

Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model

Yunne-Jai Shin^{a,*}, Philippe Cury^{b,c}

^a *Unité de recherche Géodes, Institut de recherche pour le développement (IRD), 32, avenue Henri-Varagnat, 93143 Bondy cedex, France*

^b *Marine and Coastal Management, Private Bag X2, Rogge Bay, 8012 Cape Town, South Africa*

^c *Oceanography Department, University of Cape Town, Rondebosch 7701, South Africa*

Received 22 May 2000; accepted 9 January 2001

Abstract – An individual-based model named OSMOSE (Object-oriented Simulator of Marine Ecosystems Exploitation) is used to investigate the dynamics of exploited marine fish communities. It allows the representation of age- and size-structured populations comprised of groups of individuals that interact within a spatialized food web. Within each group, which constitutes the basic interaction entity (the ‘super-individual’ in individual-based modelling terminology), fish belong to the same species, have similar biological parameters and behaviour rules. Somatic growth, reproduction, predation and starvation processes are modelled. Two rules apply for the predation process: for a given fish group, prey selection depends both on the spatial and temporal co-occurrence of the predator and its prey, and on the respective lengths of the prey versus the predator. Thus, fish feed regardless of the taxonomy of their prey. The strength of both predation and competition relationships therefore vary according to changes in relative species abundance. Preliminary investigations are conducted on a theoretical community comprising seven interacting species. The simulation results show how community stability can emerge from variability in species biomass. It is thus suggested that size-based trophic interactions, along with the existence of multiple weak links and species redundancy, favour community persistence and stability. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

multispecific model / individual-based model / trophic interactions / size-based predation / ecosystem stability

Résumé – **Interactions trophiques fondées sur la taille et dynamiques des communautés de poissons marins : exploration à l’aide d’un modèle spatial individu-centré.** Dans cet article, nous décrivons OSMOSE (Object-oriented Simulator of Marine Ecosystems Exploitation), un modèle individu-centré et dédié à l’étude de la dynamique des communautés marines exploitées. Les populations de poissons modélisées sont structurées en taille et en âge et composées de groupes d’individus qui interagissent au sein d’un réseau trophique. Ces groupes, constituant les unités écologiques élémentaires du modèle (les « super-individus » pour adopter la terminologie des modèles individu-centré), sont composés d’individus possédant les mêmes paramètres biologiques et les mêmes règles comportementales. Les processus de croissance, de reproduction, de prédation et de jeûne sont modélisés. Deux règles fondamentales sont utilisées pour modéliser le processus de prédation : la sélection des proies dépend d’une part de la co-occurrence spatiotemporelle des prédateurs et de leurs proies et, d’autre part, du rapport de la taille de la proie à celle du prédateur. Dans le modèle, la prédation n’est donc pas liée à des préférences alimentaires pré-établies sur l’identité taxonomique des proies. En conséquence, la structure du réseau trophique et la force des interactions peuvent varier en fonction des abondances relatives des espèces. A titre d’exemple d’application du modèle, une communauté théorique composée de sept espèces est simulée. Les résultats suggèrent que des interactions trophiques fondées sur la taille corporelle et de faible intensité, ainsi que l’existence d’une redondance spécifique, favorisent la persistance et la stabilité de la communauté. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

modèle multisécifique / modèle individu-centré / interactions trophiques / prédation taille-dépendante / stabilité

1. INTRODUCTION

Consideration of species interactions and their importance for fisheries management dates back to the 1960s (Larkin, 1963; Riffenburgh, 1969). There was considerable development in this field during the 1980s, coinciding with the intensifying fishing effort

on an increasing number of marine species (e.g. Mercer, 1982; May, 1984; Daan and Sissenwine, 1989). Investigating the internal structure of marine production systems seems as important as taking into account extrinsic factors such as fishing activity or environmental conditions (Kerr and Ryder, 1989; Botsford et al., 1997). In an attempt to quantify species

*Correspondence and reprints.

E-mail address: shin@bondy.ird.fr (Y.J. Shin).

interaction strength, several studies reveal the importance of energy fluxes through ecosystems. For example, Daan (1973) estimates the mean annual consumption of the North Sea cod stock during the period 1967–1970 to be 1 015 000 t (of which 359 000 t consist of exploited fish populations), i.e. more than three times its own biomass. Sissenwine (1984) estimates that Georges Bank fish consume between 60 and 90% of their own production. Likewise, an analysis of fish mortality sources in exploited marine ecosystems suggests that predation represents 2 to 35 times the fishing-induced mortality (Bax, 1991). These examples illustrate the importance of taking into account the effects of species interactions in community ecology.

The first multispecies modelling effort consisted of constructing a system from the explicit coupling of monospecies dynamics models. Kirkwood (1982) and Ströbele and Wacker (1991) among others, investigated the multispecies version of the Schaefer model, which involved the addition of linear terms of interspecific interactions. Similarly, the analytical method MSVPA (multi-species virtual population analysis) lies within the realm of classical cohort analysis with the inclusion of predation mortality rates (Andersen and Ursin, 1977; Helgason and Gislason, 1979; Pope, 1979). Developed in the North Sea ecosystem, this approach is used for the assessment of the North Sea stocks by ICES (International Council for the Exploration of the Sea). On the other hand, the pioneered Lotka–Volterra model (Volterra, 1926; Lotka, 1932) has produced a variety of multispecies dynamical models, which partly focus on predator functional and numerical responses (e.g. Holling, 1959; Arditi and Ginzburg, 1989; Yodzis, 1994).

Finally, several approaches have been developed at the ecosystem level, motivated by the observation of some recurrent patterns of marine ecosystems, suggesting that interactions within the ecosystem are important structuring factors (Dickie and Kerr, 1982). For example, a widespread observation is the stability of the production of many marine ecosystems compared to that of individual species (e.g. Sutcliffe et al., 1977; May et al., 1979; Murawski et al., 1991). The maximum sustainable yield (*MSY*) is extended to a set of exploited species that are considered to form a single stock (Brown et al., 1976; FAO, 1978): the equilibrium production of the multispecies assemblage would then be a parabolic function of fishing effort and the *MSY* would correspond to the exploitation of half the virgin biomass of the whole assemblage. More recently, Polovina (1984) and Christensen and Pauly (1992) developed the ecosystem model ECOPATH, which is widely used among fisheries scientists. In this model, species are aggregated into functional groups, which are related by fluxes of matter. Forming the basis of the model are two equations of mass conservation, describing the production and the consumption at equilibrium for each group of species.

Hence, a number of multispecies models have been developed over the last four decades, which can be categorized in two major groups. The first consists of refining the knowledge gained at the monospecies level by the coupling of a limited number of species dynamics. The second, more exhaustive in terms of the number of species considered, pays particular attention to ecosystem properties without explicitly modelling the species dynamics. By developing a new multispecies model, an attempt is made to reconcile different levels of investigation of populations dynamics. Species interactions are explicitly modelled with the objective of studying species dynamics as well as the properties of exhaustive multispecies assemblages.

The proposed model named OSMOSE (object-oriented simulator of marine ecosystems exploitation) is an individual-based model. It allows the emergence of complex trophic interactions resulting from simple individual predation rules. Unlike most marine multispecies models, species dynamics are not modelled from pre-established interactions of predation and competition: each fish can potentially be a prey or a predator, regardless of its taxonomy, but depending on an appropriate relationship between the body length of the predator versus its prey (Ursin, 1973; Sheldon et al., 1977; Peters, 1983; Cousins, 1991). Though suggested by several theoretical studies (e.g. Bond, 1979; Laevastu and Larkins, 1981; Sissenwine, 1984), this opportunism of predation is rarely considered in models. Thus, OSMOSE is a dynamic trophic web model in which piscivorous fish can shift from one prey species to another according to their relative abundance and fish size characteristics. Firstly, the model is presented: the assumptions on which it is based, its structure, as well as its implementation. Then, a preliminary application is developed to investigate how community relative stability can emerge from interacting dynamics of fish species.

2. MODEL DESCRIPTION

2.1. An individual-based model

The individual-based approach is stimulating an increasing interest among ecologists (Huston et al., 1988; DeAngelis and Gross, 1992; Van Winkle et al., 1993; DeAngelis et al., 1994; Grimm, 1999). It basically involves following the fate of all individuals through their life cycle by assigning to them behavioural rules such as local interactions between the individuals and their environment. The individual-based approach postulates that apparent minor events between individuals can have significant effects on the global state and dynamic of the populations (Uchmanski and Grimm, 1996). Concerning the study of multispecies communities, there are some cases where individual-based models shed new light on some crucial issues in ecology. For example, when populations are small, state variable models can exacerbate their probabilities of extinction (DeAngelis and Gross, 1992). In addition, predation processes modelled at the individual level along

with the explicit inclusion of spatial interactions can account for the long term coexistence of competitive species that differ little in their use of trophic resources (Uchmanski and Grimm, 1996).

Opportunism in the predation process is a strong assumption in the present model. This opportunism can be readily managed at the individual level with the application of the ‘localization principle’ which states that an individual is exclusively affected by the organisms that are located in its spatial and temporal vicinity (DeAngelis and Gross, 1992). The choice of an individual-based approach is also justified by the second assumption of our model, namely the criterion for the selection of the prey by the predator, which is based on their respective individual body sizes.

One decisive step in the elaboration of the model was the choice of the biological entity corresponding to a computer individual. To run tractable simulations, the model is not brought down to the fish level but to an aggregated level consisting of a group of fish having similar biological attributes and behaviour rules regarding the modelled processes. Indeed, the total number of fish (from eggs to adult fish) to be taken into account in the simulated system can reach a value of the order of 10^{12} . Scheffer et al. (1995) suggest that using a ‘super-individual’, a group of similar fish, permits modelling of large populations on an individual basis, while avoiding the potential bias that may be induced by the reduction of the number of individuals

in a population, i.e. by modelling only a sample of the population. The unit of interaction of the model, or the ‘super-individual’, 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). For convenience, this group will be called a ‘fish group’ in the following sections. Such an aggregative behaviour can be related to fish schooling, which, for almost 80% of fish species, occurs at least during one stage of the life cycle (Burgess and Shaw, 1979). Fish schools are actually more heterogeneous than the fish groups of the model. For example, schools size can temporally vary (Misund, 1993) as well as their species composition (Bakun and Cury, 1999). However, a strong homogeneity in body size characterizes the fish schools (Fréon, 1984; Pitcher et al., 1985). Furthermore, Pitcher (1983) suggests a general definition for fish schools, as being groups of fish that move synchronously in the same direction. The analogy between OS-MOSE fish groups and fish schools is evoked here to show that modelling super-individuals is not just a technical means but is also consistent with aggregation behaviours that are observed among fishes.

The architecture of OS-MOSE is hierarchical since a fish group belongs to a cohort, which in turn, belongs to a species. Four model classes, which represent particular ecological entities, are used: the class ‘system’, the class ‘species’, the class ‘age class’, and the

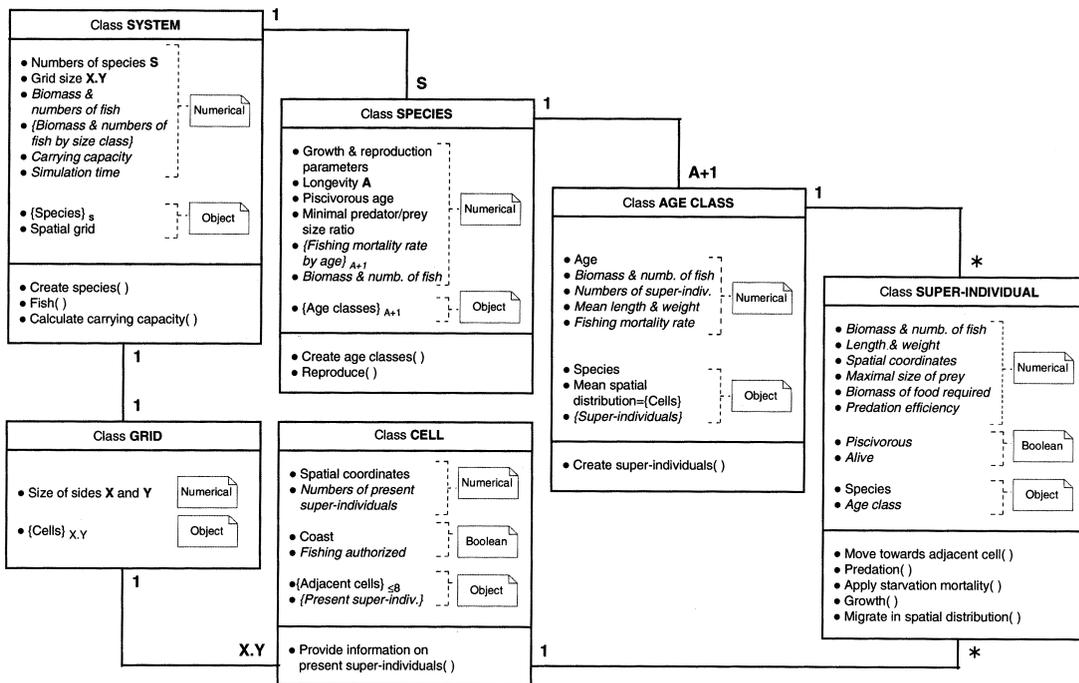


Figure 1. Class diagram of OS-MOSE model in UML formalism (Rumbaugh et al., 1999). For each class, the main attributes and methods are listed in the middle and bottom compartments, respectively. Attributes in italics can vary through time. The lines connecting the classes represent their associations in terms of multiplicity. For example, the binary association 1–S between the classes ‘system’ and ‘species’ means that one instance of the class ‘system’ is associated to S instances of the class ‘species’.

class ‘super-individual’ (figure 1). In addition, two classes represent the spatial environment of fish: the classes ‘grid’ and ‘cell’. Then, fish groups move through a two-dimensional grid, represented by a set of cells $C_{x,y}$: $\{C_{x,y} \mid x \in [0,X], y \in [0,Y]\}$ with closed boundaries, of which the sides X and Y can be defined. From each class are created a number of model objects that are part of the simulated system. The hierarchical structure of OSMOSE enables the investigation of some key variables at different levels of aggregation, in particular the abundance, the spatial distribution of fish by species and age or the ecosystem size spectrum. Indeed, as the state of each individual fish group is known, the state of the population or other aggregated entity can be simply generated by summing (or calculating the mean, variance, etc.) the attributes of all individuals of similar characteristics (e.g. age, size, species).

OSMOSE can account for different levels of species richness by the instantiation of as many species objects as required. These are characterized by several input parameters such as survival parameters (longevity, mortality rates), growth parameters (von Bertalanffy model parameters, condition factor) and reproduction ones (age at maturity, relative fecundity) that are available for many species in the literature or in databases such as FishBase (Froese and Pauly, 1997). At a higher aggregated level, the modelled system can be characterized by its species richness, by the type of species assemblage, by a carrying capacity (type of dynamic and mean value), and by a fishing scenario as is described in the following section.

2.2. Fish life cycle: hypotheses and implementation

OSMOSE is developed in the object-oriented language Java (Jdk 1.1.3, Sun Microsystems). A graphical interface allows a specific definition of the simulation framework (biological parameters, species distribution areas by age, coast line, fishing scenarios). The time step of the model is one reproductive season t , which in general, is one year in high-latitude ecosystems. This step value is adopted by default but in fact, it is divided into two series of actions (see section 2.2.7.) Depending on simulation requirements, the time step can be refined down to the month to include processes such as intra-annual migrations or seasonal reproduction. All notations used in the description of the model are listed in appendix 1.

2.2.1. Initialization

At model initialization, S ‘species’ objects are created. This stage requires the assignment of values to certain attributes for each species object s ($s = 1, \dots, S$), namely:

- A_s : longevity of species s (in years)
- a_{Ms} : age at maturity (in years)
- ϕ_s : relative fecundity (number of eggs spawned per gram of mature female)

- $L_{\infty s}$, K_s , a_{0s} : von Bertalanffy growth model parameters (in centimetres, year⁻¹, and year, respectively)
- c_s : condition factor (in grams per cubic centimetre)
- $\{F_{s,a} \mid 0 \leq a \leq A\}$: with $F_{s,a}$, the fishing mortality rate for age class a .
- $\{\mathcal{A}_{s,a} \mid 0 \leq a \leq A\}$: with $\mathcal{A}_{s,a}$ the set of cells $C_{x,y}$ constituting the mean distributional area of fish of age class a , of species s .

The cohort and fish group objects are then successively created relative to each species, inheriting species biological attributes. Thus, the mean length and weight of fish of age a , of species s , respectively $L_{s,a}$ and $W_{s,a}$, can be calculated from the von Bertalanffy growth model (von Bertalanffy, 1938):

$$L_{s,a} = L_{\infty s} (1 - e^{-K_s(a - a_{0s})}) \quad (1)$$

$$W_{s,a} = c_s L_{s,a}^3 \quad (2)$$

These mean initial values are allocated to the instantiated fish groups objects. Thus, at time $t = 0$, fish of the same age and species initially have the same values for their fish size and weight attributes. These attributes will vary over time in relation to the trophic conditions encountered by each fish group. For egg size, we allocate the value 1 mm, which appears to be a representative mean for marine fish species, whatever the size of the adults (Cury and Pauly, 2000).

Besides, the abundance of each age class is initially distributed amongst n fish groups. The initial abundance of each age class and consequently of fish group, can be determined according to two different methods depending on the available information and on the simulation objective: either from the species abundances N_s ($s = 1, \dots, S$) which can be provided as input, or from the ecosystem size spectrum (see appendix 2).

Finally, for each age class a of species s , the n fish groups are randomly distributed in their distribution area $\mathcal{A}_{s,a}$. For each simulated year t , fish life cycle can then be modelled following the steps described in figure 2.

2.2.2. Carrying capacity constraint

The existence of a carrying capacity constraint at the species level has been assumed as far back as 1838 by Verhulst. It has been extended to the ecosystem level by Sutcliffe et al. (1977) in a multispecies fishery model. In OSMOSE, the carrying capacity corresponds to the maximum total biomass of non-piscivorous fish. The piscivorous state of fish, which can be defined in the input, depends on their taxonomy and their age. By default, all age 1⁺ fish are considered to be piscivorous and all age 0, non-piscivorous. The carrying capacity dynamics can be modelled in different ways depending on the simulation requirements and on the ecosystem considered (stationary, periodic, random dynamics, or with the occurrence of an anomaly).

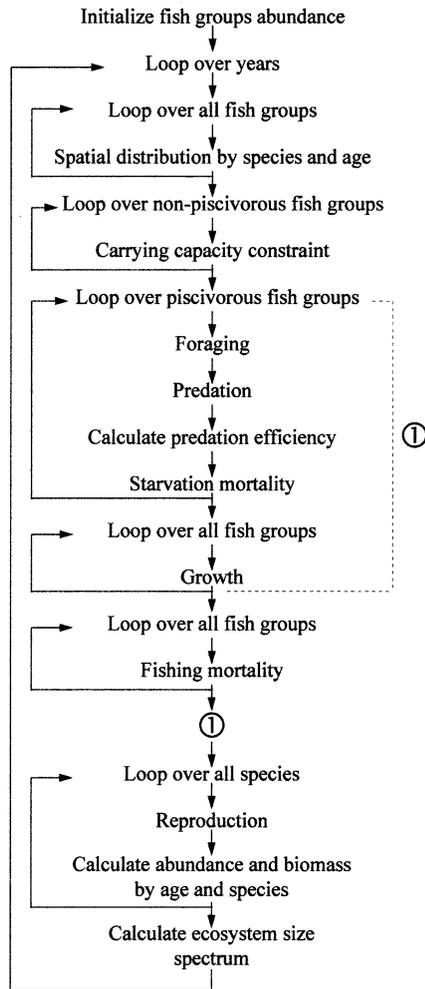


Figure 2. Different processes modelled in OSMOSE during one iteration.

Carrying capacity is assumed to be homogeneous over the whole spatial grid. Thus, at the beginning of each iteration t , a carrying capacity value can be attributed locally to each cell of the simulation grid such that:

$$\forall(x,y) \in [0, X] \cap [0, Y], CC_{t,x,y} = \frac{CC_t}{XY}$$

where CC_t is the carrying capacity value at time t , x and y the coordinates of the cell, X and Y the sizes of the grid sides.

Then, within each cell, the total biomass of non-piscivorous fish $B'_{t,x,y}$ is compared to the local carrying capacity: 1) below the carrying capacity, the constraint has no effect on fish survival, and 2) above the carrying capacity, the biomass of non-piscivorous fish is reduced down to the carrying capacity level. The reduction in biomass operates uniformly among the non-piscivorous fish groups: the same fraction of

biomass $[(B'_{t,x,y} - CC_{t,x,y})/B'_{t,x,y}]$ is removed from each fish group.

2.2.3. Foraging

This stage, as well as the predation stage (section 2.2.4), only concerns piscivorous fish. For both stages, the order in which fish groups act is randomly drawn at each new time step t . Fish group foraging consists of the evaluation of the trophic favorability of its vicinity, the latter being represented by \mathcal{V}_{x_0,y_0} , a set of cells comprising the cell C_{x_0,y_0} , in which the group is located, and its adjacent cells:

$$\mathcal{V}_{x_0,y_0} = \{C_{x,y} | (x,y) \in ([x_0 - 1, x_0 + 1] \times [y_0 - 1, y_0 + 1]) \cap ([0, X] \times [0, Y])\}$$

The criterion of fish group displacement is, in other terms, the search for the cell in which potential prey biomass is the highest. Let τ be the minimal theoretical ratio between predator and prey body length. Then, for a group indexed by i_0 , the potential prey groups are those for which the fish have a length inferior to the critical size L_{i_0}/τ .

Thus, a fish group i_0 , located in the cell C_{x_0,y_0} , will move towards the cell $C_{x',y'}$ if this latter satisfies the condition:

$$\sum_{\substack{i \in [1..n_{x,y}] \\ L_i \leq L_{i_0}/\tau}} B_{i,x',y'} = \text{Max}_{\mathcal{V}_{x_0,y_0}} \left(\sum_{\substack{i \in [1..n_{x,y}] \\ L_i \leq L_{i_0}/\tau}} B_{i,x,y} \right)$$

with $n_{x,y}$ the number of fish groups located in the cell $C_{x,y}$, L_i the length of fish belonging to group i , and $B_{i,x,y}$ the biomass of group i located in the cell $C_{x,y}$.

2.2.4. Predation

After moving to the cell having the highest prey density, each fish group feeds, causing explicit predation mortality for each targeted prey fish group.

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 , prey groups have to be located in the predator cell to be considered to be accessible), and (2) that the predator-prey size ratio is inferior to the threshold value τ (estimated approximately at 3.5 from FishBase 97; Froese and Pauly, 1997). A first consequence of these behaviour rules is that a species can occupy different trophic levels in the system, depending on the age class considered (Bond, 1979; Rice, 1995): two species can then simultaneously be a predator or a prey to each other. This predation opportunism can also account for cannibalism. Furthermore, it is consistent with the observations of very diversified and time-varying diets. These different trophic patterns, which characterise the virtual systems simulated in OSMOSE, can be observed in reality by the diet analyses that were carried out in different ecosystems in the world (e.g. Gislason and Helgason,

1985; Crawford, 1987; Alheit, 1987; Mittelbach and Persson, 1998).

Finally, at the end of the predation process, a predation efficiency ξ_i is calculated for each fish group i ($\xi_i \in [0,1]$). This coefficient is determined by the ratio between the food biomass ingested by a group and the maximal food biomass required to fulfill its vital functions. From values that are available for several species, it is estimated that a fish should annually consume 3.5 g of food per body gram (Laevastu and Larkins, 1981; Gislason and Helgason, 1985; Longhurst and Pauly, 1987). The selection of a group of prey, among those satisfying the size criterion and being located in the same cell as the one of the predator, is randomly drawn. As long as the food ration of the predator is not reached, new groups of prey are selected. When a group of fish, or a super-individual, undergoes a predation pressure, this latter does not necessarily induce the mortality of the super-individual but a decrease of the numbers of fish. The mortality of the super-individual occurs only if all the constituting fish disappear.

2.2.5. Growth

Mean annual growth rates in length of fish of age a , species s , are calculated from the von Bertalanffy model (equation 1):

$$\Delta L_{s,a} = L_{\infty s} (1 - e^{-K_s}) e^{-K_s(a - a_0s)} \quad (3)$$

This mean rate is readjusted to take into account the quantity of food ingested by each group during a time step t . Laevastu and Larkins (1981) have estimated the daily food ration for fish maintenance (i.e. for which there is neither an increase, nor a decrease in biomass) to be about 0.55% of the body weight, this value representing an annual ration of 2.01 g of food per body gram. A critical threshold ξ_{crit} can then be calculated, from which the food ration is considered to be dedicated to fish growth (ξ_{crit} = annual maintenance ration/annual mean ration = 0.57). A simple approximation is to consider that for a group i , if $\xi_i \geq \xi_{crit}$ growth rate in length varies linearly with ξ_i such that:

- for $\xi_i = \xi_{crit}$, the rate is null,
- for $\xi_i = (\xi_{max} + \xi_{crit}) / 2$, with $\xi_{max} = 1$, growth rate in length equals the mean rate $\Delta L_{s,a}$ calculated from equation 3 (figure 3a).

Thus, the growth rate in length $\Delta L_{s,a,i,t}$ of a group i , of age a , of species s , and at time t , follows the expression:

$$\begin{cases} \Delta L_{s,a,i,t} = 0 & \text{if } \xi_{i,t} < \xi_{crit} \\ \Delta L_{s,a,i,t} = \frac{2\Delta L_{s,a}}{1 - \xi_{crit}} (\xi_{i,t} - \xi_{crit}) & \text{if } \xi_{i,t} \geq \xi_{crit} \end{cases}$$

Fish body weight is subsequently calculated from the allometry relationship (equation 2).

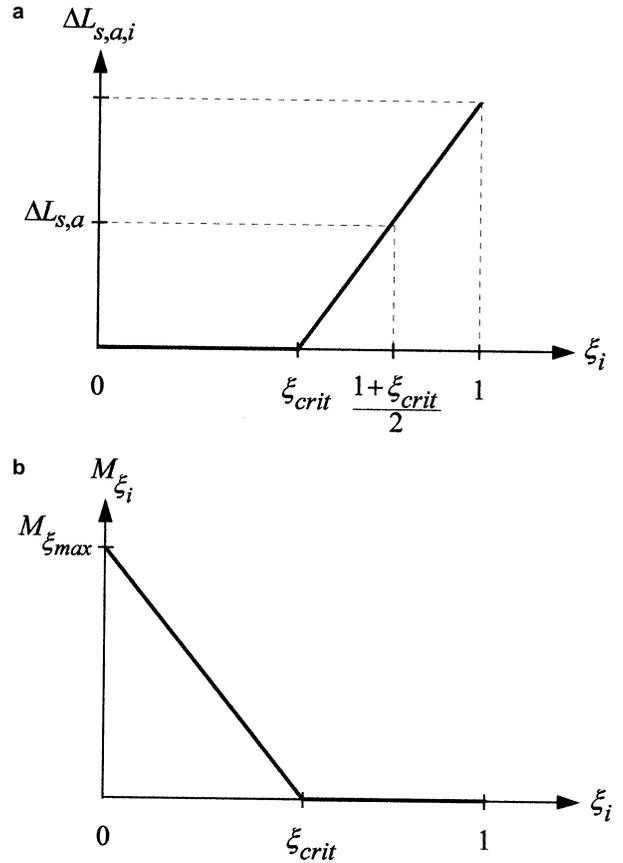


Figure 3. a. Annual growth rate in length $\Delta L_{s,a,i}$ as a function of predation efficiency ξ_i of fish group i , of age a and species s . $\Delta L_{s,a}$ represents the mean growth rate of a fish of age a , of species s , following the von Bertalanffy growth model. ξ_{crit} represents the critical predation efficiency corresponding to the fish maintenance food ration. b. Starvation mortality rate M_{ξ_i} as a function of the predation efficiency ξ_i of fish group i . $M_{\xi_{max}}$ represents the maximal starvation mortality rate, fixed at the beginning of the simulation. ξ_{crit} represents the critical predation efficiency corresponding to the fish maintenance food ration.

2.2.6. Starvation mortality

Starvation mortality is supposed to affect fish groups when the food ration is too low to provide the basic fish maintenance requirements (starvation, increased sensibility to environmental variations, to diseases, etc.). This process is poorly documented, as most multispecies models consider the decrease or the increase of a population at a global level, i.e. in terms of population biomass for which the variations simultaneously reflect somatic growth, reproduction and mortality processes. This is typically the case for Lotka–Volterra type predator-prey models. Concerning the multispecies model MSVPA, only the fishing and the predation mortalities are taken into account (Gislason and Helgason, 1985). The few studies addressing starvation mortality concern the larval stages of fish, for which this source of mortality is exacer-

bated, as the post-vitelline stage is considered to be a critical stage for recruitment success (Hewitt et al., 1985; Theilacker, 1986). In these studies, larval mortality rates are estimated but the studies do not propose models of mortality in relation to food ration that could be extended to fish adult stages. Finally, Beverton and Holt (1957) suggest the possibility that starvation mortality may occur for fish adult stages in a model which linearly links the natural mortality rate to fish density. Indeed, the authors suggest that this density-dependent mortality may result from intraspecific competition for food, which can lead to fish starvation. By considering food resources to be limiting for each species, the linear model of Beverton and Holt (1957) is used with the assumption that as fish density increases, fish food ration decreases. Thus, the starvation mortality rate M_{ξ_i} of a fish group i can be expressed linearly as a function of predation efficiency when $\xi_i \leq \xi_{crit}$ (figure 3b). The following equation is applied, with $M_{\xi_{max}}$ the maximal starvation mortality rate:

$$M_{\xi_i} = -\frac{M_{\xi_{max}}}{\xi_{crit}} \xi_i + M_{\xi_{max}}$$

Consequently, the number of fish that starve $N_{M_{\xi_i,t}}$ of group i for the time step t , can be expressed in the following form:

$$N_{M_{\xi_i,t}} = N_{i,t} (1 - e^{-M_{\xi_i,t}})$$

2.2.7. Fishing mortality

Fishing activity is represented by the vector $\{F_{s,a} | 0 \leq a \leq A_s\}$, which is set as input to the model for each species s . To determine when fishing mortality is to be applied is the next step, i.e. to determine the order within the time step t , in which the different processes affecting the abundance of each species act: predation, starvation, and fishing mortality. The first two sources of mortality are implemented at the group level. During time step t , each fish group acts and interacts successively, causing an explicit mortality of the prey groups in its environment, and resulting in a variable starvation mortality for itself. Predation and starvation mortalities can thus be considered to be continuous within the time step. According to Pope (1972), it is assumed that the annual fishing mortality rate $F_{s,a}$ is instantaneously applied in the middle of the time step $[t, t + 1]$. Hilborn and Walters (1992) consider that the error induced by this approximation is negligible if the total annual mortality rate is less than 1. Consequently, within a time step t , each fish group experiences two foraging actions and two predation actions that are interrupted by the occurrence of fishing mortality at time $(t + 1/2)$. Predation efficiency ξ of each group is then calculated twice, at the middle

and at the end of the time step, along with growth and starvation rates, which are determined consecutively (figure 2).

2.2.8. Reproduction

Each species has relative fecundity ϕ_s as an input attribute, i.e. the number of eggs spawned per gram of mature female. SB_s is species s spawning biomass, $B_{s,a}$ the biomass of age class a , a_{M_s} its age at maturity and A_s its longevity. Assuming that the sex-ratio equals 1:1 for all species, the following equation is applied:

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

As growth variability is implemented in relation to food intake, the reproductive process also depends implicitly on the food conditions that are encountered, locally in time and space, by each fish group. Besides, two arguments have presided over the choice of modelling the egg production in relation to spawning biomass, instead of directly modelling the recruitment level of each species. Firstly, it is important to model fish larval stages explicitly since they represent a significant quantity of food for adult groups, therefore influencing the dynamics of the whole system. Secondly, the reproduction process is simply represented by a linear relationship, without constraints on the stock-recruitment relationship. The recruitment level emerges from the annual survival of eggs and juveniles, in relation to the predation process and to the annual level of the carrying capacity.

3. RESULTS: SIMULATION EXAMPLES

The following simulations, which give preliminary insights into the possibilities of using OSMOSE, aim to investigate which dynamics emerge at the level of the species and the system, when scaling up from individual behaviour rules that were presented in the previous section. We particularly focus on the study of community stability, defined here as opposed to temporal variability. This temporal stability can be measured by the coefficient of variation of some ecosystem state-variables (Pimm, 1991; Tilman, 1996; Tilman, 1999).

A simulation of reference is first proposed, which concerns a multispecies community without redundancy. The species and the total biomass levels are examined as well as their variability. The effect of species interaction strength is then analysed. Finally, the effect of fishing mortality is considered in the case of the reference community, and in the case where an analogous species is added to the community.

3.1. A simulated multispecies community

A multispecies community consisting of seven interacting species is simulated. The set of species that

Table I. Biological parameters used in the reference simulation (non-exploited system, no species redundancy).

Process	Growth				Reproduction		Predation		
Parameters	L_∞ (cm)	K	a_0 (year)	c (g·cm ⁻³)	a_{mar} (year)	ϕ (g ⁻¹)	Piscivorous age (year)	Predation rate	Predator/prey size ratio
Species 1	15	0.74	-1.03	0.01	1	1000	1	3.5	3.5
Species 2	45	0.32	-	-	2	500	-	-	-
Species 3	65	0.25	-	-	2	200	-	-	-
Species 4	105	0.18	-	-	2	100	-	-	-
Species 5	165	0.14	-	-	3	30	-	-	-
Species 6	205	0.12	-	-	3	30	-	-	-
Species 7	235	0.11	-	-	3	20	-	-	-

are modelled is chosen to cover a wide range of sizes: growth parameter L_∞ varies from 25 cm to 235 cm. Other biological input parameters are listed in *table I*. All species are different, as they do not have the same biological parameters. Longevity is arbitrarily fixed at 7 years for all species. The number of fish groups per age class is fixed at 50. At the maximum, 2800 groups are thus interacting in a 15×15 lattice (7 species \times 8 age classes \times 50 groups). The size of species distribution areas is set at 80% of the total grid size (180 cells) and their location is randomly drawn for each species. Carrying capacity is set at 10^6 t, it is stationary throughout the whole simulation period (200 years). To initiate species abundance, an algorithm is developed to match the size spectrum described in the North Sea ecosystem during the period 1977–1993 (Rice and Gislason, 1996; *appendix 2*). For each configuration of the parameters of the model, 10 simulations of 100 years each have been conducted.

Results of the simulation in terms of species and community biomass dynamics are presented in *figure 4*. They show the emergence of a relative stable biomass at the level of the multispecies assemblage, contrasting with the variability observed at the level of

each population. Indeed, the mean coefficient of variation (\overline{CV}) of the total biomass, averaged over the CV s of the 10 simulation series, appears to be relatively low ($\overline{CV} = 0.348$). Apparently, this pattern is not due to the existence of one dominant species of which the dynamics would be more stable than the ones of other species (see the biomass mean values in *table II*). By contrast, biomass of the species that is located at the basis of the trophic web (species 1 with $L_\infty = 15$ cm) exhibits very high variability ($CV = 2.089$).

If the species dynamics were independent, the expected mean coefficient of variation of the overall biomass \overline{CV}_e could be calculated as follows:

$$\overline{CV}_e = \left[\frac{\sum_{n=1}^{10} \sqrt{\frac{\sum_{s=1}^S \sum_{t=0}^T (B_{n,s,t} - \overline{B}_{n,s})^2}{T}}}{\sum_{s=1}^S \overline{B}_{n,s}} \right] / 10 = 0.439$$

with n the number of the simulation, S the species number, T the simulation period, $B_{s,t}$ the biomass of

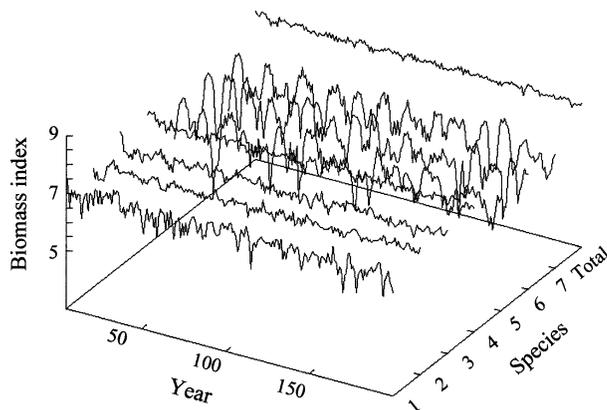


Figure 4. Species and total system $\log(\text{biomass})$ in $\log(\text{tonnes})$ over time, for the reference simulation: no fishing activity, no redundancy. The course of one 200 years-simulation, among the 10 conducted, is represented here.

Table II. Mean biomass and mean coefficients of variation (\overline{CV}) for the system of reference.

	Mean biomass (t)	\overline{CV} of biomass
Species 1	1.868×10^7	2.089
Species 2	1.812×10^7	0.326
Species 3	1.327×10^7	0.382
Species 4	2.036×10^7	0.339
Species 5	7.239×10^6	1.061
Species 6	1.096×10^7	1.085
Species 7	8.891×10^6	1.058
Total	9.753×10^7	0.348

The system of reference consists in 7 species, without fishing or species redundancy. Biomass is averaged over the mean biomass of 10 series of 200 years-simulations. CV corresponds to the mean of the CV s of the 10 series of simulations.

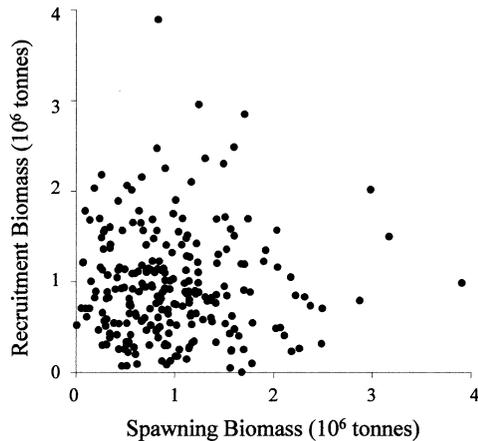


Figure 5. Recruitment biomass versus spawning biomass for species 1 in the reference simulation: no fishing activity, no redundancy. Only one 200 years-simulation is represented here.

species s at time t , and \overline{B}_s the mean biomass of species s over the period T .

The nonparametric test of Wilcoxon allows to reject the null hypothesis $H_0: P(CV < CV_e) \leq 0.5$ with a type I error inferior to 0.001 [$U_{\text{obs}} (= 3) < U_{10,10,0.001} (= 10)$]. Thus, the coefficient of variation of the total biomass of the simulated community is inferior to the one that would be obtained if the species biomass were independent.

This result shows that species interactions tend to stabilise system biomass. It may not stem from the carrying capacity constraint since: 1) the carrying capacity constraint only applies to non-piscivorous fish, and 2) it occurs at the very beginning of each iteration and is followed by predation activity, fish growth and reproduction. After these different steps, the species and community biomasses are calculated. Carrying capacity only constrains the mean biomass of the system but not the CV of the total biomass. The variability of species biomass is also illustrated in *figure 5* where no particular relationship emerges between spawning and recruitment biomass of species 1, even though the number of eggs spawned annually was modelled as linearly dependent on spawning biomass. The same pattern is observed for all the species of the simulated system, showing the potential role of species interactions in recruitment variability. In the model, recruitment depends on carrying capacity and predation intensity rather than on the state of the population.

In the next simulation, heavy fishing pressure on species 1 is modelled ($F = 5$ for age group 1^+). This fishing mortality pattern is not meant to be realistic but to simulate a scenario in which a species is exploited at an extremely high level. In this case, the total system remains at the same levels of mean biomass ($\overline{B} = 9.887 \times 10^7$ t) and variability ($CV = 0.313$) as in the case of a non-exploited scenario. Despite the

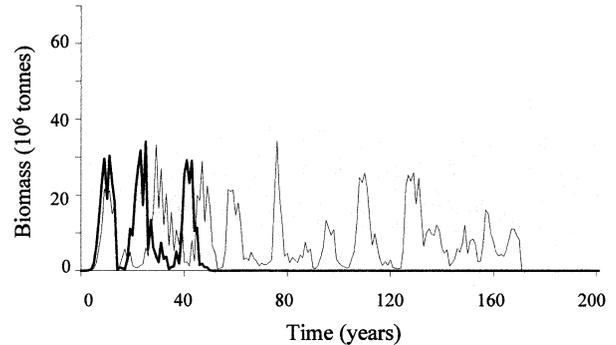


Figure 6. The simulated scenario consists of a high fishing mortality rate for species 1 ($F = 5$) with no redundancy implemented: species 5 (thick line) and species 7 (thin line) collapse. The course of one simulation, of the 10 conducted, is represented here. Species 7 remains viable in 2 simulations of the 10.

high level of exploitation, species 1 does not disappear from the system. Demographic parameters (early age at maturity, high relative fecundity) make it resistant to fishing. The mean and CV of its biomass are moreover strikingly of the same orders of magnitude to those when the species is not fished. However, the age structure of the exploited species is changed since age group 4^+ is poorly represented in the system. By contrast, an unpredictable consequence of fishing species 1 is the collapse of both species 5 and 7 (*figure 6*): if, quantitatively, the system seems resistant to fishing pressure, its structure changed.

3.2. Effect of species interaction strength

The aim of this set of simulations is to explore how the intensity of species interactions influences the stability of the previous seven species assemblage. This question can be simply investigated by allowing the number of cells of the spatial grid to vary, while leaving the total area unchanged. Indeed, a cell represents the spatial unit in which all fishes are interacting with each other through the predation process. By increasing the number of cells, we reduce their surface area, i.e. the theoretical foraging area of all fish. Consequently, predation intensity can be considered to be negatively correlated to the number of cells. The relationship between community biomass and interaction intensity is non-linear (*figure 7a*). When fish are fully accessible (one cell for the grid), some species are depleted by extreme predation pressure and system biomass is low. On the contrary, when fish groups are isolated (extreme right part of the curve), starvation occurs. System biomass is at a maximum at weak to intermediate strength links. On the other hand, this maximum observed biomass corresponds to a minimum in the CV of community biomass (*figure 7b*) as well as to a higher relative stability of the community compared to species dynamics (*figure 7c*). *Figure 7c* also shows that when interactions are too strong or too

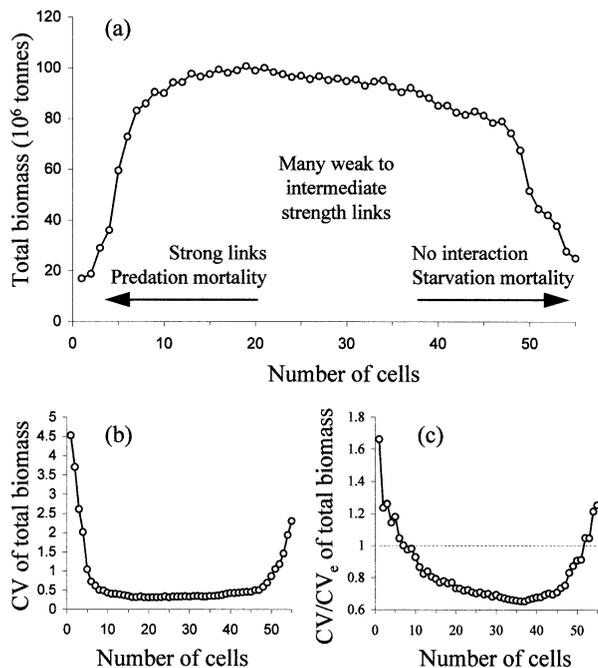


Figure 7. Influence of species interaction strength for the system of reference (no fishing activity, no redundancy) on mean system biomass (a), on the CV of system biomass (b), and on its ratio with the expected coefficient of variation CV/CV_e (c). Predation intensity is negatively correlated to cell number in the spatial grid. The more patchy the environment, the more isolated the populations: starvation occurs, system mean biomass decreases, system (b) and species (c) biomass variabilities increase. The same features are obtained when species are totally accessible to each other (one cell in the grid), due to extreme predation pressure. Each dot represents an average calculated over 10 series of simulations.

low, they induce a destabilization of the system ($CV / CV_e > 1$).

3.3. Effect of redundancy on community stability

In these simulations, a redundant species 1* is added to the system, having the same biological parameters as species 1, the same size for its distribution area but not necessarily the same location since it is randomly drawn as previously for the other species. In the non-exploited case, the biomass of species 1 and the one of its analogue have almost the same characteristics in terms of mean and CV (table III) but their dynamics are not synchronous. On the other hand, the overall biomass as well as the biomass of each species appear to be more stable than in the non-redundant system (table II). Moreover, the mean total biomass is higher. This result was not expected a priori since the carrying capacity level was unchanged for this simulation. When two species are redundant, the biomass of each species is less than if there was no redundancy. However, the mortality rate of their larvae due to the carrying capacity constraint may be lower than in the case of a single species since the mortality process is

Table III. Mean biomass and coefficients of variation for the redundant case.

	Mean biomass (t)	CV of biomass
Species 1	1.519×10^7	1.392
Species 1*	1.533×10^7	1.279
Species 2	2.592×10^7	0.315
Species 3	1.313×10^7	0.397
Species 4	2.305×10^7	0.378
Species 5	6.322×10^6	0.792
Species 6	1.012×10^7	0.691
Species 7	7.735×10^6	0.776
Total	1.167×10^8	0.286

Species 1 and 1* are redundant (same biological parameters).

locally density-dependent in a context where the total distribution area of both species is larger than for one species. Thus, the summed biomass of the two similar species is higher than the biomass obtained in the simulation without redundancy. The higher larval biomass of the two redundant species may also cause higher mortality rates for larvae of other species with which they potentially compete through the carrying capacity constraint. However, as the redundant species are at the basis of the food chain, their larger biomass can lead to lower starvation mortality of adults of other species and thereby to greater total biomass of the system.

Unlike in the non-redundant system, when fishing on species 1 ($F = 5$), the mean biomass of the exploited species is reduced by approximately one third ($\overline{B}_1 = 1.028 \times 10^7$ t). This can be perceived as a result of competition between species 1 and the redundant species. Indeed the redundant species exhibits a higher level of biomass ($\overline{B}_{1^*} = 1.681 \times 10^7$ t) in response to the decrease in biomass of species 1. This result was not trivial since the trophic place of each species in the system can not readily be inferred from the predation rules implemented in OSMOSE: the ranges of sizes occupied by species overlap so that it is not possible to determine clear competitive relationships. Finally, the mean total biomass remains stable when fishing on species 1 and contrary to the non-redundant case, the structure of the system is also preserved, at least qualitatively, since no species disappears.

4. DISCUSSION

Currently, essentially two marine multispecies models are used by the fisheries scientific community: MSVPA (Andersen and Ursin, 1977; Helgason and Gislason, 1979; Pope, 1979) and ECOPATH (Polovina, 1984; Christensen and Pauly, 1992). The success of MSVPA is mainly due to its possible use in the assessment of exploited stocks; MSVPA provides a tool to refine the estimation of natural mortality rates

of fish and to diagnose the effect of some management measures such as mesh sizes limitations or setting of quotas. Considerable work has been undertaken to apply the model to the North Sea ecosystem and has improved our knowledge of predation processes (Kerr and Ryder, 1989). However, the amount of biological data that is required makes the application to other ecosystems difficult. The ECOPATH model has been developed to estimate the trophic fluxes within an ecosystem. Applied to various marine ecosystems such as upwellings (Shannon and Jarre-Teichmann, 1999), coral reefs (Arias-Gonzales et al., 1997), oceanic (Christensen and Pauly, 1998), or coastal zones (Christensen and Pauly, 1992), ECOPATH provides a global structure of marine food webs, allows the investigation of some ecosystem indices and has therefore facilitated important results on the functioning of marine ecosystems (Pauly et al., 1998). However, this macroscopic approach does not facilitate comparisons with classical stock assessment procedures or the investigation of some ecosystem indices such as the ecosystem size spectrum or various biodiversity indices that require detailed demographic and/or morphometric features of the populations. This motivated the development of the present multispecies model (OSMOSE), which complements existing models by trying to combine: 1) the study of extensive multispecies assemblages, 2) the study of the spatial dynamics of age and size-structured populations and the simulation of different fishing scenarios in a compatible way with classical stock assessment methods, and 3) the use of simple interaction rules at a microscopic level, requiring biological data that are available in the literature, possibly to be applied to different ecosystems.

One of the limits of the OSMOSE model lies in the type of multispecies assemblage investigated: indeed, OSMOSE is essentially structured to represent the detailed dynamics of piscivorous fish of the system. The species, which are entirely non-piscivorous, as well as various species groups such as birds or marine mammals, the primary and secondary producers of the system, only appear in the model by means of a global variable or parameter.

The exploratory simulations that are presented here account for some emergent properties of marine ecosystems. In particular, the dynamics of the overall biomass appear to be more stable than the ones of individual species. This result is all the more pronounced when species interactions are not too strong. McCann et al. (1998) have shown, by using non-linear models, that weak to intermediate strength links promote community persistence and stability. In our simulations, weak links (high number of patches in the spatial grid) tend to maintain population densities further away from zero in the sense that chances for a fraction of each population to remain inaccessible to predators are greater. It seems that weak to intermediate interactions are “the glue that binds natural communities together” (McCann et al., 1998). Conversely, since no species interactions means no predation and

subsequent starvation, there is a limit to the environmental patchiness beyond which populations are too isolated to find the minimum quantity of a resource required for survival.

The relative stability of the overall biomass that was obtained in our simulations is consistent with diverse observations made on marine ecosystems (e.g. Sutcliffe et al., 1977; Murawski et al., 1991). For instance, May et al. (1979) have reported that in the North Sea, fishing activity has been marked by important changes in species composition: in the 1970s, herring and mackerel catches dropped while those of some gadoids increased. By contrast, total catches remained relatively stable. The authors assume that the fall of herring and mackerel catches, which were due to excessively high fishing pressure, led to less predation on larvae of other species and thereby to better recruitment success of other species. This explanation points out the intrinsic capacity of regulation of the system. In OSMOSE, the stability of the overall biomass is achieved through compensating dynamics between populations. If one population decreases due to fishing or to some other exogenous factor, energy is made available to other species. This system-wide, density-dependent process is made possible if the component species compete, to some degree, for trophic resources (Lawton and Brown, 1994). This is the case in our model where fish size is the predation criterion: all species are then potential trophic competitors. Both underlying hypotheses of OSMOSE, opportunistic predation and life-history omnivory, imply the existence of a multitude of trophic links between the age classes of different species. Consistently with different empirical studies (Gislason and Helgason, 1985; Gulland, 1987; Rice, 1995), fish have multiple predators and they also consume a large variety of species. On the other hand, ontogenetic omnivory, by increasing the number of potential competitive links between species, at the same time decreases their intensity since competition strength is then distributed amongst many component species and age classes: competition is diffuse. Theoretically, there are multiple competitive relationships that act to buffer system production (McCann, 2000), and the competitive species can coexist because their interactions are weak. These trophic features are assumed to be peculiar to piscivorous fish communities, whereas in other aquatic or terrestrial communities, more specificity may exist for the selection of food, i.e. there may be fewer competitive links, but those may be more intense (Kerr, 1974; Gulland, 1982; Blumenshine et al. 2000).

Thus, in fish communities, energy fluxes can use very different pathways through the system, and because of this flexibility, can be used optimally: the modelled ecosystem can be considered as being energy efficient. The cost of this is a high variability at the level of the species. Using a non-linear multispecies model, Ives et al. (1999) show that the negative covariances of species dynamics, due to the existence

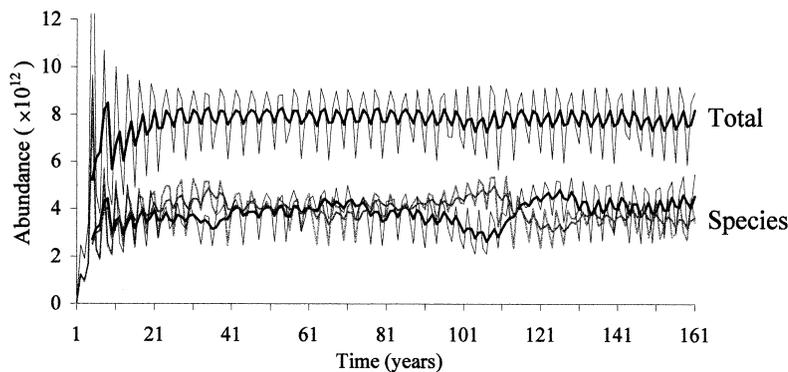


Figure 8. Simulated dynamics of two redundant species (same biological parameters) competing for the same trophic resources. The three thick lines correspond to a 5-years smoothing of respective curves.

of competition, have no significant effect on the coefficient of variation of community dynamics. By contrast, competition generates a higher variability of species dynamics. In other terms, by analogy with the simulations conducted with OSMOSE, the coefficient of variation CV of the community would remain constant, the expected coefficient of variation CV_e would increase, and hence the ratio CV/CV_e would decrease. This result is not contradictory with our study but puts its conclusions into perspective. Indeed, the simulations do not allow us to conclude that interspecies interactions act either towards a stabilization of community biomass, or towards a destabilization of species biomass. They only show that the total biomass of the simulated community is more stable than the species biomass ($CV_{total} < CV_e$) and hence, in that, they provide some kind of validation of the OSMOSE model and of the underlying mechanisms of interaction, by generating results that are consistent with observations made in different marine ecosystems.

Competition is exacerbated when two species have similar biological characteristics. In a basic simulation with two redundant species (same parameters of growth and reproduction) competing for the same trophic resources, species dynamics exhibit alternating phases of dominance (figure 8). The dynamics of the two redundant species are not synchronous: the increase in abundance of one species compensates for the decrease of the other so that the total system remains at the same level of abundance. In a more complex configuration where higher trophic levels can feed on these two redundant species, predators may switch from one species to another depending on their relative abundance. In this case, it is the asynchrony of the dynamics of the competitive species that would provide stability to the system. Thus, in the simulations presented in section 3.3, opportunistic feeding and redundancy seem to have prevented the modification of the community structure due to fishing. Simulating a high exploitation rate of a redundant species led to an increase in the biomass of its analogue, while overall biomass was practically unchanged. Not only did this compensatory effect sustain the biomass of predators, but it also contributed to the persistence of

the exploited species by enabling predators to switch their predation effort to the more abundant redundant species. The asynchrony of the simulated species dynamics can be related to the buffering effect studied by Yachi and Loreau (1999), by using a stochastic model. However, these authors do not take into account species interactions in their model but show that the differences in the response of the species to environmental fluctuations allow the system to stabilize. In their model, the asynchrony of the populations, or the different reactions of the populations, is only due to stochastic independent processes. In this context, they show that when species number increases, the productivity of the system is more stable. The insurance hypothesis that they propose is to be related to the portfolio effect, which is discussed in detail by Doak et al. (1998) and Tilman et al. (1998). This statistical effect means that the coefficient of variation of the dynamics of a group of species is necessarily inferior to the mean coefficient of variation of the species dynamics. Indeed, as the community biomass is the sum of the biomass of the component species, each varying independently through time, an increase of the species richness would tend to statistically average the fluctuations of the species dynamics and therefore to decrease the coefficient of variation of the total biomass (Doak et al. 1998). Thus, the existence of interactions is not, a priori, a necessary condition to the relative stability of a community. In our simulations, the portfolio effect is found in the calculation of the CV_e (the coefficient of variation calculated by considering that the species are independent), which is indeed inferior to the mean of the CV s of species biomass ($\overline{CV}_{species} = 0.905$). In addition to the portfolio effect, we assume that the difference in the stability of simulated community and species dynamics is exacerbated by the existence of trophic interactions ($\overline{CV}_{total} < \overline{CV}_e$). Moreover, Tilman et al. (1998) noticed that if two species are competitors, their covariance would be negative and consequently the variance of the bispecific system would be inferior to the sum of their individual variances.

The simulations that were conducted corroborate in some way the redundancy hypothesis (Walker, 1992;

Lawton, 1994), which states that some species are capable of extending their functions in an ecosystem in order to compensate for some decrease in abundance of similar species. Both aspects of redundancy are indeed illustrated by the simulations: the insurance against environmental perturbations, and the efficiency of energy transfer (Blondel, 1995). The underlying idea is that ecosystems are segregated into a certain number of functional groups within which species would have functional analogues. In this functional perspective, some species can disappear with little effects on ecosystem properties as long as each functional group is represented. In this case, other species belonging to the same functional group may increase their production as a result of competition. As a consequence of the redundancy hypothesis, it appears that ecosystems comprising the same number of species can have different functional structures thereby resulting in difficulties in comparing different species assemblages and establishing a relationship between species richness and the stability of the ecosystem. In this context, a crucial stake is to develop indices that can help to determine which species of an assemblage are redundant. This study suggests that fish size can help to better understand the trophic position or the functional role of species in the system (Cowan et al., 1996; Lundvall et al., 1999) and by extension, that the ecosystem size spectrum can be considered as being a global expression of the functional structure of ecosystems (Cousins, 1991; Hall, 1999).

Acknowledgements. We are very grateful to Lynne Shannon, Olivier Maury and Soizick Lebihan for helpful comments on the manuscript. We also thank three anonymous referees who provided very valuable suggestions for improvement. The ‘Gulf of Guinea EC Project’ and the ‘Vibes Project’ supported part of the research.

Appendix 1

Glossary of notations.

Indices

s	Species
a	Age
i	Group of similar fish, the ‘super-individual’ of the model
x, y	Spatial coordinates
t	Time step (1 year)

Parameters

T	Simulation time (year)
S	Species number
A	Terminal age, longevity (year)
n	Group number per age
C	Cell of the spatial grid
X, Y	Grid size in cell number
\mathcal{A}	Set of cells forming a distribution area
\mathcal{V}	Set of vicinity cells
a_M	Age at maturity (year)

ϕ	Relative fecundity (number of eggs per gram of mature female)
L_{∞}, K, a_0	von Bertalanffy growth model parameters (centimetres, year ⁻¹ , year)
c	Condition factor (grams per cubic centimetre)
F	Fishing mortality rate
τ	Theoretical ratio between predator and prey body lengths
ξ_{crit}	Predation efficiency corresponding to the annual maintenance food ration
$M_{\xi_{max}}$	Maximal starvation mortality
Variables	
N	Abundance
B	Biomass (tonnes)
B'	Non-piscivorous biomass (tonnes)
SB	Spawning biomass (tonnes)
$L, \Delta L$	Body length and growth rate in length (centimetres)
W	body weight (grams)
ξ	Predation efficiency
M_{ξ}	Starvation mortality rate
$N_{M_{\xi}}$	Number of dead fish by starvation
CC	Carrying capacity (tonnes)

Appendix 2

Initial conditions

The initialization of age classes and fish groups abundance can be implemented by two means: either from species abundances or from the ecosystem size spectrum.

– In the case where the abundance of each species N_s is an input of the model, a pseudocohort can be formed for each species from the conventional survival equation that follows:

$$N_{s,a+1} = N_{s,a} e^{-M_{s,a}}$$

with $N_{s,a}$ the abundance of age class a ($0 \leq a \leq A_s$), of species s ($1 \leq s \leq S$), M the natural mortality rate ($M_{s,0} = 5$ and $\forall a \in [1, A_s - 1]$, $M_{s,a} = 0.5$). The analytical expression of the abundance $N_{s,0}$ of age 0 class of species s is deduced from the above equation and then allows to constitute the age structure of species s :

$$N_{s,0} = N_s \left(1 + \sum_{a=0}^{A_s-1} e^{-\sum_{a'=0}^a M_{s,a'}} \right)^{-1}$$

– The initialization from the ecosystem size spectrum is adapted in the case of exploratory theoretical simulations, for which the ratio between the different species abundance is considered to be more important than the quantification itself of the abundance levels. The relative uniformity of the size spectra observed in different marine ecosystems justify the choice of this index to possibly initialise more realistic multispecies assemblages than those obtained by a random distribution of the species biomasses. Different measures of the size spectrum expressed in $\text{Ln}(\text{abundance})$ versus $\text{Ln}(\text{body length class})$, show that this ecosystem index

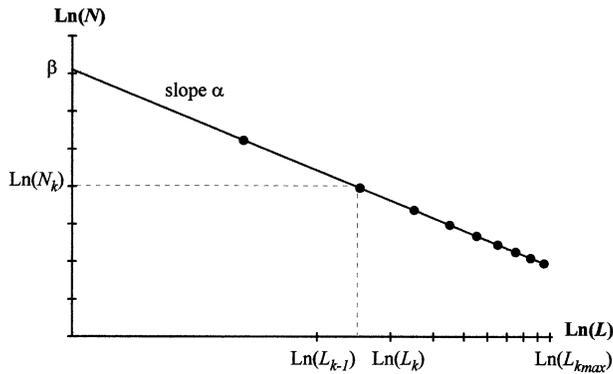


Figure 9. Theoretical ecosystem size spectrum. The natural logarithm of the average fish numbers N_k ($1 \leq k \leq k_{max}$) in the fish length interval $[L_{k-1}, L_k]$ is a linear decreasing function of the natural logarithm of the midlength in the corresponding group.

is a uniform decreasing function of organisms size (e.g. Rice and Gislason, 1996; Bianchi et al., 2000). This conservative property, despite sometimes important variability in species abundance, suggests that size of organisms is a factor of marine ecosystems structure, allowing the full occupation of their production potentials (Kerr and Ryder, 1989). This is in agreement with the hypotheses adopted in OSMOSE, and this constitutes a second reason for the use of such an index. Let the ecosystem size spectrum be represented by the following equation:

$$\ln(N_k) = \alpha \ln\left(\frac{L_k + L_{k-1}}{2}\right) + \beta$$

with N_k the abundance of fish having a body length comprised within the interval $[L_{k-1}, L_k]$, $k \in [1, \dots, k_{max}]$ is the index of length class, α et β are two fixed parameters (figure 9).

The initialisation algorithm consists of distributing the total abundance $\sum_{k=1 \dots k_{max}} N_k$ into $\sum_{s=1 \dots S} (A_s + 1)$ age classes. For each length class $[L_{k-1}, L_k]$ is first calculated n_k , the number of age classes a ($a = 0, \dots, A_s$), of species s ($s = 1 \dots S$) such that $L_{s,a} \in [L_{k-1}, L_k]$. The fish numbers $N_{s,a}$ of each age class a of species s are then initialised following the expression:

$$\forall (s,a) \in [1, \dots, S] \times [1, \dots, A_s] \left| L_{s,a} \in [L_{k-1}, L_k], N_{s,a} = \frac{N_k}{n_k} \right.$$

Finally, a readjustment of the fish numbers is undertaken to take into account the decrease of a cohort abundance with age: if $N_{s,a+1} \geq N_{s,a}$, the abundance $N_{s,a+1}$ is reduced down to $N_{s,a}$ and the residual fish number is distributed over the $(n_k - 1)$ other age classes belonging to the same size class in the limit of

the condition $N_{s,a+1} \leq N_{s,a}$. Fish groups of age a , of species s have then an initial abundance equal to n .

References

- Alheit, J., 1987. Egg cannibalism versus egg predation: their significance in anchovies, The Benguela and comparable ecosystems, Payne, A.I.L., Gulland, J.A., Brinks, K.H. (Eds.). S. Afr. J. Mar. Sci. 5, 467–470.
- Andersen, K.P., Ursin, E., 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddelelser fra Danmarks Fiskeri-og Havundersogelser 7, 319–435.
- Arditi, R., Ginzburg, L., 1989. Coupling in predator-prey dynamics: ratio-dependence. J. Theor. Biol. 139, 311–326.
- Arias-Gonzales, J., Delesalle, B., Salvat, B., Galzin, R., 1997. Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. Coral Reefs 16, 231–246.
- Bakun, A., Cury, P., 1999. The ‘school trap’: a mechanism promoting large-amplitude out-of-phase population oscillations of small pelagic fish species. Ecol. Letters 2, 349–351.
- Bax, N.J., 1991. A comparison of the fish biomass flow to fish, fisheries, and mammals on six marine ecosystems. ICES Mar. Sci. Symp. 193, 217–224.
- Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fish and fisheries series, no. 11. Chapman and Hall, London.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F., Jin, X., Zwanenburg, K., 2000. Impact of fishing on size composition and diversity of demersal fish communities. ICES J. Mar. Sci. 57, 558–571.
- Blondel, J., 1995. Biogéographie. Approche écologique et évolutive. Collection Écologie no. 27. Masson, Paris.
- Blumenshine, S.C., Lodge, D.M., Hodgson, J.R., 2000. Gradient of fish predation alters body size distributions of lake benthos. Ecology 81, 374–386.
- Bond, C.E., 1979. Biology of fishes. Saunders College Publishing, Philadelphia.
- Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. Science 277, 509–515.
- Brown, B., Brennan, J., Grosslein, M., Heyerdhal, E., Hennemuth, R., 1976. The effect of fishing on the marine fish biomass in the Northwest Atlantic from The Gulf of Maine to Cape Hatteras. ICNAF Res. Bull. 12, 49–68.
- Burgess, J.W., Shaw, E., 1979. Development and ecology of fish schooling. Oceanus 27, 11–17.
- Christensen, V., Pauly, D., 1992. ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61, 169–185.
- Christensen, V., Pauly, D., 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecol. Appl. 8, 104–109.

- Cousins, S.H., 1991. Species diversity measurement: choosing the right index. *Trends Ecol. Evol.* 6, 190–192.
- Cowan, J.H., Houde, E.D., Rose, K.A., 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. *ICES J. Mar. Sci.* 53, 23–37.
- Crawford, R.J.M., 1987. Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel, The Benguela and comparable ecosystems, Payne, A.I.L., Gulland, J.A., Brink, K.H. (Eds.). *S. Afr. J. Mar. Sci.* 5, 735–757.
- Cury, P., Pauly, D., 2000. Patterns and propensities in reproduction and growth of marine fishes. *Ecol. Res.* 15, 101–106.
- Daan, N., 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. *Neth. J. Sea Res.* 6, 479–517.
- Daan, N., Sissenwine, M.P., 1989. *ICES Mar. Sci. Symp.* 193, Multispecies models relevant to management of living resources, pp. 1–385.
- DeAngelis, D.L., Gross, M.J., 1992. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Chapman et Hall, New York.
- DeAngelis, D.L., Rose, K.A., Huston, M.A., 1994. Individual-oriented approaches to modeling ecological populations and communities. In: Levin, S.A. (Ed.), *Frontiers in mathematical biology*. Springer-Verlag, Berlin, pp. 390–410.
- Dickie, L.M., Kerr, S.R., 1982. Alternative approaches to fisheries management. In: Mercer, M.C. (Ed.), *Multispecies approaches to fisheries management advice*. Canadian special publication on fishery and aquatic science, pp. 18–23.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1988. The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* 151, 264–276.
- FAO, 1978. Some scientific problems of multi-species fisheries. Report of the expert consultation on management of multispecies fisheries. *FAO Fish. Tech. Pap.* 181, 1–42.
- Fréon, P., 1984. La variabilité des tailles individuelles à l'intérieur des cohortes et des bancs de poissons: observations et interprétation. *Oceanol. Acta* 7, 457–468.
- Froese, R., Pauly, D., 1997. *FishBase 97: concepts, design and data sources*. ICLARM, Manila.
- Gislason, H., Helgason, T., 1985. Species interaction in assessment of fish stocks with special application to the North Sea. *Dana* 5, 1–44.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol. Model.* 115, 129–148.
- Gulland, J.A., 1982. Why do fish numbers vary? *J. Theor. Biol.* 97, 69–75.
- Gulland, J.A., 1987. The effect of fishing on community structure, The Benguela and comparable ecosystems, Payne, A.I.L., Gulland, J.A., Brink, K.H. (Eds.). *S. Afr. J. Mar. Sci.* 5, 839–849.
- Hall, S.J., 1999. *The effects of fishing on marine ecosystems and communities*. Blackwell Scientific Publications Ltd, Oxford.
- Helgason, T., Gislason, H., 1979. VPA analysis with species interaction due to predation. *CIEM C.M.1979/G*. ICES, Copenhagen.
- Hewitt, R.P., Theilacker, G.H., Lo, N.C.H., 1985. Causes of mortality in young jack mackerel. *Mar. Ecol. Prog. Ser.* 26, 1–10.
- Hilborn, R., Walters, C.J., 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall Ltd, London.
- Holling, C.S., 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.* 91, 293–320.
- Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. *Bioscience* 38, 682–691.
- Ives, A.R., Gross, K., Klug, J.L., 1999. Stability and variability in competitive communities. *Science* 286, 542–544.
- Kerr, S.R., 1974. Theory of size distribution in ecological communities. *J. Fish. Res. Board Can.* 31, 1859–1862.
- Kerr, S.R., Ryder, R.A., 1989. Current approaches to multispecies analyses of marine fisheries. *Can. J. Fish. Aquat. Sci.* 46, 528–534.
- Kirkwood, G.P., 1982. Simple models for multispecies fisheries. In: Pauly, D., Murphy, G.I. (Eds.), *Theory and management of tropical fisheries*. Conference Proceedings, no. 9. ICLARM, Manila, pp. 83–98.
- Laevastu, T., Larkins, H., 1981. *Marine fisheries ecosystem. Its quantitative evaluation and management*. Fishing News Books Ltd, Farnham.
- Larkin, P.A., 1963. Interspecific competition and exploitation. *J. Fish. Res. Board Can.* 20, 647–678.
- Lawton, J., 1994. What do species do in ecosystems. *Oikos* 71, 367–374.
- Lawton, J.H., Brown, V.K., 1994. Redundancy in ecosystems. In: Schulze, E.-D., Mooney, H.A. (Eds.), *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, pp. 255–270.
- Longhurst, A.R., Pauly, D., 1987. *Ecology of tropical oceans*. Academic Press, London.
- Lotka, A.J., 1932. The growth of mixed populations: two species competing for a common food supply. *J. Wash. Acad. Sci.* 22, 461–469.
- Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Can. J. Fish. Aquat. Sci.* 56, 1285–1292.
- May, R.M., 1984. *Exploitation of marine communities*. Springer-Verlag, Berlin.
- May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J., Laws, R.M., 1979. Management of multispecies fisheries. *Science* 205, 267–277.
- McCann, K., Hastings, A., Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798.
- McCann, K., 2000. The diversity-stability debate. *Nature* 405, 228–233.

- Mercer, M.C., 1982. Multispecies approaches to fisheries management advice. Canadian special publication on fisheries and aquatic sciences, no. 59.
- Misund, O.A., 1993. Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat and saithe schools. *ICES J. Mar. Sci.* 50, 145–160.
- Mittelbach, G.G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* 55, 1454–1465.
- Murawski, S.A., Lange, A.M., Idoine, J.S., 1991. An analysis of technological interactions among Gulf of Maine mixed-species fisheries. *ICES Mar. Sci. Symp.* 193, 237–252.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F. Jr, 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Peters, R.H., 1983. The ecological implications of body size. Cambridge University Press, Cambridge.
- Pimm, S.L., 1991. The balance of nature? Ecological issues in the conservation of species and communities. The University of Chicago Press, Chicago.
- Pitcher, T.J., 1983. Heuristic definitions of shoaling behaviour. *Anim. Behav.* 31, 611–613.
- Pitcher, T.J., Magurran, A.E., Edwards, J.L., 1985. Schooling mackerel and herring choose neighbours of similar size. *Mar. Biol.* 86, 319–322.
- Polovina, J.J., 1984. Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3, 1–11.
- Pope, J.G., 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *ICNAF Res. Bull.* 9, 65–74.
- Pope, J.G., 1979. Stock assessment in multispecies fisheries. South China Sea fisheries development and coordinated programme SCS/DEV/79/19. FAO, Manila.
- Rice, J., 1995. Food web theory, marine food webs, and what climate change may do to northern marine fish populations. In: Beamish, R.J. (Ed.), *Climate change and northern fish populations*. Canadian special publication on fisheries and aquatic sciences, no. 121, pp. 561–568.
- Rice, J., Gislason, H., 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J. Mar. Sci.* 53, 1214–1225.
- Riffenburgh, R.H., 1969. A stochastic model of interpopulation dynamics in marine ecology. *J. Fish. Res. Board Can.* 26, 2843–2880.
- Rumbaugh, J., Jacobson, I., Booch, G., 1999. The unified modeling language reference manual. Addison-Wesley Publishing Company, Reading, MA.
- Scheffer, M., Baveco, J.M., DeAngelis, D.L., Rose, K.A., van Nes, E.H., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. *Ecol. Model.* 80, 161–170.
- Shannon, L.J., Jarre-Teichmann, A., 1999. A model of the trophic flows in the northern Benguela upwelling system during the. *S. Afr. J. Mar. Sci.* 21, 349–366.
- Sheldon, R.W., Sutcliffe, W.H., Paranjape, M.A., 1977. Structure of pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Board Can.* 34, 2344–2353.
- Sissenwine, M.P., 1984. Why do fish populations vary? In: May, R.M. (Ed.), *Exploitation of marine communities*. Springer-Verlag, Berlin, pp. 59–94.
- Ströbele, W.J., Wacker, H., 1991. The concept of sustainable yield in multi-species fisheries. *Ecol. Model.* 53, 61–74.
- Sutcliffe, W.H., Drinkwater, K., Muir, B.S., 1977. Correlations of fish catch and environmental factors in the Gulf of Maine. *J. Fish. Res. Board Can.* 34, 19–30.
- Theilacker, G.H., 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. *Fish. Bull.* 84, 1–17.
- Tilman, D., 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77, 350–363.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455–1474.
- Tilman, D., Lehman, C.L., Bristow, C.E., 1998. Diversity–stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* 151, 277–282.
- Uchmanski, J., Grimm, V., 1996. Individual-based modeling in ecology: what makes the difference? *Trends Ecol. Evol.* 11, 437–441.
- Ursin, E., 1973. On the prey preferences of cod and dab. *Meddr Danm. Fisk.-og Havunders* 7, 85–98.
- Van Winkle, W., Rose, K.A., Chambers, R.C., 1993. Individual-based approach to fish population dynamics: an overview. *Trans. Am. Fish. Soc.* 122, 397–403.
- Verhulst, P.F., 1838. Notice sur la loi que la population suit dans son accroissement. *Correspondances Mathématiques et Physiques* 10, 113–121.
- Volterra, V., 1926. Variations and fluctuations of the numbers of individuals in animal species living together (Translated re-edition). In: Chapman, R.N. (Ed.), *Animal ecology*. McGraw-Hill, New York, pp. 409–448.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). *Hum. Biol.* 10, 181–213.
- Walker, B., 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6, 18–23.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. USA* 96, 1463–1468.
- Yodzis, P., 1994. Predator-prey theory and management of multispecies fisheries. *Ecol. Appl.* 4, 51–58.