Fish, fishers, seals and tourists: Economic consequences of creating a marine reserve in a multi-species, multi-activity context*

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Abstract:
This paper investigates some economic consequences of creating a marine reserve on both fishing and ecotourism, when the range of controllability of fishing effort is limited and the impact of the reserve on ecosystem is considered. The issue is illustrated by the example of creating a no-take zone in part of a region where fishing is managed through a limited entry license system, and which is inhabited by two interacting stocks: a stock of prey (fish) and a stock of predators (seals). While the former is targeted by commercial fishing, the latter is not subject to harvest but is a potential basis for a commercial non-extractive activity (seal watching). Analysis is conducted with the help of a bioeconomic model combining the features of marine reserve modeling and of multispecies modeling. Following a description of the model, results of several simulation runs are presented. These show that creating a marine reserve has more complex economic implications than predicted in studies focused exclusively on one stock and/or commercial fisheries. More specifically, the model shows that the dynamics of the two interacting stocks reduces the benefits of the no-take zone for the fishing industry, while it makes the creation of this zone provide an opportunity for the development of ecotourism. Due to this dynamics, the model suggests that the optimal size of the reserve is larger when ecotourism is taken into account along with fishing activities.

Keywords : Marine protected areas, multispecies interactions, ecotourism, bioeconomic modeling

Introduction
Various achievements are expected from the creation of marine reserves (Shackell et al., 1995 ; Murray et al., 1999). The objectives pursued can usually be classified under one of the following three categories : ecosystem preservation, fisheries management and development of non-extractive recreational activities. At a general level, the degree of compatibility between these objectives is

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difficult to assess. It is bound to vary from case to case, depending on local conditions. The variety of interests at stake is a source of potential conflicts during the process of creating a marine reserve (Dixon et al., 1993; Polunin et al., 2000), which calls for the development of tools helping a global assessment of its impact (Hoagland et al., 1995), both in terms of efficiency (global surplus) and equity (distributional effects among the various categories of stakeholders).

Up to now, the economic discussion concerning marine reserves has mainly focused on their use as a fisheries management tool. Making use of a single-species multiple-cohort model incorporating a stock-recruitment relationship, Holland and Brazee (1996) have shown that marine reserves could improve sustainable catches in overexploited fisheries, given a fixed level of fishing effort. Introducing uncertainty into the harvested fraction of the stock and using a global discrete-time logistic model, Lauck et al. (1998) have advocated marine reserves as a way of implementing the precautionary principle in fisheries management. Also using a global logistic model, Hannesson (1998) and Anderson (2000) have questioned the usefulness of marine reserves as a tool for fisheries management in a deterministic context, as long as free access is accepted outside the reserve. The assumption of space homogeneity inside the fishery, which is common to the above mentioned papers, was relaxed by Sanchirico et al. (1999).

Marine reserves may also have an economic impact on ecotourism (Agardy, 1993), a term being used here for naming non-extractive recreative activities related to the ecosystem. Studies considering this question mainly deal with tropical areas (see e.g. Kenchington, 1993; Dixon et al., 1993; Davis and Harriot, 1995; Buerger, Hill et al., 2000), and treat the consequences of marine reserves on ecotourism as a direct corollary of their impact on fish biomass. The standard case is that of a coral reef, which becomes more attractive for snorkellers and scuba-divers if a fishing ban increases the number and / or size of fish within the reef or close to it. Models used for assessing reserves as fisheries management tools may be used to study this case, provided a relationship between fish abundance and tourist frequentation is worked out. Once such a relationship is incorporated, these models may be used to investigate the question of optimal reserve design and appropriate supplementary measures within the general framework of cost-benefit analysis (Hoagland et al., 1995).

However, the coral-reef case is hardly transferable to temperate areas, where observation of fish in their ecosystem (by diving, tours in glass-bottom boats or other means) in most cases cannot be regarded as a major opportunity for the development of ecotourism. If marine wildlife observation has proved to be an important attraction for ecotourism in many of these areas, the link with fish biomass, if any, is usually indirect, i.e. operates through the ecosystem. One interesting case is that of marine mammal watching, which has become a significant source of incomes in some areas (Anon., 1994; Hoyt, 1995; Hvenegaard, 1997). In the case where the diet of these mammals makes them competitors of fishers3, implementing a marine reserve in part of a fishing zone may have indirect economic consequences both on the fishing industry and ecotourism, through its impact on the stock of marine mammals. Making use of multispecies modelling is helpful to investigate such indirect consequences.

This paper presents a simple bioeconomic model describing some consequences of implementing a marine reserve in part of an area where fishing is conducted under a limited entry licence system, and which is inhabited by two interacting stocks: a stock of prey (fish) and a stock of predators (seals). While the former is targeted by commercial fishing, the latter is not subject to harvest but is a

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3 The case of direct competition for fish, which will be considered here, is not the only type of interaction between marine mammals and fisheries (Beddington et al., 1985; Trites et al., 1997)
potential basis for the development of ecotourism (seal watching). First the structure of the model is described, then the results of some simulations are presented. These results are used to discuss the direct and indirect impacts of the reserve on both fishing activities and ecotourism.

1. Description of the model

1.1 Hypothesis

The model presented here combines two topics which are usually treated separately: marine reserve modelling and multispecies modelling. The treatment of each of these topics is highly simplified, and based respectively on Hannesson (1998) and Flaaten (1989). The main biological and technical assumptions of our model follow the hypothesis made by these two authors:

- deterministic, continuous time self-regenerating model, applied to a zone considered ecologically homogeneous and relevant for the management of the living marine resources inhabiting it;
- distinction between two stocks, related by a prey-predator relationship where the instantaneous mortality rate of prey by the predators is supposed to be proportional to the biomass of predators, and the predator carrying capacity of the area is supposed to be proportional to the biomass of prey (Flaaten); in our model, prey will be called “fish” (stock $F$) and predators “seals” (stock $S$);
- global representation of each stock (or each substock in the case of fish), the natural dynamics of which follows a logistic curve;
- tendency of the fish stock to spread uniformly over the area under survey, at a rate which depends on an exogenous mobility coefficient (Hannesson);
- proportionality of CPUE to fish density inside the fishing zone (Hannesson).

However, our institutional / economic hypothesis are slightly different:

- like Hannesson, we suppose that the area under survey is split into two subspaces: a reserve, i.e. a zone where fishing is forbidden (zone 1) and a zone open to fishing (zone 2); but unlike that author, we assume a limited entry licence system, or some other regulation resulting in an effective control over fishing effort; however, we acknowledge that, due to political / social considerations, the regulator’s ability to lower fishing effort is limited.
- unlike Flaaten, we suppose that only one of the two interacting stocks is harvested: while fish are targeted both by seals and fishers, seals are not harvested, but may have some economic value as a

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4 The choice of this example was motivated by a debate on such an issue in the context of the forthcoming creation of a marine national park in the Iroise sea, a coastal sea west of Brittany (France). This area is characterised by a great variety of living marine resources (Hily et al., 1999) and shelters a small colony of seals which, local fishermen fear, might grow as a consequence of a fishing ban within the limits of the park. On the other hand, this possible development is regarded as an opportunity for new income in a region visited by many tourists (Anon., 1999).

5 As in Hannesson (1998) and Anderson (2000), a discrete time version of the model is also built for the purpose of simulations. See Appendix I.

6 For the seal stock, we assume ubiquity over the whole area, i.e. we admit that seals can move instantly from any part of this area to another and exert on each substock of fish a predation which is proportional to its biomass. Therefore no distinction is made between seals inside the reserve and seals inside the fishing zone.

7 This hypothesis seems realistic as regards a number of inshore fisheries. In France for instance, there is a general tendency for fisheries within the 12 NM to have limited entry licence systems, managed by fishers organisations under the supervision of the state (Pennanguer et al., 2001). When a limited entry licence system is introduced into a fishery, the aim is clearly to prevent any further increase in fishing effort, and possibly to gradually decrease it. However, in practice this decrease may only be achieved by attrition.
resource for a non extractive recreative use (seal watching). We assume that the demand for seal watching is a non-linear increasing function of the stock of seals in the area under survey.

All prices are treated as exogenous.

1.2 Equations

The dynamics of both stocks is modelled as follows:

\[
\frac{dX_{F1}}{dt} = r_F . X_{F1} \left(1 - \frac{X_{F1}}{\alpha . X_{Fmax}}\right) - T - \beta . X_{F1} . X_S
\]

\[
\frac{dX_{F2}}{dt} = r_F . X_{F2} \left(1 - \frac{X_{F2}}{(1 - \alpha) . X_{Fmax}}\right) + T - \beta . X_{F2} . X_S - Y_F
\]

\[
\frac{dX_S}{dt} = r_S . X_S \left(1 - \frac{\gamma . X_S}{X_{F1} + X_{F2}}\right)
\]

with:

- \(X_{Fi}\) the fraction of the fish stock biomass in sub-region \(i\) (\(i = 1, 2\))
- \(X_S\) the seal stock biomass
- \(r_F\) the intrinsic growth rate of the fish stock biomass
- \(r_S\) the intrinsic growth rate of the seal stock biomass
- \(X_{Fmax}\) the fish carrying capacity of the total region under survey
- \(T\) the net instantaneous transfer of fish from the reserve to the fishing grounds
- \(Y_F\) the instantaneous catch of fish by fishers in the region open to fishing
- \(\alpha\) the share of the reserve in the total region under survey
- \(\beta\) the predation coefficient (instantaneous fish mortality rate per seal biomass unit)
- \(\gamma\) the equilibrium ratio between fish biomass and seal biomass

The net transfer of fish from the reserve to the fishing grounds, \(T\), is supposed to be proportional to the difference between the fish biomass in the reserve and what it would be assuming uniform spread of fish over the whole area under survey:

\[
T = \sigma . [X_{F1} - \alpha . (X_{F1} + X_{F2})] = \sigma . [(1 - \alpha) . X_{F1} - \alpha . X_{F2}]
\]

with \(\sigma\) a coefficient describing the space mobility of fish.\(^8\)

The catch per unit of effort is supposed to be proportional to the density of fish in the fishing zone:

\[
T = s . (D_{F1} - D_{F2}), \text{ with } s = \sigma . \alpha . (1 - \alpha) . A.
\]

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\(^8\) At present this assumption also looks realistic in the context of several countries, including France. Non-extractive use value may be associated with a non-use value (existence value), not taken into account here.

\(^9\) This is equivalent to assuming that fish migration depends on relative density between the two areas: let \(A\) be the total surface of the area under survey, \(D_{F1} = X_{F1}/(\alpha . A)\) and \(D_{F2} = X_{F2}/(1 - \alpha) . A\) be the densities of fish in the reserve and fishing zone respectively, then we get from (4): \(T = s . (D_{F1} - D_{F2})\), with \(s = \sigma . \alpha . (1 - \alpha) . A\).
\[ \frac{Y_F}{E_F} = q \cdot D_{F2} \iff Y_F = q \cdot E_F \cdot \frac{X_F}{(1 - \alpha) \cdot A} \]

with:

- \( q \) the catchability coefficient (instantaneous fish mortality rate per unit of fishing effort and per unit of surface)
- \( E_F \) the fishing effort
- \( D_{F2} \) the fish density inside the fishing zone
- \( A \) the surface of the total area under survey

Ecotourism is supposed to be the result of combining two partly substitutable factors: natural resource (the seal stock) and production effort (an index of the anthropic inputs devoted to the promoting of ecotourism in the area under survey). For the sake of simplicity, we will assume a Cobb-Douglas type production function:

\[ Y_s = a \cdot X_s^b \cdot E_s^c \]

with:

- \( Y_s \) the flow of ecotourism visits of the area
- \( E_s \) the effort devoted to the ecotourism industry
- \( a \) a positive dimension parameter
- \( b \) the elasticity of visits with regard to the abundance of seals
- \( c \) the elasticity of visits with regard to the effort devoted to promoting ecotourism

The fishing and ecotourism rents are defined respectively as follows:

\[ R_F = P_F \cdot Y_F - C_F \cdot E_F \]
\[ R_S = P_S \cdot Y_S - C_S \cdot E_S \]

with:

- \( P_j \) the unit price of the product of activity \( j \) (\( j = F, S \))
- \( C_j \) the unit cost of effort devoted to activity \( j \) (\( j = F, S \))

For given effort levels in both activities, the system reaches equilibrium when the following conditions are satisfied simultaneously:

\[ \frac{dX_{F1}}{dt} = 0 \]
\[ \frac{dX_{F2}}{dt} = 0 \]
\[ \frac{dX_S}{dt} = 0 \]

2. Simulations
Various simulation experiments with the model were carried out using softwares Excel and Stella. For this purpose, a discrete time version of the model was built. In these simulations, the equilibrium was calculated as the asymptotic result of the dynamics of the system, assuming given initial conditions. Although the path towards equilibrium displays some interesting features, only equilibrium results will be presented here. All the figures belong therefore to comparative statics, i.e. they link various equilibrium situations but give no information about the actual move from one equilibrium to another. We shall start with a version of the model where parameter $\beta$ is set equal to zero (no mortality of fish by seals), in order to display what can be expected from the reserve in terms of fisheries management, when the ecosystemic interaction between the two stocks is not taken into account (direct effect of the reserve). Then we shall give a positive value to parameter $\beta$, which will depict how the impact of the predator-prey relationship mitigates the direct effect of the reserve for the fishing industry, and in the same time affects ecotourism. As parameters of the model are not based on real-world observations, the main features described by the simulations presented hereafter should be considered from a qualitative, rather than quantitative point of view.

2.1 Reserve effects without predator-prey interaction

In this first series of simulations, $\beta = 0$, which means no predation by seals. Under this hypothesis, the simulations are interesting only from the point of view of fisheries management (Figures 1 to 4).

Figure 1 depicts the basic effect expected from the creation of a reserve on fish biomass: while the fraction of the stock in the fishing zone tends to zero as effort increases, the fraction inside the reserve is safe, which may give some protection against stock collapse due to overfishing. This presentation is greatly simplified, as fish transfers between zones link the dynamics of the two fractions of the stock. The critical ratio here is between the intrinsic growth rate of the stock ($r_F$) and its space mobility coefficient ($\sigma$): as pointed out by Anderson (2000), the safe minimum biomass level (SMBL) achieved by the reserve will be positive only if $\sigma \leq r_F$, or, in the opposite case, if the proportion of the reserve in the total area, $\alpha$, is larger than $1 - (r_F / \sigma)$. The simulations presented here are compatible with a positive SMBL, as parameter values have been selected so that $\sigma \leq r_F$.

Figure 2 exhibits, in flow terms, what was presented in Figure 1 in terms of stocks. Under equilibrium conditions, catches realised in the fishing zone have two origins: the flow of natural increase of the fraction of the stock in this zone, and the flow of net transfer from the reserve. The first flow is the main source of catches when the fishery is lightly fished, because then net transfer from the reserve is not important. This is due to the fact that the densities of fish biomasses in both zones are close to each other when fishing mortality occurring in zone 2 is low. The net transfer from the reserve becomes more important as the increase in fishing effort broadens the gap between the densities inside the two zones. The density inside the fishing zone tends to zero, and the flow of transfer tends towards a limit proportional to the SMBL in the reserve. When the fishery is heavily fished, most of the catches come from transfers from the reserve.

Figures 3 and 4 compare several scenarios concerning the relative size of the reserve and fishing zone. As shown by Figure 3, the level of the SMBL (the asymptotic value of fish biomass in the reserve and, by extension, in the whole area when fishing effort grows indefinitely) is an increasing function of the ratio $\alpha$ representing the share of the reserve in the whole area. This protection effect of the reserve has a counterpart in terms of catches, which appears in Figure 4. Protecting the stock against

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10 See the equations of the discrete time version of the model, the values of the parameters and the initial values of the state variables in Appendix I.

11 The simulations presented in the paper were calculated with Excel, and equilibrium was considered as reached after 50 periods.
the risk of a collapse, the reserve also secures catches if fishing effort becomes very important: as was shown on figure 2, the flow of catches becomes close to the flow of net transfer from the reserve, which itself depends on the ratio \( \alpha \). However, the relation is not monotonic, because, when the fraction of the stock inside the fishing zone tends to zero, the net flow of transfer from the reserve comes close to:

\[
T^* = \alpha(1 - \alpha)X_{F1}^*
\]

where \( X_{F1}^* \) is the SMBL. The higher \( \alpha \), the higher is also \( X_{F1}^* \) (cf. Figure 3), but the lower is \( (1 - \alpha) \), the share of the fishing zone in the whole area. These two factors act in opposite directions on \( T^* \): the flow of transfer from the SMBL, which is low when the ratio \( \alpha \) is close to zero, increases with \( \alpha \) up to some point, after which it starts decreasing as \( \alpha \) tends to 1. On figure 4, \( T^* \) increases when \( \alpha \) goes from 30% to 50%, but decreases if \( \alpha \) goes from 50% to 80%.

For a lightly fished fishery, the volume of sustainable catches corresponding to a given level of effort and the ratio \( \alpha \) vary in opposite directions. This is so because in this case, net transfer from the reserve is unimportant (see Figure 2), and the main consequence of increasing \( \alpha \) is to diminish the biomass directly exploitable by fishermen.

The value of \( \alpha \) maximising catches varies according to the level of fishing effort. Low or even zero when fishing effort is not important, this value shows a tendency to rise (up to some limit) as fishing effort increases. If fishing effort and its impact on fish biomass are under perfect control, there is little to expect from the creation of a marine reserve as regards fisheries management: the maximum maximorum of catches (and, a fortiori, of fishing rent\(^{12} \)) is achieved with a zero \( \alpha \). However, as was stated by Holland and Brazee (1996), if the control of fishing effort is bounded by social / political constraints, the creation of a reserve may in some cases be regarded as a second best solution, because once a certain level of effort is attained, sustainable catches become more important with a reserve than without it, caeteris paribus. This feature, added to the benefits of “bet-hedging” advocated by Lauck et al. (1998), suggests that in many real world cases, characterised both by the existence of some control of fishing effort and by the political inability of the regulator to bring it down to the “first best” level, marine reserves should be regarded as a useful tool for fisheries management. The benefits of this solution are jeopardised if the creation of the reserve is followed by an increase in total fishing effort, which is the type of problem addressed by Hannesson (1998) and Anderson (2000), when they make the hypothesis of free access to the resource outside the reserve.

2.2 Consequences of the predator-prey interaction

We now turn to the case where \( \beta > 0 \), i.e. we suppose that seals, along with fishers, exert some predation on the fish stock (Figures 5 to 9). Compared to the former simulations, those performed under this hypothesis will help to assess the indirect impact of the reserve on the fishing industry (i.e. the consequences due to ecosystemic interactions), as well as the impact of the reserve on ecotourism (seal watching). The dotted line on each figure recalls the situation when there is no predation by seals \((\beta = 0)\).

Figures 5 and 6 illustrate the impact of the predator-prey relation on biomasses and catches in relation to fishing effort, for a given size of the reserve. The comparison between the dotted line and the continuous line on Figure 5 shows that taking into account the prey-predator relation lowers the level of equilibrium fish biomass for each level of fishing effort. In particular, the SMBL is lower when the predator-prey interaction is taken into account, and varies inversely to the rate of predation by seals

\(^{12}\) The level of effort maximising rent being systematically lower than the one maximising catches, as soon as the marginal cost of fishing effort is positive.
(see Appendix II for a demonstration). However, the negative effect of the predator-prey interaction, which is the consequence of predation by seals, becomes less important when fishing effort grows, because the food shortage which this growth induces for seals results in a decrease of their equilibrium stock (see lower line on Figure 5).

Figure 6 illustrates how, under equilibrium conditions, the flow of natural growth of the fish biomass is shared between fishermen and seals, for various levels of fishing effort and for a given size of the reserve. The flow of predation by seals, which is equal to the total flow of natural growth of the fish biomass when there is no fishing effort, decreases both in absolute and relative terms when fishing effort grows, making the competition for food tougher for seals, and thereby diminishing their stock (see Figure 5). Figure 6 also shows that, for any given level of effort, taking into account the prey-predator relation results in lowering the level of equilibrium catches by fishermen.

Figures 7, 8 and 9 display some consequences of the prey-predator interaction in relation to the size of reserve, for a given level of fishing effort.

Figure 7 shows that the impact of this relation on the equilibrium fish biomass is more important when the share of the reserve in the total area is large. This is due to the fact that any increase in food abundance (a consequence of increasing the reserve size with a given level of effort) results in increasing the seal stock: under the assumptions of the prey-predator model used here, not only do seals eat more when there is plenty of food, but they become more numerous\(^\text{13}\). While the predator-prey interaction may be regarded as an unnecessary refinement of the analysis in the case of a small \(\alpha\), this parameter becomes critical if the relative size of the planned reserve is large, a condition which is often regarded as necessary if the reserve is meant to generate significant impacts on the situation of the fishery (Lauck et al., 1996; Sladek Nowlis and Roberts, 1999).

Figure 8 depicts the consequences in terms of flows. It shows that, while the total flow of increase in fish biomass is a monotonically growing function of the relative size of the reserve, for large values of \(\alpha\) this phenomenon benefits seals rather than fishers. Two factors explain this feature: 1) the switch to a larger relative size of reserve increases the seal stock (see Figure 7), while fishing effort is assumed to be unchanged; 2) while fishermen respect the fishing ban inside the reserve (also by assumption), seals ignore it and pursue their prey over the whole area, whatever the level of \(\alpha\) adopted by the fishery regulator.

Figure 9 translates the features displayed by Figure 8 in terms of economic rent, and illustrates the trade-off between the fishing industry and ecotourism according to the relative size of reserve which is adopted. It should be stressed that, because the values of parameters are arbitrary (and in particular the prices and unit costs of each activity), the indications given by the figure are qualitative. The economic parameters of the model have been fixed at levels such that the fishery rent is zero when there is no reserve, and the break-even point for the ecotourism industry corresponds to a 10% relative size of the reserve. This case is of course just an example.

According to Figure 9, the steady-state rent derived from the fishery increases with the relative size of the reserve, for an unchanged level of effort, up to an \(\alpha\), between 30% and 40% of the total area in the case illustrated here. This is the direct consequence of the increase in catches (see Figure 8), which is itself the result of the increase in the fish biomass protected by the reserve. However, beyond this level of \(\alpha\), catches decrease because the net transfer of fish from the reserve is not important enough to compensate for the negative impact of the decrease in the size of the fishing zone. So does the

\(^{13}\) Joining equations (1), (2), (3) and (11) shows that, under equilibrium conditions, predation by seals is proportional to the square of the fish biomass.
fishery rent, the level of effort and unit prices being unchanged by assumption. The comparison of the fishery rent curve with the dotted line (fishery rent when $\beta = 0$) shows that, for any value of $\alpha$, the predator-prey interaction reduces the benefits of the reserve for fishers (the importance of this effect will depend on the actual size of the impact of predation by seals on fish biomass). At the same time, the growth in the seal stock generated by a higher relative size of the reserve increases the opportunity of making money through ecotourism. Unlike the relation between fishery rent and $\alpha$, the relation between ecotourism rent and $\alpha$ is monotonic, because 1) the seal stock increases monotonically with $\alpha$, and 2) the number of visits by ecotourists is assumed to be an increasing function of the seal stock. As a result, the higher is $\alpha$, the larger the gap is between the total economic surplus generated by the marine reserve and the fishery rent. A corollary is that the optimal reserve size, according to a global cost-benefit analysis, is larger than the one which looks optimal if fisheries management is the only objective (within the interval between the two corresponding $\alpha$s, the net marginal loss for the fishing industry induced by an increase in the relative size of the reserve being lower, in absolute value, than the corresponding net marginal gain for the ecotourism industry). As long as the reserve size is kept below the level maximising fishery rent, any marginal increase in $\alpha$ benefits simultaneously both activities (Pareto-improving change). Beyond this level, any further increase in the reserve size will still improve overall efficiency of the reserve, provided $\alpha$ is kept below the level maximising global economic surplus. However, this improvement will be realised at the detriment of the fishing industry, which suggests that the fishing sectors might seek compensation of some sort for lost revenues. A such, policy makers seeking to put marine reserves in place may need to be sensitive to these losses, in order to enlist necessary support.

**Conclusions**

The aim of the simulation model presented in this paper is to develop further insights to the economics of marine reserves, from a multispecies perspective and taking into account non-extractive uses of marine ecosystems. The complexity of ecosystemic interactions is sometimes advocated for keeping up with monospecific modelling, because little advantage is expected from the integration of trophic competition or predator-prey relations between stocks as far as economic assessment of marine reserves is concerned (Holland and Brazee, 1996). In some cases however, multispecies modelling is necessary to deal with the economic problem which is addressed. A case in point is the situation where a marine reserve is planned inside an area sheltering a stock of fish targeted by fishers and a stock of predators which is protected by law from any extractive use, but which may provide benefits from non-extractive uses. Though based on real world considerations (both as regards biology and institutions), the model presented here does not pretend to entirely capture the complexity of ecosystemic interactions at stake. Moreover, due to the arbitrary parameter values used in the simulations, the significance of the conclusions which may be drawn from these simulations is mainly qualitative. These conclusions may be summed up as follows:

1. The model supports the idea that implementing a marine reserve in part of a highly fished fishery may constitute a second best solution as regards fisheries management, in the case where the entry into the fishery is limited but the regulator’s ability to lower fishing effort is bounded by social / political constraints. This idea, which was put forward by Holland and Brazee (1996) in a monospecific context, still holds when the area is inhabited by a non-harvested stock of predators competing for fish with fishers and taking advantage of the creation of the reserve.

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For instance, the global treatment of fish does not allow the model to deal with the fact that, in most marine systems, the largest predator of fish are other fish, not marine mammals. However, the reasons why we give a special treatment to the seal-fish relation in the model are not biological, but institutional and economic: we suppose that, as opposed to various fish stocks, marine mammals are protected by law and may derive an economic value from non-extractive uses. These seem to be realistic assumptions in a number of temperate inshore waters cases.
2. The predator-prey interaction results in lowering the benefits of the reserve for fishers. This affects the steady-state fishery rent for any given level of fishing effort, but also the expected results of the reserve in terms of conservation effects, as the safe minimum fish biomass level provided by the implementation of the reserve is reduced by the fish mortality due to the unharvested stock of predators.

3. In the case where the stock of predators may be economically valued by means of a non-extractive use (ecotourism), the implementation of the reserve generates additional incomes through this channel. According to local circumstances, these extra incomes will partly or totally offset the negative impact of the predator-prey interaction on the fishery rent.

4. In this case, the model suggests that the optimal relative size of the reserve, from a global cost-benefit analysis point of view, is larger than when only fishery rent is considered.

Conclusions 3 and 4 raise the issue of the distributional impact of the reserve, and of the possibility for fishers to participate in the benefits generated by ecotourism. This issue could be addressed by incorporating some relations into the model that depict more explicitly the costs and benefits to fishers of diversifying their activity\textsuperscript{15}.

\textsuperscript{15} A preliminary investigation of this question was realised, in the Iroise Sea case, by Boncoeur et al.(2000).
Figures

Fig. 1. Relation between fishing effort and fish biomasses
(intrinsic growth rate of fish biomass = 0.3; mobility coeff. = 0.2; reserve = 30% of total area; no predation)

Fig. 2. Relation between fishing effort, net transfer from the reserve to the fishing zone and catches
(intrinsic growth rate of fish biomass = 0.3; mobility coeff. = 0.2; reserve = 30% of total area; no predation)
Fig. 3. Relation between fishing effort and total fish biomass according to the relative size of the reserve (intrinsic growth rate of fish biomass = 0.3; mobility coeff. = 0.2; no predation).

Fig. 4. Relation between fishing effort and catches according to the relative size of the reserve (intrinsic growth rate of fish biomass = 0.3; mobility coeff. = 0.2; no predation).
Fig. 5. Relation between fishing effort, fish biomass and seal biomass
(intrinsic growth of fish biomass = 0.3; mobility = 0.2; reserve = 0.3; predation of fish by seals)

Fig. 6. Relation between fishing effort, catches and predation by seals
(intrinsic growth of fish biomass = 0.3; mobility = 0.2; reserve = 0.3; predation of fish by seals)
Fig. 7. Relation between relative size of the reserve and biomass levels for a given level of fishing effort (intrinsic growth of fish biomass = 0.3; mobility = 0.2; effort = 100; predation of fish by seals).

Fig. 8. Relation between relative size of the reserve, catches and predation by seals for a given level of fishing effort (intrinsic growth of fish biomass = 0.3; mobility = 0.2; effort = 100).
Fig. 9. Relation between relative size of the reserve and economic rents for a given level of fishing effort (intrinsic growth of fish biomass = 0.3; mobility = 0.2; fishing effort = 100; predation by seals)

Relative size of the reserve, as a percentage of total area

Rent types:
- Fishery rent
- Ecotourism rent
- Total rent (fishery + ecotourism)
- Fishery rent when there is no predation by seals
References


ANON. (1999) Etude économique des activités liées à la mer d’Iroise. ADEUPA / Portances / SAFI, Brest, France (3 volumes).


Appendix I : the discrete time version of the model

A discrete time version of the model was built for the sake of simulations. The transition from the continuous to the discrete version rests on some simplifying assumptions. Following Hannesson (1998) and Anderson (2000), we assume that, for each period, natural growth and migration of fish biomass take place after catches and are independent (they are in fact treated as discrete jumps at the end of each period)\(^{16}\). Moreover, we assume that catches by fishers and predation by seals are simultaneous, and that the natural growth of seal biomass also takes place at the end of each period. Under these assumptions, the equations of the discrete time version of the model may be written as :

\begin{align*}
1') & \quad X_{F1(t+1)} = (X_{F1(t)} - Z_{1(t)}) \left[ 1 + r_F \left( 1 - \frac{X_{F1(t)} - Z_{1(t)}}{\alpha X_{F_{max}}} \right) \right] - T_{(t)} \\
2') & \quad X_{F2(t+1)} = (X_{F2(t)} - Z_{2(t)} - Y_{F(t)}) \left[ 1 + r_F \left( 1 - \frac{X_{F2(t)} - Z_{2(t)} - Y_{F(t)}}{(1 - \alpha) X_{F_{max}}} \right) \right] + T_{(t)} \\
3') & \quad X_{S(t+1)} = X_{S(t)} \left[ 1 + r_S \left( 1 - \frac{\gamma X_{S(t)}}{X_{F1(t)} + X_{F2(t)}} \right) \right] \\
4') & \quad T_{(t)} = \sigma \left[ (1 - \alpha) \left( X_{F1(t)} - Z_{1(t)} \right) - \alpha \left( X_{F2(t)} - Z_{2(t)} - Y_{F(t)} \right) \right] \\
5') & \quad Z_{1(t)} = X_{F1(t)} \left( 1 - e^{-\beta X_{S(t)}} \right) \\
6') & \quad Z_{2(t)} = \left( \frac{\beta X_{S(t)} - \gamma E_{F(t)}}{\beta X_{S(t)} + \frac{q.E_{F}}{(1 - \alpha) A}} \right) \cdot X_{F2(t)} \left( 1 - e^{-\beta X_{S(t)} - \frac{q.E_{F}}{(1 - \alpha) A}} \right) \\
7') & \quad Y_{F(t)} = \left( \frac{\gamma E_{F}}{(1 - \alpha) A} - \frac{q.E_{F}}{(1 - \alpha) A} \cdot X_{F2(t)} \left( 1 - e^{-\beta X_{S(t)} - \frac{q.E_{F}}{(1 - \alpha) A}} \right) \right) \\
8') & \quad Y_{S(t)} = a.b.X_{S(t)}^{b}, E_{S}^{c} \\
9') & \quad R_{F(t)} = P_{F}Y_{F(t)} - C_{F}E_{F} \\
10') & \quad R_{S(t)} = P_{S}Y_{S(t)} - C_{S}E_{S}
\end{align*}

**Endogenous variables :**

\begin{align*}
X_{F(t)} & \quad \text{Fish biomass inside zone } i (i = 1, 2) \text{ at the beginning of period } [t ; t+1[ \\
X_{S(t)} & \quad \text{Seal biomass at the beginning of period } [t ; t+1[ \\
Z_{i(t)} & \quad \text{Predation of fish by seals inside zone } i (i = 1, 2) \text{ during period } [t ; t+1[ \\
Y_{F(t)} & \quad \text{Catches of fish by fishers during period } [t ; t+1[ \\
T_{(t)} & \quad \text{Net transfer of fish from zone 1 to zone 2 at the end of period } [t ; t+1[ \\
Y_{S(t)} & \quad \text{Seal watching visits during period } [t ; t+1[ \\
R_{j(t)} & \quad \text{Rent generated by activity } j (j = F, S) \text{ during period } [t ; t+1[ \\
\end{align*}

\(^{16}\) Anderson (2000) considers that they follow semi-continuous time processes (each period being divided into a fishing time and a growth-and-migration time, which makes it more difficult to consider growth and migration processes as independent).
Exogenous variables and parameters:

- $r_j$: intrinsic growth rate of biomass $j$ ($j = F, S$)
- $X_{F_{\text{max}}}$: fish carrying capacity of the whole area (zones 1 and 2)
- $\alpha$: share of the reserve in the whole area
- $A$: surface of the whole area
- $\sigma$: fish mobility coefficient
- $\beta$: predation coefficient
- $\gamma$: equilibrium ratio between fish biomass and seal biomass
- $q$: catchability coefficient
- $E_j$: anthropic effort in activity $j$ ($j = F, S$)
- $a$: dimension parameter of the ecotourism attraction function
- $b$: elasticity of visits with regard to the abundance of seals
- $c$: elasticity of visits with regard to the ecotourism attraction effort
- $P_j$: unit price of the product of activity $j$ ($j = F, S$)
- $C_j$: unit cost of effort devoted to activity $j$ ($j = F, S$)

The simulations presented in the paper were based on the following initial conditions and parameter values:

<table>
<thead>
<tr>
<th>Initial conditions</th>
<th>Values of parameters and exogenous variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>$X_F(t = 0) = 0,5, \alpha X_{F_{\text{max}}}$</td>
<td>$r_F = 0,3$</td>
</tr>
<tr>
<td>$X_S(t = 0) = 0,5, (1 - \alpha) X_{F_{\text{max}}}$</td>
<td>$r_S = 0,1$</td>
</tr>
<tr>
<td>$X_S(t = 0) = 0,5, X_{F_{\text{max}}} / \gamma$</td>
<td>$X_{F_{\text{max}}} = 1000$</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>$0$ to $1$ according to simulations</td>
</tr>
<tr>
<td>$A$</td>
<td>$1$</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>$0,2$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>$0,001$</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>$10$</td>
</tr>
<tr>
<td>$q$</td>
<td>$0,0025$</td>
</tr>
<tr>
<td>$E_F$</td>
<td>$0$ to $300$ according to simulations</td>
</tr>
<tr>
<td>$E_S$</td>
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</tr>
<tr>
<td>$a$</td>
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</tr>
<tr>
<td>$b$</td>
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</tr>
<tr>
<td>$c$</td>
<td>$0,2$</td>
</tr>
<tr>
<td>$P_F$</td>
<td>$5$</td>
</tr>
<tr>
<td>$P_S$</td>
<td>$6$</td>
</tr>
<tr>
<td>$C_F$</td>
<td>$0,9$</td>
</tr>
<tr>
<td>$C_S$</td>
<td>$60$</td>
</tr>
</tbody>
</table>
Appendix II: the effect of the predator-prey interaction on the safe minimum fish biomass level provided by the reserve

Joining equations (1) and (9), we get the equilibrium condition of the fish biomass inside the reserve:

\[
0 = r_F.X_{F1}.\left(1 - \frac{X_{F1}}{\alpha.X_{F\text{max}}}\right) - T - \beta.X_{F1}.X_S
\]

In the same way, joining equations (3) and (11) gives us the equilibrium condition of seal biomass:

\[
0 = 1 - \frac{\gamma.X_s}{X_{F1} + X_{F2}} \iff X_s = \frac{X_{F1} + X_{F2}}{\gamma}
\]

Joining (12), (13) and (4), we then get:

\[
-\left(\frac{r_F}{\alpha.X_{F\text{max}}} + \frac{\beta}{\gamma}\right).X_{F1} + \left(r_F - \sigma(1-\alpha) - \frac{\beta}{\gamma}.X_{F2}\right).X_{F1} + \sigma.\alpha.X_{F2} = 0
\]

Solving this quadratic polynomial in \(X_{F1}\) and selecting the relevant solution gives the equilibrium relation between the two fractions of the fish stock:

\[
X_{F1} = \frac{\left(r_F - \sigma(1-\alpha) - \frac{\beta}{\gamma}.X_{F2}\right) + \sqrt{\left(r_F - \sigma(1-\alpha) - \frac{\beta}{\gamma}.X_{F2}\right)^2 + 4\left(\frac{r_F}{\alpha.X_{F\text{max}}} + \frac{\beta}{\gamma}\right)\sigma.\alpha.X_{F2}}}{2\left(\frac{r_F}{\alpha.X_{F\text{max}}} + \frac{\beta}{\gamma}\right)}
\]

The fish SMBL is the equilibrium level \(X_{F1}^*\) of fish biomass inside the reserve which is observed when the fish biomass in the fishing zone \(X_{F2}\) falls to zero, i.e. :

\[
X_{F1}^* = \frac{r_F - \sigma(1-\alpha)}{r_F} \frac{X_{F2}}{\alpha.X_{F\text{max}}} + \frac{\beta}{\gamma}
\]

In the particular case where \(\beta\) is equal to zero (no predation by seals), the expression of the SMBL becomes:

\[
X_{F1}^* = \alpha.X_{F\text{max}}\left(1 - \frac{\sigma(1-\alpha)}{r_F}\right)
\]

which is the expression obtained by Anderson (2000). In the general case \((\beta \geq 0)\), expression (16) shows that the SMBL is positive provided:

\[
\alpha > 1 - \frac{r_F}{\sigma}
\]

a condition which is always satisfied in the case where \(\sigma \leq r_F\), and which is independent of the predator-prey interaction (parameters \(\beta\) and \(\gamma\)). However, when the above condition is satisfied, the level of the SMBL is a decreasing function of the ratio \((\beta/\gamma)\), which means that the predator-prey interaction has a negative impact on the protective effect of the reserve, as regards fisheries management.