximum harvest, or h^{msy} , b) Max current profit, or h^{mey} , c) Open access, or h^∞ , and finally, d) Maximum sustainable yield in the reserve, or maximum dispersal out of the reserve h^{mm} .

a) Maximum harvest h^{msy}

In this regime we are simply concerned with finding the maximum value of the *ISYF*. When $dh(X_1)/dX_1 = 0$, equation (4) yields $F'(X_1) = -G'(R(X_1))R'(X_1)$. As this equation is a third degree polynomial for the specified functional forms, it is generally not possible to find an

analytical solution for X_1 , and hence h^{msy} . However, it is seen that this solution may either be characterised by $F' > 0$ together with $G' < 0$, the opposite, or simply $F' = G' = 0$. In Fig. 2, which gives management options for $0 < \beta < 1$, h^{msy} is described when $F' < 0$ and $G' > 0$.

When taking the total differential of the above condition characterising h^{msy} , it is not possible to say anything definite about what happens when β shifts up. However, there is good reason to suspect that a higher β will give a higher h^{msy} as more fish then, *ceteris paribus*, flows out of the reserve and adds to the fishable population. This is confirmed by the numerical examples in the next section.

Fig. 2 about here

b) Maximum current profit h^{mey}

To assess profitability, effort use has to be included. When introducing the Schaefer function $h = qEX_2$ with E being effort use and q being the catchability coefficient, the current profit reads $\pi = (p - c/qX_2)h$. p and c are the unit landing price and effort cost, respectively, both assumed to be fixed. The profit maximising problem is accordingly to maximise $\pi = (p - c/qR(X_1))h$, subject to $h = h(X_1)$.

For various reasons (see also below) the most illuminating way to solve this problem is to work with isoprofit curves. When taking the total differential of the profit and keeping

π fixed, $\pi = \bar{\pi}$ (cf. Fig. 2), the slope reads $dh/dX_1 = -\frac{hc/qR(X_1)^2}{(p-c/qR(X_1))}R'(X) < 0$. It can be

shown that the isoprofit curves are quasiconcave, and the profit level increases outwards in the $X_1 - h$ plane. The tangency point between an isoprofit curve and $h(X_1)$ therefore gives the solution to this problem and h^{mey} . Compared to the previous case a) problem of finding h^{msy} , it follows directly that the stock abundance in the reserve will be larger under the present management goal of profit maximisation. See also Fig. 2. This fits with the intuition and is not very surprising as there are no forces (e.g., discounting) that counteract the working of stock dependent harvesting costs.

As the β parameter influences the isoprofit curves as well as the $ISYF$, it is difficult to say anything analytically about how, say, a situation with $\beta > 1$ compared to the standard models with $\beta = 1$ influences profitability, the amount of harvest and the stock abundance in the reserve. We will return to this in the numerical analysis in the next section. However, because the $ISYF$ is affected only by the ecology, and not the economy, it is clear that a higher price-cost ratio gives a less negative slope of the isoprofit curves, and hence a lower stock in the reserve. Accordingly, the result is a higher harvest h^{mey} . The economic reason is that more effort is introduced in the outer area accompanied by a smaller stock here, and this unambiguously affects the reserve. The dispersal M therefore always increases under such circumstances either through increased outflow, or through reduced inflow into the reserve (the latter which happens only when $0 \leq \beta \leq 1$).

c) *Open access* h^∞ .

When applying the standard open access assumption that the profit π equals zero, the stock in the fishable area reads $X_2 = c / pq$. When inserting into equation (1) in equilibrium, we find

an explicit expression for the stock size within the reserve as

$$X_1 = \frac{K_1}{2} \left[1 - \frac{m\beta}{r_1 K_1} + \sqrt{\left(1 - \frac{m\beta}{r_1 K_1}\right)^2 + \frac{4mc}{r_1 K_1 K_2 pq}} \right].$$

This solution may also be seen in light of the

ISYF as the isoprofit curves asymptotically approach the open access stock size

$R(X_1) = c/pq$ when the profit approaches zero, cf. the above expression for the slope of the isoprofit curve (see also Fig. 2). Depending on the size of β as well as the other ecological and economic parameters, the open access stock size in the reserve may be either below or above that of the h^{msy} level. If, say, the price-cost ratio is high, and hence the effort level is high, we may typically find that the reserve stock will be lower than h^{msy} . A high price-cost ratio, as depicted in Fig. 2, therefore also works in the direction of a low stock abundance in the reserve, and the mechanism is just as in the previous case (cf. also Sanchirico and Wilen, 2001).

While the open access stock size outside the reserve is unaffected by the degree of asymmetry in the dispersion as well as the other biological parameters due to the Schäfer harvesting function assumption, we observe that a higher β means a smaller open access stock in the reserve. Hence, $\beta > 1$, implying detrimental conditions within the reserve, reduces the stock size compared to the standard models with $\beta = 1$. The reason for this is that a higher β , for a fixed density in the outer area, means more dispersal. In a next step, this translates into a higher natural growth through the equilibrium condition

$F(X_1) = M(X_1, X_2)$, and hence, a smaller stock abundance. The effect on the size of the

harvest is, however, unclear as the X_1 stock associated with h^∞ may be either located to the right or the left hand side of the stock associated with h^{msy} .

The dispersal between the areas under open access may also be calculated, and after some

tedious rearrangements we find $M = m \left\{ \frac{\beta}{2} \left[\left(1 - \frac{m\beta}{r_1 K_1}\right) + \sqrt{\left(1 - \frac{m\beta}{r_1 K_1}\right)^2 + \frac{4mc}{r_1 K_1 K_2 pq}} \right] - \frac{c}{K_2 pq} \right\}$,

which may be either positive or negative. The stylized fact situation of heavy harvesting pressure outside the reserve due to the nature of open access makes the reserve a source, $M > 0$, and this is the situation depicted in Fig. 2. On the other hand, favorable conditions in the reserve so that $\beta < 1$, combined with a low price-cost ratio and a low harvesting pressure, may give an inflow to the reserve even under open access.

d) Maximum sustainable yield in the reserve, or maximum dispersal out h^{mm} .

Maximum dispersal out of the reserve coincides with the maximum natural growth level within the reserve, $K_1/2$, as equation (1) yields $F(X_1) = M$ in equilibrium. Hence, we

have $M = r_1 K_1 / 4$ as the maximum dispersal which is independent of the size of β as well as the economy, and the ecological parameters in the outer area. The corresponding stock level here becomes $X_2 = (K_2/2)(\beta - r_1 K_1 / 2m)$ when inserting into $F(X_1) = M$. A higher β translates therefore unambiguously into a higher fishable stock size under the management option of maximum dispersal, and the effect is quite substantial as we have

$\partial X_2 / \partial \beta = K_2 / 2$ (cf. also the numerical examples below).

It is also possible to find an analytical expression for the harvest by inserting for X_2 and M into equation (2) in equilibrium and solving for h . The result is

$$h^{mm} = \frac{r_2 K_2}{4} \left(\beta - \frac{r_1 K_1}{2m} \right) \left(2 - \beta + \frac{r_1 K_1}{2m} \right) + \frac{r_1 K_1}{4}$$

which is independent of economic factors as well.

This harvest may either be smaller or larger than that of the open access, or maximum economic yield. In Fig. 2, h^{mm} is depicted as being above the open access harvest level. However, when being lower than h^∞ , lower profitability than that of the open access; i.e., negative profit, is possible (cf. the isoprofit curve in figure 2).

Numerical illustrations

The above regimes will now be illustrated numerically with data that fits the North East Atlantic cod fishery in a stylised way. The baseline parameter values are given in Table 1. The economic and technological data applied are for an average trawl vessel in the Norwegian fishing fleet, as trawlers harvest 60-70% of the total allowable catch (see Armstrong, 1999). The biological data are approximations of intrinsic growth rates and stock size described in Eide (1997) for the North East Atlantic cod stock. The total carrying capacity $K_1 + K_2$ is divided in two parts, one held as a reserve, the other as the remaining fishable area. In the baseline simulations they are equal. Simulations allowing different K -values were run, without this adding any further insight⁸. The dispersion parameter m is set equal to 1300, illustrating the fact that the cod stock is highly migratory. Little is known about cod and density dependent migration, but it is clear that there are several important density dependent effects in the life-cycle of the cod; spawning, recruitment to the fishable stock, and cannibalism (Bogstad *et.al.*1994, and Eide, 1997). Hence, density dependent

dispersal between the fishable area and the reserve could be seen as an approximation of these effects, making closures relate to geographic areas in the migratory life-cycle of the cod stock. This fits in well with proposals made by some interest groups desiring closures of areas where young cod congregate, and yet others requiring closures of spawning areas.

Table 1 about here

As demonstrated above, the ecological parameter β is crucial for what happens. This parameter will therefore be varied throughout the simulations and we use three different values for β , with $\beta = 1.5$ and $\beta = 0.5$ representing either the reserve or the fishable area as detrimental, respectively. To compare with the standard model with symmetric dispersal, we also illustrate when $\beta = 1$. These results are found in Table 2.

Table 2 about here

In the following we analyse the numerical results from two main perspectives. We first compare the results as regards stock size, harvest, profit etc. of the different management options a)-d) for the two β values. This focus is therefore *inter-managerial*, comparing the various management regimes to one another. The second perspective is how sensitive the different management regimes are to the value of β . This analysis shows how choice of management regime can be affected by the uncertainty of the ecological conditions inside and outside the reserve and is hence *intra-managerial*.

Inter-managerial comparison

One striking observation when studying Table 2 is the fact that the maximum dispersal case d) gives negative profit due to the small stock size in the reserve and overall when $\beta = 0.5$. In actuality the situation of high effort level and negative profits will only emerge in the short term, by allowing some form of subsidy or alternative valuation of fishing activity, as no rational agent will otherwise continue harvesting past the 0 profit point. However, given this possibility, even the open access scenario c) yields higher stock sizes than h^{mm} in the reserve when the outside area is detrimental (but $\beta = 1.5$ showed the opposite case). This clearly has management implications, and contrasts purely biological management to management where economic issues are included. For $\beta = 1.5$ the stock size X_2 increases dramatically in the d) scenario compared to the other management schemes as anticipated from the theoretical analysis, and is just equal the maximum harvest case a). However, this equality is a construct of the parameter values, and under such circumstances we thus also have the highest natural growth in the fishable area $G'(R(X_1)) = 0$, as h^{msy} is characterised by

$F'(X_1) = -G'(R(X_1))R'(X_1)$ (cf. section three). The switch in the β value changes the scenario that gives minimum harvest from the open access case c) when $\beta = 1.5$ to the maximum dispersal out of the reserve case d) for $\beta = 0.5$. This may also clearly be relevant for management decisions.

A switch is also found for lowest migration, existing under the open access case c) when $\beta = 1.5$, and the maximum economic yield case b) for $\beta = 0.5$. The Maximum current profit scenario gives the highest stock sizes, both inside and outside the reserve, compared to all the other scenarios. As already mentioned, this is quite reasonable since this is a static

analysis with no discounting involved so that the h^{mey} solution always take place to the right hand side of the peak value of the *ISYF*. Profits are considerably reduced when $\beta = 0.5$ as compared to when $\beta = 1.5$, and this is particularly so for the maximum dispersal case d). It is also seen that profits show greater variation between the various scenarios when β is low. As would be expected, the profit maximising scenario b) demands the lowest effort, and open access c) results in the highest effort level.

We observe that for neither $\beta = 1.5$ nor $\beta = 0.5$ presented in Table 2 is the picture regarding stock size differences among the various scenarios the same as those we find on the Fig. 2 *ISYF*. However, this does happen when we have the standard model of symmetric dispersal of $\beta = 1$ in Table 2.

When comparing $\beta = 1$ with $\beta = 1.5$ and $\beta = 0.5$ in Table 2 we observe that the assumption of symmetry poses the greatest danger of overexploitation when the environment outside the reserve actually is detrimental, i.e., $\beta < 1$. Harvest levels would then be set too high for all the management options. This will especially be so for management option d) of ensuring maximum sustainable yield in the reserve. If alternatively the actual situation is such that the environment inside the reserve is detrimental and $\beta > 1$, quotas would be set too low under the assumption of symmetry. Only the open access harvesting c) would be lower than anticipated.

Intra-managerial comparison

Looking at the effects of the increase in β upon the different management scenarios in Table 2, we observe that X_1 is non-increasing for all cases. All scenarios obtain increased X_2 for increased β , except the open access scenario c) where the stock level is unchanged as it is determined by the economic parameters only. As already observed, the change is particularly substantial for case d). The dispersal M is increasing under scenario a) and b), while it first increases and then decreases under the open access case c). Growth in the fishable area G increases under schemes a) and d) while it first increases and then decreases under the maximum economic yield case b). Under the open access case c) there is of course no change as the fishable stock, and hence, the accompanying natural growth, are determined by economic factors only. Harvest and profit increase for all scenarios except case c) where harvest decreases, and profits of course all the time remain zero. Not unexpected from the theoretical analysis, there is no clear pattern for the effort use E as β increases.

As β functions as a relative concept between the area within and outside the reserve, the analysis may indicate that depending on the management preferences, the chosen area to close may differ⁹. If the manager wishes to maximise harvests as in case a), closing the detrimental area is the best option. This is also so under the maximum profit scenario of b). On the other hand, if the goal is to maximise employment in the shape of effort as in the open access scenario c), the best option is to close the ecologically more attractive area; that is, the area with the lowest β . It is also seen that closing the most detrimental area is by far the best option under the maximum dispersal goal d). Indeed, doing the opposite may have substantial negative economic consequences.

Concluding remarks

The ecological conditions within a marine reserve can be expected to differ from conditions outside a reserve due to exploitation and habitat effects. In the present paper this is analysed by assuming asymmetric density dependent dispersal between a reserve and an outside fishable area. It is demonstrated that this may give substantially different results compared to the standard models of symmetric dispersal. This is shown analytically by introducing the Induced Sustainable Yield Function (*ISYF*), and by running numerical examples. Altogether, four different management options are analysed.

The comparisons between symmetric and asymmetric dispersal show that if the environment is detrimental outside the reserve, a situation easily imagined, there are clear dangers of incorrectly assuming symmetry when managing a fishery, as over-harvesting would ensue. As many reserves are imposed in order to protect unique habitats or habitats of special importance to marine life, this issue seems of great relevance. Furthermore, a management scenario inside the reserve given by maximum sustainable yield, or maximum dispersal out of the reserve, has most serious consequences, in the shape of potentially negative profits and small total stock size, if it is mistakenly assumed that migration is symmetric when the actual situation outside the reserve is detrimental.

The analysis may also indicate that depending on what the management goal is, the preferable areas to close may differ. Hence in the management of the North East Atlantic cod fishery, which from the Norwegian side (also Russia and other countries fish upon this stock) has had to answer for a plethora of management goals such as securing viable communities,

environmental requirements as well as economic aims, it is not clear as to which of the examples studied here should apply. In recent years, however, the economic goals have increasingly been underlined (Johnsen, 2002), and hence a management goal of profit maximisation combined with the closing of more detrimental areas would be relevant. This would presumably also be easier to get acceptance for politically, as the ecologically attractive areas are also usually the areas that have the greatest fisheries concentration and importance, but nonetheless contrasting the desire shown by biologists to close productive or pristine areas.

The case of symmetric density dependence is overall quite improbable, as expecting different habitats or ecosystems to have equal densities seems a strong and idealized assumption. Hence when this idealized assumption implies serious consequences for management, as presented here, it should be applied with great care.

References

Armstrong, C.W., 1999. Sharing a resource - bioeconomic analysis of an applied allocation rule. *Environmental and Resource Economics.*, 13:75-94.

Armstrong, C.W. and Reithe, S., 2001. Marine Reserves – will they accomplish more with management costs? A comment. *Marine Resource Economics*, 16:165-175.

Bogstad, B., Lilly, G.R., Mehl, S., Pálsson Ó.K. and Stefánsson, G., 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua*) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). *ICES Mar. Sci. Symp.*, 198:576-599.

Attwood, C.G., Harris, J.M. and Williams, A.J., 1997. International experience of marine protected areas and their relevance to South Africa. *South African Journal of Marine Science*, 18:311-332.

Botsford, L.W., Castilla, J.C. and Peterson, C.H., 1997. The Management of Fisheries and Marine Ecosystems. *Science*, 277(5325):509-515.

Conrad, J., 1999. The bioeconomics of marine sanctuaries. *Journal of Bioeconomics*, 1:205-217.

Delong, A.K. and Lamberson, R.H., 1999 . A habitat based model for the distribution of forest interior nesting birds in a fragmented landscape. *Natural Resource Modeling*, 12:129-146.

Eide, A, 1997. Stock variations due to symbiotic behaviour - An attempt to understand the fluctuations in the cod fisheries in the Barents Sea. In: McDonald and McAleer (Editors) *MODSIM 97*, International Congress on Modelling and Simulation Proceedings, pp.1599-1604.

Fosså, J.H., Mortensen, P.B. and Furevik, D.M., 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fisheries impacts. *Hydrobiologia*, 471:1-12.

Hannesson, R., 1998. Marine reserves: what would they accomplish? *Marine Resource Economics*, 13:159-170.

Hastings, A., 1982. The dynamics of a single species in a spatially varying environment: The stabilising role of high dispersion rates. *Journal of Mathematical Biology*, 16:49-55.

Holland, D.S. and Brazee, R.J., 1996. Marine Reserves for Fisheries Management. *Marine Resource Economics*, 11:157-171.

Holt, R., 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology*, 28:181-208.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T. P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. and Warner, R.R., 2003. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science*, 293(5530): 629-638.

Johnsen, J.P., 2002. The fisherman that disappeared? A study of depopulation, overpopulation and processes of change in Norwegian fisheries (in Norwegian). Phd Thesis, Norwegian College of Fishery Science, University of Tromsø, Norway.

Mortensen, P.B., 2000. *Lophelia pertusa* (Scleractinia) in Norwegian waters. Distribution, growth, and associated fauna. Dr. scient. Thesis, University of Bergen, Norway.

Myers, R.A. and Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, 423(6937): 280-283.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. *The American Naturalist*, 132: 652-661.

Reithe, S., 2002. Quotas, marine reserves and fishing the line. When does reserve creation pay? Working paper Series 04/2003, Department of economics, University of Tromsø, Norway. http://www.nfh.uit.no/working_papers/ifo/reithe2003.pdf.

Sanchirico, J.N., 2004. Designing a cost-effective marine reserve network: A bioeconomic metapopulation analysis. *Marine Resource Economics*, 19(1):41-66.

Sanchirico, J.N. and Wilen, J.E. 1999. Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environment Economics and Management*, 37:129-150.

Sanchirico, J.N. and Wilen, J.E., 2001. A Bioeconomic Model of Marine Reserve Creation. *Journal of Environmental Economics and Management*, 42:257-276.

Sanchirico, J.N. and Wilen, J.E., 2002. The impacts of marine reserves on limited entry fisheries. *Natural Resource Modeling*, 15(3):291-310.

Schnier, K.E., 2005. Biological “hotspots” and their effects on optimal bioeconomic marine reserve formation. *Ecological Economics*, 52(4):453-468..

Skonhofs, A. and Armstrong, C.W., 2005. Conservation of wildlife. A bioeconomic model of a wildlife reserve under pressure of habitat destruction and harvesting outside the reserve. *Natural Resource Modeling*, 18:69-90s .

Smith, M.D. and Wilen, J.E., 2003. Economic impacts of marine reserves: the importance of spatial behaviour. *Journal of Environmental Economics and Management*, 46(2):183-206.

Sumaila, U.R., 1998. Protected marine reserves as fisheries management tools: a bioeconomic analysis. *Fisheries Research*, 37: 287-296.

Sumaila, U. R. and Armstrong, C.W., 2003. Distributional effects of Marine Protected Areas: A study of the North-East Atlantic cod fishery. Working paper series Department of Economics and Management. Norwegian College of Fishery Science, University of Tromsø, Norway, 02/2003.

http://www.nfh.uit.no/working_papers/ifo/sumaila_and_armstrong2003.pdf.

Tuck, G.N. and Possingham, H., 1994. Optimal harvesting strategies for a metapopulation. *Bulletin Math. Biology*, 56: 107-127.

Appendix

The ISYF curve

For the specific functional forms, $h(X_1)$ will generally be a fourth degree polynomial. The *ISYF* is defined when $h(X_1) \geq 0$ for all $X_1 > 0$ that ensures a positive $X_2 = R(X_1)$. We only look at the case where the X_1 -isocline is defined for all positive X_1 that is, $K_1 - m\beta / r_1 < 0$. We then have $h(0) = 0$ together with $h(K_1) = G(K_2\beta)$, and accordingly $h(K_1) = 0$ for $\beta = 0$ and $\beta=1$, and $h(K_1) > 0$ for $0 < \beta < 1$ while not being defined when $\beta > 1$ (see also the main text). Differentiation yields $dh/dX_1 = F' + G'R'$. Because $R' > 0$ for all positive X_1 , h increases for small values and decreases for large values of X_1 . We have extreme values when $F' + G'R' = 0$. This is a third degree polynomial, but we can suspect one peak value of $h(X_1)$ in the actual interval. Furthermore, we find $d^2h/dX_1^2 = F'' + G''R'R' + G'R''$. As we

have $R'' > 0$, $h(X_1)$ is strictly concave when $G' < 0$, i.e., for large values of X_1 . However, it may not hold for small values of X_1 as $G' > 0$ then is large and may dominate. Numerical simulations have confirmed that $h(X_1)$ will reach one peak value when $h(X_1) > 0$ and be strictly concave for large values of X_1 .

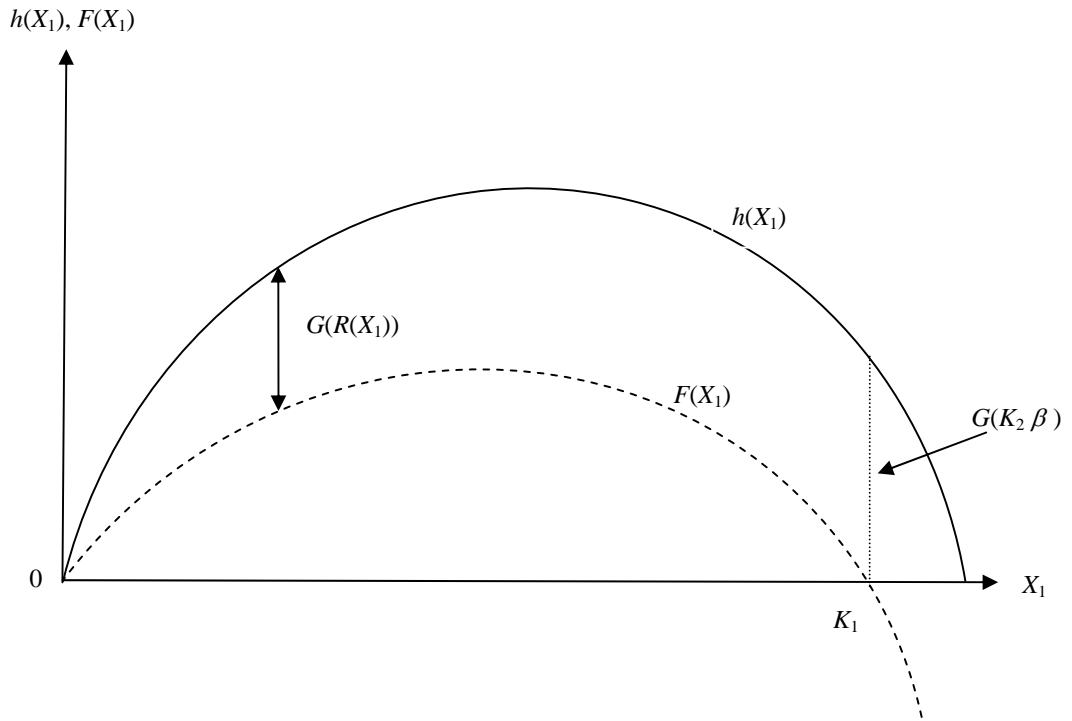


Fig. 1a.

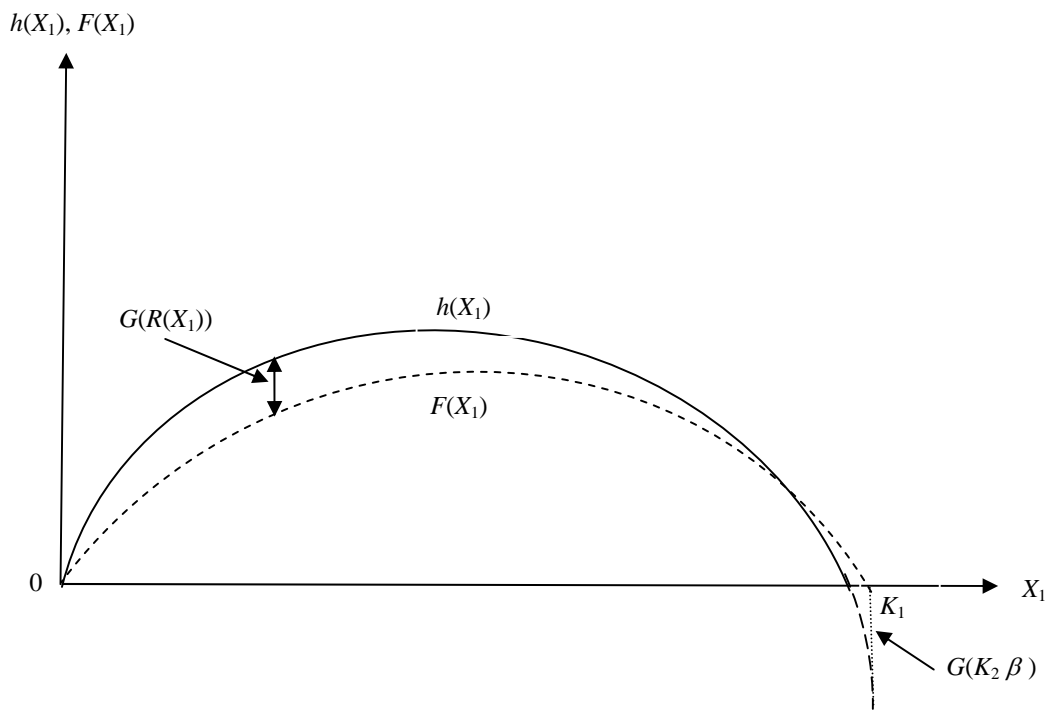


Fig. 1b.

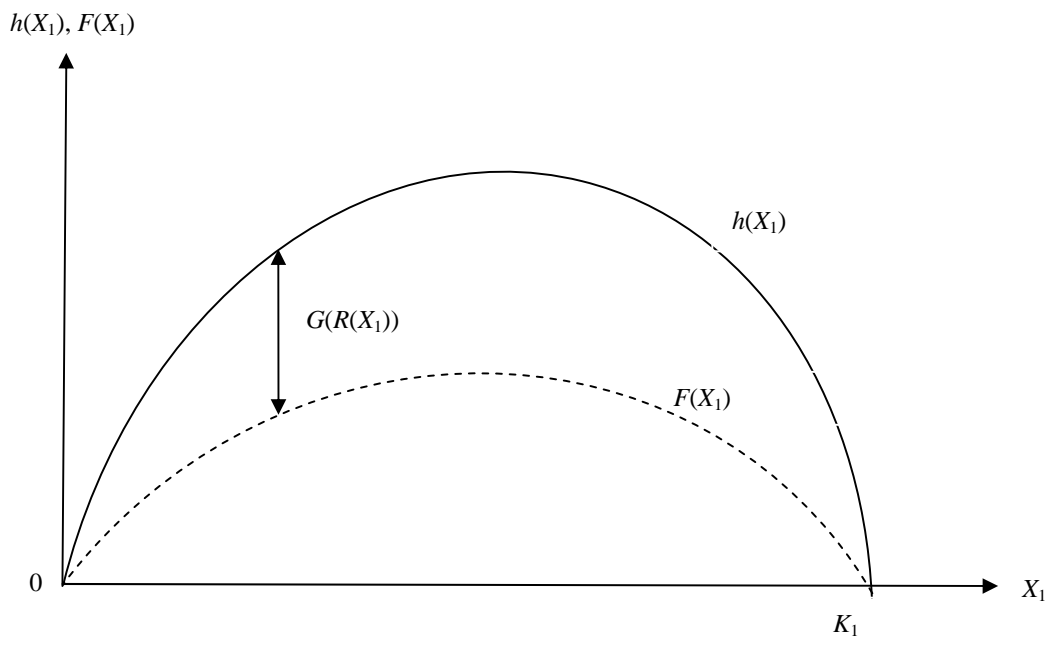


Fig. 1c.

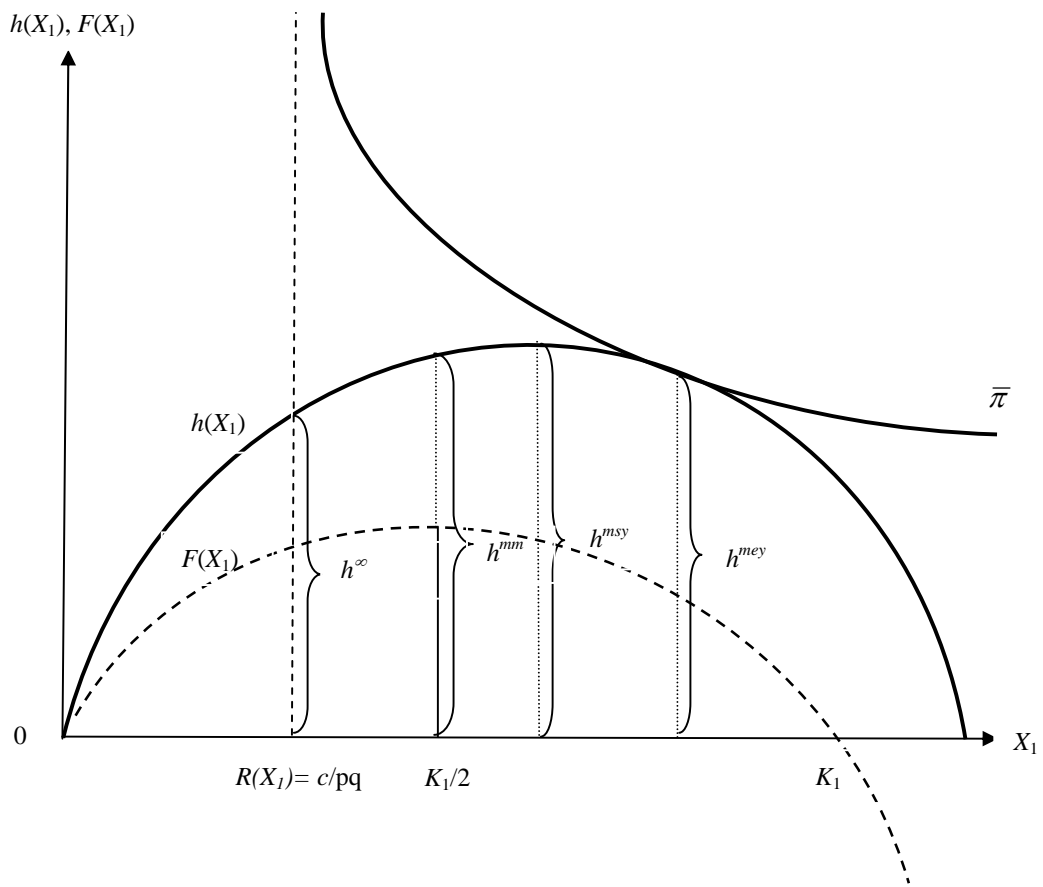


Fig. 2.

Table 1. Baseline values; prices and costs, ecological parameters and other parameters.

Parameter	Description	Value
r_1	Maximum specific growth rate reserve	0.5
r_2	Maximum specific growth rate outer area	0.5
K_1	Carrying capacity reserve	2500 (tonne)
K_2	Carrying capacity outer area	2500 (tonne)
m	Dispersion	1300 (tonne)
p	Landing price fish	7.6 (NOK/kg)
c	Effort cost	18.6 (mill NOK/ trawl vessel)
q	Catchability coefficient	0.0066 (1/trawl vessel)

Table note: The price is based on average data for 1992, and the cost and catchability parameters are averaged over the years 1990-1993 (see Armstrong, 1999). Ecological data are approximations of Eide (1997).

Table 2. The effects of different β values; $\beta = 0.5$; the environment *outside* the reserve is detrimental, $\beta = 1.0$; symmetric dispersal, $\beta = 1.5$; and the environment *inside* the reserve is detrimental. Stock sizes X_i (1000 tonne biomass), natural growth $F(X_1)$ and $G(X_2)$ and harvest h (1000 tonne biomass), profit π (million NOK) and effort E (number of trawl vessels)

β -value	Management	X_1	X_2	$F(X_1)=M$	G	h	π	E
Scenario:								
$\beta = 0.5$	a) Max harvest h^{msy}	1950	563	215	218	432	1120	116
	b) Max profit h^{mey}	2300	973	92	297	389	1831	61
	c) Open access h^∞	1750	370	263	158	420	0	172
	d) Max dispersal h^{mm}	1250	24	313	12	324	-3558	2045
$\beta = 1.0$	a) Max harvest h^{msy}	1600	1046	288	304	592	2905	86
	b) Max profit h^{mey}	1800	1315	252	312	564	3076	65
	c) Open access h^∞	930	370	292	158	450	0	185
	d) Max dispersal h^{mm}	1250	649	313	240	553	1801	129
$\beta = 1.5$	a) Max harvest h^{msy}	1250	1274	313	312	625	3367	74
	b) Max profit h^{mey}	1400	1508	308	299	607	3480	61
	c) Open access h^∞	510	370	203	158	361	0	146
	d) Max dispersal h^{mm}	1250	1274	313	312	625	3367	74

Figure captions

Fig. 1a. The Induced Sustainable Yield Function; *ISYF* ($0 < \beta < 1$).

Fig. 1b. The Induced Sustainable Yield Function; *ISYF* ($\beta > 1$).

Fig. 1c. The Induced Sustainable Yield Function; *ISYF* ($\beta = 1$).

Fig. 2. Harvest under a) Maximum harvest, or h^{msy} , b) Max current profit, or h^{mey} , c) Open access, or h^∞ , and finally, d) Maximum sustainable yield in the reserve, or maximum dispersal out of the reserve h^{mm} ($0 < \beta < 1$).

¹ The history of terrestrial reserves is old, but these nature reserves appeared long after hunting had become completely marginalised compared to farming. Hence terrestrial reserves never had a commercial management approach. The oceans, however, still sustain a large degree of hunting, in the shape of fisheries, making the marine reserve approach a very different one to the terrestrial. The marine reserve focus is increasingly upon the area *outside* the reserve, while the terrestrial reserve concentrates on the conditions *within* the reserve.

² Sanchirico and Wilen (2001) initially describe a general model as presented here, but the entire analysis is done with more limiting assumptions with regard to dispersal.

³ Sanchirico and Wilen (2002) and Sanchirico (2004) model limited-entry allowing some profits, while Conrad (1999), Sumaila and Armstrong (2003), and Schnier (2005) implicitly investigate optimal management by determining optimal reserve sizes through optimising simulation processes.

⁴ Hence we refrain from studying optimal reserve size as done in Hannesson (1998). It is assumed that a given reserve is introduced, and the question remaining is how to manage a fishery in this context.

⁵ It is clear, however, that an aggregation of species could create compounding effects on the dispersal, not specifically discussed here.

⁶ The parameter β may clearly be a dynamic variable that evolves over an adjustment period to a steady-state level. We are however focusing on steady-state equilibrium, following the creation of a marine reserve, and hence assume that β is constant.

⁷ It can be shown that the X_1 -isocline of equation (1) yields X_2 as a convex function of X_1 while the X_2 -isocline of equation (2), for a fixed h , is a concave function. The system

generally has two equilibria, where the one with positive X -values is stable (see also the main text below). Outside equilibrium, starting with for instance a small X_1 and large X_2 , X_1 grows while X_2 initially decreases, before it eventually starts growing as well. During the transitional phase where both sub-populations grow, the dispersal may change sign with inflow into the reserve area being replaced by outflow; that is, the reserve area changes from being a sink to being a source. The same shift in dispersal may happen when starting with a small X_2 as well as a small X_1 .

⁸ As could be expected, profits increase and stock size in the reserve decreases for smaller reserve size.

⁹ Notice that due to the actual parameter values (cf. Table 1), the two areas are totally symmetric except for the value of β .