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Impact of trophic interactions on production functions and on the ecosystem response to fishing: A simulation approach

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Abstract – A simulation model is developed to analyse the variability of production functions in an exploited virtual ecosystem. We assume that a complex food web can be represented by a set of trophic components interacting through predation. Each component has a set of recruitment, growth, and survival models, a catch level and trophic preference function. Prey are consumed according to their abundance and predators' trophic preference functions are estimated in a pristine system. A parameter for the food consumption per unit biomass describes foraging for each trophic component. The FishBase database is used to parameterise some of the major processes in a generic model. A commercial fishery targets mostly high trophic levels through a set selectivity function. Some key ecosystem features are assessed in simulations: the intensity of top-down and of bottom-up controls, and the degree of trophic opportunism. Top-down control is the regulation of lower food-web components by one or several upper-levels predators. Bottom-up control is the regulation of trophic components by their prey. Results show that biological production functions are highly dependent on predation parameters and vary differently according to trophic level. Fishing activity modifies the biomass distribution between components and strongly affects higher trophic levels more sensitive to exploitation. Trophic dynamics within the system are altered through the rates of predation mortality. In systems where predation mortality is high, top-down control dominates and fishing affects all food web components. These "fishing-controlled" systems display compensatory mechanisms through a released predation control. We also show that systems where productivity is dependent on prey abundance are more "environment-controlled" and seem more sensitive to overexploitation, particularly the higher trophic levels. Trophic opportunism tends to dampen the propagation of top-down or bottom-up controls through the food web and thus stabilizes the ecosystem. Trophic relationships are therefore essential ecosystems characteristics that determine production and response to exploitation. Their routine analysis is a key part of the ecosystem approach.

Key words: Bottom-up / Top-down controls / Fishing effects / Multi-specific / Predation / Production function / Simulation / Trophic level

Résumé – Impact des interactions trophiques sur les fonctions de production et sur la réponse des écosystèmes à la pêche : approche par simulation. Un modèle de simulation est développé afin d'étudier la variabilité des fonctions de production au sein d'un écosystème virtuel exploité. Nous faisons l'hypothèse qu'un réseau trophique complexe peut être représenté par un ensemble de classes trophiques interagissant par prédation. A chaque classe est associé un modèle de recrutement, croissance, survie, capture et une fonction de préférence trophique. Les proies sont sélectionnées en fonction de leur abondance dans le système et de la fonction de préférence trophique des classes prédatrices, estimée à l'état vierge. Un paramètre de consommation de nourriture par gramme corporel définit l'importance de la ration alimentaire de chaque classe trophique. L'utilisation de la base de données FishBase pour paramétrer certain des principaux processus modélisés permet de replacer le simulateur dans un cadre très général. La pêcherie cible majoritairement les hauts niveaux trophiques suivant une fonction de sélectivité donnée. Certains traits majeurs du fonctionnement de l'écosystème sont testés à partir de simulations : l'intensité des contrôles descendants et ascendants et le degré d'opportunisme trophique. Le contrôle descendant correspond à la régulation des composantes de bas niveaux trophiques par un ou plusieurs prédateurs supérieurs. Le contrôle ascendant est la régulation des composantes du réseau

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trophique par leurs proies. Les résultats montrent que les fonctions de production sont très dépendantes des jeux de paramètres de prédation simulés et varient différemment selon les niveaux trophiques. L'activité de pêche modifie la distribution de la biomasse et affecte particulièrement les hauts niveaux trophiques plus sensibles à l'exploitation. Ceci a pour effet d'altérer les dynamiques trophiques au sein du système par le biais des taux de mortalité par prédation. Dans les systèmes où la mortalité par prédation est importante, le contrôle descendant prédomine et la pêche affecte alors tous les compartiments du réseau trophique. Ces systèmes contrôlés par la pêche présentent des mécanismes de compensation par relâchement de la prédation. Nous montrons également que les systèmes où la productivité dépend de l'abondance des proies sont plutôt contrôlés par l'environnement et semblent plus sensibles à une surexploitation, surtout dans les hauts niveaux trophiques. L'opportunisme trophique tend à modérer la diffusion du contrôle descendant ou ascendant le long du réseau trophique et stabilise ainsi l'écosystème. Les relations trophiques constituent ainsi des facteurs essentiels des écosystèmes qui déterminent leur production et leur réponse à l'exploitation. L'étude en routine de ces paramètres est l'un des facteurs clés de l'approche écosystémique.

1 Introduction

Quantifying the effects of fishing on marine ecosystems is an important question in fisheries science (Jennings and Kaiser 1998; Hall 1999), particularly interspecific flows within the ecosystem (Kerr and Ryder 1989). Difficulties stem from the high complexity of marine food webs, with a great number of interacting species and types of interactions. Fishing can lead to dramatic changes in fish community structure (Pinnegar et al. 2002; Laurans et al. 2004) by affecting the abundance of most species through interactions. Among these interactions, predation is a major source of natural mortality for many fish populations (Bax 1998) and greatly influences fish stocks dynamics. In this perspective, a simulation model is built to analyse the variability of production functions in a virtual ecosystem. Production functions describe the biological production of a population at equilibrium given its abundance in the system. It is also the potential fish production at equilibrium. They are a function of the nature and strength of links within the food web, of fishing intensity on targeted species and of characteristics of ecosystem functioning. We describe a complex food web by a set of trophic components interacting though predation. The simulator provides a high flexibility to test hypotheses of ecosystem functioning. The main objective of the analysis is to explore the effect of predation on the production functions and ecosystem reaction capacity to fishing exploitation. Three main parameters are considered, measuring the intensity of top-down control (ζ), bottom-up control (ψ) and the degree of omnivory in the system (θ). The aim of the paper is to answer the following questions: (i) How does fishing modify the distribution of biomass within the system? (ii) How do production functions vary according to the ecosystem characteristics? (iii) Are there systems that display a higher resilience to fishing overexploitation than others?

2 Materials and methods

2.1 Model description

The model simulates a virtual ecosystem in which all compartments interact through trophic relationships. The compartments represent trophic components ranging from trophic level 2.0 for secondary producers (strict herbivores and zooplankton) to 5.0 for top-predators in 0.1 intervals. At first, we consider organisms recruited to a trophic component permanently. This point will be discussed further. Each trophic component is age-structured with growth, survival, yield and recruitment functions for its biomass. The parameters of natural and fishing mortality are considered constant for all ages in each trophic component but differ across trophic component. The biomass of trophic level 1.0 is assumed to be non-limiting in the system. The pristine situation (no fishing) is the state of reference from which different steady-state scenarios are simulated. The model is run with an annual time step and solved by iteration. We first present the models followed by the simulation scenarios. Symbols and abbreviations used are summarized in Table 1.

Individual growth

A model of individual growth is defined using the von Bertalanffy Growth Function (VBGF; von Bertalanffy 1938) for each trophic component or class *i*. Parameters are estimated from empirical linear regressions (Figs. 1a,b) between the asymptotic length ($L_{\infty,i}$; cm) or the growth rate (K_i, t^{-1}) and the mean trophic level of the species using data from the FishBase database (Froese and Pauly 2000). These provide estimates for the individual weight (W_i) in each trophic component *i* at age *t* (Fig. 1d):

$$W_i(t) = a_i \times L_{\infty,i}^{b_i} \times \left(1 - e^{-K_i \times (t - t_0)}\right)^{b_i} \quad (1)$$

where a_i and b_i are parameters of the allometric length-weight relationship, with a_i estimated by linear regression using FishBase (Fig. 1c) and b_i is fixed at 3. We set t_0 (integration constant) to 0. All other parameters are specific to each trophic component.

Survival

Following the classic model of Beverton and Holt (1957), we consider a trophic cohort *i* that is subject to both natural (M_i) and fishing mortality (F_i) assumed constant during its fishable life-span. In order to describe interspecific relationships, natural mortality is partitioned into $M_i = M1_i + M2_i$.

The survival equation for a trophic cohort in function of age *t* is expressed as:

$$N_i(t) = R_i \times e^{-(F_i + M1_i + M2_i) \times (t - t_r)} \quad (2)$$

where $N_i(t)$ is the number of individuals of age *t* in the trophic cohort, *R* is the yearly recruitment of the trophic cohort (see below), $M1_i$ is the natural mortality rate without predation,

Table 1. Symbols and abbreviations used in the study.

Parameter	Definition	Value	Equation
B	Biomass	Estimated	3
Y	Yield	Estimated	8
$M1$	Mortality rate due to other causes than predation	Set to 0.05	2
$M2$	Mortality rate due to predation	Estimated	2
F	Fishing mortality rate	Set to 0.2 or 0.4	2
t_r	Age at recruitment	Set to 1	2
α	Parameter of the S-R relationship	Fixed (calibration)	9
β	Parameter of the S-R relationship	Fixed (calibration)	9
ρ	Coefficient of trophic preference	Estimated (pristine state)	4
K	Parameter of the VBGF, of dimension year-1	Estimated (FishBase)	1
L_∞	Parameter of the VBGF, asymptotic length in cm	Estimated (FishBase)	1
a	Parameter of the length-weight relationship	Estimated (FishBase)	1
b	Parameter of the length-weight relationship	Set to 3	1
η	Parameter of the selectivity function	Fixed (Table 2)	7
TL_{50}	Trophic level at which the selectivity is 50%	Fixed (Table 2)	7
$TLj\text{-}\gamma$	Mean of the function of trophic preference of the predator j	Estimated (pristine state)	-
Q/B	Food consumption per unit biomass	Estimated (FishBase)	6
φ	Available biomass	Estimated	4
ψ	Parameter defining the intensity of bottom-up control	Fixed (Table 2)	10
ζ	Parameter defining the intensity of top-down control	Fixed (Table 2)	-
θ	Parameter defining the trophic opportunism	Fixed (Table 2)	11
χ	Mean of the pristine biomass trophic spectrum	Fixed (Table 2)	-
δ	Standard deviation of the pristine biomass trophic spectrum	Fixed (Table 2)	-
A	Specific food conversion efficiency	Set to 0.5	12

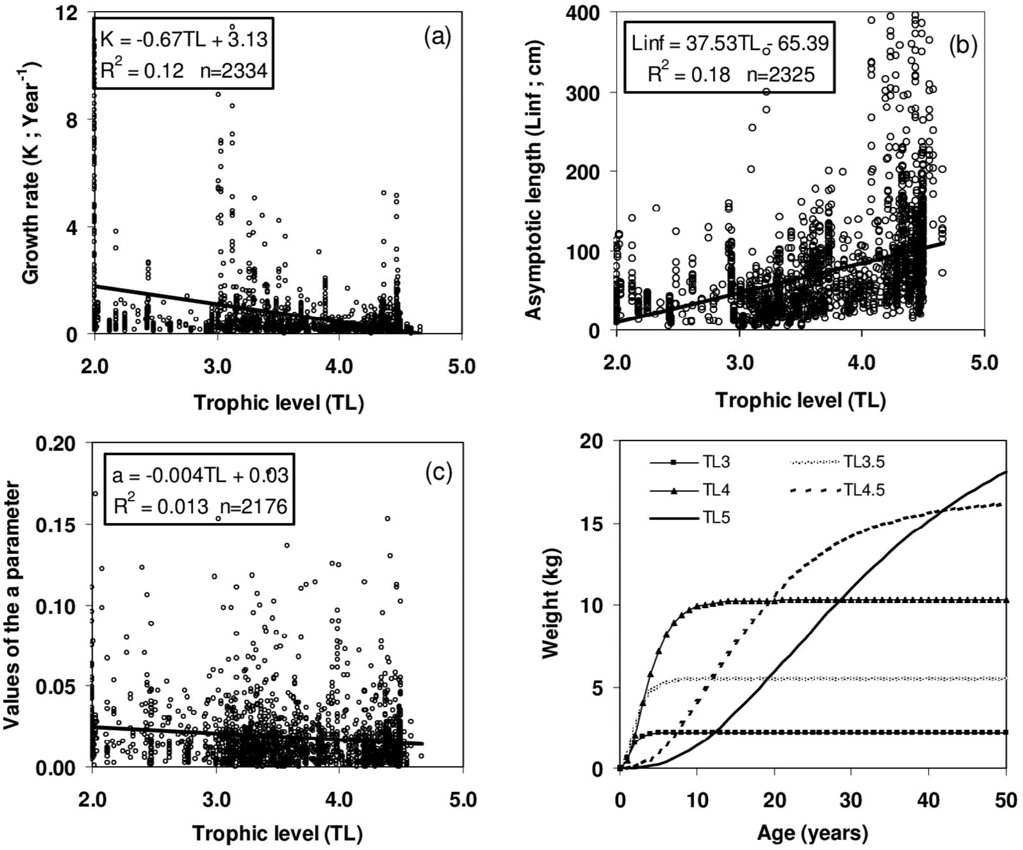


Fig. 1. Relationship between the parameters of the von Bertalanffy Growth Function (von Bertalanffy 1938), mean trophic level of fish species and corresponding growth functions for some trophic levels of the simulation model. Data come from FishBase (Froese and Pauly 2000); a) Growth rate, K; b) Asymptotic length, L_{inf}; c) Parameter a of the length-weight relationship; d) Growth functions in weight (kg).

$M2_i$ is the predation mortality and t_r is the age at recruitment (Eq. (4)). t_r is set to 1 in the model.

In a steady-state situation, the total biomass B_i of a trophic component i can be estimated by integrating the following equation:

$$B_i = \int_0^{\infty} N_i(t)\ W_i(t)\ \mathrm{d}t. \tag{3}$$

Trophic preference

In the model, each predator j is given a function of trophic preference that defines a selection coefficient (ρ_{jk}) for its prey k in the system ($\rho_{jk} < 1$). This function is estimated in the pristine situation and then assumed constant, as an intrinsic characteristic of each trophic component. We assume that ρ_{jk} follows a normal distribution with mean $\mu_j = TL_j - \gamma_j$ and standard deviation (σ_j) increasing with trophic levels. γ_j represents the difference between the trophic level of predator j and of its preferred prey (generally assumed equal to 1). The diet of trophic components is assumed to become more generalist with increasing trophic levels, a trend illustrated by plotting fish omnivory indices versus their trophic levels in FishBase (Froese and Pauly 2000).

The food available to component j from component k is $\varphi_{jk} = \rho_{jk} \times B_k$. The total available biomass φ_j for a given predator j is:

$$\varphi_j = \sum_k \varphi_{jk} = \sum_k \rho_{jk} \times B_k. \tag{4}$$

The γ_j parameters are estimated in a pristine situation by solving the trophic level equations for all trophic components:

$$TL_j = 1 + \sum_k DC_{kj} \times TL_k = 1 + \sum_k \frac{\varphi_{jk}}{\varphi_j} \times TL_k \tag{5}$$

where TL_k and TL_j are the trophic levels of the prey and predators respectively and DC_{kj} is the diet composition i.e., the contribution of food item k to the diet of j.

Predators are thus assumed to have access to all prey equally (same vulnerability) and their diet composition directly reflects the proportion of each prey in the overall prey biomass. Trophic cannibalism i.e., consumption on the same trophic component, and predation on higher trophic levels are assumed to be minor (less than 5%).

Predation mortality

The rate of predation mortality ($M2_k$) for a trophic component k is considered equal for all ages. It is the proportion of prey that disappears each year through predation and is given by the ratio of the total amount of prey k eaten by all its predators j over the total biomass of prey:

$$M2_k = \frac{\sum_j \left(\frac{Q}{B}\right)_j \times B_j \times \frac{\varphi_{j,k}}{\varphi_j}}{B_k} \tag{6}$$

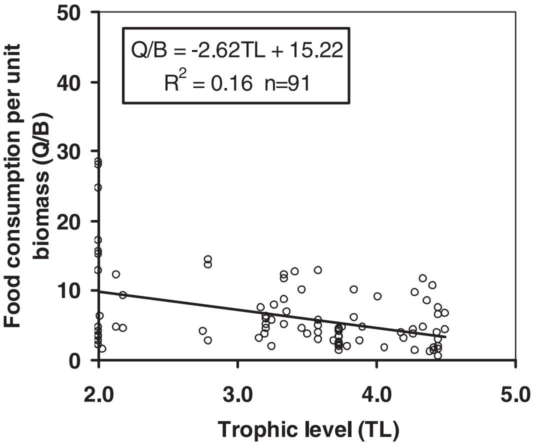


Fig. 2. Relationship between the food consumption per unit of biomass (*Q/B*) and the mean trophic level (*TL*) of fish species. Data come from FishBase (Froese and Pauly 2000).

where $(Q/B)_j$ is the annual food consumption of the predator per unit biomass, B_j is the predator biomass, B_k is the prey biomass and φ is the available biomass of prey (Eq. (4)). An empirical function between food consumption per unit biomass (*Q/B*) and trophic levels was first estimated from FishBase (Froese and Pauly 2000; Fig. 2), and the parameter *Q/B* is considered constant. In a second step, a *Q/B* varying with total mortality will be considered (see below). The estimated $M2_k$ is used in Eq. (2). The estimation of $M2_i$ from numbers or biomass leads to the same results because mortality is taken to be the same across all ages within a trophic component.

Yield

Following the standard model of Beverton and Holt (1957), we estimate the catches corresponding to a steady state in each trophic component. Therefore, the annual yield is the same as the yield throughout the fishable life-span of any one year-class. In order to define the trophic components preferentially targeted by the fishery, the fishing mortality (F_i) is weighted by a gear selectivity (s_i) modelled with a trophic level-dependent (TL_i) relationship:

$$s_i = \frac{TL_i^{\eta}}{TL_{50}^{\eta} + TL_i^{\eta}} \tag{7}$$

where TL_{50} is a parameter of the selectivity function indicating the trophic level at which selectivity is 50% and η is a parameter that gives the rate at which maximum selectivity is approached. From the Beverton and Holt equation, the yield (Y_i) is given by:

$$Y_i = R_i \times s_i \times m_F \times F \times W_{\infty,i} \times \sum_{n=0}^{3} \Omega_n \times \frac{e^{-nK_i}}{Z_i + nK_i} \tag{8}$$

where R is recruitment, s selectivity (Eq. (7)), m_F is a fishing mortality multiplier, F is the current fishing mortality, W_∞ the asymptotic weight, K the VBGF growth rate, Z is the total mortality and Ω_n are coefficients with $\Omega_0 = 1$; $\Omega_1 = -3$; $\Omega_2 = 3$; $\Omega_3 = -1$.

Recruitment

In order to get a self-regenerating simulated ecosystem, a Beverton and Holt (1957) deterministic stock-recruitment (S-R) function is defined for each trophic component:

$$R_i = \frac{\alpha_i \times B_i}{\beta_i + B_i} \tag{9}$$

where R_i is recruitment, B_i biomass and α_i and β_i are parameters of the S-R relationship. The main assumption here is that recruitment of a given component i only depends on its biomass B_i. The α_i parameters are used to calibrate the model. To this end, the α_i values are estimated in a pristine situation (no fishing). This pristine biomass trophic spectrum (Gascuel et al. 2002) corresponds to the biomass distribution by trophic level and is empirically chosen as a normal distribution with mean 1 and standard deviation 0.7.

2.2 Simulation scenarios

Fishing effects

At first, the system is simulated in a reference situation for the yield, biomass, trophic preference, diet composition, recruitment and rates of predation mortality. The total biomass, yield and their distribution by trophic component are calculated for different sets of model parameters (Table 2) and a fishing mortality multiplier m_F increasing from 0 to 2 by 0.1 steps.

Top-down and bottom-up control

Top-down control i.e., the regulation of lower food-web components by one or several upper-levels predators (Cury et al. 2003) is explicitly formulated through the predation mortality parameter. Its intensity is fixed through the parameter of food consumption per unit biomass (*Q/B*). Multiplying this parameter by a coefficient ζ according to the range of values observed in Figure 2 leads to increasing predation mortality in the total mortality affecting trophic components. Increasing this parameter increases top-down processes. Increasing values for the top-down parameter ζ were used for low and high fishing mortalities (Table 2). Bottom-up control i.e., the regulation of food-web components via the abundance of their prey is introduced through the growth rate (K_i) of each predator. K_i is assumed to depend on the proportion of available prey relatively to the pristine situation:

$$K_i = K_{i,\,\text{virgin}} \times \left(\frac{\varphi_i}{\varphi_{i,\,\text{pristine}}}\right)^{\psi} \tag{10}$$

where $K_{i,\,\text{pristine}}$ is the growth rate in the pristine state, φ_i is the prey biomass available for i (Eq. (4)), $\varphi_{i,\,\text{pristine}}$ is the prey biomass available in the pristine situation and ψ is a parameter defining the intensity of bottom-up control. This parameter allows growth to be faster when there is more food available than in the pristine situation. Conversely, in years with less food available growth will be slower. At first, changes in the abundance of trophic level 1.0 are simulated for different values of σ without fishing (Table 2). Second, the biomass of trophic level 1.0 is considered constant and non-limiting, at different fishing intensities (Table 2).

Trophic opportunism

Various degrees of opportunism corresponding to various types of ecosystem functioning are simulated. For this purpose, a linear relationship is assumed between the standard deviation of the trophic preference distribution (σ_i) and the trophic level (TL_i) with a slope θ:

$$\sigma_i = \theta \times TL_i. \tag{11}$$

Increasing θ simulates more generalist systems with trophic components preying on a wider range of prey.

Modelling age-structured effects

The parameter *Q/B* (see above) is assumed to be constant at first. However, the VBGF is derived from specific assumptions regarding energy assimilation and costs (von Bertalanffy 1938). The “specialized VBGF” assumes a consumption rate proportionate to body size to 2/3 power (Beverton and Holt 1957; Essington et al. 2001). Integrating the consumption (Q) at population level gives at equilibrium:

$$Q_i = R_i \times \frac{3K_i W_{\infty,\,i}}{A} \sum_{n=0}^{2} \Omega'_n \times \frac{e^{-nK_i}}{Z_i + nK_i} \tag{12}$$

where K is the VGBF growth rate, W_∞ the asymptotic weight, A the specific food conversion efficiency (caloric and indigestible correction), and Z the total mortality. As previously, the age at recruitment t_r was set to 1 and the parameter t_0 (integration constant) was set to 0. A is set to 0.5 and considered constant in the simulations for all trophic components. $\Omega'_0 = 1$; $\Omega'_1 = -2$; $\Omega'_2 = 1$. *Q/B* is estimated from Eqs. (8) and (12) by dividing *Q/R* by *B/R*. It shows that *Q/B* will increase with Z because younger age classes tend to predominate in a population submitted to increasing fishing pressure. Parameters used in the simulation dealing with top-down control (Table 2) were used with the new values of *Q/B* to estimate the impact on the results.

3 Results

3.1 Fishing effects

The trophic structure of the ecosystem is modified by a fishing activity that mainly targets the higher trophic levels and has a direct impact on their abundance (Fig. 3). These variations in biomass are transferred within the food web through the rates of predation mortality affected by biomass variations. Consequently, fishing not only affects the trophic components targeted but results in modifications of all components in the system by removing high trophic levels biomass. The degree of fishing impact is closely linked to the values of the predation parameters ζ, ψ and θ that can either propagate or restrict the extent of the effects. According to the growth function defined for each trophic component, high trophic levels are more sensitive to overexploitation than lower trophic levels (Fig. 4). This is due to their relative slower growth characterized by lower growth rates (K, Fig. 1a) and larger asymptotic lengths (L_∞, Fig. 1b) than for lower trophic levels.

Table 2. Values of the parameters used in the simulations; *TL* Trophic level.

	F	TL_{50}	η	$B_{TL1.0}$	ζ	ψ	θ
Reference	0.2	3.0	30	5.4×10^{14}	1	0.1	0.05
Biomass trophic spectra (Fig. 3)	0.2	3.0	30	5.4×10^{14}	1	0.1	0.05
Yield-per-recruit (Fig. 4)	0.4	0.0	30	5.4×10^{14}	1	0.1	0.05
Top-down control (Figs. 5a-b)	0.2	3.0	30	5.4×10^{14}	0.5 to 2	0.1	0.05
Top-down control (Fig. 5c)	0.6	3.0	200	5.4×10^{14}	0.5 to 2	0.1	0.05
Bottom-up control (Figs. 6a-b)	0.4	3.0	30	5.4×10^{14}	1	0 to 0.6	0.05
Bottom-up control (Fig. 6c)	0.6	3	30	5.4×10^{14}	1	0 to 0.6	0.05
Variation in $TL_{1.0}$ abundance (Fig. 7)	0	3.0	30	$5. \times 10^{13}$ to 5.3×10^{15}	1	0.2	0.02 to 0.08
Trophic opportunism (Fig. 8)	0.2	3.0	30	5.4×10^{14}	1	0.1	0.02 to 0.08
Trophic cascade (Fig. 9)	1	3.5	200	5.4×10^{14}	1	0.1	0.02 to 0.08
Variable *Q/B* (Fig. 10)	0.2	3.0	30	5.4×10^{14}	2	0.1	0.05

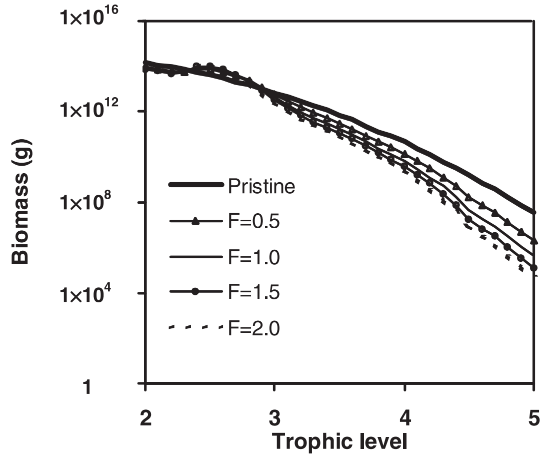


Fig. 3. Biomass trophic spectra giving the distribution of biomass by trophic level for different values of fishing mortality.

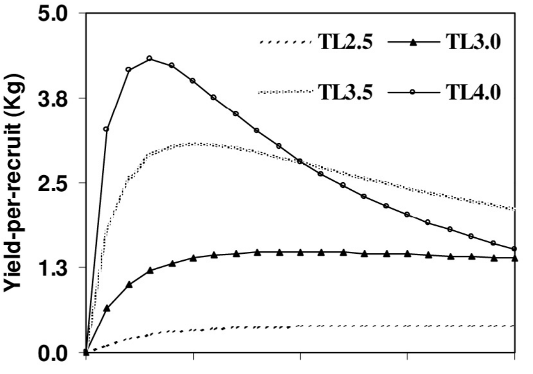


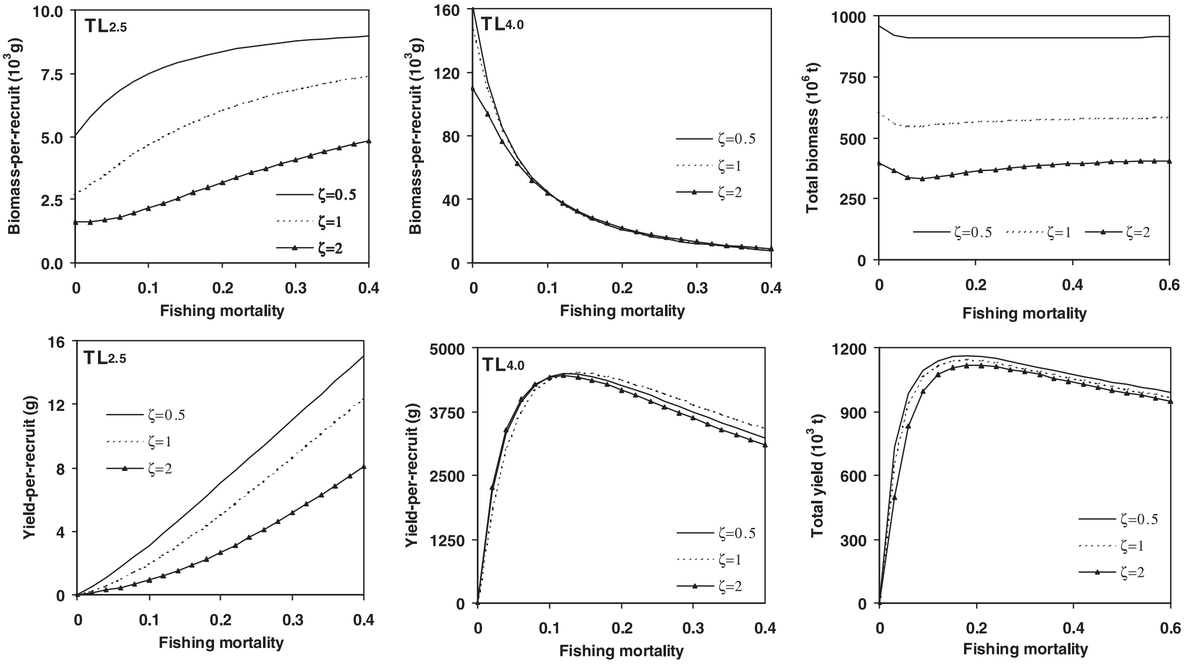
Fig. 4. Yield-per-recruit functions for some trophic levels of the system.

3.2 Top-down control

Simulations for different levels of top-down control show that production functions depend on the position of the trophic component in the food web (Figs. 5a *TL2.5* and 5b *TL4.0*). At low trophic levels, yield-per-recruit functions vary widely with the control exerted in the ecosystem. As primary production is assumed to be non-limiting and lower trophic levels are less exploited by fishing, their biomass depends mostly on predation mortality exerted by higher trophic levels. Therefore, increasing grazing rates strongly affects biomass by modifying the rates of predation mortality. Trophic components directly preyed upon by exploited trophic levels display a higher yield-per-recruit when a top-down control releases predation pressure. This has a decreasing effect as trophic level increases because the parameter *Q/B* decreases with trophic levels (Fig. 2) and the biomass in high trophic levels is lower. It is therefore dependent on the biomass trophic spectrum chosen. The magnitude of top-down impact within the food web seems closely linked to the ratio of predation mortality to the total mortality encountered by a trophic component. Trophic levels characterized by a high ratio are very sensitive to the intensity of top-down control. Systems described by a weak top-down control display higher catches and higher overall biomass consequently to the decrease in predation mortality on all their components. However, the global production curve for the whole ecosystem shows a maximum of yield for lower fishing mortalities in the case of weak top-down control (Fig. 5c). Conversely, systems showing an intense control by the predators seem to resist overexploitation better although the total yield remain lower. Indeed, release from predation control increases with the intensity of the top-down control and can cause an increase in the total biomass of the system (Fig. 5c).

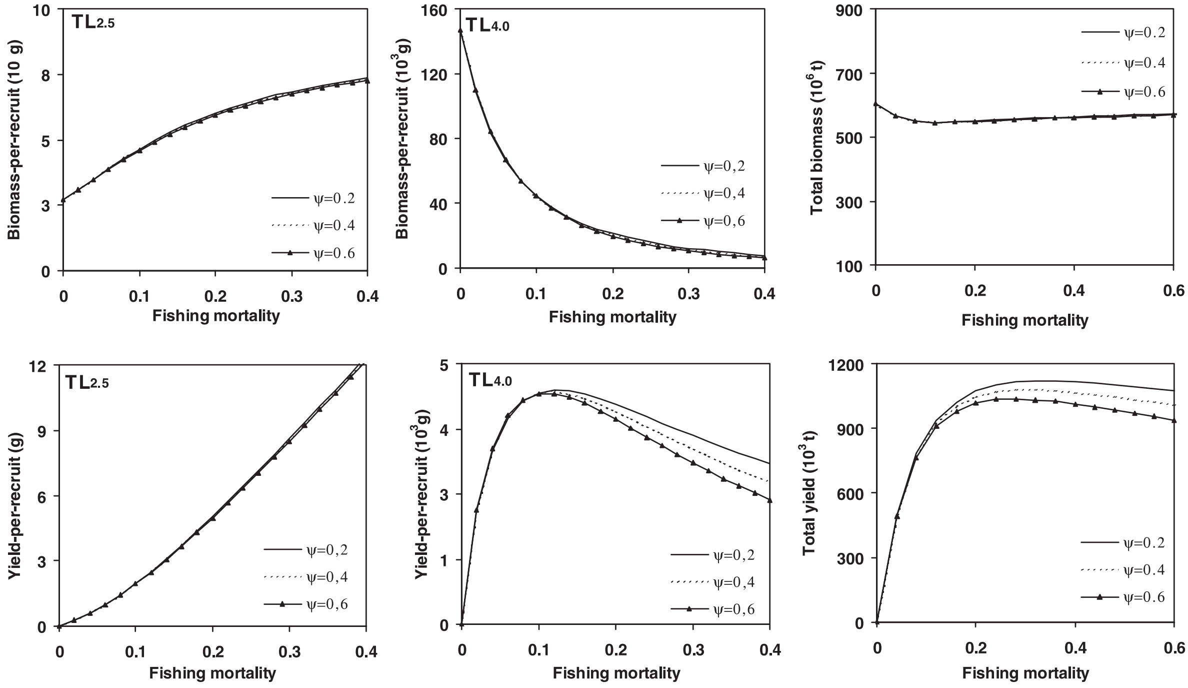
3.3 Bottom-up control

The variability of the yield-per-recruit functions estimated for different degrees of bottom-up control simulated is greatly dependent on trophic levels (Fig. 6). Production functions in low trophic levels are poorly affected by an increase in the intensity of bottom-up control. Indeed, the abundance of their prey does not vary much relative to the pristine situation because the biomass of trophic level 1.0 is assumed non-limiting and constant in the model and low trophic levels are not exploited (Fig. 6a). On the other hand, high trophic levels display variable production functions according to the degree of bottom-up control. By reducing the prey biomass of the high trophic levels, the fishing activity generates a decrease in the parameter K of their growth function according to Eq. (10).



(a) (b) (c)

Fig. 5. Top-down control. Yield-per-recruit and corresponding biomass-per-recruit functions for trophic levels 2.5 and 4.0 and total yield and biomass according to different intensities of top-down control in the system. Trophic level 1.0 is not included in the total biomass. ζ is the parameter defining the intensity of top-down control (see text for details).



(a) (b) (c)

Fig. 6. Bottom-up control. Yield-per-recruit functions and corresponding biomass-per-recruit functions for trophic levels 2.5 and 4.0 and total yield and biomass according to different intensities of bottom-up control in the system. Trophic level 1.0 is not included in the total biomass. ψ is the parameter defining the intensity of bottom-up control (Eq. (10)).

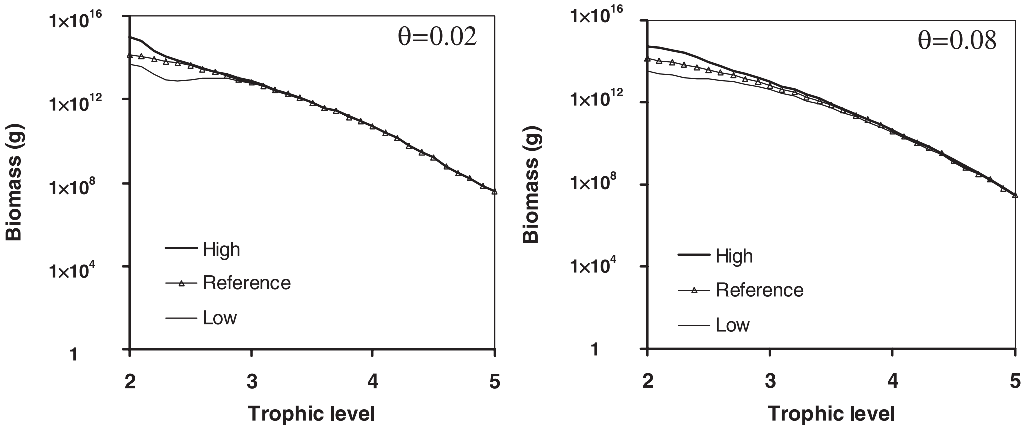


Fig. 7. Biomass trophic spectra for three levels of abundance of trophic level 1.0 in the system and according to different values of θ see text for details).

The decrease in the value of K with increasing values of the bottom-up parameter ψ implies a decrease in yield-per-recruit for a given fishing mortality (F) and thus generates states of growth overexploitation for lower fishing mortalities (Fig. 6b). Considering the total yield in the ecosystem, the bottom-up control accelerates the overexploitation of high trophic levels by reducing their prey biomass and this generates an earlier state of ecosystem overexploitation for high values of ψ (Fig. 6c). The whole biomass of the ecosystem does not display strong variations due to bottom-up control because it is mostly predominated by very low trophic levels almost not affected by fishing. Simulating variations in phytoplankton abundance mostly modifies low trophic level biomass following the intensity of bottom-up control used. The effect propagates further up through the food web but is dampened for increasing values of θ (Fig. 7). However, it rarely cascades upward to affect the high trophic levels because the bottom-up control is only accounted for the growth parameter.

3.4 Trophic opportunism

Increasing the trophic opportunism modifies the predation mortality and therefore the biomass of all the compartments of the food web. Production functions thus display different responses according to the trophic component considered and to the magnitude of trophic opportunism simulated in the system (Fig. 8). Decreasing θ generates a decrease in the predation mortality affecting lower trophic levels. Therefore, they display higher biomasses and higher yield-per-recruit for a similar fishing mortality. In the same way, for intermediate and high trophic levels, the increase in trophic opportunism increases the predation mortality and thus implies a lower biomass and lower yield-per-recruit for a given fishing effort. Trophic cascades are simulated for increasing values of trophic opportunism. For a value of 0.02 for the parameter θ, the functions of trophic preference are very narrow and define very specialist trophic components, mainly preying upon trophic levels just below. The trophic cascade simulated is then straightforward because fishing decreases the biomass of high trophic levels and generates a release from predation control for intermediate trophic levels. This increases their biomass and consequently the predation mortality affecting lower trophic levels that then display a decrease in biomass (Fig. 9a). The trophic cascade is dampened for increasing values of θ defining more generalist systems (Fig. 9b).

3.5 Taking account of age-structured effects in the model

Simulations including a parameter *Q/B* that varies with fishing mortality (Eq. (11)) show that yield-per-recruit and biomass-per-recruit functions are affected at all trophic levels but in relatively minor importance. All figures are not presented here for reasons of clarity but results show that the general patterns observed with a constant *Q/B* (Figs. 3 to 9) are maintained. Taking into account the variable *Q/B* leads to higher predation mortality in the system submitted to fishing because of higher *Q/B*. For a given fishing mortality, systems with variable *Q/B* thus display a stronger top-down control than for constant values. This is traduced in the simulation by a higher release from predation when the predators abundance decreases (Fig. 10).

4 Discussion

Estimating the links between predator and prey populations and their impacts on population dynamics has been a major task in ecology since the pioneer works of Lotka (1924) and Volterra (1926). In fisheries science, the past two decades have seen an explosive growth in the number and type of multispecies models developed to quantify the effects of trophic interactions on fish populations (for a review see Hollowed et al. 2000; Whipple et al. 2000). Notably, the Ecopath with Ecosim software (Christensen and Pauly 1992; Walters et al. 1997) has been widely used to investigate the ecosystem functioning and estimate the effects of fishing (Christensen and Pauly 2004). However, all these models generally require large data sets that are difficult to collect. The approach taken here allows the definition of a very general framework with parameters derived from the FishBase database available worldwide. This notably enables the avoidance of results that could

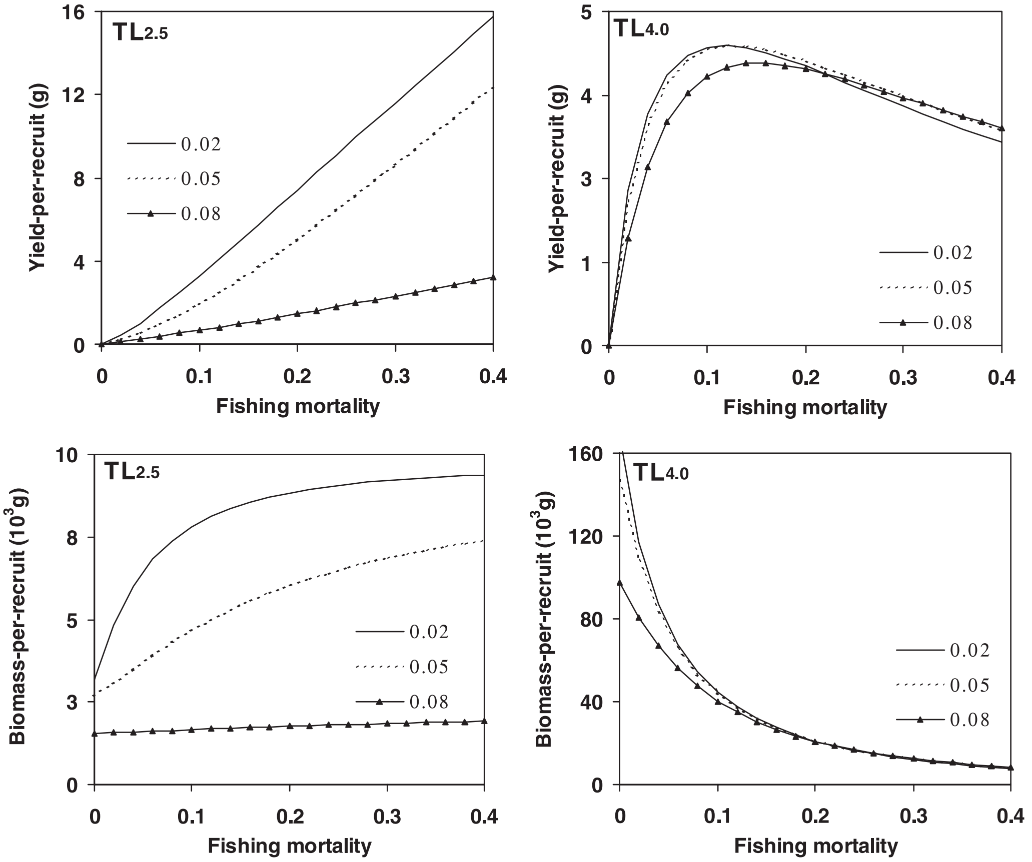


Fig. 8. Yield-per-recruit functions and corresponding biomass-per-recruit functions for trophic levels 2.5 and 4.0 according to different degrees of trophic opportunism in the system. θ is the parameter defining the magnitude of trophic opportunism (Eq. (11)).

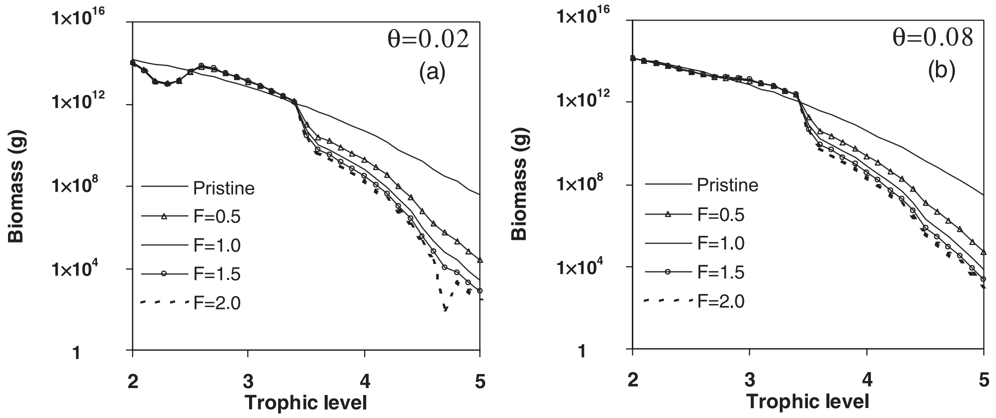


Fig. 9. Biomass trophic spectra for different levels of fishing mortality and according to different values of θ; a) $\theta = 0.02$; b) $\theta = 0.08$.

be linked to specific ecosystems. Using a simulation model enables a high flexibility regarding the assumptions and parameters employed. 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, some necessary assumptions on the functioning of exploited marine ecosystems are made. The model is based on predation processes because predation appears to be the most central organizing concept in ecology (Martinez 1995). All species are aggregated by trophic class as suggested by the trophic species concept (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 enables the definition of a trophic-species web (Martinez 1991) that is easier to describe and analyse. Here, species are not grouped into compartments according to their

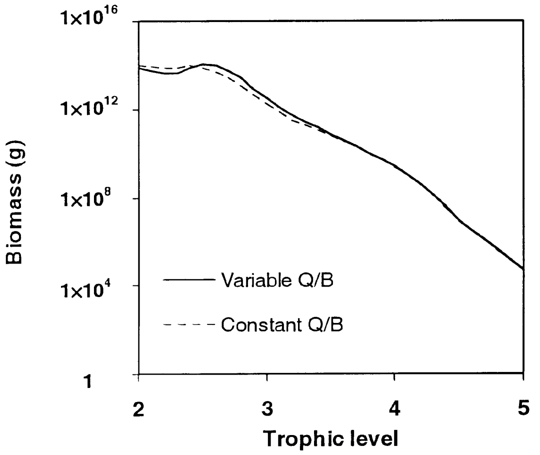


Fig. 10. Biomass trophic spectra considering (a) constant *Q/B* derived from FishBase and (b) *Q/B* varying with total fishing mortality according to the VBGF assumptions.

diet composition as in Ecopath models (Christensen and Pauly 1992) but the whole biomass is distributed in classes defined by their trophic level. This choice of modelling approach is closer to a model of energy flows and enables a higher flexibility to represent trophic relationships within the food web (see below). The coefficient M1 is the rate of natural mortality excluding predation but it could also account for possible shifts of species with age from one trophic component to another due to ontogeny. Trophic components would then represent a compartment gathering various species according to the age considered. In this case, estimated growth equations would be naturally questionable. However, global dynamics of the system would certainly remain in the same order of magnitude and general results obtained would be poorly modified. Within a trophic component, species are given a mean profile that should represent inter-individual and inter-specific variability. The species composition of each class remains however essential. Using different sets of parameters (ζ, ψ, θ) should allow us to represent ecosystems displaying different species compositions. In the model, recruitment of each trophic component is assumed independent on the abundance of the other interacting classes. Indeed, in nature, fish recruitment mainly depends on the physical environment and primary productivity (Cushing 1982; Cury and Roy 1989; Platt et al. 2003). Abundance of trophic level 1 corresponding to phytoplankton, algae and detritus is assumed non-limiting in the food web. Here, the analysis mainly focuses on the exploited part of the ecosystem and pelagic marine food webs are characterized by a weak coupling between phytoplankton and herbivores (Micheli 1999). Recruitment in the simulator is considered as a mean recruitment allowing the realization of short-term predictions as in current yield-per-recruit analyses. Simulating a variable recruitment for some trophic components due to changes in climate for instance (Watters et al. 2003) and estimating its effects on the food web could be done with the model but would go beyond the scope of this paper.

In the model, the parameters of predation mortality are supposed constant across all ages of each trophic component. This is a strong and unrealistic assumption of the present analysis. However, such an assumption is usually made in stock assessment methods regarding natural mortality. In the same way, we chose to consider a constant fishing mortality at all sizes of a given trophic component associated with a curve of fishing selectivity defining the components preferentially targeted. These choices allow to greatly simplify the system studied and to rely on the classic model of Beverton and Holt (1957). Adding complexity through differential predation mortality based on size preference would require the definition of large sets of parameters (e.g. matrices of trophic preference) and this would weaken the general framework of modelling adopted.

Trophic preference

Defining the predators and prey requires to define properly their trophic preference functions. Based on the niche theory in which niche relationships are modelled with bell-shaped curves (May 1976), we chose normal distributions to model the trophic preference of each class. 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 this theoretical "prey window" defined, predation in the model only depends on the available biomass of prey. Functions of trophic preference are assumed constant and calibrated relative to the pristine situation. They are thus highly dependent on the initial biomass distribution that varies according to the types of ecosystems (Chassot and Gascuel 2003).

Fishing effects

Growth characteristics for each trophic component imply a higher sensibility of high trophic levels to growth overexploitation than low trophic levels for a similar fishing mortality. Indeed, high trophic levels present a slower growth due to the growth parameter (K) and asymptotic length (L_∞) estimated in FishBase and a longer life-span. Regression linear models that are used explain a low proportion of variance but express the simple and robust idea that high trophic levels globally display higher sizes and slower growth than low trophic levels. 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 and bottom-up controls

Simulations illustrate that top-predators production functions are logically poorly subjected to predation and therefore relatively insensitive to changes in top-down control intensity. On the other hand, low trophic levels display very different yield-per-recruit functions according to the level of predation in the system. An essential parameter determining the observed patterns is the relative part of the mortality by predation on the total mortality encountered by a given trophic component. The parameter ζ used to simulate various intensities of top-down control is related to the specific assimilation efficiency (A). High values of ζ correspond in fact to low values of efficiency associated with a strong top-down control (and reciprocally). Simulations carried out with constant and variable Q/B globally lead to the same qualitative results. Using a variable Q/B was more coherent with the assumptions inherent to the use of a VBGF and implied stronger top-down control. Actually, two opposite effects occurred in the simulation when fishing the species preying upon a given trophic component: a decrease in predation mortality when the predators abundance decreases, limited at the same time by an increase in the predation mortality linked to the increase in Q/B for the remaining predators. In nature, age-structured effects can thus limit the extent of top-down control although this compensation effect at the population level must be of minor importance relative to the effects of a decrease in predator abundance. However, using a variable Q/B required to add the parameter A assumed constant for all trophic levels. This seems an unrealistic assumption and it did not strongly modify the general results. Although it is difficult to establish clear links when several prey and predators are involved (May et al. 1979; Cox et al. 2002), it has been shown by meta-analysis that predators can suppress lower trophic levels in oceanic food webs as they do in lakes, streams and coastal waters (Worm and Myers 2003). Therefore, top-down control is a general pattern observed in many marine ecosystems (Cury et al. 2003). Ecosystems characterized by high levels of predation control seem to be more resistant to overexploitation because of a stronger compensation effect due to predation release. This can lead to an increase in the total biomass of the exploited ecosystem. Therefore, global overexploitation of an ecosystem characterized by a strong top-down control would require targeting low trophic levels that often display low prices (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).

Bottom-up control is assumed to explain many observations of fluctuations in predator populations following changes in abundance of forage fish (Cury et al. 2000). Systems where donor control predominates are supposed to greatly depend on primary producers. Here, this control is considered in its global sense i.e., the abundance of prey drives the abundance of predators and it is not restricted to primary producers. Indeed, a bottom-up perturbation of marine ecosystems is defined as an alteration of resource availability (Micheli 1999). Although bottom-up effects are relatively easy to figure out when dealing with the effects of nutrients on phytoplankton abundance, the link is not straightforward when we refer to an effect between upper trophic levels such as small pelagics and their predators. Clearly defining and identifying the relative part of the components of bottom-up control that might act at different temporal scales seems a necessary task to better understand its consequences in a food web. Although food availability does not influence growth directly, it does so indirectly via reserve energy (Kooijman 2000). It is simulated in the model through an empirical power type function that modifies the predator growth according to the abundance of prey in the system. This could represent a gain of energy linked to a decrease in time searching when prey abundance increases. On the contrary, the less food available, the greater the costs of hunting, locating and capturing its prey for the animal, thus leading to pronounced effects on growth efficiency (Ryther 1969). Despite the difference in the mathematical formulation used, the same approach was taken in the extended MultiSpecies Virtual Population Analysis (MSGVPA; Gislason 1999). Not considering effects of prey abundance on recruitment remains a choice of modelling that leads to more straightforward results and allows to avoid a higher complexity calling for more assumptions and parameters in the simulator. The model is thus based on the strong hypothesis that recruitment is mostly driven by environment rather than predation processes. Simulating an increase in phytoplankton abundance favoured the abundance of their direct predators according to the intensity of control. The magnitude of the effect and its propagation upward through the food web depend on the growth variability and on the degree of trophic opportunism. Simulation results highlight that high trophic levels are the classes particularly affected by bottom-up control when their prey are also targeted by fishing. Therefore, systems dominated by donor-control tend to be more subject to overexploitation. To sum up, ecosystems predominated by top-down control are more driven by fishing exploitation but can display an important reaction capacity. On the other hand, donor-controlled systems depend more on environment but appear to be more sensitive to exploitation. The balance of top-down vs. bottom-up control defines the production functions of each trophic class according to their place within the food web. Fishing modifies this balance and seems to shift the ecosystem functioning towards a more bottom-up control by removing major predators out of the system and altering consumer-resource relationship. Because predation is supposed to favour stability, fishing could lead to systems driven by donor control and thus becoming more dependent on climate variability and more subject to overexploitation. Defining the relative importance of each process is a difficult task (Cury et al. 2000) but should help in understanding the ecosystem dynamics and its response to exploitation. Trophic relationships are essential because they determine the production and stability of the ecosystem. However, they depend on prey biomass and on the functions of trophic preference within the food web and are thus variable in time and space. Therefore, an ecosystem approach requires analysing trophic relationships routinely in order to improve our perception of the ecosystem functioning.

Trophic opportunism and trophic cascades

A crucial point to analyse consumer-resource relationships lies in the definition of trophic preference because it considerably affects the trophic dynamics within the system and it eventually modifies the production functions of each trophic component. Simulation results show that trophic opportunism seems to dampen the effects of top-down or bottom-up control by diffusing them within the food web. Food webs described by a high opportunism display numerous weak interactions that seem to provide more stability to the system (Shin and Cury 2001), a pattern observed in nature (McCann et al. 1998).

As an illustration, 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). 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 component having a large range of prey. Observing a clear top-down effect that cascades downward required narrow functions of trophic preference. Indeed, trophic cascades can be dampened or eliminated by numerous compensatory mechanisms such as omnivory and complexity of food webs (Micheli 1999; Pace et al. 1999). They have been simulated (Harvey et al. 2003) and observed in marine ecosystems (e.g. Pinnegar et al. 2000; Jackson et al. 2001) although they may seldom occur (Cury et al. 2003). Indeed, because predation in marine food webs is essentially based on prey size (Kerr 1974) and therefore opportunistic, functions of trophic preference might be very large in nature, especially in pelagic food webs. Observing a clear trophic cascade thus requires specific conditions that might be rare in marine food webs.

Conclusion

The general modelling framework adopted in the present study allowed the finding of results and patterns already observed in nature or simulated with models applied to specific ecosystems. Notably, systems characterized by high predation mortality seem to be driven by top-down control and are thus "fishing controlled". Systems where productivity is dependent on prey abundance are predominated by bottom-up control and are thus more "environment controlled". The balance between top-down and bottom-up controls will specify the production functions and their variability inherent to fishing and environment, and this will eventually define the resilience of the ecosystem. Some of the major processes responsible for those controls are linked to the energy transfers occurring within the food web which are directly dependent on the energetic requirements at the individual and population levels. Lack of knowledge for many parameters dealing with energetic grounds calls for more work in this field in order to ultimately reconcile traditional yield models (i.e., classic population dynamics) with food web analysis.

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