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Claire W. Armstrong and Anders Skonhoft

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**Department of Economics and Management
Norwegian College of Fishery Science
University of Tromsø
Norway**

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

Abstract

A static bioeconomic model of a marine reserve is introduced, allowing asymmetric density dependent migration between the reserve and the fishable area. This allows for habitat or ecosystem differences within and outside a reserve not described in earlier studies. Four 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 focus 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, a detrimental or 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 (Anderson 2002, Conrad 1999, Hannesson 1998, Lauck *et al.* 1998, Pezzey, *et. al.* 2000, Sanchirico and Wilen 1999, 2001, Smith and Wilen 2003 and Sumaila 1998). Hence the idea of using marine reserves as a fisheries management tool has appeared. 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 paper studies a general bioeconomic model with 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 paper 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 (2003), 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 dispersion. This paper expands the model in Skonhøft and Armstrong (2003) to a marine analysis, and studies how the dispersal asymmetry affects the management of the outside area.

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

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.

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 economic research within marine reserves does not study optimal management (one exception is Reithe 2002). 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, 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 degree of conservation measured as fish density in the reserve.

The paper is organised as follows. In the next section the ecological model is presented. Here we introduce the Induced Sustainable Yield Function (*ISYF*), giving the relationship between fish abundance in the reserve and harvesting taking place outside. 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 sizes², 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 present.

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

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

and

² 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.

$$(2) \quad dX_2/dt = G(X_2) + M(X_1, X_2) - h$$

$$= r_2 X_2 (1 - X_2/K_2) + m(\beta X_1/K_1 - X_2/K_2) - h$$

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 and Pezzey *et al.* 2000). 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.* 2000 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. Hence, $\beta=1$ in their models.

The above system is analysed only in ecological equilibrium, and hence, $dX_1 / dt = 0$ and $dX_2 / dt = 0$ are assumed to hold all the time³. The X_1 -isocline of equation (1) may be expressed as:

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

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

³ 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

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, $R'(X_1) > 0$.

Combination of equations (1) and (2) when $dX_i / dt = 0$ ($i = 1, 2$), and (3) yields:

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

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

being a source. The same shift in dispersal may happen when starting with a small X_2 as well as a small X_1 .

over the interval $[0, K_1 - m\beta/r_1)$ and $h(K_1 - m\beta/r_1) = 0$. However, also in this situation $h(K_1) = G(K_2\beta)$.

Figure 1 about here

Figure 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 Figure 1 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.

Figure 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 $\beta = 0$, as portrayed in Figure 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 Figure 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.

b) *Maximum current profit h^{mey}*

To assess profitability, effort use has to be included. When introducing the Schäfer 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 $h = h(X_1)$.

Figure 2 about here

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

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

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 Figure 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 Figure 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 that

of the h^{msy} level. A high price-cost ratio, as depicted in Figure 2, works therefore also now 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 Figure 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 in the outer area 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

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

well. This harvest may either be smaller or larger than that of the open access, or maximum economic yield. In Figure 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

(Armstrong 1999). The biological data are approximations of intrinsic growth rates and stock size described in Eide (1997). The total carrying capacity $K_1 + K_2$ is divided in two equal parts, one held as a reserve, the other as the remaining fishable area. 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, Eide 1997). Hence, density dependent dispersal between the fishable area and the reserve could be seen as an approximation of these effects. As demonstrated above, the ecological parameter β is crucial for what happens. This parameter will therefore be varied throughout the simulations and we use two values, $\beta = 1.5$ and $\beta = 0.5$, representing either the reserve or the fishable area as detrimental, and where the results are reported in Table 2 and Table 3, respectively. To compare with the standard model with symmetric dispersal, we also illustrate when $\beta = 1$. These results are found in Table 4.

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/ trawlvessel)
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 (Armstrong 1999). Ecological data are approximations of Eide (1997).

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 different 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 comparing Tables 2 and 3 is the fact that the maximum dispersal case d) gives negative profit due to the small stock size in the reserve and overall when $\beta = 0.5$. Hence, even the open access scenario c) yields higher stock sizes than h^{mm} in the reserve when the outside area is detrimental (but Figure 2 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 happens only by accident, 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.

Table 2. Environment *inside* the reserve is detrimental, $\beta = 1.5$. 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)

Management scenario:	X_1	X_2	$F(X_1)=M$	G	h	π	E
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

Table 3. Environment *outside* the reserve is detrimental, $\beta = 0.5$. 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)

Management Scenario:	X_1	X_2	$F(X_1)=M$	G	h	π	E
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

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 case of β presented in Tables 2 and 3 is the picture regarding stock size differences among the various scenarios the same as those we find on the Figure 2 *ISYF*. However, this happens when we have the standard model of symmetric dispersal of $\beta = 1$ in Table 4.

When comparing with Tables 2 and 3 we observe that the assumption of symmetry poses the greatest danger of overexploitation when the environment outside the reserve actually is detrimental, i.e., $\beta < 1$ as in Table 3. 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 was 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.

Table 4. Symmetric dispersal, $\beta = 1.0$. 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).

Management Scenario:	X_1	X_2	$F(X_1)=M$	G	h	π	E
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

Intra-managerial comparison

Looking at the effects of the increase in β upon the different management scenarios in Tables 2, 3 and 4, 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 differ⁴. 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

⁴Notice that due to the actual parameter values (cf. Table 1), the two areas are totally symmetric except for the value of β .

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 introducing 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 overharvesting 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 focus on the well-being of the reserve in the shape of maximum sustainable yield, or maximum dispersal out of the reserve, has most serious consequences, in the shape of negative profits and small total stock, 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.

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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 β

> 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 .

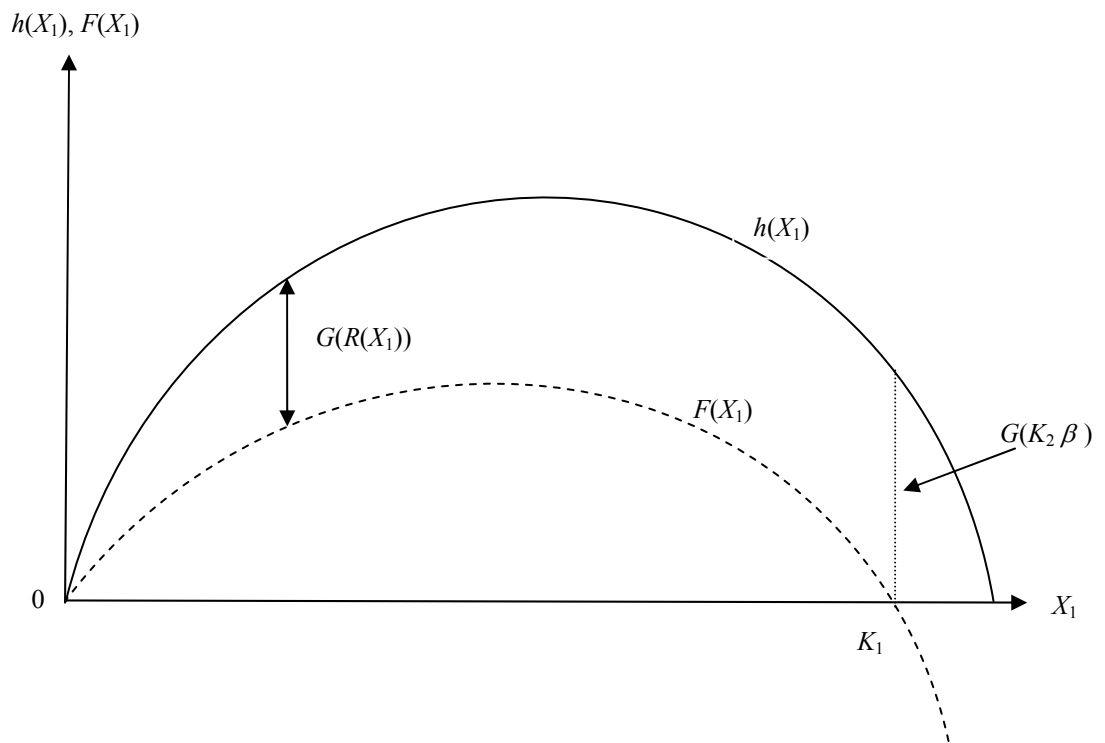


Figure 1a. The Induced Sustainable Yield Function; *ISYF* ($0 < \beta < 1$).

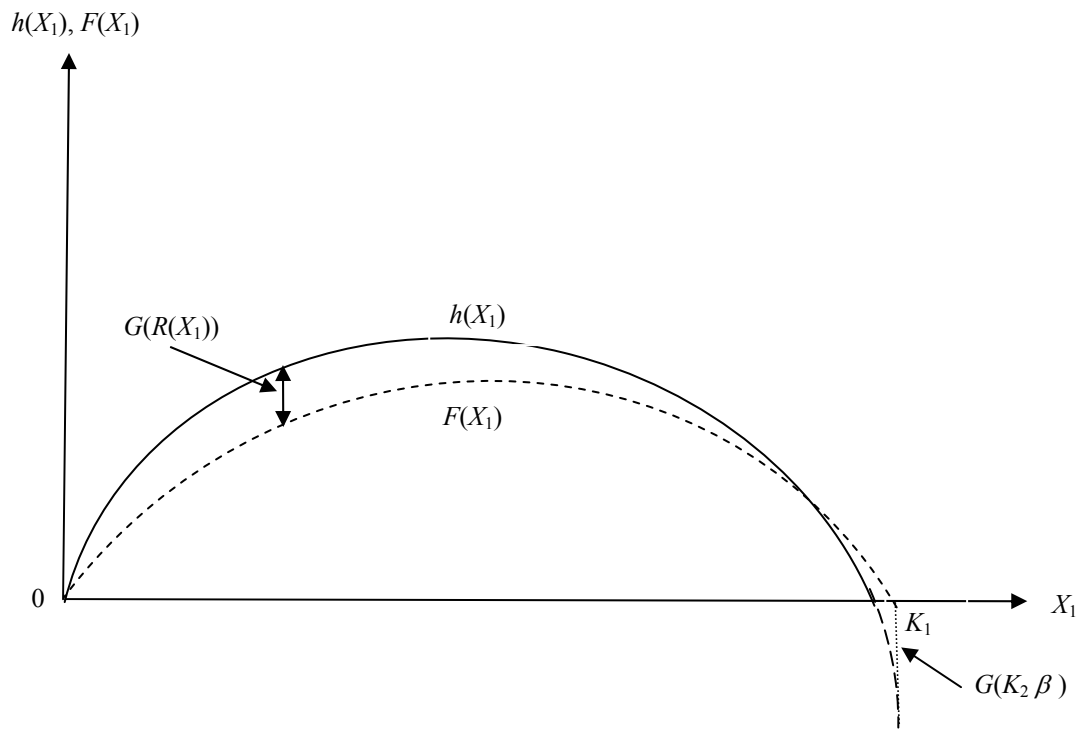


Figure 1b. The Induced Sustainable Yield Function; *ISYF* ($\beta > 1$).

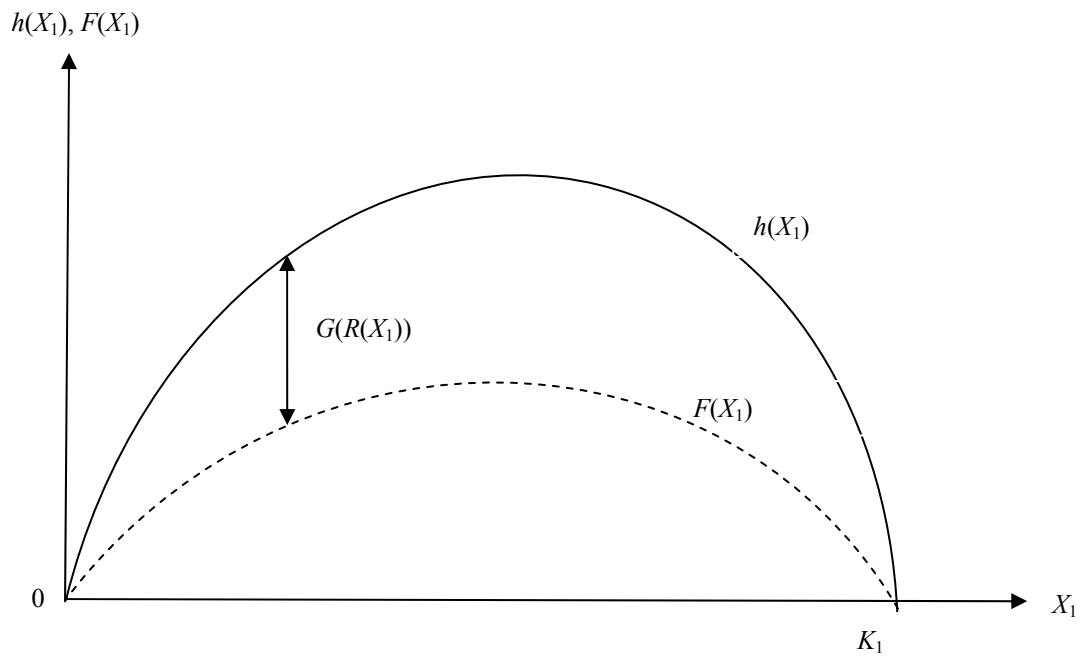


Figure 1c. The Induced Sustainable Yield Function; *ISYF* ($\beta = 1$).

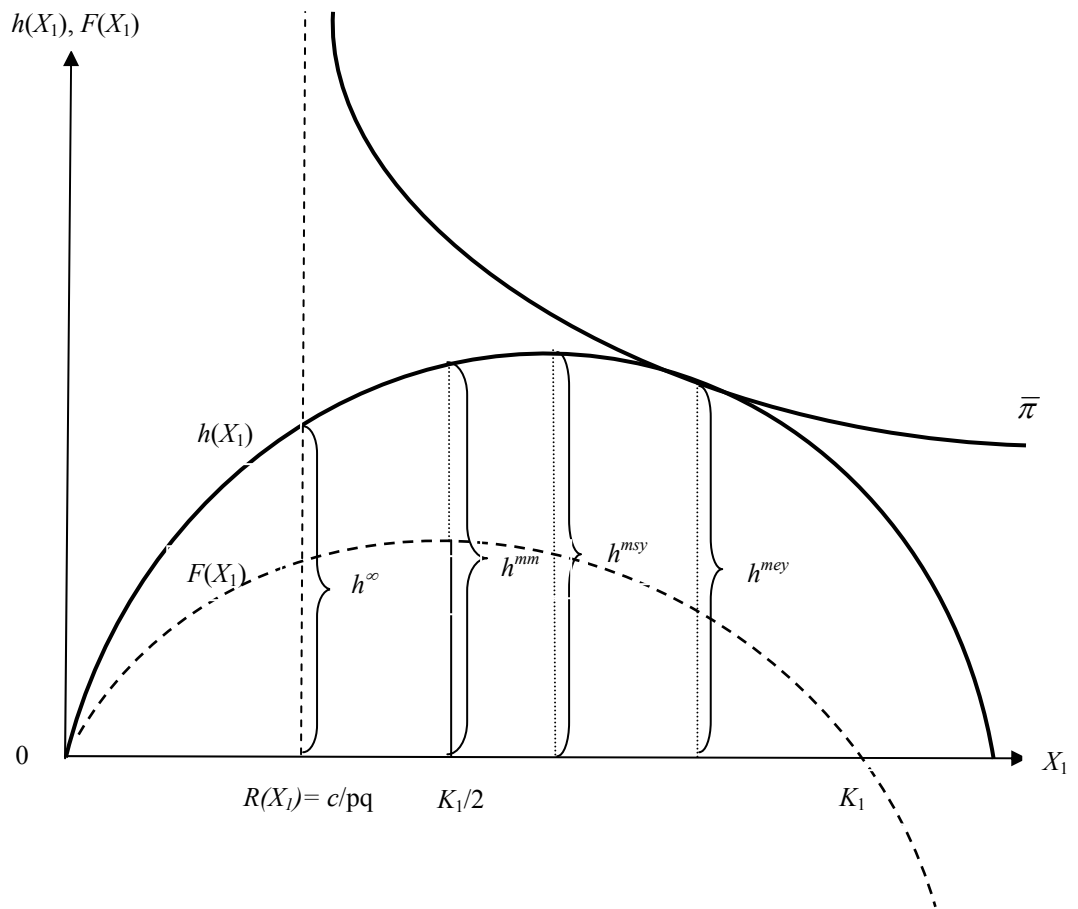


Figure 2. Harvest under a) Maximum harvest, or h^{msy} , b) Max current profit, or h^{mey} , c) Open access, or h^∞ , and finally, d) Maximum sustainable yield in the reserve, or maximum dispersal out of the reserve h^{mm} ($0 < \beta < 1$).