

# Marine Reserves and Quotas as Fisheries Management Tools: When does Marine Reserve Creation Pay?

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## Abstract

This paper explores the issue of using marine reserves in combination with quotas as fisheries management tools. The underlying biological dynamics are described by a patchy environment model, in which a metapopulation is built up by linked sub-populations that are distributed across a set of spatially discrete habitats or patches. The size of each sub-population depends on its own specific population dynamics, which is described by the logistic growth function, and dispersal from other patches. The rent generated by fishing on the total population, using optimal quotas as a management tool, is compared to the rent from the fishery when managed with quotas and a marine reserve. This is done under two different assumptions regarding the type of dispersal mechanisms between the sub-populations in the different patches: A source-sink system (unidirectional flow of individuals) and density dependent migration. The cost per unit harvest is assumed to be lower in the patches open to fishing when the fishery is managed by quotas and a reserve than in the same patches when the fishery is managed by quotas solely. It is shown that the rent maximizing management strategy will vary, depending on the characteristics of the dispersal rates linking the sub-populations and the degree of stock dependent harvesting costs.

KEY WORDS: Marine reserves, optimal quotas, metapopulation model.

## 1. INTRODUCTION

Marine reserves, also called no-take areas, are zones in the marine habitat in which fishing is prohibited for certain parts of the time, or at all times. As conventional fisheries management has been shown to suffer obvious shortcomings (for instance, Guénette et al. 1998), attention has been drawn towards alternative methods of management, marine reserves being one of them (see Sumaila 1998a and Conover, et al. 2000). Reserves may have several potential benefits (see for instance Bohnsack 1993, and Roberts & Polunin 1993); protection of spawning biomass, provision of recruitment sources for the surrounding areas, supplemental restocking of fished areas through emigration, maintenance of natural population age structure and sex ratio, maintenance of undisturbed habitats and insurance against management failures in fished areas. Conservation biologists have been enthusiastic about reserves, but the question whether marine reserves may enhance fisheries or not is still much disputed as empirical evidence is scarce. A few studies that do not contradict the theory do however exist (McClanahan & Kaunda-Arara 1996, Russ & Alcala 1996, Roberts et al. 2001).

Some theoretical bioeconomic studies have been done on the effectiveness of marine reserves. Hannesson (1998) found that a reserve combined with open access would result in a lower stock size, lower catches and a higher exploitation rate than optimal quotas for all relevant sizes of reserves and migration rates. Armstrong and Reithe (2001) found that these results are modified if management costs are included in the calculations. Both Sumaila (1998b) and Conrad (1999) compared the use of optimally set quotas only to both quotas and marine reserves, finding that in a deterministic setting, the former is the rent maximizing strategy. In all of the work mentioned above, it is assumed that the fish is homogeneously distributed over an area. It is further assumed that the reserve may be of size 0 to 100 % of this area, measured on a continuous scale, and that the sub-stocks and their growth will be proportional to the size of the area they live in.

Sanchirico & Wilen (2001) also compares solely open access to a marine reserve combined with open access, but as opposed to the above-mentioned studies their work includes the spatial dimension is included both in the biological and economic part of the model. In this type of model the management

unit is the metapopulation<sup>1</sup>, which is assumed to consist of a group of linked sub-populations distributed across a set of spatially discrete habitats or patches. The reserve consists of the patches of one or more sub-stocks. Each sub-stock has its own population dynamics, but some or all are connected through different dispersal mechanisms. Sanchirico & Wilen (2001) show that when patches are linked through unidirectional flow of individuals (sink-source system) or density dependent migration, reserve creation may increase stock and harvest if the cost / price ratio is low and for given values of the intrinsic growth rate / migration rate ratio. Brown and Roughgarden (1997) use a metapopulation model to find optimal management of barnacles. The barnacle has a two-stage life cycle, the first lived in a common oceanic larval pool, the second at a local coastal site. They show that the optimal strategy, in terms of maximizing discounted net benefits, is to harvest on one patch only, setting the other patches off as nurseries or reserves. Hence, it seems as if reserves may have the greatest potential as being beneficial in the management of species whose population dynamics may be described with metapopulation models.

In the following, the biological part of the type of metapopulation model applied by Sanchirico & Wilen (2001) will be used to compare the per period equilibrium rent of a fishery managed by the use of quotas solely and quotas in combination with a reserve. The economic part of the model is however formulated differently as other issues are addressed here. Hence, this work differs from previous theoretical bioeconomic studies of marine reserves in that a metapopulation model applied in the analyses of reserves combined with optimal quotas. It also differs in that a new harvesting and cost per unit harvest function is introduced. This is done in order to take all the benefits from reserve creation to be taken into account. In order to keep the modeling framework simple, benefits from the fishery are restricted to account for any rent generated.

## 2. THE MODEL

This section provides a brief presentation of the general modeling framework. The biological model is based on Sanchirico and Wilen (1999 and 2001) and is in line with the works of Levin (1974, 1976), Hastings (1982, 1983), Vance (1984) and Holt (1985). For a more in depth discussion of this model and general aspects concerning metapopulation modeling, see the above references.

The following equation describes the instantaneous net change in biomass of sub-population  $i$ .

$$(1) \quad \dot{x}_i = f(x_i)x_i + d_{ii}x_i + \sum_{\substack{j=1 \\ j \neq i}}^n d_{ij}x_j$$

The dynamics of  $n$  sub-populations may be expressed in matrix form:

$$(2) \quad \dot{\mathbf{x}} = \mathbf{F}(\mathbf{x})\mathbf{x} + \mathbf{D}\mathbf{x}$$

Where

$\dot{\mathbf{x}}$  =  $n \times 1$  vector of the instantaneous change in biomass ( $\dot{x}_i$ ) in patch  $i$  at time  $t$

$\mathbf{F}(\mathbf{x})$  =  $n \times n$  diagonal matrix where the average growth of patch  $i$  ( $f(x_i)$ ) constitute the diagonal elements

$\mathbf{x}$  =  $n \times 1$  vector of the level of biomass in patch  $i$  at time  $t$  expressed as relative densities<sup>2</sup>. The sum of this vector is the size of the metapopulation.

$\mathbf{D}$  =  $n \times n$  matrix of dispersal rates ( $d_{ij}$ )

The growth process of the sub-stocks will be expressed by the logistic growth function<sup>3</sup>.

<sup>1</sup> Hanski & Gilpin (1991) define the term metapopulation as a set of local populations of a single species that interact as members migrate among local populations.

<sup>2</sup>  $x = X/K$ , where  $X$  is the absolute stock level and  $K$  is the carrying capacity. In order to calculate absolute growth/harvest from the stock size when it is expressed as relative density, one must multiply the parameter  $r$  with  $K$ .

<sup>3</sup>  $f(x_i) = r_i(1-x_i) \ln(1)$ .

The restriction  $\sum_{i=1}^n d_{ik} = 0$  is imposed on the dispersal matrix and implies that no death or birth occurs during migration, or in other words, the same amount that leaves one patch shows up in another. It is further assumed that  $d_{ii} \leq 0$  is emigration from patch  $i$  and  $d_{ij} \geq 0$  is immigration to patch  $i$  from patch  $j$ . With this type of model it is possible to describe the most commonly observed links and dispersal mechanisms between the sub-populations (Sanchirico & Wilen 1999): fully integrated systems, closed patches, sink-source and spatially linear systems. Fully integrated systems are systems in which all sub-populations are linked through some dispersal process, while closed systems are comprised of sub-populations between which no migration occur. Sink-source systems consist of local populations that are linked through a unidirectional flow of individuals. The last category mentioned, a linearly linked system, is one in which migration only occurs between neighboring patches. This case nests other spatial configurations of patches, such as a circle and a square. The migration may be unidirectional or density dependent. The simplest example of density dependent migration is a two patch system in which  $d_{12} = d_{21}$ , that is, migration rates from both patches are equal. In this case net migration will always go from the patch with the highest density towards the patch with the lowest density.

In the quota case the harvest function is defined as the standard  $H_i = q_i E_i x_i$ , where  $E_i$  is the fishing effort in patch  $i$ ,  $x_i$  the stock level in patch  $i$  and  $q_i$  is a constant of proportionality between an increase in effort or stock level and an increase in harvest. We shall assume that  $q_i = 1$  in all cases. If one further assumes a constant patch specific cost of effort  $c_i$ , and a linear cost function equal to  $TC_i(E_i) = c_i E_i$ , the cost per unit harvest becomes  $c_i/x_i$ . Hence the per period equilibrium rent from the fishery when managed by quotas alone may be expressed by the following function:

$$(3) \quad \pi_Q = \sum_{i=1}^n (p r_i x_i (1 - x_i) - \frac{c_i}{x_i} (r_i x_i (1 - x_i))) \quad i = 1, 2, \dots, n$$

Where  $p$  is a constant price and the term in the last parenthesis is the equilibrium harvest.

When managed by both quotas and a reserve it is assumed that the harvest in patch  $i$  at time  $t$  depends both on the stock level and the net migration from the reserve at that given point in time. Thus, harvest

in patch  $i$  is defined as  $H_i = q_i E_i (x_i + d_{ii} x_i + \sum_{\substack{j=1 \\ i \neq j}}^n d_{ij} x_j)$ . Where subscript  $i$  denote stock level in the

fishable area and subscript  $j$  the stock level in the reserve and the two last terms in the parenthesis express the net immigration to the fishable area. This is an approximation as any net migration to the fishable area will mingle and become part of the stock level in patch  $i$ . It is done however, in order to allow us to take into account that when there is a net migration to the fishable area, there is a higher density of fish, which should lead to a lower cost per unit harvest. With a the cost function  $TC_i(E_i) =$

$c_i E_i$ , the cost per unit of harvest now becomes  $c_i / (x_i + d_{ii} + \sum_{\substack{j=1 \\ i \neq j}}^n d_{ij} x_j)$ . The per period equilibrium rent

expressed as a function of stock level then becomes

$$(4) \quad \pi_R = \sum_{i=1}^n (p (r_i x_i (1 - x_i) + d_{ii} x_i + \sum_{\substack{j=1 \\ j \neq i}}^n d_{ij} x_j) - \frac{c_i}{x_i + d_{ii} x_i + \sum_{\substack{j=1 \\ j \neq i}}^n d_{ij} x_j} (r_i x_i (1 - x_i) + d_{ii} x_i + \sum_{i=1}^n d_{ij} x_j)), \quad i = 1, 2, \dots, n$$

Reserve creation is economically rational if  $\Delta\pi = \pi_R^* - \pi_Q^* > 0$ , where the stars are used to indicate that it is the maximum rent from both cases. Two main factors determine the sign and size of  $\Delta\pi$ . First we have what will be called the *dispersal effect*, namely the new equilibrium level of emigration from the reserve to the fishable area due to a larger source stock minus the pre-reserve catch from the closed area. If the net migration from the reserve to the fishable area is greater than the loss of pre-reserve catch, the dispersal effect is positive. The second part is here called the *cost effect* of reserve creation. This term refers to the fact that the cost per unit harvest is lower when there is a reserve than in the pure quota case. As a result, the cost effect will always pull towards a higher optimal stock level in the

fishable area of the reserve case, than in the quota case. None of the above mentioned works on marine reserves have used different cost functions for reserves and other management strategies, but it will be shown below that it is an important factor in determining the profitability of reserves. The terms will be discussed more thoroughly below. In the following two cases regarding the dispersal process will be examined: A two-patch source-sink system and a two-patch system with density dependent migration.

### 3. RESULTS

#### 3.1. Managing the fishery with quotas

For simplicity we shall first assume that the biological and the economic characteristics of the patches are identical. That is, they have the same intrinsic growth rate, carrying capacity, prices and costs. With the biological and economic parameters of the different patches being equal and the restriction that requires the dispersal vector to sum up to zero, the problem of maximizing equilibrium profits from a fishery consisting of two patches becomes

$$(5) \quad \underset{x_1, x_2}{Max} \quad \pi_Q = p \sum_{i=1}^2 r x_i (1 - x_i) - \sum_{i=1}^2 \frac{c}{x_i} r x_i (1 - x_i) \quad i = 1, 2$$

Which is a standard, well-known problem in bioeconomics. Differentiating the profit function with respect to  $x_1$  and  $x_2$ , equating these differentials to zero and solving for the  $x$ 's gives the optimal stock levels

$$(6) \quad x_{1, MEY} = x_{2, MEY} = 0.5(1 + c/p)$$

As the cost parameter approaches zero, the optimal stock level ( $X_{MEY}$ ) in both patches will approach that giving maximum sustainable yield ( $X_{MSY} = 0.5$ ). The greater the cost parameter is compared to the price, the greater the difference between  $X_{MEY}$  and  $X_{MSY}$ . If one allows for different harvesting costs in the two patches, optimal stock levels will differ, depending on the patch specific  $c/p$  ratio. Differences in the intrinsic growth rate will only affect the level of rent, not the optimal stock level.

#### 3.2. Managing the fishery with quotas and a marine reserve

##### 3.2.1. Sink-source dynamics

Also here it is first assumed that patches are homogeneous. The two-patch sink-source system may then be described by the following system of equations:

$$(7) \quad \begin{aligned} \dot{x}_1 &= r x_1 (1 - x_1) - d x_1 && \text{Source} \\ \dot{x}_2 &= r x_2 (1 - x_2) + d x_1 && \text{Sink} \end{aligned}$$

Where stock 1 would be the source and stock 2 the sink. The parameter  $d$  denotes the migration rate from the source to the sink. Since the profitability of marine reserves depends on spillover or migration from the reserve to the fishable area, closing the sink in a sink-source system never pays (Sanchirico & Wilen 2001). Assume therefore that we close the source. The equilibrium stock level in the reserve is found by equating  $\dot{x}_1$  to zero and solving for  $x_1$ . This gives

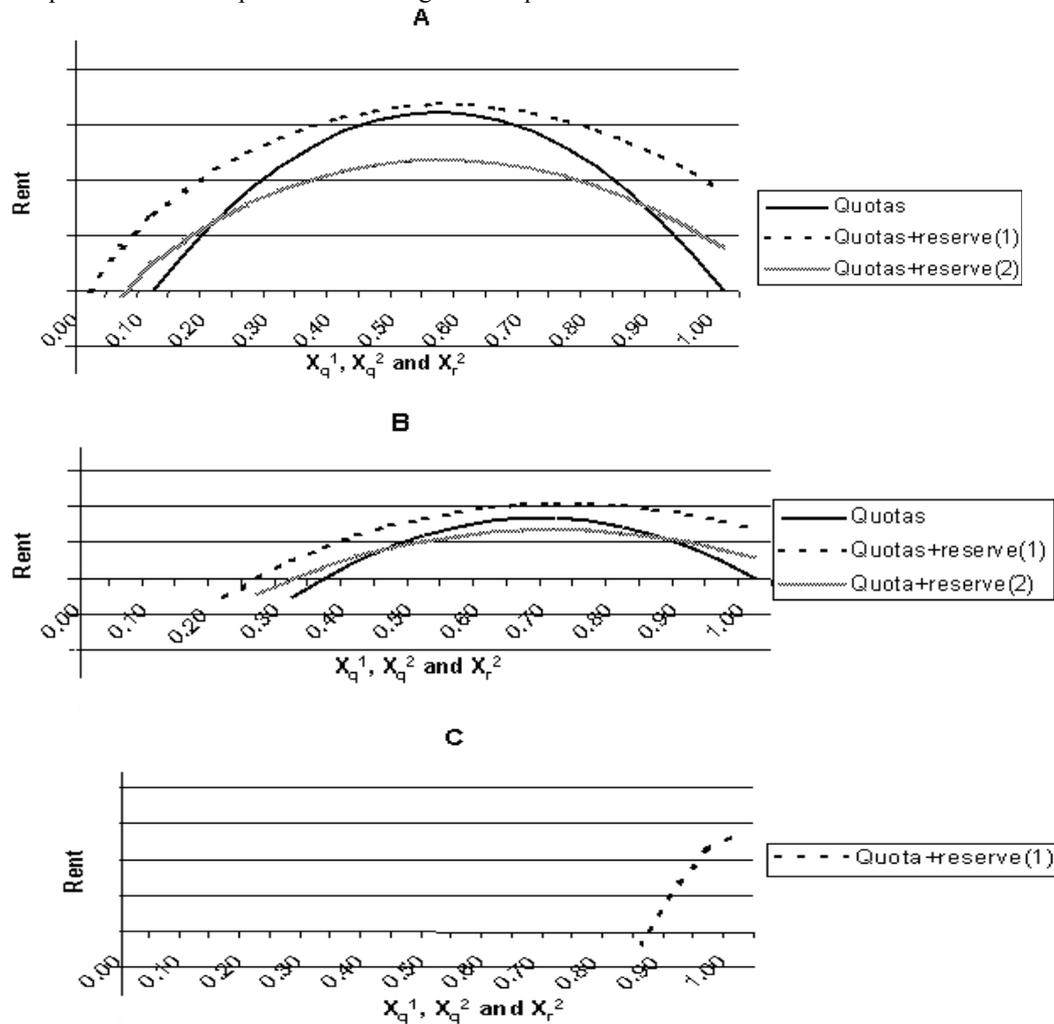
$$(8) \quad \tilde{x}_1 = 1 - d/r$$

With harvesting the equilibrium stock level of patch 2 is determined by solving the following maximizing problem:

$$(9) \quad \underset{x_2}{Max} \pi_R = \left( p - \frac{c}{(x_2 + d\tilde{x}_1)} \right) (rx_2(1-x_2) + d\tilde{x}_1)$$

The analytical solution to this problem is hard to interpret and it is difficult to isolate the effects of a change in any of the parameters. Hence the discussion below is based on numerical calculations<sup>4</sup>. The equilibrium properties in terms of stability are listed in the appendix.

The numerical calculations show that the optimal stock level in the fishable area depends only on the size of  $c$  compared to  $p$  and the rate of migration  $d$  relative to the intrinsic growth rate  $r$ . As in the quota case, when the costs of harvesting are very low compared to the price, optimal stock level is close to  $X_{MSY}$  and increasing with increasing costs, other things equal. This is illustrated in figure 1 where the profit from the fishery when managed with quotas alone is compared to that obtained when managed with both quotas and a marine reserve. The intrinsic growth rate  $r$  is set equal to 0.4. The cost parameter is adjusted to exhibit three situations. Panel A shows the situation that will be referred to as the low cost case. Here the per unit profit in the quota case is 84.4 % of the price. Panel B illustrates the medium cost case where the per unit profit in the quota case is 50 % of the price. Panel C exhibit a situation where the fishery managed with quotas alone is no longer profitable while the per unit profit as % of the price when managed with quotas and a reserve is 13.6.



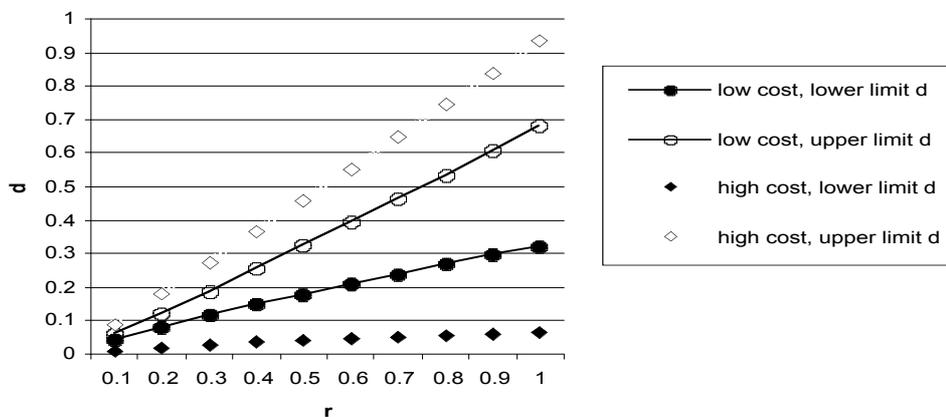
**Figure 1.** Rent generated from the fishery when managed through quotas alone and with quotas in combination with a reserve<sup>1</sup>.

<sup>4</sup> The numerical estimates were conducted in Excel.

<sup>1)</sup> Quota+reserve(1) refers to the case when  $d = 0.2$ ,  $r = 0.4$ . Quota+reserve(2) refers to the case when  $d = 0.1$ ,  $r = 0.4$ . Subscript is used to identify stock levels under different management regimes, where  $q$  denotes the case of quotas and  $r$  the case of quotas and a reserve. Superscript is used to identify sub-populations.

In the sink source case the dispersal effect will be constant for a given cost level, as the flow of individuals is unidirectional. At zero costs the loss of pre-reserve catch is exactly offset by the dispersal from the reserve. As  $c$  increases a lower  $d$  is required to make the dispersal effect equal to zero, or in other words, for a given  $d$  an increase in costs causes the dispersal effect to increase. This because while migration from the reserve remains constant, the loss due to reserve creation in terms of equilibrium harvest in the quota case decreases<sup>5</sup>.  $\Delta\pi$  will always have its' maximum value when  $d = r/2$ , as this gives the maximum migration from the reserve to the fishable area. If  $d > r/2$ , the stock level in the reserve becomes lower and so do the migration measured in absolute numbers. The change in the dispersal effect due to an increase in cost may be isolated in figure 1 as the increase in distance between the quota curves and the quotas+reserve(1) curves, or as the decrease in distance between the quota curves and the quotas+reserve(2) curves, when going from panel A to panel B. The cost effect may be visualized as the different optimal stock levels in panel B, or by the fact that for high costs the fishery may remain profitable when managed by quotas and a reserve while being unprofitable when managed by quotas solely as in panel C. In panel A the costs are too low to have a visible effect.

For any combination of  $r$  and level of harvesting cost, there is one low ( $d_l < r/2$ ) and one high value ( $d_h > r/2$ ) of  $d$ , that gives  $\Delta\pi = 0$ . The value of  $d_l$  decreases with increasing harvesting costs and increases with increasing  $r$ . The value of  $d_h$  increases with increasing  $c$  and  $r$ . This is illustrated in figure 2. For all  $d_l < d < d_h$ ,  $\Delta\pi > 0$ , corresponding to the areas between the gray lines with diamond markers in the high cost case, and the black lines with circular markers in the low cost case in figure 2. We see that the range of migration rates leading to  $\Delta\pi > 0$  increases with increasing  $r$  and  $c$ , everything else constant. Hence, for a specie with a low intrinsic growth rate and/or low harvesting costs (relative to price) marine reserves will have small chances of being profitable, whereas for species with high intrinsic growth rates and/or high harvesting costs, the chances that reserve creation may pay are much greater.

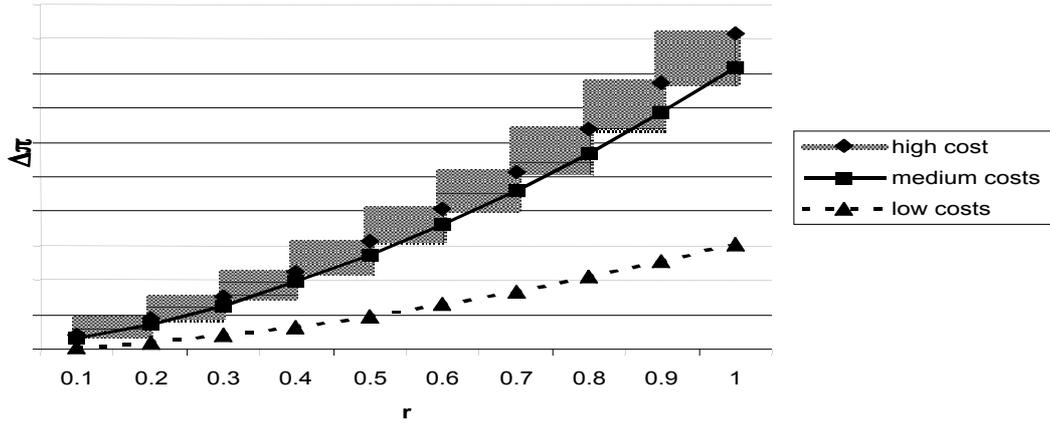


**Figure 2.** The low and high values of  $d$  that result in  $\Delta\pi = 0$ <sup>II</sup>.

<sup>II)</sup> Low cost case refers to the case when the unit profit in the quota case is 84.4% of the price.  
High cost case refers to the case when the unit profit in the quota case is 20% of the price.

It is also the case that the absolute value of  $\Delta\pi$  increases with increasing  $c$  and  $r$ . This is illustrated in figure 3 where  $\Delta\pi$  is plotted for the three cost levels and  $d = r/2$ .

<sup>5</sup> This is because the optimal stock level is greater than  $x_{MSY}$ . Using the logistic growth function to describe population dynamics this implies that a decrease in stock level results in an increase in equilibrium catch.



**Figure 3.** Maximum difference in rent generated from a fishery when managed by quotas alone and when managed by quotas and a reserve.

Allowing for heterogeneity between patches does not alter the qualitative nature of the results only the absolute level of rent generated from the fishery.

### 3.2.2. Density dependent migration

We first assume that patches are homogeneous in terms of intrinsic growth rates and harvesting costs. The population dynamics of the two-patch system with density dependent migration is described with the following equations:

$$(10) \quad \begin{aligned} \dot{x}_1 &= rx_1(1-x_1) - dx_1 + ax_2 \\ \dot{x}_2 &= rx_2(1-x_2) + dx_1 - ax_2 \end{aligned}$$

Where  $d$  is the migration rate from patch 1 to patch 2 and  $a$  is the migration rate from patch 2 to patch 1. Closing area 1 gives equilibrium stock size ( $\tilde{x}_1$ ) equal to

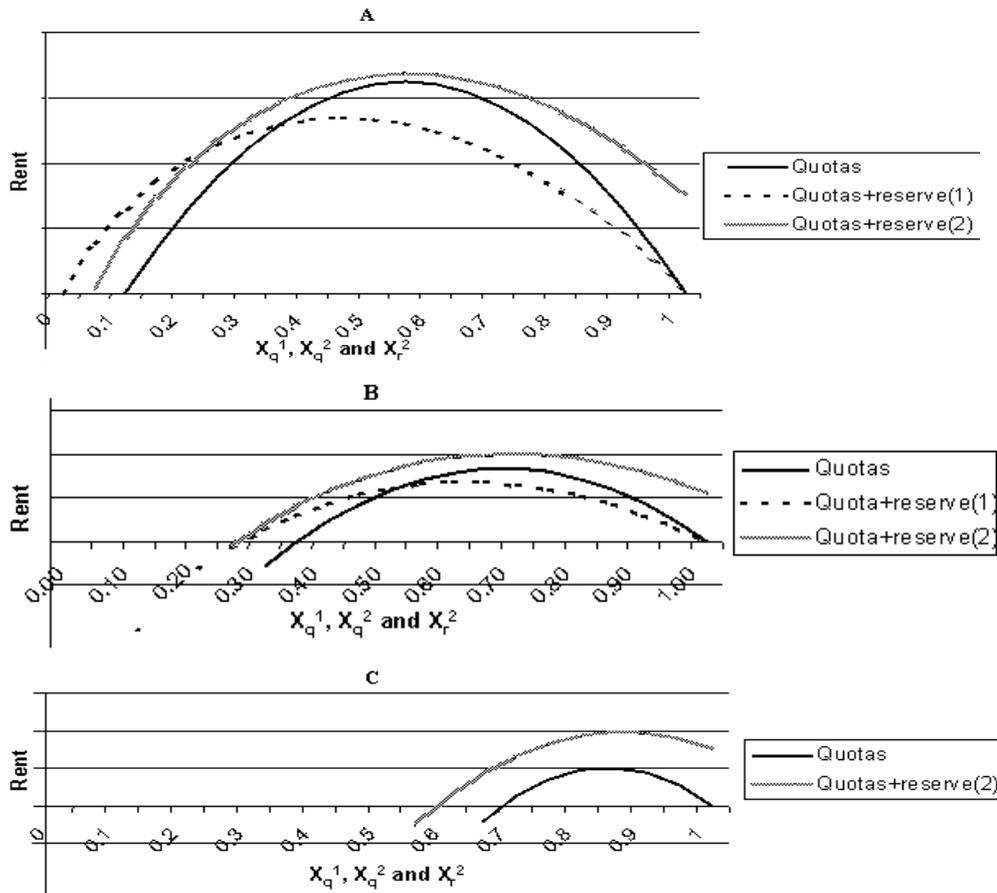
$$(11) \quad \tilde{x}_1 = -\frac{d-r-\sqrt{(r-d)^2+4arx_2}}{2r}$$

The maximizing problem in this case is

$$(12) \quad \max_{x_1, x_2} \pi_r = \left( p - \frac{c}{(x_2 + d\tilde{x}_1 - ax_2)} \right) (rx_2(1-x_2) + d\tilde{x}_1 - ax_2)$$

Differentiating (12) with respect to both  $x_1$  and  $x_2$  and equating the differentials to zero gave no appropriate answers. Hence optimal stock levels were derived by differentiating (12) with respect to  $x_2$ , equating the differential to zero, and using the answer to calculate  $\tilde{x}_1$  and  $x_2$  numerically. But as it turns out, maximum profit from the fishery now depends on the parameters  $a$  and  $d$  relative to  $r$ , and the  $c/p$  ratio. In figure 4 equilibrium rent for the different stock levels for both management strategies are shown for the three different cost levels. Also here panel A, B and C exhibit the low, medium and high cost case respectively. First of all we should observe that reserve creation is unprofitable when the dispersal rates  $a$  and  $d$  are equal, unless costs are very high. Secondly, if  $d > a$  it may be profitable to create a reserve. Further we see from panel A that for low levels of costs and a low value of the parameter  $d$  (compared to  $a$ ) the optimal stock level in the reserve is lower than  $x_{MSY}$ . This is a result of the dispersal effect, which is no longer constant. When  $d$  is low, the stock in the reserve is large. Hence it pays to keep the stock level in the fishable area low to ensure a high net migration in absolute numbers. As the value of  $d$  increases, the stock level within the reserve decreases and the gain in harvest in terms of net migration from the reserve is offset by an increase in the stock level in the fishable area with the following increase in catch and the cost effect. In the low cost case (panel A) we have that when  $d = 0.38$  the loss of pre-reserve catch is exactly offset by the net migration from the

reserve. The corresponding values of  $d$  in the medium and high cost case are 0.34 and 0.26 respectively.



**Figure 4.** Rent generated from the fishery in the medium cost case when managed by quotas alone and with quotas in combination with a marine reserve<sup>III</sup>.

<sup>III</sup>) Quotas+reserve(1) refers to the case when  $a = d = 0.2$  and  $r = 0.4$ . Quotas+reserve(2) refers to the case when  $a = 0.2$ ,  $d = 0.4$  and  $r = 0.4$ .

The trend regarding the change in  $\Delta\pi$  following an increase in  $r$  and  $c$  were also found to be similar to that of the sink source case (see figure 3). Given the value of  $a$ , as  $r$  or  $c$  increases, the relative profitability of reserve creation increases. Also similar to the sink-source case, for a given value of  $a$  there is an upper and lower limit to  $d$  that makes  $\Delta\pi = 0$  and the range between  $d_l$  and  $d_h$  where  $\Delta\pi > 0$  increases with increasing  $r$  and  $c$  (see figure 2).

If we allow for different harvesting costs in the two patches and density dependent migration the question becomes; which patch should be closed to fishing? Numerical estimates show that it is optimal to close the patch that has the lowest per unit profit as % of the price. This is the opposite result of what Sanchirico & Wilen (2000) found for marine reserves and open access. They found that closing the patch with the lowest cost / price ratio would be optimal in the sense of increased harvest. This because with a low cost / price ratio and open access the stock level and hence also equilibrium harvest is low and the loss of pre-reserve catch is less than that for patches with a higher cost / price ratio. In the case of optimal quotas, closing the patch with the highest harvesting costs and thereby the lowest per unit profit, would give the lowest loss of pre-reserve catch (see footnote 5). An other interesting result is that with different cost levels and a common migration rate between the patches ( $a = d$ ) reserve creation may be profitable. We have e.g. that if the cost levels are low and medium, or high and medium in the two patches,  $\Delta\pi > 0$  when the patch with the highest level of harvesting costs is closed. This result contradicts the conclusions of Sumaila (1998b) and Conrad (1999) that stated that

reserve creation was unprofitable in a deterministic setting and density dependent migration with a common migration rate, but in these works differences between the cost levels of the two patches was not taken into consideration.

#### **4. SUMMARY AND CONCLUDING REMARKS**

In this paper the potential for an increase in rent due to reserve creation in a fishery already managed by optimally set quotas has been assessed. This has been done by comparing the per period rent the fishery yields in equilibrium under the two management strategies, assuming two different dispersal mechanisms between the patches; unidirectional and density dependent. Through numeric calculations it has been shown that under certain biological and economic circumstances the use of quotas and a marine reserve may be the rent maximizing management strategy.

In the sink-source case it has been shown that the profitability of reserve creation depends on the migration rate relative to the intrinsic growth rate and the cost / price ratio. Furthermore, the higher the costs and the higher the intrinsic growth rate the wider the range of migration rates that allows for profitable implementations of reserves. The profitability of a reserve was also seen to increase with increasing costs and intrinsic growth rate. In the case where the patches were assumed to be linked through density dependent migration the profitability of a reserve depends on the rate of migration back to the reserve, the migration from the reserve relative to the intrinsic growth rates and the level of costs.

These results contradict the findings of Sumaila (1998b) and Conrad (1999) who show that quotas in combination with a marine reserve is an inferior management strategy compared to optimally set quotas solely, when analyzed in a deterministic setting. I can see two reasons for the contradiction. First neither of the mentioned works allowed for a difference between the rate of migration from the reserve to the fishable area and from the fishable area to the reserve. The second reason lies in that the cost per unit harvest in the reserve case is lower than in the quota case in this paper, a difference that was not made in the other papers mentioned.

Many of the results in this paper depend on the way the harvesting cost function is formulated. This highlights the need for empirical research; what are the true functional form and parameter values of the harvesting costs function after a reserve has been implemented? Also on the biological side there are some major questions that need to be addressed: What are realistic ranges of values of migration and the intrinsic growth rate? And do the values of the parameters found to make reserve creation profitable fall within the realistic intervals? In addition, there are several complicating factors concerning reserve creation that are not included in this analysis. First we have multispecies dynamics. Boncoeur et al. (forthcoming) analyses the issue of reserve creation when interactions between fish and seals are taken into consideration. They show that the dynamics of the two stocks reduces the benefits to the benefits of the reserve for the fishing industry, but creates an opportunity for developing ecotourism (seal watching). As a result, it is found that the optimal size of the reserve is greater when ecotourism is taken into account along with fishing activities. Second, the value of catch in an area prior to reserve creation, versus the value of spillover from a reserve is an issue that has not been discussed in this paper. Here it has been assumed that these values are equal, although this may not always be the case. E.g. if the migratory part of the stock consist of juveniles or parts of the stock that are in some other way differ from the targeted group prior to reserve creation, the value of the spillover versus pre-reserve catch may be less than what has been pictured here. Hence, although the results of this paper indicate that reserves may be the profit maximizing management strategy under certain conditions, much work is needed before the debate over marine reserves and fisheries enhancement may be settled.

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## 6. REFERENCES

- Armstrong, C.W. & S. Reithe. Comment: Marine reserves: Will They Accomplish More With Management Costs? *Marine Resource Economics*, 16, 165-175, 2001.
- Bohnsack, J.A. Marine Reserves. They Enhance Fisheries, Reduce Conflicts, and Protect Resources. *Oceanus*, fall, 1993.
- Boncoeur J., F. Alban, O. Guyader & O. Thébaud. Fish, fishers, seals and tourists: Economic consequences of creating a marine reserve in a multi-species, multi-activity context. Forthcoming in *Natural Resource Modelling*.
- Brown, G. & J. Roughgarden. A metapopulation model with private property and a common pool. *Ecological Economics*, 22, 65-71, 1997.
- Conover, D.O., J. Travis & F.C. Coleman. Essential fish habitat and marine reserves: an introduction to the Second Mote Symposium in Fisheries Ecology. *Bulletin of Marine Science*, 66(3), 527-534, 2000.
- Conrad, J.M. The Bioeconomics of Marine Sanctuaries. *Journal of Bioeconomics*, 1, 205-217, 1999.
- Guénette, S., Lauck, T., and Clark, C. Marine reserves: from Beverton and Holt to the present. *Reviews in Fish Biology and Fisheries*, 8, 251-272, 1998.
- Hannesson, R. Marine Reserves: What Would They Accomplish? *Marine Resource Economics*, vol. 13, 159-170, 1998.
- Hanski & Gilpin. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42, 3-16, 1991.
- Hastings, A. Dynamics of a single species in a spatially varying habitat: The stabilizing role of high dispersal rates, *J. Math. Biol.*, 16, 49-55, 1982.
- Hastings, A. Can spatial variation alone lead to selection for dispersal, *Theoret. Population Biol.*, 24, 244-251, 1983.
- Holt, R.D. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theoret. Population Biol.*, 28, 181-208, 1985.
- Levin, S.A. Dispersion and population interactions. *American Naturalist*, 108, 207-227, 1974.
- Levin, S.A. Population dynamic models in heterogeneous environments. *Ann. Rev. Ecology Syst.*, 7, 287-310, 1976.
- McClanahan, T.R. & B. Kaunda-Arara. Fishery recovery in a coral reef marine park and its effect on the adjacent waters. *Conservation Biology*, 10, 1187-1199, 1996.
- Roberts, C. M. & N.V.C. Polunin. Marine Reserves: Simple Solutions to Managing Complex Fisheries. *Ambio*, 22(6), 363-368, 1993.
- Roberts, C. M., J.A. Bohnsack, F. Gell, J.P. Hawkins & R. Goodbridge. Effects of Marine Reserves on Adjacent fisheries. *Science*, 294, November, 1920-1923, 2001.
- Russ, G.R. & A.C. Alcala. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series*, 132, 1-9, 1996.
- Sanchirico, J.N. & J.E. Wilen. Bioeconomics of Spatial Exploitation in a Patchy Environment. *Journal of Environmental Economics and Management*, 37, 129-150, 1999.
- Sanchirico, J.N. & J.E. Wilen. A Bioeconomic Model of Marine Reserve Creation. *Journal of Environmental Economics and Management*, 42, 257-276, 2001.
- Sumaila, U. R. Protected marine reserves as hedge against uncertainty: an economist's perspective. In: T. J. Pitcher, D. Pauly, and P. Hart, eds., *Reinventing fisheries management*, Chapman and Hall, London, England, Vancouver, BC, Canada, 303-309, 1998a.
- Sumaila, U.R. Protected marine reserves as fisheries management tools: a bioeconomic analysis. *Fisheries Research*, 37, 287-296, 1998b.
- Vance, R. The effects of dispersal on population stability in one-species, discrete space population growth models, *American Naturalist*, 123(2), 230-254, 1984.

## 7. APPENDIX . EQUILIBRIUM CHARACTERISTICS.

The Jacobian matrix of the sink-source case:

$$A_{ss} = \begin{bmatrix} r - 2rx_1 - d & 0 \\ d & r - 2rx_2 \end{bmatrix}$$

In the density dependent case:

$$A_{dd} = \begin{bmatrix} r - 2rx_1 - d & a \\ d & r - 2rx_2 - a \end{bmatrix}$$

For all of the parameter values used in this paper we have that the trace of A (tr(A)) is less than zero, the determinant of A ( $|A|$ ) is greater than zero,  $\text{tr}(A)^2 - 4|A| > 0$  and the eigenvalues are negative when evaluated in optimum, which are the characteristics of an asymptotically stable improper node.