

Simulation of the Effects of Marine Protected Areas on Yield and Diversity Using a Multispecies, Spatially Explicit, Individual-Based Model

Yunne-Jai Shin

Institut de Recherche pour le Développement, Laboratory LIA, Bondy, France

Philippe Cury

University of Cape Town, Oceanography Department, Rondebosch, South Africa

Abstract

The OSMOSE (Object-oriented Simulator of Marine biOdiverSity Exploitation) multispecies model is used to simulate the effects of Marine Protected Areas (MPAs) in the framework of nontargeted multispecies fisheries. The modeled theoretical populations are structured according to age and size. The predatory behavior rules by which they interact are implemented at the fish school level. Each species is attributed a mean distribution area within which, at each simulated year, the larval production is randomly distributed. The results of the simulations show that at high fishing rates, the setting of an MPA can enable the maintenance of the mean overall catches at a high level. In particular, for exploitation rates resulting in mortality rates greater than F_{MSY} , implementing different sizes of MPA highlights the existence of an optimal size for the MPA. Furthermore, the comparison of the effects induced by the direct reduction of the fishing effort, and by the closing of some fishing areas, suggests that this latter management measure is more efficient in terms of catch maximization and biodiversity conservation. This theoretical advantage is supposed to result from a particularity inherent to implementation of MPAs, which would indeed enable the preservation of not only a global fraction of the populations but also a set of trophic interactions that are localized in space and time. However, these results must be cautiously considered, as other po-

tentially important parameters have not been taken into account in the present work such as diffusive and migratory characteristics of the resource.

Introduction

With fishing effort intensifying on an increasing number of marine species, marine biodiversity conservation is becoming a critical issue for management (Hammer et al. 1993, Carlton and Butman 1995, Boehlert 1996, Eichbaum et al. 1996, Richards and Maguire 1998). One approach which is advocated for protecting marine biodiversity and promoting the sustainable use of marine resources is the implementation of Marine Protected Areas (Plan Development Team 1990, Ticco 1995, Bohnsack and Ault 1996, Eichbaum et al. 1996, Botsford et al. 1997, Hall 1998, Lauck et al. 1998, Castilla 1999). MPAs would allow the re-creation of natural refuges, which in the past have been too deep, isolated, and inaccessible to the exploitation (Dugan and Davis 1993). Along with this aim of conserving natural ecosystems, MPAs also provide an insurance against stock collapse (Attwood et al. 1997). Empirical and theoretical studies suggest that MPAs would allow increased yields, particularly when fishing mortality rates are important (e.g., Russ and Alcala 1990, Dugan and Davis 1993, Man et al. 1995, Lauck et al. 1998, Guénette and Pitcher 1999). Testifying to the increasing interest given to marine refuges for the maintenance of coastal ecosystems, the World Conservation Union has set before itself the objective to ban fishing from 20% of coastal waters by the year 2000 (IUCN 1992). However, there is still currently a lack of criteria to determine the optimal spatial limits of protected areas, as well as a lack of in situ observations to judge their long term consequences. Modeling work on marine reserves, then, takes its whole importance by allowing simulation of the effects of refuges in different configurations of the exploitation and the resource. On the other hand, the necessity of considering interactions between species in the study of MPAs is highlighted but scarcely taken into account in practice (Hall 1998). In this context, the individual-based model OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation) is used to investigate the potential effects induced by the implementation of an MPA on the exploitation of multispecies assemblages. The study is limited to the influence of refuge size and initial fishing level on both catches and diversity of the exploited ecosystem.

Methods

The Multispecies Model OSMOSE

An Individual-Based Model

The individual-based approach consists in following the fate of all individuals in a population, by assigning them some behavior rules that take

into account local interactions between individuals and with their environment (Huston et al. 1988, DeAngelis and Gross 1992, Van Winkle et al. 1993). It indeed postulates that minor events between individuals can have significant effects on the dynamic and the global state of the populations (Judson 1994).

One of the main hypotheses of the OSMOSE model is predation opportunism. This opportunism can readily be managed at the individual level by applying the "localization principle" which establishes that an individual is affected exclusively by the organisms that are located in its spatio-temporal vicinity (DeAngelis and Gross 1992). The choice of an individual-based approach is also justified by the second modeling hypothesis, namely that the criterion for the selection of prey is based on body size, and this can be characterized at the individual level.

OSMOSE is developed in the object-oriented language Java (JDK 1.1.3, Sun Microsystems). One important step in the development of OSMOSE was the choice of the biological entity corresponding to a computer individual. To allow significant gain in calculation time, the model is not brought down to the individual fish level but to an aggregated level corresponding to a group of fish having similar biological attributes and behavior rules regarding the modeled processes. The "super-individual" of the model, i.e., the unit of action and interaction, is a group of fish having the same size, the same spatial coordinates, requiring similar food, and belonging to the same species (therefore having similar physiological and morphological characteristics). Such aggregative behavior can be related to schooling behavior which occurs during at least one stage in the life cycle of about 80% of fish species (Burgess and Shaw 1979). Fish schools, however, appear to be more heterogeneous than those ideally implemented in the model. Pitcher (1983) suggests a general definition for schooling as being a group of fish in polarized and synchronized swimming. The size of schools can vary with time (Misund 1993) as well as its species composition (Bakun and Cury 1999, Fréon and Misund 1999). Despite these observations, strong homogeneity characterizes fish schools regarding fish size and body form (Fréon 1984, Pitcher et al. 1985). Thus, for convenience, the "super-individual" of the model will be called a fish school in the following sections.

OSMOSE architecture is based on a hierarchy since a fish school belongs to an age class, which in turn, belongs to a species. Four computer classes are then implemented: the class "system," the class "species," the class "cohort," and the class "fish school." This structure allows the study of some key variables at different levels of aggregation, in particular the abundance or the biomass of fish by age and by species.

The Biological Processes at Stake

The hypotheses of the model OSMOSE, as well as their implementation, are presented in detail by Shin and Cury 2001. This multispecies model allows the study of the spatial dynamics, structured in age and size, of a great number of species that interact. The time step of the model is one

reproductive period t , which in general, is one year in high-latitude ecosystems (Russel 1976, Froese and Pauly 1997). This step value is adopted by default for the set of simulations that will be subsequently described. Fish schools displace in a two-dimensional grid with closed boundaries. At model initialization, a certain number of object "species" are created, with the assignment of some attributes such as von Bertalanffy growth parameters, reproduction parameters (age at maturity, relative fecundity), longevity, and mean distribution areas by species and age. The object age classes and schools, which inherit their species biological parameters, are then successively created. The abundance of each age class and fish school can be determined by two different methods depending on the available information and the simulation objective: either from species abundances that are provided as input to the model, or from the ecosystem size spectrum (Shin and Cury 2001). Finally, each school is randomly distributed in the area attributed to its species and age class. Within each simulated year t , the fish life cycle can then be modeled, following the stages that are now described in an order which reflects the one implemented in the model.

Carrying Capacity Constraint. In OSMOSE, the carrying capacity corresponds to the upper limit of the viable biomass of all nonpiscivorous fish of the system. The piscivorous state of fish, that can be specified in the input, depends on their taxonomic identity and their age. For the set of simulations on MPAs, we chose to have age 1+ fish considered as piscivorous, and age 0 nonpiscivorous. The carrying capacity dynamic can be modeled in different ways depending on the investigated ecosystem (stationary, periodic, random, or with the occurrence of an anomaly).

At the beginning of each iteration t , the total biomass of nonpiscivorous fish is compared to the system carrying capacity. If it exceeds the carrying capacity, then the abundance of nonpiscivorous fish schools is reduced down to the implemented level of carrying capacity. The reduction in biomass operates uniformly among the nonpiscivorous schools: the same fraction of biomass is removed.

Foraging and Predation. This stage only concerns the piscivorous fish of the system. The order in which fish schools act is randomly set at each new time step t . School displacement is directed by the search of the adjacent cell with the highest biomass in potential preys. Once it has moved (or stayed in its cell), each fish school proceeds to the feeding phase, thereby causing an explicit predation mortality for each school preyed upon. It is remembered that two criteria form the basis of the predation process: an individual can potentially feed on any species provided that (1) there is a spatio-temporal co-occurrence (at time t , fish schools have to be located in the same cell to be considered accessible); and (2) the predator/prey size ratio does not exceed a certain threshold (estimated at about 3.5 in FishBase 97, Froese and Pauly 1997). An initial consequence of these rules is that a species can occupy different trophic levels in the system depending on the

age class considered (Bond 1979, Rice 1995). Therefore, two species can simultaneously be predator and prey of each other and predation opportunism takes into account the possibility of cannibalism. These trophic patterns are consistent with the observations of very diversified and time-varying diets of fish in different ecosystems in the world (e.g. Gislason and Helgason 1985, Crawford 1987, Alheit 1987, Mittelbach and Persson 1998).

Finally, when all fish schools have achieved feeding activity, a predation efficiency ξ is calculated for each fish school. This coefficient is determined by the ratio between the food biomass ingested by a school and the food biomass required to fulfill its vital functions. From values available for several species, it is estimated that a fish should annually consume 3.5 grams of food per body gram (Laevastu and Larkins 1981, Gislason and Helgason 1985, Longhurst and Pauly 1987).

Growth. Mean annual growth rates in length are calculated from the von Bertalanffy model (1938). This mean rate is readjusted to take into account the amount of food consumed by a fish school during a time step. A critical threshold ξ_{crit} can be determined for predation efficiency beyond which it is considered that the food ration is dedicated to fish growth. A simple approximation is to consider that if a school predation efficiency $\xi \geq \xi_{crit}$, then growth rate in length varies linearly with ξ such that (1) for $\xi = \xi_{crit}$ the rate is null, (2) for $\xi = (\xi_{max} + \xi_{crit})/2$, with $\xi_{max} = 1$, growth rate equals the mean growth rate calculated by the von Bertalanffy model.

Starvation Mortality. Starvation mortality is supposed to affect fish schools when the food ration is too low for fish maintenance requirements. Beverton and Holt (1957) advocate the possible existence of a starvation mortality for adult stages of fish in a linear model linking natural mortality rates to fish density. By considering that, for each species, nutritional resources are limited, this linear model is applied with the hypothesis that the greater the density of fish, the less the fish food ration will be. Hence, starvation mortality rates of fish schools are linearly expressed in relation to predation efficiency when $\xi \leq \xi_{crit}$.

Reproduction. Let Φ_s be the relative fecundity of species s , SB_s its spawning biomass, $B_{s,a}$ the biomass of age class a , a_{Ms} its age at maturity, and A_s its longevity. Assuming that the sex ratio equals 1:1 for all species, and noting $N_{s,0,t+1}$ the number of eggs spawned by species s at the end of the time step t , the following equation is applied:

$$N_{s,0,t+1} = \Phi_s SB_{s,t} \quad \text{with} \quad SB_{s,t} = \frac{1}{2} \sum_{a=a_{Ms}}^{A_s} B_{s,a,t}$$

Hence, the number of eggs spawned each year depends explicitly on fish growth. And as growth variability is implemented in relation to the

food intake, the reproduction process also depends implicitly on the food conditions that are encountered, locally in time and space, by each fish school. On the other hand, from this linear relationship, recruitment levels emerge as a consequence of the annual survival of eggs and juveniles, in relation with the predation process and with the annual level of the system carrying capacity.

Marine Refuge Implementation

Assumptions

For the set of realized simulations, marine reserves are considered to be permanent and consist of areas that are protected from all types of biomass extraction, regardless of the species considered (Bohnsack and Ault 1996). Marine reserves are explicitly represented in space and are characterized by a relative size RS , expressed in percentage of the total distribution area of the exploited species. In the circumstances, all species of the system are considered to be exploited: MPA size is then expressed in percentage of the whole grid of simulation. As for the fishery, it is considered as being nontargeting and as exerting a global annual fishing mortality F for all species and ages (recruitment age is fixed at 1 for all species). Hence, the underlying assumptions are an identical catchability for all species and a homogeneous distribution of fishing effort. This exploitation configuration is generally the one for artisanal fisheries which are strongly opportunistic and for which a single trawl or purse-seine haul can contain a great number of commercial species. The fishing scenario that is implemented is certainly simplifying, but the principle is to represent a fishery that is flexible enough for natural transfers of fishing effort to occur from one species to another, when setting up a marine refuge.

When establishing an MPA, fishing effort, which generates a fishing mortality rate F , is considered to be redistributed on the reduced area which is accessible to fishing. This redistribution is global; it is applied independently of stock identity. Thus, fish that are located out of the marine reserve are submitted to an effective annual fishing mortality rate F_e increasing with reserve size (Gu enette and Pitcher 1999):

$$F_e = F(1 - RS)^{-1} \quad (1)$$

Based on Pope's (1972) analysis, it is assumed that fishing mortality rate is instantaneously applied in the middle of the simulated year. Hilborn and Walters (1992) consider the error induced by this approximation as negligible if the total annual mortality rate is less than 1. The spatial distribution of the fishing effort is not taken into account, as it is uniformly applied to all fish schools in age of recruitment (ages 1+). Other sources of mortality (by predation and starvation) occur during the whole time step, when local successive actions are accomplished by each fish school of the system.

Biomass transfer out of MPAs is supposed to occur since age 1+ fish execute local displacements in a time step. By contrast, no large-scale migration has been implemented: all age groups of the same species are assumed to have the same distribution area. Concerning age 0 fish schools, they are uniformly distributed over their species distribution area, consecutively to the annual reproduction stage. This assumption, which is supposed to account for large-scale processes of larval dispersion and diffusion (in particular by physical currents), is often used in models of marine reserves (Quinn et al. 1993, Attwood and Bennett 1995, Hastings and Botsford 1999).

Simulation Parameters

A set of $S = 50$ species is implemented, species biological parameters and distribution areas being randomly attributed. The simulated species are all assumed to be piscivorous from their second year of life (ages 1+). For the sake of simplicity, the distribution areas which are represented by a set of 150 adjacent cells are only defined at the species level without differentiation regarding fish age. Fish schools, of which the number is fixed at 50 per age class, move and interact in a grid of 15×15 cells. Carrying capacity is fixed at 10^6 tons and its dynamic is assumed to be stationary. To initialize species abundances, the size spectrum of the North Sea ecosystem during the period 1977-1993 is used (Rice and Gislason 1996). Preliminary simulations have allowed for the selection of a species sample. The species kept for the study are those which are viable without exploitation for 100 simulations, each simulation being 200 years in length. A set of 21 species among the 50 initial ones were then selected, for which different fishing scenarios have been simulated. For each set of fishing mortality and reserve size parameters, 100 simulations of 200 years have been carried out, from which have been calculated the mean results that are expounded in the next section. RS is allowed to vary between 0 and 0.8, assuming that equation (1) is valid in this range of reserve size, i.e., fisheries maintain their activity up to a limit of 20% of accessible zone. Each RS value corresponds to a single set of contiguous cells, i.e., to a single refuge area, of which the localization is randomly chosen for each simulation.

Results

Effects of Reserve Size on Fishing Yields

To investigate the potential effects of marine refuges on multispecies assemblages, we first focused on the overall catch of the system, all species combined. The results, which are expressed in terms of the total catch averaged on 100 series of 200 years of simulation, are represented in Fig. 1. It is assumed that the time series produced by the simulations correspond to catch oscillations around the equilibrium. Then, mean catches provide an estimation of equilibrium values.

The *MSY* (maximum sustainable yield) of the multispecies assemblage without MPA is obtained for $F = 0.3$. For F values lower than F_{MSY} , refuges have a negative effect on fishing yields regardless of their size. For F values greater than F_{MSY} , it appears that the larger the MPA, the more the *MSY* is obtained for higher values of fishing mortality. On the other hand, from a certain size of the refuge, namely beyond a relative size *RS* of 50%, the shape of the relationship changes: up to a maximal value of $F = 0.8$, mean yields do not decrease. Rather, they level off.

Two management measures can then be compared, the first consisting of directly reducing fishing mortality, the second consisting of reducing the area accessible to fishing. Consider, for example, the extreme case where all species are exploited at a rate of $F = 0.8$. At constant catchability, the measure which would consist of reducing the fishing effort by half ($F = 0.4$) would result in a negligible increase in yield. By contrast, the implementation of an MPA of $RS = 50\%$ would result, on average, in an appreciable increase in yield. The catch level which would be reached is indeed less by only 7% than the total *MSY* obtained without refuge, i.e., the theoretical maximal level of yield in the long term. At this exploitation level, the reduction of 50% of the fishing zone would correspond to an optimum in the refuge size as mean overall catches are concerned.

In general, for exploitation rates greater than F_{MSY} , the observed relationship between mean total catch and MPA size is nonlinear. Indeed, an optimal size of the MPA exists for each exploitation level. For $F = 0.5$ for example, the optimal relative size would equal 40% (Fig. 2).

Effects of MPA Size on Species Diversity

Along with the analysis on mean yields, the Shannon index of diversity H' has been calculated for the same set of simulations. This index, which corresponds to a cardinal measure of biodiversity (Cousins 1991), can account for species richness as well as for species evenness, i.e., the distribution of species relative abundances. It is a common measure of ecosystem biodiversity (Begon et al. 1996):

$$H' = - \sum_{s=1}^{S-21} \frac{N_s}{N} \log_2 \left(\frac{N_s}{N} \right) \quad \text{with} \quad N = \sum_{s=1}^S N_s$$

Here, N_s represents an average on 100 simulations, of the mean abundance of species s , calculated over the duration of each simulation, namely 200 years.

In the case of a scenario without marine reserve, Fig. 3 shows that the Shannon index remains remarkably constant over a large range of fishing mortalities, even beyond $F_{MSY} = 0.3$. Species diversity begins to change dramatically for a fishing mortality value greater than 0.45. Implementing an MPA thus allows for an appreciable increase in the assemblage diversity. For an initial situation where fishing causes a mortality rate of 0.6, for

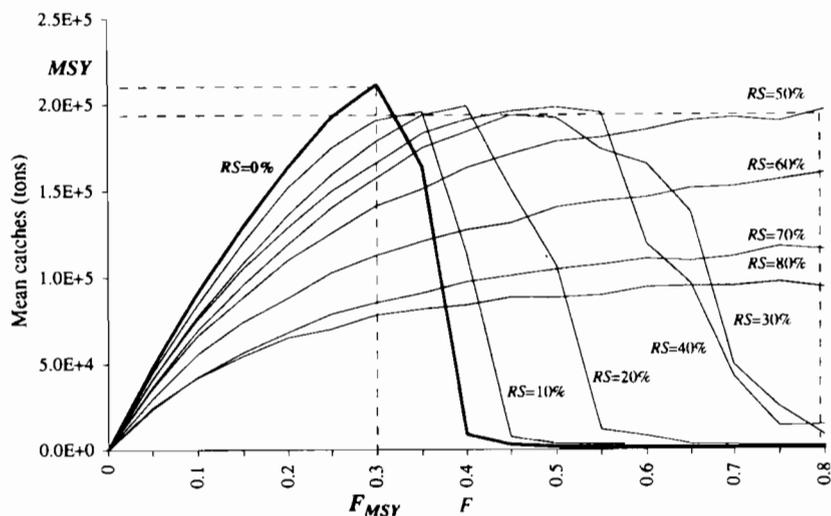


Figure 1. Mean catch, all species together, against fishing mortality rate F . Different MPA relative sizes are implemented (RS in % of the total distribution area of the species). The thick curve represents the mean catch obtained without MPA implementation.

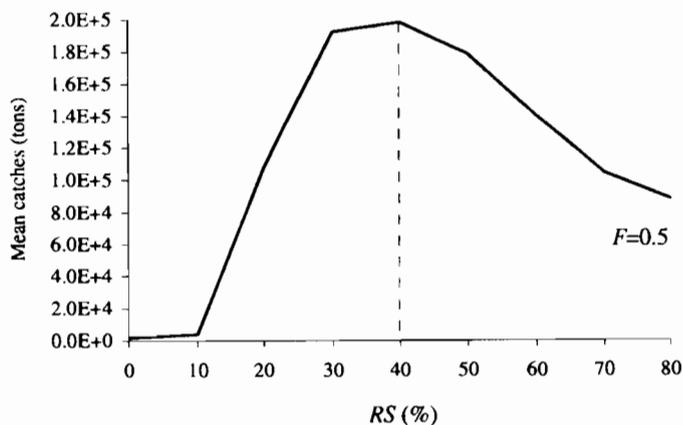


Figure 2. Mean catch, all species together, against MPA relative size for a fishing mortality rate F equal to 0.5.

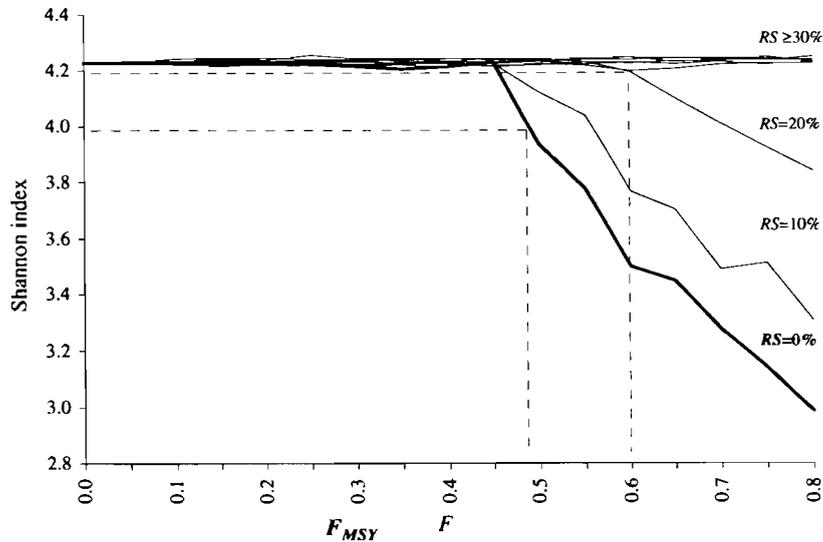


Figure 3. Shannon diversity index H' against fishing mortality rate F . Different MPA relative sizes are simulated (RS ranges from 0% to 80%). The thick curve represents the diversity index obtained without MPA implementation.

example, the diversity index obtained in the long term by closing 20% of the fishing area ($H' = 4.19$) would be superior to the one obtained by reducing the fishing effort by 20% ($H' = 3.98$). In parallel, for the same exploitation configuration, these two management measures appear to be equivalent in terms of yield increase. The theoretical gain obtained is negligible in this case (Fig. 2). For a given exploitation rate, the general shapes of the curves of the Shannon diversity index and of the yield against MPA size are different. Indeed, there is no optimal size of the refuges concerning Shannon diversity since globally, the larger the MPA, the higher the species diversity with a plateau obtained for relative sizes superior to 30%, whatever the implemented fishing mortality rate might be (Fig. 3).

Discussion

The present work affords new considerations on how to integrate multispecies assemblages for MPAs considered as a tool for fisheries management. The variables that are studied are indeed global (overall catch and diversity index). They concern the dynamics of multispecies assemblages, hence allowing particular aspects of ecosystem management to be addressed. The implemented fishing scenarios are simplified and first allow for the corroboration of results already obtained at the species level. A

result that is frequently obtained when modeling MPAs is that at high exploitation rates, refuges indeed prevent the long-term decrease of the catches (e.g., Polacheck 1990, Man et al. 1995, Guénette and Pitcher 1999, Hastings and Botsford 1999). In the framework of generalist multispecies fisheries and for exploitation rates greater than F_{MSY} , the simulations that were undertaken with OSMOSE show that the implementation of MPAs would further permit overall catches to increase at a level often greater than the one obtained by a directly equivalent reduction of fishing effort. At each exploitation level (greater than F_{MSY}), there is an optimal size of the MPA in terms of fishing yield in the long term. The relationship between fishing yield and reserve size is indeed nonlinear (Fig. 2) for high fishing mortality rates: on the left part of the curve, yields increase with the reserve size. This phenomenon is probably linked to a better survival of fish within the MPA, resulting in an age structure of the populations that include more mature and aged individuals. Growth and recruitment overexploitation can thus be avoided, while allowing fishing yields to increase by the diffusion of adults out of the protected areas as well as by the dispersion of larval production (Dugan and Davis 1993, Rowley 1994, Guénette and Pitcher 1999, Maury and Gascuel 1999). On the right part of the curve, yields decrease with marine reserve size. In this configuration, it is assumed that the system has reached its carrying capacity level, this latter indirectly determining the maximum recruitment level, all species confounded (Shin and Cury 2001).

The variation of species diversity with MPA size has been simulated as well. For this management criterion and in the case where $F > 0.45$, the larger the MPA size, the higher the Shannon diversity index. For high exploitation rates, the implementation of a refuge area cannot necessarily significantly increase the long-term yields but, in contrast, can induce an appreciable increase in the Shannon diversity index. This result assumes a long-term reversibility of the phenomenon of population biomass decrease; i.e., the minimal condition is that no species goes extinct. Indeed, the Shannon index quantifies both species richness (species number) and species evenness. In the case where no MPA is implemented, simulation results show that species richness does not decrease for $F < 0.7$. Thus, for fishing mortality rates ranging between 0.45 and 0.7, these values being theoretical, one can consider that implementing an MPA results in an increase of the exploited multispecies assemblage in the long term.

The simulations thus suggest that by implementing MPAs, there can theoretically be a compromise between both objectives of yield maximization and marine biodiversity protection. For both criteria, the results show that in the case of a global management of fishing resource, the reduction of fishing area can have a greater impact than an equivalent direct reduction of fishing effort. First, by preserving an area where fishing is banished, a fraction of each species biomass is preserved, as is already the case for diverse measures of fishing effort reduction (e.g., quotas, fishing gear number, mesh sizes). Second, by implementing MPAs, a trophic web is

preserved; i.e., a set of species and interactions that are localized in space and time. By contrast, the global reduction of fishing effort does not result in avoidance of local overexploitation phenomena, which in turn, can lead to the disappearance of links between species which are important in the global dynamic of the system.

Refuge implementation, however, remains a complex problem with the necessity to determine their localization as well as their size, even sometimes their duration and their restriction to a few species and activities of biomass extraction. Our simulations are restricted to the investigation of the effects of the MPA size. The results show that this parameter is really to be taken into account if the management goal is the maximization of catches in the long term. In 1992, the World Conservation Union (IUCN 1992) had an aim to close 20% of the world coastal waters to fishing by the year 2000. This general measure, which was essentially intended to avoid resource collapse, can be considered to be an application of the precautionary approach in a context where 60-70% of world marine resources appear to be fully exploited to overexploited (Garcia et al. 1999). The simulations indeed show that for overexploited stocks (in the condition that $0.45 < F < 0.7$), the implementation of arbitrarily sized MPAs could permit the diversity of ecosystems to increase. The investigation of some particular ecosystems should hereafter enable the search for optimal sizes of MPAs in an attempt to increase yields, in particular, by taking into account the resource initial level of exploitation. In addition, numerous studies show that the more or less diffusive and migratory characteristics of the resource condition the effects of MPAs (Beverton and Holt 1957, Polacheck 1990, Attwood and Bennett 1995, Guénette and Pitcher 1999, Maury and Gascuel 1999). This is not considered in the present study.

The results are hence to be related to the simulation context where fish school displacements are linked to the search of the highest densities in potential prey (Shin and Cury 2001). Maury et al. (2001) show that such local movement can be observed for Atlantic yellowfin tuna. In the model, the extent to which fish schools can displace each year is theoretical and linked to cell size. Implementing different sizes of the simulation grid (in cell number) can make the cell size and hence the foraging range of fish vary. Shin and Cury (2001) show that when grid size varies from 10 to 35 cells, there is little effect on the level of system biomass.

On the other hand, the larvae dispersion hypothesis, which reproduces the fact that larval retention areas and adult distribution areas are not necessarily the same for many species, is likely to influence MPA efficiency since it regularly provides the fishing zones with new recruits (Guénette et al. 1998). Thus, the refuge plays the part of the source and fishing the one of sink (Roberts 1998).

In this particular frame of simulation, the OSMOSE model has produced some simple results by confronting two criteria of management of multispecies communities exploitation, with the purpose of better understanding the phenomena that occur with MPA implementation. When the

investigation of real cases is foreseen in the future, species migration and diffusion schemes will then have to be taken into account.

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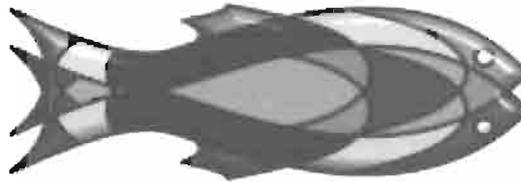
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University of Alaska Sea Grant
P.O. Box 755040
203 O'Neill Bldg.
Fairbanks, Alaska 99775-5040
Toll free (888) 789-0090
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