

EcoTroph: Modelling marine ecosystem functioning and impact of fishing

Didier Gascuel^{a,*}, Daniel Pauly^b

^a Université Européenne de Bretagne, Agrocampus Ouest, Pôle halieutique/Fisheries and Aquatic Sciences Center, UMR Ecologie et Santé des Ecosystèmes, 65 rue de Saint Briec, CS 84215, 35042 Rennes Cedex, France

^b University of British Columbia, Fisheries Centre, Sea Around Us Project, 2202 Main Mall, Vancouver, BC, V6T 1Z4, Canada

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ABSTRACT

EcoTroph (ET) is a model articulated around the idea that the functioning of aquatic ecosystems may be viewed as a biomass flow moving from lower to higher trophic levels, due to predation and ontogenetic processes. Thus, we show that the ecosystem biomass present at a given trophic level may be estimated from two simple equations, one describing biomass flow, the other their kinetics (which quantifies the velocity of biomass transfers towards top predators). The flow kinetic of prey partly depends on the abundance of their predators, and a top-down equation expressing this is included in the model. Based on these relationships, we simulated the impact on a virtual ecosystem of various exploitation patterns. Specifically, we show that the EcoTroph approach is able to mimic the effects of increased fishing effort on ecosystem biomass expected from theory. Particularly, the model exhibits complex patterns observed in field data, notably cascading effects and ‘fishing down the food web’. EcoTroph also provides diagnostic tools for examining the relationships between catch and fishing effort at the ecosystem scale and the effects of strong top-down controls and fast-flow kinetics on ecosystems resilience. Finally, a dynamic version of the model is derived from the steady-state version, thus allowing simulations of time series of ecosystem biomass and catches. Using this dynamic model, we explore the propagation of environmental variability in the food web, and illustrated how exploitation can induce a decrease of ecosystem stability. The potential for applying EcoTroph to specific ecosystems, based on field data, and similarities between EcoTroph and Ecopath with Ecosim (EwE) are finally discussed.

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1. Introduction

One of the first approaches, pioneered by Elton (1927) and Lindeman (1942) for describing aquatic ecosystem, was to assign the individual numbers or biomass or the biological production by its component species onto integer trophic levels (TLs), and thus represent the ecosystem as a pyramid of number, biomass or production. This approach, which differentiated between primary producers and detritus (TL = 1), first-order consumers (TL = 2), second-order consumer (TL = 3), etc., was dominant until the early 1970s, and served, for example, as a major structuring element of the International Biological Program (Golley, 1993).

This approach was sharply criticized by Rigler (1975), who pointed out that most aquatic animals feed at more than one trophic level, and that, therefore, TLs cannot be used to structure ecosystem data (see also Cousin, 1985). Thus, he suggested, trophic levels were only conceptual entities, not parameters that could be derived from empirical data. This critique was devastatingly effective, and for a while, the TL concept faded from view. However, in the same year

that Rigler's critique appeared, Odum and Heald (1975) published an alternative to trophic-levels-as-a-concept, i.e., fractional trophic level. These can be estimated from different types of empirical data (see e.g., Kline and Pauly, 1998), and which hence, by Rigler's own criteria, have as legitimate a place in ecology as, for example, sea surface temperature.

The emergence of Ecopath as a widely used approach and software for modelling aquatic ecosystems (Polovina, 1984; Christensen and Pauly, 1992), contributed in a major way to the resurgence of trophic levels, especially as they were not an input to Ecopath, but an output, i.e., parameters that were estimated by Ecopath. And, as the use of Ecopath spread worldwide, so did the trophic level concept (Pauly et al., 2000). Two other developments also contributed to increasing familiarity with trophic levels. One is the emergence of FishBase (Froese and Pauly, 2000), the online database on fish, covering all fish species in the world (over 30,000), and which present estimates of trophic levels for nearly half of these species. The other is the demonstration of the worldwide occurrence of the phenomenon now widely known as ‘fishing down marine food webs’ (Pauly et al., 1998).

Here, we present EcoTroph as a trophic-level based ecosystem modelling approach which makes full use on the conceptual advances heralded by Odum and Heald (1975). This approach is not

* Corresponding author. Tel.: +44 223 48 55 34; fax: +44 223 48 55 35.
E-mail address: Didier.Gascuel@agrocampus-ouest.fr (D. Gascuel).

an elaboration (i.e., complexification) of previous food web modelling effort, nor does it aim to replace more comprehensive (and often more complex) models. On the contrary, EcoTroph results from attempts to simplify trophic modelling. Within the family of tropho-dynamic models, it may be regarded as constituting an ultimate stage, wherein species as such disappear behind trophic levels. EcoTroph thus may be seen as providing an oversimplified, but useful caricature, thereby offering another interpretation of available data, and another view of ecosystems.

After publication of a first version of a trophic-level based model (Gascuel, 2005), an in-depth comparison, equation by equation, with the well-established Ecopath with Ecosim model revealed inconsistencies in its formulation. This applied particularly to the implementation of top-down control, and to the catch equation, which was made compatible with standard formulations. Additionally, simulations based on parameters of flow kinetics were updated using a recently published empirical model (Gascuel et al., 2008a).

This paper thus presents a new version of the trophic-level based model, from now called EcoTroph. We also aim to assess the ability of the model to mimic the generic rules which appear to regulate the functioning of marine ecosystems, with emphasis on the impact of fishing. In a first step, the general principles and assumptions of the model are presented, and their mathematical formulations are detailed. Then, we show that the model is an efficient theoretical tool to build generic relationships between parameters (for instance between fishing effort and catch, or ecosystem biomass) and that it gives a consistent representation of the trophic functioning of ecosystems. The model is then used to analyse the impact of fishing on ecosystem biomass given various exploitation patterns and to explore the propagation of environmental variability in the food web. The sensitivity of the model to input parameters is also explored. Practical use of EcoTroph for case studies is briefly discussed in the last section, where we also present EcoTroph as a module of EWE (vers. 6).

2. Method

2.1. General principle: modelling ecosystem functioning as a trophic flow

The trophic level of an organism or the mean trophic level of a population is defined as:

$$\tau_i = 1 + \sum_j (D_{ij} \cdot \tau_j) \quad (1)$$

where D_{ij} is the proportion of the prey j in the diet of consumer i , and τ_j is the mean trophic level of the prey, with the trophic level of primary producers and detritus being conventionally set equal to unity. Thus, trophic level emerges from the diet of individuals. It constitutes a state variable characterizing each unit of biomass in an ecosystem and defining its position within the food web.

The first key point of EcoTroph is that it deals with the continuous distribution of the biomass occurring in an ecosystem, as a function of trophic levels (Fig. 1). Biomass enters the food web at trophic level 1, as generated by the photosynthetic activity of the primary producers, and recycling by the microbial loop. With the exception of semi-autotrophic organisms with small biomasses in some ecosystems (e.g. coral polyps, tridacnid clams), there is usually no biomass between trophic levels 1 and 2. Herbivorous and detritivorous are at trophic level 2. Then, at trophic levels higher than 2, the biomass is distributed along a continuum of trophic level values. Some trophic levels may contain more or less biomass, but the variability of the diet of the different consumers of an ecosystem should result in all trophic levels being 'occupied'.

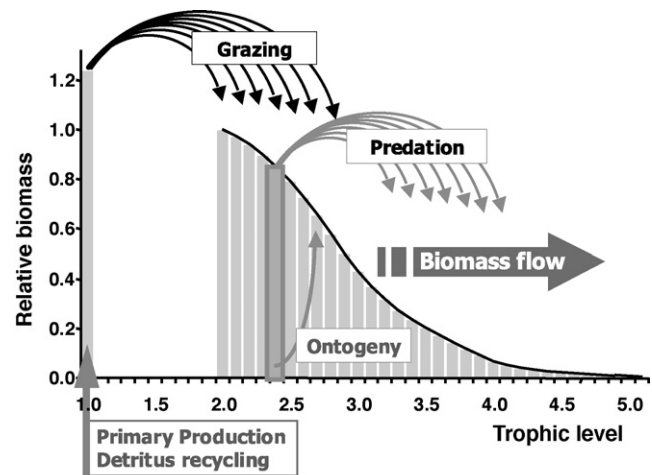


Fig. 1. Diagram of the trophic functioning of an ecosystem: theoretical distribution of the biomass by trophic level and trophic transfers processes, given an arbitrary input of biomass (fixed equal to 1 for TL = 2).

As a consequence, the EcoTroph equations are based on a continuous approach and the model aims to simulate the state variable $B(t, \tau)$, i.e., the density of biomass occurring in the ecosystem at time t , at trophic level τ (see notations in Table 1). Firstly, we present a steady-state version of the model, wherein the state variable is $B(\tau)$, i.e., the distribution of the ecosystem biomass by trophic level. In a second step we will move to a dynamic version of EcoTroph referring to time.

A discrete approximation of the continuous distribution is used for mathematical simplification and visual representation. Thus, the distribution of the ecosystem biomass is split into fractional classes (see Fig. 1). Conventionally, we consider trophic classes of $\Delta\tau = 0.1$ trophic level, from trophic level 2, corresponding to first-order consumers, to trophic level 5, sufficient to cover all top predators likely to occur in marine systems (Pauly et al., 1998; Cortés, 1999). Thus, the state variable becomes B_τ , the biomass in the $[\tau, \tau + \Delta\tau]$ trophic class. The resulting bivariate graph (B_τ as a function of τ) represents a key aspect of ecosystem functioning and constitutes what is called a 'biomass trophic spectrum' (Gascuel et al., 2005).

The second key idea of EcoTroph is that the trophic functioning of marine ecosystems can be modelled as a continuous flow of biomass surging up the food web, from lower to higher trophic levels. All of the organic particles start in the food web with photosynthesis or detritus recycling at trophic level 1. From there, they move up more or less rapidly in the food web, jumping for each predation event to a trophic level, which is defined by the mean diet of the predator. The fate of a given particle is thus characterized by continuous processes (ontogenic changes in trophic levels) and abrupt jumps (of 1 TL on average) caused by predation. Few particles reach the highest trophic levels, and most will stop long before that, due to non-predation mortality, excretion or respiration. But the particles that move up in the food web constitute a biomass flow which has to be considered as a whole. All particles jointly have a wide range of trajectories whose mean is a continuous curve. Thus, using a continuous model is not an approximation of the discrete trajectories; it is the mean process itself, expressed as biomass flow (see Gascuel et al., 2008a).

2.2. Biomass and flow equations

2.2.1. Biomass equation

In flux physics, quantities related to a flow of liquid, moving for instance in a canal, are linked by the following equation

Table 1Trophic level-based modelling: parameters definition and suggested units^a.

| Variable | Parameter definition | Dimension (units) |
|-----------------------|---|---|
| $B(t, \tau)$ | Density of biomass at time t and trophic level τ | Mass·TL ⁻¹ (t TL ⁻¹) |
| B_τ | Biomass in the $[\tau, \tau + \Delta\tau]$ trophic class | Mass (tonnes) |
| $B_{\text{ref},\tau}$ | Biomass in the $[\tau, \tau + \Delta\tau]$ trophic class for the reference situation (unexploited or current ecosystem) | Mass (tonnes) |
| B_τ^* | Accessible biomass in the $[\tau, \tau + \Delta\tau]$ trophic class | Mass (tonnes) |
| $\Phi(\tau)$ | Biomass flow at trophic level τ | Mass·time ⁻¹ (t year ⁻¹) |
| Φ_τ | Mean biomass flow in the $[\tau, \tau + \Delta\tau]$ trophic class | Mass·time ⁻¹ (t year ⁻¹) |
| Φ_τ^* | Accessible trophic flow in the $[\tau, \tau + \Delta\tau]$ trophic class | Mass·time ⁻¹ (t year ⁻¹) |
| μ_τ | Natural loss rate of biomass flow, in the $[\tau, \tau + \Delta\tau]$ trophic class | TL ⁻¹ |
| μ_τ^* | Net natural loss rate of the accessible biomass flow | TL ⁻¹ |
| φ_τ | Fishing loss rate of biomass flow, in the $[\tau, \tau + \Delta\tau]$ trophic class | TL ⁻¹ |
| φ_τ^* | Fishing loss rate of the accessible biomass flow | TL ⁻¹ |
| M_τ | Natural mortality in the $[\tau, \tau + \Delta\tau]$ trophic class | 1/time (year ⁻¹) |
| $M_{\text{ref},\tau}$ | Natural mortality in the $[\tau, \tau + \Delta\tau]$ trophic class for the reference situation (unexploited or current ecosystem) | 1/time (year ⁻¹) |
| F_τ | Fishing mortality in the $[\tau, \tau + \Delta\tau]$ trophic class | 1/time (year ⁻¹) |
| $\Delta\tau/\Delta t$ | Speed of the trophic flow (also called flow kinetics) | TL·time ⁻¹ (TL year ⁻¹) |
| Δt | Time required by a unit of biomass to go from level τ to level $\tau + \Delta\tau$ | Time (year) |
| α_τ | Coefficient of top-down control | – |
| γ | Shape parameter of the predator/preys relationship | – |
| S_τ | Selectivity coefficient by trophic level | – |
| E_τ | Exploitation rate | – |
| Y_τ | Yield per unit of time in the $[\tau, \tau + \Delta\tau]$ trophic class | Mass·time ⁻¹ (t year ⁻¹) |

^a The logic of EcoTroph is not bound to the specific units used here, but to their dimensions. Note also that mass (tonnes) should be in most case, expressed as density (t km⁻²). This is omitted here for the sake of clarity.

(see e.g. Kot, 2001):

$$\Phi(t, x) = \sigma(t, x) D(t, x) \quad (2)$$

where $\Phi(t, x)$ is the flow at time t and point x , expressed for instance in l s⁻¹; $D(x, t)$ is a density of liquid expressed in l m⁻¹ and $\sigma(x, t)$ is the speed of the flux in m s⁻¹.

Here, we consider biomass as ‘flowing’ not through space according to x , but through trophic levels τ , according to ontogeny and predation. In a steady-state, the parameters remain constant in the course of time and Eq. (2) becomes:

$$\Phi(\tau) = \sigma(\tau) B(\tau) \quad (3)$$

The ‘flow’ $\Phi(\tau)$ refers to the amount of biomass that moves up the food web through trophic level τ and can be expressed in tonnes per year (t year⁻¹) or equivalent units for any trophic level. The speed of the trophic flow $\sigma(\tau)$ measures the kinetics of the process at trophic level τ . In other words, each of the particles (and thus the biomass that they contribute to), starting at a trophic level of 1, reaches the higher upper levels after a certain time. Thus, the speed of the flow quantifies the velocity of biomass transfers in the food web. It can be expressed in term of the number of trophic levels passed per year (TL year⁻¹). Finally, $B(\tau)$ is the density of biomass expressed in tonnes per trophic level (t TL⁻¹).

The biomass B_τ , present at every moment in a given trophic class of width $\Delta\tau$, is:

$$B_\tau = \int_\tau^{\tau+\Delta\tau} B(\tau) d\tau = \int_\tau^{\tau+\Delta\tau} \frac{\Phi(\tau)}{\sigma(\tau)} d\tau \quad (4)$$

Finally, using a discrete approximation of the integral in (4), the biomass equation is expressed as:

$$B_\tau = \frac{\Phi_\tau}{\Delta\tau/\Delta t} \cdot \Delta\tau \quad (5)$$

where Φ_τ is the mean biomass flow passing through the trophic class $[\tau, \tau + \Delta\tau]$ and $\Delta\tau/\Delta t$ is the mean speed of the flow through that class.

2.2.2. Flow equation

Due to natural losses occurring during trophic transfers (non-predation mortalities, respiration, egestion and excretion), the biomass flow is not conservative and decreases as a function of

trophic level. Adding to this natural process, exploitation by fisheries can be considered as a diversion of one part of the trophic flow and expressed in the same manner as the natural flow loss. These processes can be expressed as follows:

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \cdot \exp[-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau] \quad (6)$$

where μ_τ is the net natural loss rate of biomass flow, and φ_τ is the loss rate of biomass flow due to fishing. The loss rates are defined as mean coefficients per trophic class, and they are expressed in TL⁻¹. We will later see that φ_τ is related to fishing mortality (F_τ), while μ_τ is not directly related to natural mortality (M_τ). Eq. (6) defines the term $\exp(-\mu_\tau)$ as the transfer efficiency (TE) between trophic levels.

This flow equation allows us to estimate the biomass flow at any trophic level, based on knowledge of the flow at the level below, the fishing loss rate by trophic class φ_τ and an estimate of TE. Additionally, integration of Eq. (6) leads to specify the relationship between the mean flow Φ_τ passing through interval $[\tau, \tau + \Delta\tau]$ and the value $\Phi(\tau)$ at trophic level τ :

$$\Phi_\tau = \frac{1}{\Delta\tau} \cdot \int_0^{\Delta\tau} \Phi(\tau + s) \cdot ds = \frac{1}{\Delta\tau} \cdot \left[\frac{\Phi(\tau) \cdot \exp[-(\mu_\tau + \varphi_\tau) \cdot s]}{-(\mu_\tau + \varphi_\tau)} \right]_0^{\Delta\tau}$$

$$\text{Thus : } \Phi_\tau = \Phi(\tau) \cdot \frac{1 - \exp[-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau]}{(\mu_\tau + \varphi_\tau) \cdot \Delta\tau} \quad (7)$$

2.3. Flow kinetic equation and top-down control

Globally, the speed of the trophic flow should be a decreasing function of the trophic level. Indeed, metabolism at low trophic levels is generally very fast, involving small organisms belonging to the phytoplankton, zooplankton or micro- and meiobenthos, which exhibit high turn-over (only few species, such as herbivorous fishes, should constitute exceptions to this general rule). Such fast turn-over and short life cycles induce fast trophic transfers from the lowest toward the higher trophic levels. Conversely, high-trophic level predators are generally large and long-lived, and have few predators. Thus, the trophic flows they mediate should be characterized by slow kinetics. The temperature of the environment also impacts the metabolism of organisms, biochemical reactions being faster at higher than at lower temperatures.

Therefore, to facilitate use of EcoTroph in theoretical or data poor contexts, an empirical model was developed expressing the $\Delta\tau/\Delta t$ ratio as a function of trophic level (τ) and mean water temperature (θ in °C) (Gascuel et al., 2008a). The model was fitted to 1718 data triplets (P/B , TL and temperature) extracted from 55 well documented Ecopath models, assuming that the P/B ratios can be used to represent flow speed. This empirical model has the form:

$$\frac{\Delta\tau}{\Delta t} = 20.2 \cdot \tau^{-3.26} \cdot \exp(0.041 \cdot \theta) \quad (8)$$

This model will be considered in the following for the reference state of our virtual ecosystem.

We also have to consider that the speed of the trophic flow should vary with the intensity of exploitation and predation to which each trophic class is exposed. Indeed, when the fishing mortality and/or the predation increase, the life expectancy of preys decreases. Even if they are caught and thus never reach the upper trophic levels, the average individual spends less time in its trophic class. Thus, the speed of the trophic flow is increased. We expressed this mechanism using:

$$\left(\frac{\Delta\tau}{\Delta t}\right)_\tau = F_\tau + M_\tau \quad (9)$$

This equation is consistent with Allen's relationships (1971) indicating that under equilibrium assumption, the P/B ratio, which is a measure of the speed of the flow (Gascuel et al., 2008a), is equal to total mortality (Z).

'Top-down control' implies that the abundance of prey is, at least partly, determined by the abundance of predators. While bottom-up control is implicit in Eq. (6), accounting for such top-down control must be introduced through an additional, explicit equation. Since the more the predators there are, the faster the prey are likely to be eaten (Eq. (9)), top-down control can operate if a fraction of the natural mortality of prey depends on predator abundance, i.e.:

$$M_\tau = \alpha_\tau \cdot M_{\text{ref},\tau} \cdot \left(\frac{B_{\text{pred}}}{B_{\text{pred,ref}}}\right)^\gamma + (1 - \alpha_\tau) \cdot M_{\text{ref},\tau} \quad (10)$$

This leads to the top-down control equation we used:

$$\left(\frac{\Delta\tau}{\Delta t}\right)_\tau = \left[\left(\frac{\Delta\tau}{\Delta t}\right)_{\text{ref},\tau} - F_{\text{ref},\tau}\right] \cdot \left[1 + \alpha_\tau \cdot \frac{B_{\text{pred}}^\gamma - B_{\text{pred,ref}}^\gamma}{B_{\text{pred,ref}}^\gamma}\right] + F_\tau \quad (11)$$

where

- $(\Delta\tau/\Delta t)_\tau$ and $(\Delta\tau/\Delta t)_{\text{ref},\tau}$ are the speed of the trophic flow at trophic level τ , respectively for any state of the ecosystem and for the reference state.
- F_τ , $F_{\text{ref},\tau}$, M_τ and $M_{\text{ref},\tau}$ are the fishing mortality and the natural mortality at trophic level τ , respectively in any state of the ecosystem and in a given state being used as reference.
- B_{pred} and $B_{\text{pred,ref}}$ are the biomass of predators in any state and in the reference state respectively. The ratio $B_{\text{pred}}/B_{\text{pred,ref}}$ defines the relative change in abundance of predators. Thus, the speed of the flow at trophic level τ is calculated according to the relative abundance encountered at level $\tau+1$ (in practice, biomass from trophic classes $\tau+0.8$ to $\tau+1.3$ are considered).
- The alpha coefficient (α_τ) expresses the fraction of the natural mortality ($M_{\text{ref},\tau}$) which depends on predator abundance. This coefficient may theoretically vary between 0 and 1, and defines the intensity of the top-down control that affects trophic level τ . The coefficient $\alpha_\tau=0$ pertains to a situation dominated by bottom-up processes, and where changes in predators abundance have no effects on preys. Conversely, a coefficient $\alpha_\tau=1$ defines

a completely top-down controlled situation, where the speed of the flow strongly depends on predators abundance.

- The gamma coefficient (γ) is a shape parameter, varying between 0 and 1 which defines the functional relationship between prey and predators. The value $\gamma=1$ relates to a situation where predators abundance has a linear effect on the speed of the flow of their preys. Such relationship may be assimilated to a Holling type I functional response, while a coefficient smaller than 1 implies non-linear relationships, closer to type II functional response (Holling, 1965).

Eq. (11) implies that the speed of the flow is expressed in relation to a given state being used as the reference. Therefore, the speed of the flow is estimated for the reference state using Eq. (8), while Eq. (11) allows its computation for all other states, for any values of the α_τ and γ coefficients, given an estimate of predator biomass obtained, e.g., from Eqs. (5) and (6). As Eq. (5) also includes flow speed, the solution must involve an iterative procedure, starting with the reference values of $(\Delta\tau/\Delta t)_{\text{ref}}$, estimating $\Delta\tau/\Delta t$, then estimating B for each iteration, and continue until stabilisation (see also Fig. 3).

2.4. Accessibility and catch simulation

For ecological or technological reasons, only a fraction of the ecosystem biomass is usually accessible to fisheries. As a consequence, a selectivity coefficient S_τ must be introduced into the model, expressing the fraction of the biomass B_τ accessible to fisheries in trophic class $[\tau, \tau + \Delta\tau]$. This biomass fraction will be referred as B_τ^* (with $B_\tau^* = B_\tau \cdot S_\tau$). In the present study devoted to theoretical simulations, a logistic curve is used for S_τ , to mimic the increase of accessibilities from low values at low trophic levels to full accessibility at higher trophic levels.

We assumed that the flow kinetics is similar whether the biomass is accessible or not. Then, based on the selectivity defined in the reference state ($S_{\text{ref},\tau}$), we can deduce new parameters:

- $\Phi_{\text{ref},\tau}^* = \Phi_{\text{ref},\tau} \cdot S_{\text{ref},\tau}$ defines the reference accessible trophic flow;
- $\varphi_{\text{ref},\tau}^* = \varphi_{\text{ref},\tau} / S_{\text{ref},\tau}$ is the fishing loss rate in the reference situation;
- The net natural loss rate of the accessible biomass flow is derived from the reference values using the inverse of Eq. (6):

$$\mu_\tau^* = \text{Ln} \left(\frac{\Phi_{\text{ref},\tau}^*}{\Phi_{\text{ref},\tau+\Delta\tau}^*} \right) \cdot \frac{1}{\Delta\tau} - \varphi_{\text{ref},\tau}^* \quad (12)$$

These parameters allows simulation of the accessible biomass flow, for any value of the fishing loss rate φ_τ^* . The computations are initialised by:

$$\Phi_2^* = \Phi_{\text{ref},2}^* \cdot \frac{\Phi_2}{\Phi_{\text{ref},2}} = \Phi_2 \cdot S_\tau \quad (13a)$$

$$\text{and then : } \Phi_{\tau+\Delta\tau}^* = \Phi_\tau^* \cdot \exp[-(\mu_\tau^* + \varphi_\tau^*) \cdot \Delta\tau] \quad (13b)$$

The logistic selectivity curve we used implies that the fraction of accessible biomass and accessible flow increases from low values to the highest targeted trophic levels. As a consequence, the term μ_τ^* , expressing the flow loss rate, will exhibit negative values, as it results from the balance between real losses (due to non-predation mortality, excretion and respiration) and gains due to the transition of biomass flow from the inaccessible to the accessible state. Such transition may be considered as a 'recruitment' into the accessible biomass flow and the μ_τ^* parameters, calculated from the reference state, are considered biological features of the exploited species,

independently of ecosystem state; this point is discussed further below.

Finally, catches per trophic class and per time unit are deduced from previous equations. They can be expressed either as the integration over time of instantaneous catches dY/dt , or as the integration over trophic level of catch density per trophic level $dY/d\tau$, leading to:

$$Y_{\tau} = \int_{t=0}^1 \frac{\varphi_{\tau}^*}{\varphi_{\tau}^* + \mu_{\tau}^*} \cdot [\Phi *(\tau) - \Phi *(\tau + \Delta\tau)] \cdot dt \quad (14a)$$

$$\text{or: } Y_{\tau} = \int_{s=0}^{\Delta\tau} \varphi_{\tau}^* \cdot \Phi *(\tau + s) \cdot ds \quad (14b)$$

Eq. (14a) indicates that catches are equal to the fraction of flow loss due to the fishery, while Eq. (14b) stems from the definition of the fishing loss rate. Using (13b), integration of (14a) or (14b) both leads to the catch equation, which can be expressed after simplification based on Eq. (7):

$$Y_{\tau} = \varphi_{\tau}^* \cdot \Phi_{\tau}^* \cdot \Delta\tau \quad (15)$$

Additionally, Eq. (15) allows specifying the relationship that exists between the fishing loss rate φ_{τ}^* and the fishing mortality F_{τ}^* occurring in a trophic class. By definition F_{τ}^* is equal to the ratio Y_{τ}/B_{τ}^* . Thus:

$$F_{\tau}^* = \varphi_{\tau}^* \cdot \frac{\Delta\tau}{\Delta t} \quad (16)$$

2.5. From steady-state to time-dynamic modelling

A dynamic model that allows time-dynamic simulations can be derived from the steady-state equations presented below. From Eq. (2), the variables of interest (such as the biomass, the flow or the catch) must be expressed as functions of trophic level and time, while some of the required parameters (especially the natural loss rate and the top-down control coefficients) are considered as ecological characteristic constant in the course of time.

The dynamic model requires some preliminary rearrangement, however. In the steady-state model, all trophic classes have the same $\Delta\tau$ wide range, conventionally equal to 0.1 trophic level. Biomass moves from trophic level τ to trophic level $\tau + \Delta\tau$ in a time equal to Δt . Due to the slowing down of the trophic flow from low to upper trophic levels, these time intervals Δt differ from one trophic class to the other. This is changed when building the dynamic model and we used constant time intervals $\Delta t'$ (conventionally equal to 0.1 year), which correspond to unequal trophic classes $\Delta\tau'$, wider at low trophic levels. This ensures that, at each simulated time step, biomass moves up one trophic class. Using values from the flow kinetics equation (8), the width of each trophic class is calculated as:

$$\Delta\tau' = \Delta t' \cdot \frac{\Delta\tau}{\Delta t} \quad (17)$$

The time-dynamic model is then based on the following steps:

- Computations are initialised each time step t by a value $\Phi(2, t)$, the biomass flow at trophic level 2. Biomass and biomass flow per trophic class must also be specified for the first time step, possibly using the steady-state model. This first time step is used as reference for the computation of flow kinetics, when top-down controls are taken into account;
- The flow equation of the dynamic model, derived from (6), allows estimating the trophic flow by trophic level and for all time steps:

$$\Phi(\tau + \Delta\tau', t + \Delta t') = \Phi(\tau, t) \cdot \exp[-(\mu_{\tau} + \varphi_{\tau, t}) \cdot \Delta\tau'] \quad (18)$$

- The biomass per trophic class and the catches may then be calculated for each time step, using respectively Eqs. (5) and (15), where $\Delta\tau/\Delta t$ and $\Delta\tau$ are simply replaced by $\Delta\tau'/\Delta t'$ and $\Delta\tau'$.

2.6. Analysing a virtual ecosystem: simulation steps

The EcoTroph model can be used to simulate virtual ecosystems facing various exploitation patterns. First, we consider an ecosystem under steady-state conditions; we then move to the time-dynamic version of the model.

The ecosystem used as the reference state is unexploited ($\varphi_{\tau} = 0$) and has the following features.

- **Initialisation:** the value of primary production $\Phi_{\text{ref},1}$ was set at 1000 arbitrary units, such that the biomass flow of the first trophic class considered in the model ($\Phi_{\text{ref},2}$) is equal to 100 when a standard transfer efficiency of 10% is used (see Pauly and Christensen, 1995);
- **Transfer efficiency:** a unique standard value of $\exp(-\mu) = 0.10$ was used for all trophic levels; for sensitivity purpose, low and high transfer efficiencies were also simulated using values equal to 0.07 and 0.15, respectively;
- **Flow kinetics:** standard flow kinetics were considered, based on the empirical equation (8) for a mean water temperature of 15 °C. (Doing this, we assumed that the empirical model of the speed of the flow is sufficient to initialise the unexploited state, even if initially this model was in fact not based on data from unexploited ecosystems). Slower and faster transfers were also simulated using the same equation with water temperatures of 5 and 25 °C, respectively;
- **Top-down control:** the effects of top-down controls were analysed using two values of the alpha coefficient: a value $\alpha = 0$ (here for all trophic levels) defines a 'bottom-up' controlled ecosystem, while $\alpha = 0.6$ refers to a 'top-down' controlled ecosystem'. The shape parameter gamma was fixed at 0.5.

The impact of increasing fishing efforts on biomass were simulated based on several (logistic) selectivity curve (Fig. 2). Each curve may be defined by the trophic level where S_{τ} is equal to 50%, noted τ_{50} , which, in analogy to the mean length at first capture (Beverton and Holt, 1957), may be called 'trophic level at first capture'. The reference scenario refers to a trophic level $\tau_{50} = 3.0$; alternative scenarios correspond to lower ($\tau_{50} = 2.5$) or higher ($\tau_{50} = 3.5$) trophic levels at first capture.

For each selectivity curve, biomass and catch trophic spectra were simulated based on the equations defining the steady-state model and using, for all trophic levels, the same fishing mortal-

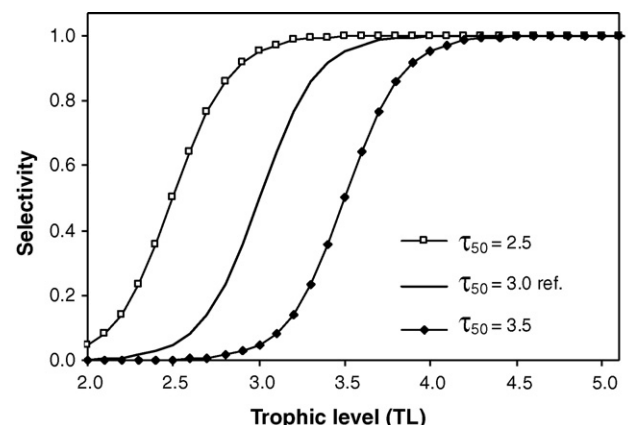


Fig. 2. Selectivity curves used in simulations (see text).

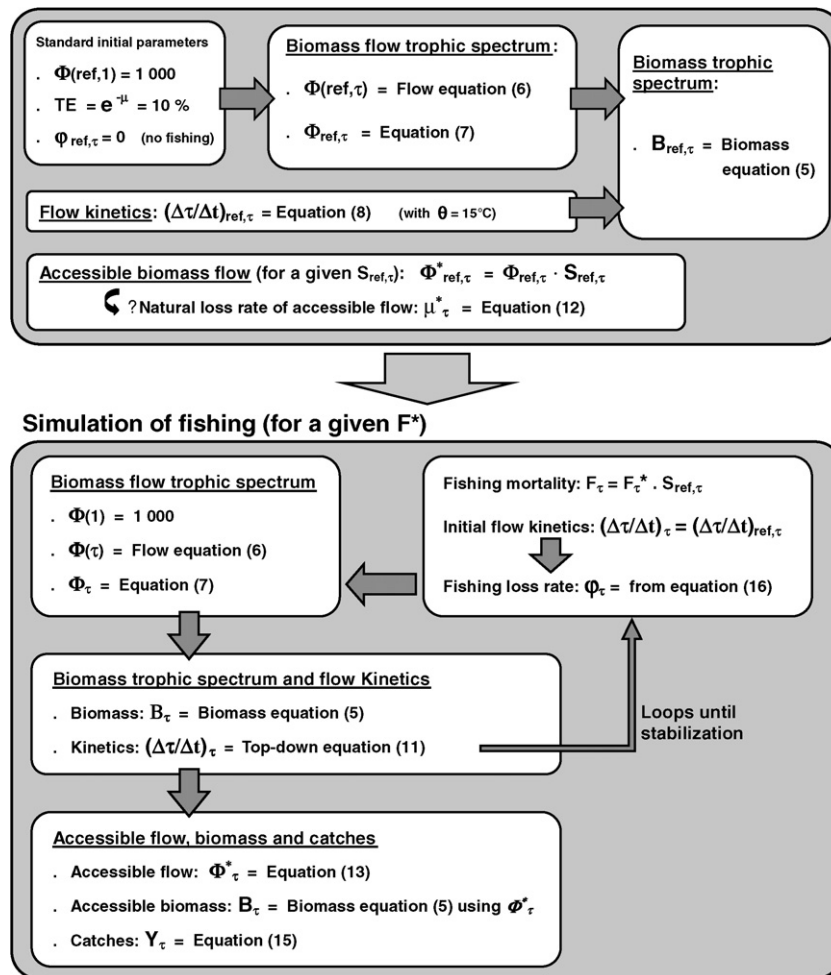


Fig. 3. Diagram of the simulation steps in EcoTroph (see notations in Table 2).

ity F^* applied to the accessible biomass. Thus, the fishing mortality applied to the whole biomass ($F_\tau = F^* \cdot S_\tau$) follows a logistic curve. In simulations F^* varies between 0 (no fishing) and 1 (strong fishing). Simulation steps are summarized in Fig. 3.

A mean flow exploitation rate was calculated measuring the fraction of trophic flow loss due to fishing:

$$E_\phi = \frac{\varphi_{\text{moy}}}{\varphi_{\text{moy}} + \mu} \quad (19)$$

where φ_{moy} is the mean fishing loss rate, conventionally calculated for trophic levels between 3.5 and 5.0. From the simulated biomass trophic spectra and catch trophic spectra, we also deduced total catch, total biomass and biomass of predators (conventionally referring to $\tau \geq 3.5$). The mean trophic levels of catch and ecosystem biomass were calculated as well.

Finally, a dynamic model was constructed to explore the propagation of environmental variability throughout the food web. Two sources of variability were considered, the first due to primary production fluctuations, the second generating changes in the transfer efficiencies. This was achieved by adding a log-normally distributed random factor to the model, based on either of the two equations:

$$\Phi_1(t) = \Phi_1 \cdot \varepsilon_1(t) \quad \text{or} \quad \mu(t) = \mu \cdot \varepsilon_2(t) \quad (20)$$

The dynamic simulations started with the reference steady-state model and ran for 100 years, of which the 50 firsts were unexploited. Based on the reference selectivity curve and a given fishing mortality F^* , exploitation started in year 51 and then remained constant. For the two periods (with and without exploita-

tion, excluding the transition phase; i.e. from time steps 11 to 50 and 61 to 100, respectively) and the two sources of variability, coefficients of variation of yearly catches and biomass were estimated for each trophic level and for the total. Various values of $\sigma(\varepsilon)$ were considered for the standard deviation of the random factor ε_1 or ε_2 , defining various levels of environmental variability. Based on a reference value of $\sigma(\varepsilon)$ (0.2 for ε_1 and 0.1 for ε_2), we also considered several values for the fishing mortality, from 0.2 to 1 year⁻¹. For each value of the parameters tested as input, 30 simulations were performed and the mean estimate (and the confident limits) of the output parameters were estimated.

3. Results

3.1. Impact of fishing on biomass

Exploitation affects biomass flow and flow kinetics eventually affecting ecosystem biomass as well (Fig. 4), with total biomass decreasing with increasing exploitation rate. In a 'bottom-up ecosystem' (Fig. 4, left), only the exploited trophic levels are affected. Increasing fishing pressure decreases the biomass flow, with cumulative effects for the highest trophic levels (even if they are not targeted by fishing). Due to decrease in life expectancy, the higher the fishing mortality, the faster the speed of the flow. The two effects contribute to the decrease of biomass, which is especially strong for the highest trophic levels because they are affected both by loss of their prey and the direct impact of the catch. We observe, for example, a more than 12-fold reduction in the

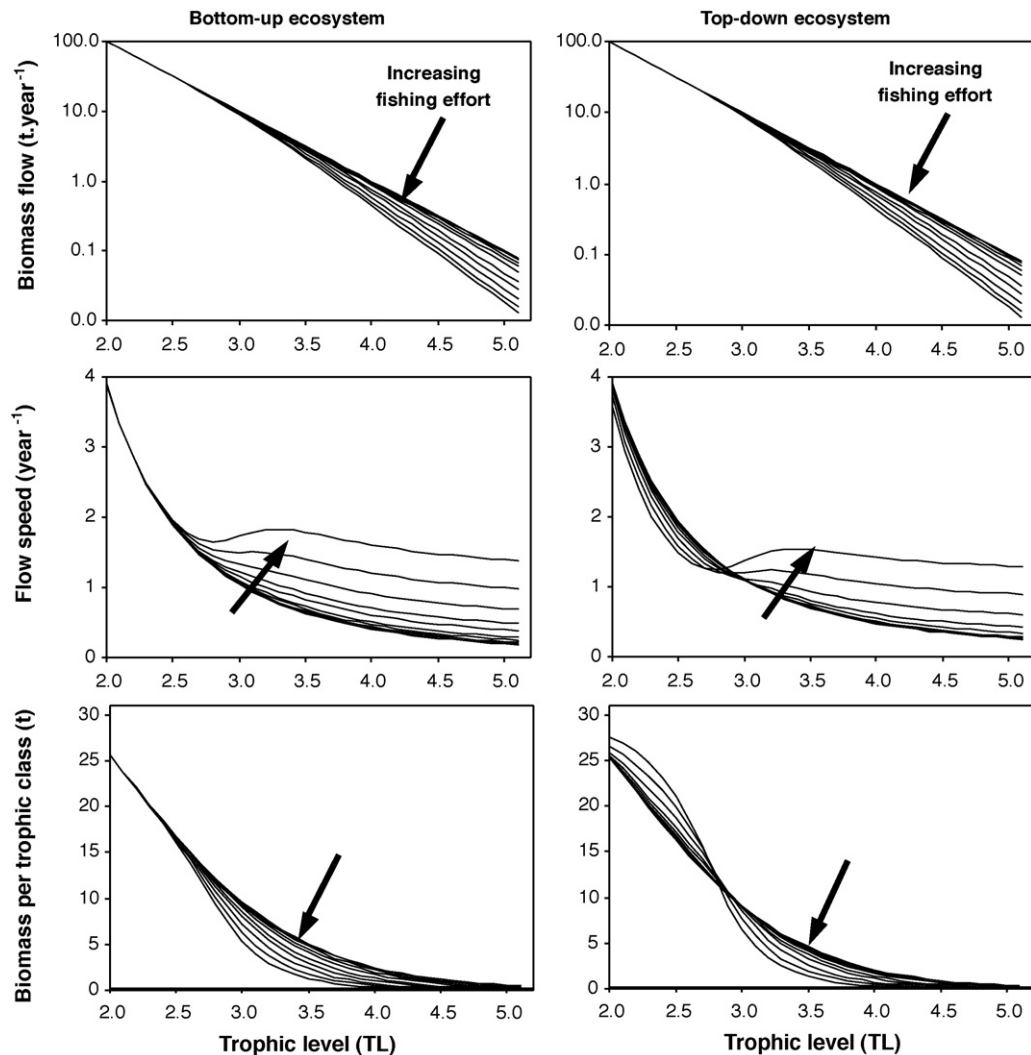


Fig. 4. Impact of increasing fishing mortality on the biomass flow (top), the flow speed (middle) and the biomass trophic spectrum (bottom). Left panels refer to a 'bottom-up ecosystem'; right panels to a 'top-down ecosystem'.

biomass of the trophic level 4.5. In a 'top-down ecosystem' (Fig. 4, right), the fishery-induced decrease in predator abundance leads to a release of predation. This does not affect the biomass flow, but induces a decrease in the speed of the flow for the prey (their life expectancy is increased) and thus an increase of their biomass. Subsequently, predators benefit from this increase and are slightly less

affected than in the case of a 'bottom-up ecosystem'; for instance, the biomass of trophic level 4.5 is reduced 'only' by a factor of 10.

Obviously, starting exploitation at lower trophic levels induces a stronger biomass decrease in the ecosystem as a whole (Fig. 5). In a 'bottom-up ecosystem', exploitation has a large impact on total ecosystem biomass, and may lead to strong biomass depletion

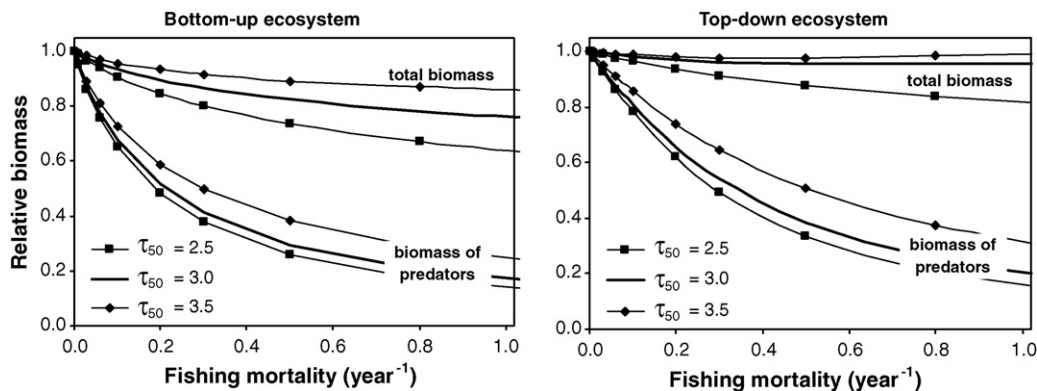


Fig. 5. Impact of increasing fishing mortality on the total biomass or biomass of predators (standardized values), for a 'bottom-up ecosystem' (left) and a 'top-down ecosystem' (right).

when the mean trophic level at first capture is low (Fig. 5, left). For instance, in our simulations, the reduction in total biomass reaches almost 40% for $\tau_{50} = 2.5$. The decrease is especially strong for predators and can be caused even by low fishing mortality. For instance, with the reference selectivity, we obtained a twofold decrease in predators abundance using a value $F = 0.2 \text{ year}^{-1}$, and a more than 80% reduction for $F = 1.0 \text{ year}^{-1}$.

In a 'top-down ecosystem', the release of predation compensates, at least partially, for fishing pressure on prey, and thus can induce an increase in their abundance, if the lower trophic levels are not too strongly exploited (Fig. 5, right). More generally, top-down control leads to limited impacts in total biomass, even for the strongest exploitation rates (but top predators tend to disappear when strongly exploited). This is particularly true when the lowest trophic levels remain unexploited ($\tau_{50} = 3.0\text{--}3.5$). In other words, top-down control increases the resilience of ecosystems to fishing. But this resilience has limits and vanishes when low trophic levels are exploited.

The accessible biomass, which includes predators, is of course the most affected (Fig. 6). Additionally, top-down control has the effect that predation release leads to an increase in prey biomass, especially in species which are not targeted by fishing. Thus, an increase in the inaccessible biomass is observed (Fig. 6, bottom). In a way, the sea 'fills up' with undesirable species, while the targeted species tend to disappear.

The above simulations refer to standard values of transfer efficiencies and flow kinetics parameters, but modifying these values allows us to analyse their influence on the ecosystem response to fishing. We especially observed that increasing transfer efficiencies leads to higher fishing impact on the total biomass (Fig. 7, left). In this case, the natural loss rates are smaller and a given fishing loss rate induces a higher exploitation rate ($\varphi/(\varphi + \mu)$). This

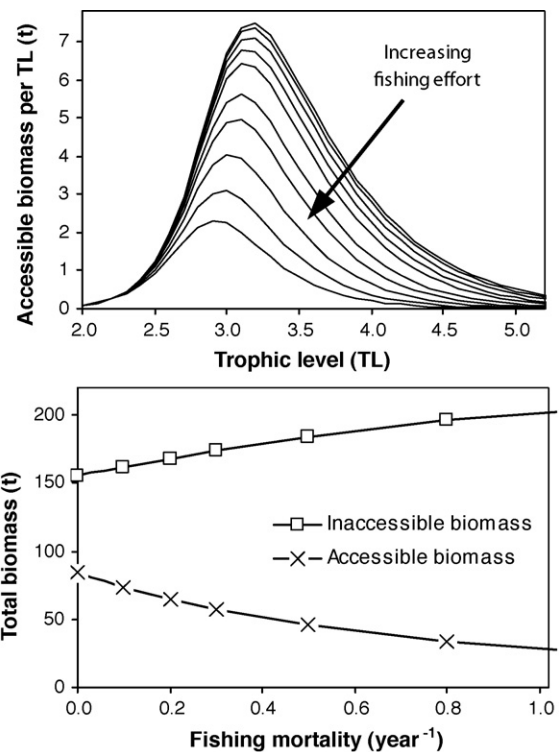


Fig. 6. Changes in the accessible (to fishing) biomass trophic spectrum (top) and in the total accessible and inaccessible biomass (bottom), in a 'Top-down ecosystem' (based on parameter reference values).

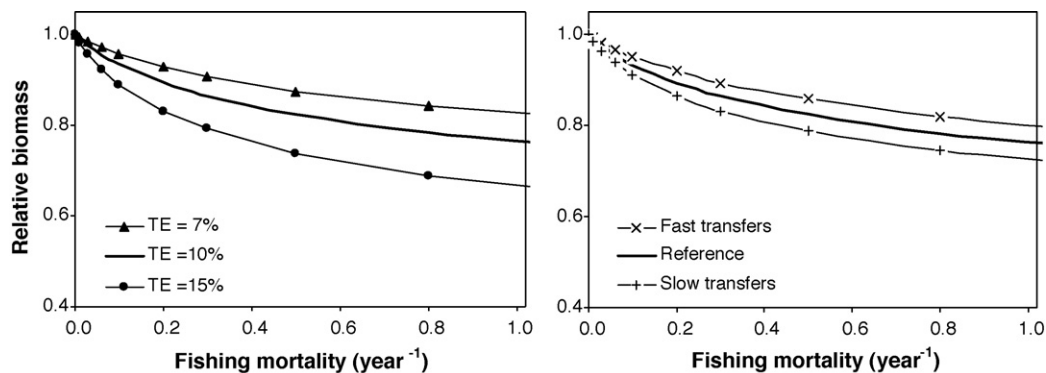


Fig. 7. Impact of transfer efficiency (left) and of flow speed (right) on ecosystem sensitivity to fishing (results refer to a bottom-up ecosystem).

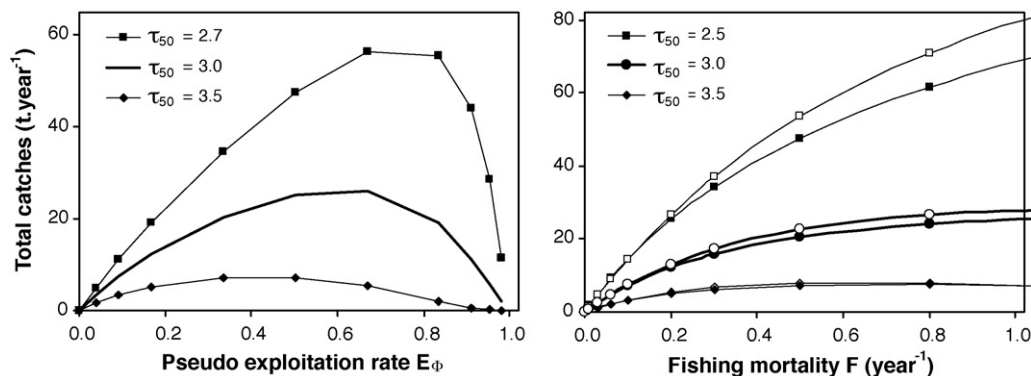


Fig. 8. Relationship between catches and fishing intensity expressed as a function of flow exploitation rate (left; note that $E_{\phi} = 1$ corresponds to $F = \infty$) or fishing mortality (right), for three mean trophic levels at first capture (black marks refer to a 'bottom-up ecosystem'; white dots refer to a 'top-down ecosystem').

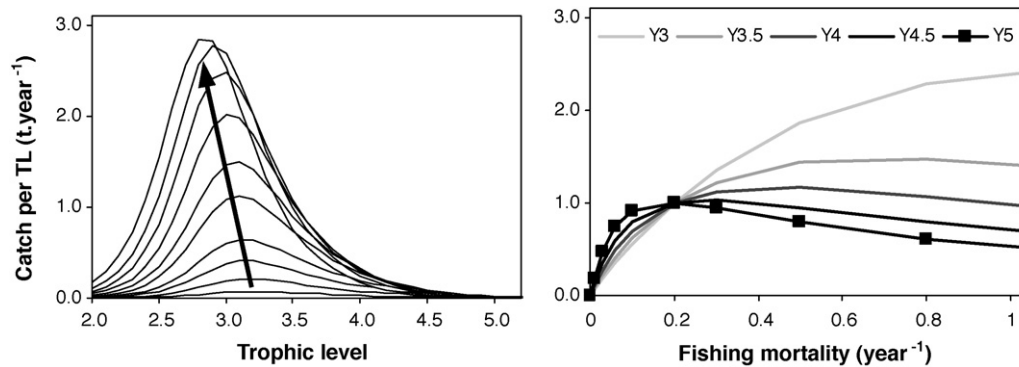


Fig. 9. Simulation of catch trophic spectra (left; arrow indicates increasing fishing mortality) and catch by trophic class (right; values Y_T are standardized for 1 for $F = 0.2 \text{ year}^{-1}$) ('Bottom-up ecosystem'; $\tau_{50} = 3.0$).

increased sensitivity is also a direct consequence of a change in biomass distribution: high transfer efficiencies lead to high abundances of predators, which are most affected by fishing. As for flow speed (Fig. 7, right), the ecosystems characterized by fast transfers appear less sensitive to fishing pressure. Biomass regeneration is faster, and thus fisheries catches are more easily compensated for.

3.2. Catch simulations

When fishing mortality increases, yields tends towards a value equal to the all the accessible biomass flow. This flow, however, decreases with fishing pressure (as does the accessible biomass; see Fig. 6, top), and thus the catch, expressed as a function of exploitation rate, is dome-shaped, and tends toward zero at the highest fishing mortality (Fig. 8, left). In other words, total catches at the ecosystem scale exhibits a maximum value, defining something akin to 'Maximum Sustainable Ecosystem Yield' (MSEY). For fishing mortalities higher than F_{MSEY} , ecosystem over-exploitation occurs.

Nevertheless, the fishing loss rates of the low or intermediate trophic levels are usually small compared to the natural loss rates. As a consequence, ecosystem overfishing is observed only for high fishing mortalities, especially when low trophic levels are targeted. For instance, for $\tau_{50} = 2.5$, the F_{MSEY} is around 5 year^{-1} and the catch therefore appears a growing function for the explored values of fishing mortality (Fig. 8, right). Conversely, for $\tau_{50} = 3.5$, F_{MSEY} is approximately equal to 0.9 year^{-1} what appears realistic at ecosystem scale.

In addition, the lower the trophic level of first catch, the more the total yield increases. For instance, in case of a medium fishing pressure ($F = 0.5 \text{ year}^{-1}$), moving from $\tau_{50} = 3.0$ to $\tau_{50} = 2.5$ in our simulations more than doubles total yield. In other words, targeting secondary producers enables higher and almost indefinitely growing catches. Conversely, targeting higher trophic levels leads to lower catches; moreover, overfishing occurs more readily. Indeed, the higher the mean trophic level at first capture, the easier overfishing occurs.

In a 'top-down ecosystem', overall potential yield is increased by the release of predation at low trophic levels (Fig. 8, right). In such case, the increase in prey biomass, which also slightly benefits the predators, induces a catch increase. Thus, the gain of total catch induced by top-down control is about 10% with the reference selectivity curve ($\tau_{50} = 3.0$), while it is higher than 15% when prey are targeted ($\tau_{50} = 2.5$) and close to zero if only predators are fished ($\tau_{50} = 3.5$).

When fishing effort increases, the catch tends to originate increasingly from the low trophic levels (Fig. 9, left), even if these low levels are not specifically targeted. The high trophic levels appear more sensitive to fishing and are the first to be overex-

ploited (Fig. 9, right). In the reference simulation, full exploitation is, for instance, reached with $F = 0.2 \text{ year}^{-1}$ for trophic level 5, with $F = 0.3 \text{ year}^{-1}$ for trophic level 4.5, and with $F = 0.8 \text{ year}^{-1}$ for trophic level 3.5. This higher sensitivity of high trophic levels is a major characteristic of ecosystem functioning, mainly due to the kinetic of transfers.

A consequence of the higher sensitivity of upper trophic levels is that fishing strongly affects the mean trophic level of the catch, and of the residual biomass in the ecosystem (Fig. 10), all the way to the disappearance of the predators. Of course, this phenomenon, which is obviously a manifestation of the 'fishing down marine food webs' (Pauly et al., 1998), also depends on the scenario used to define the fishing pattern. Thus, targeting only high trophic levels leads to a weaker reduction of biomass trophic levels than when

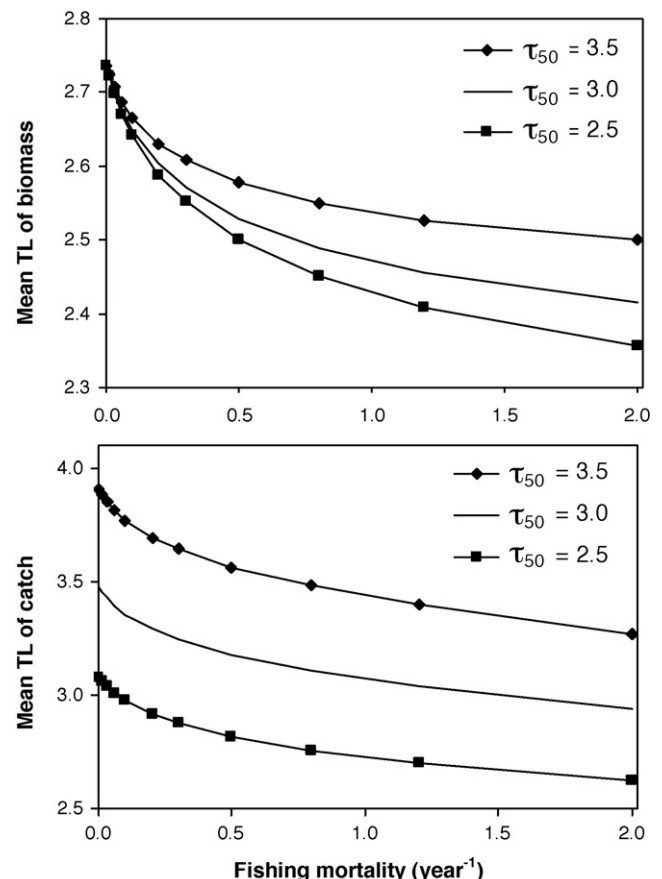


Fig. 10. Mean trophic level of ecosystem biomass (top) and of catch (bottom).

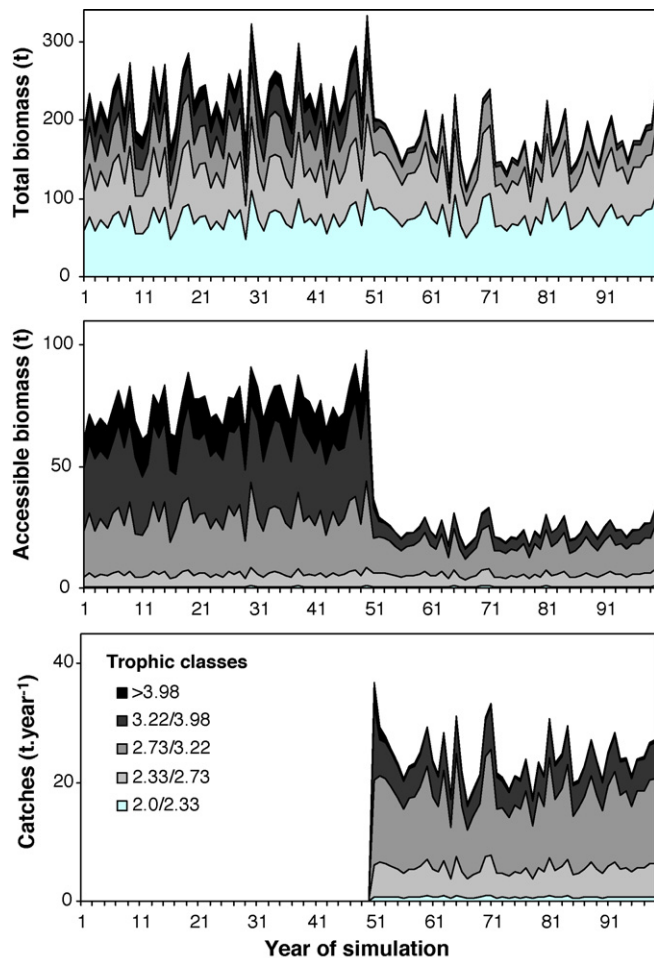


Fig. 11. Simulation of biomass, accessible biomass and catches time series, using the dynamic version of EcoTroph (based on the values: $F^* = 1$; $\varepsilon_1 = 0.2$ and $\varepsilon_2 = 0$; trophic classes aggregated for clarity). Exploitation starts in year 51 with high catches and a short transition phase is observed during the following years.

targeting low trophic levels (Fig. 10, top). The mean trophic level of the catch follows a similar trend, and decreases as a function of fishing mortality, whatever the trophic level at first capture is (Fig. 10, bottom).

3.3. Dynamic model: impact of fishing on stability of ecosystem biomass

Using the dynamic model, we simulated times series of biomass, accessible biomass and catch (Fig. 11). The model properly mimics how the input variability at trophic level 1, as a representation of the environmental fluctuations of primary production, propagates through the food web. The fishery, which starts at year 51, induces a 30% reduction in total biomass, which is consistent with the results of the steady-state model. Here also, predators are the most affected, the biomass at trophic levels higher than 4 almost completely disappearing, while the overall accessible biomass experiences a fourfold reduction. In the very first years of the fishery, a transition phase is observed, where the biomass at higher trophic levels remains substantial, and catches are especially high, before stabilising around a lower mean value.

Because trophic level 3.5 is reached in 1 year, the propagation of environmental fluctuations is fast and a lag is observed only for the highest trophic classes, whose relative biomass in the ecosystem is small. Similarly, the transition phase which follows the start of the fishery is short. Nevertheless, on average and for the simulated

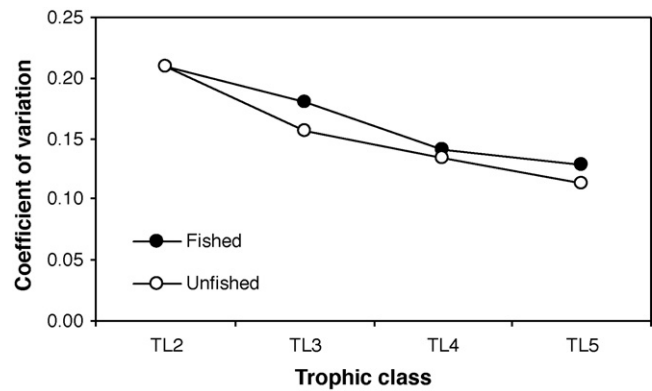


Fig. 12. Decrease in the instability of the biomass as a function of trophic levels, measured from the year-to-year coefficient of variation in biomass for entire trophic classes (simulation for: $F^* = 1$; $\varepsilon_1 = 0.2$ and $\varepsilon_2 = 0$).

conditions, this transition phase lasts 3 years near trophic level 4, and 5 years at trophic level 5.

Due to the slowing down of the speed of the trophic flow, the year-to-year variability of biomass declines with increasing trophic levels (Fig. 12). For instance, the standard deviation experiences a twofold decline, between trophic levels 2 and 4. This decrease is slightly less pronounced when fishing occurs, because the mean trophic level increases within each trophic class. The key point, however, is the confirmation that the biomass at high trophic level is characterized by a high stability.

As a consequence, the simulations show that the variability of the biomass of the whole ecosystem is significantly increased by fishing ($p < 0.001$) (Fig. 13). Logically, a high variability of primary production will result in a high variability of the total biomass, though the slope of this relationship will be higher when fishing occurs (Fig. 13, top). Thus, whatever the strength of the environmental fluctuations, the simulated fishery leads to an increase in the coefficient of variation of the biomass. This increase is especially strong when the fishing pressure is high; also, it is much stronger for the accessible biomass than for the total biomass (Fig. 13, bottom). This also applies to catches, whose coefficient of variation follows the same trend as the accessible biomass and which become very unstable for high fishing pressures.

Considering the variability of the trophic efficiency does not substantially modify these results. In that case, not only the secondary production and thus the biomass input into the model change from year to year, but also the natural loss rates at all trophic levels. Thus, (simulated) environmental variability appears to be important to all trophic classes, including high trophic level predators, especially as it may mask the stability-reducing effect of fishing. Nevertheless, a significant increase of the biomass coefficient of variation is still observed ($p < 0.001$), especially for the accessible biomass (see Fig. 13, bottom).

4. Discussion

4.1. EcoTroph and Ecopath with Ecosim

We recently showed (Gascuel et al., 2008a) that there are strong similarities, even homologies, in the way trophic transfers and predation are accommodated by EcoTroph and the well-established Ecopath model (Polovina, 1984; Christensen and Pauly, 1992). Additionally, the dynamic version of EcoTroph exhibits obvious similarities with Ecosim (Walters et al., 1997). Of course, the two modelling approaches are different, Ecopath (and Ecosim) being based on flows between boxes representing (groups of) species, while EcoTroph considers continuous trophic classes only, without references to particular species or groups thereof (Table 2).

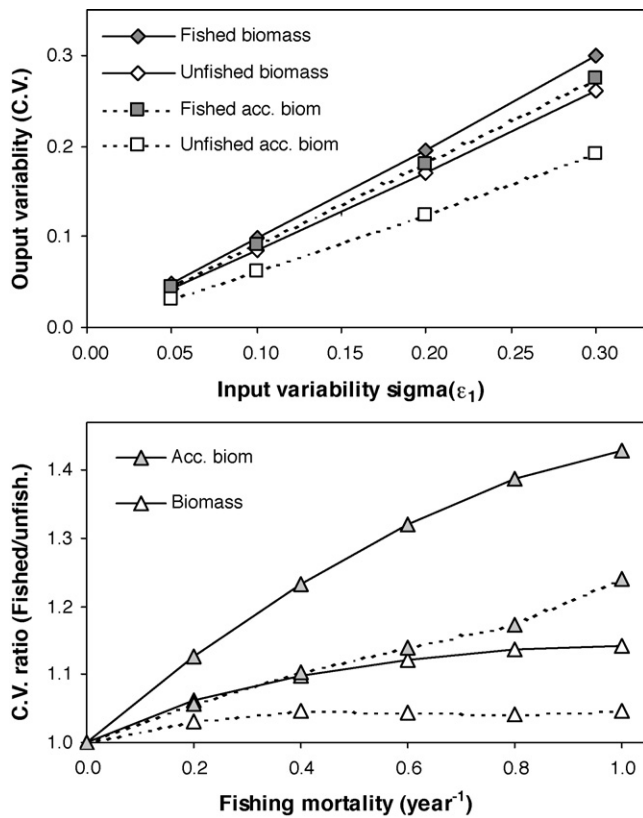


Fig. 13. Propagation of the input variability to the ecosystem biomass. Top: impact of increasing variability in the primary production on the variability of the biomass or accessible biomass (mean estimates for a set of 30 simulations, based on $F^* = 1$ and $\varepsilon_2 = 0$, transition phase excluded). Bottom: impact of increasing fishing effort on the relative variability of the biomass and accessible biomass; the input variability either affects the primary production (solid lines) or the transfer efficiency (dashed lines) (mean estimates for a set of 30 simulations, based on the reference values for ε_1 and ε_2 , transition phase excluded).

However, in both cases, the ecosystem is represented as a trophic flow moving from lower to upper trophic levels, losses due to non-predation mortality, catches, excretion and respiration (Fig. 14).

The homologies between Ecopath and EcoTroph help us better understand aspects of the both models. In particular, trophic flow appears to be the consequence of two processes: predation, by which biomass is transferred from a prey to a predator, and growth, through which the predator converts the biomass of trophic level τ into its own biomass, on average at trophic level $\tau + 1$. During this transfer, losses occur due to the four processes: catches, non-predation mortality, excretion and respiration. The catch pro-

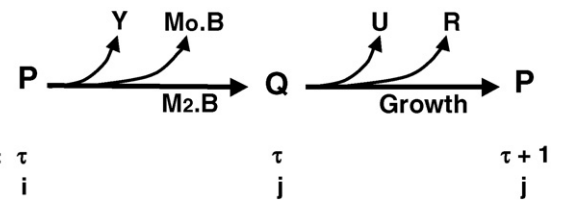


Fig. 14. Schematic representation of the conceptualisation of biomass flow in Eco-path: The production P of the prey i at trophic level τ is split into three parts: predation ($M_2.B = Q$), losses due to non-predation mortality ($M_0.B$) and fisheries catches ($F.B = Y$). Of the amount Q , only a small.

cess is taken into account in the flow equation (6) using the fishing loss rate parameter φ_τ , while the three others are implicit in the natural loss rate parameter μ_τ . In other words, natural loss rate (μ_τ), and thus trophic efficiency (TE), are not directly linked to natural mortality (M). Rather, TE depends on non-predation mortality (M_0), excretion and respiration, with this last term being, in most cases, the most important. As for the natural mortality $M (=M_0 + M_2)$, its M_2 component is directly linked to the magnitude of the upward trophic transfer due to predation, and cannot, thus, be considered a 'loss' term.

Overall, the two approaches differ more in their parameterisation than in their conceptualisation of predation and related processes. While Ecopath requires a value of each parameter (P/B , Q/B , etc.) per box, or functional group, EcoTroph is based on parameters expressed as functions of trophic level. Perhaps more importantly, Ecopath is based on knowledge of diet, consumption and production rates, with trophic levels estimated as outputs of the model. Conversely, EcoTroph is based on trophic level estimates, and requires neither diet compositions, nor Q/B values. This leads, for EcoTroph, to a very strong reduction in the number of required parameters, but also to a loss of flexibility and realism. Therefore, it must be seen as complementary, and not as alternative to Ecopath.

4.2. What's new in the present EcoTroph version?

A first version of the trophic-level based model was published as a theoretical representation of ecosystem functioning (Gascuel, 2005). A significant set of improvement to this first approach emerged from comparing its logic, equation by equation, with that of the Ecopath model. This led to introduction of three major changes into the present version.

First, the comparison suggested that the implementation of top-down control in the first version of EcoTroph was inconsistent. Indeed, top-down control was assumed to result from the coefficient of natural flow loss (μ_τ) depending on predator abundance. In fact, this coefficient is not related to the predation process itself, but to the losses which occur during transfers (see Fig. 14). Conversely,

Table 2

A first comparison between key features of EcoTroph and Ecopath (see Table 1 for notation of EcoTroph parameters).

| | Ecopath | EcoTroph | Link equations |
|--|--|---|---|
| <i>General structure</i> | | | |
| Model structure | Aggregation of species into discrete trophic groups called boxes | Continuous distribution of the biomass | – |
| Parameters | One value of each parameter per box | Parameters expressed as functions of TL | – |
| Trophic parameters | DC_{ij} ; Q/B_i ^a | TLs | – |
| <i>Relationship between main parameters</i> | | | |
| Production P | | Biomass flow Φ | $\Phi = -dP/d\tau$, or $P = \Phi \cdot \Delta\tau$ |
| Biomass B_i | | Biomass B_τ | $B = \Phi/(P/B)$ |
| Productivity P/B | | Flow speed $d\tau/dt$ | $P/B = d\tau/dt = \Delta\tau/\Delta t$ |
| Fishing mortality F | | Fishing loss rate φ_τ | $F_\tau = \varphi_\tau \cdot \Delta\tau/\Delta t$ |
| "Partition" of production P and consumption Q ^b | | Natural loss rate μ | $\mu = (M_0 \cdot B + R + U)/P$ |

^a Ecopath parameters: DC_{ij} is the diet composition defining the proportion of prey j in the diet of consumer i , Q and B are the consumption and the production of the predator i .

^b In Ecopath the production and the consumption of each box are split into various terms. EcoTroph aggregates non-predation mortality, respiration and excretion, which are separate in Ecopath, and defined for each box.

the kinetic of the flow depends on the life expectation of animals as prey, and thus on predation. As a consequence, top-down control has to impact the speed of the flow $\Delta\tau/\Delta t$, as it does in Eq. (11), rather than the natural loss rate μ_τ .

The catch equation was also reformulated, based on definition of fishing mortality and related parameters leading to simulation results that are consistent with the theory of fishing. Notably, we took into account that a large part of the biomass is not accessible to fishing, especially for low trophic levels. According to Eq. (13a), the 'recruitment' into the accessible biomass flow is proportional to the total biomass at trophic level 2. Therefore, when the biomass flow increases at trophic level 1 or 2 (for instance, when climatic events affect the primary production) it positively impacts the accessible biomass flow (for trophic level 2 and consequently for all higher trophic levels) and thus the accessible biomass itself. Conversely, we assumed that the transfers between inaccessible and accessible biomass flow depend on the accessible biomass flow itself and are not affected by changes affecting the inaccessible biomass. In other words, an increase in undesirable species will not directly induce an increase in the targeted species.

The third major improvement of the model came from the comparison between EcoTroph and Ecopath: we showed that the P/B ratio, used as a key input parameter in Ecopath, may be considered a measure of the speed of the biomass flow. In fact, the total mortality Z , the P/B ratio and the flow speed $\Delta\tau/\Delta t$ are all different ways to look at the same kinetics, i.e., that by which biomass dies and is regenerated at the same time it moves through the food web (Gascuel et al., 2008a). This allowed us to propose an empirical model (Eq. (8)) to estimate a parameter previously thought to be elusive, and showed that previously assumed values of this parameter (Gascuel, 2005) were erroneous. Nevertheless, the general pattern of the expected relationship between flow speed and trophic level was correct, and similar to those presented above.

Generally, and quite surprisingly, these three major improvements had little impact on the general behaviour of EcoTroph. The absolute values of estimates (of biomass, catches, kinetics...) changed, but not the general rules that were inferred. Of course, the correction of these erroneous inputs gives us more confidence in the present EcoTroph output.

Some important qualitative results in Gascuel (2005) remain unchanged and hence are not revisited here. This applies particularly to the demonstration that cascade effect can be simulated (in case of top-down control), if a fishery targets only high trophic levels. Conversely, a low selectivity, simulating a fishery targeting a wide range of trophic levels leads to fairly constant biomasses for all prey, the predation release by top predators being more or less compensated for at intermediate and low trophic levels. This suggests that when top-down control occurs, applying a low fishing mortality to a wide range of trophic levels may be the best way to maintain the resilience of exploited ecosystems.

Finally, a major improvement was adding a dynamic component to the steady-state version of the model. In the present study, we used it for theoretical simulation, but it may also be used for hind- and forecasting (Gascuel et al., 2009). In the former case, the dynamic model may be fitted to observed time series, leading to improvement of available estimates of the required parameters (for instance, of trophic efficiency TE or the α coefficient of top-down control). In the case of forecasts, various exploitation patterns and trends may be simulated, especially for the purpose of analysing fishing policies.

4.3. Building a model of ecosystem functioning based on trophic levels

The EcoTroph model presents some similarities with body-size based models and size spectrum analysis, where all species are

aggregated as well, and the biomass is continuously distributed by the size (e.g., length or weight) of the organisms therein (reviews by Bianchi et al., 2000; Benoît and Rochet, 2004; Andersen and Beyer, 2006). With such approaches, body size is the key parameter used to investigate trophic relationships among fish and is considered as one of the main factor determining ecosystem dynamics. In fact, body size can then be regarded as a cause, whereas trophic level may appear as an emergent property, of these dynamics, providing an *a posteriori* metric of the trophic processes involved. Both parameters, body size and trophic level, are correlated at the community level (Jennings et al., 2001), but their relationships remain complex and a model structured around body sizes will not have the same properties as one structured around trophic levels. Many publications have explored the usefulness of body size spectra, notably as a tool for assessing fishing impact on aquatic ecosystems (e.g. Kerr and Dickie, 2001; Gislason and Rice, 1998).

However, the structure of the two types of models is very different. Size-based models usually derive from the mass balance partial differential equation (PDE) of McKendrick-von Forster model (in Kot, 2001) and includes explicit representations for growth, mortality and predation (Silvert and Platt, 1980; Benoît and Rochet, 2004). In EcoTroph, we use only Eq. (2) to link the flow, the biomass and the speed of the flow. What is new here is that we use a well established equation from hydrodynamics (or flux physics) to model the flow through TLs. This allows us to formalize an explicit relationship between the production (the biomass flow) and the biomass itself (Eq. (5)). As far as we know, such an equation, where the speed of the trophic flow is the link factor between biomass and production, has not been proposed before for an ecological application. This master equation of EcoTroph allows the biomass can be calculated, by combining the two sub-models: one expressing the fact that the biomass flow is not conservative (because of losses occurring during the transfers in the food-web; Eq. (6)), the other based on an empirical model embodying the idea that transfers are faster at low trophic levels (Eq. (8)).

Thus, using the TLs metric leads to a very simple model which is able to mimic ecosystem functioning. This does not mean we consider TLs to be driving ecosystems dynamics. Rather, we suggest that trophic relationships are driving ecosystems, an assumption also made in virtually all ecosystem models, including EwE or body size spectra. The TL of an organism or the mean TL of a population is the metric that emerges as the result of the trophic functioning of ecosystems and using this metric appear promising to explore ecosystems dynamics.

Of course, the trophic level of an organism may change during ontogeny and may also vary in time and space, as the function of the prey fields it encounters. Still, most consumers are anatomically and behaviourally adapted to a relatively narrow range of prey. This constrains the range of trophic levels that they can have, and justifies its representation through a mean, expressing the ecological characteristic of a population of organisms in term of their position in an ecosystem's food web. In that sense, TL appears a state variable characterizing each unit of biomass in an ecosystem. Additionally, it should be noted that it is never assumed in EcoTroph that the TL of organisms or populations does not change. On the contrary such changes are considered, albeit implicitly in our theoretical simulations.

The fact they can be considered a state variable does not mean that trophic levels are easy to estimate in the field. Because diets are variable and often opportunistic, more work is still needed to estimate not only mean trophic levels but also their variability in time or space (see Karachle and Stergiou, 2006, or Chassot et al., 2008 for an example of the type of study needed). Obviously, ecosystem modelling requires data on trophic relationships, which probably implies to develop costly observation systems. Isotopic and gut contents analyses thus appear to be a key step for implementing

marine ecosystem modelling and ecosystem approach to fisheries. However, estimate should not be confused with the concept itself (i.e., even if difficult to measure, TLs exist) and developing trophic-level based models constitutes a useful step forward in theoretical context, as well as for specific case studies.

4.4. From theoretical model to specific case studies

Using EcoTroph in order to analyse ecosystem functioning and fishing impact in specific ecosystems does not present any particular conceptual difficulties. Nevertheless, using field data rather than an idealized system modifies several aspects of the model.

First, the flow speed model can be modified. In specific ecosystems, the speed of the flow depends on the species composition encountered at each trophic level. This is so because each species is characterized by a particular physiology and growth, which determine its turnover rate, and by different predators, which impact on the speed of the trophic flow. As a result, actual $\Delta\tau/\Delta t$ ratios plotted against trophic levels need not have the same shape as the monotonously decreasing curves inferred from Eq. (8). Observed kinetics, for instance based on P/B ratios from Ecopath, will exhibit a more or less complex pattern, frequently non-monotonous (Gascuel et al., 2008b). As a consequence, the biomass trophic spectrum may also present a complex pattern and a non-monotonous shape. This explains why trophic pyramids of biomass can be topsy-turvy, while pyramids of production must exhibit declining production by trophic levels (Gascuel et al., 2005).

Secondly, the fact must be taken into account that primary production is consumed not only by herbivores (i.e., strict secondary producers), but also by animals at higher trophic levels. The same applies to detritus, which is not consumed only by strict detritivores (see Fig. 1). Thus, if we consider trophic levels higher than 2 (i.e., animals), biomass can be seen as entering the system not only at trophic level 2, but at higher trophic level as well. This implies that gains of biomass flow can occur at different trophic levels, and not only losses. As a result, the μ_τ coefficients express the balance between real losses and feeding on trophic level 1. They may exhibit negative values and thus the term $\exp(-\mu_\tau)$ is not any more equivalent to trophic efficiency (TE). Nevertheless, secondary producers are generally abundant and plants or detritus often constitute a small part of the diet of higher order consumers. Thus, by far the highest biomass input occurs as a flow at trophic level equal or close to 2. For all other trophic levels, the trophic flow will decrease (and $\exp(-\mu_\tau)$ can be considered equivalent to TE).

There are two ways to apply EcoTroph to specific ecosystems (Gascuel et al., 2009). The first is to build an observed biomass trophic spectrum and a biomass flow trophic spectrum (both jointly defining an 'observed' model of the flow speed). One obvious way this can be done is when an Ecopath model has already been built for the considered ecosystem. In such case, EcoTroph may be seen as a complementary module to EwE, enabling the exploration of various fishing scenarios (including estimate of the biomass spectrum of the unexploited state). The second way to use EcoTroph is as a stand-alone application, using the Catch Trophic Spectrum Analysis (CTSA) to generate biomass trophic spectrum. This last routine, not presented here, is based on a reverse form of EcoTroph equations and allows users to estimate fishing mortalities and biomasses by trophic levels, using catches as input (see Gascuel and Chassot, 2008).

4.5. Summary

Overall, EcoTroph, as a trophic-level based model, relies on a few elementary and robust assumptions. The first basic assumption is that secondary production transits through the food web, from lower to higher trophic levels, and that these transfers incur

losses, whose magnitude depends on both natural factors and fishing. The second basic assumption is that the kinetics of the biomass flow is characterized by faster transfers at low trophic levels, due to the higher metabolism rate of the animals therein. The third basic assumption is that biomass of prey may (but need not) depend on the biomass of predators.

Of course this model, only based on trophic levels, is a caricature of the functioning of real ecosystems. We obviously know that the species composition of an ecosystem has major effect on its functioning. However, not explicitly taking its species composition into account does not imply that their effect cannot be included in a model. Specific composition determines, among other things, transfer efficiencies per trophic class and flow kinetics, as well as the extent of top-down controls. Here, all parameters of the model are assumed to be constant. In a sense, they are considered characteristics of a given ecosystem, just as growth, for instance, is considered a constant characteristic of species in most simple single-species dynamic models. This is a strong assumption, and a more sophisticated model may be conceived which would not require a hypothesis of constant parameters, defining for instance density dependent relationships for trophic efficiencies or top-down controls. But the lack of real observations makes this unrealistic. Thus, for the present model, we accept variable parameter (i.e., density-dependence) only for flow kinetics.

As a result, we found that taking into account the few simple processes discussed above appears sufficient to simulate the biomass distribution patterns and responses to fishing pressure observed in real ecosystems. The best argument for the trophic-level based model presented here is that it appears to be a useful tool for understanding ecosystem functioning in both ecological and fisheries contexts. It provides the theoretical basis to explain the distribution of biomass of an ecosystem over its various trophic levels, and the impact of fishing on this distribution. For example: it provides consistent relationships between parameters (e.g. catches versus fishing mortalities); it shows that slower flow implies slower biomass regeneration, which causes (usually large) high-trophic level species to be intrinsically more vulnerable to fishing (see also Cheung et al., 2005, 2007); it mimics the decline under exploitation of the mean trophic level of catches now known as 'fishing down marine food webs' (Pauly et al., 1998), and it explains key changes in the species composition of ecosystems, e.g., the relative (and sometimes absolute) increase of unfished biomass induced by exploitation.

The model also explains more complicated patterns, such as the increasing instability of ecosystems biomass and catches when intensively fished. It suggests that cascade effects can only occur with particular fishing patterns, strictly and strongly targeting highest trophic levels (as in the study of Myers et al., 2007, where only the large sharks were fished). It suggests that, when top-down control occurs, applying a low fishing mortality to a wide range of trophic levels may be the best way to maintain the resilience of exploited ecosystems (such 'shaving off' of trophic pyramids is illustrated in Palomares and Pauly, 2000). It shows, more generally, that low transfer efficiencies, fast transfers and strong top-down controls may contribute to the resilience of marine ecosystems in face of fishing.

5. Conclusion

EcoTroph is now available as a plug-in module of EwE Version 6 (Christensen and Lai, 2007). By concentrating on biomass flow as a quasi-physical process, this approach allows aspects of ecosystem functioning to be explored which are complementary to EwE. Of course, we must not forget that in the face of the actual complexity of evolved (and evolving!) ecosystems, all attempts at reducing them to equations are equally vain. The question thus is one of

utility, i.e., how useful (or informative) a model is, relative to the time and other resources invested in its construction. These resources, in the case of EcoTroph are minimal, especially when, as we suggest here, EcoTroph is used as a complement, rather than an alternative to other approaches.

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