

Estimation of the impact of trophic interactions on biological production functions in an ecosystem.

Emmanuel Chassot and Didier Gascuel

Abstract

A simulation model is developed in order to estimate the impact of trophic interspecific relations on the biological production functions of an ecosystem. Exploitable biomass of a theoretical ecosystem is allocated by trophic class, each class including all the species and organisms of a given range of trophic levels. These species and organisms are given individual growth, recruitment and survival models. Biomass and yields per recruit models based on the usual approach of Beverton and Holt are thus estimated by trophic class for different theoretical levels of fishing mortality.

The parameters of the growth and survival models are estimated to define a coherent biological production function for each trophic class. A recruitment term is also introduced for each class in order to get a biomass distribution in the ecosystem similar to different biomass trophic spectra pre-determined. The natural mortality encountered by each trophic class is supposed to include a term of mortality dependent on the predators biomass and a term of residual mortality considered constant. Predation is based on a function of trophic preference between the classes. We show that trophic interactions existing in an ecosystem affect the biological production functions according to the trophic class considered within the food web. Low trophic levels functions are highly variable according to the level of top-down control considered and the shape of the virgin spectrum. High trophic levels functions display low variations because their biomass is generally low and they are poorly subjected to predation. In this context, ecosystems characterized by a strong top-down control and a high biomass in the low trophic levels seem more resistant to overexploitation. Predation relaxation and selectivity of the fishing gear explain the observed patterns. We thus show that the biomass spectrum and the level of top-down control (predation) are two essential factors of the ecosystems functioning and particularly of their ability to react to a given exploitation. These characteristics should eventually be taken into account in the perspective of an ecosystem management.

Keywords: ecosystem overexploitation, growth, multispecies, predation, production function, top-down, trophic class, trophic level, steady state, yield-per-recruit

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Introduction

Ecosystem management is a concept precisely defined very recently (Christensen et al., 1996; Garcia et al., *in press*). It notably presupposes that fisheries management must take into account multispecies interactions in a community of fish species, and their dependence on underlying ecosystem dynamics (Larkin, 1996; Link, 2002). In fact, the interest in holistic approaches has been recognized since a long time (Andersen and Ursin, 1977; May et al., 1979; Mercer, 1982; Daan, 1987; Kerr and Ryder, 1989) and has emerged within ICES with the use of the Multi-Species Virtual Population Analysis (MSVPA; Sparre, 1991) and its predictive version, the Multi-Species Forecast (MSFOR). However, these models only focus on the predation process for a limited number of species. Moreover, they require a huge amount of data that limits their general application (Gislason and Helgason, 1985). In this context, current models in fisheries sciences are mostly performed on individual stocks and some essential input parameters such as the natural mortality (M) are usually considered constant (Caddy, 1991). Therefore, analysing the variability of the production functions for a given species within an ecosystem due to the potential variations of the predation mortality appears an essential but very difficult task that could improve stock assessments and eventually fisheries management.

Marine food webs are characterized by a high complexity mainly due to the high number of interacting species, the types of interactions and the strong ontogenic shifts affecting fish species in the course of their life (Polis et al., 1989). A key to improve our understanding of the marine ecosystems functioning lies in the analysis of the energy flows (Cury et al., 2003). In this sense, trophic levels represent an interesting approach because the concept constitutes an important abstraction that improves our vision of energy transfers (Pahl-Wostl, 1997) and trophic position weigh trophic connections according to their relative energetic importance (Vander Zanden et al., 1997). Therefore, it is assumed that the structure of a complex food web can be represented by a set of trophic classes. Each trophic class corresponds to a small range of trophic positions and can be viewed as a dynamic entity characterized by a biological production that can be exploited. The central process of interest is the predation that takes place between the trophic classes because predation is essential in marine ecosystems (e.g. Bax, 1998) and appears to be the most central organizing concept in ecology (Martinez, 1995).

In this perspective, a simulation model is developed in order to analyse the variability of the production functions along the trophic continuum of the ecosystem. Thus, for a given fishing pattern, the predation mortality of each trophic class is determined according to some major characteristics of the ecosystems. The features of interest are the distribution of the biomass in the virgin ecosystem, the level of the top-down control and the function of trophic preference of each trophic class. The main assumptions of the simulator as well as the sub-models of growth, catch, recruitment and survival are first introduced. Then, as an illustration, some simulations results enable to stress out which seem to be some of the most important features of the ecosystem that drive the production functions of the trophic classes.

Materials and methods

The symbols and abbreviations used in this study are summarized in table 1.

The simulator represents a virtual ecosystem in which the total biomass (1000g) is allocated between trophic classes. All organisms are given a trophic class between 2.0 for the secondary producers (herbivores, zooplankton) and 5.0 (top-predators) according to their trophic position, the classes being separated by step of 0.1. A recruitment and individual growth function are defined for each class. Also, a survival equation describing the decrease of the biomass with age in each trophic class enables to introduce the predation mortality due to other trophic classes. Finally a yield-per-recruit model in the form of Beverton and Holt (1957) is applied to each class.

Table 1. Symbols and abbreviations used in the study

Parameter	Definition
TL_i	Trophic level of the class of index i
$M1$	Instantaneous mortality rate due to other causes than predation (starvation, disease,...)
$M2$	Instantaneous mortality rate due to predation
$M3$	Instantaneous 'pseudo-recruitment' rate; difference between the biomass of organisms entering and leaving a trophic class by unit of time (metamorphosis,...)
F_{simu}	Fishing mortality of reference
mF	Fishing mortality multiplier
g_{ij}	Coefficient of trophic preference of the predator i to the prey j
t_r	Age at recruitment
t_c	Age at first capture
K	Parameter of the VBGF, of dimension $year^{-1}$, expressing the rate at which the asymptotic length (or weight) is approached
L_∞	Asymptotic length in cm; parameter of the VBGF expressing the mean length that the fish would reach if they were to grow indefinitely
t_0	Parameter of the VBGF expressing the theoretical 'age' in years the fish would have at length zero if they had always grown as described by the VBGF
a_i	Rate of effective search
s	Selectivity
α	Parameter of the selectivity function considered constant
TL_{50}	Parameter of the selectivity function indicating the trophic level at which the selectivity is 50%
VBGF	Von Bertalanffy growth function

Survival Equation

Like in the usual model of Beverton and Holt (1957), we consider a trophic cohort i that is subject to both a natural mortality and a fishing mortality assumed constant during its fishable life-span. We thus analyse the system in a steady state for different scenarios of fishing or functioning of the ecosystem. In order to describe interspecific relationships, natural mortality is partitioned into $M_i=M1_i+M2_i+M3_i$.

The survival equation for a trophic cohort is expressed as:

$$\frac{dB_i(t)}{dt} = -(F_i + M1_i + M2_i + M3_i) \times B_i(t) \quad (1)$$

$M1_i$ and $M3_i$ are supposed constant and equals for all the trophic classes. Predation mortality $M2_i$ is explicit in the model and depends on the rate of effective search a_j of each predator weighted by its trophic preference g_{ji} .

The instantaneous rate of predation mortality by the predators j is the same on the whole lifespan of the class i and is expressed as:

$$M2_i = \sum_j a_j \times g_{ji} \times B_j \times B_i$$

A theoretical function of trophic preference is assigned to each trophic class, defining a coefficient of selection for each prey (Figure 1). The trophic level 1.0 is included in the diet as a complement of the levels between 2.0 and 5.0. A normal distribution is assumed with a mean $\mu = TL_j - 1$ and an increasing standard deviation estimated in order that the trophic level of the predator satisfies the equation:

$$TL_j = 1 + \sum_i g_{ji} \times TL_i$$

In the model, the trophic level is initially assigned to each class and enables to define their prey selection or “prey window” (Pahl-Wostl, 1997). The estimation of the standard deviation presupposes an ideal situation in which all the preys are available to the predator in infinite quantity. The standard deviations estimated increase with the trophic level, showing a diet more and more generalist at the top of the trophic web. This trend is observed when plotting the omnivory index versus the trophic level of the fish species given in Fishbase data (Froese and Pauly, 2000). Trophic preferences established imply trophic cannibalism (consumption on the same trophic class) and predation on higher trophic levels in minor proportion.

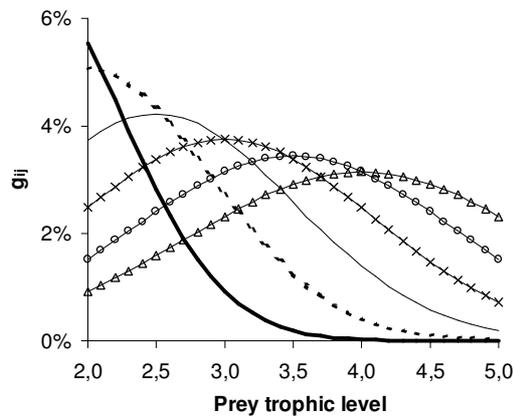


Fig. 1. Functions of trophic preference for certain classes of the simulation model. Solid line= $g_{2.5,i}$; dashed line= $g_{3.0,i}$; thin line= $g_{3.5,i}$; line with crosses= $g_{4.0,i}$; line with circles= $g_{4.5,i}$; line with triangles= $g_{5.0,i}$.

Individual growth model

Based on the Von Bertalanffy growth function (1938), a model of individual growth for each trophic class is defined. The parameters are estimated from empirical relationships between the asymptotic length (L_{inf} , cm), the rate at which the asymptotic length is approached (K , t^{-1}) and the mean trophic level of the species (Figure 2). Data come from the Fishbase database (Froese and Pauly, 2000). From these parameters, the individual weight of any individual of a trophic class can be estimated with age (Figure 3).

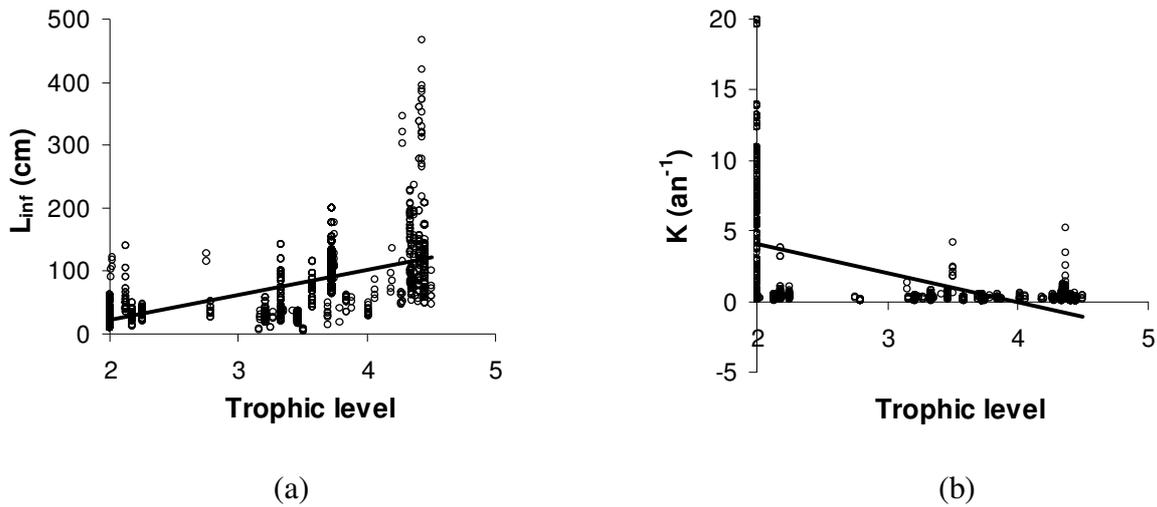


Fig. 2. Relationship between the parameters of the Von Bertalanffy growth function and the mean trophic level of fish species. Data from Fishbase (Froese and Pauly, 2000). (a) Asymptotic length, L_{inf} ; (b) Rate at which the asymptotic length is approached, K .

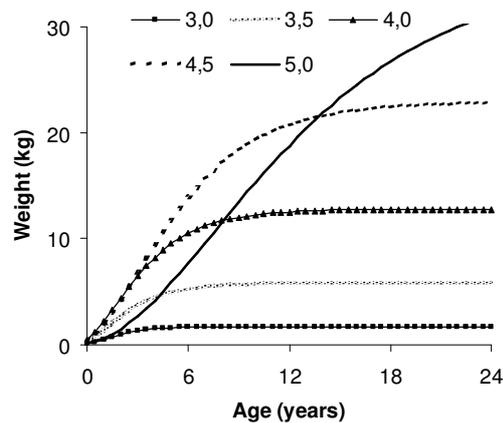


Fig. 3. Growth curves for some trophic classes used in the simulation model.

Yield-per-recruit model

A yield-per-recruit model of Beverton and Holt type (1957) is used. The fishing mortality is weighted by a gear selectivity modelled with a trophic level-dependent relationship. The selectivity function defines the magnitude at which the trophic classes are

targeted by the fishery (Figure 4). This function assumes that fisheries preferentially direct their exploitation towards high trophic levels than lower ones, despite a possible expansion of pelagic fisheries observed in some ecosystems (Pinnegar et al., 2002). Different fishing efforts are simulated from a fishing mortality of reference (F_{simu}) in order to represent a large range of fishing pressure going from under to overexploitation (effort multiplier evolving from 0 to 2 by 0.1 steps).

$$\left\{ \begin{array}{l} Y/R = s \times mF \times F_{simu} \times e^{-M(t_c - t_r)} \times W_{\infty} \times \sum_{n=0}^3 \Omega_n \times \frac{e^{-nK(t_c - t_0)}}{Z + nK} \\ s = \frac{TL^{\alpha}}{TL_{50}^{\alpha} + TL^{\alpha}} \end{array} \right.$$

Where Y is the yield, R is the recruitment, M is the total natural mortality and Z is the total mortality; $\Omega_0=1$; $\Omega_1=-3$; $\Omega_2=3$; $\Omega_3=-1$.

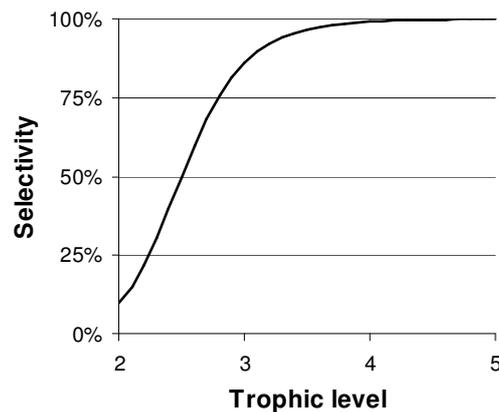


Fig. 4. Selectivity function of the fishery used in the simulation model.

Trophic spectra and biomass model

A trophic spectrum displays the distribution of the biomass of an ecosystem by trophic level (Gascuel, *in press*). In order to analyse the production functions in different types of ecosystems, different trophic spectra representing different levels of biomass accumulation in the system are simulated in accordance with observed situations. In this perspective, trophic spectra are constructed from Ecopath data to describe various potential biomass distributions by trophic level (Figure 5a). According to the ecosystem considered, the biomass can be either stored in the low trophic levels or more spread along the trophic continuum, characterizing a lower accumulation at the bottom of the trophic web. Therefore, the biomass in the simulator is modelled with a normal distribution centred in μ and of variable standard deviation (σ). To represent the exploitable biomass instead of the total biomass of the ecosystem, some simulations were also conducted with a spectrum centred in the trophic level of 3.0 (Figure 5b). Then, the total biomass of the ecosystem and total catches can be estimated for each level of exploitation rate:

$$\begin{cases} Y = Y/R \times R \\ B = B/R \times R \end{cases}$$

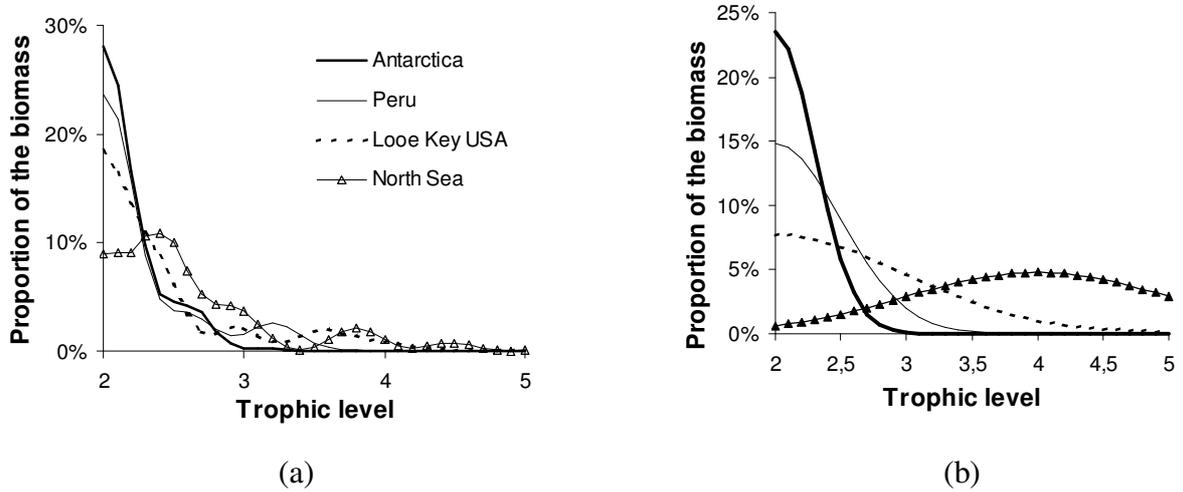


Fig. 5. (a) Trophic spectra representing the biomass distribution by trophic level in 4 ecosystems: the North Sea, the upwelling area of Peru, the marine reserve of Looe Key in the United States and the Weddell Sea in Antarctica (source: <http://www.Ecopath.org>). (b) Simulated trophic spectra in the simulation model. Line with triangles represents the biomass accessible to exploitation in the ecosystem.

Recruitment model

A recruitment is assumed for each trophic class according to a trophic spectrum pre-determined and the model of biomass per recruit. The recruitment is considered constant and can be viewed as a mean recruitment expected in a predictive approach. The recruitment is estimated from the virgin situation (no fishing activity):

$$R_i = \frac{B_{i,v}}{(B/R)_{i,v}}$$

Where $B_{i,v}$ is the biomass of the trophic class i defined by the trophic spectra in the virgin situation. $(B/R)_{i,v}$ is the biomass per recruit estimated in the pristine situation by a biomass-per-recruit model:

$$B/R = e^{-M(t_c - t_r)} \times W_\infty \times \sum_{n=0}^3 \Omega_n \times \frac{e^{-nK(t_c - t_0)}}{Z + nK}$$

Simulations

First, simulations are carried out in order to test the impact of the different trophic spectra on the production functions in the model. Then, different levels of predation are

considered, describing different ecosystems in which the predation mortality is taking an increasing part in the total mortality affecting the trophic classes. The rates of effective search a_{ji} that represent the instantaneous mortality rate on prey i caused by one unit of predator j biomass (Walters et al., 1997) are thus given increasing values. As already mentioned, these parameters are assumed independent on the type of prey but are weighted by a coefficient of trophic preference. The aim of these simulations is to quantify the impact of the ‘predation efficiency’ on the production functions, according to their place in the food web and on the total ecosystem production (Table 2).

Table 2. Values of the parameters used in the simulations

Simulation	Top-down control (a_j)	Spectrum (μ, σ)	F_{simu}
Simulation 1: top-down control	0.00005	2, 1.0	0.15
	0.00001	2, 1.0	0.15
	0.000001	2, 1.0	0.15
Simulation 2: trophic spectra	0.000015	2, 0.3	0.05
	0.000015	2, 0.5	0.05
	0.000015	2, 1.0	0.05
Simulation 3: accessible biomass	0.000015	3; 1.0	0.05

Results

Fishing effects

According to the VBGF defined for each trophic class, the same fishing pressure implies a state of overexploitation for the high trophic levels whereas the low trophic levels remain under-exploited (Figure 6). This is due to the slower growth of the high trophic levels and remains true for a large range of fishing mortalities of reference (F_{simu}).

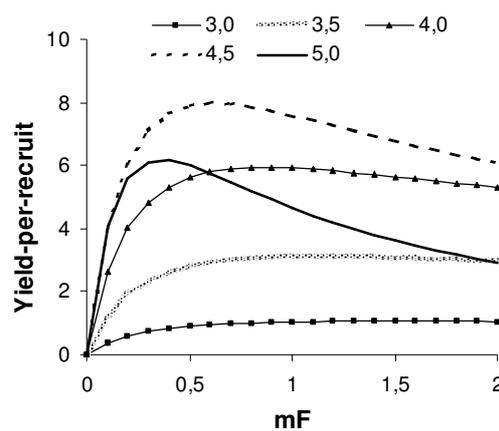


Fig. 6. Yield-per-recruit curves for some trophic levels of the system. $F_{simu}=0.1$.

The fishing activity modifies the biomass spectrum by preferentially targeting some trophic levels of the ecosystem (Figure 7). Thus, the spectrum can change from an initial spectrum modelled by a normal distribution of standard deviation 1.0 to a spectrum less spread along the food web, characterizing a decrease in the biomass of the high trophic levels

and an increase in the low trophic levels. The decrease of the predators biomass thus implies an increase in abundance of the preys.

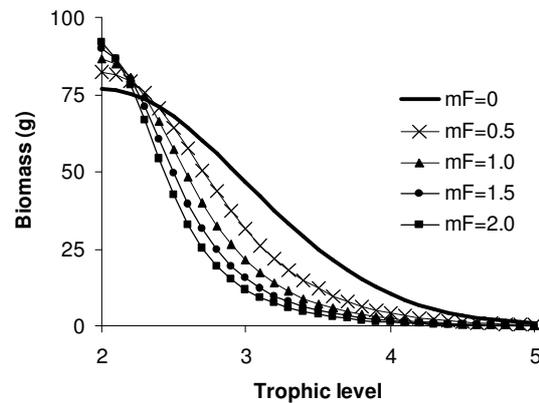


Fig. 7. Variation of the biomass trophic spectra with fishing.

Production functions variability

Simulations carried out for different levels of top-down control show that biomass-per-recruit and yield-per-recruit functions depend on the place of the trophic class in the food web (Figure 8). In the low trophic levels, the biomass-per-recruit function is highly variable according to the control exerted in the ecosystem, the biomass being lower for increasing 'rates of effective search' simulated (Figure 8a). The effect of the top-down control on the functions seems to decrease with the trophic level. Above the trophic level 4.0, the top-down control does not affect the biomass and yield functions (Figure 8c).

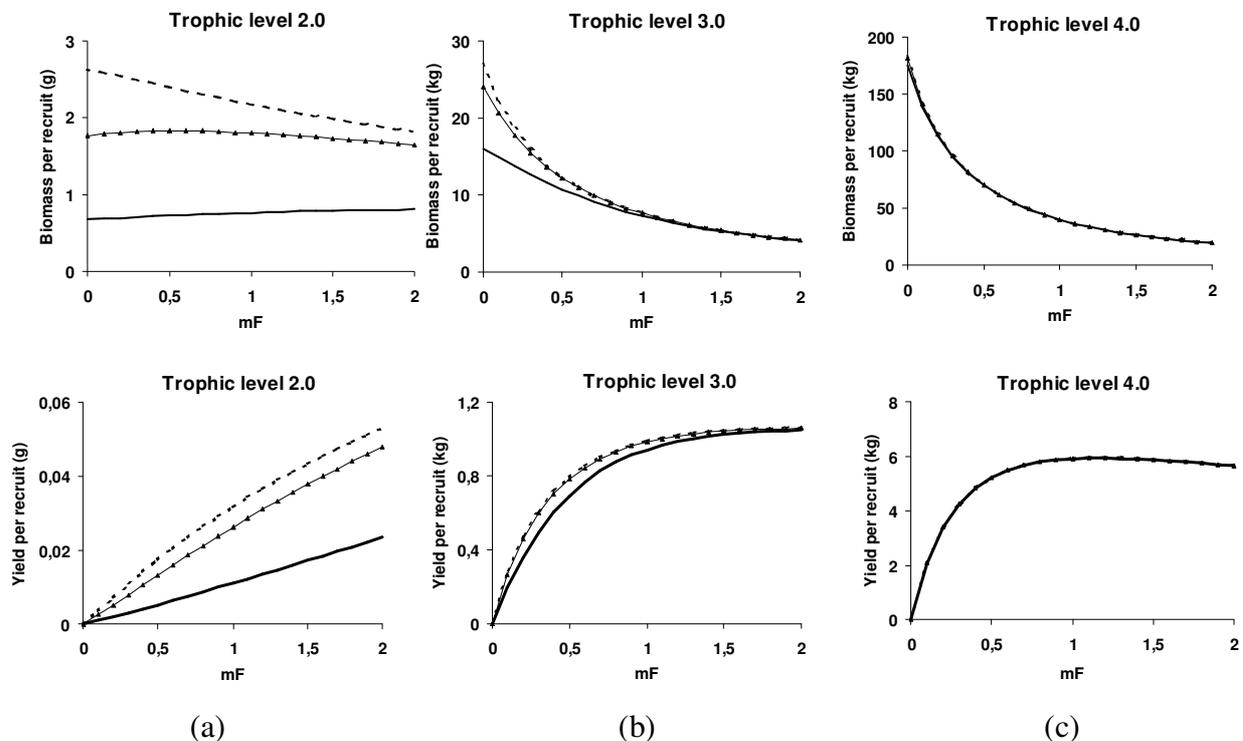


Fig. 8. Biomass-per-recruit and yield-per-recruit functions according to the trophic level of the class for different levels of top-down control. High predation, solid line; intermediary predation, solid line with triangles; low predation, dashed line. Parameters used are defined in table 2 (Simulation 1).

Biomass trophic spectra used in the simulation to define the biomass distribution by trophic level in the virgin ecosystem also have an impact on the biomass-per-recruit functions (Figure 9). The degree of variability of the functions seems also linked to the trophic level of the class of interest, the low trophic levels being more affected by a variation in the spectrum than the higher levels. For the trophic level 2.0, the biomass functions are very different according to the simulated spectrum and show a slight increase with the fishing effort. Trophic classes above the trophic level 4.0 seem poorly affected by the initial spectrum used.

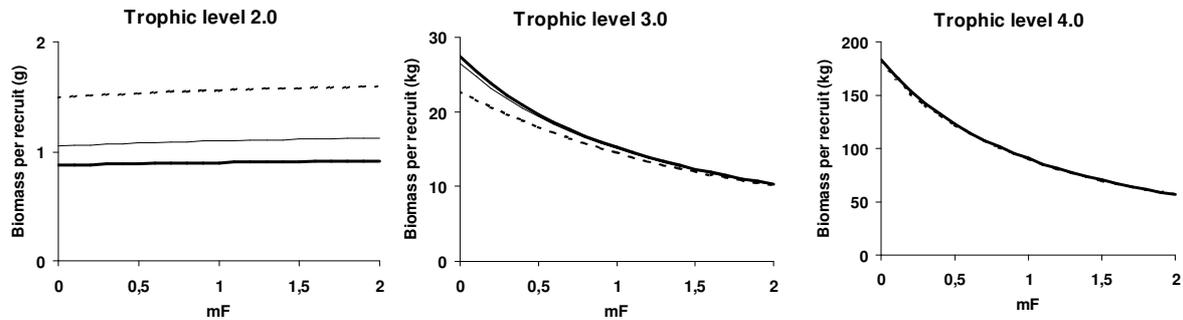
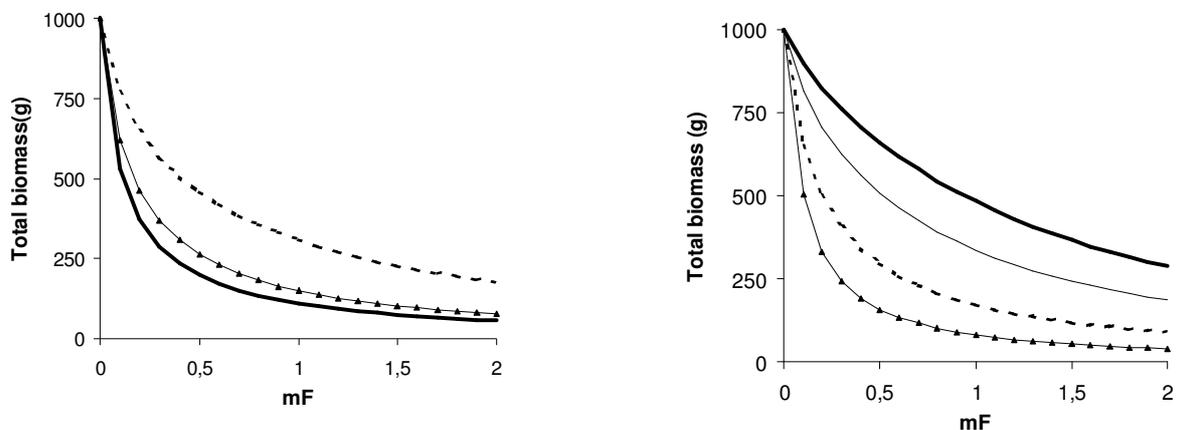


Fig. 9. Biomass-per-recruit functions according to the trophic level of the class for different initial biomass trophic spectra modelled by a normal distribution of mean 2 and variable standard deviation (σ). $\sigma=0.3$, solid line; $\sigma=0.5$, solid line with triangles; $\sigma=1.0$, dashed line. Parameters used are defined in table 2 (Simulation 2).

Ecosystem overexploitation

The biomass distribution along the trophic continuum and the magnitude of the top-down control in the ecosystem both affect the biomass-per-recruit of the trophic classes and therefore their production functions. Thus, the total production of the ecosystem, corresponding to the sum of the yields of all the trophic classes targeted, is strongly linked to both factors. The total catches within the food web increases with increasing top-down control and shows a maximum of exploitation higher for a strong top-down control (Figure 10a). In the same way, the ecosystem presents more resistance to overexploitation when the trophic spectrum is narrow, i.e. when most of the biomass is stored in the low trophic levels (Figure 10b). The trophic spectrum representing the accessible biomass to exploitation implies a rapid overexploitation.



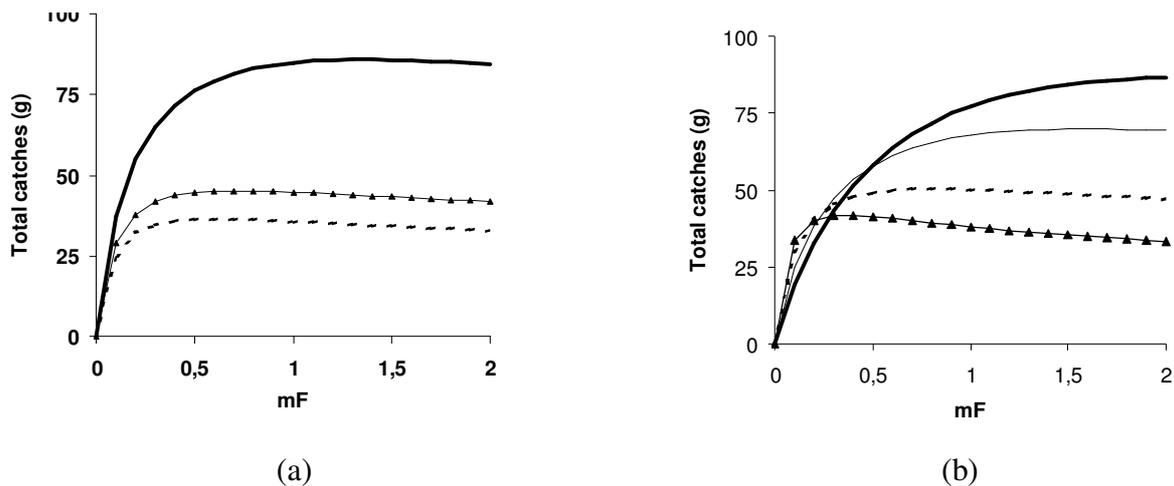


Fig. 10. Ecosystem biomass and total catches for (a) Different levels of top-down control. High predation, solid line; intermediary predation, solid line with triangles; low predation, dashed line (Simulation 1 with $F_{simu}=1$) (b) Different trophic spectra modelled by a normal distribution of mean μ and variable standard deviation (σ). $\mu=2$ $\sigma=0.3$, thick solid line; $\mu=2$ $\sigma=0.5$, thin solid line; $\mu=2$ $\sigma=1.0$, dashed line. Solid lines with triangles represents a spectrum of accessible biomass ($\mu=3$, $\sigma=1$). Parameters used are defined in table 2 (Simulation 2 with $F_{simu}=1$).

Discussion

Model assumptions and limits

Using a simulation model enables a high flexibility regarding the assumptions and parameters employed. However, defining a high number of parameters may also cause some difficulties for their estimation, and eventually the application of the model to real data. Nevertheless, the interest in such a virtual laboratory is to explore different possible realities by inferring them from a set of assumptions on the functioning of the ecosystem. In this sense, virtual experimentation is the natural extension of modelling (Maury and Gascuel, 1999).

In the simulator, a number of weaknesses can arise from some of the assumptions made. First, the trophic level 1 corresponding to both phytoplankton, algae and detritus is not included in the analysis. Yet, food availability is considered to be one of the main factors affecting fish recruitment and ultimately fish abundance (Cury et al., 2003). Including primary production and nutrients recycling complicates greatly the system to model and the analysis mainly focuses on the exploited part of the ecosystem. Moreover, pelagic marine food webs are characterized by a weak coupling between phytoplankton and herbivores (Micheli, 1999). A second limit of the model concerns the recruitment of the trophic classes that is supposed constant in the model. Indeed, the simulator does not take into account the impact of the predators abundance on the recruitment of the different trophic classes. This presupposes that the recruitment only depends on the primary productivity of the system and on the environment and is not linked to the trophic relations between preys and predators, an assumption often verified in nature (Cushing, 1982; Cury and Roy, 1989; Cury et al., 2003, Platt et al., 2003). The recruitment used can be viewed as a mean value allowing to realize short-term predictions as in current yield-per-recruit analyses. The use of a stock-recruitment relationship by trophic class could improve the model by defining a limit of biomass from which the recruitment can decline. No bottom-up control is included in the analysis. Indeed, the production of the different trophic classes generated through the consumption process is not considered contrary to current predator-prey models (see for a review Jost, 1998). The

fishery and the trophic classes are assumed to be in a steady state and the model estimates analytically the annual yield by taking into account a predation process affecting each trophic cohort. A bottom-up control in the form of a positive parameter in the survival equation corresponding to a 'resistance' to predation in function of the prey biomass in the system could be included in further analysis. In the same way, a variation of the growth parameter (K) and the asymptotic length (L_{∞}) of the VBGF with the amount of available prey could be an alternative to include a bottom-up control in the model.

The model also includes a term of endogenous recruitment that represents potential exchanges between trophic classes. Because of a lack of information about this parameter, it is supposed constant at equilibrium and equal between the trophic classes. Otherwise, accumulation of biomass would occur and the biomass spectrum of reference would be modified. Another potential weakness of the simulator lies in the linear functional (biomass of preys consumed per unit area per unit time by a unit of biomass of predator) response retained (Lotka, 1924; Volterra, 1926). The simulated situation dubbed « laissez-faire » in which no predator interference or facilitation is considered does not represent satiation by predators. However, data of stomach contents in aquatic ecosystems show that most consumers are rarely able to achieve satiation (Walters et al., 1997). Including predator dependence or ratio-dependence (e.g. Jost, 1998) in the model could be an interesting task but would greatly complicate the mathematical resolution of the equations and increase the number of parameters of the model.

Trophic level and trophic preference

A species' trophic level indicates the number of times chemical energy is transformed from a consumer's diet into a consumer's biomass along the food chains that lead to the species (Williams and Martinez, 2002). Although the concept has been criticized to a certain extent (Cousins, 1987), trophic levels have found a broad application throughout ecology. In aquatic ecosystems, mean trophic levels available on Fishbase (Froese and Pauly, 2000) are estimated through gut contents analyses and/or Ecopath models. Because of high costs and difficulties in sampling stomach contents, the quality and reliability of the trophic levels estimated is highly variable. In this context, development of stable isotope techniques (e.g. Post, 2002) is very promising and their recent application to marine ecosystems is encouraging (Pinnegar et al., 2002). Moreover, comparisons between the 2 methods show strong correlations between the values of trophic position estimated (Vander Zanden et al. 1997; Davenport and Bax, 1998; Kline and Pauly, 1998).

In the model, all the species are aggregated by trophic classes that are in concordance with the trophic species concept of Briand and Cohen (1987): "a collection of organisms that feed on a common set of organisms and are fed by a common set of organisms". Lumping organisms into a trophic hierarchy thus enables to define a trophic-species web (Martinez, 1991) easier to describe and analyse. Defining the predators and preys however requires to define properly the trophic preference functions. Based on the niche theory in which niche relationships are modelled with bell-shaped curves (May, 1976), and size preference curves related to log-normal probability functions (Andersen and Ursin, 1977), we chose normal distributions to model the preference of each class. According to the definition of the "flow-based trophic level" of Adams et al. (1983), the mean of the distribution is the trophic level of the predator minus 1. The standard deviations estimated allow the existence of trophic cannibalism, looping, omnivory and predation on higher trophic levels in minor proportions (Williams and Martinez, 2000) as well as the overlap in prey use by predators (Cohen, 1978). Within the theoretical "prey window" defined, predation in the model only depends on the available biomass of the preys. Therefore, trophic positions estimated with the current flow-

based trophic level equation (Adams et al., 1983) might differ from the trophic classes defined a priori. Indeed, the model does not consider constant diet compositions independent on the prey biomasses present in the system as in Ecopath and Ecosim models (Christensen and Pauly, 1992; Walters et al., 1997). Thus, the trophic level equation is only used to define the trophic preference of each class. In nature, food consumption is also linked to the quality of the diet, the energy requirements and the assimilation efficiencies of the predator (Trites, 2003).

Fishing effects

Parameters of the VBGF estimated for each trophic class imply a higher sensibility of high trophic levels to growth overexploitation whereas low trophic levels seem more resistant to exploitation. Indeed, high trophic levels are defined by a slower growth due to the growth parameter (K) and asymptotic length (L_{∞}) estimated in the simulation model, a longer lifespan and are also strongly targeted by the fishery. In marine ecosystems, larger and later maturing species are less able to withstand a given rate of fishing mortality than their smaller earlier maturing counterparts (Jennings et al., 1998). Because trophic position and size are correlated at the community level (Jennings et al., 2001), high trophic levels seem to be more vulnerable to exploitation than low trophic levels.

Top-down control

The level of top-down control modifies the production functions according to the place of the trophic class within the food web. Top-predators production functions are poorly subjected to predation and therefore relatively insensitive to changes in the top-down control. In the same way, trophic classes above the trophic level 3.5 are also poorly affected by a variation in the top-down control because their biomass is low and they are mainly targeted by the fishing gear simulated. On the other hand, low trophic levels display very different biomass-per-recruit functions according to the level of predation in the system. Indeed, they are targeted in minor proportion by the fishery but display a high number of predators due to the structure of the food web. Therefore, low trophic levels are subjected to a stronger predation release because of the harvesting of their predators' biomass for an increasing top-down control in the system.

Trophic cascades are defined as reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one food-link in a food web (Pace et al., 1999). They have been observed in marine ecosystems (Hughes, 1994; Sala et al., 1998 ; Pace et al., 1999; Pinnegar et al., 2000; Jackson et al., 2001 ; Worm and Myers, 2003) although they may seldom occur (Cury et al., 2003). Simulating trophic cascades was not straightforward because the system is not composed of a simple linear chain but represents a complex food web with multiple links, each trophic class having a large range of preys. Because the food web buffers the consumer-resource interactions (Micheli, 1999), observing a clear top-down effect that cascades downward required very high rates of effective search. Indeed, trophic cascades can be dampened or eliminated by numerous compensatory mechanisms such as omnivory and complexity of food webs (Pace et al., 1999).

Fishing modifies the biomass trophic spectrum of the ecosystem by removing important biomasses out of the system and altering the consumer-resource relationships. Ecosystems characterized by high levels of predation seem to be more resistant to overexploitation because of a stronger compensation effect due to the predation release. Therefore, global overexploitation of an ecosystem characterized by a strong top-down

control seems doubtful and would require to target the low trophic levels. Moreover, low trophic levels often display lower prices than high trophic levels (Pinnegar et al., 2002) and remain difficult to exploit. However, fishing down marine food webs has been currently observed in marine ecosystems (Pauly et al., 1998). As an illustration, the rapid development of fishing in West Africa in a few decades has led to a succession in the exploitation going from large demersal fishes such as the white grouper (*Epiphenelus aenus*) to the shrimp (*Penaeus duorarum norialis*) via the octopus (*Octopus vulgaris*) (Poinsard and Garcia, 1984; Faure, 2000). This succession seems mainly due to a new fishing activity linked up to the overexploitation of the demersal community (Gascuel, *in press*) and the impact of the environment on the abundance of the resource. Nevertheless, it could also be linked to a strong predation relaxation following the decrease in biomass affecting a high number of demersal stocks (Faure, 2000; Laurans et al., *submitted*).

Trophic spectrum and ecosystem maturity

Simulating different trophic spectra under pristine (unfished) conditions determines the production functions obtained. Indeed, low trophic levels seem very sensitive to the spectra used whereas biomass-per-recruit functions of high levels are relatively independent on the spectrum. Indeed, because the exploitation mainly targets high trophic levels, assigning a more important part of the food web to high trophic levels implies a stronger predation relaxation, as discussed above. Thus, an important feature of the ecosystem appears to be the shape of the trophic spectrum which describes the distribution of the biomass between trophic levels in the pristine ecosystem. Spectra of low standard deviation are characterized by a lower trophic diversity, a high productivity, a high biomass, a small size of organism often related to a r strategy and match therefore some of the attributes defining a “young ecosystem” (Odum, 1969). Because exploitation seems to reduce the extent of the biomass trophic spectrum, it acts as a perturbation that modifies the ecosystem from a more mature to a younger state. Thus, defining a pristine spectrum of reference and analysing its variability with time could therefore serve as quantifying the level of development of the system with exploitation.

Conclusion

The interest of the simulation model is to integrate some of the patterns currently observed in marine ecology despite the absence of a general theory on the functioning of the ecosystems (Cury et al., 2003). The aim was thus to simulate some potential characteristics of the ecosystems functioning and evaluate their impact on the production functions. Because the energy flows within the systems are a way of exploring their behaviour, one crucial point to analyse the consumer-resource relationships remains in the definition of the trophic preference between trophic classes. Indeed, current approaches used in fisheries sciences deal with size preference but size is strongly linked to the trophic position at the community level (Jennings et al., 2001) and might only be a proxy of the trophic level.

Describing the trophic spectrum of the ecosystem and analysing its temporal variability could help in characterizing its functioning and eventually defining its sensibility to overexploitation. In this perspective, a key component to understand the energy flows within the system is the estimation of the predation efficiency along the trophic continuum. Using ecosystem indicators such as the ecotrophic efficiencies from ECOPATH (Christensen and Pauly, 1992) or transfer efficiencies (Jennings et al., 2002) within the systems to quantify the levels of top-down control appears a necessary task in order to improve our understanding of the responses of different trophic webs to exploitation. Other indices quantifying the

variation in strength of species interactions exist (Berlow et al., 1999) but have not been yet performed in marine ecosystems in this perspective. The biomass spectrum and the level of top-down control (predation) are two essential factors of the ecosystems functioning and particularly of their ability to react to a given exploitation. These characteristics should eventually be taken into account in the perspective of an ecosystem management.

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