



The trophic-level based model: A theoretical approach of fishing effects on marine ecosystems

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Received 29 July 2004; received in revised form 9 March 2005; accepted 29 March 2005
Available online 11 July 2005

Abstract

We propose the trophic-level based model as a new approach to analyse the functioning of marine ecosystems in both ecological and fisheries contexts. The model considers a virtual ecosystem where all the animal biomass is distributed along a continuum of trophic level classes. Biomass moves from one class to the upper ones according to predation and ontogenic processes. From a given secondary production occurring at trophic level 2, the ecosystem biomass distribution can therefore be expressed as the result of the biomass flow passing through the ecosystem, from low to upper trophic levels. The model is based on two main equations. One is regarding biomass flow, which decreases according to fishing and natural losses occurring during transfers. The other expresses the speed of the flow per trophic level, assuming that high metabolism rates induce fast transfers at the lower trophic levels. Additionally, various hypotheses of ecosystem functioning are considered, dealing with the extent of top-down controls, the intensity of feedback effects on secondary production through biomass recycling and the occurrence of a biomass inaccessible to fisheries.

Depending on which trophic levels are targeted, various scenarios are simulated. Results highlight the impact of increasing fishing efforts on the ecosystem, in term of total biomass, biomass distribution and mean trophic level. We notably show that high fishing pressure and low trophic level of first catch may lead to severe biomass depletions, even if no overfishing is generally observed. Transfer efficiencies as well as flow kinetics appear as key characteristics of the ecosystems functioning, determining its response to fishing pressure. Feedback effects on secondary production amplify the fishing effects. Conversely, the top-down control may be a major feature of the ecosystem resistance to fishing. It implies that any catch may have effects for all trophic levels and can induce cascade effects in the ecosystem.

More generally, we show that the trophic-level based model, built from a small number of very simple and rather unquestionable assumptions, leads to a relevant representation of ecosystem impacts of fishing. It might be regarded as a theoretical basis contributing to our understanding of such impacts. We finally discuss on the use of the model in real cases and we address its usefulness to build a general theory on marine ecosystem functioning.

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Keywords: Ecosystem modelling; Fishing impact; Trophic level; Biomass flow; Transfer efficiency; Kinetics of transfer; Top-down control

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1. Introduction

Fisheries management is nowadays still largely based on single species approaches, using models of population dynamic-developed since the 1950s. Stock assessment procedures are thus applied to each of the main targeted species and particularly intend to generate stock-specific annual advices and management recommendations like total allowable catches (TAC). Nevertheless, over the last decade improving ecosystem approach to fisheries has progressively been recognised as a necessity (Garcia, 2005) and we assist to the development of a wide range of models dealing with fishing effects at ecosystem scale. These new approaches should be considered more as complementary than alternatives to the single species ones. Indeed, ecosystem-based fisheries management is not meant to replace stock-assessments, which could be considered as tactical, but to provide a strategic context to it and criteria to choose TAC's (Christensen and Pauly, 2004).

In this context, a general consensus has emerged in the community of fisheries scientists that studying trophodynamics is a major concern to improve our understanding of marine ecosystems functioning (Pitcher and Cochrane, 2002; Cury et al., 2003). Since a few years, many ecosystem case studies have been analysed, generally using models that express trophic flows between the various groups present in the ecosystem. The most popular model and software that relies on the allocation of biomass in discrete groups is the mass-balanced Ecopath model (Polovina, 1984; Christensen and Pauly, 1992) and its dynamic extension Ecosim (Walters et al., 1997). Each group merges all species characterized by similar preys and predators and is considered as a functional group in the ecosystem. Such models appear as useful tools to investigate the ecosystem functioning and to analyse the past and present effects of fishing. Nevertheless, they do not provide a general theory on ecosystem impact of fisheries. Probably due to their high number of parameters, they also appear until now as poor tools of forecasts.

We propose here the trophic-level based model as a theoretical representation of ecosystem functioning and impact of fishing. This model can be regarded as a new step in the trophodynamic approach; it does not consider species any more but is directly based on trophic levels. The trophic level may be considered as the metric, which expresses the trophic process itself.

It is the result of what is eaten and represents a state variable characterising each unit of biomass present in an ecosystem. Thus, trophic levels can be used in order to analyse and model transfers in the food web, due to predation which implies discrete transfers of biomass from each prey to its predator, as well as to ontogenic processes characterized by continuous changes according to growth.

The trophic-level based model considers all the animal biomass of the ecosystem, distributed along a continuum of trophic level values split into fractional classes. Biomass moves from one class to the upper ones according to biomass flow equations, depending on natural processes and fishing.

Considering here a virtual ecosystem under steady state, theoretical simulations were conducted in order to analyse consequences of fishing on catches and ecosystem biomass, per trophic level or at the whole ecosystem scale. The model is firstly presented. Various hypotheses of ecosystem functioning are considered, dealing with: the extent of top-down controls, the intensity of feedback effects on secondary production and the occurrence of a biomass inaccessible to fishing. Simulations are then conducted with increasing fishing efforts and various scenarios in term of trophic levels targeted. We show the effects of the considered ecological hypothesis on yield, biomass and trophic levels trends.

We finally discuss the use of the trophic-level based model in real cases and we address its usefulness to analyse ecosystem effects of fishing and to build a general theory on marine ecosystem functioning.

2. Method

2.1. Biomass equations

The trophic level concept was firstly introduced by Lindeman (1942) to characterise the position of organisms within the food webs: 1 for primary producers and detritus, 2 for secondary producers, 3 for their predators, etc. Odum and Heald (1975) and Adams et al. (1983) defined fractional trophic levels for mixed regimes; thus, trophic levels of animals appear continuously distributed in the ecosystem.

Conventionally, the trophic-level based model is structured by trophic classes of $\Delta\tau=0.1$ range step,

from trophic level 2 corresponding to secondary producers to trophic level 5, value of 5 being considered as sufficient to cover almost all top predators. Biomass enters the system at trophic level 2 according to three processes: secondary production due to grazing on primary producers, biomass recycling by the microbial loops, and hatching for species whose early-stage larvae feed on phytoplankton. We assume that carnivorous larvae account for small inputs of biomass and can be neglected. Thus, biomasses at trophic levels higher than 2 come from the lower levels, not only by predation but also by ontogenic processes, since ontogeny is generally associated with changes in trophic levels or organisms during their life history. Finally, biomass outputs occur at all trophic levels involving fishing mortality and natural mortality other than predation.

Each process is not explicitly modelled. We just consider the global biomass flow passing through the ecosystem from low to upper trophic levels, according to predation and ontogeny. Under steady state and for a given amount of biomass entering trophic level 2, biomass per trophic level is then expressed as the result of this biomass flow:

$$B_\tau = \int_\tau^{\tau+0.1} \frac{B(t, \tau)}{d\tau} \times d\tau = \int_\tau^{\tau+0.1} \Phi(\tau) \times \frac{d\tau}{d\tau} \times d\tau \tag{1}$$

where $B(t, \tau)/d\tau$ is the density of biomass present in the ecosystem at time t and trophic level τ , B_τ the biomass present in the trophic class ranging from trophic level τ to trophic level $\tau + 0.1$ and $\Phi(\tau) = \frac{dB(t, \tau)}{d\tau}$ is the constant biomass flow passing through trophic level τ under steady state (see also definition of parameters used in Table 1).

The $\frac{d\tau}{dt}$ term is the inverse of a flow speed. Eq. (1) then traduces that biomass at a given trophic level is equal to the biomass flow divided by the speed of the flow. Consequently, the trophic level based model is built using two equations, one for biomass flow and the other for flow kinetics.

The biomass flow is assumed to follow a decreasing curve due to natural losses occurring during trophic and ontogenic transfers (non-predation mortality, egestion and excretion, dissipation of energy by respiration, ...) and to fishing losses (catches). Those processes are formalized using for each trophic class a coefficient of total loss equal to the instantaneous loss rate of biomass

flow:

$$\psi_\tau = \mu_\tau + \varphi_\tau = -\frac{1}{\Phi(\tau)} \times \frac{d\Phi(\tau)}{d\tau} \tag{2.1}$$

hence,

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \times \exp[-(\mu_\tau + \varphi_\tau) \times \Delta\tau] \tag{2.2}$$

where μ_τ is the natural loss rate of biomass flow and φ_τ is the fishing loss rate of biomass flow. Flow Eq. (2.2) implies that the natural transfer efficiency between trophic levels corresponds to $\exp(-\mu_\tau)$.

In our simulations, we use a simple form of this equation considering that in unexploited situations transfers efficiencies are equal for all trophic levels. Based on values commonly cited in the literature, a conventional transfer efficiency equal to 15% is considered as a standard value. Low and high transfer efficiencies are also simulated using values equal to 10 and 20%, respectively (Fig. 1).

The second equation required by the biomass model concerns the kinetics of transfers. Those ones are seldom analysed or quantified in the literature. No formal expression has been proposed to characterise them. Hence, an empirical model is used assuming that the time required to go from trophic level τ to trophic level $\tau + \Delta\tau$ follows a logistic curve. Such an assumption allows to define the kinetics of transfers as follows:

$$\tau = a \times \ln \left(\frac{e^{b \times t} - 1}{c} \right) \tag{3.1}$$

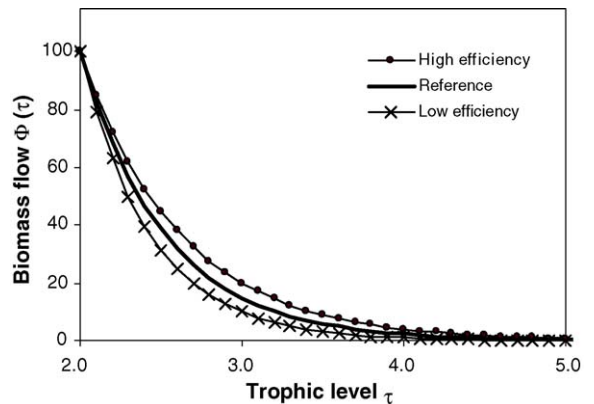


Fig. 1. Biomass flow model: biomass flow per trophic level (arbitrary units) for the three considered values of transfer efficiency (see Table 1).

Table 1
The trophic-level based model: parameters definitions and values used in the simulations

Notation	Parameter definition	Values used in simulations
$B(t, \tau)$	Instantaneous biomass at time t and trophic level τ	
B_τ	Biomass in the interval $[\tau, \tau + \Delta\tau]$	Estimated from Eq. (4)
Bv_τ	Biomass in the interval $[\tau, \tau + \Delta\tau]$ in the unexploited situation	Estimated from Eq. (4), with $\varphi_\tau = 0$
B_{ac}, B_{in}	Accessible and inaccessible biomasses	Estimated from Eqs. (9.1) and (9.2)
$\Phi(\tau)$	Biomass flow at trophic level τ	$\Phi(2)$ estimated from Eqs. (6.1) and (6.2), $\Phi(\tau \neq 2)$ estimated from Eqs. (2.1) and (2.2)
μ_τ	Natural loss rate of biomass flow, in the interval $[\tau, \tau + \Delta\tau]$	Estimated from Eq. (5)
μv_τ	Natural loss rate of biomass flow in the unexploited situation	Exploring values for $e^{-\mu_\tau} = 0.1, 0.15$ and 0.2
φ_τ	Fishing loss rate of biomass flow, in the interval $[\tau, \tau + \Delta\tau]$	Definite by Eq. (8)
S_τ	Selectivity coefficient by trophic level	Conventional logistic curves (Fig. 3)
mf	Fishing effort	mf = 0–2, by 0.2 range step
Δt	Time required by a unit of biomass to go from level τ to level $\tau + \Delta\tau$	Estimated from Eqs. (3.1) and (3.2)
a, b, c	Coefficients of the transfer kinetics model (Eqs. (3.1) and (3.2))	Empirical values corresponding to a range of realistic curves (cf. Fig. 3)
α_τ	Coefficient of top-down control (Eq. (5))	0 (“bottom-up ecosystem”) or 0.8 (“top-down ecosystem”)
β	Coefficient of biomass input control (Eqs. (6.1) and (6.2))	0 (“primary production-based ecosystem”) or 0.5 (“detritus-based ecosystem”)
ρ_τ	Rate of transfer between inaccessible and accessible biomass, at level τ	Estimated from Eqs. (9.1) and (9.2), in unexploited situation
Y_τ	Yield per unit of time in the interval $[\tau, \tau + \Delta\tau]$	Estimated from Eq. (7)

hence,

$$\frac{dt}{d\tau} = \frac{1}{a \times b} \times \frac{c}{c + e^{-\tau/a}} \quad (3.2)$$

with a, b and c parameters of the flow kinetics.

In our simulations, a, b and c are arbitrarily chosen in a range of empirical values corresponding to realistic curves (Fig. 2). Kinetics Eq. (3.1) may be interpreted as determining the trophic level reached at time t , by a unit of biomass starting at level 1 at a time close to zero. Formally, the theoretical model has no dimension. But if we accept that time is expressed in years, then parameters used correspond to the idea that a unit of biomass produced at level 1 at time zero reaches level 2 in some days, level 3 in some weeks and level 4 after around 6 months (Fig. 2a). Logistic curve (Eq. (3.2)) corresponds to fast transfers at low trophic levels, according to high metabolism, and to slower transfers at intermediate or high trophic levels. It also implies that the speed of the flow, and therefore the time required to go from one trophic level to the upper one, tends to an asymptote for the highest trophic levels. But parameters a, b and c may be chosen in order to display various types of curves, corresponding to a slowing of biomass flow which occurs at different trophic levels (Fig. 2b

and Table 1). A non-monotonous curve is also manually defined in order to simulate poorly predated species, at a given trophic level (around 3.0 here), whose presence should induce a slowing in the biomass flow.

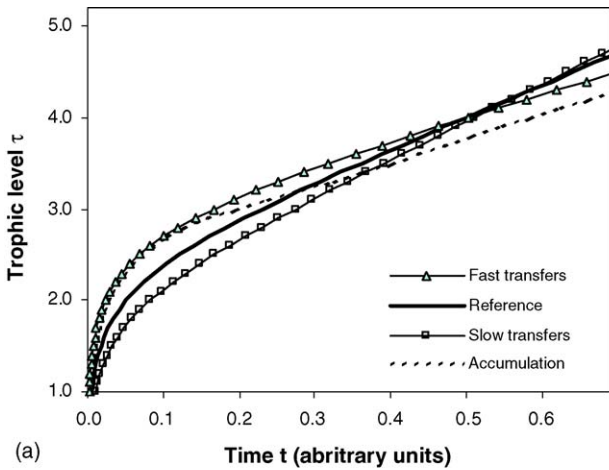
Finally, biomass Eq. (1) is reexpressed using a discrete approximation of Eq. (3.2):

$$B_\tau \approx \frac{\Delta t}{\Delta \tau} \times \int_0^{\Delta \tau} \Phi(\tau + x) \times dx = \frac{\Delta t}{\Delta \tau} \times \Phi(\tau) \times \frac{1 - \exp[-(\mu_\tau + \varphi_\tau) \times \Delta \tau]}{\mu_\tau + \varphi_\tau} \quad (4)$$

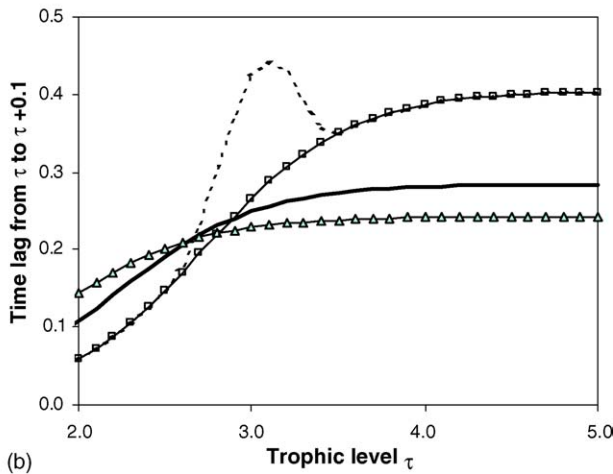
For a given biomass flow $\Phi(2)$ entering the system at trophic level 2, Eqs. (2.2) and (4) allow to estimate the biomass flow $\Phi(\tau)$ for each trophic level τ and the biomass B_τ for each trophic class $[\tau, \tau + 0.1]$. Obviously, these quantities depend on transfer efficiencies (μ_τ parameters), transfers kinetics (a, b, c) and fishing parameters (φ_τ).

2.2. Top-down control and biomass input control – Initialisation

Two types of considerations imply to go a little bit further than this very simple model and to intro-



(a) Time t (arbitrary units)



(b) Trophic level τ

Fig. 2. Model of the transfers kinetics: (a) relationship between the time and the trophic level reached by a unit of biomass and (b) time required by a biomass unit to go from trophic level τ to trophic level τ + 0.1. The four curves correspond to various sets of empirical parameters, used in order to simulate more or less fast transfers. Dashed line traduces the presence of poorly predated species around trophic level 3.

duce additional equations. First, if biomass flow at a given trophic level is independent of its predators abundance, then the model only admits bottom-up control. Conversely, top-down control can be introduced in the model by the mean of a relationship linking the natural loss rate of biomass flow at trophic level τ, and therefore the biomass flow and the biomass itself, to the biomass of predators at trophic level τ + 1. We assume that the natural loss rates are known in the unexploited situation. When predators abundance decreases

due to fishing, the natural loss rate of their preys also decreases, according to:

$$\mu_{\tau} = (1 - \alpha_{\tau}) \times \mu_{v_{\tau}} + \alpha_{\tau} \times \mu_{v_{\tau}} \times \frac{B_{\tau+1}}{B_{v_{\tau+1}}} \quad (5)$$

where α_{τ} is a coefficient expressing the extent of top-down control at trophic level τ and μ_{v} and B_{v} are the natural loss rate and the biomass in the unexploited situation, respectively.

In our theoretical simulations, a simple form of Eq. (5) is used with a constant coefficient $\alpha_{\tau} = \alpha$ for all trophic levels. Two empirical extreme values of α are considered, in order to analyse effects of top-down control: $\alpha = 0$ traduces an ecosystem without any top-down control and conventionally called “bottom-up ecosystem” and $\alpha = 0.8$ corresponds to strong top-down controls in a “top-down ecosystem”.

The second point deals with the amount of initial biomass flow introduced in the system at trophic level 2. This flow is partly due to recycling of detritus and to hatching. Then, we may reasonably assume that it is partly dependent on the biomass present in the system, which one is itself dependent on the biomass flow at trophic level 2. This process introduces a feedback effect on secondary production, that we call “biomass input control”. We also assume that top-down control may occur for trophic level 2. Therefore, according to Eq. (2.2) calculi are initialised using:

$$\Phi(2) = \Phi(1) \times \exp \left[- \sum_{\tau=1}^{1.9} \mu_{\tau} \times \Delta\tau \right] \quad (6.1)$$

and

$$\Phi(1) = (1 - \beta) \times \Phi_{v(1)} + \beta \times \Phi_{v(1)} \times \frac{B_{tot}}{B_{v_{tot}}} \quad (6.2)$$

where β is a coefficient expressing the extent of biomass input control, μ_{τ} is defined by Eq. (5), $\Phi_{v(1)}$ the fixed value of virgin biomass flow at trophic level 1, B_{tot} and $B_{v_{tot}}$ are the total biomass (for $\tau \geq 2$) in the exploited and unexploited situations, respectively.

Simulations are conducted for two empirical extreme values. $\beta = 0$ traduces an ecosystem where all secondary production is issued from predation on primary producers, detritus recycling and hatching being considered as insignificant in terms of biomass input; such an ecosystem is conventionally called “primary producers-based ecosystem”. Conversely, $\beta = 0.5$ corresponds to an ecosystem where detritus and/or hatch-

ing represent a major part of biomass input and therefore are of great importance in the ecosystem functioning. Such ecosystems are called “detritus-based ecosystems”. Conventionally, the value $\Phi_v(1)$ is dimensioned in such a way that B_2 , the biomass for the first trophic class, is equal to 1 when neither top-down control nor biomass input control occur ($\alpha = \beta = 0$) and with standard parameters for transfer efficiencies and flow kinetics. This allows to easily look at the consequences of those effects and parameters on biomass per trophic class.

2.3. Catch simulations

Catches per trophic class are deduced from previous equations. During the period of time $\Delta\tau$, required to go from τ to $\tau + \Delta\tau$, catches for each value of interval $[\tau, \tau + \Delta\tau]$ are equal to $\varphi_\tau \times \Phi(\tau)$. Hence, we deduce the catch made on this interval for a time unit:

$$Y_\tau = \Delta t \times \int_\tau^{\tau+\Delta\tau} \varphi_\tau \times \Phi(\tau) \times d\tau = \Delta t \times \frac{\varphi_\tau}{\mu_\tau + \varphi_\tau} \times \Phi(\tau) \times (1 - \exp[-(\mu_\tau + \varphi_\tau) \times \Delta\tau]) \quad (7)$$

Eq. (7) also traduces that catch made during a Δt period of time is equal to the fraction of the loss of biomass flow, which is imputable to fishing.

Catches are simulated under various scenarios of fishing, each corresponding to a selectivity curve S_τ defining which trophic levels are targeted (Fig. 3). In all simulations, fishing loss rates are specified relatively to the natural loss rate μv_τ , as:

$$\varphi_\tau = mf \times S_\tau \times \mu v_\tau \quad (8)$$

where mf is a fishing effort ranking from 0 (no fishing) to 2 (strong fishing) in the simulations, by 0.2 range step.

A reference scenario is defined corresponding to a trophic level $\tau_{50} = 2.5$ (i.e. $S_\tau = 0.5$ at trophic level 2.5) and $\tau_{95} = 3.0$; it traduces a fishery poorly targeting low trophic levels but nearly all levels higher than 3. Alternative scenarios correspond to lower ($\tau_{50} = 2.0$) or higher ($\tau_{50} = 3.0$) first trophic levels targeted, with two selectivity curve shapes for this last case (see Fig. 3).

In these four scenarios we admit that all the biomass can be caught, even if poorly targeted. Conversely, a fifth and last scenario is built assuming that only a

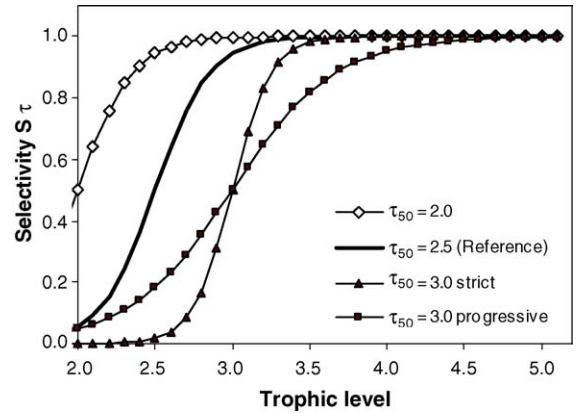


Fig. 3. Selectivity curves used for catch simulations. Each curve is defined by a “trophic level of first catch” τ_{50} , which conventionally corresponds to selectivity equal to 50%. For $\tau_{50} = 3$, two curve shapes are considered.

part of the ecosystem biomass is accessible to fisheries, due to ecological, technological or market reasons. In such a case no selectivity is considered for the fishing loss rate ($\varphi_\tau = mf \times \mu v_\tau$), but yields are calculated by Eq. (7) where the biomass flow $\Phi(\tau)$ is replaced by an accessible biomass flow $\Phi_{ac}(\tau)$. This one is defined by two equations:

$$\Phi_{vac}(\tau) = S_\tau \times \Phi_v(\tau) \quad (9.1)$$

and

$$\frac{d\Phi_{ac}(\tau)}{d\tau} = -(\mu_\tau + \varphi_\tau) \times \Phi_{ac}(\tau) + \rho_\tau \times \Phi_{in}(\tau) \quad (9.2)$$

where Φ_{vac} is the virgin accessible biomass flow, S_τ the reference selectivity, Φ_{ac} and Φ_{in} the accessible and the inaccessible biomass flow and ρ_τ is a rate of transfer between those two biomasses for trophic level τ . The ρ_τ are firstly calculated using relationship (9.2) applied to an unexploited situation (thus Φ_{ac} and Φ_{in} are known by Eq. (9.1)). Then, they are used in Eq. (9.2) to estimate the $\Phi_{ac}(\tau)$ and Y_τ for various exploitation schemes.

Simulations are conducted using Excel sheets and visual basic macros. Some parameters are cross-dependent and equations must be solved by iterations until convergence. We firstly look at the effects of transfer efficiency and flow kinetics on the biomass distribution in an unexploited ecosystem. Using standard values for those parameters, we then analyse fishing

impact on biomass and yields, with mf ranking from 0 to 2, for the five scenarios of fishing patterns previously defined. Four types of virtual ecosystems are here considered, depending on whether they are “bottom-up or top-down controlled” and “primary producers or detritus-based”. Finally, we get back on efficiency and kinetics parameters briefly studying their impact on the ecosystem response to fishing. For each simulation, we calculate: yield and biomass per trophic level, total yield and biomass, mean trophic level for yields and biomass. Yield and biomass per trophic class are plotted according to trophic level, which graphical representation corresponds to trophic spectrum as proposed by Gascuel et al. (2005a). Only most significant results are of course presented hereafter.

3. Results

3.1. Impact of transfer efficiency and kinetics of transfer, on unexploited biomass

In an unexploited ecosystem, transfer efficiencies and flow kinetics determine the amount of biomass and its distribution per trophic level. Top-down and biomass input controls have here no effect since they only occur when fishing decreases the biomass. Transfer efficiencies have a direct impact on abundance of high trophic levels (Fig. 4a). For a given biomass flow entering trophic level 2, ecosystems with low transfer efficiencies will be characterized by a small biomass and dominated by low trophic levels. On the contrary, supporting high abundance of top predators in an ecosystem implies high transfer efficiencies.

The flow kinetics also affect the biomass distribution, but including now low trophic levels (Fig. 4b). They notably induce an accumulation of biomass in trophic levels characterized by slow transfers. For a given biomass flow, fast transfers lead to low biomasses, because the flow just passes through trophic classes, while slow transfers imply high biomasses, due to an accumulation of biomass in each trophic class. This phenomenon of biomass accumulation is well illustrated by simulating a slowing flow at intermediate trophic levels corresponding for instance to the presence of poorly predated species (dashed line on Fig. 4b). Flow kinetics thus appears as a key factor of ecosystem functioning and of biomass distribution

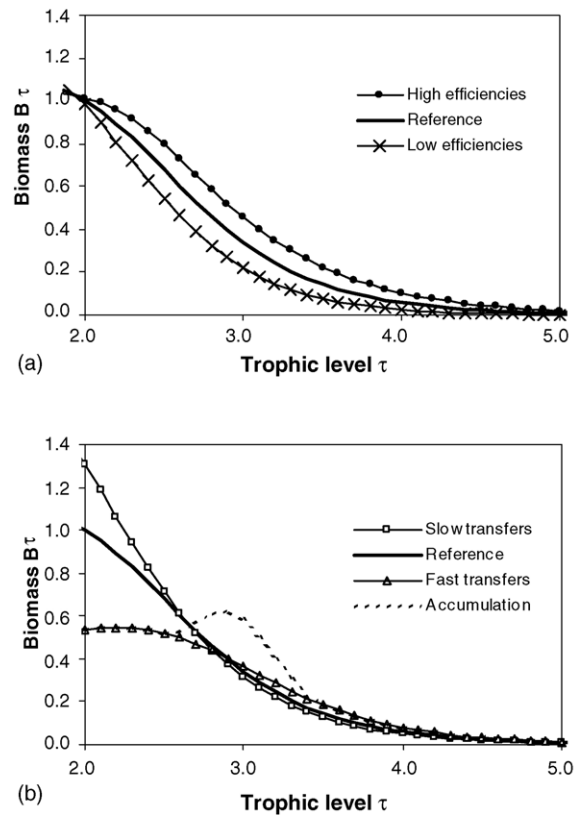


Fig. 4. Impact of transfer efficiencies (a) and kinetics of transfers (b), on the biomass distribution per trophic level, in an unexploited ecosystem. Efficiencies and kinetics used refer to Figs. 1 and 2 for (a) and (b), respectively.

in the food web. They particularly allow to explain non-monotonous distributions of biomass according to trophic level, while biomass flow could only exhibit a continuous decreasing curve, due to flow losses occurring during predation or ontogenic transfers.

3.2. Impact of fishing on ecosystem biomass

Exploitation does not affect kinetics of transfers but impacts the biomass flow, eventually affecting the ecosystem biomass (Fig. 5). Logically, the higher the exploitation rate is, the more the total biomass decreases. In the same way, starting exploitation at lower trophic levels leads to a stronger biomass decrease.

More precisely, impact of fishing differs according to the considered ecosystem functioning. In a “bottom-up ecosystem”, exploitation has a large impact on the

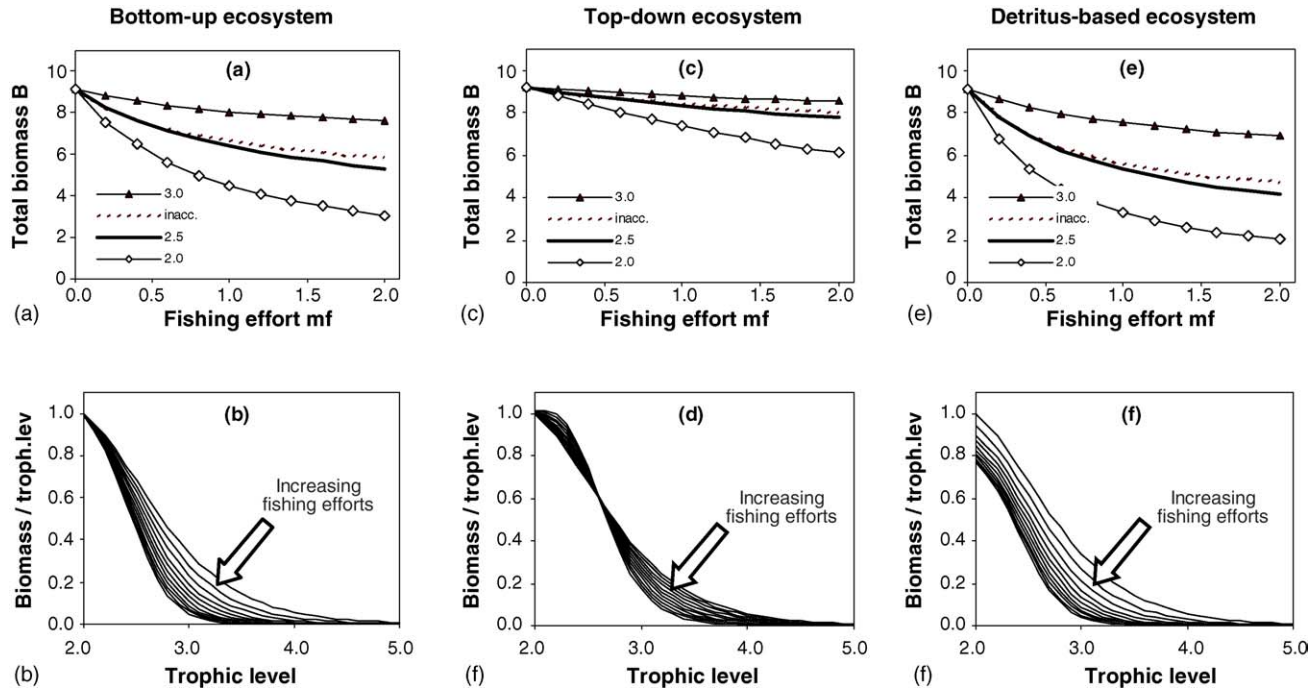


Fig. 5. Impact of fishing on the ecosystem biomass. First line displays trends in the total ecosystem biomass according to fishing effort, for three types of ecosystem functioning and four selectivity curves (defined each by their trophic level of first catch (see Fig. 3); dashed line refers to the occurrence of inaccessible biomass). Second line displays impact of increasing fishing efforts on the biomass trophic spectrum (i.e. the biomass distributions per trophic level), for the same ecosystems but for the reference selectivity only.

total ecosystem biomass (Fig. 5a and b). It may lead to strong biomass depletion when first trophic levels targeted are low. In our simulations, reduction in total biomass can reach for instance a factor more than 3, for $\tau_{50} = 2.0$. In such “bottom-up ecosystems”, all exploited trophic levels are affected by fishing. The decrease is especially marked for the highest ones because they combine a loss of their preys and the direct impact of catch. For example, with the reference selectivity, we simulate a more than 95% reduction for trophic levels higher than 3.5.

In a “top-down ecosystem”, the decrease in predators abundance leads to a release from predation. This compensates, at least partially, the fishing pressure on preys. It can induce an increase in abundance, notably for the less exploited low trophic levels (Fig. 5d). More generally, in all cases of fishing patterns, top-down controls contribute to the stability of the total biomass (Fig. 5c) and thus appear to induce an ecosystem ability to react to exploitation. Except when the first trophic level of catch is very low, the total biomass reduction appears limited even for the strongest exploitation rates. Of course, it does not mean that no change occurs in the ecosystem and we notably observe that top predators tend here too to disappear with fishing. Additional results can be observed for some fishing patterns. If the fishery only targets high trophic levels with a strong selectivity ($\tau_{50} = 3$), a cascade effect is simulated (Fig. 6a); biomasses at intermediate trophic levels significantly increase while the lowest ones decrease. We notice that such an effect only occurs if a strict selectivity is considered, leading to a marked biomass decrease for top predators only. Inversely, selectivity increasing on a large range of trophic levels leads to fairly constant biomasses for all preys, predation release being compensated by fishing (Fig. 6b). Such a simulation exhibits a high resilience of the biomass ecosystem in face of fishing. It shows that exploitation may have a low impact of the ecosystem biomasses, if top-down controls exist and for some particular fishing patterns.

When taking into account biomass input control, the fishing impact on ecosystem biomass appears logically as being raised (Fig. 5e and f). The biomass decrease directly due to catching implies fewer genitors and detrital biomasses, and then a lower biomass recycling and recruitment that amplifies the initial reduction. Therefore, “detritus-based ecosystems” should be more sensitive to fishing pressure than the “primary

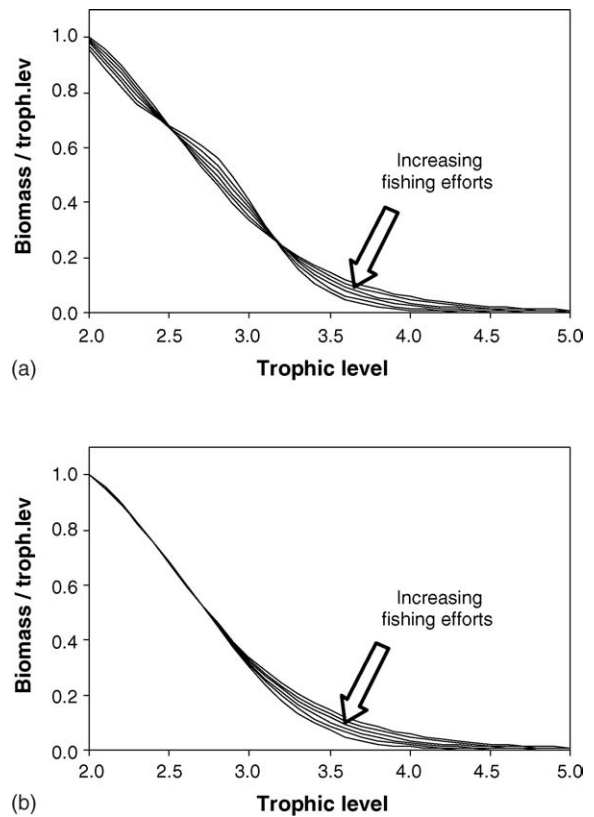


Fig. 6. Cascade effect (a) and resilience effect (b), in a top-down ecosystem: impact of increasing fishing efforts on the biomass trophic spectrum (a) corresponds to the selectivity curve noted “ $\tau_{50} = 3.0$ strict” and (b) to “ $\tau_{50} = 3.0$ progressive” (see Fig. 3).

producers-based ones”. High exploitation rates associated to low trophic levels for first catches can lead to a collapse of total biomass, with for instance a five times reduction in our simulations. Nevertheless, such a sensitivity of “detritus-based ecosystems” is only observed when no top-down control occurs. Indeed, we have seen here before that this last control leads to low impact of fishing. It induces a small detritus or genitors reduction, and then a small effects for the biomass input control. Consequently, considering both effects, biomass input and top-down control, leads to results (not shown) which are very close to those obtained for primary production based and top-down control ecosystems (Fig. 5c and d). In other words, top-down control appears as an important factor for ecosystem’s resistance to fishing. Not only it may induce a partial but direct compensation between catches and predation

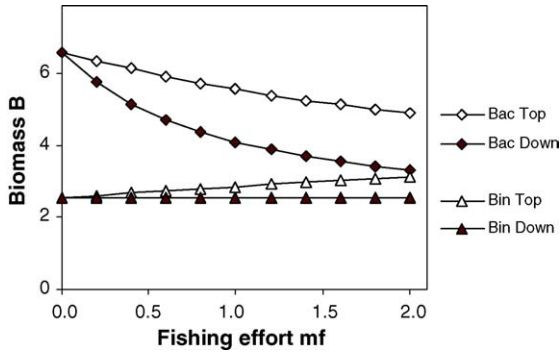


Fig. 7. Trends in accessible and inaccessible biomasses (B_{ac} and B_{in}), according to fishing effort. Simulations have been conducted for a bottom-up and a top-down ecosystem.

release, but also it tends to inhibit feedback effects that fishing could imply through the reduction of biomass recycling.

Considering now that low trophic levels are partly inaccessible to fishing does not strongly modify estimates of total biomass decrease due to fishing. Indeed, in the four considered cases of ecosystem functioning, the fishing impacts biomass in the same order of magnitude, either selectivity is used to define exploitation rates applied to the whole biomass, or that it is used to define the accessible biomass (Fig. 5). Nevertheless, the composition of the biomass has been modified (Fig. 7). In bottom-up ecosystem, increasing fishing effort has logically no effect on inaccessible biomass. Thus, the reduction of total biomass conceals a much more higher reduction for the accessible biomass. In our standard simulation, the first one is around 35%, while the second reaches 50%. When top-down control is considered we additionally observe an increase in the inaccessible biomass. In a way, the sea “fills up” with unexploitable species while the targeted ones tend to disappear.

All simulations presented above refer to standard values of transfer efficiencies and flow kinetics parameters. Modifying these values does not affect our qualitative results. On the other hand, it allows us to look at their influence on the ecosystem response to fishing. We notably observe that increasing transfer efficiencies leads to higher fishing impact on the total biomass (Table 2). In the same way, ecosystems characterized by fast transfers appear more sensitive to fishing pressure. In both cases, this increased sensitivity is a direct

consequence of a change in the biomass distribution, high transfer efficiencies and fast biomass flow leading to high abundances of predators, which are the most affected by fishing.

3.3. Catches simulation

In all virtual simulated ecosystems and for all considered fishing patterns, total yield appears as a monotonous growing function of fishing effort (Fig. 8). In bottom-up ecosystem, yield tends towards an asymptote (Fig. 8a). It is easy to demonstrate that this one corresponds to the catch of the whole biomass present in the first exploited trophic class, before fishing. Consequently, the lower the trophic level of first catch is, the more the total yield increases. In other words, targeting close to secondary production enables higher catches. This is besides true, whatever the fishing pressure is. For example, moving from $\tau_{50} = 3$ to 2 in our simulations induces a four time increase in total yield.

In top-down ecosystem, potential of yield is greatly augmented, due to higher biomasses induced by predation release on low trophic levels (Fig. 8b). In such case, increasing effort leads to increasing biomass of preys and thus to increasing total catch. Consequently, the potential yield appears extremely high, easily exceeding the initial amount of biomass at trophic level 2 (conventionally fixed equal to 1 in simulations). Here too, this potential is of course as much higher than trophic level of first catch is low.

Considering biomass input control leads to different results (Fig. 8c). The biomass input reduction induced by fishing implies here limited potentials for yield. Comparatively to the reference case, catches are around 30% reduced by the simulated biomass input control. Thus, detritus-based ecosystem eventually appears sensitive to fishing, in terms of impact on biomass, and poorly productive, in terms of catch. Of course, as for biomass, this is only true if no top-down effect inhibits the biomass input control.

More generally, the fact that no global overfishing, characterised by decreasing catches for highest exploitation rates, is observed in our range of simulation may seem a quite surprising result. In fact, it is the consequence of the biomass distribution, which is generally strongly decreasing for the targeted trophic levels. Hence, when fishing effort increases, catch moves increasingly on low and more abundant trophic levels

Table 2

Influence of transfer efficiencies and transfer kinetics on the ecosystem response to fishing: total biomass without ($mf=0$) and with ($mf=2$) fishing, and residual biomass after fishing ($B_{tot}(mf=2)/B_{tot}(mf=0)$), for the various values of efficiency and kinetics parameters

	Parameter value	$B_{tot}(mf=0)$	$B_{tot}(mf=2)$	Residual biomass (%)
Influence of transfer efficiencies				
Bottom-up ecosystem	$e^{-\mu_{v,\tau}} = 0.10$	7.16	4.43	61.2
	$e^{-\mu_{v,\tau}} = 0.15$	9.15	5.32	58.1
	$e^{-\mu_{v,\tau}} = 0.20$	11.23	6.22	55.4
Top-down ecosystem	$e^{-\mu_{v,\tau}} = 0.10$	7.16	6.57	91.8
	$e^{-\mu_{v,\tau}} = 0.15$	9.15	7.76	84.8
	$e^{-\mu_{v,\tau}} = 0.20$	11.23	8.90	79.3
Influence of transfer kinetics (cf. Fig. 2)				
Bottom-up ecosystem	Slow transfers	9.80	6.15	62.8
	Reference	9.15	5.32	58.1
	Fast transfers	7.57	3.57	47.2

Simulations have been conducted for reference selectivity curve and for a primary production-based ecosystem.

(Fig. 9a). Even if these low levels are less targeted, they are able to produce high catches for strong exploitation rates. Considering inaccessible biomasses does not modify this result, because flow coming from inaccessible biomass regenerates the accessible biomass depleted by fishing. Here too, total yield rises to an asymptote, which corresponds now to the catch of the whole input of accessible biomass. At last, it appears that global overfishing may only occurs in assuming strong biomass accumulation for a given range of trophic levels, and for a strict selectivity with fisheries only targeting those levels. It may be for instance simulated while applying very high exploitation rates to our biomass distribution coming from the presence of a poorly predated species (Fig. 10). In such case, biomass input control logically aggravates overfishing.

While global overfishing may only be simulated for particular biomass distributions and fishing patterns, it is currently observed in all simulations at the scale of some trophic classes (Fig. 9b). Indeed, high trophic levels are more sensitive to fishing and are thus the firstly over-exploited ones when fishing effort increases. In the reference simulation, full exploitation is for instance reached with $mf=0.4$ for trophic levels higher than 4, with $mf=0.6$ for trophic level 3.5 and with $mf=1$ for trophic level 3. This higher sensitivity of high trophic levels appears as a major characteristic of the ecosystem functioning. It is not only due to addition of direct impact by catching and indirect impact due to prey's reduction, but more essentially to the slower biomass transfers in upper trophic levels. Slower flow implies slower biomass regeneration and leads to more

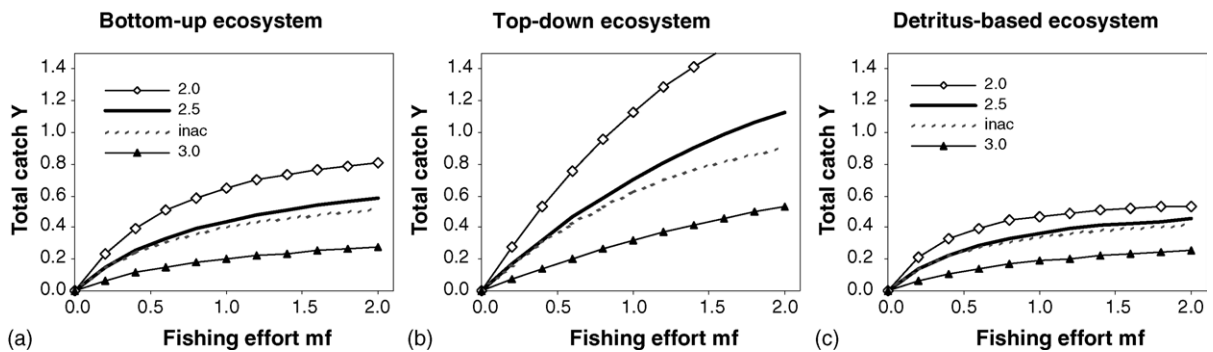


Fig. 8. Catches simulation: variation of total yield according to fishing effort, for three types of ecosystems functioning and four selectivity curves (see Fig. 3).

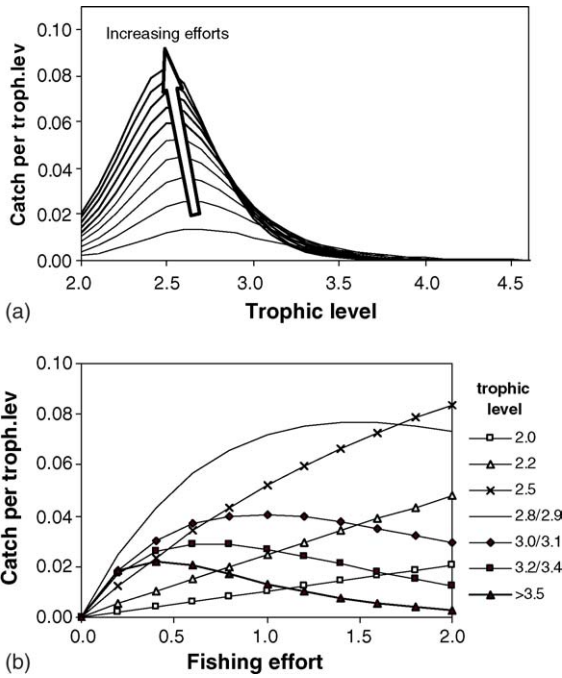


Fig. 9. Catches simulation: (a) catch trophic spectra (i.e. catch distributions per trophic level) obtained for increasing fishing efforts and (b) trends in catches per trophic level according to fishing effort (only some trophic levels are presented). Simulations have been conducted for the reference selectivity curve, and a bottom-up primary production-based ecosystem.

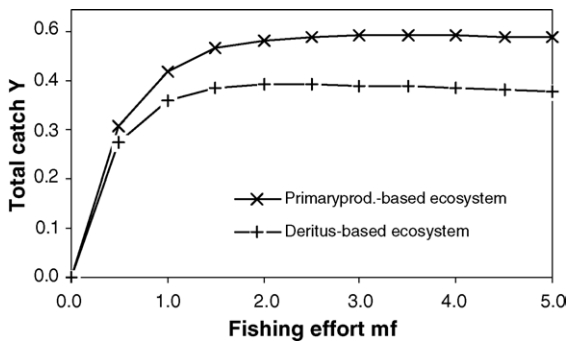


Fig. 10. Overfishing simulation. Curves corresponding to an overfishing phenomenon are obtained for a biomass distribution traducing an accumulation of poorly predated species around trophic level 3 (dashed line on Fig. 2 and for a particular selectivity curve ($S_\tau = 0$ for $\tau < 2.5$ and $S_\tau = 1$ otherwise)). Only bottom-up ecosystems are considered.

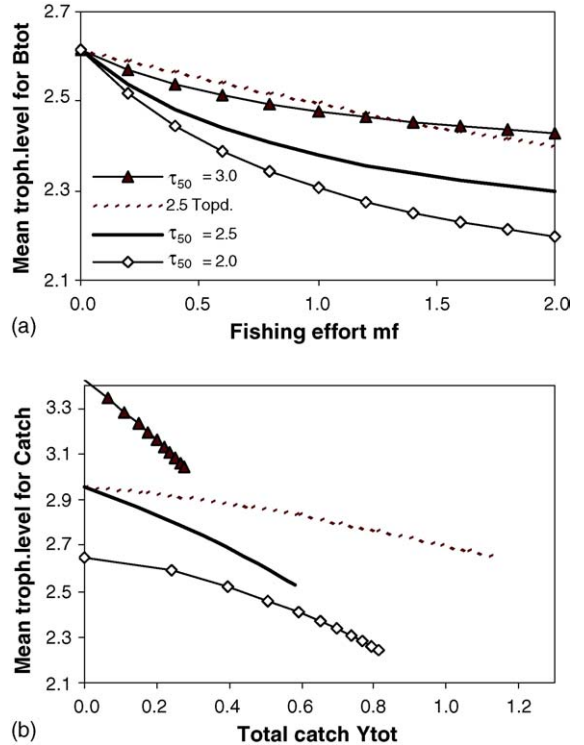


Fig. 11. Trends of the mean trophic levels: (a) trends in the biomass mean trophic level, according to fishing efforts, for various scenarios of selectivities and controls and (b) relationships between catch and mean trophic level of catch, for the same scenarios.

vulnerable resources. Thus, once again, transfer kinetics appear as a major factor for our understanding of ecosystem response to fishing.

A consequence of the higher sensitivity of upper trophic levels is the decrease of mean trophic levels induced by fishing. When fishing effort increases, the mean trophic level of the ecosystem biomass decreases, at the same time that predators tend to disappear (Fig. 11a). This phenomenon is observed even if exploitation rates are equal for all trophic levels. It directly results from the slowing of the flow at upper trophic levels. Of course, it also depends on the scenario used in terms of fishing pattern. We have seen before that targeting low trophic levels induces higher biomass reduction; it then leads to a stronger decrease for the mean trophic level (from 2.6 to 2.2 in our standard simulation). Conversely, targeting only high trophic levels leads to a small decrease in terms of total biomass as well as in terms of mean trophic level (from 2.6 to 2.4).

In all cases, top-down control may reduce the mean trophic level decrease, by reducing the biomass depletion itself.

On the other hand, the mean trophic level of yield follows quite similar trends whatever the trophic level of first catch is. Expressing it according to the amount of catches gives a synthetic overview of quantitative and qualitative changes occurring when fishing effort increases (Fig. 11b). Ranking from no fishing to intense fishing ($mf = 2$) approximately induces a 0.4 decrease in the mean trophic level of catch, for all simulated fishing pattern, and even if this amount of yield is very different. Here too, top-down control limits the decrease, in the same time as potential yield is augmented.

4. Discussion

4.1. Building a theoretical model of ecosystem functioning

In oceans, predation appears to be the main process, which structures biological communities and determines ecosystem dynamics (Martinez, 1995; Hall, 1999). Comparatively to terrestrial ecosystems, habitats are probably distributed more continuously, but trophic relationships may be significantly more complicated. Two species can for instance be alternatively prey and predator one to each other, at various stages of their life and food chains appear generally longer than for terrestrial animals.

Therefore, quantifying and modelling biomass distribution in the food web, and the biomass flows as well, is recognized by most marine ecologists as a key to improve our understanding of ecosystems functioning (Pahl-Wostl, 1997; Cury et al., 2003). This trophic functioning is particularly supposed to determine the ecosystem response to fishing.

Usual ecosystem models, as Ecopath with Ecosim (Christensen and Pauly, 1992; Walters et al., 1997), are built with discrete trophic boxes, bringing together all species or all biological stages whose place in the food web is considered to be sufficiently close. In a way, such models remain based on species, whose mean trophic level emerges as the result of their diet or of their trophic preferences. The trophic-level based model does not anymore consider species, and takes into account all transfers together, that they result from predation or

ontogenic processes. Ecosystem biomass is here distributed along a continuum of trophic level values, and trophic classes are only used as an approximation of the continuous distribution. Therefore, each biomass unit is characterized by its trophic level, whatever his species. Reciprocally, each species may be distributed over a range of trophic classes, changing not only with ontogeny but also with the ecosystem state. We can thus consider that changes in the biomass distribution induced by fishing, not only correspond to changes in the specific composition but also from modifications of mean trophic level and trophic distribution for each species.

The model presents some similarities with body-size based models and size spectra analysis, where all species are aggregated too, and the biomass is continuously distributed according to animals' length (reviews by Bianchi et al., 2000; Benoît and Rochet, 2004; Shin et al., 2005). In such approaches length is the key parameter used to investigate trophic relationships among fish and is considered as one of the main factor determining ecosystem dynamics. It can then be regarded as the cause, whereas trophic level may appear as an emergent result of these dynamics, providing an a posteriori metric of the trophic processes involved. Even if both parameters, body size and trophic level, are correlated at the community level (Jennings et al., 2001), their relationship remains quite complex and it is easier to build trophodynamic models directly based on the metric of trophic levels itself. It appears as a complementary approach to length based models, which are more adapted to analyse the determinism of predators/preys relationships.

Of course, specific composition of an ecosystem remains a major factor of its functioning. But not explicitly taking species into account does not imply that they have no effects in the model. Specific composition notably determines transfer efficiencies per trophic class and flow kinetics, as well as the extent of top-down and biomass input controls. For instance, we have seen how considering the presence of poorly predated species may affect the biomass distribution and the ecosystem dynamics. Nevertheless, all parameters except transfer efficiencies are assumed to be constant whatever the ecosystem state. In a sense, they are considered as ecological characteristics of a given ecosystem, in the same way as growth is for instance considered as a biological and constant characteris-

tic of each species in simple mono-specific models. It remains that assuming constant values of such parameters is a strong assumption of the model, implying that they are independent of changes occurring for each trophic class in its specific composition, notably due to fishing. Of course, a more sophisticated model could be built to raise this hypothesis, defining for instance density dependent relationships for kinetics or top-down control. But the lack of real observations makes it illusory and a simpler model is certainly more useful for the moment. In the context of a theoretical purpose, we thus have chosen to accept a density-dependence only for efficiencies.

An other characteristic of our approach is that it is not based on one or several case studies. The trophic-level based model is here built as a theoretical tool, in order to analyse fishing impacts in a virtual ecosystem. At the same time, the model is supposed to represent the functioning of real ecosystems, in a more or less realistic way. This implies judicious choices in term of considered processes, used formalisations and value of parameters. Regarding this last aspect, the choice of transfer efficiencies is probably the less problematic one. Because our transfers include ontogenic processes, we used a value equal to 15% which appears rather high comparing to the about 10% commonly cited in the literature for trophic efficiency (Pauly and Christensen, 1995; Jennings et al., 2002). Besides, 10 and 20% values are used too. It allows us to cover the range of transfer efficiencies that seems realistic.

Choosing flow kinetics parameters remains more problematic because this aspect is less studied in the literature. Some authors have analysed the delay occurring between events of primary production blooms and corresponding abundance peaks for predators. For example, Maury (1998) mentions a 3–6 months lag from primary production to Yellowfin tuna concentration in Atlantic fisheries. We used here an empirical equation parameterised in such a way that the time required to go from level 1 to 4 is equal to 6 months too. This value is probably not unreasonable but remains largely unknown. Thus, further investigations are unquestionably needed on transfer kinetics. Nevertheless, the choice of parameters appears not essential for a theoretical approach, from the moment we admit that the speed of the flow decreases from low to upper trophic levels. Indeed, such a hypothesis, which seems undoubted, is finally sufficient to determine the main

part of our qualitative results, whatever we use as mathematical formulation of the slowing of the flow.

Top-down control is recognised by various authors as an important factor of ecosystem functioning (e.g. Hunter and Price, 1992; Cury et al., 2003; Chassot et al., 2005), but few quantitative models of this process have been developed until now. Once again, we use a large range of values, assuming they are sufficient to cover the realistic extents of top-down control. Due to the lack of real observations, we also accept in simulations a very simple model with a parameter α that is the same for all trophic levels. Nevertheless, no theoretical difficulty exists, except estimate, to build a more complex trophic-level based model, where control effects would be defined by trophic level. Here, in a virtual simulation context the simplest model appears sufficient.

Probably more important is the mathematical formulation that we have chosen to formalise the top-down effect. Assuming that the transfer efficiency of a given trophic level depends on its predators abundance, implies an adaptation process of the predator/preys relationship to the ecosystem state. When predators abundance decreases, various ecological mechanisms may interfere. Probably one of the most important is the decrease of intra-specific competition between predators, leading to an increase of their individual food ratio and to a better productivity, eventually inducing higher trophic transfers from their preys. Additionally, we can imagine that preys, whose abundance and intra-specific competition increase, may be urged to change their diet towards upper trophic levels, leading to higher ontogenic transfers. In a way, formalisation used for top-down effect corresponds to the introduction in the model of a generalised density dependent relationship, by which production of each trophic level is finally dependent on biomasses present in all trophic levels.

The model is built using a conventional and fixed value for the secondary production, occurring without fishing. Thus, it does not take into account the natural variability of primary production and climate effects on secondary production. Nevertheless, all results must be considered as being relative to a given environment state and would not qualitatively change for other conditions. Besides, any relationship identified between environment and primary and/or secondary production could easily be added to the model and would thus allow to analyse environment effects on yield. On the other hand, indirect effects of fishing on secondary produc-

tion are considered in the model, by the mean of the equation of biomass input control.

At last, whatever its parameterisation and even its mathematical formulation are, the trophic-level based model relies on very simple and little questionable assumptions. The first one is that secondary production transits in the food web, from low to upper trophic levels, and that these transfers occur with some losses depending on natural factors and on fishing. The second one is that kinetics of the biomass flow is characterised by faster transfers at low trophic levels, according to higher metabolism rates. Probably the key point of the model is that we have found that biomass, present at a given trophic level under steady state conditions, is simply the biomass flow divided by the speed of the flow. The third assumption is that biomass of preys may be (or may be not) dependent on their predators. As previously discussed, such top-down control introduces a density dependent effect in the model. And finally, we consider that secondary production may be partly dependent on biomass recycling or larvae recruitment.

Of course the model is a strong simplification of the ecosystem complexity and many others factors may have some great effects on its functioning. Nevertheless, we have found that taking into account only these very simple processes appears sufficient to explain various functioning patterns and various responses to fishing pressure observed in real ecosystems. The best argument of the trophic-level based model must be that it appears as a useful tool for our understanding of ecosystem's functioning in both ecological and fisheries contexts.

4.2. *Learning from the model*

What do we have finally learned from the model? Firstly, the model confirms that parameters and processes taken into account may have a great influence on the ecosystem functioning. It notably highlights that, for a given secondary production, biomass distribution in the food web depends on three major characteristics of the ecosystem dynamics: the transfer efficiency, the speed of the biomass flow and the extent of top-down control. Consequently, the corresponding parameters are of great interest for modelling ecosystems. This is already well known for transfer efficiencies, which are intensively studied by numerous authors (e.g. Pauly and Christensen, 1995; Jennings et al., 2002). Kinetics

of biomass transfers appear comparatively much less studied. A noticeable result of the model is that the flow speed appears as a key characteristic of ecosystem dynamics too. It allows to convert biomass flows into biomasses present at each trophic level and would then require to be analysed in real cases. Reciprocally, kinetics could be estimated and used for simulations, knowing the flows and biomasses per trophic level for a given steady state.

On the other hand, efficiency and kinetics notably determine the occurrence of top predators and then should act upon ecosystem functional biodiversity. It is generally recognized that mature ecosystems display higher biodiversity (Odum, 1969). That means that ecosystem maturation should occur with increasing efficiencies and biomass flow speed. Conversely, low efficiencies and/or slow transfers, leading to biomass accumulations at low trophic levels, would characterize disturbed ecosystems. In a way, fishing constitutes such a disturbance, by adding “fishing losses” to the natural losses occurring during biomass transfers towards higher trophic levels.

Extent of top-down control is another important factor of ecosystem functioning. This control does not replace bottom-up control but may add to it. Logically, considering biomass flows leads to the conclusion that predators must always depend on they preys; in a way, everybody needs to eat (and begins his life at low trophic level in our simple model). Reciprocal relationship is not always true, because some species could be not or less predated. Nobody needs to be eaten by predator at his end (and to moves upon upper trophic levels by ontogeny)! Nevertheless, we know that predation is a major reason for natural mortality and may then induce top-down control (Hunter and Price, 1992; Sala et al., 1998).

In case of fishing, this control implies that catch on a given trophic levels impacts all the levels. It notably induces a biomass increase for the lower ones, whose effect has been observed in several ecosystems (e.g. Reid et al., 2000; Worm and Myers, 2003). In West Africa for instance, fast increase of the fishing pressure during the last decades leads to a severe over-exploitation for species of upper trophic levels (Gascuel et al., 2005b), and would be responsible of low level's increase, notably observed for octopus or prawn populations (Caverivière, 1993; Laurans et al., 2004; Gascuel et al., 2005a). Such effects are generally

considered as a major aspect of the ecosystem impact of fishing (e.g. Goñi, 1998; Jennings and Kaiser, 1998; Hall, 1999).

Cascade effects due to fisheries, involving increasing biomass at intermediate trophic levels and a decrease for the lower ones, are more difficult to observe in real ecosystems (Pace et al., 1999; Pinnegar et al., 2000; Cury et al., 2003). Model shows that such cascade effects only occur for some particular fishing patterns, strictly and strongly targeting highest trophic levels. It also indicates that top-down effects may oppositely lead to rather constant biomasses for all trophic levels whatever the fishing pressure. Additionally, considering the natural variability and measure errors, easily explains that such effects may be quite unobservable in open oceans.

Otherwise, the model allows us to identify some main factors determining the sensitivity of an ecosystem in face of fishing. Indeed, results show that high transfer efficiencies, fast biomass flows and strong feedback effects on biomass recycling lead to sensitive ecosystems, where fishing may induce severe biomass depletions. Of course, this depends on fishing pattern too, and notably on the trophic level of first catch, biomass decrease being of as much stronger that this level is low. Conversely, we have seen that top-down control appears as an important feature of ecosystem resistance to fishing. It induces a relative stability of the total biomass and may inhibit feedback effects of fishing on biomass input.

More generally, the model appears as a relevant representation of ecosystem impact of fishing. It highlights biomass and mean trophic level decreases, induced by increasing fishing pressure, which changes are now well demonstrated in many ecosystems (Pauly et al., 1998, 2002). It also explains some changes in specific composition of the ecosystem, as for instance, the relative or absolute increase of unfishable biomass induced by exploitation. The model can thus be considered as a relevant theoretical basis to explain the distribution per trophic level of the ecosystem biomass, and fishing impact on this distribution. It therefore constitutes the theoretical basis for the use of biomass trophic spectrum as a new ecosystem indicator (Gascuel et al., 2005a).

A noteworthy but at least logical result of the model is that a global overfishing, leading to decreasing total catches, seems difficult to obtain. The oceanic

biomasses existing at low trophic levels allow to imagine very high yields, from the moment we accept and are able to catch them. The world secondary production of the sea is notably estimated around 1900 millions tonnes (Ryther, 1969), when fisheries production is around 85 millions tonnes. Nevertheless, until now and probably for a long time, lower levels remain largely unexploited for technological and commercial reasons.

In the same time, the nearly indefinite increase of total yield with fishing pressure does not mean that this increase may occur without inducing strong difficulties. First, biomass collapse may occur and should be considered as a loss of our natural patrimony. It induces a decrease in functional biodiversity that could have strong consequences regarding ecosystem resilience facing the natural variability of environment. It also induces a decrease in fisheries efficiency, the remaining biomass being more and more difficult to catch. Strong fishing pressure eventually leads to significant over-exploitation for resources of high trophic level. Top predators tend to disappear from ecosystem and catches. The decrease of mean trophic level could additionally induce a decrease of product price, adding profitability loss to the decrease of fisheries efficiency. Both ecological and economic disasters are then able to occur. Unfortunately, such situations are currently observed in many real cases.

Even if the model leads to consistent results compared with real observations, it has been presented until now as a theoretical approach considering a virtual ecosystem. We wish finally to briefly discuss its ability to be applied to real case studies. Indeed, in a recent paper (Gascuel and Chassot, submitted for publication) we propose the catch trophic spectrum analysis (CTSA) as a method to estimate biomasses and fishing loss rates per trophic level, based on catch data. This approach uses reverse forms of the trophic-level based model equations, and may be directly sustained by simulations using the model itself. In order to test the method, CTSA has been applied to Celtic Sea and North Sea fisheries, as well to simulated data. Sensitivity analysis show that relative results appear robust even if the absolute values remains largely doubtful, because of the lack of information for some input parameters, like notably those defining transfer kinetics. More important, this test allows us to conclude that no theoretical difficulties exist to apply the trophic level based approach to real case studies. Practical difficul-

ties come from parameters estimate. They finally show that ecosystem approach to fisheries logically requires strong research efforts in order to routinely estimate not only catches per trophic level but also parameters as transfer efficiencies and flow kinetics too. Multiplying comparative analysis, using a trophic-level based approach applied to real ecosystems, should also help us to better evaluate the realistic range of some parameters as extent of top-down control. It appears as the next step required to improve the methodology.

5. Conclusion

During nearly half a century, fisheries management has been essentially based on mono-specific approaches using simple models of the harvesting population's dynamic. These models constitute simultaneously theoretical and practical tools. Indeed, they allow a theoretical representation of fishing effects on a virtual population, in term of biomass or age structure. Everybody knows, for example, how a [Schaefer model \(1954\)](#) can be used in order to illustrate concepts as overfishing or maximum sustainable yield. In usual age structured models ([Ricker, 1954](#)), theoretical simulations may be conducted in order to analyse impact of fishing mortality or selectivity curve on catches, without any reference to a given stock. In the same time, these mono-specific models may be applied to real data, in order to provide diagnosis and forecasts. They are currently used for TAC's estimations and to analyse consequences of various management options.

In the field of ecosystem modelling, Ecopath with Ecosim software becomes now largely used as a tool for the representation and simulation of various particular ecosystems ([Christensen and Walters, 2004](#)). The trophic-level based model appears as a complementary way of modelling. Considering biomass flows through the food web, it is based on a closer approach to physical considerations and allows a more theoretical view on ecosystem functioning, without any reference to a given case study. The model presents some similarities with a usual mono-specific age structured model. Fishes move in it from each trophic class to the upper ones according to their trophic levels, as they move in an age structured model from one age group to the upper one, according to age ([Gascuel, 2002](#)). Of course, considering not only numbers or biomasses but also

flows, and introducing top-down and biomass input controls leads to strong differences between both models.

It remains that the trophic-level based model allows catches and biomasses theoretical simulations at an ecosystem scale, in the same way as an age structured model allows this at a single species population scale. In that sense, we have shown here that the proposed model may contribute to our understanding of ecosystem functioning in both ecological and fisheries context. Even if more researches are needed, first tests also tend to demonstrate that the model may be a practical tool for diagnosis and forecast in real cases. It should then be considered as a promising way for improving ecosystem approach to fisheries.

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