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EcoTroph (ET):

**a trophic level based software
for assessing the impacts of
fishing on aquatic ecosystems**

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**ECOTROPH (ET): A TROPHIC LEVEL BASED SOFTWARE
FOR ASSESSING THE IMPACTS OF FISHING
ON AQUATIC ECOSYSTEMS**

D. Gascuel ⁽¹⁾, L. Tremblay-Boyer ⁽²⁾ and D. Pauly ⁽²⁾

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DIRECTOR'S FOREWORD

Many researchers at the Fisheries Centre, from faculty to graduate students are involved in ecosystem modelling, and not surprisingly this has resulted in the FC becoming well-known for expertise in this challenging field.

This is obviously what motivated Prof. Gascuel to spend a sabbatical year at the Fisheries Centre, and this report, co-authored by one of our graduate students and one of our faculty, is the product of his visit.

The ecosystem model and software presented in this report, called EcoTroph, represent both a stand-alone application and a module of the Ecopath with Ecosim (EwE) software, the flagship product of the FC. EcoTroph is thus not an alternative to Ecopath, but a useful complement, an alternative way of looking at ecosystems, and I hope to see more applications of this type – even from my own discipline, ecological/fisheries economics. This will enable us to get a full view of aquatic ecosystems and the services they provide.

Finally, I wish to congratulate the institution that sponsored the study visits of Prof. Gascuel to Vancouver in Canada, and of Ms. Tremblay-Boyer to Rennes, in France, for having enabled the exchanges, which led to this report. It is initiatives of this sort which are the lifeblood of successful research as documented in this report.

Rashid Sumaila, FC Director

ABSTRACT

This report documents EcoTroph, an approach and software for modelling marine and freshwater ecosystems, and which is articulated entirely around trophic levels. EcoTroph's key displays are bivariate plots, with trophic level as the abscissa, and biomass flows or related quantities as ordinate. Thus, trophic ecosystem functioning can be modelled as a continuous flow of biomass surging up the food web, from lower to higher trophic levels, because of predation and ontogenetic processes. Such an approach, wherein species as such disappear, may be regarded as constituting the ultimate stage in the use of the trophic level metric for ecosystem modelling, providing a simplified but potentially useful caricature of ecosystem functioning and impact of fishing.

Following a historical introduction to the trophic level concept, part I of this report presents the definitions of the concepts upon which EcoTroph is based, and the equations which implement these. As well, the differences from and similarities to conventional trophic models are highlighted, notably in relation to the recently-released version 6 of Ecopath with Ecosim (EwE). We simulate fishing impact on a virtual ecosystem and show that the model is able to mimic the effects of various exploitation patterns on ecosystem biomass expected from theory. Particularly, the model provides consistent relationships between catches or biomass and fishing mortalities; it may exhibit complex patterns, e.g., cascading effects and 'fishing down the food web'; and it provides the theoretical basis to explain the effect of strong top-down controls and fast-flow kinetics on ecosystem resilience. Using an inverse form of the EcoTroph model, we also present the Catch Trophic Spectrum Analysis (CTSA), as a method for estimating biomass and fishing mortalities at the ecosystem scale. We show that such a method may be seen as the 'VPA' (Virtual Population Analysis) of ecosystem approaches and provides robust estimates when catches per trophic level and primary or secondary production are known.

Part II of this report is a **User Guide** for the EcoTroph plug-in available in the Ecopath with Ecosim (version 6) software environment. Thus, the design and use of EcoTroph (ET) as a new software are presented, with some emphasis on the routines which pre-process the input data, again with some emphasis on their differences from and similarities to EwE. The inputs, operation and output of ET are presented for both cases, i.e., when it is used a stand-alone program, and as a plug-in routine of EwE. We then provide more specific information about each of EcoTroph's four sub-routines, organised into 'What it does', 'How it works' and 'How to use it' sections. These routines are:

- **ET-Transpose** can be used to extract biomass and catch trophic spectra from an Ecopath model, thus providing the user with an alternative, synthetic overview of the ecosystem;
- **ET-CTSA** performs Catch Trophic Spectrum Analysis and generates an estimate of the biomass trophic spectrum related to the current ecosystem state given catches by trophic levels;
- **ET-Diagnosis** simulates the effects of increasing fishing pressures on ecosystem functioning. This provides a global diagnosis of ecosystem state as well as simple forecasts of total catch and biomass;
- **ET-Dynamics** is the time-dynamic version of EcoTroph. It can be used either for manually fitting biomass and/or catch time series, or for simulation and forecast.

We illustrate the usefulness of these four sub-routines using the Guinean shelf ecosystem as a case study.

INTRODUCTION

There are numerous ways to define and represent an ecosystem, and the choice of approach used by practitioners will depend on a complex of reasons. Key among these are: (i) the availability of input data from the system to be studied; (ii), whether or not other ecosystems have been previously studied using the approach in question (and hence are available for comparison), and (iii) the background and skills of the would-be modeller(s).

One approach, 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 can not 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 hence, by Rigler's own criteria, they 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 this 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, due to its new role as stepping stone to time-dynamic modelling using Ecosim (Walters *et al.* 1997) and spatial modelling using Ecospace (Walters *et al.* 1998), so did the trophic level concept (Pauly *et al.* 2000).

Two other developments were occurring at the same time which also widely contributed to increasing familiarity with trophic levels. One is the emergence of FishBase (Froese and Pauly 2000), the online database on fish (www.fishbase.org), which covers all fish species in the world (over 30,000 spp.), and which, in late 2008, achieved over 30 million 'hits' per month from over 1 million users. FishBase presents estimates of trophic level for nearly half of these 30,000 species, based either on diet compositions or food items entered in the database, or inferred from the size reached by the different species and their taxonomic affinities to species with diet compositions or food item data.

The second development which increased interest in trophic levels, at least since the late 1990s, is the demonstration of the worldwide occurrence of the phenomenon now widely known as 'fishing down marine food webs' by Pauly *et al.* (1998). Although it was contested at first (Caddy *et al.* 1998), subsequent research has corroborated the findings of Pauly *et al.* (1998), using various data sets, at different geographic scales (Pauly and Palomares 1995).

The stage is thus set for the trophic level based ecosystem modelling approach to be presented here, which, building on earlier work (Gascuel 2001 and 2005; Gascuel and Chassot 2008; Gascuel *et al.* 2005, 2008a, 2008b), makes full use of the conceptual advances heralded by Odum and Heald (1973). Here, the EcoTroph model is proposed as an extension of the Ecopath with Ecosim (EwE) approach. Within this family of models, it may be regarded as constituting an ultimate stage, wherein species as such disappear behind trophic levels. However, we must stress that EcoTroph is not an elaboration (i.e., complexification) of previous food web modelling effort. Rather, EcoTroph results from attempts to rethink and simplify trophic modelling, thereby offering another interpretation of available data, and another view of ecosystems.

The view thus provided may be seen as an oversimplified, but useful caricature. However, 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 suggested here, EcoTroph is used as a complement, rather than an alternative to Ecopath with Ecosim.

PART I – THE TROPHIC LEVEL BASED MODEL: THEORETICAL APPROACH

Part I of this report aims to introduce theoretical basis of the EcoTroph model. In a first step, general principles and assumptions of the model are presented and mathematical formulations are detailed and justified. Then, we show that the model is a useful theoretical tool to build generic relationships between parameters (for instance between fishing effort and catches or ecosystem biomass) and that it gives a consistent representation of the trophic functioning of marine ecosystems. This theoretical approach pertains to a virtual ecosystem. Finally, returning to the real world, we present the Catch Trophic Spectrum Analysis (CTSA) which is a method devoted to the estimate of parameters required in real case studies.

Part II of the report will then be devoted to the presentation of subroutines that have been developed to work as part of EwE, and thus to facilitate the use of EcoTroph for practical analysis of real data.

1. Building the model: principles, assumptions and equations

1.1. Origin of the model

- ***A first version based on single-species yield par recruit approaches***

The first steps toward what was to become the EcoTroph model for trophic level based modelling of ecosystems were presented at a conference in France in 2001, whose proceedings were published in the grey literature (Gascuel, 2001; Gascuel, 2002). In this first version, the model was explicitly based on an adaptation, at the ecosystem scale, of well-tested single-species approaches, based on an age-structured representation of the dynamics of fish populations (Ricker 1975). With such approaches, equations are initialised by a given recruitment. Then, the number of survivors and the biomass of the cohort are successively calculated, while accounting for observed catches, for each age group, for the entire cohort from its recruitment to the death of the oldest age group. Two key equations are used: one referring to survival, the other to catch. Cumulating biomass and catch over all age groups leads to biomass and yield per recruit models (Beverton and Holt 1957), which are still widely used, especially in Western Europe, to analyse the state of the stock, to evaluate the impact of fishing, and to predict expected catches and biomass under various fishery management scenarios.

These age-structured biomass and yield per recruit models may be regarded as flow models, wherein fish move from one year class to the next as a function of their age. In Gascuel (2001, 2002), the trophic level based ecosystem model was built using the same logic and equations, with two crucial differences: (1) it did not consider a single species, but all species of the ecosystem in question, and (2) the flows did not occur along the time axis (from one age group to the next) but from one trophic level to the next. Herein, the biomass was seen as ‘entering’ the ecosystem at trophic level 1 (as primary production, which is treated as analogous to ‘recruitment’ to the system) and moves from one trophic class to the next, as mediated by ontogenic and predation processes. Of course, this re-interpretation involved some modifications of the key equations, the main one being the replacement of the time (age) dimension by trophic level. Additional equations were introduced, notably to take into account the feedback effects caused by top-down control, a theme to which we shall return further below.

As in many single-species populations dynamic models, this first version of the trophic level based model was formulated in terms of numbers. The feasibility of re-expressing the model in terms of biomass flows was mentioned in an annex, but otherwise, any consideration of flows and trophic kinetics, which, as we will see later, is crucial to EcoTroph, was missing. Nevertheless, because population and catch numbers can be converted to biomass and yield, the model could output biomass and yield as a function of fishing patterns. Notably, the model generated results whose gross features were similar to those of the more fully

developed subsequent versions. Thus, there is some justification in perceiving the EcoTroph as a multi-species yield or biomass per recruit model in which the time axis is replaced by a trophic level scale, and we shall make use of this as heuristic device further on.

- ***From the trophic level based model to EcoTroph***

A second version of the trophic level based model, which incorporated biomass flow and flow kinetics equations was then developed as a theoretical representation of ecosystem functioning (Gascuel, 2005). Here, the model expressed the trophic functioning of a virtual ecosystem, without references to any particular field data or case study. The aim was to formulate generic relationships between parameters, but not to analyse the dynamic or the state of a given ecosystem; thus, parameter values based on apparently reasonable, but arbitrary considerations, were used for the simulations. This appeared sufficient to build or analyse general rules on ecosystems functioning. However, a first attempt to apply the model to real case studies (Gascuel and Chassot, 2008) led to the realization that uncertainty concerning some of the required parameters strongly limited model implementation.

A third set of improvement to the trophic level approach emerged from comparing its logic, equation by equation, with that of the well-established Ecopath with Ecosim model (EwE) described above, which revealed deep similarities between the two approaches. Exploiting these similarities led a new version of the trophic level based model, which was renamed EcoTroph (ET), and whose software implementation works both as a stand-alone software, and as a module of EwE (version 6).

The comparison of ET with EwE suggested that the implementation of top-down control in ET was inconsistent, and a new, correct formulation was introduced. This showed that the previous version was robust in that it produced correct results, if for the wrong reasons. 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. Also, examination of parameter estimates used in EwE revealed that a number of approximations previously used in ET were not consistent. However, because the inter-relationships between these parameter values were realistic, the erroneous absolute values had no impact on the general behaviour of ET. Nevertheless, the correction of these erroneous inputs gives us more confidence in the ET output. Also, these corrections removed difficulties that had appeared previously in some case studies, thus improving our confidence in the result of ET.

Overall, we have been able to learn from over 20 years of experience with Ecopath; so far possible, we use here the concepts, definitions and notation also used in Ecopath, in the hope that this will facilitate assimilation of EcoTroph. We note, finally, that the version of EcoTroph presented here replaces all previous implementations of the trophic level based modelling approach distributed by the first author.

1.2. EcoTroph: general principles

1.2.1. Recalling the trophic level metric

Trophic levels, as initially conceived (Lindeman, 1942) characterized the position of organisms within the food webs: 1 for primary producers and detritus, 2 for first-order consumers, 3 for their predators, etc. This conceptual approach leads, among other things, representation of ecosystem as trophic pyramids, where the biomass of each of the various components of ecosystems had to be shoehorned into one of a few integer trophic levels. As mentioned above, this approach has been (rightly) questioned, because most consumers feed on different prey, each with its own trophic level. The result, as noted by Odum and Heald (1975) and Adams *et al.* (1983), is that these consumers have fractional trophic levels, which can be calculated from:

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

where D_{ij} is the proportion of the prey j in the diet of consumer i , and is τ_j the mean trophic level of its prey.

The trophic level of an organism may change during ontogeny (Pauly *et al.* 2001), 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 sizes. This constrains the range of trophic levels that they can have, and justifies its representation through a mean trophic level, expressing the ecological characteristic of a population of organisms in term of their position in an ecosystem's food web. More generally, trophic level appears a state variable characterizing each unit of biomass in an ecosystem.

1.2.2. The biomass distribution: continuous representation and discrete approximation

Now, let examine the theoretically expected 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. Obviously, a large amount of biomass occurs all the time at trophic level 1, continuously subject to mortality and continuously regenerated by primary production and detritus recycling. Conversely, with the exception of semi-autotrophic organisms with small biomasses in some ecosystems (e.g., coral polyps and tridacnid clams), there is usually no biomass between trophic levels 1 and 2. According to the trophic level metric, herbivorous and detritivores are at trophic level 2. In other words, plants and detritus belong to level 1, animals belong to levels 2 (and higher), and there is no biomass between 1 and 2.

On the other hand, at trophic levels higher than 2, the biomass is distributed along a continuum of trophic level values. Of course, some trophic levels may contain more or less biomass, but none of them should be completely 'empty'. The variability of the diet of the different consumers of an ecosystem should result in all trophic levels being 'occupied' (Fig. 1).

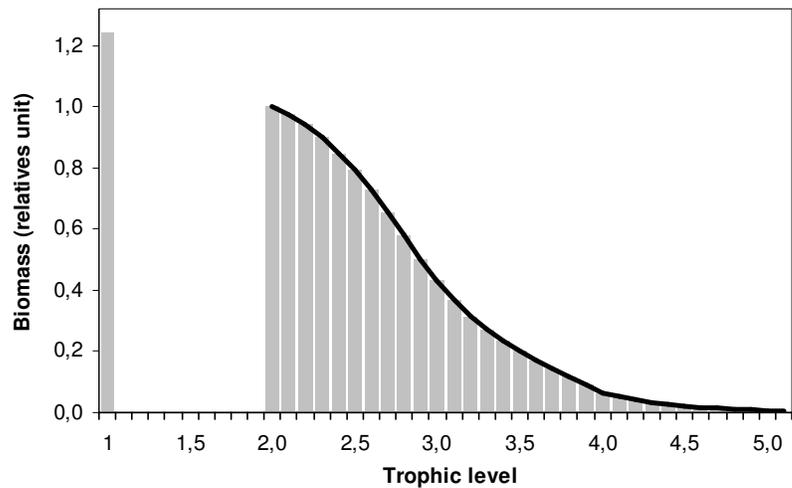


Figure 1 – Theoretical distribution of the biomass of an ecosystem by trophic level

Thus, the first key point of EcoTroph is that it deals with as continuous distribution of the biomass. The model aims to simulate the state variable $B(t, \tau)$, i.e., the biomass occurring in the ecosystem at time t , at trophic level τ .

As a consequence, the EcoTroph equations are based on a continuous approach. We will present further below a dynamic version of EcoTroph, which of course refers to time. However, the initial version refers to a steady state, wherein the state variable is $B(\tau)$, i.e., the distribution of the ecosystem biomass by trophic level. Additionally, 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 usually sufficient to cover all top predators likely to occur in marine systems (Pauly *et al.* 1998; Cortes 1999). The resulting bivariate graph represents a key aspect of ecosystem functioning and constitutes what is called a 'biomass trophic spectrum' (Gascuel *et al.*, 2005).

1.2.3. Trophic flow: from a discrete process to a continuous model

In ecosystems, biomass moves from lower to higher trophic levels due to growth and predation, as can be best illustrated by the fate of a single particle (e.g., a carbon atom) drawn schematically in Fig. 2 (dotted line). This particle enters the ecosystem at time $t = 0$, through a primary producer of trophic level = 1, for instance a phytoplanktonic organism. Then, it jumps very rapidly to trophic level 2 due to grazing by a small zooplankter. It may stay here for a short time, and then be consumed by a fish, e.g., a juvenile sardine. This juvenile sardine will increase its own trophic level, as it graduates, in the course of its ontogeny, from feeding on small, herbivorous zooplankton to feeding on a mixture of small and larger zooplankton, some of it carnivorous. After say, a year, this sardine is then eaten by an adult cod, with a trophic level of 4.1. This cod will not experience an ontogenic increase of its trophic level, but survive more than two years before becoming the prey of a top predator, whose own trophic level is higher than 5.

The fate of our particle is thus characterized by continuous processes (ontogenic changes in trophic levels) and abrupt jumps caused by predation. The example illustrates the specific fate of a given particle,

and other particles will have different fates. Yet there are generalities: with the exception of those in semi-autotrophic organisms, all of the particles start with photosynthesis or detritus recycling at trophic level 1; from there, they move up more or less rapidly, jumping, at each predation event, to trophic levels defined by the average diet of the predators. Few particles, however, reach the highest trophic levels, and most will stop long before that, due to non-predation mortality, excretion or respiration. The particles that move up the food web have a wide range of trajectories, as illustrated in Figure 2 (grey lines). As a consequence, the flow of particles can be considered a continuous process. In fact, the continuous model (solid black line in Fig. 2) is not an approximation of the discrete process. It is the mean process itself, expressed as flow of biomass.

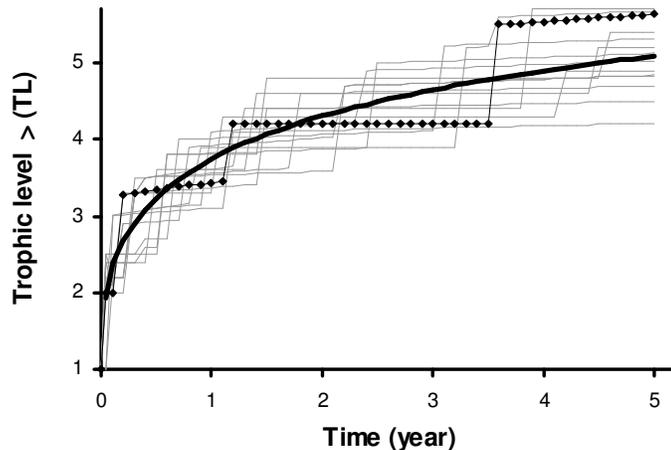


Figure 2 – Illustrating the transition from a discrete to a continuous representation of biomass flow in an ecosystem. Grey broken lines refer to the trajectories of single particles along trophic, while the continuous line refers to the mean trajectory of biomass flow from low to upper trophic levels

This is the second key idea of EcoTroph: 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.

1.2.4. Viewing ecosystem functioning as a flow

For the reasons given above, biomass can be considered as ‘flowing’ through each trophic level of an ecosystem. Herein, ‘flow’ refers to the amount of biomass that moves up the food web, which can be expressed in tonnes per year ($t \cdot \text{year}^{-1}$) or equivalent units for any trophic level. Obviously, this flow decreases from low to high trophic levels, due to respiration and non-predation mortality. On the other hand, the trophic flow is also characterised by a speed, which measures the kinetics of the process. In other words, particles starting at a trophic level of 1 (and therefore biomass itself) reach the upper levels only after a certain time. Thus, the speed of the biomass flow quantifies the velocity of biomass transfers in the food web. This speed can be expressed in term of number of trophic levels passed per year ($\text{TL} \cdot \text{year}^{-1}$).

Comparison with the jet of a fountain, such as the famous one in Geneva (Fig. 3) may be one way to visualize the processes involved here. The trophic flow, which starts at trophic level 1, is driven by a pump, corresponding to primary production. It reaches trophic level 5 or higher, but in the course of the required trophic transfers, losses occur, most particles falling back to the detritus (non predation mortality) or as respiration, before reaching the highest levels (i.e., the top predator). At each point (of the water column in Fig. 3), the flow is moving upwards. But in steady-state conditions, it may be characterized by a constant rate of (biomass) flow (e.g., in litres·s⁻¹; here: t·year⁻¹) and by a constant value of the flow speed (e.g., in m·s⁻¹; here TL·year⁻¹). Thus, from the bottom to the top of the column, the biomass flow decreases, due to the losses mentioned above. At the same time, the speed of the flow also appears a decreasing function of trophic level.

1.2.5. The input of biomass into the system

In the followings, we will only consider trophic levels higher than 2. Thus, the water jet of Figure 3 will not adequately represent biomass input into the system. 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. Thus, once we disregard the input at TL = 1, biomass can be seen as entering the system not only at trophic level 2, but at higher trophic level as well (Fig. 4). Of course, because herbivores (=secondary producers) are generally abundant and plants or detritus often constitute a small part of the diet of higher-order consumers, by far the highest biomass input occurs at trophic level 2. But it is not the only one. Thus, hatching also represents a biomass input to ecosystems: early stage larvae commonly feed on phytoplankton, and this biomass input mainly relates to trophic level 2.

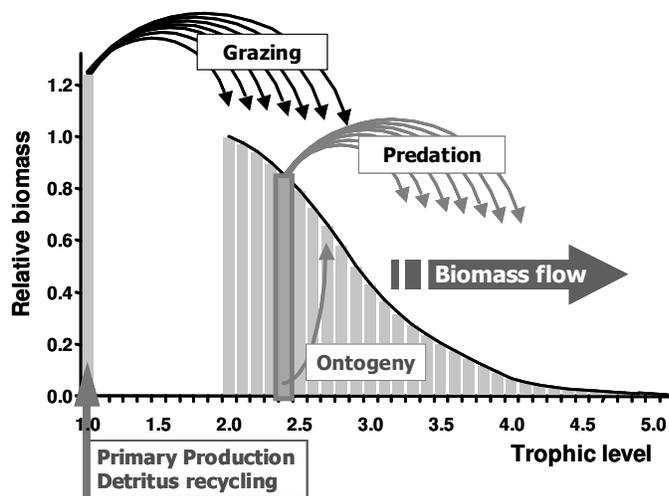


Figure 4 – Diagram of the trophic functioning of an ecosystem: biomass inputs and trophic transfer processes

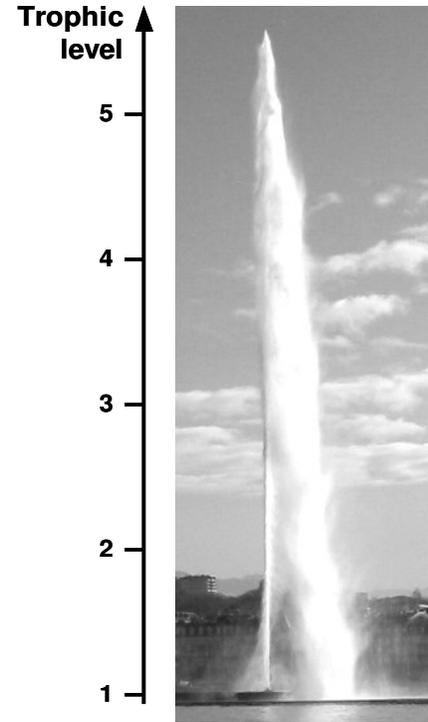


Figure 3 The water jet of Geneva, illustrating the concept of biomass flow

Biomass inputs at trophic levels higher than 2 stem from the discontinuity of the trophic process itself, notably between the first and higher trophic levels. But this does not invalidate the representation of an ecosystem as a continuous flow of biomass. Rather, it implies that gains of biomass can occur at different trophic levels, and not only losses. The ‘trophic fountain’, differs from that in Fig. 3 in that it is ‘fed’ at all trophic levels, although the contribution of the lowest trophic level considered (here: 2) will always be predominant. Thus, the main processes involved in ecosystems functioning, and which EcoTroph implicitly takes account of, are: the biomass inputs due to feeding on primary production and recruitment; the trophic transfers due to ontogeny and predation which induce a biomass flow towards high levels; and the losses from the system due to non-predation mortality and fishing.

1.3. **EcoTroph: biomass and flow equations**

Table 1 lists and defines the variables to be used in the following. Note that variables followed by parentheses, such as $B(\tau)$ or $\Phi(\tau)$ refer to continuous functions of trophic levels, while variable with subscripted indices (B_τ or Φ_τ) refer to cumulative or mean values in a trophic class $[\tau, \tau+\Delta\tau]$.

Table 1 – Trophic level-based modelling: parameters definition and suggested units*.

Variable	Parameter definition	Dimension (units)
$B(t,\tau)$	Density of biomass at time t and trophic level τ	Mass·TL ⁻¹ (tonne·TL ⁻¹)
B_τ	Biomass in the $[\tau, \tau+\Delta\tau]$ trophic class	Mass (tonne)
$B_{ref,\tau}$	Biomass in the $[\tau, \tau+\Delta\tau]$ trophic class for the reference situation (unexploited or current ecosystem)	Mass (tonne)
B^*_τ	Accessible biomass in the $[\tau, \tau+\Delta\tau]$ trophic class	Mass (tonne)
$\Phi(\tau)$	Biomass flow at trophic level τ	Mass·time ⁻¹ (t·year ⁻¹)
Φ_τ	Mean biomass flow in the trophic class $[\tau, \tau+\Delta\tau]$	Mass·time ⁻¹ (t·year ⁻¹)
Φ^*_τ	Accessible trophic flow in trophic class $[\tau, \tau+\Delta\tau]$	Mass·time ⁻¹ (t·year ⁻¹)
P_τ	Production in trophic class $[\tau, \tau+\Delta\tau]$	Mass·TL·time (t·TL·year ⁻¹)
Ψ_τ	Total loss rate of biomass flow in trophic class $[\tau, \tau+\Delta\tau]$	TL ⁻¹
μ_τ	Natural loss rate of biomass flow in trophic class $[\tau, \tau+\Delta\tau]$	TL ⁻¹
μ^*_τ	Net natural loss rate of the accessible biomass flow	TL ⁻¹
φ_τ	Fishing loss rate of biomass flow in trophic class $[\tau, \tau+\Delta\tau]$	TL ⁻¹
φ^*_τ	Fishing loss rate of the accessible biomass flow	TL ⁻¹
M_τ	Natural mortality in trophic class $[\tau, \tau+\Delta\tau]$	1/time (year ⁻¹)
$M_{ref,\tau}$	Natural mortality in trophic class $[\tau, \tau+\Delta\tau]$ for the reference situation (unexploited or current ecosystem)	1/time (year ⁻¹)
$M_{0\tau}$	Non predation natural mortality in trophic class $[\tau, \tau+\Delta\tau]$	1/time (year ⁻¹)
$M_{2\tau}$	Predation natural mortality in trophic class $[\tau, \tau+\Delta\tau]$	1/time (year ⁻¹)
F_τ	Fishing mortality in trophic class $[\tau, \tau+\Delta\tau]$	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 move from trophic level τ to trophic level $\tau+\Delta\tau$	Time (year)
a, b	Coefficient of the general empirical model of flow kinetic	-
α_τ	Coefficient of top-down control	-
γ	Shape parameter of the predator/preys relationship	-
β	Coefficient of biomass input-control	-
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)

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

1.3.1. Biomass = flow divided by speed

In hydrology, it is well known (and easy to understand) that the water quantity which is present at any moment into a section of a water jet (Fig. 3) can be calculated as the flow (e.g., in $l \cdot s^{-1}$) divided by the flow speed ($m \cdot s^{-1}$), multiplied by the length of the section considered (m). Similarly, the biomass $B\tau$, present at every moment in a given trophic class of width $\Delta\tau$ (here: 0.1 TL), can be deduced from both the biomass flow and the flow kinetics. Thus, the **biomass equation** is:

$$B\tau = \frac{\Phi\tau}{\Delta\tau/\Delta t} \cdot \Delta\tau \quad \dots 2)$$

where $\Phi\tau$ 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.

This equation is expressed for a trophic class, and is derived from the discrete approximation of a continuous process. On one hand, it may be deduced from the continuous formulation used in flux physics:

$$\Phi(\tau) = B(\tau) \cdot \frac{d\tau}{dt} \quad \dots 3)$$

where $\Phi(\tau)$ is the biomass flow at trophic level τ ; $B(\tau)$ is a density of biomass per trophic level (at trophic level τ); and $d\tau/dt$ is the exact value of the flow speed at trophic level τ .

$$\text{On the other hand: } B\tau = \int_{\tau}^{\tau+\Delta\tau} B(\tau) \cdot d\tau \quad \dots 4)$$

and replacing (3) into (4) leads to (2).

From equation (2), we may also infer that:

$$B\tau = \Phi\tau \cdot \Delta t \quad \dots 5)$$

where Δt is the mean time required by a unit of biomass to move from trophic level τ to $\tau+\Delta\tau$.

Finally, equations (3) and (5) are only different forms of equation (2), i.e., the first main equation of the trophic level based model. It implies that the biomass distribution by trophic level can be deduced from two functions, one considering the biomass flow, the other related to flow kinetics. The next step is therefore to elaborate on these two related equations.

1.3.2. Biomass flow equation

Due to natural losses occurring during trophic transfers (non-predation mortality, respiration, egestion and excretion), the biomass flow expressed as a function of the trophic level should exhibit a declining trend. Only the lowest trophic levels, where significant input may occur due to direct grazing on primary production (see above), can be an exception to this very general rule. For all other trophic levels, the trophic flow will decrease. Adding to this natural trend, 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 thus be formalized by defining a total loss rate of biomass flow $\psi(\tau)$ equal to:

$$\psi(\tau) = \mu(\tau) + \varphi(\tau) = - \frac{1}{\Phi(\tau)} \cdot \frac{d\Phi(\tau)}{d\tau} \quad \dots 6)$$

where $\mu(\tau)$ is the net natural loss rate of biomass flow, and $\varphi(\tau)$ is the loss rate of biomass flow due to fishing. The loss rates $\psi(\tau)$, $\mu(\tau)$ and $\varphi(\tau)$ are expressed in TL^{-1} . We will later see that $\varphi(\tau)$ is related to

fishing mortality $F(\tau)$. The loss rate parameter $\mu(\tau)$, on the other hand, is not directly related to natural mortality $M(\tau)$.

The rates of flow loss are defined as continuous processes. In practice, however, only mean coefficients per trophic class are used (ψ_τ , μ_τ and ϕ_τ). This does not mean that these rates are supposed to be constant in each class, but only that mean coefficients are sufficient to describe the variability between classes. On the other hand, it does not appear useful to take account of within-class variability.

Based on integration of the differential equation (6), we deduce the **flow equation** which is the second main equation of EcoTroph:

$$\Phi(\tau+\Delta\tau) = \Phi(\tau) \cdot \exp[-(\mu_\tau + \phi_\tau) \cdot \Delta\tau] \quad \dots 7)$$

Equation (7) defines the term $\exp(-\mu_\tau)$ as the transfer efficiency (TE) between trophic levels. Therefore, this equation allows estimation of 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 (which may be estimated using the Catch Trophic Spectrum Analysis, see §3), and an estimate of TE.

Transfer efficiencies between the trophic levels of ecosystems are not straightforwardly estimated, notably because they are not equal to the gross efficiency ($K_1 = \text{production/ingestion}$) of an animal population (Ivlev 1966; Pauly 1986), notwithstanding many authors using estimates of K_1 as substitutes for TE. The Ecopath approach and software, however, allows for the rigorous estimation of TE (Christensen and Pauly 1992), and its application to a number of marine ecosystems showed that TE usually ranges between 0.05 and 0.15, with a mean at 0.10 (Pauly and Christensen 1995), confirming earlier anecdotal evidence (Morowitz 1991).

Additionally, equation (7) leads to an expression of the mean flow Φ_τ through interval $[\tau, \tau+\Delta\tau]$:

$$\Phi_\tau = \frac{1}{\Delta\tau} \cdot \int_{s=0}^{s=\Delta\tau} \Phi(\tau) \cdot \exp[-(\mu_\tau + \phi_\tau) \cdot s] \cdot ds \quad \dots 8)$$

Thus:

$$\Phi_\tau = \Phi(\tau) \cdot \frac{1 - \exp[-(\mu_\tau + \phi_\tau) \cdot \Delta\tau]}{(\mu_\tau + \phi_\tau) \cdot \Delta\tau} \quad \dots 9)$$

1.4. EcoTroph and Ecopath: first comparison

The EcoTroph approach, based on a continuous representation of the trophic flow, differs from the Ecopath model, whose biomass is split between various trophic boxes. In Ecopath, during each time unit, each box generates a biomass production (P) at trophic level τ , of which a part Q is consumed by predators, whose production occurs on average at trophic level $\tau+1$ (Fig. 5). Thus, the production $P(\tau+1)$ constitutes a trophic flow transferred from level τ to level $\tau+1$. It is usually expressed in $t \cdot \text{year}^{-1}$, but it implicitly refers to a one trophic level jump. Thus, seen in continuous perspective, it should be expressed in $t \cdot \text{TL} \cdot \text{year}^{-1}$.

Assuming that transfers mainly result from predation illustrates the strong similarities between EcoTroph and Ecopath. 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). 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. Therefore, from this analogy, it follows that the production of the trophic class $[\tau, \tau+\Delta\tau]$ is:

$$P_\tau = \Phi_\tau \cdot \Delta\tau \quad \dots 10)$$

More precisely, this means that the production of a trophic class during one unit of time is proportional to the mean flow passing through the trophic class during that period and to the wide range of the class. Referring not any longer to a trophic class $[\tau, \tau+\Delta\tau]$, but to the exact value τ implies that the flow $\Phi(\tau)$ is in fact a density of production and may be expressed as follows:

$$\Phi(\tau) = -\frac{dP}{d\tau} \quad \dots 11)$$

where the minus sign is consistent with the fact that $P(\tau)$ is a decreasing function of τ .

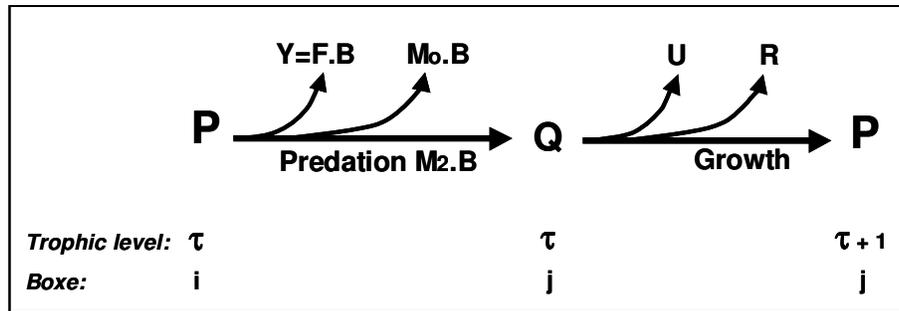


Figure 5 – Schematic representation of the conceptualisation of biomass flow in Ecopath:

The production P of the prey i at trophic level τ is split into three parts: predation ($M_2 \cdot B = Q$), losses due to non-predation mortality ($M_0 \cdot B$) and fisheries catches ($F \cdot B = Y$). Of the amount Q , only a small fraction is transferred by the predator j from trophic level τ to $\tau+1$, due to losses connected with excretion (U) and respiration (R) (see Christensen and Pauly, 1992).

Based on equations (2) and (9), an expression for the flow speed can be deduced:

$$\Delta\tau/\Delta t = (P/B)\tau \quad \dots 12)$$

where $(P/B)\tau$ is the mean P/B ratio in the trophic class $[\tau, \tau+\Delta\tau]$.

Therefore, the P/B ratio applying to a specific box in Ecopath can be seen, in practice, as a measure of the average speed of the trophic flow that passes through that box.

More generally, the homologies between Ecopath and EcoTroph help us better understand aspects of both models. In particular, trophic flows 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 first of these four processes is taken into account in the flow equation (7) using the fishing loss rate parameter ϕ_τ , which is related to fishing mortality F_τ (see §1.6). The three others are implicit in the natural loss rate parameter μ_τ .

On Figure 5, the upward arrows (Y , $M_0 \cdot B$, U and R) are related to loss terms, while the terms F , M_0 , U/B and R/B refer to loss rates. Formally, using standard equations of population dynamics, this implies:

$$P_{\tau+1} = P_\tau \cdot \exp[-(F+M_0+U/B+R/B) \cdot \Delta t] \quad \dots 13)$$

which, combined with (7) and (12), leads to:

$$\mu = \frac{M_0 + U/B + R/B}{\Delta\tau/\Delta t} = \frac{M_0 \cdot B + U + R}{P} \quad \dots 14)$$

In other words, natural loss rate, and thus trophic efficiency (TE), are not directly linked to natural mortality. Rather, TE is an aggregate of three processes: non-predation mortality (or 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.

Table 2 – A first comparison between key features of EcoTroph and Ecopath

	Ecopath	EcoTroph	Link equations
General structure			
Model structure	Aggregation of species into 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	TLs	--
Relationship between main parameters			
	Production (P)	Biomass flow (Φ)	$\Phi = -dP/d\tau$, or $P = \Phi \cdot \Delta\tau$
	Biomass (B_i)	Biomass ($B\tau$)	$B = \Phi / (P/B)$
	Productivity (P/B)	Flow speed ($d\tau/dt$)	$P/B = d\tau/dt = \Delta\tau/\Delta t$
	Fishing mortality (F)	Fishing loss rate ($\phi\tau$)	$F\tau = \phi\tau \cdot \Delta\tau/\Delta t$
	'cutting the pie' *	Natural loss rate (μ)	$\mu = (M_0 \cdot B + R + U)/P$

* In Ecopath the production and the consumption of each box are split into various terms (this is what Villy Christensen calls 'cutting the pie'), while EcoTroph aggregates three terms (non-predation mortality, respiration and excretion) into one parameter, μ .

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. This is the reason why it must be seen as complementary, and not as alternative to Ecopath.

1.5. Flow kinetic equation

1.5.1. Theoretical approach

Globally, the speed of the trophic flow should be a decreasing function of 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 (e.g., rabbitfish of the Family Siganidae, which feed predominantly on seagrass), should constitute exceptions to this general rule. Thus, high metabolism, fast turn-over and short life cycles induce fast trophic transfers from the lowest 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. Thus, trophic kinetics should be particularly fast in warm-water ecosystems.

To facilitate use of EcoTroph, an empirical model was developed by Gascuel *et al.* (2008b) for predicting the speed of the trophic flow from trophic level and temperature. The model was fitted to 1,718 data triplets (P/B, TL and temperature, in °C) extracted from 55 well documented Ecopath models, assuming that the P/B ratios can be used to represent flow speed (see above). This model, expressing the $\Delta\tau/\Delta t$ ratio as a function of trophic level (τ) and mean water temperature (θ), has the form:

$$\Delta\tau/\Delta t = 20.2 \cdot (\tau^{-3.26}) \cdot \exp(0.041 \cdot \theta) \quad \dots 15)$$

Equation (15) predicts that, depending on water temperature, the speed of the trophic flow ranges from 2-7 TL \cdot year $^{-1}$ for secondary producers to 0.1-0.3 TL \cdot year $^{-1}$ for top predator groups (Fig. 6a). Figure 6a also illustrates that the predicted speeds vary by a factor of about 3 between cold (5 °C) and warm (25°C) waters.

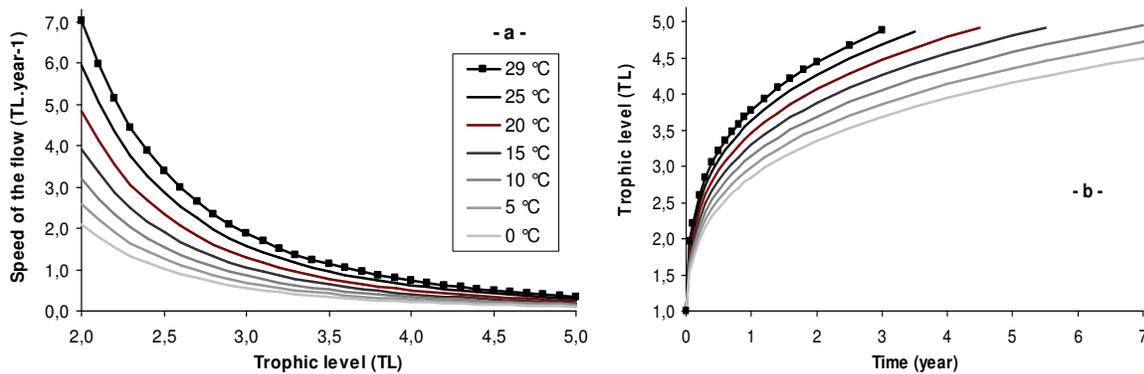


Figure 6 - Theoretical model of flow kinetics (from Gascuel *et al.*, 2008b): (a) speed of the flow as a function of trophic level; (b) relationship between time and trophic level.

In a given ecosystem, with a given mean water temperature, the speed of the trophic flow is simply a power function of trophic level. Thus, in a continuous formulation, equation (13) can be re-expressed as:

$$\frac{d\tau}{dt} = a \cdot \tau^{-b} \quad \dots 16)$$

Equation (16) allows estimation of the speed of the flow, and based thereon, the biomass present under steady-state conditions at each trophic class ($\Delta\tau$).

$$\text{Equations (16) can also be expressed as:} \quad dt = \frac{1}{a} \cdot \tau^{-b} \cdot d\tau \quad \dots 17)$$

Integration leads to an explicit relationship between time t and trophic level τ :

$$t = \frac{1}{a \cdot (b+1)} \cdot \left[\tau^{b+1} - 1 \right] \quad \dots 18)$$

wherein t may be interpreted as the mean time required by a unit of biomass to move from trophic level 1 (primary producers) to trophic level τ . In other words, it defines the mean age of biomass present at trophic level τ . The reciprocal of this expression leads to equation (19):

$$\tau = \left[1 + a \cdot (b+1) \cdot t \right]^{\frac{1}{b+1}} \quad \dots 19)$$

where τ is the mean trophic level reached, at time t , by a unit of biomass fixed in the food web at time zero.

Based on parameters of equation (15), we also have:

$$\tau = [1 + 86.0 \cdot \exp(0.041 \cdot \theta) \cdot t]^{0.235} \quad \dots(20)$$

This expression is the empirical representation of the theoretical schema presented as Figure 2, and also characterizes the kinetics of trophic flows at different water temperatures (Fig. 6b). For instance, Equation (20) indicates that the mean age of the biomass present at trophic level 4 is 3.5 years in cold water and 1.5 years in warm water (i.e., 5 and 25°C respectively). Or, put differently: in 2 years, the biomass 'entering' the food web at trophic level 1 reaches trophic level 3.5 in cold waters, and level 4.3 in warm water.

1.5.2. Equation of the flow kinetics: practical approach in a reference situation

The empirical model presented here as Equation (15) provides estimates of $\Delta\tau/\Delta t$ for marine ecosystems in general. However, in specific ecosystems, the speed of the flow depends on the species composition encountered at each trophic level. This is so because each (group of) 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, in a specific ecosystem, have the exact same shape as the monotonously decreasing curves in Figure 6.

In practice, the speed of the flow $\Delta\tau/\Delta t$ must be estimated for each trophic class [$\tau, \tau+\Delta\tau$]. This can be done using four different methods:

- Using P/B ratios estimated by field measures of P and B (see e.g., Winberg 1971), or from empirical equations to predict P/B ratios as a function of easy-to-estimate parameters, such as body weight, temperature and taxonomic affinities (see e.g., Brey 2001). Such equations are commonly used in the construction of Ecopath models and may be completed by equations proposed in Gascuel *et al.* (2008b)¹. In that case, P/B values are estimated by species or ecological group; a unique curve expressed as a function of the trophic level then derived, using an aggregation procedure (see the 'ET-Smooth' procedure in Part II of this report);
- Using P/B ratios derived from a previous Ecopath model (see 'ET-Transpose' procedure in Part II);
- Using the ratio between the biomass flow and the biomass (from equation 2, i.e., using $\Delta\tau/\Delta t = \Phi\tau/B\tau\Delta\tau$), when both of these parameters are known; and
- Using the general empirical model (equation 15) when no other value is available. Such estimates should be subsequently corrected, using literature data or expert knowledge.

¹ Under equilibrium assumptions, and for most growth functions (including the von Bertalanffy growth function), the identity hold that $P/B=Z$ (Allen, 1971). Thus, P/B can be estimated (as Z) from standard methods in fisheries science, i.e., catch curves (Beverton and Holt 1957; Ricker 1975), length-converted catch curves (Pauly 1998), or mean lengths (Beverton and Holt 1956; Pauly 1998) in exploited stocks, and from unexploited stocks (as M) from various empirical equations, notably Pauly's (1980) approximation, i.e., $M = 0.985 \cdot K^{0.6543} \cdot L_{inf}^{-0.279} \cdot \theta^{0.4634}$.

Gascuel *et al.* (in press) propose three additional equations:

. The first is based on the same model as equation (15), but was fitted for fish only, using 162 unexploited fish stocks for which the required parameters ($P/B=M, \tau, \theta$) were available in FishBase; this model is expressed as follows: $P/B = 2.31 \cdot \tau^{-1.72} \cdot \exp(0.053 \cdot \theta)$, with $R^2 = 0.37$.

. The second, also for fish, was fitted on the same dataset; it links P/B, the trophic level and the von Bertalanffy growth coefficient as follows: $P/B = 2.56 \cdot \tau^{-0.78} \cdot K^{0.70} \cdot \exp(0.020 \cdot \theta)$, with $R^2 = 0.68$; simplified forms without τ or θ are also provided, including the simple linear relationship: $P/B = 1.89 \cdot K$ ($R^2 = 63$).

. The third, applying to any taxon, is presented here as Equation (15).

1.5.3. Change in the flow kinetic due to fishing

In the previous version of EcoTroph, the flow kinetic was assumed an ecological characteristic not related to ecosystem status and fishing intensity. Comparison with Ecopath suggests that this assumption is not valid, as indicated by Figure 5. The speed of the trophic flow is related to predation processes, on the left part of the graph. These processes imply that fishing mortality F , non-predation mortality M_0 , and predation mortality M_2 determine the average time a given organism lives. This time can be a few days, month, or even years. Conversely, the processes involved in the right part of the graph (Fig. 5) are very fast and we can assume that the time required by a consumer to transform ingested food (Q) into production (P) is negligible in term of flow kinetics.

In other words, when fishing mortality increases, the life expectancy of individual consumers 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, and we have:

$$\frac{\Delta\tau}{\Delta t} = F + M \quad \dots 21)$$

Equation (21) is consistent with Allen's relationships (1971), i.e., it shows that under equilibrium assumption, the P/B ratio (which equals $F+M$), is a measure of the speed of the flows equal to total mortality Z (see footnote 1).

1.6. Top-down control and biomass input control

The previous equations are sufficient for analysing the impact of trophic efficiencies and flow kinetics on the biomass of an ecosystem at various trophic levels. However, examination of the effect of fishing (or other exogenous disturbances) required the introduction of two additional equations: one expressing the top-down controls that may exist in some ecosystems and/or for some trophic levels, the other dealing with the impact of total biomass reduction on recycling by the microbial loop.

1.6.1. The top-down control equation

The biomass flow equation (7) implies that changes occurring to a given trophic level impact the higher trophic levels. This is a form of 'bottom-up' control, linking the abundance of predators to the abundance of their prey. Conversely, 'top-down control' implies that the abundance of prey is determined by the abundance of predators. While bottom-up control is implicit in EcoTroph, accounting for 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 (equation 21), top-down control can operate only if at least a fraction of the natural mortality of prey depends on predator abundance, i.e.,

$$M\tau = \alpha\tau \cdot M_{ref,\tau} \cdot \left(\frac{B_{pred}}{B_{pred,ref}} \right)^\gamma + (1-\alpha\tau) \cdot M_{ref,\tau} \quad \dots 22)$$

This leads to the top-down control equation ²:

$$\left(\frac{\Delta\tau}{\Delta t} \right)_\tau = \left(\frac{P}{B} \right)_\tau = \alpha\tau \cdot M_{ref,\tau} \cdot \left(\frac{B_{pred}}{B_{pred,ref}} \right)^\gamma + (1-\alpha\tau) \cdot M_{ref,\tau} + F\tau \quad \dots 23)$$

² In Gascuel (2005), top-down control was assumed to result from the coefficient of natural flow loss ($\mu\tau$) depending on predator abundance. Deeper reflection suggests, however, that this coefficient is in fact not related to the predation process itself, but only to the losses which occur during transfers (see §1.5.3 above). Conversely, the kinetic of the flow depends on the life expectation of each animal (as a prey) and thus on abundance of predators. Therefore, top-down control should impact the speed of the flow $\Delta\tau/\Delta t$ rather than the natural loss rate $\mu\tau$.

where:

- $(\Delta\tau/\Delta t)_\tau$ and $(P/B)_\tau$ are two expressions of the speed of the trophic flow at trophic level τ ;
- $M_{ref,\tau}$ is the natural mortality at trophic level τ , for a given state of the ecosystem, this state being used as reference (which can be either the unexploited state, or the present situation; see below). This implies that the speed of the flow is expressed in relation to the reference state;
- B_{pred} and $B_{pred,ref}$ are the biomass of predators in any state and in the reference state respectively. The ratio $B_{pred}/B_{pred,ref}$ thus defines the relative change in abundance of predators relative to the reference state. That means that 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) expresses the fraction of the natural mortality $M_{ref,\tau}$ which depends on predator abundance. It may theoretically vary between 0 and 1 and defines the intensity of the top-down control that affects the trophic level τ . The coefficient $\alpha = 0$ pertains to a situation dominated by bottom-up processes, and where changes in predator abundance have no effects on prey (in that case: $\Delta\tau/\Delta t = M_{ref} + F$). Conversely, a coefficient $\alpha = 1$ defines a completely top-down controlled situation, where the speed of the flow strongly depends on predator abundance ³;
- 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, similar to type II functional response (Holling 1965). More to the point, this relationship allows for direct comparison with the vulnerability parameter of foraging arena theory (Walter and Juanes 1993; Walters *et al.* 1997) built into Ecosim (see footnotes 4).

For practical use, equation (23) may be rearranged in the following form (for the sake of simplicity, τ indices are here omitted):

$$\frac{\Delta\tau}{\Delta t} = \frac{P}{B} = M_{ref} \cdot \left[1 + \alpha \cdot \frac{B_{pred}^\gamma - B_{pred,ref}^\gamma}{B_{pred,ref}^\gamma} \right] + F \quad \dots 24)$$

However, the M_{ref} parameter is usually not known; an alternative equation may then be used:

$$\frac{\Delta\tau}{\Delta t} = \frac{P}{B} = \left[\left(\frac{P}{B} \right)_{ref} - F_{ref} \right] \cdot \left[1 + \alpha \cdot \frac{B_{pred}^\gamma - B_{pred,ref}^\gamma}{B_{pred,ref}^\gamma} \right] + F \quad \dots 25)$$

Therefore, if the speed of the flow has been estimated for the reference state, equation (25) allows its computation for all other states, for any values of the α and γ coefficients, given an estimate of predator biomass obtained, e.g., from equations (2) and (7). As equation (2) also includes flow speed, the solution must involve an iterative procedure, starting with the reference values of $(P/B)_{ref}$, estimating $\Delta\tau/\Delta t$, then estimating B for each iteration, and continue until stabilisation.

Here also, there is a deep analogy with the expression of vulnerability in Ecosim, and an explicit relationship between coefficients used in the two models can be demonstrated, at least under certain

³ The ratio between predation mortality (M_2) and total natural mortality (M) may be viewed as a first estimate of the alpha coefficient. However, according to foraging arena theory (Walter and Juanes 1993), both M_2 and M change with prey biomass, thus complicating the relationship between α and M_2/M .

conditions 4. More importantly, this indicates that the top-down equation has, in the EcoTroph model, the same purpose as the vulnerability used in Ecosim, i.e., both define the functional relationship between prey and predators.

1.6.2. The equation of biomass input-control

A second important process determines ecosystem functioning, i.e., the biomass flow introduced into the system at trophic level 2. This flow is partly due to recycling of detritus and to recruitment. Thus, we may reasonably assume that it depends, in part at least, on the biomass of whole system. This process introduces a feedback effect on secondary production, called here 'biomass input-control'. We also assume that top-down control may occur between trophic levels 1 and 2. Therefore, according to equation (7), computation may be initialised using:

$$\Phi(2) = \Phi(1) \cdot \exp(-\mu\tau) \quad ..26)$$

and

$$\Phi(1) = (1 - \beta) \cdot \Phi_{ref}(1) + \beta \cdot \Phi_{ref}(1) \cdot \frac{B_{tot}}{B_{tot,ref}} \quad ...27)$$

where β is a coefficient expressing the extent of biomass input-control, $\Phi_{ref}(1)$ is the value of biomass flow at trophic level 1 in the reference state, and B_{tot} and $B_{tot,ref}$ are the total biomasses (for $\tau \geq 2$) in the current and reference states, respectively.

Therefore, a value $\beta = 0$ refers to an ecosystem where all secondary production originates from grazing on primary producers, detritus recycling and recruitment being insignificant in terms of biomass input. We shall call such ecosystems 'primary producers-based' ecosystems. Conversely, a value of β closer to 1 corresponds to an ecosystem where detritus and/or recruitment contribute a major part of the biomass input. We shall refer to such ecosystems as a 'detritus-based' ecosystems.

⁴ The function used to express top-down control in EcoTroph and in Ecosim can be compared.

In EcoTroph, for $\gamma = 1$, equation (22) leads to: $\frac{M}{M_{ref}} = \alpha \cdot \frac{B_{pred}}{B_{pred,ref}} + 1 - \alpha$

In Ecosim, $M_2 = \frac{a \cdot V \cdot B_{pred}}{B_{prey}}$ and at equilibrium (Walters *et al.*, 1997): $V = \frac{v \cdot B_{prey}}{2 \cdot v + a \cdot B_{pred}}$

where v is the Ecosim vulnerability coefficient, B_{prey} is the total prey biomass, V is the biomass of prey vulnerable to predators, and a is constant. Thus:

$$M_2 = \frac{a \cdot v \cdot B_{pred}}{2 \cdot v + a \cdot B_{pred}} \quad \text{and} \quad M_{2ref} = \frac{a \cdot v \cdot B_{pred,ref}}{2 \cdot v + a \cdot B_{pred,ref}}$$

If we assume that $M/M_{ref} \approx M_2/M_{2ref}$ (which corresponds to the assumption that the non predation mortality M_0 either changes like M_2 or is negligible), then replacing M and M_{ref} into the first equation by these two expressions of M_2 and M_{2ref} leads, after simplification, to:

$$\alpha \approx \frac{2 \cdot v}{2 \cdot v + a \cdot B_{pred}} = \frac{2 \cdot V}{B_{prey}}$$

In Ecosim, in the case of complete top-down control, vulnerability v tends to infinity, and thus the vulnerable biomass tends to $V = B_{prey}/2$. This equation implies that α is then close to 1 -which is the value we assumed for EcoTroph; therefore the two approaches appears consistent. In the case of complete bottom-up control, in Ecosim, $v = 1$, corresponding to $\alpha = 0$ in EcoTroph (what indicates that the biomass vulnerable to predators tends to zero).

1.7. Catch equation and accessibility

1.7.1. The catch equation

Catches per trophic class Y_τ are deduced from previous equations. They can be expressed as the integration over time of instantaneous catches, i.e.,

$$Y_\tau = \int_{t=0}^1 \frac{dY}{dt} \cdot dt = \int_{t=0}^1 \frac{\varphi_\tau}{\varphi_\tau + \mu_\tau} \cdot \Delta\Phi \cdot dt \quad \dots 28)$$

where $\Delta\Phi$ is the flow loss occurring in the whole trophic class $[\tau, \tau + \Delta\tau]$; thus catches are equal to the fraction of flow loss due to the fishery.

Alternatively, catches per trophic class can be expressed as the integration over trophic level of catch density per trophic level $dY/d\tau$:

$$Y_\tau = \int_{\tau}^{\tau + \Delta\tau} \frac{dY}{d\tau} \cdot d\tau = \int_{s=0}^{\Delta\tau} \varphi_\tau \cdot \Phi(\tau + s) \cdot ds \quad \dots 29)$$

where equation (6), which defines the fishing loss rate φ_τ , is used to express catch density.

Integration of (22) or (23) both leads to the catch equations⁵, which can be expressed with regard either to flow φ_τ , or biomass B_τ :

$$Y_\tau = \varphi_\tau \cdot \Phi_\tau \cdot \Delta\tau \quad \dots 30a)$$

or

$$Y_\tau = \varphi_\tau \cdot B_\tau \cdot \frac{\Delta\tau}{\Delta t} \quad \dots 30b)$$

Equation (30) also allows specifying the relationship that exists between the fishing loss rate of biomass flow φ_τ and the fishing mortality F_τ occurring in a trophic class. Indeed, by definition F_τ is equal to the ratio Y_τ/B_τ . Thus:

$$F_\tau = \varphi_\tau \cdot \frac{\Delta\tau}{\Delta t} \quad \dots 31)$$

Equation (31) shows that a constant fishing mortality F_τ over all trophic levels would imply increasing fishing loss rates φ_τ for the higher trophic levels, due to decreasing speeds of the flow.

⁵ Regarding equation (28), by definition the flow loss is: $\Delta\Phi = \Phi(\tau) - \Phi(\tau + \Delta\tau)$

Thus: $\Delta\Phi = \Phi(\tau) \cdot [1 - \exp(-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau)]$, which doesn't depend on time.

Therefore, replacing in equation (28) implies: $Y_\tau = \frac{\varphi_\tau}{\varphi_\tau + \mu_\tau} \cdot \Phi(\tau) \cdot [1 - \exp(-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau)]$.

According to equation (9), this leads to $Y_\tau = \varphi_\tau \cdot \Phi_\tau \cdot \Delta\tau$, which is equation (30a).

As for equation (29), according to equation (7): $Y_\tau = \int_{s=0}^{\Delta\tau} \varphi_\tau \cdot \Phi_\tau \cdot \exp(-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau) \cdot ds$

Then: $Y_\tau = \frac{\varphi_\tau}{\mu_\tau + \varphi_\tau} \cdot \Phi_\tau \cdot [1 - \exp(-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau)]$. Replacing by equation (9) also leads to equation (30a)

Finally, the catch equation can be expressed using the parameters of Ecopath:

$$Y_{\tau} = \varphi_{\tau} \cdot P_{\tau} = \varphi_{\tau} \cdot B_{\tau} \cdot (P/B)_{\tau} = F_{\tau} \cdot B_{\tau} \quad \dots 32)$$

Equation (32) also means that the fishing loss rate φ_{τ} is in fact the ratio between catch and production, while the fishing mortality F_{τ} is the ratio between catch and biomass.

1.7.2. Accessibility and catch simulations

For ecological or technological reasons (the latter sometimes reflecting the marketability of products), only a fraction of the ecosystem biomass is usually accessible to fisheries. Thus, using the catch equation (30) as if all the biomass could be harvested leads to unrealistic simulations.

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 the trophic class $[\tau, \tau + \Delta\tau]$. This biomass fraction will be referred as $B^{*\tau}$ (with $B^{*\tau} = B_{\tau} \cdot S_{\tau}$). As we shall see later (in §3), in practice, the selectivity coefficient S_{τ} and therefore the accessible biomass $B^{*\tau}$ can be estimated for all trophic levels using Catch Trophic Spectrum Analysis (see below). On the other hand, a logistic curve, frequently used in selectivity studies (see e.g., Gayanilo *et al.* 1996), will be used for S_{τ} in theoretical simulations, to mimic the increase of accessibility, from low values at low trophic levels to full accessibility at higher trophic levels.

We assume that the flow kinetics is similar whether the biomass is accessible or not. Then, based on the selectivity and the accessible biomass in a reference state (either in the unexploited ecosystem or the current state), we can infer new parameters and equations:

- The reference accessible trophic flow is given by:

$$\Phi^{*ref,\tau} = \Phi_{ref,\tau} \cdot S_{ref,\tau} \quad \dots 33)$$

- The net natural loss rates of the accessible biomass flow are derived from the reference values using the inverse of equation (7):

$$\mu^{*\tau} = \text{Ln} \left(\frac{\Phi^{*ref,\tau}}{\Phi^{*ref,\tau+\Delta\tau}} \right) \cdot \frac{1}{\Delta\tau} - \varphi^{*ref,\tau} \quad \dots 34)$$

where $\varphi^{*ref,\tau} = \frac{\Phi_{ref,\tau}}{S_{ref,\tau}}$ is the fishing loss rate of the accessible biomass in the reference situation.

- This allows simulation of the accessible biomass flow, for any value of the fishing loss rate $\varphi^{*\tau}$. The computations are initialised by:

$$\Phi^{*2} = \Phi^{*ref,2} \cdot \frac{\Phi_2}{\Phi_{ref,2}} = \Phi_2 \cdot S_{\tau} \quad \dots 35)$$

$$\text{and then:} \quad \Phi^{*\tau+\Delta\tau} = \Phi^{*\tau} \cdot \exp[-(\mu^{*\tau} + \varphi^{*\tau}) \cdot \Delta\tau] \quad \dots 36)$$

The logistic selectivity curve we use implies that the fraction of accessible biomass and flow increases from low values to the highest targeted trophic levels. As a consequence, the term $\mu^{*\tau}$, expressing the flow loss rate, will exhibit negative values, as it pertains to 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 ‘recruitment’ into the accessible biomass flow. Indeed, this is analogous to classical fish population dynamics, where the term ‘recruitment’ is used from the transition, or migration of young fish from their shallow nurseries to the adult feeding grounds, where they become accessible to fisheries (see Beverton and Holt 1957)

The μ^*_τ parameters are considered biological features of the exploited species, independently of ecosystem state. According to equation (35), 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 variability affects 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 assume 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.

Based on (30), the simulated catches are:

$$Y_\tau = \varphi^*_\tau \cdot \Phi^*_\tau \cdot \Delta\tau \quad \dots 37)$$

Finally, based on equation (2), the total biomass and the accessible biomass are, respectively:

$$B_\tau = \frac{\Phi_\tau}{\Delta\tau/\Delta t} \cdot \Delta\tau \quad \dots 38a)$$

and

$$B^*_\tau = \frac{\Phi^*_\tau}{\Delta\tau/\Delta t} \cdot \Delta\tau \quad \dots 38b)$$

In such simulations, the effect of increasing fishing mortality on the accessible biomass can be analysed, and the catches calculated. We may, for instance, consider multipliers applied to the coefficient of fishing loss rate $\varphi^*_{\text{ref},\tau}$, or to the fishing mortality F_τ . Total biomass and biomass flow are also simulated. Once again, estimates of trophic flow $\Delta\tau/\Delta t$ and biomass B_τ are dependent on each others, and thus must be estimated using iterative procedures. Note also that the fraction of the biomass that is accessible, and thus the selectivity S_τ , changes with the fishing mortality (see §2 for theoretical simulations, and the ET-Diagnosis procedure in Part II for practical applications).

1.8. From steady-state to time-dynamic modelling

Because the model includes an explicit relationship between trophic level and time, it is quite easy to derive from the steady-state equations presented above a dynamic model that allows fitting to time series or time-dynamic simulations. 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 (such as the natural loss rate, the top-down or biomass input control coefficients) are considered system properties, and assumed to remain constant.

The dynamic model requires some preliminary rearrangement, however. In the steady-state model, all trophic classes have the same $\Delta\tau$ width, 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 different in the time-dynamic model, where we use constant time intervals $\Delta t'$ (conventionally equal to 0.1 year), which correspond to unequal trophic classes $\Delta\tau'$ (Fig. 7), wider at low trophic levels. This ensures that, biomass moves up one trophic class at each simulated time step.

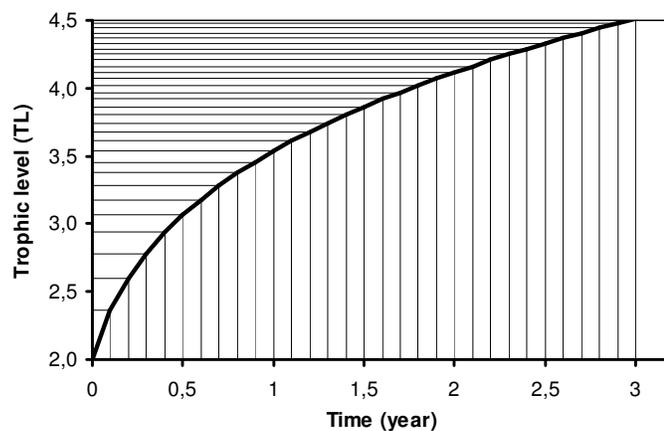


Figure 7 – The flow kinetic relationship (see §1.3.3) allows defining unequal trophic classes, related to constant intervals of time $\Delta t = 0.1$ year

The width of each trophic class is calculated from the flow kinetics equation:

$$\Delta\tau' = \Delta t' \cdot \frac{\Delta\tau}{\Delta t} \quad \dots 39)$$

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

- Computations are initialised each time step by a secondary production $\Phi_{2,t}$, which may be inferred from primary production using the biomass input-control equation (27). Biomass and/or 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 (7), allows estimating the trophic flow by trophic level:

$$\Phi_{\tau+\Delta\tau',t+\Delta t'} = \Phi_{\tau,t} \cdot \exp[-(\mu_{\tau} + \varphi_{\tau,t}) \cdot \Delta\tau'] \quad \dots 40)$$

- The biomass per trophic class is thus:

$$B_{\tau,t} = \frac{\Phi_{\tau,t}}{\Delta\tau'/\Delta t'} \cdot \Delta\tau' \quad \dots 41)$$

- Flow kinetics $\Delta\tau'/\Delta t'$ must be recalculated for each time step using equation (25). Because the flow kinetics and the biomass are interdependent, equations (25) and (41) are successively used in an iterative procedure, until stabilisation (as in the case of the steady-state model).

- Finally, catches are calculated from:

$$Y_{\tau,t} = \varphi_{\tau,t} \cdot \Phi_{\tau,t} \cdot \Delta\tau' = \varphi_{\tau,t} \cdot B_{\tau,t} \cdot \frac{\Delta\tau'}{\Delta t'} \quad \dots 42)$$

The dynamic model may be used in two different ways, either for hindcasting or for simulation and forecast. In the former case, catches per trophic class are usually known for several years and allow estimating times series of fishing loss rate $\varphi_{\tau,t}$ (using the inverse of equation 42), biomass $B_{\tau,t}$ (equation 41), biomass flow $\Phi_{\tau,t}$ (equation 40), fishing mortality $F_{\tau,t}$, etc ⁶.

These time series depend on the parameters used in the model, and especially on the natural loss rate μ_{τ} , the top-down coefficients α_{τ} and γ , and the biomass input-control coefficient β . If observed time

⁶ Hindcasting

Note that the fishing loss rate estimated over the time interval t (from the inverse of equation 42) relates to the model of flow loss between t and $t+\Delta t'$. According to equation (40), it is also used to calculate the mean biomass flow of the time interval, $t+\Delta t'$ from that of interval t . This approximation would be rendered superfluous by using the equations of the Catch Trophic Spectrum Analysis (see §3) and a clear distinction between instantaneous values referring to the beginning of each time interval and mean values related to the whole interval.

Another technical point complicates hindcasting: catches usually refer to yearly intervals while time steps Δt conventionally refer to intervals of 0.1 year. Therefore, simulations can be conventionally conducted using tenths of year and tenths of annual catches (which assumes a lack of seasonality in fishing operations). However, some of previous equations must also be modified when explicitly considering ten time intervals occurring from one year to the next. The Flow equation (40) is thus replaced by:

$$\Phi_{\tau+\sum_{i=1}^{10} \Delta\tau'_i, t+10\cdot\Delta t'} = \Phi_{\tau,t} \cdot \exp \left[\sum_{i=1}^{10} -(\mu_{\tau_i} + \varphi_{\tau_i}) \cdot \Delta\tau'_i \right]$$

where the fishing loss rates are inferred from tenths of the annual catches and the $\Delta\tau'_i$, μ_{τ_i} and φ_{τ_i} refer to the 10 successive trophic class through which the trophic flow passes during a year.

series are available, particularly of biomass, the dynamic model may be fitted to these observed values, by changing one or several of the parameters above.

In the case of forecasts, the fishing mortalities or fishing loss rates are used as input parameters of the dynamic model, while catches and biomass are the outputs. Various exploitation patterns and trends may be simulated, either for the purpose of analysing fishing policies or for exploring the ecological functioning of ecosystems. As in the steady-state model, selectivity coefficients must be considered for realistic simulations of catches. Thus, the same procedure than the one described through equations (33) to (37) is used (but with two indices, one for τ the other for t).

Theoretical forecasts are presented in Paragraph 2, while the ET-Dynamic procedure in Part II includes an application of the past analysis.

2. Learning from the model: some generic rules about ecosystem functioning ⁷

In this section, the EcoTroph model is used to simulate ecosystems, and to assess the ability of the model to mimic the generic rules which seem to regulate the functioning of marine ecosystems, with emphasis on the impact of fishing on ecosystem biomass given various exploitation patterns. The sensitivity of the model to the input parameters is also explored. First, we consider an ecosystem under steady-state conditions; we then move to the time-dynamic version of the model.

2.1. Simulation of a virtual ecosystem: method

2.1.1. Common features

In this simulation of the effect of increasing fishing effort, the unexploited state was used as reference state. The ecosystem used as the reference/unexploited state has the following features.

Initialisation: the value of primary production $\Phi_{ref,1}$ was set at 1000 arbitrary units, such that the biomass flow of the first trophic class considered in the model ($\Phi_{ref,2}$) is equal to 100 when a standard transfer efficiency of 10% is used (see below). This facilitates the analysis of the effect of fishing and sensitivity of the model.

Transfer efficiency: a unique standard value of $\exp(-\mu) = 0.10$ was used for all trophic levels; low and high transfer efficiencies were also simulated using values equal to 0.07 and 0.15 respectively.

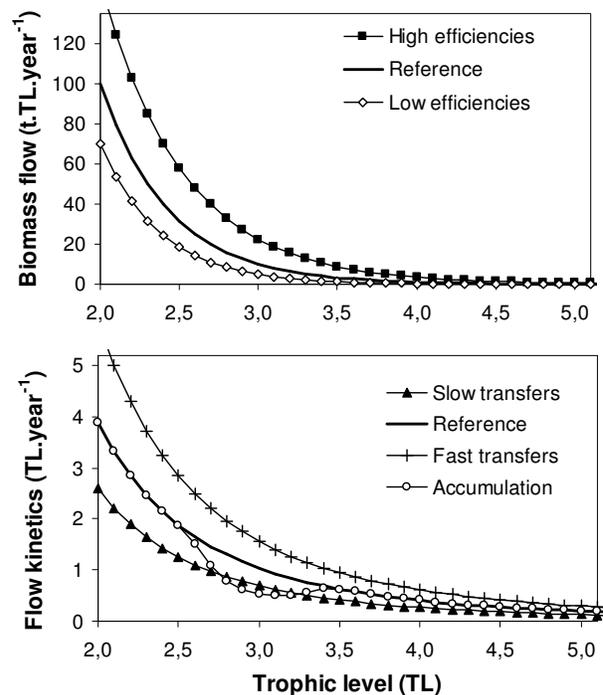


Figure 8 - Biomass flow model (top) and flow kinetics model (bottom) used for simulations of an ecosystem: reference curves and alternatives curves used for sensitivity analyses

⁷ This paragraph is inspired from Gascuel (2005); however, the results and text have been harmonized with the present version of EcoTroph; also some new results were added. The dynamic model is also new.

Therefore, the trophic flow in the reference state can be estimated for all trophic levels using equation (7) (Fig. 8, top).

Flow kinetics: standard flow kinetics were considered, based on the empirical equation (15) for a mean water temperature of 15°C. Slower and faster transfers were also simulated using the same equation with water temperatures of 5 and 25°C, respectively. Additionally, a non-monotonous curve is presented (Fig. 8, bottom, open squares) which simulates flow kinetics of species with few predators (here around trophic level $\tau=3.0$), whose presence should induce a slowing-down of the biomass flow.

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.

Biomass input-control: impact of the biomass input control was explored using two values for the beta coefficient of equation (27): $\beta=0$ defining a 'primary producer-based ecosystem' and $\beta=0.4$ for a 'detritus-based ecosystem'.

2.1.2. Simulation steps

1. First, the sensitivity of the biomass estimates to the input parameters was explored for the case of an unexploited ecosystem. The effects of transfer efficiencies and flow kinetics on the biomass trophic spectrum were also analyzed.

2. Second, the impact of increasing fishing efforts on biomass were simulated based on various selectivity curves. Logistic curves were used, which all implied a selectivity close to 0 for low, and close to 1 for high trophic levels, but with a different transition from low to high (see Figure 9). Each logistic curve may be defined by the steepness of the selectivity and the trophic level where $S\tau$ is equal to 50 %, noted τ_{50} , which, in analogy to the mean length at first capture (Beverton and Holt 1957), may be called 'mean 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 ($\tau_{50} = 3.5$) mean trophic levels at first capture, and to a smaller steepness of the selectivity curve (see Figure 9).

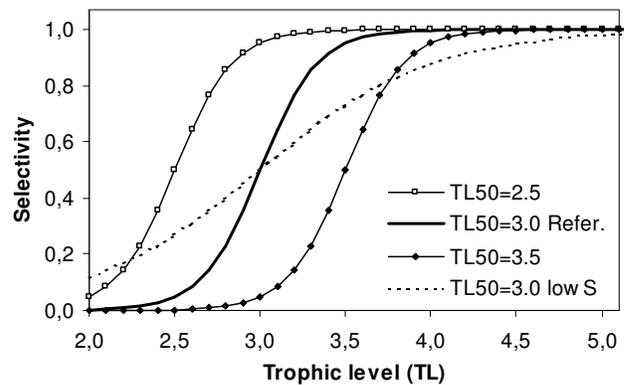


Figure 9 - Selectivity curves used in simulations (see text)

3. For each selectivity curve, biomass and catches were simulated based on the equations defining the steady-state model and using, for all trophic levels, the same fishing mortality 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 2 (strong fishing). Therefore, according to equation (31), the fishing loss rates are:

$$\varphi\tau = \frac{F^* \cdot S\tau}{\Delta\tau/\Delta t} \quad \dots 43)$$

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

$$E' = \frac{\varphi_{moy}}{\varphi_{moy} + \mu} \quad \dots 44)$$

where φ_{moy} is the mean fishing loss rate, conventionally calculated only for high trophic levels, between 3.5 and 5.0.

From the simulated biomass trophic spectra and catch trophic spectra, we 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.

4. 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 normally distributed random factor to the model, based on either of the equations:

$$\Phi_1(t) = \Phi_1 \cdot \mathcal{E}_1(t) \quad \text{or} \quad \mu(t) = \mu \cdot \mathcal{E}_1(t) \quad \dots 45)$$

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 fishing mortality F^* , exploitation started in year 51 and then remained constant. For the two periods (with and without exploitation, 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 $\sigma(\epsilon)$ 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 $\sigma(\epsilon)$ (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 parameter tested as input, 30 simulations were performed and the mean estimate (and the confident limits) of the output parameters were estimated.

2.2. Impact of transfer efficiency and flow kinetics on unexploited biomass

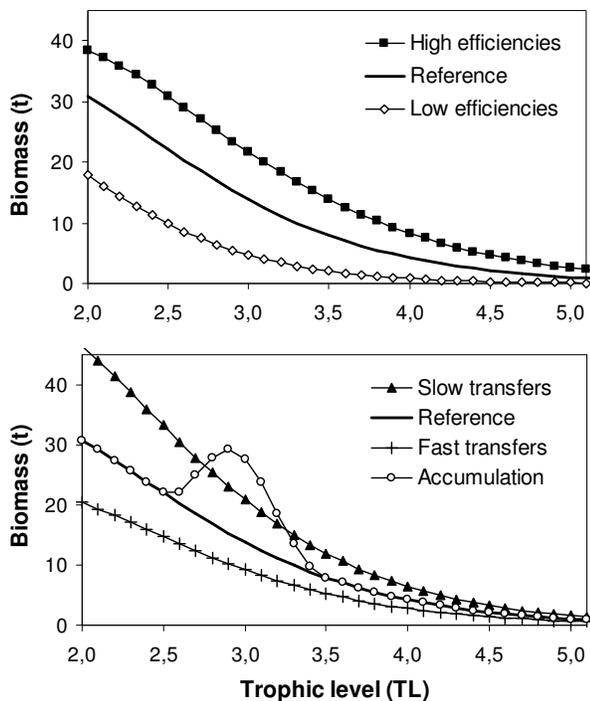


Figure 10 - Impact of the trophic efficiency (top) and the flow kinetics (bottom), on the biomass trophic spectrum, in a virtual unexploited ecosystem

In an unexploited ecosystem, given a certain primary production, the transfer efficiencies and flow kinetics determine the overall amount biomass and its distribution by trophic level. Top-down and biomass input controls have no effect – they become noticeable only when fishing impacts on the biomass. Transfer efficiencies have a direct impact on abundance at all trophic levels (Fig. 10, top). For a given primary production, ecosystems with low transfer efficiencies are characterized by a small biomass, concentrated at low trophic levels. Conversely, high abundance of top predators implies high transfer efficiencies.

Flow kinetics also affects the biomass distribution, especially at the lowest trophic levels (Fig. 10, bottom). 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 biomass accumulation in all trophic classes. This phenomenon of biomass accumulation can be illustrated by simulating a slowing down of the biomass flow at intermediate trophic levels, due, e.g., to the presence of abundant species experiencing little predation ('Accumulation' line on Fig. 10). Flow kinetics thus appear the key to ecosystem functioning and biomass distribution

within the food web. Particularly, they explain the non-monotonous distributions of biomass by trophic level. This differs from biomass flow, which can only exhibit a monotonous decrease, due to flow losses occurring as a result of respiration (and excretion and non-predation mortalities).

2.3. Impact of fishing on biomass

Exploitation affects biomass flow and flow kinetics, eventually affecting ecosystem biomass as well (Fig. 11). Not surprisingly, the higher the exploitation rate is, the more total biomass decreases. Similarly, starting exploitation at lower trophic levels leads to a stronger biomass decrease in the ecosystem as a whole.

More precisely, the impact of fishing differs according to the ecosystem control. In a 'bottom-up ecosystem', exploitation has a large impact on total ecosystem biomass (Fig. 11, top), and may lead to strong biomass depletion when the mean trophic level at first capture is low. For instance, in our simulations, the reduction in total biomass reaches almost 50% for $\tau_{50} = 2.5$. The decrease is especially strong at high trophic levels, because they are affected both by the loss of their prey and the direct impact of the catch. For instance, with the reference selectivity, we obtained a reduction in abundance > 90 % for trophic levels > 3.5. Strong biomass reductions can be caused by low fishing mortality; thus, a value $F=0.2 \text{ year}^{-1}$, for example, induces a two-fold decrease in predators' abundance.

In a 'top-down ecosystem', a fishery-induced decrease in predator abundance leads to a release of predation. This 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. 11, center left). 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 ($\tau_{50} = 3.0-3.5$). In other words, top-down controls increases the resilience of ecosystems to fishing. But this resilience has limits and vanishes when low trophic levels are exploited.

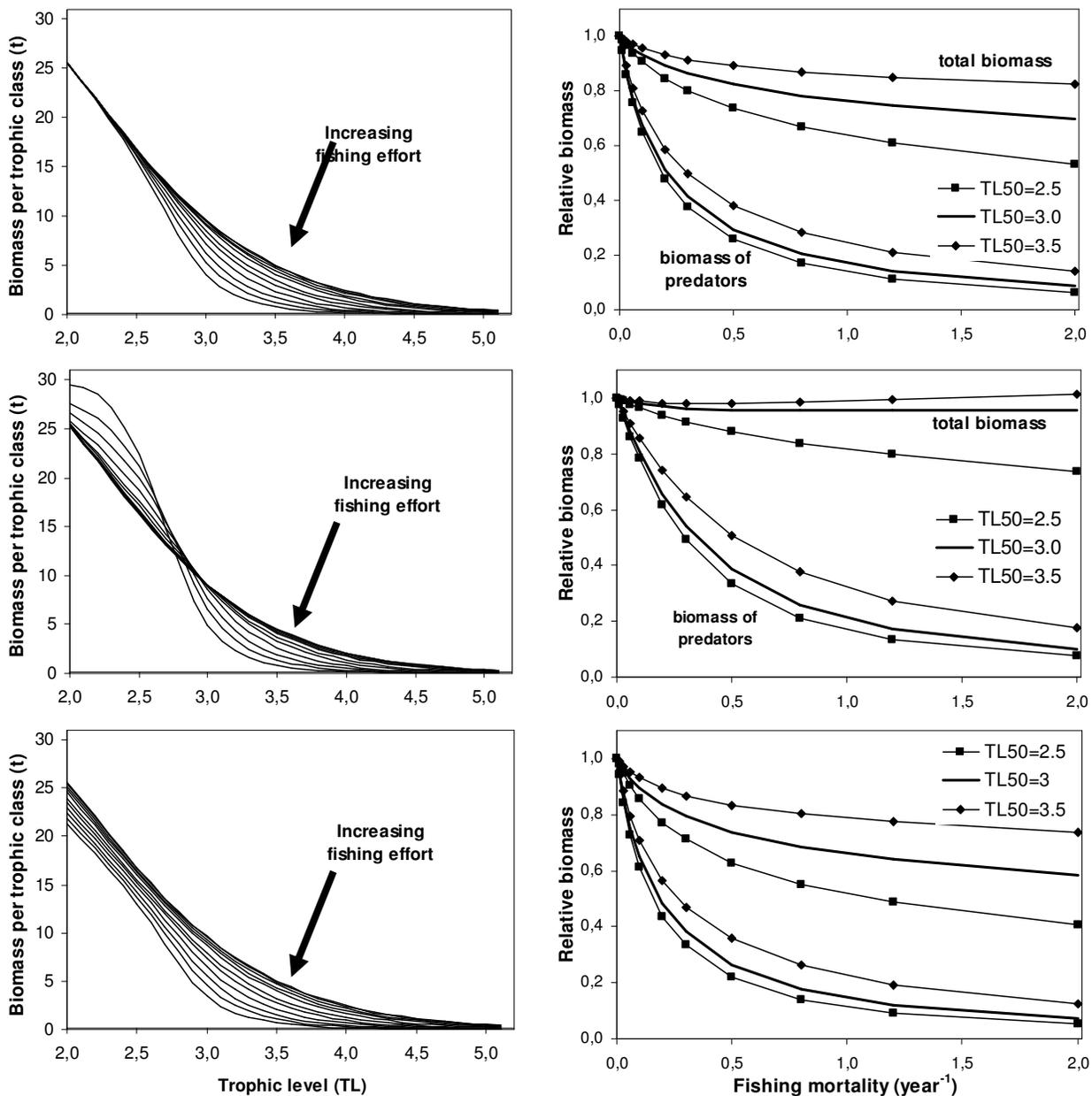


Figure 11 – Impact of increasing fishing mortality on the biomass trophic spectrum (on the left, for the reference selectivity curve) and the total biomass or biomass of predators (on the right, values are standardized to 1, for an unexploited ecosystem). Top panels refer to a ‘bottom-up ecosystem’ primary producers-based; central panels refer to a top-down ecosystem based on primary producers; bottom panels refer to a detritus-based ecosystem.

The accessible biomass, which includes predators, is of course the most affected (Fig. 12, top). Therefore, top-down control has another effect that must be mentioned: 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. 12, bottom). In a way, the sea ‘fills up’ with undesirable species, while the targeted species decline.

When taking into account biomass input-control, the fishing impact on the ecosystem biomass appears to increase, as expected (Fig. 11, bottom). The biomass decrease due to catches implies a reduced detrital biomass; this leads to a smaller input of recycled biomass, which amplifies the initial reduction. Therefore, 'detritus-based' ecosystems are more sensitive to fishing pressure than primary producers-based ecosystems. High exploitation rates associated with a low trophic level of first catches can lead to a collapse of total biomass with, for instance, an almost three times reduction in our simulations.

Nevertheless, such a sensitivity of 'detritus-based' ecosystems is only observed when top-down control does not occur. Indeed, as we saw above, top-down control reduces the impact of fishing. It induces a limited detritus reduction, and thus a weak effect for the biomass input control. Consequently, taking into account both effects, biomass input and top-down controls, leads to results (not shown) which are very close to those obtained without any effects, i.e. for primary production-based and bottom-up control ecosystems. In other words, top-down control appears as an important factor for ecosystem's resistance to fishing. Not only does it appear to induce a direct (albeit partial) compensation between catches and predation release, but also it inhibits the feedback effects that fishing could cause through reduction of biomass recycling.

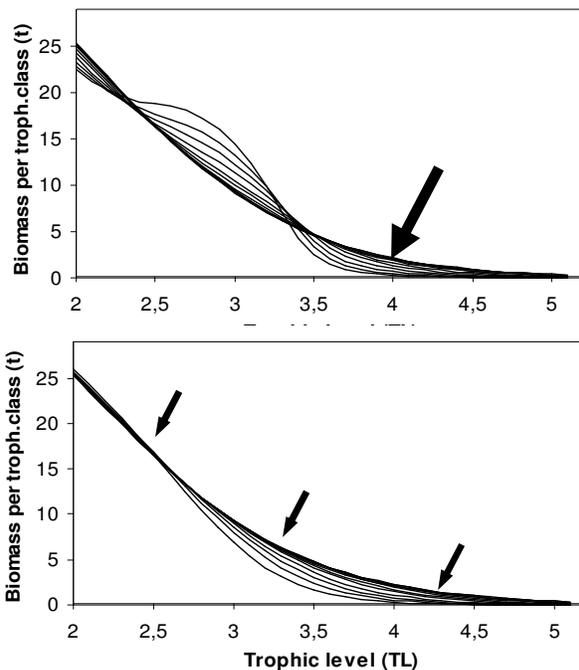


Figure 13 – Simulation of a cascade effect (top) and of a more resilient ecosystem (bottom). See text

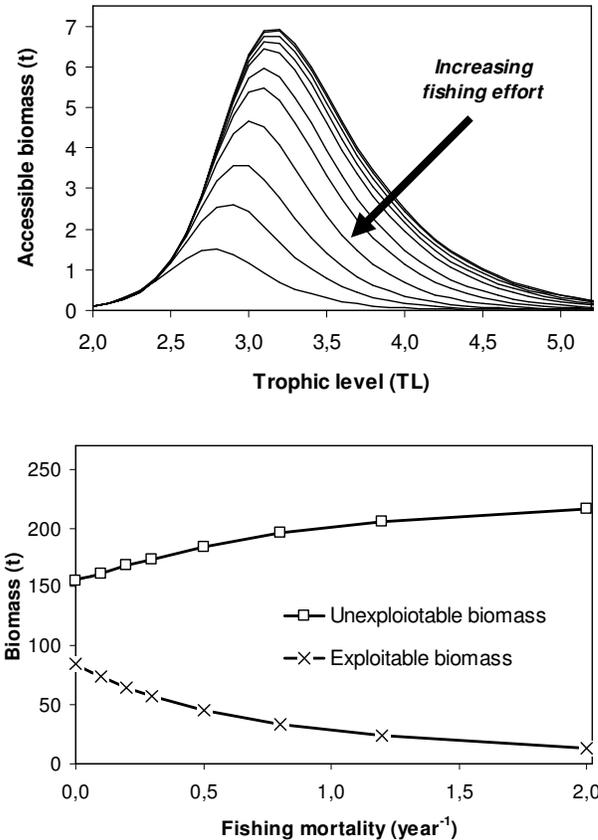


Figure 12 – Changes in the trophic spectrum of the exploitable biomass (top) and in the total exploitable and unexploitable biomass (bottom), in a "Top-down" ecosystem (based on reference values of the parameters).

However, the sensitivity which is observed in ET model for 'detritus based' ecosystem, only refers to steady state conditions. In dynamic simulations, Vasconcellos *et al.* (1997) observed that systems with high-detritus recycling recover better from a shock (such as a strong pulse of fishing).

Additional insights can be obtained from particular fishing patterns. In case of top-down control and if the fishery only targets high trophic levels ($\tau_{50} = 3.5$), a cascade effect is simulated (Fig. 13, top). Due to the decrease of top predators, prey biomass at intermediate trophic levels increases, while the prey of the prey decreases at the lowest trophic levels.

Conversely, a low selectivity, simulating a fishery targeting a large 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 (Fig. 13, bottom). 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 ecosystems⁸. (In fact, this is probably what authors mean when they write about ‘ecosystem-based management’ without defining the term).

The above simulations refer to standard values of transfer efficiencies and flow kinetics parameters. Modifying these values does not affect these results substantially. However, it allows us to analyse their influence on the ecosystem response to fishing; notably, that increasing transfer efficiencies leads to higher fishing impact on total biomass (Table 3). In this case, the natural loss rates are smaller and a given fishing loss rate induces a higher flow exploitation rate ($\phi/(\phi+\mu)$). This 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, 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.

Table 3-Effects of transfer efficiencies and transfer kinetics on ecosystem response to fishing. Total biomass without ($F=0$) and with ($F=2 \text{ year}^{-1}$) fishing, and residual biomass after fishing ($B_{\text{tot}}(F=2) / B_{\text{tot}}(F=0)$), for the various values of efficiency and kinetics parameters. The simulations apply to the reference selectivity curve and a ‘primary production-based’ ecosystem.

Ecosystem control	Parameter value	$B_{\text{tot}} (F=0)$	$B_{\text{tot}} (F=2 \text{ year}^{-1})$	Residual biomass (%)
Effect of transfer efficiencies				
Bottom-up ecosystem	$e^{-\mu v \tau} = 0.07$	200.0	154.0	77.0
	$e^{-\mu v \tau} = 0.10$	253.0	177.1	70.0
	$e^{-\mu v \tau} = 0.15$	357.2	212.1	59.4
Top-down ecosystem	$e^{-\mu v \tau} = 0.07$	191.8	199.1	103.8
	$e^{-\mu v \tau} = 0.10$	240.0	230.0	95.8
	$e^{-\mu v \tau} = 0.15$	331.6	276.0	83.2
Effect of transfer kinetics				
Bottom-up ecosystem	Slow transfers	381.2	252.5	66.2
	Reference	253.0	177.1	70.0
	Fast transfers	167.9	123.9	73.8

2.4. Catch simulations

In bottom-up (model) ecosystems, yields tends towards an asymptote, corresponding to the whole exploitable biomass, i.e., the biomass present (before exploitation) upward of τ_{50} . Nevertheless, because the exploitable biomass, when plotted against fishing mortality, follows a dome-shaped curve (Fig. 12), the catch expressed as a function of exploitation rate is dome-shaped as well (Fig. 14), with the maximum catch tending

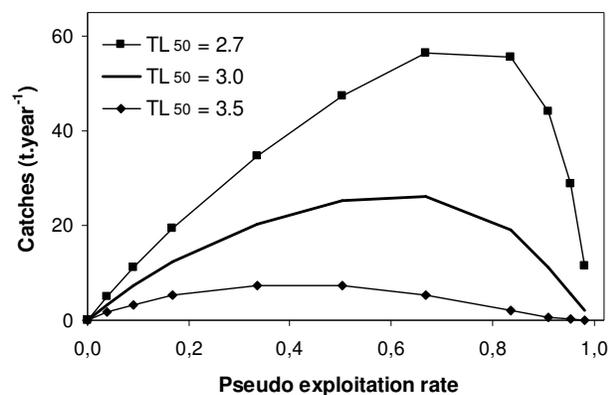


Figure 14 - Total catch expressed as a function of pseudo exploitation rate (simulation for a ‘bottom-up’ ecosystem).

⁸ Such ‘shaving off’ of trophic pyramids is illustrated in Palomares and Pauly (2000; see http://www.fishbase.org/manual/English/fishbasetrophic_ecology00002693.htm).

toward zero for the highest values of fishing mortality.

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. This is documented in Figure 14, for different trophic levels at first capture. Note that the rapid decline of yield with exploitation rate is due to the highly non-linear nature of the abscissa scale of Figure 14, where 1 corresponds to a fishing mortality equal to infinity.

Nevertheless, the fishing loss rates of the low trophic levels are usually small compared to the natural loss rates. For the trophic class $\tau = 2.5$ for instance, we assumed value of $\varphi\tau = 1 \text{ TL}^{-1}$ when $F\tau = 2 \text{ year}^{-1}$, while $\mu\tau = 2.3 \text{ TL}^{-1}$. As a consequence, for $\tau_{50} = 2.5$ ecosystem overfishing is observed only for very high fishing mortalities (F_{MSEY} is around 5 year^{-1}) and the catch therefore is an increasing function of fishing mortality, in the range we explored (Fig. 15). Conversely, for $\tau_{50} = 3.5$ F_{MSEY} is approximately equal to 0.9 year^{-1} , which appears realistic at the ecosystem scale. In addition, the lower the trophic level of first catch, the more 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 the secondary producers enables higher catches that seemingly increase without bounds.

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 more easily overfishing can occur.

In a top-down ecosystem, overall potential yield is slightly increased by the release of predation at low trophic levels (Fig. 15, center). In such case, the increase in prey biomass, which also slightly benefits the predators, induces a catch increase. The gain of total catch induced by top-down control is about 10% with the reference selectivity curve ($TL_{50}=3.0$).

Biomass-input control (i.e., due to the feedback effect on detritus recycling) leads to opposite results (Fig. 15, bottom). Compared to the reference case, the catch reduction due to this effect is about 20%. Thus, detritus-based ecosystems appear very sensitive to fishing (in terms of its impact on biomass), and less productive (in terms of catch), other things being equal. Of course, as for the changes in biomass, these generalizations are true only if the biomass input control is uninhibited by top-down effects.

When fishing effort increases, the catch tends to originate increasingly from low trophic levels (Fig. 16, left), even if low levels are not specifically targeted. The low trophic levels, indeed, can generate large catches when exploitation rates are strong. Global overfishing can occur, however, when fishing becomes intense, particularly when a large part of the biomass

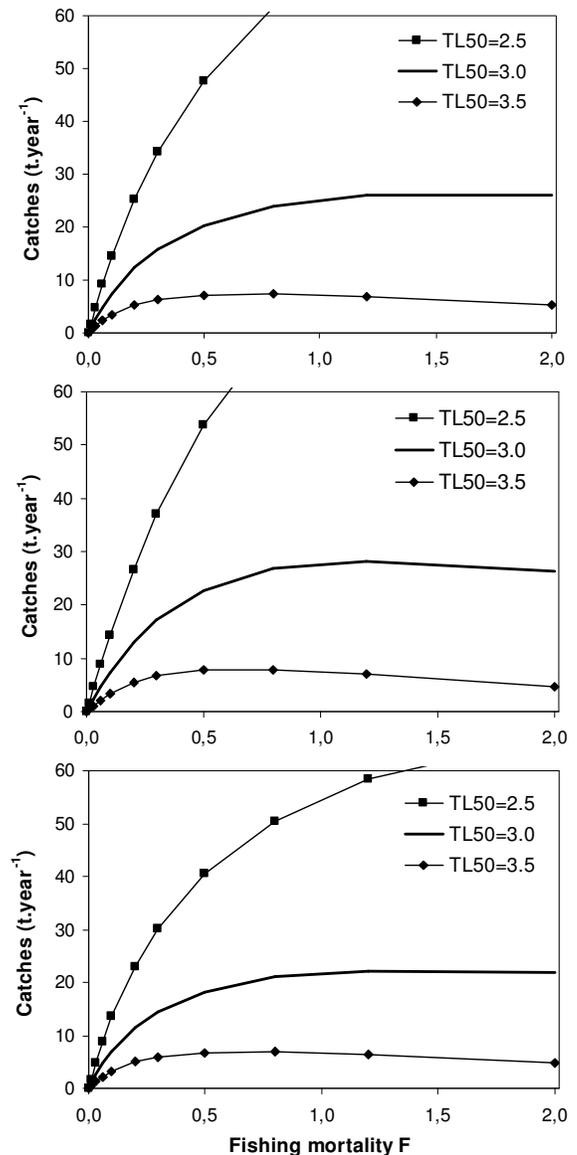


Figure 15 – Total catches as a function of fishing mortality and trophic level of first catch, in a bottom-up ecosystem (top), a top-down ecosystem (center) and a detritus-based ecosystem (bottom)

at low trophic levels is not exploitable, which is frequently the case in real ecosystems. Still, it is the high trophic levels which are more sensitive to fishing and which are the first to be overexploited when fishing effort increases (Fig. 16, 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.

This is not only due to the combination of the direct effect of catches and indirect effects of prey reduction, but more fundamentally, to the slow biomass transfers in the upper trophic levels. 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, 2006). Thus, once again, transfer kinetics appear as a major factor for our understanding of ecosystem response to fishing.

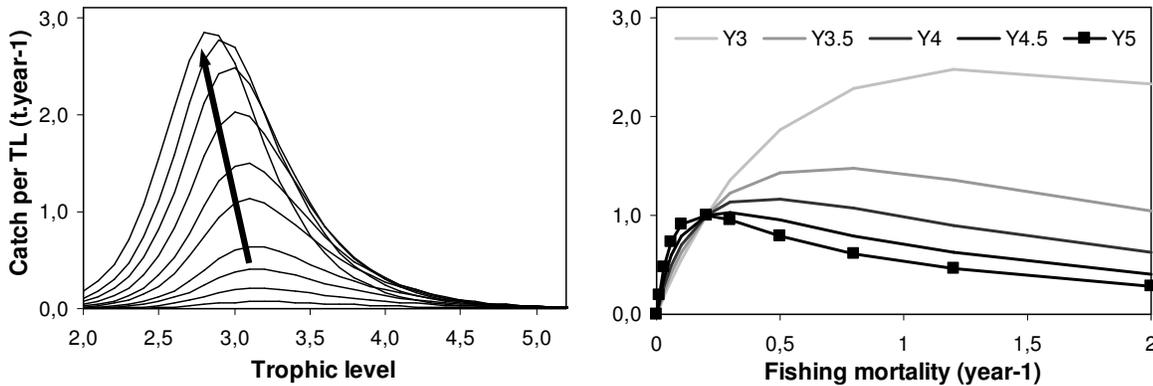


Figure 16 – Simulation of Catch trophic spectra (left; arrow indicates increasing fishing mortality) and catch by trophic class (right; values are standardized for 1 for $F=0.2$) ('Bottom-up ecosystem'; $TL_{50}=3.0$)

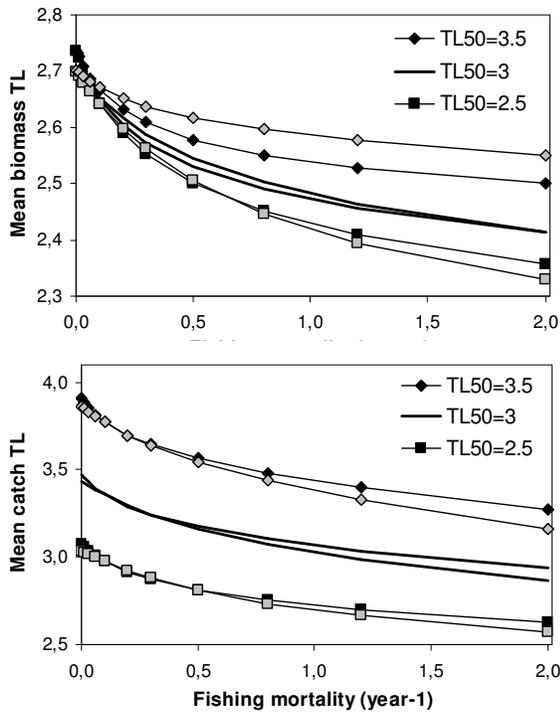


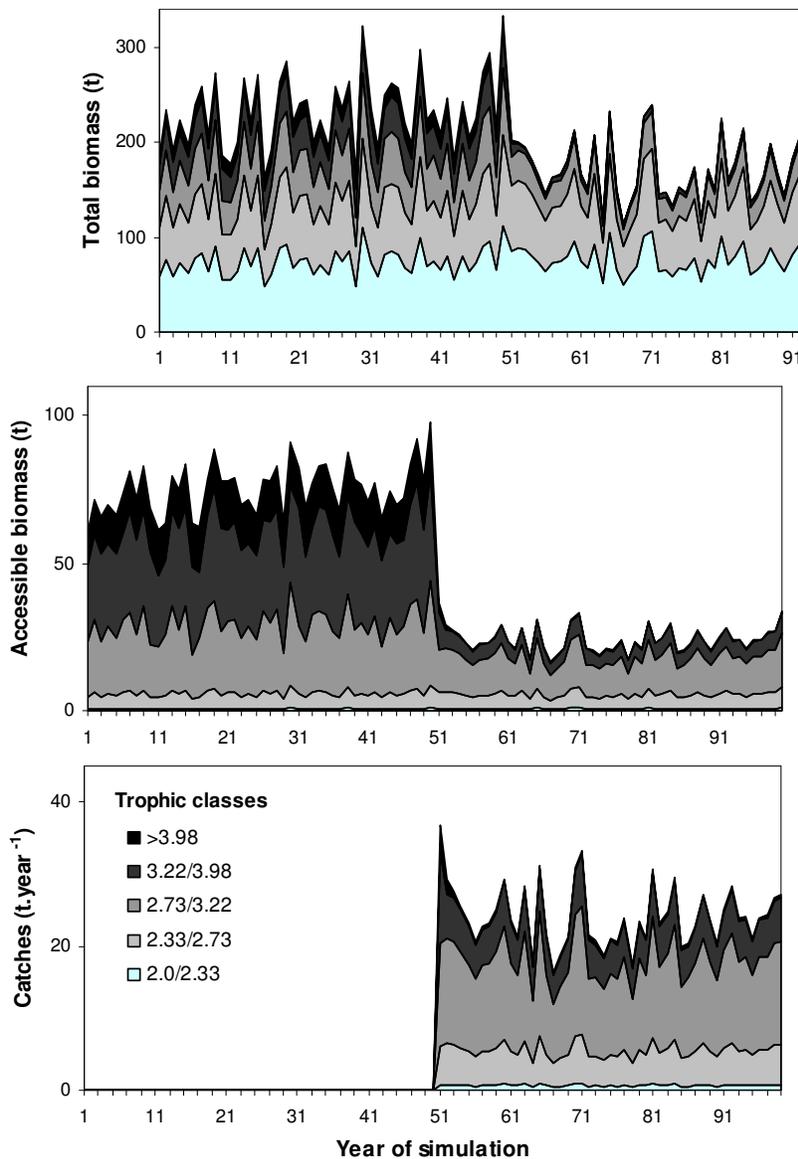
Figure 17 - Mean trophic level of the ecosystem biomass (top) and of the catch (bottom); black marks refer to a bottom-up ecosystem, while gray marks refer to a top-down ecosystem.

A consequence of the higher sensitivity of upper trophic levels is that fishing strongly affects the mean trophic level of the catch, and the one of the residual biomass in the ecosystem (Fig. 17), all the way to the disappearance of the predators. Of course, this phenomenon, which is obviously a manifestation of what Pauly *et al.* (1998) call 'fishing down marine food webs', also depends on the scenario used to define the fishing pattern. Thus, targeting only high trophic levels leads to less of a reduction of the mean trophic level of the biomass than when targeting low trophic levels (Fig. 17).

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. 17, bottom). Top-down control has contradictory effects: on one hand, predation release increases the abundance and thus the catch of prey, leading to a strong decrease of the mean trophic level; on the other hand, top-down control also limits the total decrease of biomass, including that of top predators. Thus, the overall effect of top down control on mean trophic level appears to be limited.

2.5. Dynamic model: impact of fishing on ecosystem stability

Using the dynamic model, we simulated times series of biomass, accessible biomass and catch (Fig. 18). 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 stabilizing around a lower mean value.



Because trophic level 3.5 is reached in one 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 conditions, this transition phase lasts three years near trophic level 4, and five years at trophic level 5.

Figure 18 - Simulation of biomass, accessible biomass and catches time series, using the dynamic version of EcoTroph (based on the values: $F^* = 1 \text{ year}^{-1}$; $\varepsilon_1 = 0.2$ and $\varepsilon_2 = 0$; trophic classes aggregated for clarity)

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.19). For instance, the standard deviation displays a twofold decline, between trophic level 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 another indication that the biomass at high trophic level is characterized by a high stability.

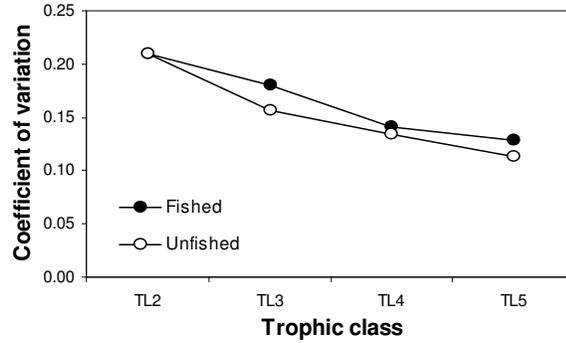


Figure 19. Decrease in the instability of the biomass as a function of trophic levels, measured from the year-to-year coefficient of variation in biomass and for entire trophic classes (Simulation for: $F^* = 1$; $\epsilon_1 = 0.2$ and $\epsilon_2 = 0$)

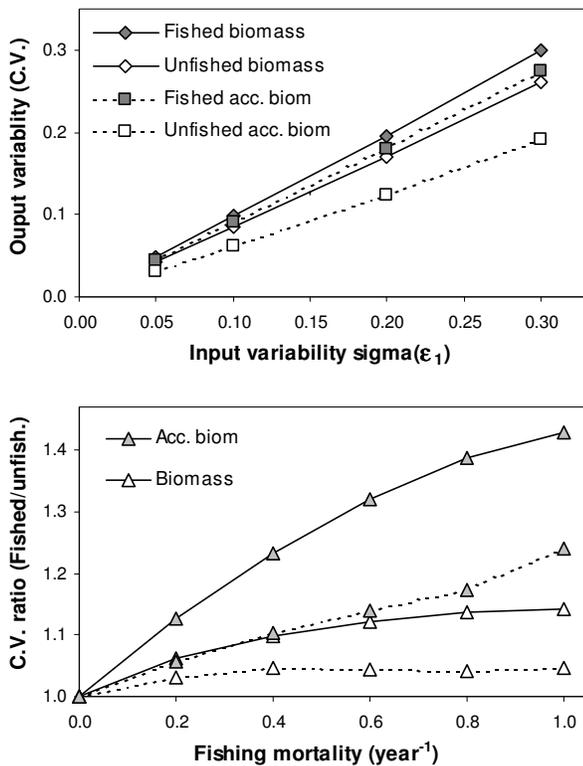


Figure 20 - Propagation of the input variability to the ecosystem biomass. Top: impact of increasing variability in the primary production on the variability of the biomass or accessible biomass (mean estimates for a set of 30 simulations, based on $F^* = 1$ and $\epsilon_2 = 0$). Bottom: impact of increasing 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).

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. 20). From first principles, it can be expected that 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. 20, 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. 20, bottom). For $F^* = 1 \text{ year}^{-1}$, for instance, the fishery induces a 15 % increase in the coefficient of variation of total ecosystem biomass, while for the same fishing mortality, the increase for the accessible biomass reaches almost 50 %. This also applies to catches, whose coefficient of variation follows the same trend as the accessible biomass.

Also 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 strong increase of the coefficient of variation of the biomass is still observed ($p < 0.001$), especially for the accessible biomass (see Fig. 20, bottom).

2.6. Concluding remarks on the theoretical approach

- ***An ecosystem model without species?***

Of course, 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 and biomass-input controls. For instance, we saw how considering the presence of species relatively immune to predation can affect both biomass distribution and ecosystem dynamic. Nevertheless, in spite of the changes that would be brought about by, e.g., different exploitation regimes, all parameters of the model (with the exception of those regulation flow kinetics) 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 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.

- ***Top-down control***

The extent to which top-down control occurs is an important element of ecosystem functioning. However, in actual ecosystems, top-down control may not replace bottom-up control, but occurs simultaneously with it (see Cury *et al.* 2003). Or put differently: predators must depend on their prey, because without prey, there can be no predators; conversely, prey are impacted by the abundance of their predators. However, such reciprocal relationships may not always apply, because certain (potential) prey may experience little predation, depending on their behaviour (Walters *et al.* 1997). Be as it may, we know that predation is a major cause of natural mortality, and frequently leads to top-down control (Hunter and Price 1992; Sala *et al.* 1998, Walters *et al.* 1997, Cury *et al.* 2003).

In case of fishing, top-down control implies that catch at a given trophic level impacts all other levels. Notably, fishing may induce a biomass increase at lower trophic levels. In West Africa, fast increase of fishing pressure in the last decades led to a severe overexploitation of upper trophic level species (Gascuel *et al.*, 2004), and is probably responsible for increase in abundance of species at lower trophic levels, octopus and penaeid shrimp populations (Caverivière 1993; Laurans *et al.* 2004; Gascuel *et al.* 2005). Such effects are generally considered a major indirect effect fishing (e.g. Gonie 1998; Jennings and Kaiser 1998; Hall 1999).

Fisheries-induced cascade effects, 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), although they may have been off the mid-Atlantic coast of the USA and Chesapeake Bay (Myers *et al.* 2007). The EcoTroph model suggests that such 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.

- ***Speed of the flow and resilience***

We saw that P/B ratio can be considered a measure of the speed of the trophic flow. Assuming equilibrium, this P/B ratio is equal to the total mortality rate Z (Allen, 1971), which means that the total mortality rate Z is also a measure of the speed of the trophic flow. When a fishery develops, inducing an increasing fishing mortality F , equilibrium can be maintained only if the productivity P/B increases. This may be the result of density-dependant effects, increasing exploitation rates leading to a biomass reduction and thus to reduced competition between individuals. Also, old individuals tend to disappear, leaving the various populations dominated by younger individuals. Thus, the fishery first induces a higher biological productivity (see also Ricker, 1975, p. 309). At the same time, the speed of the trophic flow increases,

because biomass production increases and because a larger part of the newly generated biomass moves up the food web, or is fished. Such a process of increasing trophic kinetics with F has been observed in actual cases studies (e.g. Jennings and Blanchard 2004). It was explicitly taken into account in the formulation of EcoTroph (equation 23), but is generally not captured by Ecopath with Ecosim models (Gascuel *et al.* 2008b). Aydin (2004) already noticed that density-dependence, which is at the basis of single-species surplus production models (Ricker 1975), may be underestimated by EwE models ⁹.

Top-down control is another process affecting the speed of trophic flows, and it may contribute to maintain equilibrium when fishing pressure increases. Indeed, predation release, discussed in the sections above, may induce slower transfers and thus an accumulation of prey biomass, leading to compensatory effect in term of total biomass.

Therefore, the speed of the trophic flow is a factor that partly determines ecosystem responses to natural or human disturbances, especially fishing. Trophic groups or ecosystems characterized by fast transfers (and thus by a fast regeneration capacity) would exhibit a higher resilience. This is the case for most low trophic level species, which are characterized by a high productivity, a high turnover rate and a high resilience (with same exceptions, such as e.g., abalone; see e.g., Roger-Bennett *et al.* 2007).

Conversely, top predators generally exhibit low turnover rates, and are the most vulnerable in face of fishing (Cheung *et al.* 2007). Such general rule remains globally true at the whole ecosystems level. Immature ecosystems (*sensu* Odum 1969) are usually dominated by low trophic levels and characterized by a high productivity, but a relatively small total biomass (Christensen, 1995), with the exception of upwelling ecosystems, which can be seen as immature, but whose biomass may be very high, because of the very high primary production prevailing in such ecosystems.

Additionally, immature ecosystems are less complex, and generally less stable than more mature ecosystems (Odum 1969); as well, their trophic transfers, which pass through simple food chains, are very fast. In other words, intense, simple and fast trophic transfers may be seen as an adaptation to unstable conditions. This, combined with a rapid return to previous conditions following perturbations, enable that these ecosystems to exhibit a high resilience to fishing, with catches being compensated for by increased productivity. On the other hand, mature ecosystems tend to have higher biomass and slower trophic transfers. Stability is usually high, but productivity low, notably because of strong competition between species or groups. Indeed, complex food webs and low trophic efficiencies may be way that these ecosystems maintain their high biomass and diversity (Christensen and Pauly 1998). This leads to more vulnerable ecosystems, strong perturbations undermining the maintenance of such high biomass and maturity (see also Gunderson and Holling 2001). Thus, there is evidence of fisheries strongly impacting on such ecosystems, notably by reducing their maturity (see e.g. Arreguin-Sanchez *et al.* 2002; Coll *et al.* 2006).

▪ **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. Probably the key point of the model is that, under steady-state conditions, the biomass present at a given trophic level is simply the biomass flow divided by the speed of the flow. The third basic assumption is that biomass of prey may (but need not) depend on the biomass of predators. As previously discussed, the simulation of top-down control requires the introduction of density dependence in the model. Finally, secondary production may be partly dependent on biomass recycling, or, to a lesser extent, on larval recruitment.

⁹ One way to capture density-dependence in EwE models is by splitting each state variable ('box') into a series of stanzas, each having its own set of parameters, which can be done straightforwardly only in the most recent versions of EwE.

Of course the ET model is a caricature of the functioning of real ecosystems. Nevertheless, 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, however, that it appears to be a useful tool for understanding ecosystem functioning in both ecological and fisheries contexts. For example, it mimics the decline under exploitation of the mean trophic level of catches now known as ‘fishing down marine food webs’, and which has been demonstrated to occur in many ecosystems (Pauly *et al.*, 1998, 2002, Pauly and Palomares 2005). It also 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 can thus provide 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.

3. The Catch Trophic Spectrum Analysis (CTSA) ¹⁰

3.1. From EcoTroph to the CTSA

In standard single-species population dynamic models, fishes move from one age to another according to time. In EcoTroph, the biomass of the ecosystem is distributed by trophic classes and moves from one class to the next. Thus, trophic level based models can be viewed as transposition of an age-structured model on an ecosystem scale (see §1.1). Age is ‘converted’ into trophic level, and an equation expresses the kinetics of the underlying process, just as a growth equation expresses the kinetics of growth in a length-based single-species model. In the following, we show how this analogy allows us to adapt Virtual Population Analysis (VPA; Gulland 1965), and its close relative, Cohort Analysis (Pope 1972), to our needs.

In analogy to cohort analysis, we assume that the catch in interval $[\tau, \tau+\Delta\tau]$ occurs precisely at trophic level $t+\Delta t/2$. Just before that trophic level, the biomass flow is equal to:

$$\Phi(\tau) \cdot e^{-\mu\tau \cdot \Delta\tau/2} \quad \dots 46a)$$

Just after trophic level $t+\Delta t/2$, it is:

$$\Phi(\tau+\Delta\tau) \cdot e^{\mu\tau \cdot \Delta\tau/2} \quad \dots 46b)$$

The difference between these two values is equal to the catch made on the trophic class and for a unit of time:

$$Y\tau = \Phi(\tau) \cdot e^{-\mu\tau \cdot \Delta\tau/2} - \Phi(\tau+\Delta\tau) \cdot e^{\mu\tau \cdot \Delta\tau/2} \quad \dots 47)$$

Therefore:

$$\Phi(\tau) = \Phi(\tau+\Delta\tau) \cdot e^{\mu\tau \cdot \Delta\tau} + Y\tau \cdot e^{\mu\tau \cdot \Delta\tau/2} \quad \dots 48)$$

which is equivalent to J.G. Pope’s formulation of Cohort Analysis’ (Pope 1972). Thus, equation (48) allows back-calculating biomass flow, its value at trophic level τ being deduced from the value at trophic level $\tau+\Delta\tau$ and the catch $Y\tau$. Furthermore, based on the inverse of the flow equation (7), the corresponding fishing flow loss rates are calculated:

$$\varphi_\tau = \frac{1}{\Delta\tau} \cdot \text{Ln} \left(\frac{\Phi(\tau)}{\Phi(\tau+1)} \right) - \mu_\tau \quad \dots 49)$$

¹⁰ This paragraph is inspired from Gascuel and Chassot (2008; originally presented in 2004), but the equations and results have been updated to match to the version presented in this document.

If the flow kinetics are known for the current state, biomass per trophic class B_τ can be inferred from the biomass equation (2). Conversely, if independent biomass estimates are available, flow kinetics can be deduced from the same biomass equation (2). Here, we inferred flow kinetics from the general empirical model presented in §1.3.3 (equation 15), assuming that this model refers to the unexploited state of the ecosystem. Therefore, the top-down equation (25) is re-arranged in the following form:

$$\frac{\Delta\tau}{\Delta t} = \frac{P}{B} = \left(\frac{P}{B}\right)_v \cdot \left[1 + \alpha \cdot \frac{B_{pred}^\gamma - B_{pred,v}^\gamma}{B_{pred,v}^\gamma} \right] + F \quad \dots 50)$$

where $(P/B)_v$ is the speed of the trophic flow in the unexploited state, as inferred from equation (15).

From this, fishing mortalities are estimated based on equation (31). In addition, a flow exploitation rate, expressing the proportion of flow losses due to fishing, is defined as follows:

$$E\Phi_\tau = \frac{\varphi_\tau}{\varphi_\tau + \mu_\tau} \quad \dots 51)$$

The catch trophic spectrum analysis requires catches per trophic level Y_τ , natural loss rates μ_τ , and coefficients α and γ of the top-down equation as inputs (here a single value of α is used for all trophic levels). In addition, as in cohort analysis, the computations must be initialised, for the highest trophic level, with an estimate of 'terminal' fishing loss rate. Then, for each trophic level τ , biomass flow $\Phi(\tau)$, fishing flow loss φ_τ , biomass B_τ , flow kinetics $(\Delta\tau/\Delta t)_\tau$, fishing mortality F_τ and flow exploitation rate $E\Phi_\tau$ are estimated from values at level $\tau + \Delta\tau$ using equations (48), (49), (2), (50), (31) and (51) respectively. Because B_τ and $(\Delta\tau/\Delta t)_\tau$ are interdependent, the system of equations must be solved iteratively. The first step $(\Delta\tau/\Delta t)_\tau$ is initialised with a reference values $(P/B)_v$; for each subsequent iteration, the equations lead to improved estimates of $\Phi(\tau)$, B_τ and $(\Delta\tau/\Delta t)_\tau$. The iterations are stopped after the convergence criterion is met.

3.2. Testing the method on simulated data

We used simulated data (i.e. simulated catches based on an EcoTroph model using a given set of parameters) to test the CTSA. More specifically, the convergence properties of the method were investigated and the sensitivity of estimates, to the parameters used as input, was analysed.

3.2.1. Convergence properties of the CTSA

In cohort analysis, it is well-known that estimates converge towards the 'true value', independently of the terminal fishing mortality used as input. Such a property, first observed by Jones (1961), is important in that it allows uncertainty in the terminal fishing parameter used as input, with little impact on the output estimates. Thus, the convergence property was explored for the CTSA, since the inclusion of flow kinetics and the addition of the top-down equation could have altered the convergence process.

First, a theoretical catch trophic spectrum was simulated with EcoTroph, using the following parameters: the natural loss rates $\mu_\tau = 2.3$ ($\exp(-\mu_\tau) = 0.10$); the transfer kinetics deduced from Equations 15 and 50 based on a mean temperature equal to 15°C; a coefficient of top-down control intensity (α) equal to 0.4; a fishing mortality of 0.5 year⁻¹ and the standard logistic selectivity curve (with $\tau_{50} = 3.0$). These simulated data were subsequently used as input of the CTSA and the convergence of the method for biomass, fishing loss rates and fishing mortalities estimates was investigated, with computations initialised using different terminal fishing mortalities, from 0.2 to 1 year⁻¹.

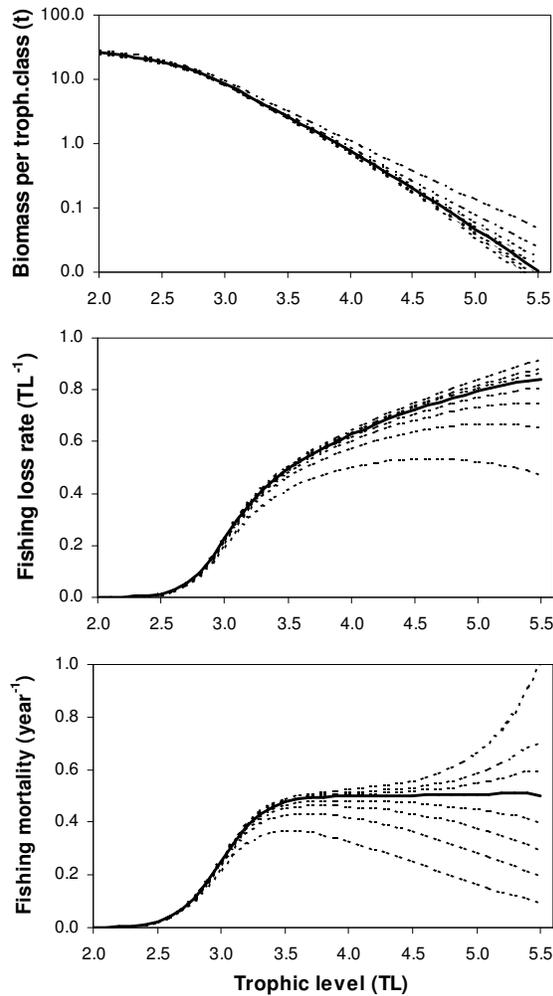


Figure 21 – Illustrating that the convergence properties CTSA are similar to those of cohort analysis. Top: biomass estimates; center: fishing loss rate estimates; bottom: fishing mortality estimates (see text).

3.2.2. CTSA sensitivity to input parameters

A catch trophic spectrum (i.e., catches per trophic level, built using the ET-Smooth or equivalent procedure; see Part II) is the minimum input required for CTSA. When no previously-built Ecopath model is available, P/Bs per trophic level are not available, and the empirical model of trophic kinetics might be used instead. Similarly, empirical values might be assumed for the mean trophic efficiencies and for the top-down coefficient. Of course, uncertainty in parameters used as input of the CTSA will impact the output estimates, especially fishing mortality, biomass flow and biomass.

Thus, the sensitivity of CTSA estimates was explored for three key parameters: transfer kinetics, natural loss rates (linked to transfer efficiency) and intensity of top-down control. Non-standard values defined in 2.1.1 (see Figure 8) were considered for transfer kinetics and efficiency; and a range of values, from 0 (bottom-up ecosystem) to 0.6, was explored for the top-down coefficient. For each case, catches were simulated using the same fishing mortality ($F^* = 0.5 \text{ year}^{-1}$) and the logistic selectivity curve (with $\tau_{50} = 3.0$). These simulated catches were used as input in the CTSA where only standard parameters were considered. In other words, the ‘true values’ of all the tested parameters used in simulations were considered as

As expected, using standard parameters and a terminal fishing mortality equal to 0.5, the CTSA routine leads to outputs equal to the input data used during catches simulation. Especially, the method provides estimates of the ecosystem biomass per trophic class, the fishing mortality and the fishing loss rate coefficient (Fig. 21). Only one value of the terminal fishing mortality (the ‘correct’ one) allows us to find a curve with stable values for high trophic levels, linked to the shape of the selectivity curve.

For other terminal fishing mortalities used as input, convergence is observed, especially at intermediate or low trophic levels. Thus, in analogy to cohort analysis, where the relative error of fishing mortality estimates decreases with decreasing age of a cohort, the relative error of fishing mortality estimates decreases with decreasing trophic level. Biomass estimates also converge in terms of relative error, leading to estimates for trophic level 2 which are very little affected by the value chosen for the terminal fishing mortality.

Additionally, we observed that the higher the fishing mortality, the faster the convergence occurs. In other words, the more intensively exploited the ecosystem, the more reliable the estimates from CTSA. For instance in our simulation, when the terminal fishing mortality is over-estimated, biomass or fishing mortalities estimates remain very close to their true values, for all trophic levels lower than 4. Conversely, estimates can be highly uncertain in case of low exploitation rates.

unknown in the CTSA, which only uses in computation the standard (and erroneous) values. CTSA estimates of fishing mortalities, biomass flow and biomass can therefore be compared to their 'true values', allowing us to analyse the impact of using erroneous parameters for CTSA computations.

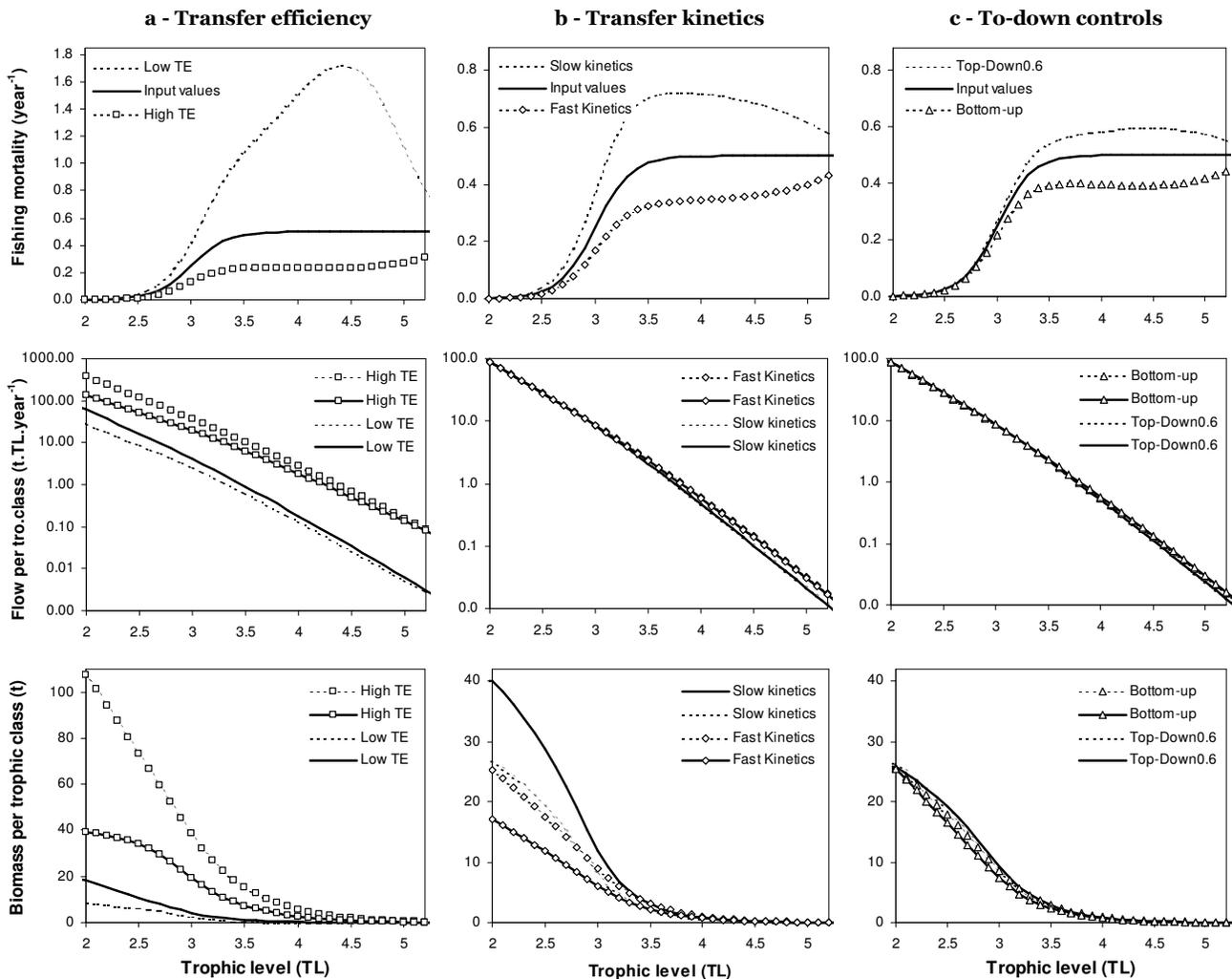


Figure 22 - Sensitivity analysis of the CTSA estimates (fishing mortalities, biomass flow and biomass per trophic class), to the three main parameters used as input: mean transfer efficiency, flow kinetics and intensity of top-down controls. Solid lines refer to the true values (i.e. values used as input for simulation of catches), while dotted lines are the CTSA estimates based on standard (and 'erroneous') parameters.

The CTSA estimates of fishing mortality, biomass flow and biomass appear sensitive to the parameters used as input for calculation (Fig. 22). If the transfer efficiencies, or the speed of the biomass flow are over-estimated, or if the extent of top-down control is underestimated, then fishing mortalities are over-estimated and conversely for biomass flow and biomass.

Nevertheless, the sensitivity is not the same for the three tested parameters.

- Intensity of top-down controls has the smallest impact on estimates (Fig. 22, right column). When a standard parameter ($\alpha = 0.4$) is assumed during CTSA computations, the relative error in fishing mortality estimates may reach 25% if the system is in fact completely bottom-up ($\alpha = 0$) or top-down ($\alpha = 0.6$). But at the same time, biomass flow estimates are correct with relative error smaller than 5%, while a relative error on biomass estimates is around 10%. Note that the top-down parameter mainly affects estimates for the highest TLs.

- Transfer kinetics have a significant effect on fishing mortality and biomass estimates but, due to the structure of EcoTroph, they do not affect the biomass flow estimates (Fig.22, center column). Assuming a flow kinetics model based on a mean water temperature equal to 15°C, while the true values relate to a model based on a temperature equal to 5 or 25°C, induces a relative error of about 50% for the fishing mortality and the biomass estimates. Of course, an under- or overestimation of temperature by 10°C is unrealistic, but the model of flow kinetics we use is an empirical equation and using a wide range of temperature values is a way of simulating the uncertainty associated with the true values of flow kinetics.
- The third parameter we tested, the transfer efficiency, has the highest impact on CTSA estimates (Fig.22, left column). Assuming a transfer efficiency equal to 10% while the true value is 7 or 15% induces relative errors higher than 100% for the three estimated parameters: fishing mortality, biomass flow and biomass. The absolute errors are especially high for low trophic levels, where no exploitation occurs and where, therefore, the flow and biomass estimates strongly depends on the assumed transfer efficiency.

Finally, it can be concluded that biomass estimates are highly sensitive to the values of the transfer kinetics and even more to the transfer efficiency used as input parameter for CTSA computations. Conversely, this means that if the shape of the biomass distribution or the absolute value of biomass or biomass flow at trophic levels 1 or 2, were available as independent estimates (for instance from remote sensing imagery, which can lead to primary production estimate), then the CTSA could be calibrated and should provide reliable estimates for higher trophic levels.

This result is not different from what is observed when VPA is applied to single-species assessment. In this case, fishing mortalities and stock biomass estimates strongly depend on the natural mortality M , which is often poorly estimated. Only experience and comparative analyses between periods of time or between various stocks are able to confirm (or to correct) the reliability of the M values that are used.. In the case of CTSA, more work is obviously needed, involving detailed case studies and comparisons between them, until users get a sense of the parameter values required as input. In this context, it may be useful to use both the backward and the forward CTSA, where computations are initialized by the terminal fishing mortality or by the initial biomass flow (at TL 1 or 2) respectively. Thus, these two approaches have been implemented in the EcoTroph plug-in presented in Part II of the present document.

3.3. Application to real case studies

The CTSA is a tool especially adapted to data-poor environments because it allows the reconstruction of the state of the whole ecosystem with very little data. The minimum data requirement are the total catches per species or groups in the ecosystem in question, and estimates of the mean trophic level of each species or group. In absence of other data, the means of trophic levels in FishBase (see www.fishbase.org) can be used for fish. SeaLifeBase is an increasingly good source of trophic levels for invertebrates and non-fish vertebrates (see www.sealifebase.org).

Based on these catches and TLs data, a preliminary step before applying the CTSA is to build the catch trophic spectrum. A conventional smoothing technique is applied to spread catches of each species around its mean trophic level, i.e., to simulate the fact that the fish in question have trophic level that may change with ontogeny (Pauly *et al.* 2001), or season (see e.g., Karachle and Stergiou 2008; Chassot *et al.* 2008). This method is based on the assumption that the distribution of the biomass of a species or group around its mean trophic level follows a lognormal curve. It is detailed in Part II of the present document (see procedure ET-Smooth, p 47).

When no other data are available, CTSA computations can be performed, using the following input: the catch trophic spectrum, the empirical model of flow kinetics considered as characterizing the unexploited state of the ecosystem (thus, only the mean water temperature is required in order to specify this model), assumed values for the trophic efficiency (the default value is 10%) and the top-down coefficient ($\alpha=0.4$ might be considered the default value). An example of such a CTSA application is provided in Part II of the present document, based on the Guinean case study (see §3.4).

Of course, using assumed or poorly estimated values for some of the CTSA input parameters leads to high uncertainty in output estimates. We thus advise to perform sensitivity analyses. Also, attempts should be undertaken to calibrate the method using independent estimates, especially for primary production or biomass.

Another way to improve the reliability of estimates is to use additional information, such as that available in a previously built Ecopath model. For example, the P/Bs ratios of the model's 'boxes' can be used as a measure of the flow kinetics (Gascuel *et al.* 2008b) instead of the empirical model. In that case, the 'observed kinetics' will exhibit a more or less complex pattern, frequently non-monotonous unlike the empirical model. This is because each species or group 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, the biomass trophic spectrum estimated from the CTSA may also present a complex pattern and a non-monotonous shape, that is probably more realistic than the curve obtained from the empirical model of flow kinetics.

Finally, the analogy between CTSA and Cohort Analysis makes the former easy to understand and helps to solve the equations through the use of a well-established theory. As in classical stock-assessments, following the CTSA step, projections can be conducted for different values of effort multiplier, based on a mean recruitment (here: secondary production) and a constant exploitation pattern for the trophic levels that are targeted. More sophisticated simulations could also easily be performed.

4. Conclusion: the trophic level based approach

For the whole second half of the 20th century, fisheries management was essentially based on single-species approaches using relatively simple models of the dynamic of the exploited population, i.e., the holistic model of Schaefer (1954, 1957), and the analytic models of Beverton and Holt (1957) and Ricker (1975). These models are both theoretical and practical tools. Thus, the surplus-production model of Schaefer (1954) can be used both to illustrate theoretical concepts such as optimum fishing effort or maximum sustainable yield, and to estimate their values in specific fisheries. Similarly, age-structured models (Beverton and Holt 1957; Ricker 1975), which can be used to analyse the theoretical impact of fishing mortality or different selection patterns on catch without reference to a specific stock, can be used with field data to forecast actual catches. Indeed, these models are the forerunners, and often still the backbone of the models currently used for the estimation of Total Allowable Catch (TAC) and to explore management option in many single species fisheries throughout the world.

The last decade has seen the ascent of Ecopath with Ecosim (EwE) as the most widely use software for modelling aquatic ecosystems, be it Ecopath, used for representing a snapshots of the biomass and trophic flows in ecosystems (Christensen and Pauly 1992), Ecosim, used for tracking and/or simulated temporal changes in ecosystems (Walters *et al.* 1997), Ecospace, for mapping trophic interactions onto geographic space (Walters *et al.* 1998), or using all three for comprehensive diagnoses of ecosystem (Pauly *et al.* 2000; Christensen and Walters 2004).

The trophic level based model outlined here mediates between single-species analytic models and whole-ecosystem approach, as represented by EwE. Thus, biomass in ecosystems moves from lower to higher trophic levels in a fashion similar to the manner in which fish populations graduate from one age group to the next (Gascuel 2002). On the other hand, by concentrating on biomass flow as a quasi-physical process, the approach presented here allows aspects of ecosystem functioning to be explored which are not represented in the EwE approach as conceived to date. It is particularly in this sense that EcoTroph is complementary to EwE; it is also the reason why it is presented, in the following section, as a plug-in module of EwE Version 6 (Christensen and Lai 2007), which was designed to accommodate extensions of this sort.

PART II - ECOTROPH: A NEW TOOL IN THE EWE FAMILY

Part II of this report is a user guide for the EcoTroph plug-in available in the Ecopath with Ecosim (version 6) software environment. The EcoTroph plug-in can be used as a stand-alone application or with an existing Ecopath model. We start with basic information about the plug-in, including a general overview of what it can do. We then provide more specific information about each of EcoTroph's sub-routines, organised into 'What it does', 'How it works' and 'How to use it' sections. Additionally, we conclude the description of each sub-routine with an example of its application to real data.

The theoretical basis and equations implemented in the Ecotroph routines are presented in Part I of this document and references to them (either by section or equation number) are included as often as possible. Please note that this manual applies to the first version of the EcoTroph plug-in.

1. General information

1.1. Structure of the EcoTroph routines:

The general organization of the various components of EcoTroph is as follows (Fig. 23):

ET-Main Table includes all parameters required for an EcoTroph simulation. This table is also a way to look at the functioning of the ecosystem under study for the reference situation, as well as to explore how sensitive the reference state is to assumptions about parameter values. ET-Main Table can be created from an Ecopath model using the ET-Transpose routine or from catch data using ET-CTSA.

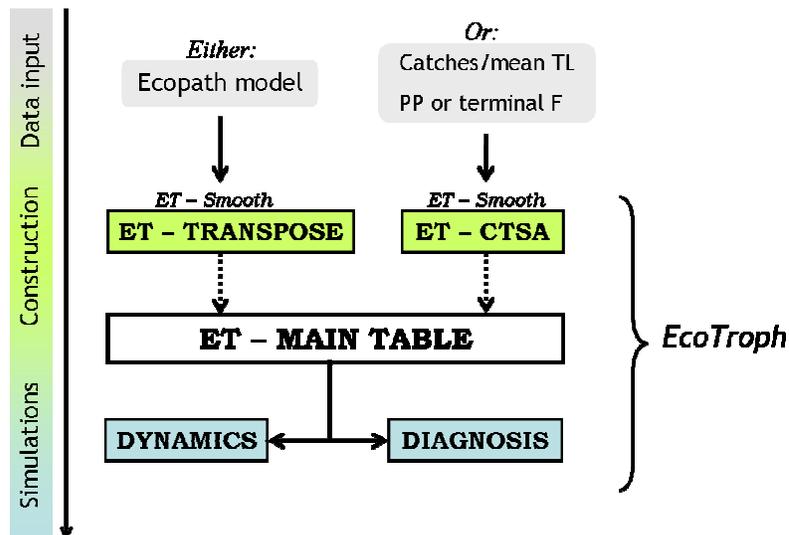


Figure 23 - EcoTroph flow chart: subroutines and data flow

EcoTroph routines:

- **ET-Transpose** has a dual purpose. On its own, it can be used to extract biomass and catch trophic spectra from an Ecopath model, thus providing the user with an alternative, synthetic overview of the

ecosystem. The other is to transform biomass and catch from an Ecopath model into the format required by the Main Table of EcoTroph as a preliminary step to simulations with ET-Diagnosis and/or ET-Dynamics.

- **ET-CTSA** performs Catch Trophic Spectrum Analysis. ET-CTSA generates an estimate of the biomass trophic spectrum related to the current ecosystem state given catches by trophic levels, as well as a corresponding unexploited state of the ecosystem. The resulting model (and accompanying ET-Main Table) can be used to run the other routines of EcoTroph.
- **ET-Diagnosis** simulates the effects of increasing fishing pressures on ecosystem functioning. Starting with the reference situation (saved in the ET-Main Table), ET-Diagnosis simulates catch and biomass trophic spectra for a range of fishing effort multipliers (conventionally from 0 to 2 or 5). This provides a global diagnosis of ecosystem state as well as simple forecasts of total catch and biomass.
- **ET-Dynamics** is the time-dynamic version of EcoTroph. It can be used either for manually fitting biomass and/or catch time series, thereby improving the model's parameterization, or for simulation and forecast according to a user-defined exploitation pattern.

1.2. Installation of the plug-in

Ecopath With Ecosim 6 must be installed (download from www.ecopath.org) in order to use the EcoTroph plug-in. The plug-in EwEEcotroph.dll can be obtained directly from:

- . Sherman Lai: s.lai@fisheries.ubc.ca
- . Didier Gascuel: didier.gascuel@agrocampus-ouest.fr
- . Villy Christensen: v.christensen@fisheries.ubc.ca

In order to use it from EwE, the .dll has to be copied into the same directory that contains EwE (typically C:/Program Files/Ecopath With Ecosim 6/). Once EwE 6 is open, the plug-in is activated by going under Tools -> Options -> Plug-ins , selecting 'EwEEcotroph', making sure the box 'Enable this plug-in module' is ticked and clicking OK. This only has to be done the first time the plug-in is used. The EcoTroph plug-in is located under the navigator tree (on the left) as Parameterization (Ecopath) -> Tools -> Eco Troph plug-in (Fig. 24).

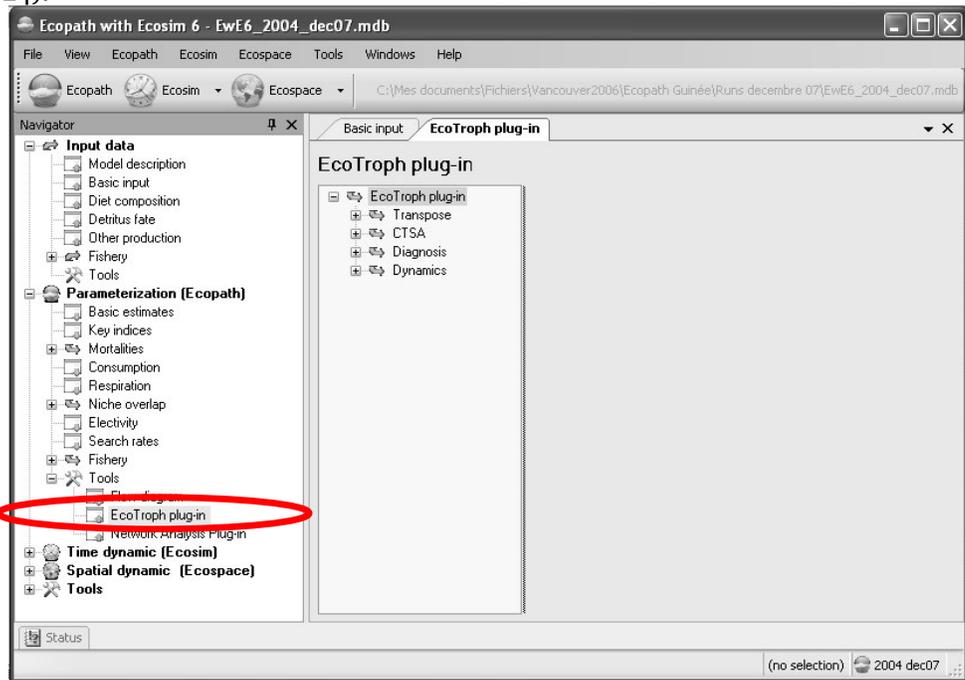


Figure 24 – Position of the EcoTroph submenu in the EwE navigator tree

1.3. Additional information

1.3.1. Range of trophic levels in the results

The plug-in provides results for trophic levels going from 1 to 7, by intervals of 0.1 (except between trophic levels 1 and 2 where no intermediary values are possible). Realistically however, trophic levels over 6 are almost probably not observed in nature and high trophic level catches are badly estimated, so it is advised to focus the analysis of results on trophic levels 5.9 and below, or whatever range is considered representative of the ecosystem under study. Values for trophic levels of up to 7 are derived in EcoTroph because it is necessary to compute the biomass of predators of higher trophic levels to capture the top-down effect on a given trophic level (see § 1.6.1).

1.3.2. Data used in the manual's figures

The data used as illustrations of the EcoTroph model in the subsequent sections are derived from the Guinean shelf ecosystem, where a fast and strong increase in the fishing pressure occurred over the past 25 years (Gascuel *et al.* 2008a and in prep.). Data on catch and scientific survey were initially provided by the Guinean institute CNSHB (in French: Centre National des Sciences Halieutiques de Boussoura). Based on 'catch reconstructions' (*sensu* Zeller *et al.*, 2007) and GLMs procedures applied to surveys data, catches and biomass per trophic group were estimated over the 1985 to 2004 period. Two separate Ecopath models were built for 1985 and 2004. Models take into account 34 ecological groups, including 24 fish groups defined accordingly to their ecology (especially their diet) and to data availability. Parameters required by these models (mainly P/B, Q/B and diet) were estimated based on a previous Ecopath model (Gu nette and Diallo, 2004) and on complementary *ad hoc* procedures detailed in Gascuel *et al.* (in prep.). Of course, our aim here is not to analyse these Ecopath models or the detailed functioning of the Guinean ecosystem, but to illustrate the use of the various EcoTroph routines with real data.

2. ET-Transpose: looking at an Ecopath model using EcoTroph

2.1. What is it used for?

ET-Transpose allows to translate the content of an Ecopath model into an EcoTroph model to produce, amongst other things, biomass and catch trophic spectra (curves of biomass (or catch) of an ecosystem obtained by summing the relevant variable over trophic levels). Ecopath and EcoTroph are ecosystem models that share many similarities (see § 1.4), especially in the way they represent the transfer of biomass flow between organisms and in the functional relationships between predators and their preys. Their final representation of ecosystems is different but complementary. Viewing an Ecopath model with ET-Transpose provides a synthetic overview of an ecosystem and is a good tool to help users think at an ecosystem scale.

ET-Transpose can also be used as a starting point for further analyses, like those performed in ET-Diagnosis and ET-Dynamics. In other words, ET-Transpose can be considered as a method to estimate input parameters of simulations starting from an Ecopath model. Also, if time-series of Ecopath models are available for a given ecosystem, ET-Transpose can produce corresponding series of biomass and catch trophic spectra to be analyzed in light of the ecosystem's fishing history.

2.2. How it works

EcoTroph summarizes ecosystem properties by trophic level while Ecopath splits biomass between boxes representing species or group of species. ET-Transpose translates the information contained in

Ecopath into an EcoTroph model by using a procedure called ET-Smooth (see 'ET-Smooth box') and the biomass/production calculated by Ecopath for each species/group of species.

Procedure:

- 1) The Ecopath model provides data for each box, more specifically biomass B , P/B ratios and catch per fleet Y_f . The production (or biomass flow) of the box is calculated as $P=(P/B)*B$
- 2) ET-Smooth is applied to biomass B , catch per fleet Y_f and production P for each Ecopath box in order to produce continuous distributions of those variables over trophic levels. The idea behind this is that the mean trophic level of a group does not fully reflect its function within an ecosystem, because not all individuals in the group are exactly at that mean trophic level. Biomass, catches and/or production are partitioned around the mean trophic level of the species they refer to, according to an estimate of the trophic level variability within the group. The user can choose between three different ways of estimating trophic level variability, which are described in detail in the box 'ET-Smooth' below.
- 3) The trophic spectra for biomass, production and catch are calculated by summing over trophic levels the values obtained in step 2 for all boxes. The flow kinetics at each trophic level can then be derived from biomass and production, using equation 2.
- 4) Given a selectivity manually defined by user for each Ecopath species/species group (i.e. the proportion of the biomass that is accessible to fisheries), the accessible biomass and accessible flow are calculated.
- 5) Once the biomass, the accessible biomass, the flow, the kinetics and the catches by trophic level are derived, it is possible to compute EcoTroph reminding variables, that is, the fishing loss rate and accessible fishing loss rate, the fishing mortality and the accessible fishing mortality, the natural loss rate and the mean age of the biomass at each trophic level.

The output of ET-Transpose, the 'Main Table', summarizes the main properties of an ecosystem as represented by an EcoTroph model (described under Table 4) and can serve as a basis to run ET-Diagnosis and ET-Dynamics.

Box 1: ET-Smooth

ET-Smooth converts data pertaining to specific taxa or functional groupings into data by trophic classes. Data can be catches, leading to Catch Trophic Spectra (CTS), or biomasses, leading to Biomass Trophic Spectra (BTS). Taxa or functional groups can be species or guilds, or Ecopath 'boxes', or any groups whose position in a food web can be defined by a single trophic level (and its variance, see below). The resulting BTS and CTS range from trophic levels 2.0 to 6.9 and are sliced in classes of 0.1, in addition of a trophic class for trophic level 1.

The main assumption in ET-Smooth is that the distribution of the biomass or catch of a trophic group around its mean trophic level follows a lognormal curve. The curve is defined by a mean (the mean TL of a trophic group) and a standard deviation (*sigma*), which is a measure of trophic level variability within the group. Knowing these two parameters for a group or a species allows the allocation of the biomass and/or catch data to a set of trophic classes in the neighbourhood of the mean. The distributions are then defined by the lognormal function $LN(\text{meanTL}, \text{sigma})$.

The standard deviation (*sigma*) defining the shape of the group's distribution is a key parameter of the procedure. Ideally, it should have been previously estimated, based on a set of trophic level estimates from a representative sample of individual animals of the group. Usually however, these data are not available so the ET-Smooth procedure offers the user three options:

- The default choice is a **theoretical model** that assumes that the TL variability within an ecological group increases log-linearly with the mean trophic level of the group. Defining the slope of this increase (parameter 'Smooth') is sufficient to build theoretical distributions for all trophic classes (see Figure 25b). $\text{Sigma}(\text{TL})$ is thus defined as $\text{sigma}(\text{TL}) = \text{Smooth} * \ln(\text{TL} - 0.05)$, where the subtraction of 0.05 accounts for the half interval range of the trophic class. Note that the EcoTroph module gives the user the option of changing the value for the slope 'Smooth', currently set at a default value of 0.07.

- The **standard deviation of estimates of trophic levels from Ecopath models** are derived as the square root of the omnivory index of Christensen and Pauly (1992) and are available in many Ecopath models. ET-Transpose can extract these variables from the Ecopath model and use them in ET-Smooth.

Note that there is no direct relationship between the Ecopath standard deviation of TLs (which measures the variability of the prey of a group of species), and *sigma*, which measures the variability between individual predators. For example, within a population of predators, if all animals have the same omnivorous diet they will also all have the same mean trophic level associated with a high omnivory index, even though there might be no TL variability between individuals. Conversely, it is possible to imagine a population where all individuals exhibit very different diets, thus inducing a high standard deviation of mean TLs, but where each individual is very specialized so that the omnivory index is low. Nevertheless in practice the two notions are often linked, since variability at the level of individuals will tend to induce variability at the level of the population, and so the option is given to the user of setting *sigma* as a function of the omnivory index derived from the Ecopath model.

- The user can **manually define sigma** for each group, using, for instance, independent data from the field or the data available from FishBase for trophic levels estimated from diet compositions (see www.fishbase.org).

Technical notes:

In case (2) or (3) standard deviations usually refer to normal distributions. Therefore, the routine expects normal mean TL and sigma values, and will automatically transform them to their log-normal equivalent (since ET-Smooth assumes a lognormal distribution of TLs around the mean). In other words, the user inputs mean TL and *sigma* defined for normal distributions, and the routine transforms and outputs them as log-normal (the normal distribution $N(\text{meanTL}, \text{sigma})$ is approximated by the distribution $\text{meanTL} \cdot LN(\text{meanTL}, \text{sigma}/\text{meanTL})$, where LN refers to the lognormal function).

It is important to note that because there can be a lot of uncertainty in *sigma* coefficients, we recommend that the user perform a sensitivity analysis of the results to *sigma*, which can easily be done with the EcoTroph plug-in by using, for instance, various empirical values for the 'Smooth factor'. Based on the case studies analysed previously, it appears however that the sensitivity of the final results of EcoTroph simulations are not affected much by the strength of the smoothing applied to the input data. Such a low sensitivity is in fact expected as the magnitude of the biomass should be more important than the details of how it is split between trophic classes.

Figure 25 illustrates how ET-Smooth converts biomass data into biomass trophic spectra by using the Guinean Ecopath model. The biomass of the 34 trophic groups of the Guinean model are first assigned to trophic classes, according to their mean trophic level (Fig. 25a). For instance, the bonga (*Ethmalosa*), whose mean TL is equal to 2.57, is assigned the trophic class comprised between 2.5 and 2.6. Then, lognormal distributions are calculated for all the trophic classes, according to their mean TL values and to their standard deviation σ (here defined by the theoretical model); each distribution is standardized in such a way that it sums to one (Fig. 25b). Then, the biomass of each group is divided between various trophic classes, according to its standardized distribution. The Biomass Trophic Spectrum is the curve obtained by summing all the distributed biomasses (Fig. 25c).

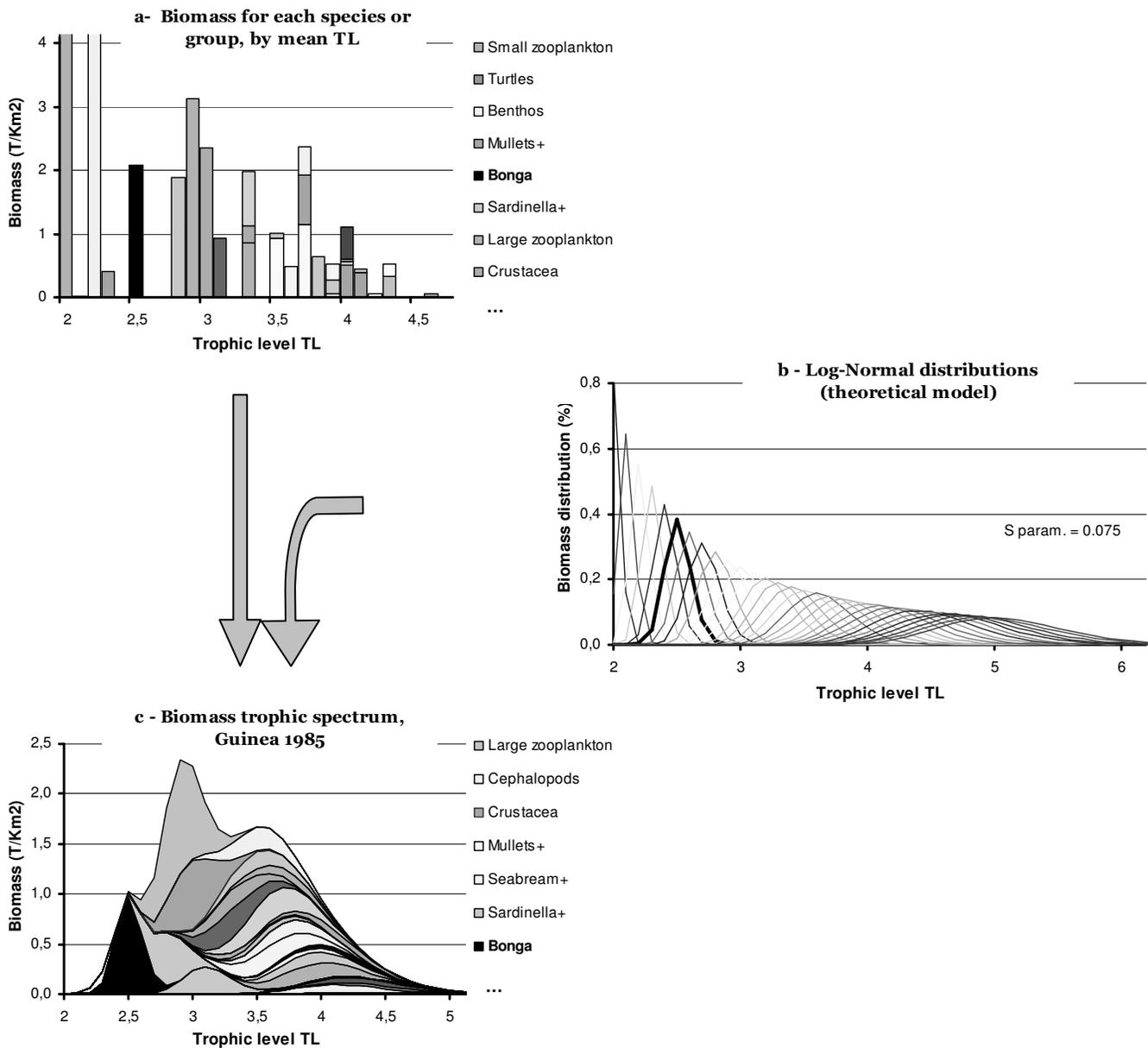


Figure 25 - ET-Smooth: an illustration of the procedure, applied to the Guinean Ecopath model. a. Biomass per Ecopath group, ranked by their mean trophic level; b. Lognormal distributions for all trophic classes, using the theoretical model

(see text); c. Distributions of biomass per groups; the cumulative curve is the Biomass Trophic Spectrum (for clarity, Small zooplankton and benthos which are very abundant were removed from c; Bonga is in black).

Table 4: Definitions of the variables presented in ET-Main table.

	Description	Symbol	Unit	Reference section
Biomass	Amount of organic matter present in the ecosystem by trophic level.	B_{τ}	Tonne t	1.3.1
Accessible biomass	Ecosystem biomass accessible to fisheries.	B^*_{τ}	Tonne t	21-22
Production (biomass flow)	Amount of biomass that passes through each trophic level in a year.	$\Phi(\tau)$	t.year ⁻¹	1.3
Kinetic	Speed of the biomass flow passing through the trophic level.	$\Delta\tau/\Delta t$	TL.year ⁻¹	1.5
Catches	Amount of biomass extracted from the ecosystem by fishing.	Y_{τ}	t.year ⁻¹	1.7
Fishing loss rate	Proportion of the biomass flow that is diverted by fishing.	φ_{τ}	TL ⁻¹	1.3.2; 1.7.1
Accessible fishing loss rate	Proportion of the accessible biomass flow that is diverted by fishing.	φ^*_{τ}	TL ⁻¹	1.7.2
Natural loss rate	Proportion of the biomass flow lost at each trophic level due to digestion, excretion, etc.	μ_{τ}	TL ⁻¹	1.3.2
Fishing mortality	Proportion of the biomass of each trophic level that is removed by fishing.	μ^*_{τ}	year ⁻¹	1.7.1
Accessible fishing mortality	Proportion of the accessible biomass removed by fishing.	F_{τ}	year ⁻¹	1.7.2
Selectivity	Proportion of each trophic level's biomass that is accessible to fishing	S_{τ}		1.7.2
Time	Average time it takes an unit of biomass produced at the first trophic level to reach a given trophic level, or, average age of the biomass present at each trophic level.	Δt	year	1.5.1

2.3. How to use it

Summary: To run ET-Transpose open the Ecopath model of interest and select the desired mean of estimating trophic level variability. Once the default ET-Main table is computed, accessibility/selectivity can be adjusted for each Ecopath group under the 'Accessible biomass' tab and parameters can be adjusted for the 'Automatic smooth' and 'User-defined' sigma options. For the settings to be registered, ET-Main Table must be updated by clicking on 'Calculate'. The up-dated ET-Main Table can be used in runs of ET-Diagnosis or ET-Dynamics.

To set-up the initial version of ET-Main Table, open the Ecopath model of interest. In the Ecotroph plug-in menu, select ET-Transpose and choose between the three options available to set TL variability in the ET-Smooth procedure: Automatic Smooth, Omnivory index, User-defined sigma (see Box ET-Smooth). ET-Transpose will compute the default ET-Main Table (1), accessible biomass (2), production (3), biomass (4) and catch per fleet (6), by Ecopath boxes over trophic levels (as shown in Fig. 26). A table is also provided that sums the catch per fleet for all Ecopath boxes (5). Lastly, a table shows the distribution of output trophic levels given the input Ecopath level (7).

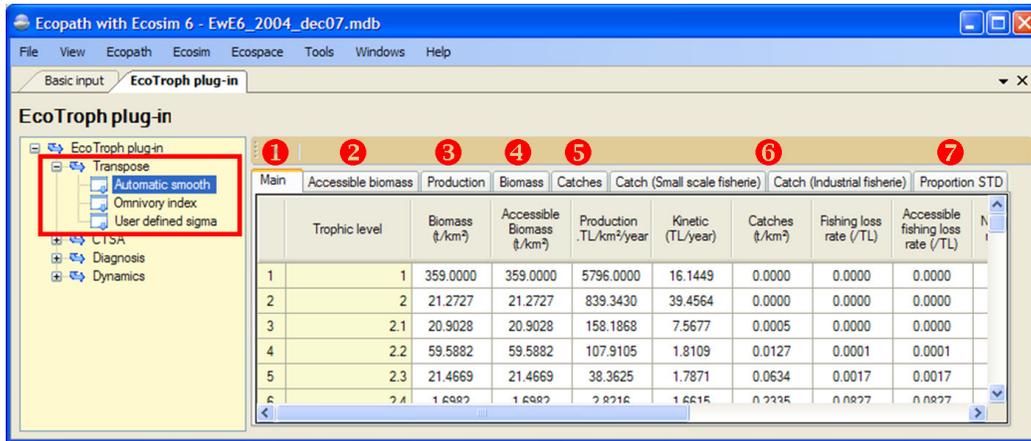


Figure 26 - Output tables 'Main' of ET-Transpose under 'Automatic smooth'

The accessibility is set under the 'Accessible biomass' tab, by entering the appropriate value for each Ecopath group and clicking 'Calculate' to re-run ET-Transpose with the new settings (Fig. 27). Note that these values of accessibility have no effect on the Smooth procedure and thus on the biomass or catch trophic spectrum. They only impact the accessible biomass and the related parameters included in the ET-Main Table (accessible fishing mortality and accessible fishing loss rate). Selectivity, defined by the values of accessibility for each group, becomes a key factor for the next steps, when using ET-Diagnosis or ET-Dynamics for simulation purposes.

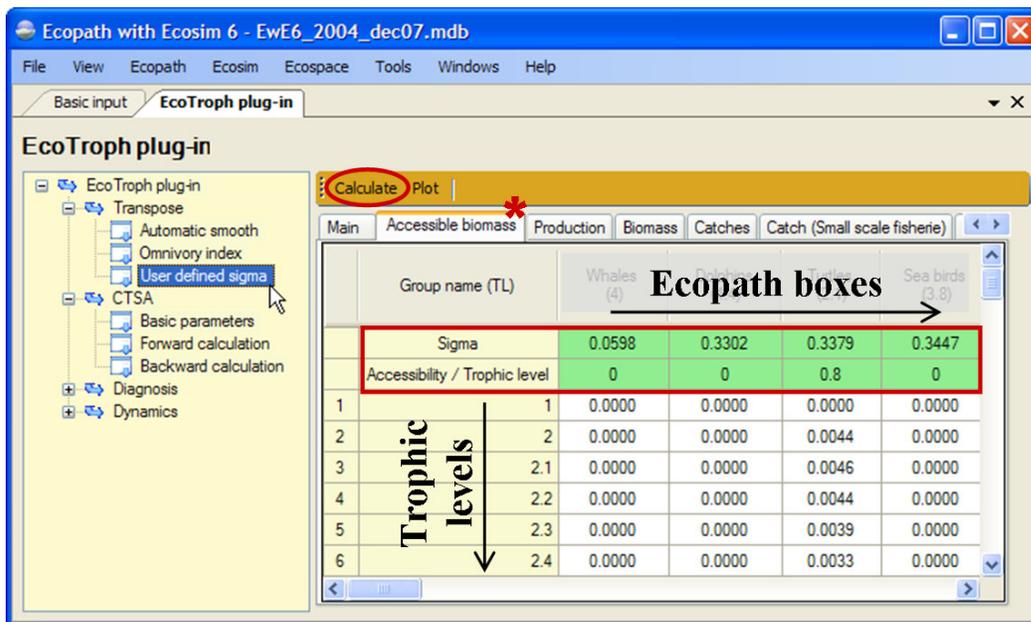


Figure 27 - Output table 'Accessible biomass' of ET-Transpose under 'User defined sigma'.

Under 'Automatic Smooth' the user can set the smooth parameter (default = 0.07). Under 'User-defined sigma' the trophic level variability or each Ecopath group (where sigma describes the normal distribution) can be set under the 'Accessible biomass' tab (or other tabs that contains the Ecopath groups). There are no user-defined settings when one chooses the 'Omnivory index' option. For any setting to take

effect, 'Calculate' must be pressed. Those settings will then be used if the option ET-Transpose is used to input baseline data into ET-Diagnosis or ET-Dynamics.

Clicking on 'Plot' under the tab 'Main' will produce two figures on the same window (Fig. 28), the first one with the biomass, accessible biomass, production, catches and kinetics over trophic levels (on a log-scale) and the second one with fishing loss rates and mortalities over trophic levels for both the accessible and inaccessible biomass.

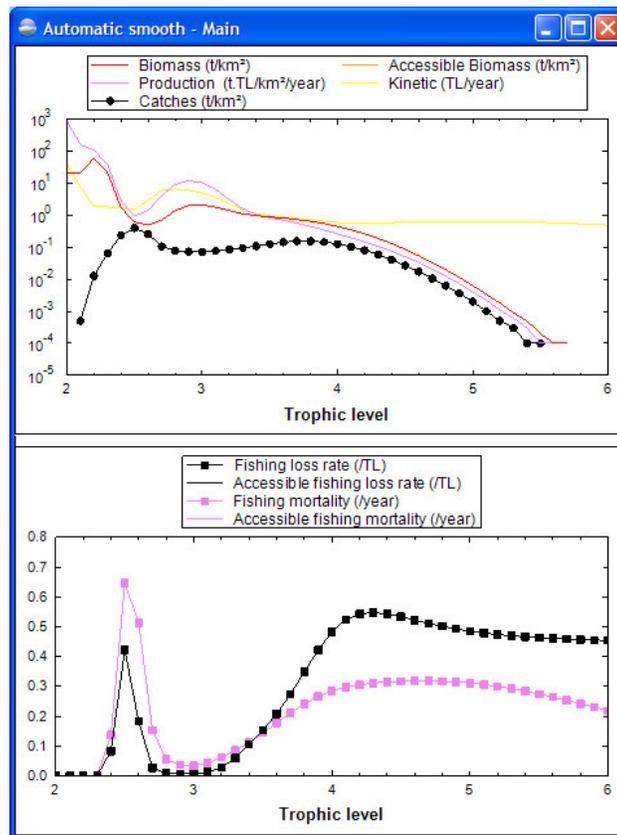


Figure 28 - Example of a figure produced by selecting 'Plot' under ET-Transpose 'Summary' tab

Similarly, the data in the other tabs ('Accessible biomass', 'Production', etc.) can also be visualized (Fig. 29, left). The figure produced by selecting 'Plot' under a given tab will show distributions of the variable of interest (say Production if 'Plot' was selected under the 'Production' tab) for each Ecopath group by trophic levels, with one colored area by category (species/species group, fleet category type, etc.). The areas are juxtaposed in the order the data appears in the column (i.e. first column is the front-most area), so that areas for some columns might be hidden behind others. Note that it is possible to select specific columns to be included in the figure by holding Shift and clicking on the columns of interest.

An alternative representation of the distribution of the variable of interest over trophic levels by category can easily be obtained by copying-and-pasting the table into Excel and producing a juxtaposed area graph (Fig. 29 right). This also allows to visualize the trophic spectra of the variable of interest and the relative contribution of each species/functional group to the trophic spectrum.

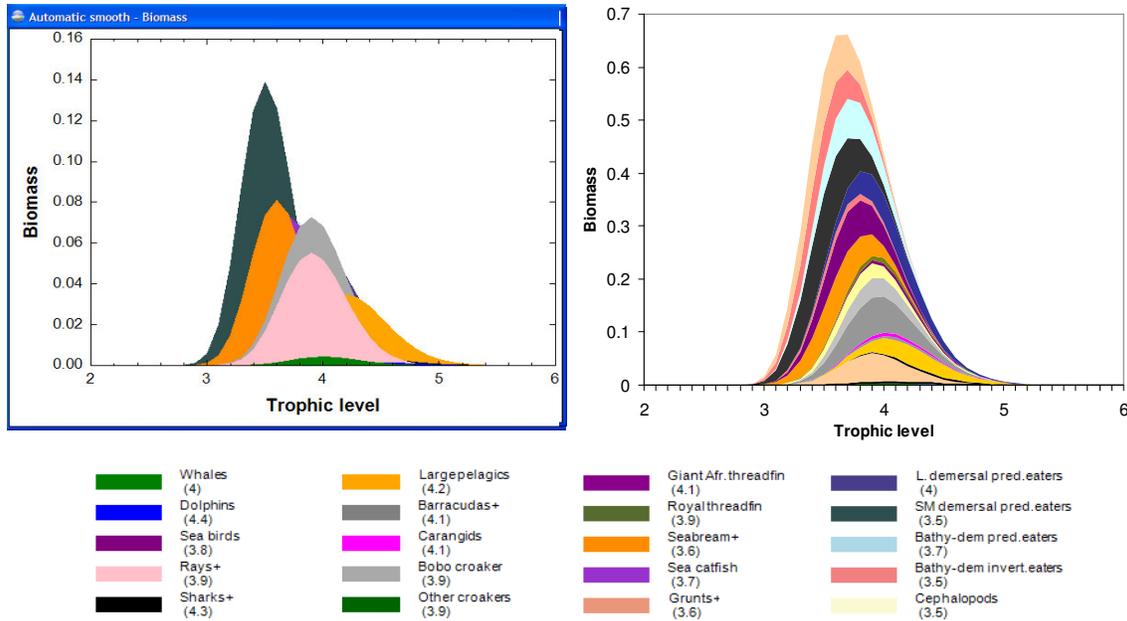


Figure 29 - Area plot produced by selecting 'Plot' under the detailed tables of ET-Transpose (left), compared with the same data pasted in Excel and plotted as a juxtaposited area plot (right).

2.4. Example of application

Figure 8 illustrates the usefulness and pertinence of using ET-Transpose as a complementary tool of the Ecopath approach in order to obtain a synthetic overview of the ecosystem (from Gascuel *et al.* 2008a). For instance, we clearly observe between 1985 and 2004 the global decline in the biomass of the various trophic groups of the Guinean ecosystem (Fig. 30 top). This decrease is especially pronounced in the highest trophic levels; groups such as croakers (Fam. Sciaenidae; TL>4.0) almost disappear. During the same period, catches increased and fishing mortality increased 5 fold (Fig. 30 bottom). Low trophic levels (i.e., mainly the Bonga shad *Ethmalosa fimbriata*) are exploited only by the small-scale fishery, while higher levels are targeted by the two sectors, industrial and small-scale. In recent years, TLs above 4 experienced high fishing pressure; in terms of fishing loss rates (not shown here), these levels are the most impacted.

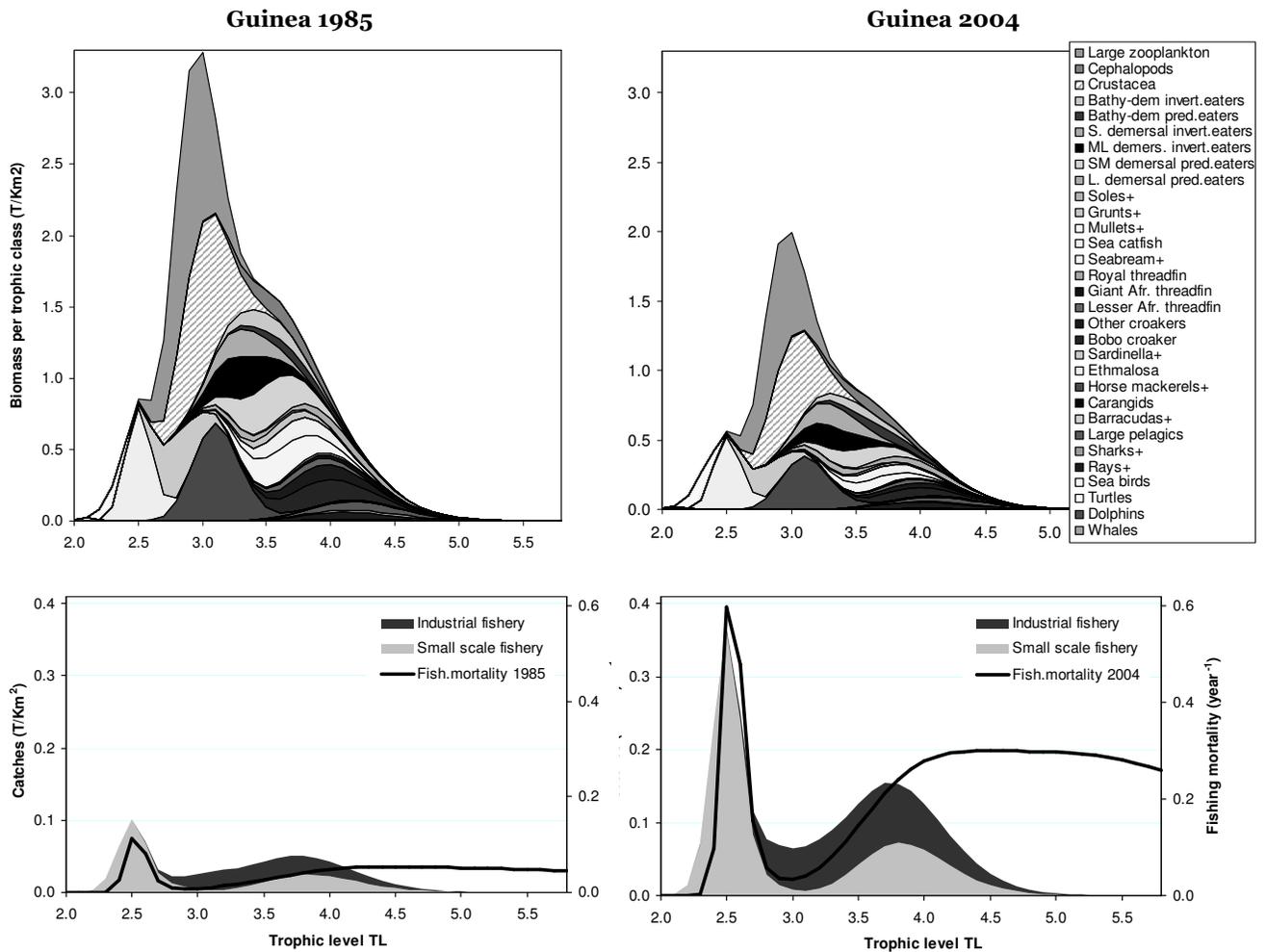


Figure 30 - A representation of the two Guinean Ecopath models, for 1985 (left) and 2004 (right), as interpreted by EcoTroph using ET-Transpose: biomass distribution by Ecopath group and trophic levels (top; small zooplankton and detritus were removed for clarity); catch per fishery and aggregate fishing mortality, by trophic level.

3. ET-CTSA: estimating input parameters of EcoTroph

3.1. What is it used for?

A trophic level based model like EcoTroph can be seen as an ecosystem-scale age-structured model where, instead of having individuals flowing through ages, biomass flows through trophic levels. This analogy allows the application of a Virtual Population Analysis-like approach in an EcoTroph context to reconstruct ecosystem biomass based on catch by trophic level (see § 3). The Catch Trophic Spectrum Analysis (CTSA) uses a catch trophic spectrum and an estimate of ecosystem flow kinetics to derive, either in the forward direction (from low to high trophic levels) or in the backward direction (from high to low trophic levels), biomass trophic spectra for the current state of the ecosystem (i.e. from which the catch data originates) and a reference state where no fishing occurs (called 'unexploited').

The ET-CTSA routine can be used on its own to generate biomass trophic spectra and estimate the ecosystem biomass. The comparison between the current and the unexploited biomass trophic spectrum can be used to analyze the impacts of fishing at the ecosystem-scale. ET-CTSA also serves as an intermediate

step to create ET-Main table, as the baseline to be used by ET-Diagnosis and ET-Dynamics (see Table 5 for a comparison).

Table 5 – Comparison of the data required to derive ET-Main Table given the starting routine used. Values in bold must be provided independently by the user, values in italics can be set according to an empirical model or a default value (on which sensitivity analysis can later be performed)

ET-Transpose	ET-CTSA Forward	ET-CTSA Backward
<ul style="list-style-type: none"> • balanced Ecopath model, including estimates for each group of at least three of the following: biomass; P/B; ecotrophic efficiency; consumption/biomass or production/consumption 	<ul style="list-style-type: none"> • <i>flow kinetics (temperature)</i> • catch by trophic level • <i>trophic level variability</i> • <i>top-down parameters</i> • <i>natural loss rate (TE)</i> 	<ul style="list-style-type: none"> • <i>flow kinetics (temperature)</i> • catch by trophic level • <i>trophic level variability</i> • <i>top-down parameters</i> • <i>natural loss rate (TE)</i>
<ul style="list-style-type: none"> • <i>selectivity</i> 	<ul style="list-style-type: none"> • estimate of biomass or production at TL 1 or 2 	<ul style="list-style-type: none"> • terminal accessible fishing mortality or fishing loss rate
<ul style="list-style-type: none"> • <i>trophic level variability</i> 		<ul style="list-style-type: none"> • <i>highest trophic level</i>

3.2. How it works

Virtual population analysis (VPA) re-constructs the state of populations by modelling how individuals move from one age-class to the next while accounting for age-specific catches and mortality. The analogous variable in EcoTroph is the biomass flow, which is the amount of biomass that passes through trophic levels over time (see § 1.2.4). This value is directly affected by fishing since the catches for each trophic level are directly removed from the biomass flow at each step. ET-CTSA infers what the flow at the next (or previous) trophic level must be given the catch at the current trophic level and the transfer efficiency (i.e. the rate at which the biomass flow is naturally reduced) (see § 3.1). Using this approach and the remainder of the EcoTroph structure, that is, the model describing the flow kinetics and how it relates to biomass, it is possible to reconstruct ecosystem biomass by trophic level. ET-CTSA, like a VPA, must be initialized either at the very beginning (trophic level 1 or 2 in ET-CTSA Forward) or at the end (trophic level around 5 in ET-CTSA Backward). The algorithm then works down (or up) trophic levels by assuming that catches are taken exactly half way between trophic level intervals and deriving biomass flow based on equation 48 (which basically says that the biomass flow at trophic level $TL - \Delta TL$ is equal to the flow it would have taken to produce both the existing flow and the catches at trophic level TL , given the rate at which the biomass flow is naturally reduced) (see Fig. 31).

In order to reconstruct the ecosystem state from biomass flow, one needs either the biomass or the flow kinetics by trophic level. Here the empirical model for flow kinetics (P/B) is used to initialize the algorithm and once the biomass and biomass flow have been derived, an up-dated P/B is recalculated to account for the effect of fishing and for a possible top-down effect. The CTSA is then run again until the input and output P/B converge (see § 3.1).

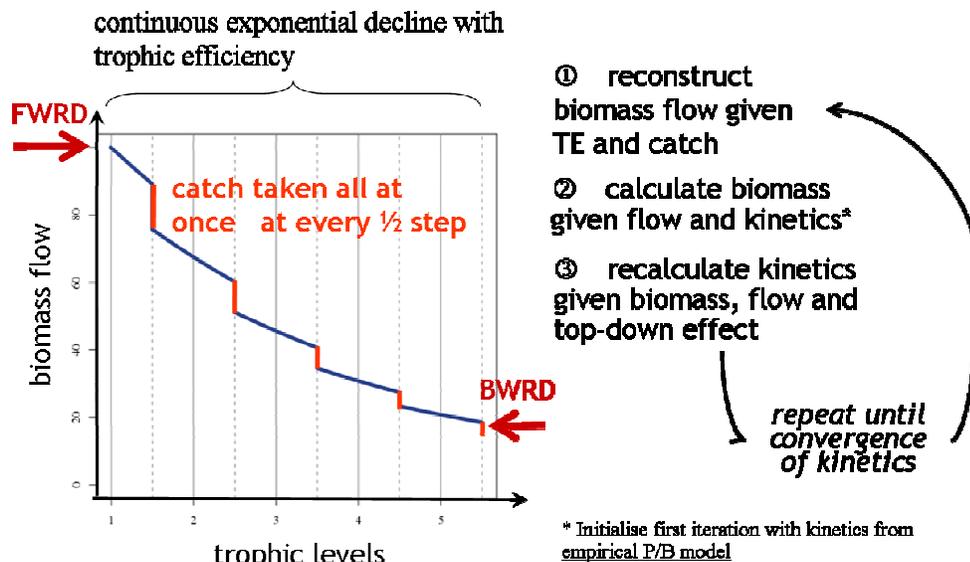


Figure 31 - Schematic representation of how ET-CTSA works.

The unexploited state of the ecosystem is calculated by assuming that the empirical P/B model refers to the unexploited state and that the biomass flow at the primary producers' level is the same in the exploited and unexploited states. The biomass flow for consumers of trophic levels 2 and above is then calculated from the primary production and the transfer efficiency (since fishing loss rate is 0). The unexploited biomass flow is combined with the empirical P/B model (equation 2) to calculate biomass by trophic levels. The final output of the CTSA is thus biomass trophic spectra for the ecosystem in the exploited and unexploited states, in addition to the other ecosystem variables defining the EcoTroph model as found in ET-Main table.

The CTSA is a great tool in data-poor systems because it allows the reconstruction of the state of the whole ecosystem with little data. However, one must be careful upon interpreting the results as the model can be sensitive to errors in the input parameters. When running both the forward and backward versions of the CTSA, we advice to use different values for the input parameters in order to explore the sensitivity of the model's results to assumptions. Additionally, the model's results should be verified against an independent data set, which can then be used as a guideline to adjust uncertain parameters such as the trophic efficiency.

3.3. How to use

Summary: To run the ET-CTSA routine, enter the required parameters under 'Basic parameters', making sure to import properly formatted .csv files if working directly with catch data. Run a default version of the algorithm of choice by selecting 'Forward calculations' or 'Backward calculations', select the type of initialising value under the 'Unexploited' tab, enter the corresponding value in the highlighted green cell and click 'Calculate' to compute the final version of the model.

3.3.1. Basic parameters

▪ Catch trophic spectrum

In order to run ET-CTSA, first click on CTSA 'Basic parameters'. Figure 32 shows the 'Basic parameters' table. If a catch trophic spectrum is already available for the ecosystem, it can be entered manually under the green cells by the 'Catches' column. If using an independent set of catch data for the

ecosystem under focus, the catch/mean TL data need to be entered in a .csv file, after which it can be imported in the CTSA routine which will automatically transform it to a catch trophic spectrum during the import process.

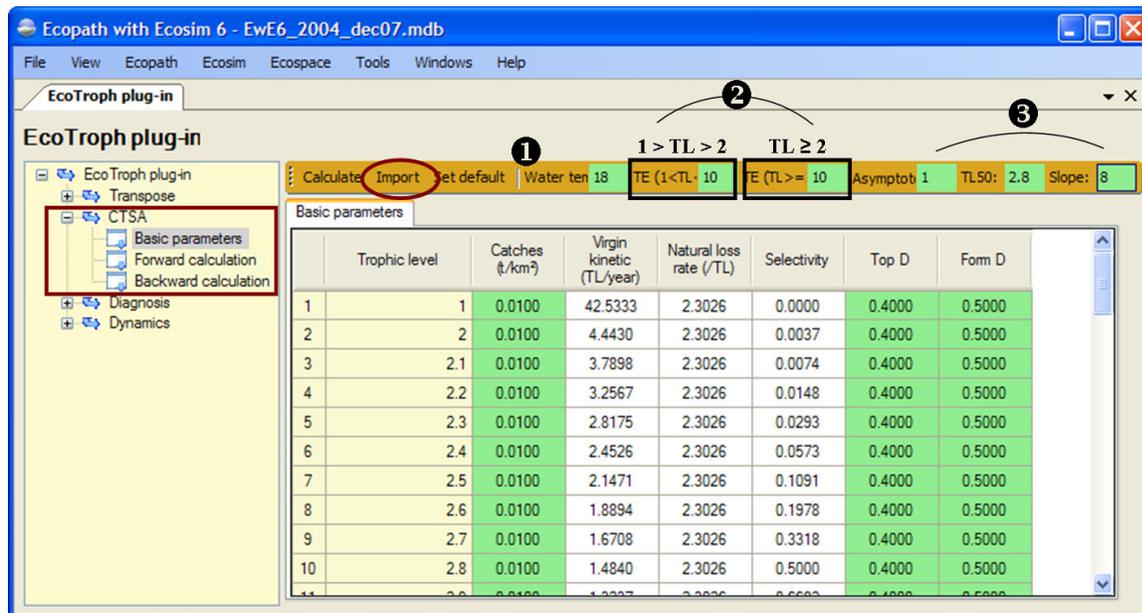


Figure 32 - Basic parameters table of ET-CTSA

The input data file can easily be created in Excel, from which it can then be saved as a .csv file. The required file format is described below for both the 'Automatic smooth' and 'User defined sigma' options (see 'ET-smooth' box in Part I for more details on smoothing – note that the omnivory index option is only available when an Ecopath model is used as a data source). Once the file has been created in the required format, click 'Import' to select the file and the smoothed catch data will be imported into the routine.

- *Other parameters*

Once the catch data is imported, the remaining parameters can be set in the 'Basic parameters' table (use Fig. 32 as a reference for the explanation below). The reference flow kinetics is calculated from the theoretical P/B model using the water temperature which is set in Celsius under (1) (default=18 °C). Transfer efficiency is set under (2) as the proportion of biomass flow left (expressed in %) for each +1 step in trophic level (default =10%). Different values can be put for the interval between trophic levels 1 and 2 and trophic levels 2 and higher. Selectivity is assumed to follow a logistic curve over trophic levels and its shape can be set at (3) by defining the asymptotic value, the trophic level at which the curve reaches half of its asymptotic value and the strength of the slope of the curve (default values are 1, 2.8, 8 respectively). Top-down alpha (Top D) and shape (Form D) parameters can be directly entered in the table for each trophic level under the green cells. When all the basic parameters are set to the desired value, click on 'Calculate' for the settings to take effect.

- *File format if using 'Automatic smooth' for the catch trophic spectrum*

Use Figure 33 as a reference. The top-most row of the Excel spreadsheet should indicate 'Automatic smooth' (Fig. 33, cell A1) and the first cell of the second row should contain the value for the smooth parameter (cell A2). The first column from the third row onwards contains the name of the species/species group corresponding to the catch data (column A), the second column has their trophic level (column B), the other columns contain the catch. If catch occurs for more than one fishery type, the corresponding catch data can be entered in separate columns (for e.g., columns C and D).

	A	B	C	D	E
1	Automatic smooth				
2		0.075			
3	Whales	4.021554	0	0	
4	Dolphins	4.631557	0	0	
5	Turtles	2.19375	0	0	
6	Sea birds	3.810006	0	0	
7	Rays+	4.12213	0.012	0.024	
8	Sharks+	4.342297	0.007	0.003	
9	Large pelagics	4.318938	0.025	0.069	
10	Barracudas+	4.123038	0.009	0.022	
11	Carangids	4.200097	0.01	0.024	
12	Horse mackerels+	3.129251	0	0.115	
13	Ethmalosa	2.53125	0.946	0	
14	Sardinella+	2.882645	0.058	0.139	
15	Bobo croaker	3.997563	0.191	0.069	
16	Other croakers	3.979	0.074	0.06	
17	Lesser Afr. threadfin	3.925325	0.002	0.075	
18	Giant Afr. threadfin	4.05512	0.023	0.004	
19	Royal threadfin	3.953913	0.007	0.004	
20	Seabream+	3.680943	0.038	0.07	
21	Sea catfish	3.700952	0.183	0.035	

Figure 33 - Required format of an Excel spreadsheet to input catch data with the Automatic smooth model, to be saved as a .csv file.

- *File format if using 'User defined sigma' for the catch trophic spectrum:*

Use Figure 34 as a reference. The first cell of the Excel spreadsheet contains 'User defined sigma' (Fig 12, cell A1), the first column from the second row onwards should contain the name of the species/species group corresponding to the catch data (column A), the second column has their trophic level (column B) and the other columns contain the catch. Catches taken in more than one fishery type can be entered in separate columns (for e.g., columns C and D). The user-specified species/species group TL standard deviation (*sigma*) is entered in the **last** column (column E).

	A	B	C	D	E
1	User defined sigma				
2	Whales	4.021554	0	0	0.059
3	Dolphins	4.631557	0	0	0.331
4	Turtles	2.19375	0	0	0.338
5	Sea birds	3.810006	0	0	0.353
6	Rays+	4.12213	0.012	0.024	0.329
7	Sharks+	4.342297	0.007	0.003	0.633
8	Large pelagics	4.318938	0.025	0.069	0.263
9	Barracudas+	4.123038	0.009	0.022	0.259
10	Carangids	4.200097	0.01	0.024	0.1346
11	Horse mackerels+	3.129251	0	0.115	0.3671
12	Ethmalosa	2.53125	0.946	0	0.2868
13	Sardinella+	2.882645	0.058	0.139	0.6095
14	Bobo croaker	3.997563	0.191	0.069	0.0644
15	Other croakers	3.979	0.074	0.06	0.1311
16	Lesser Afr. threadfin	3.925325	0.002	0.075	0.0983
17	Giant Afr. threadfin	4.05512	0.023	0.004	0.1264
18	Royal threadfin	3.953913	0.007	0.004	0.0552
19	Seabream+	3.680943	0.038	0.07	0.4937
20	Sea catfish	3.700952	0.183	0.035	0.2437

Figure 34 - Example of format of an Excel spreadsheet when entering catch data to be smoothed using a user defined sigma.

3.3.2. CTSA Forward

When selecting 'Forward calculation', a default version of the Forward CTSA is calculated and presented under the 'Main' tab for the current ecosystem state and under the 'Unexploited' tab for the unexploited state of the ecosystem. Under the 'Unexploited' tab, the Forward CTSA can be initialized with either biomass or production at trophic level one or two. Choose the appropriate option under the 'Initialization' drop-down menu and the cell where the initial value should be entered will be highlighted in

green (Fig. 35). Click ‘Calculate’ once the required value is entered and the CTSA Forward algorithm will run again and update the values in the ‘Main’ and ‘Unexploited’ tables accordingly.

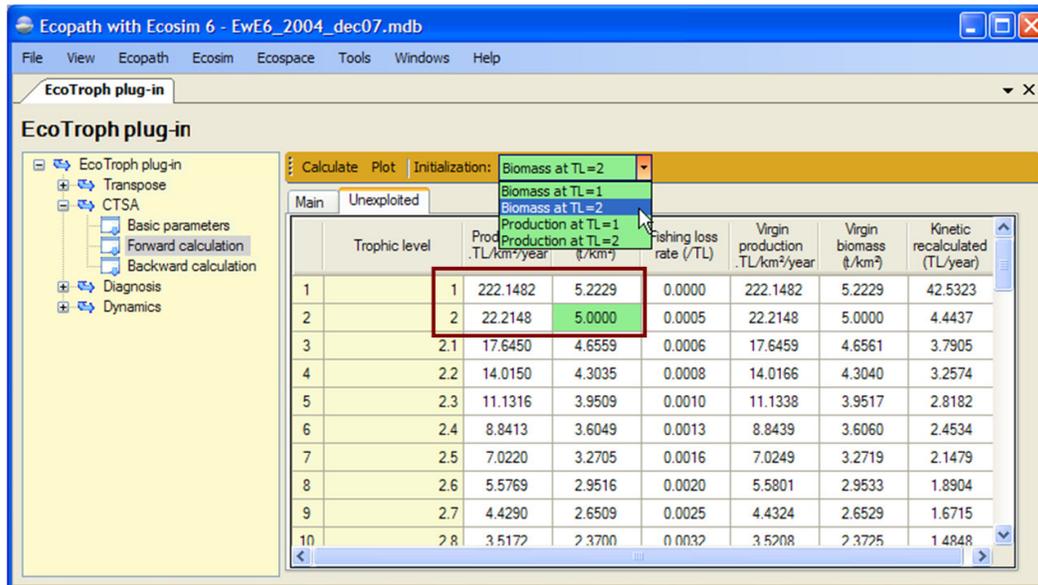


Figure 35 - ET-CTSA Forward calculation

3.3.3. CTSA Backward

As for the CTSA Forward, a default version of the Backward CTSA is calculated when selecting ‘Backward calculation’, the ‘Main’ tab shows values for the current ecosystem state and the ‘Unexploited’ tab shows values for the unexploited state of the ecosystem. Additional parameters can be adjusted under the ‘Unexploited’ tab. In the Backward CTSA the user defines the value of the terminal trophic level (‘Terminal TL’) and initialises the model with the accessible fishing mortality or fishing loss rate at that trophic level (Fig. 36). Select the desired option under ‘Initialization’ and scroll down the table to the row with the terminal trophic level to input the corresponding value in the cell highlighted in green. Press ‘Calculate’ for the settings to take effect and for the updated versions of the ‘Main’ and ‘Unexploited’ tables to become available.

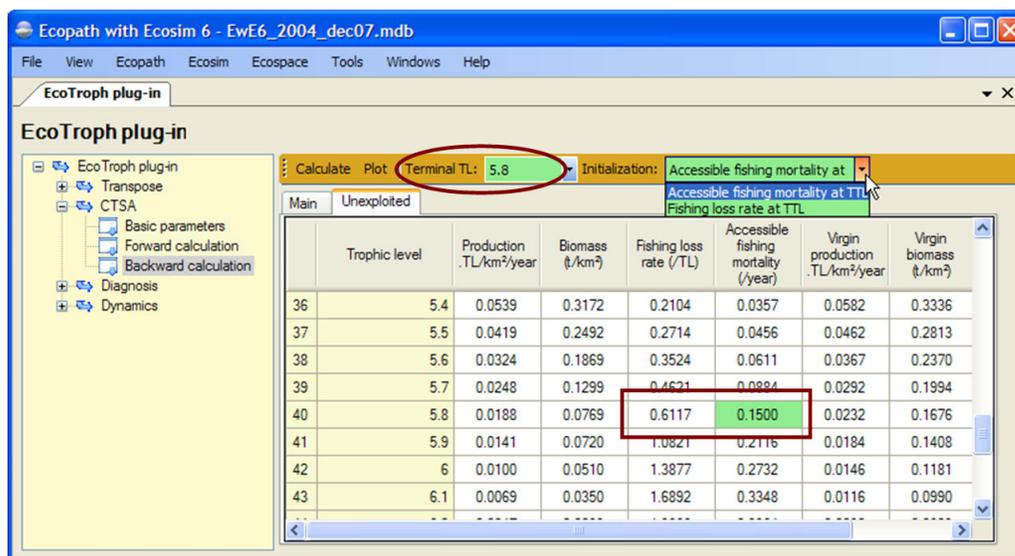


Figure 36 - ET-CTSA Backward calculation

It is advised to set the terminal trophic level to values around 5, corresponding to what is observed in many marine systems. The CTSA tables show values up to trophic level 7 because of the top-down effect included in EcoTroph which requires an estimate of biomass for higher trophic levels in order to evaluate biomass at current trophic levels. Note also that the CTSA calculation automatically extends trophic levels to 7 so that the biomass at the terminal trophic level can be estimated, but the backward model is still initialized at the value set by the user.

3.3.4. Results

The CTSA routine produces an EcoTroph model from catch data and a set of additional parameters. The model's attributes are presented under the 'ET-Main' tab for the current ecosystem state (that is, the one that yielded the input catch trophic spectrum) and under the 'Unexploited' tab for the state of the ecosystem where no fishing takes place. A summary plot comparing the current state to the unfished one can be produced by selecting 'Plot' under the 'Unexploited' tab for both the CTSA Forward and Backward (see Fig. 37): the top-most plot compares biomass and production trophic spectra for exploited and unexploited states, as well as shows catches. The center plot summarizes fishing loss rate and accessible fishing mortality by trophic level. The bottom plot shows compares kinetics under exploited and unexploited states.

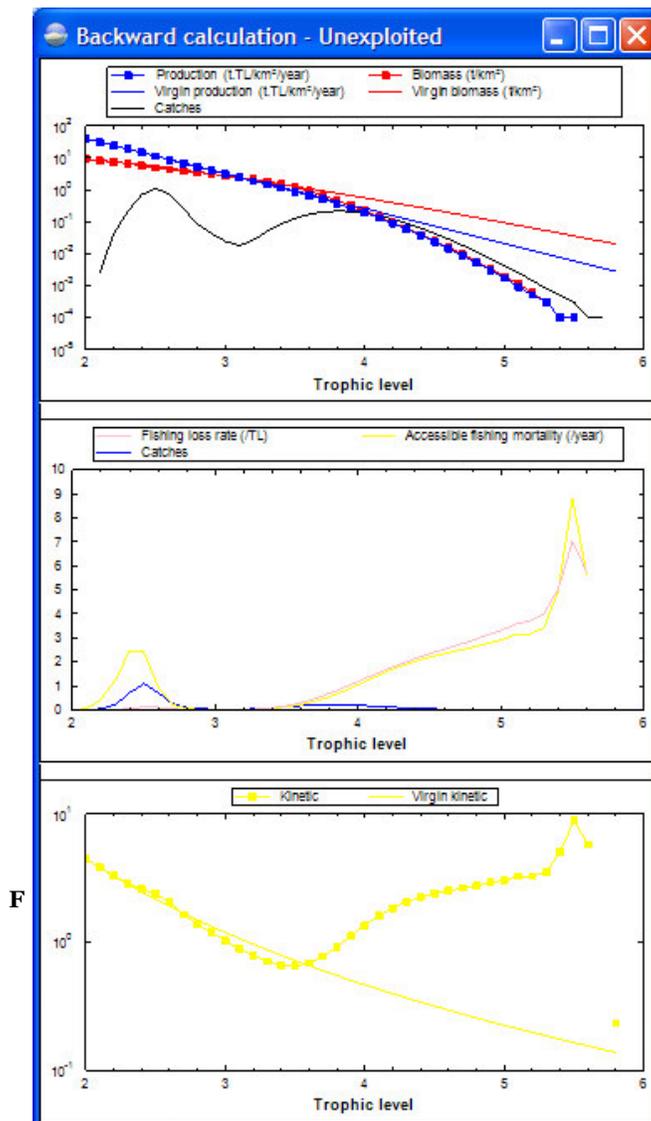


Figure 37 - Example of figures produced under the 'Unexploited' tab of ET-CTSA

3.4. Example of application

Catch and mean TL data for the Guinea Current ecosystem in 2004 were used as input to the CTSA-backward routine (Fig. 38). Mean trophic efficiency was set at 8% for TL>2 and a water temperature of 28 °C was used to define the theoretical P/B.

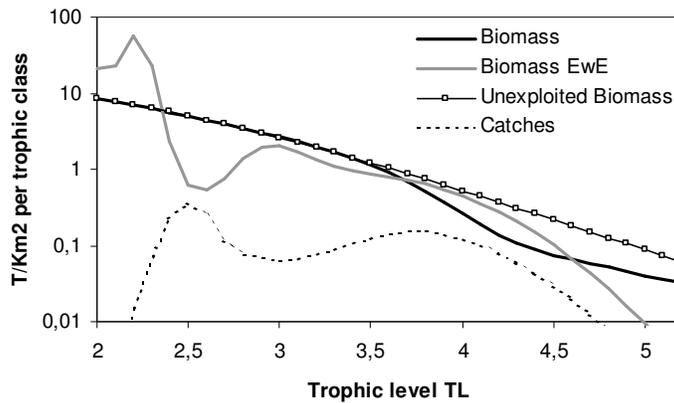


Figure 38 - Biomass trophic spectrum estimated from the CTSA data applied to the 2004 Guinean catch data; comparison with independent Ecopath estimate

Figure 16 shows the biomass, unexploited biomass and catch trophic spectra derived with the CTSA backward as well as the biomass trophic spectrum from the Guinea Current Ecopath model for comparison. The CTSA-derived biomass values per trophic levels are consistent with the Ecopath model and scientific surveys, showing a three-fold decrease in biomass for high trophic levels. The shape of the biomass trophic spectrum is however much smoother than that obtained from the Ecopath model, which can be explained by the use of a monotonous kinetics model.

4. ET-Diagnosis: using EcoTroph for simulation and global diagnosis

4.1. What is it used for?

ET-Transpose and ET-CTSA allow to obtain a picture of an ecosystem under a given fishing mortality. ET-Diagnosis is a routine that can simulate how this baseline ecosystem would be impacted by increasing or decreasing fishing effort. Ecosystem-wide effects of altering fishing effort include potential changes of biomass, accessible biomass, production, kinetics and catch trophic spectra as well as impacts on the mean trophic level of the catch, biomass and accessible biomass (see § 2.4).

Additionally, ET-Diagnosis can be a useful exploratory tool for ecosystem-based management by simulating how reducing or increasing fishing effort and/or preferentially targeting different trophic levels could improve yield at the ecosystem scale.

Lastly, ET-Diagnosis allows to view how different assumptions about ecosystem functioning, more specifically the extent recycling ('biomass-input control'; see § 1.6.2) or trophic control by higher trophic levels ('top-down'; see § 1.6.1), can have effects on both trophic level specific and ecosystem-wide properties in relation to fishing.

4.2. How it works

The ET-Diagnosis routine simulates the effects of changing fishing effort given a baseline EcoTroph model generated through ET-Transpose or ET-CTSA. The change in fishing effort is induced by multiplying the fishing mortality from the baseline model for each trophic level by a constant factor (set automatically or by the user; see below). Since the primary production is assumed to be unaffected by fishing effort, the biomass flow can be recalculated from the primary production of the baseline model, the transfer efficiency and the new values for the fishing mortalities using the following equation:

$$\Phi_{\tau+\Delta\tau} = \Phi_{\tau} \cdot \exp[-\mu_{\tau} + FM \cdot \phi_{\tau} \cdot \Delta\tau]$$

where FM is the effort multiplier, which is constant over all trophic levels.

The model is initialised by updating the baseline kinetics (P/B) with the new fishing mortality, recalculating biomass given the new biomass flow and up-dating P/B to account for the top-down effect (equation 25). Once the input and output P/B have converged, the biomass flow at trophic level one is recalculated to account for biomass-input control (equation 27) until input and output primary productions converge.

4.3. How to use it

Summary: *To run ET-Diagnosis, select the model source under ‘Basic parameter’, (making sure accessibility/selectivity was set to the desired values when the model was initially constructed), and enter a value for biomass-input control (beta) and the top-down effect (Top D and Form D). To run the model, click on the desired effort multiplier option. If using the ‘User defined effort multipliers’ option, select the option and then enter the desired effort multiplier under any of the results tables past the ‘Summary’ table.*

4.3.1. Basic parameters

To use the ET-Diagnosis routine, first select ‘Basic parameters’ under the Diagnosis option of the EcoTroph plug-in tree. There needs to be an already built EcoTroph model available, constructed either through ET-Transpose or ET-CTSA as described in previous sections of this manual. Click ‘Main from’ and select the desired option from the drop-down menu (Fig. 39, option 1). Note that user-settings specified when initially building the model under Transpose or CTSA (like selectivity) will be conserved when the corresponding ET-Main table is imported in the Diagnosis routine.

Enter the biomass-input control parameter (beta) (see § 1.6.2) (Fig. 39, option 2), and the top-down parameters, ‘Top D’ (alpha) and ‘Shape D’ (gamma) (see § 1.6.1) (option 3). Note that both beta and Top D are values between 0 and 1. Alternatively, clicking ‘Set default’ will set beta at 0, Top D at 0.4 and Shape D at 0.5 for all trophic levels. Once all the basic parameters are entered and the data source for the model is selected, click ‘Calculate’ (option 4) to import values into the routine.

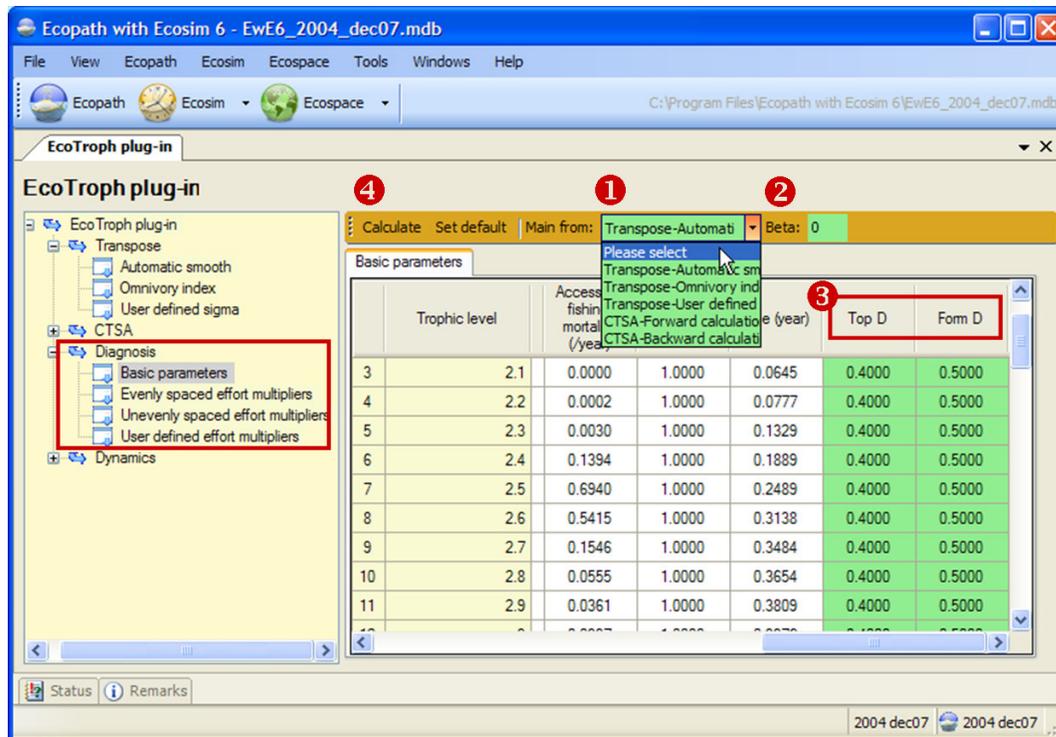


Figure 39 - ET-Diagnosis 'Basic parameters' input

4.3.2. Running the routine:

ET-Diagnosis multiplies the reference ecosystem's fishing effort by a range of values and recalculates relevant ecosystem properties for each new fishing state. There are three options available to define the values by which the reference fishing effort is to be multiplied:

- 1) Evenly spaced effort multiplier: multiplies the reference fishing effort by values between 0 and 2, evenly spaced in intervals of 0.2;
- 2) Unevenly spaced effort multiplier: the reference fishing effort is multiplied by values in the 0 to 5 range, with smaller intervals between 0 and 1;
- 3) User-defined effort multiplier: the user can manually specify the effort multiplier values to be used by clicking on any results tabs after the 'Summary' tab and entering the desired effort multipliers in the first row, with one value per column (the input row is highlighted in green) (Fig. 40 option 1).

Options 1 and 2 run automatically when selected under the EcoTroph Plug-in tree. Option 3 requires the user to manually set the desired effort multiplier values, as explained above.

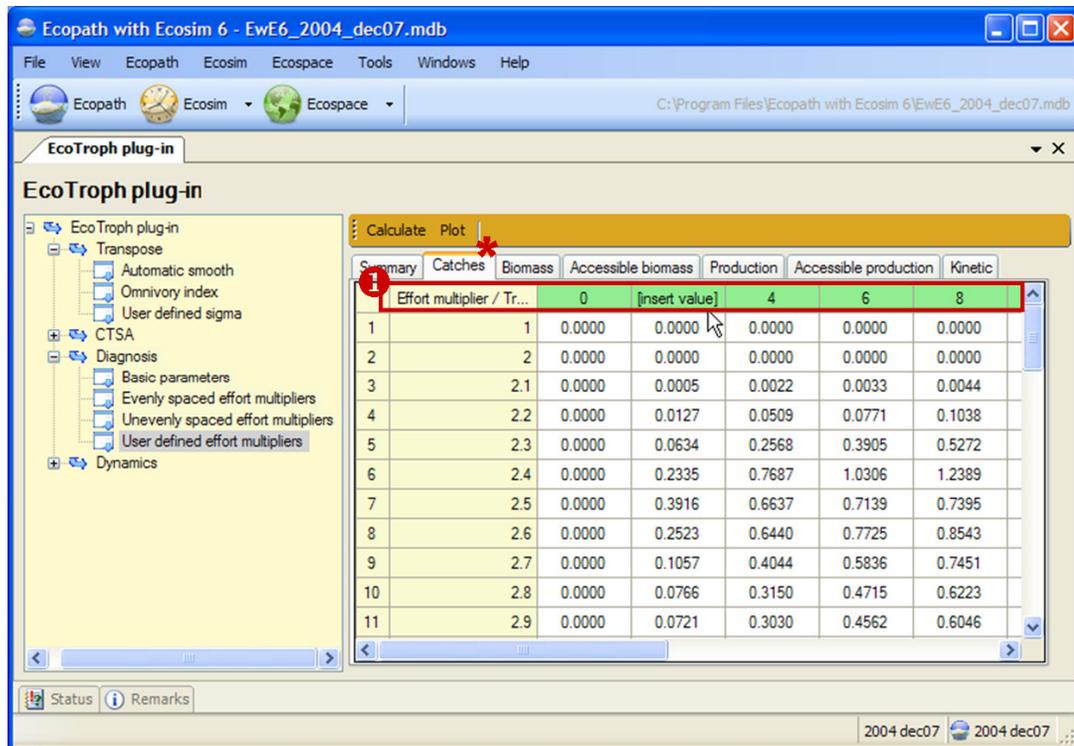


Figure 40 - ET-Diagnosis 'User defined effort multipliers' input

4.3.3. Results

The ET-Diagnosis routine provides two types of results for each different fishing effort simulated: (1) summary statistics for the whole ecosystem, including absolute and relative values compared to the baseline scenario ('Summary' tab); (2) catches, total and accessible biomass and production, kinetics for all trophic levels (each under a separate tab).

- Summary statistics:** For each fishing effort multiplier, ecosystem values (that is, summed over all TLs) for biomass, predator biomass, production, catch and predator catch are presented in absolute format (that is, the actual value in tons/km² for the ecosystem) and in relative value compared to the baseline scenario (where the fishing effort multiplier = 1). Note that the predator biomass conventionally refers to trophic levels 3.5 and higher. The mean trophic level of the total and accessible biomass and of the catch is also provided, allowing to detect trends like 'fishing down the food web' and ecosystem-wide trophic impacts of fishing. Two different plots are produced by the 'Summary' tab (Fig. 41). The top one compares relative values of biomass, predator biomass and catch by fishing effort multiplier. The bottom one shows the mean trophic level of the biomass, production and catch by fishing effort multiplier.
- Ecosystem properties by trophic levels:** Trophic level-specific values are presented for each effort multiplier under a separate tab for the following variables: catches, total and accessible biomass and production, kinetics. The effort multipliers are in columns and the trophic levels in rows. The figures produced by clicking the 'Plot' button under each tab overlay line plots of the variable of interest by trophic level (say catches if you press 'Plot' under the 'Catches' tab), with different colours for each effort multiplier (Fig. 42).

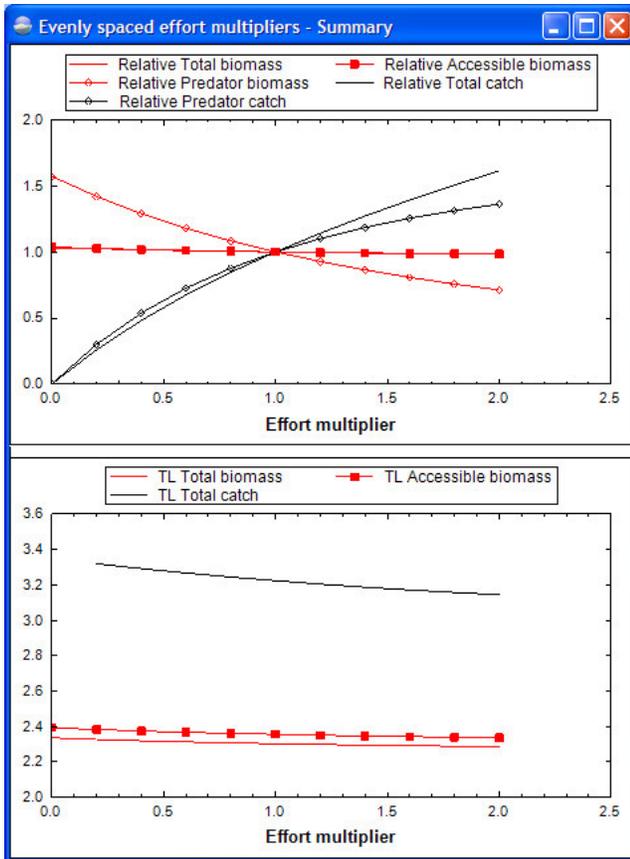


Figure 41 - Plot produced under ET-Diagnosis 'Summary' tab

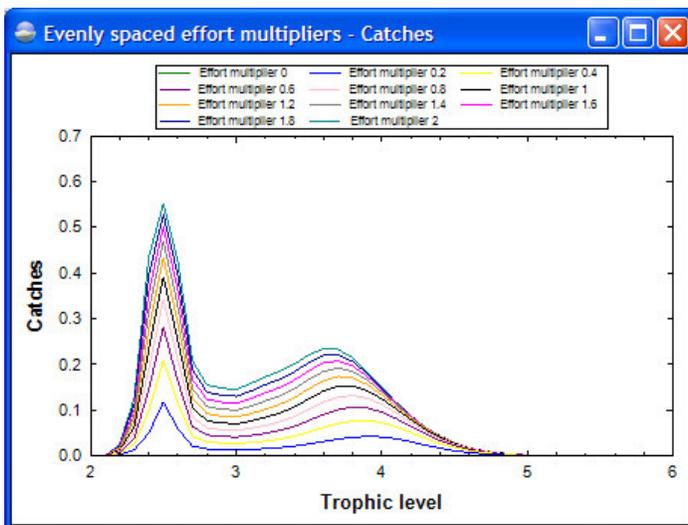


Figure 42 - Plot produced under ET-Diagnosis 'Detailed results' tab.

4.4. Example of application:

An EcoTroph model of the Guinea Current ecosystem for the year 2004 was used as a baseline to run the ET-Diagnosis routine using fishing effort multipliers between 0 and 5 (Gascuel *et al.* 2008a). The simulation highlighted a three-fold decrease in biomass of high trophic levels from the unfished (fishing effort multiplier = 0) to the current state (fishing effort multiplier = 1) (Fig. 43 bottom left). This result is consistent with independent scientific surveys, which are available since the beginning of the fishery in the

80s and also indicate an around three-fold decrease in abundance of high TLs (Gascuel *et al.* 2004; Laurans *et al.* 2004). Consequently, the decreased abundances result in an over-exploitation of the high trophic levels, as shown by a decline in relative catch with increasing fishing effort (Fig. 43 bottom right). These results confirm and generalize previous single species assessments (Gascuel *et al.*, 2004, Sidibé *et al.*, 2004). Simulating fishing effort higher than the baseline 2004 state (fishing effort multiplier >1) also shows that ecosystem yield could increase, but with a decrease in the mean trophic level of the catch (Fig. 43 top right). This would, however, induce a further decrease in the abundance of high trophic levels, with likely impacts on ecosystem structure, function and health.

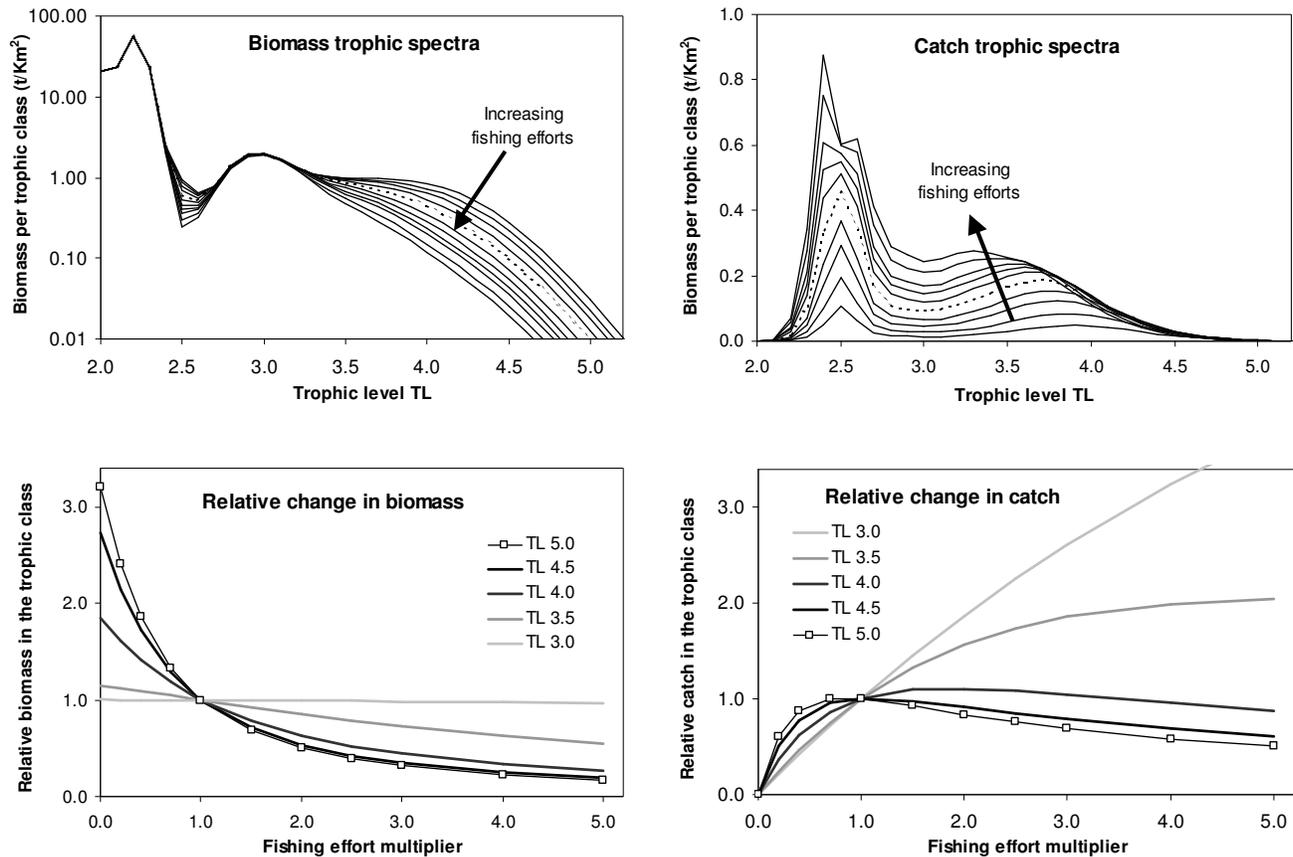


Figure 43 - Simulation of impact of increasing fishing effort on biomass (right) and catches (left) of the Guinean ecosystem. Top panels refer to biomass and catch trophic spectrum, where dashed lines represent the 'current' (i.e. 2004) situation. In the bottom panels, the relative values of biomass and catch for the trophic classes are expressed as a function of the multiplier of the current fishing mortality.

5. ET-Dynamic: using EcoTroph with time series

5.1. What is it used for?

The EcoTroph routines presented so far give a static representation of the state of the ecosystem, that is, a snapshot of how the ecosystem is at one point in time. However, the EcoTroph model also has a temporal dimension through the speed of the flow by trophic level (i.e. the kinetics), which is in TL.year⁻¹. It is thus possible to extend the model into time to obtain a dynamic version of EcoTroph. The ET-Dynamics routine is a tool that can apply the dynamic version of EcoTroph to derive representations of the ecosystem of interest for past and future years, given that an EcoTroph model is available for at least one year.

ET-Diagnosis can hindcast ecosystem properties when provided with a time-series of catch trophic spectra (which EcoTroph can create from a time-series of catch data, given the trophic levels of the catch). In addition of the biomass trophic spectra, an interesting output of this exercise is the time-series of fishing mortality by trophic level, which allows to study how or whether a fishery has shifted its trophic focus over time.

ET-Dynamics can also forecast fishing mortalities and ecosystem properties like catch and biomass. Different exploitation patterns can be simulated in order to evaluate the potential ecosystem impact of fishing policies, both in terms of the optimal fishing effort to be applied and the trophic levels that should be targeted to optimize a given policy objective (for e.g. maximize ecosystem yield on the long-term). Moreover, ecological questions about ecosystem functioning can be explored, for instance by looking at the interaction between the top-down effect and the consequences of fishing on ecosystem properties.

5.2. How it works

The dynamic version of EcoTroph (see § 1.8) is derived by taking advantage of the fact that time is already accounted for in the flow kinetics, that is, the units of the speed of the flow are TL year⁻¹. This property can be used as a building block to transform the equations describing an EcoTroph model so that they are in function both of time instead and trophic level.

Before doing this however, in order to have constant time intervals one must account for the fact that the kinetics are not constant over trophic levels since the flow slows down at higher levels (i.e. it takes more time for biomass to move between levels 4 and 5 than between levels 2 and 3). Therefore, trophic level intervals have to be adjusted to the correct length such that each interval corresponds to a constant time unit, set at 0.1 year. This results in shorter intervals for lower trophic levels and larger intervals for higher trophic levels (see Fig. 7 in § 1.8; equation 39).

Each time step is initialised with production at TL=2, which is derived from the primary production and beta (the biomass input control parameter) using equations 26 and 27. Additionally, the first iteration must be initialised with either the biomass or the flow, which allows to compute kinetics for the first time-step. To derive the biomass flow, an estimate of fishing mortalities is required. When hindcasting, catches are used as input and fishing mortalities are derived from equation 42. When forecasting, the user directly provides a time-series of fishing mortalities, which are used in the calculation of the biomass flow and also to produce a time-series of catches by trophic level. Given the transfer efficiency and the fishing loss rate, the biomass flow at time step $t+0.1$ and trophic level $\tau+\Delta\tau$ can then derived from the flow at time t and trophic level τ (equation 40).

Once the flow is calculated, the biomass can be derived given the flow and the kinetics (equation 41). As with the steady-state model, the kinetics must be updated iteratively since they are related to the biomass with the top-down effect. The ET-dynamics algorithm is thus repeated for each time step until stabilisation of the kinetics, that is, when the input P/B are equal to the output P/B.

Note that in order to simulate different environmental conditions, it is possible to set a primary production index ('Index PP') which multiplies by a user-defined factor the primary production from the baseline model. Similarly, different fishing pressures can be represented by setting a 'Catch multiplier', which multiplies the fishing mortality from the baseline model by a user-defined value.

5.3. How to use it

Summary: To run ET-Dynamics, first make sure a baseline EcoTroph model is available and import it under 'Basic Parameters'. Biomass-input control and the top-down effect are also set in 'Basic Parameters'. To forecast, click on 'Catch forecast', enter the baseline year and number of years to be forecasted, set 'Index PP' and 'Catch multiplier' parameters, and press 'Calculate' in order to simulate catches, biomass

and biomass flow for the coming years. To hindcast, first construct a properly formatted file of historical catch data and import it by clicking 'Catch past analysis', set 'Index PP' and 'Catch multiplier' parameters, and click 'Calculate' to estimates biomass, biomass flow and fishing mortalities, per trophic class and for the whole ecosystem, for each year of the past time series.

5.3.1. Input parameters

To use ET-Dynamics, first construct a baseline EcoTroph model from either ET-Transpose or ET-CTSA, making sure selectivity/accessibility by trophic level has been updated to the desired values. Select 'Basic parameters' under 'Dynamics' in the EcoTroph plug-in tree, choose the routine from which to extract the EcoTroph model under the drop-down menu (Fig.44 option 1) and click 'Calculate'. Two tables, 'Basic parameters' and 'Interpolated parameters', are produced. 'Basic parameters' is the usual version of EcoTroph Main table referring to the first year of the dynamic simulation. 'Interpolated parameters' presents the same variables but interpolated over trophic levels intervals that correspond to constant time-steps of 0.1 year, as explained in § 5.2. Under the 'Interpolated parameters' tab, biomass-input control (ref. § 1.6.2) can be set from a value of 0 to 1 under 'Beta' (Fig.44 option 2) and top-down control (ref. § 1.6.1) can be set under 'Top D' and 'Form D' (Fig.44 option 3 – the last two columns in the table).

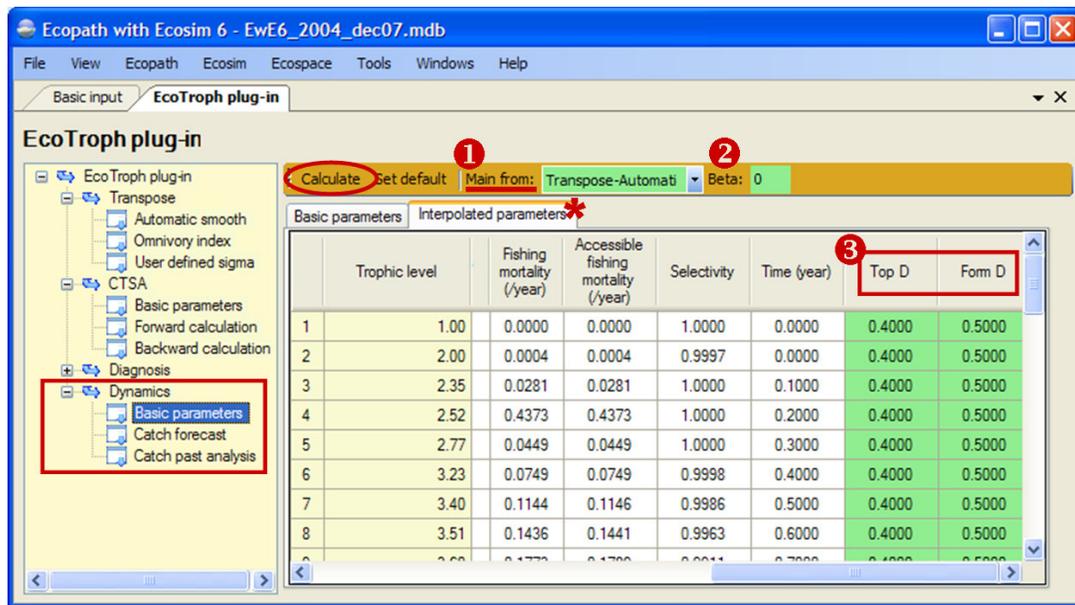


Figure 44 - Screenshot of 'Basic parameters' window of ET-Dynamics

5.3.2. Catch forecast

To forecast the EcoTroph model in time and predict biomass and catch trophic spectra, select 'Catch forecast'. Enter the reference year (Fig.45 option 1) and the number of years to be forecasted (Fig.45 option 2). For each of the forecasted years, enter under 'Catch multiplier' the value by which the fishing mortality for the baseline model should be multiplied and under 'Index PP' the value by which the primary production should be multiplied (leave it at one if it stays constant over time) (Fig.45 option 3). Press 'Calculate' once all the values have been entered.

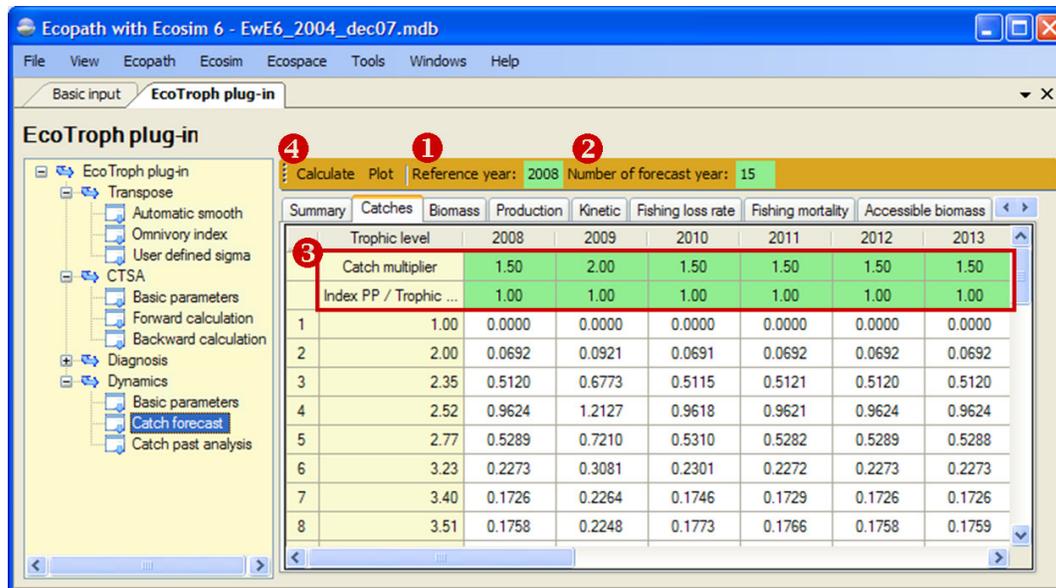


Figure 45 - Screenshot of 'Catch forecast' window of ET-Dynamics

5.3.3. Catch past analysis

To hindcast the EcoTroph model from historical catch data and derive biomass trophic spectra and fishing mortalities, first make sure to have a properly formatted historical catch data file. The catch data has to be smoothed and the user has the option of using the theoretical smooth model (see the 'ET-Smooth' box) or setting the sigma manually for each species/species group. The file can easily be created by entering the data in an Excel spreadsheet and saving as a .csv file.

- *File format if using 'Automatic smooth' for the catch trophic spectrum:*

Use figure 46 as a reference. Enter 'Automatic smooth' in the first row of the spreadsheet (Fig.46, cell A1) and type the value for the smooth factor in the second row (cell A2). In the third row, from the first column onwards input the year vector for the historical catch data, starting with the oldest (one year per column – cells C1 onwards). From the fourth row onwards, enter in the first column the names of the species/species group for which there is catch data (column A), in the second column the corresponding trophic levels of the species/species group (column B) and the reminding columns the catch data for the species/species group by year (column C onwards, so that years in row 3 cells C1+ correspond to catches in cells C3+). Save the file as a .csv file when all the data is entered.

	A	B	C	D	E
1	Automatic smooth				
2	0.075				
3	1985	1986	1987	1988	1989
4	Whales	4.021554	0	0	0
5	Dolphins	4.631557	0	0	0
6	Turtles	2.19375	0	0	0
7	Sea birds	3.810006	0	0	0
8	Rays+	4.12213	0.0132	0.0164	0.0187
9	Sharks+	4.342297	0.0089	0.0108	0.0125
10	Large pelagic	4.318938	0.0323	0.0231	0.0254
11	Barracudas+	4.123038	0.0073	0.0095	0.0106
12	Carangids	4.200097	0.007	0.0093	0.0102
13	Horse macke	3.129251	0.0731	0.102	0.1096
14	Ethmalosa	2.53125	0.2611	0.3125	0.3639
15	Sardinella+	2.882645	0.0472	0.0592	0.0673

Figure 46 - Example of format for a spreadsheet with historical catch data to be smoothed using the Automatic smooth model.

- *File format if using 'User defined sigma' for the catch trophic spectrum:*

Use Figure 47 as a reference. If manually entering the standard deviation values for each species/species group (see the 'ET-Smooth' box for more information), proceed similarly but enter 'User defined sigma' in the first row of the spreadsheet (Fig.47 cell A1), the species, trophic levels and historical catch data by year as above (columns A, B and C to G) and input the standard deviations in the very last column (i.e. directly after the most recent year for which catch data is available) (Fig.47 column H). Save as a .csv file.

	A	B	C	D	E	F	G	H
1	User defined sigma							
2	1985	1986	...	2003	2004			
3	Whales	4.021554	0	0	...	0	0	0.059
4	Dolphins	4.631557	0	0	...	0	0	0.331
5	Turtles	2.19375	0	0	...	0	0	0.338
6	Sea birds	3.810006	0	0	...	0	0	0.353
7	Rays+	4.12213	0.0132	0.0164	...	0.0311	0.0246	0.329
8	Sharks+	4.342297	0.0089	0.0108	...	0.0095	0.0045	0.633
9	Large pelagic	4.318938	0.0323	0.0231	...	0.1087	0.0989	0.263
10	Barracudas+	4.123038	0.0073	0.0095	...	0.0279	0.0251	0.259
11	Carangids	4.200097	0.007	0.0093	...	0.0242	0.0452	0.1346
12	Horse macke	3.129251	0.0731	0.102	...	0.1222	0.0794	0.3671
13	Ethmalosa	2.53125	0.2611	0.3125	...	1.2301	0.7586	0.2868
14	Sardinella+	2.882645	0.0472	0.0592	...	0.2376	0.1792	0.6095

Figure 47 - Example of format for a spreadsheet with historical catch data when manually entering standard deviations for each species/species group.

- *Running the routine*

Once the data file has been created in the proper format, click 'Catch past analysis'. This will open a directory window, from which the file to be used as a data source can be selected. Press OK and the routine runs with default values of the primary production index. To adjust the PPindex, enter for each year a value by which to multiply the baseline EcoTroph model's primary production in the row 'Index PP' highlighted in green (this can be done under any tab of 'Catch past analysis') (Fig.48 option 1) and press 'Calculate'. The results presented now account for the new values of the primary production index.

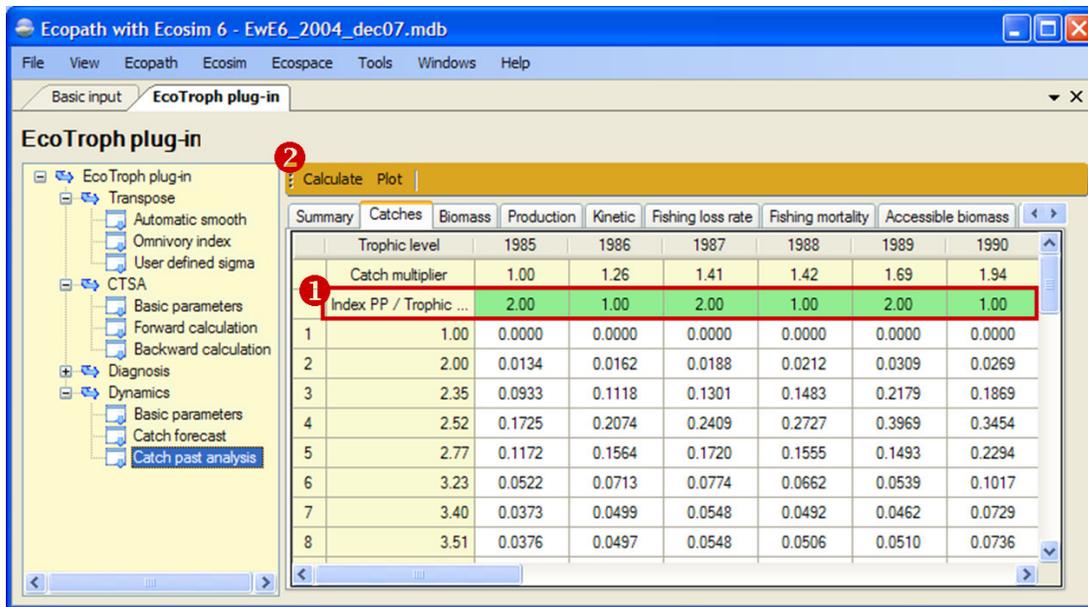


Figure 48 - Screenshot of 'Catch past analysis' window of ET-Dynamics

5.3.4. Results

Both the 'Catch forecast' and 'Catch past analysis' routines provide a summary table where total, accessible and predator biomass and production are given for each year, as well as total catch and predator catch (predators defined as TL > 3.5). The figure produced under the 'Summary' tab shows, in the first plot, the accessible biomass and production over time, and in the second plot the total catch and predator biomass, production and catch over time (Fig. 49).

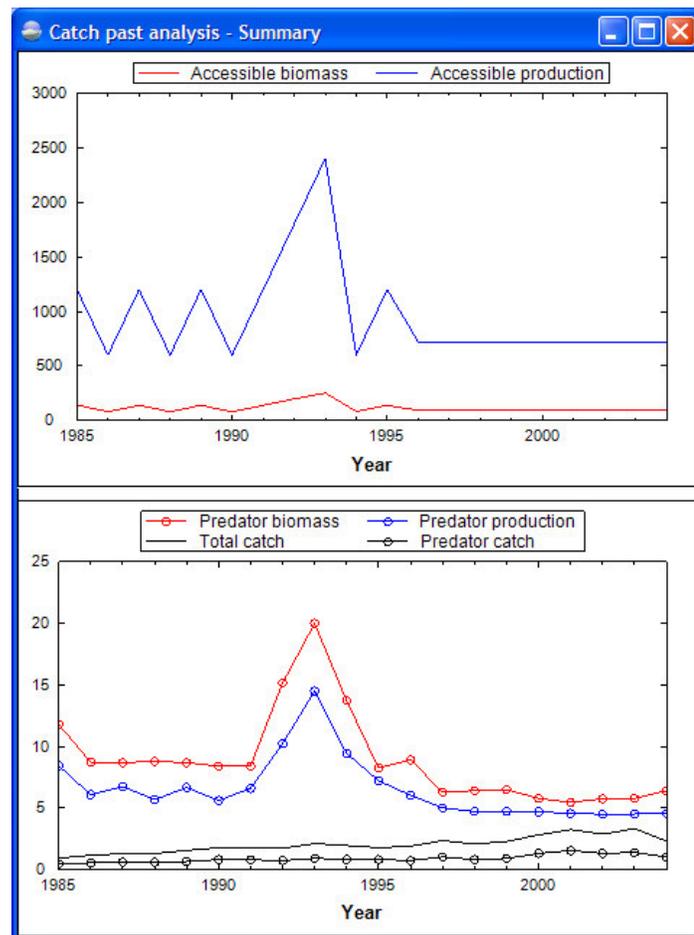


Figure 49 - Example of a plot produced under ET-Diagnosis 'Summary'

Additionally, the following values are given by trophic levels for each year (with the trophic level intervals spaced to be equivalent to 0.1 time step): catches, biomass, production, kinetic, fishing loss rate, fishing mortality, accessible biomass, accessible fishing loss rate, accessible production, the updated kinetics and the predator biomass (each under their individual tab). A line plot can be produced for any variable by clicking 'Plot', with each line representing a different year. Figure 50 shows as an example catch trophic spectra over time, computed with the 'Catch past analysis' routine.

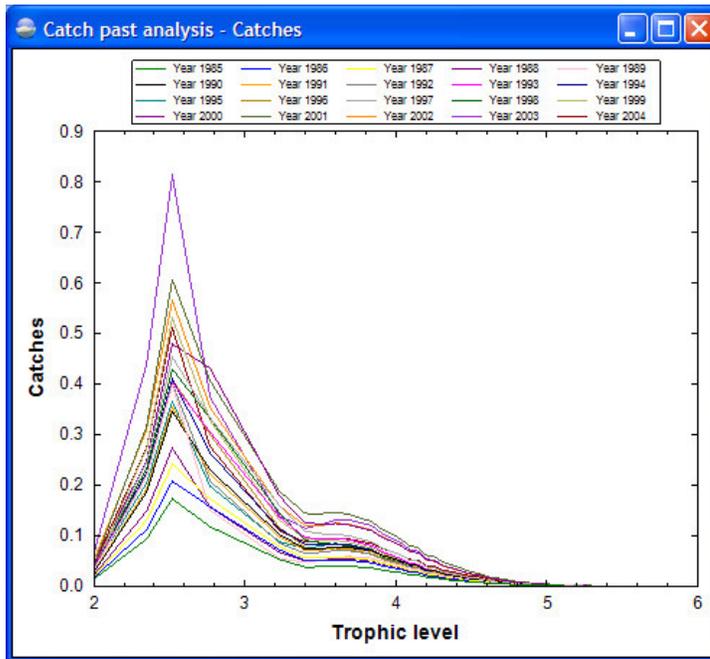


Figure 50 - Example of a plot (catch) produced under ET-Dynamics' detailed results tables.

5.4. Example of application

The Guinean case study illustrates the use of ET-Dynamic for hindcasting (Fig.51). The model is initialised by a baseline EcoTroph model derived from the 1985 Ecopath model (using ET-Transpose). Catch trophic spectra for each year of the 1985 to 2004 period are used as input, assuming a constant primary production. During that period of time, the fishing effort strongly and progressively increased, inducing greater catches for all trophic levels (Fig. 51, left panel). The ET-Dynamic routine allows us to estimate biomass trophic spectra and thus total biomass for each year of the period. Thus, we reconstructed the history of the ecosystem biomass over the past 20 years.

Low trophic levels (TL lower than 3) provide high catches (mainly due to the bonga exploitation), but appear little affected by the increasing fishing intensity. Biomass of these TLs is very high and decreases by less than 5%. Conversely, higher trophic levels are more impacted, with decreases in abundance that reach 20% for TLs 3.5 or 4.0 and around 50% for higher TLs (Fig.51, right panel). Globally, these results appear consistent with the decrease observed in scientific surveys or single species stocks assessment. Nevertheless, the decrease based on the EcoTroph dynamic simulation seems a bit underestimated (independent observations indicate a three-fold decrease, see above). This could be due either to a bias in the baseline EcoTroph model (inducing for instance an over-estimation in the mean trophic efficiency), or to a failure in the hypothesis of constant primary productions. More investigations are needed to evaluate these potential explanations.

Additionally, the model indicates that the decrease in biomass did not occur smoothly. It was slow during the first 10 years and accelerated during the 1999 to 2002 period. This observation might be linked to a rapid increase in the fishing mortality at the ecosystem scale (not shown here).

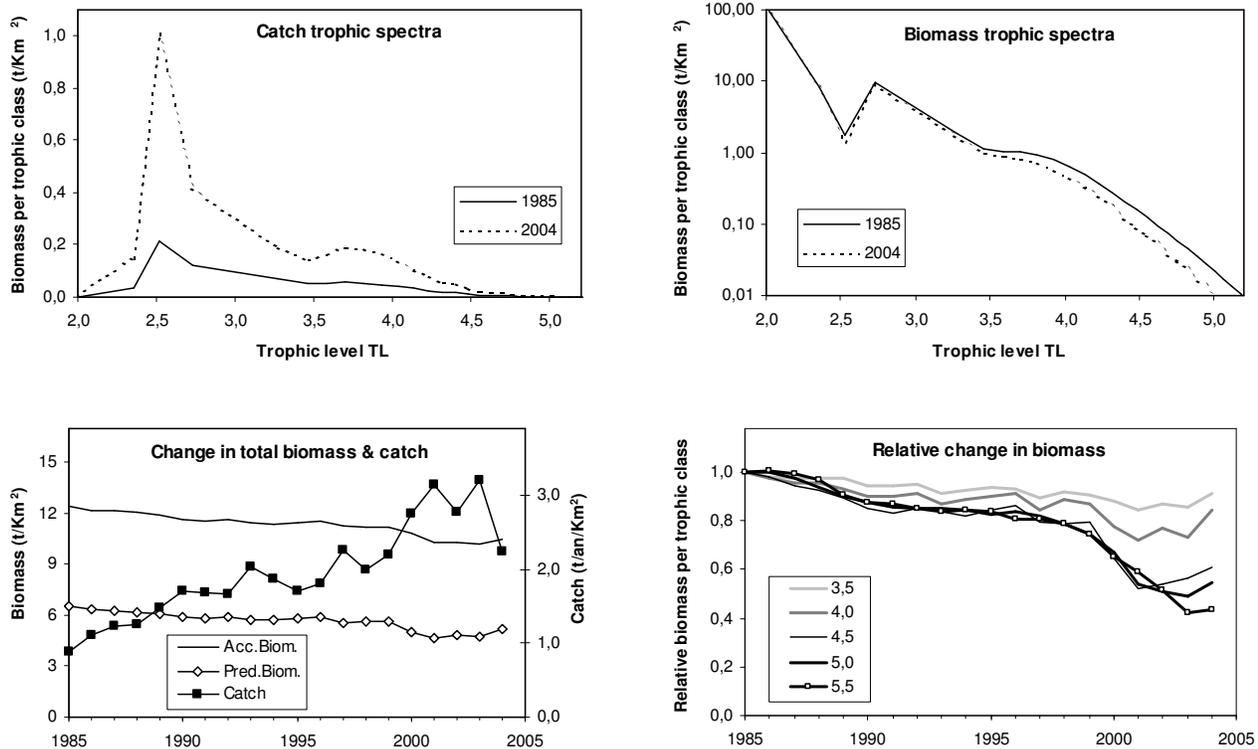


Figure 51 – Hindcasting of the functioning of the Guinean ecosystem, over the 1985 to 2004 period. Catch trophic spectra are used as input (top left panel; only years 1985 and 2004 are presented for clarity). ET-Dynamic provides estimates of biomass trophic spectra (top right), from where we deduced estimates of relative changes in biomass per trophic class (bottom right) or changes in the total ecosystem biomass (bottom left).

Finally, even if still preliminary, these results confirm the global reliability of both the Ecopath or EcoTroph models of the Guinean ecosystem functioning and the usefulness of the ET-Dynamic routine. The latter provides a useful tool to analyse the story of the ecosystem and its exploitation. It might also be used to calibrate the value of an uncertain parameter by comparing between the output of the model and independent observations. Finally, it allows users to test various scenarios regarding the past (for instance linking the primary production to known environmental indices) or the near future (for instance in order to analyse various fishing scenarios). This routine eventually appears for EcoTroph as equivalent to the Ecosim model, compared to Ecopath.

When the required data are available, it is of course strongly advised to develop both the ET-Dynamic and the Ecosim model as complementary tools for analysing the ecosystem functioning. Conversely, in data-poor situations, EcoTroph dynamic simulations might constitute a first and useful step in ecosystem modelling.

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APPENDIX II - ESTIMATING TRANSFER EFFICIENCY FROM CATCH DATA

Transfer efficiency (TE) represents the proportion of the production of lower trophic levels that is transferred to higher trophic levels (see § 1.3.2 in main text). TE accounts for individual energy losses due to respiration, digestion, excretion, etc., as well as losses due to non-predatory mortality, e.g. when individuals are not being consumed because they are protected from predation or because consumers are saturated, such as may happen during phytoplankton blooms (Cushing 1973). TE is thus a general measure of an ecosystem's efficiency at transferring energy from low to high trophic levels.

In EcoTroph, the decline of production between trophic levels is modelled as a declining exponential function, with TE representing the proportion of production left over a transfer of one TL unit. In other words:

$$\text{Production}(\text{TL}_{n+1}) = \text{Production}(\text{TL}_n) \times \exp(\log(\text{TE}))$$

In EcoTroph, most especially in the catch trophic spectrum analysis (CTSA), results are very sensitive to the value of TE (see § 3.2.2 in main text). Also, in marine ecology and in fisheries science in general, TE is an essential parameter involved in answering a number of important questions, such as the fraction of total primary production that is used by fisheries (Pauly and Christensen 1995), the effects of fishing at an ecosystem scale (Libralato *et al.* 2008), or the energy used by different groups of fish (Jennings *et al.* 2008). An average value of TE=10% is obtained for marine ecosystems in general (Pauly and Christensen 1995), which, perhaps surprisingly, also seems to apply to other systems (Morowitz 1991). However, the average value estimated by Pauly and Christensen (1995) masks a great variability between ecosystem types (Pauly and Christensen 1993; Jarre-Teichmann and Christensen 1998). Thus, having access to ecosystem-specific estimates of TE would greatly contribute to our understanding of ecosystem functioning and its interaction with fishing.

Here, we elaborate on a method previously presented in Pauly and Palomares (2005) to estimate the transfer efficiency of an ecosystem based on time-series of catch and TL data. This method assumes that, for a given ecosystem, the proportion of production exploited at each trophic level is constant, so that we would expect total catches to decrease with increasing mean TL of the catch at a rate that is proportional to TE (see Fig. A4). Assuming that production declines exponentially with trophic levels (as modelled in EcoTroph), the relationship between the mean trophic level of the catch and the $\log(\text{catch})$ is thus linear, and the TE can be extracted from the slope as $\text{TE}=10^b$, where b is the slope and the mean trophic level is the explanatory variable.

For this method to work optimally, the total catch/mean TL time-series used need to have sufficient contrast in the mean TL of the catch, and not be affected by major changes in the effort patterns of the underlying fleet. Moreover, the catch must come from the same ecosystem (or a relatively small region); otherwise an observed increase of the catch could reflect a geographic expansion of the fleet (Bhathal and Pauly 2008). If dealing with catch data from larger regions (e.g. FAO areas, as in Pauly and Palomares

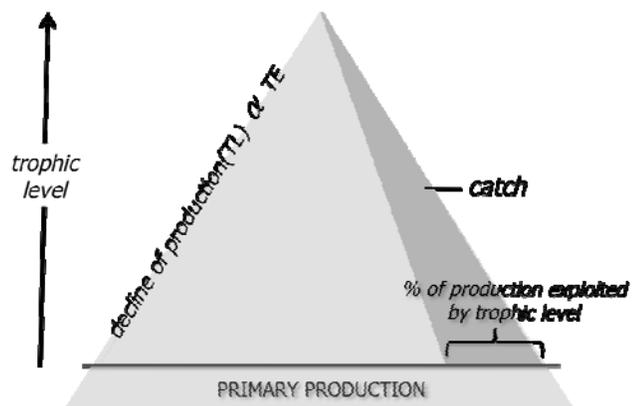


Figure A4 - Illustration of the rationale behind the estimation of TE from mean TL/catch time-series. If the proportion of production exploited is constant between TLs, catch should decline with increasing TL at a rate proportional to TE, reflecting the concurrent decline in production by TL.

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APPENDIX I – A NON-CONTINUOUS SIMULATION OF ECOTROPH

One of the main hypothesis of EcoTroph is to assume that the biomass resulting from abrupt trophic level jumps due to predation events can be modeled using an equation of continuous flow (see §1.2.3). Following a suggestion of Carl Walters, we developed a modified version of EcoTroph where this assumption is released for all trophic levels higher than 3 and we compared the results with the standard version of EcoTroph.

A theoretical fishery that targets only trophic levels in the 3.0-3.3 range is used to compare the two versions of the model. In the standard EcoTroph model (Fig. A1), this exploitation pattern induces an increase in the flow kinetics (graph P/B) for the exploited trophic levels and a decrease in the biomass flow (graph flow P) that starts at TL 3 and propagates to upper trophic levels. As a result, the biomass decreases for all trophic classes higher than 3.

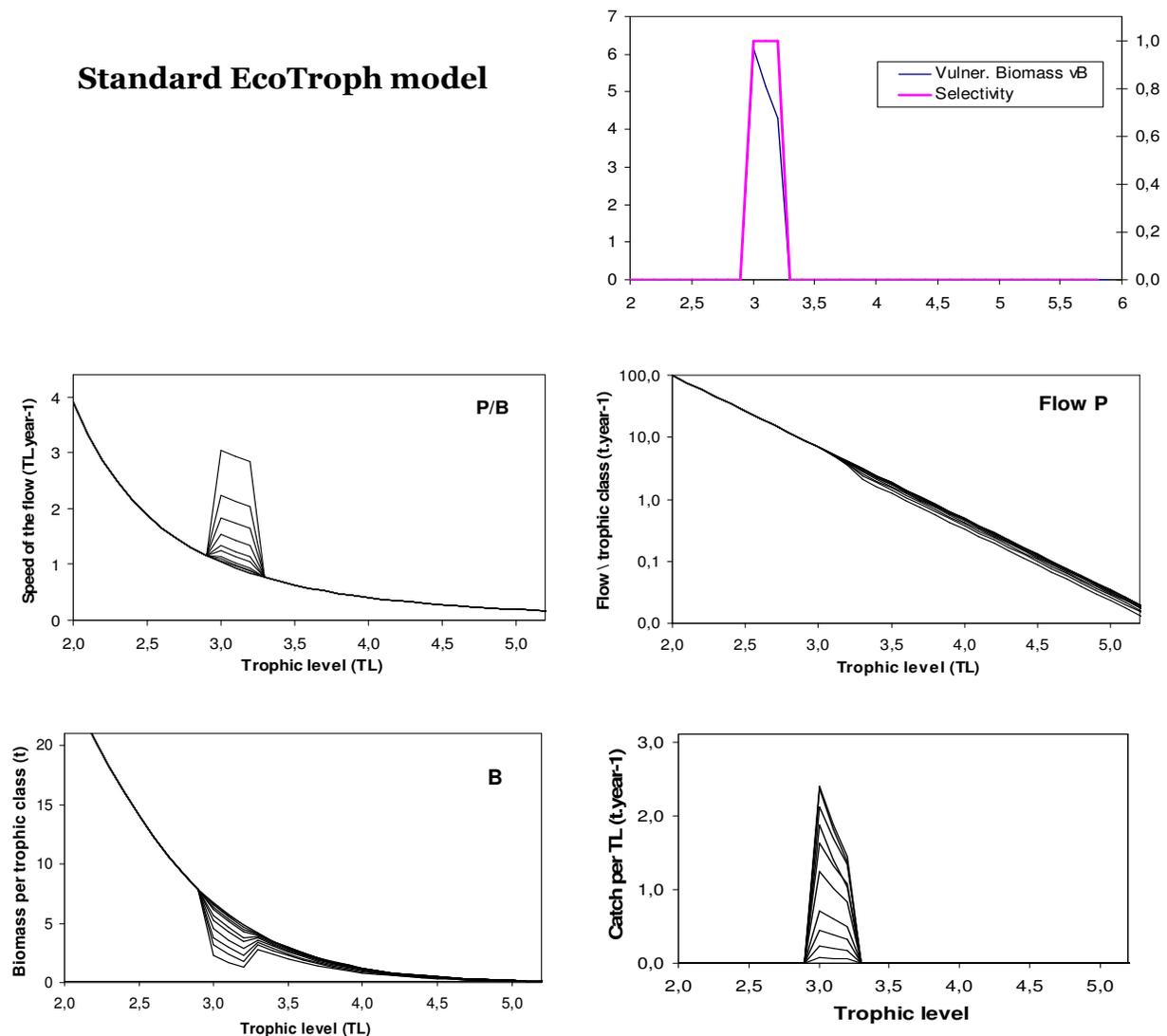


Figure A1 – A theoretical simulation of catch and fishing impact on biomass flow, kinetics (P/B) and biomass, using the standard version of EcoTroph.

In the modified version of EcoTroph (Fig. A2), the same exploitation pattern induced a similar increase in the flow kinetics. The pattern for the biomass flow is, however, different. It does decrease for the exploited trophic classes but since biomass is set to jump abruptly between trophic levels (at intervals of 1), the flow of higher trophic levels is not affected until it reaches levels 4.0 and levels higher than 4.3 are not affected. A biomass decrease is thus observed for the exploited TL 3.0-3.3 and the levels that feed on them, TL 4.0-4.3, but the effect is most pronounced for the former since two effects cumulates: the decrease in biomass flow and the increase in the speed of the flow (P/B).

Modified EcoTroph model

$$\Phi_{\tau+1} = \phi_{\tau} \cdot \exp(-\phi - \mu)$$

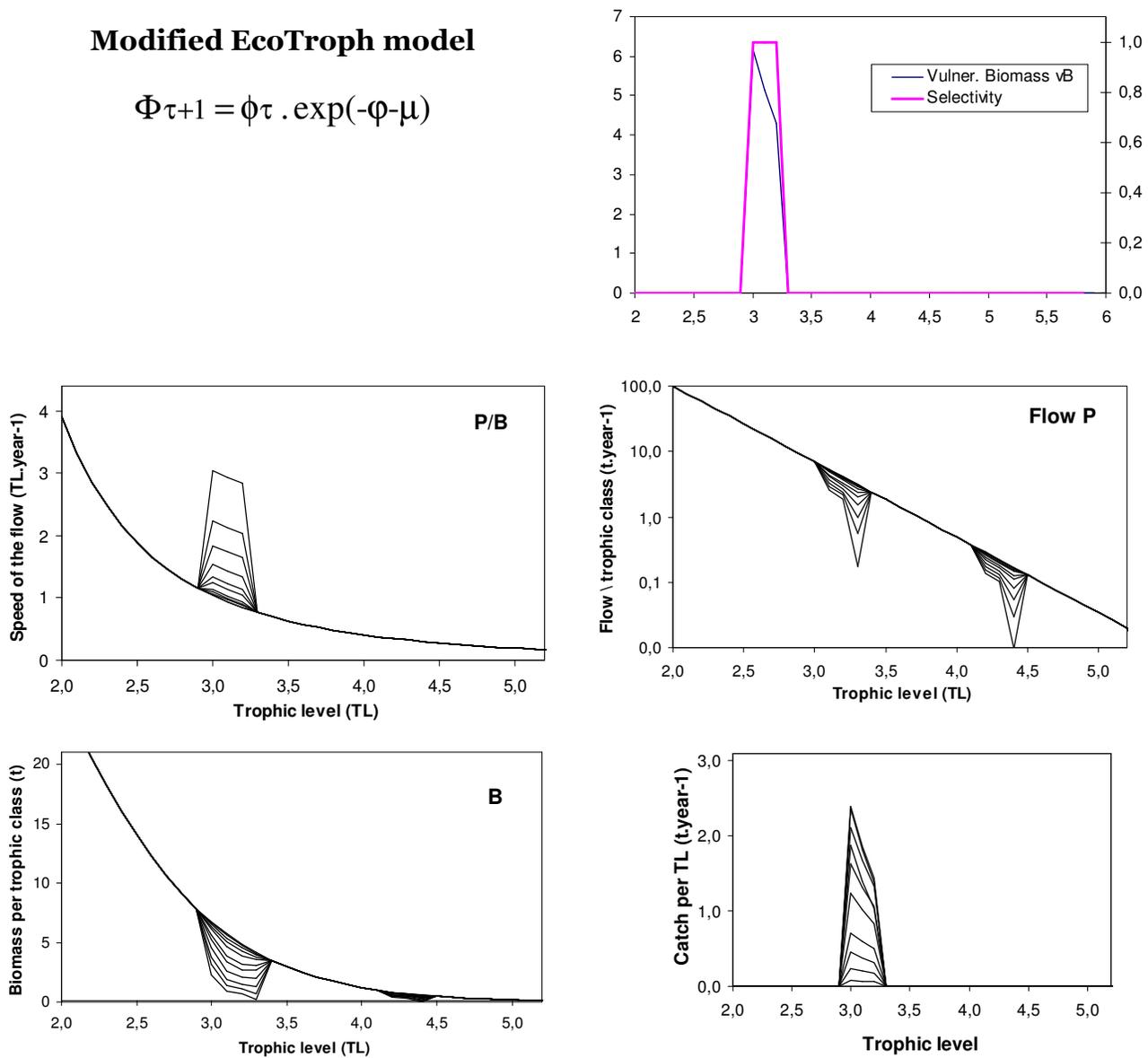


Figure A2 – A theoretical simulation of catch and fishing impact on biomass flow, kinetics (P/B) and biomass, using a modified version of EcoTroph.

The modified version of EcoTroph thus changes the estimate of biomass per trophic level for trophic levels higher than 3.3. Nevertheless, changes are limited and when considering the total ecosystem biomass, accessible biomass or catches (Fig.A3), both version of EcoTroph lead to very similar results.

We thus conclude that modeling the trophic flow (and its abrupt jumps) through an equation that represents a continuous process is an acceptable representation of the functioning of marine ecosystems.

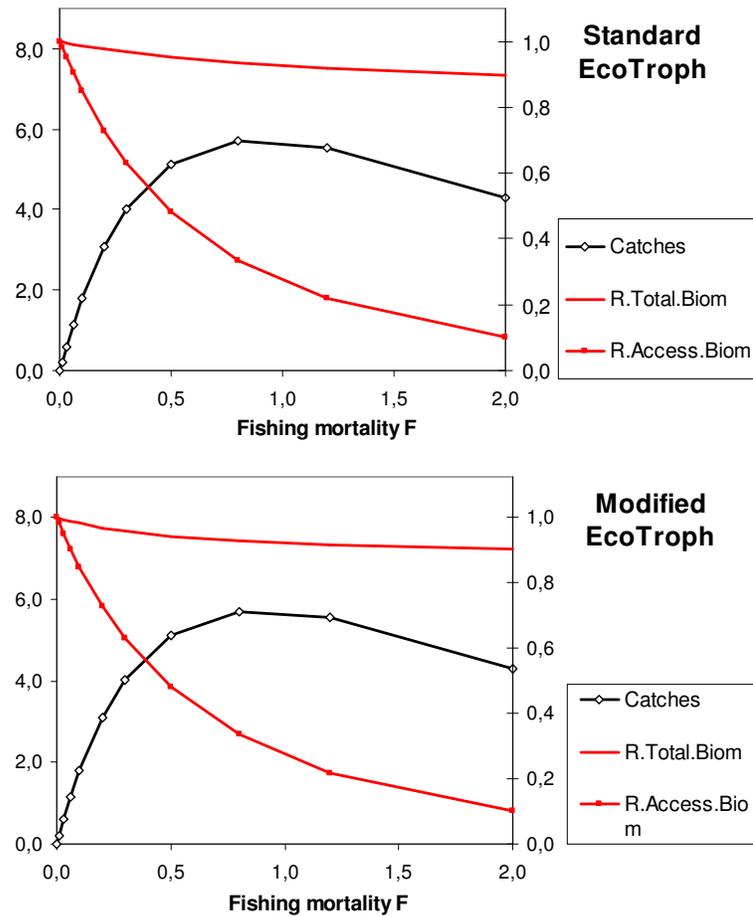


Figure A3 – Comparison of results of the two version of EcoTroph at the ecosystem scale

APPENDIX II - ESTIMATING TRANSFER EFFICIENCY FROM CATCH DATA

Transfer efficiency (TE) represents the proportion of the production of lower trophic levels that is transferred to higher trophic levels (see § 1.3.2 in main text). TE accounts for individual energy losses due to respiration, digestion, excretion, etc., as well as losses due to non-predatory mortality, e.g. when individuals are not being consumed because they are protected from predation or because consumers are saturated, such as may happen during phytoplankton blooms (Cushing 1973). TE is thus a general measure of an ecosystem's efficiency at transferring energy from low to high trophic levels.

In EcoTroph, the decline of production between trophic levels is modelled as a declining exponential function, with TE representing the proportion of production left over a transfer of one TL unit. In other words:

$$\text{Production}(\text{TL}_{n+1}) = \text{Production}(\text{TL}_n) \times \exp(\log(\text{TE}))$$

In EcoTroph, most especially in the catch trophic spectrum analysis (CTSA), results are very sensitive to the value of TE (see § 3.2.2 in main text). Also, in marine ecology and in fisheries science in general, TE is an essential parameter involved in answering a number of important questions, such as the fraction of total primary production that is used by fisheries (Pauly and Christensen 1995), the effects of fishing at an ecosystem scale (Libralato *et al.* 2008), or the energy used by different groups of fish (Jennings *et al.* 2008). An average value of TE=10% is obtained for marine ecosystems in general (Pauly and Christensen 1995), which, perhaps surprisingly, also seems to apply to other systems (Morowitz 1991). However, the average value estimated by Pauly and Christensen (1995) masks a great variability between ecosystem types (Pauly and Christensen 1993; Jarre-Teichmann and Christensen 1998). Thus, having access to ecosystem-specific estimates of TE would greatly contribute to our understanding of ecosystem functioning and its interaction with fishing.

Here, we elaborate on a method previously presented in Pauly and Palomares (2005) to estimate the transfer efficiency of an ecosystem based on time-series of catch and TL data. This method assumes that, for a given ecosystem, the proportion of production exploited at each trophic level is constant, so that we would expect total catches to decrease with increasing mean TL of the catch at a rate that is proportional to TE (see Fig. A4). Assuming that production declines exponentially with trophic levels (as modelled in EcoTroph), the relationship between the mean trophic level of the catch and the $\log(\text{catch})$ is thus linear, and the TE can be extracted from the slope as $\text{TE}=10^b$, where b is the slope and the mean trophic level is the explanatory variable.

For this method to work optimally, the total catch/mean TL time-series used need to have sufficient contrast in the mean TL of the catch, and not be affected by major changes in the effort patterns of the underlying fleet. Moreover, the catch must come from the same ecosystem (or a relatively small region); otherwise an observed increase of the catch could reflect a geographic expansion of the fleet (Bhathal and Pauly 2008). If dealing with catch data from larger regions (e.g. FAO areas, as in Pauly and Palomares

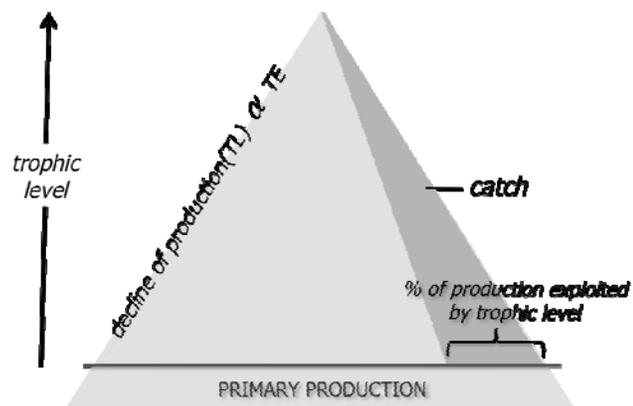


Figure A4 - Illustration of the rationale behind the estimation of TE from mean TL/catch time-series. If the proportion of production exploited is constant between TLs, catch should decline with increasing TL at a rate proportional to TE, reflecting the concurrent decline in production by TL.

2005), this issue can be addressed by computing the Fishing-in-Balance (FiB) indices for the time-series and using only those periods where the FiB index is constant, since they correspond to periods where the fleet was using the same fishing grounds (Bhathal and Pauly 2008).

We present an example of the application of the method to three different types of large marine ecosystems (LMEs): the California Current (upwelling), the South China Sea (tropical) and the Sea of Japan (temperate) (Fig. A5). The catch data originate from the *Sea Around Us* Project global fisheries database, which presents catches spatialized at a resolution of 0.5 degree Lat./Long. (Watson *et al.* 2004) and the trophic levels from FishBase (www.fishbase.org) We randomly selected three 0.5 degree square cell in each LME from a subset of cells that satisfy the conditions listed above. The mean trophic level of the catch is calculated as:

$$TL_y = \frac{\sum_i (TL_i \times Y_{iy})}{\sum_i (Y_{iy})}$$

with Y_{iy} the catch of species group i in year y and TL_i the trophic level of species group i . To reduce the noise induced by abrupt changes in the species targeted by the fishing fleet, years where the mean trophic level of the total catch changes by more than 10% are not used in the linear regression. Also, we consider half-degree cells to be small enough for an expansion of the fisheries over the cells' area to be a negligible factor. Therefore, unlike Pauly and Palomares (2005), we did not use the FiB index to identify periods where the area of the fishing grounds was constant.

We estimate transfer efficiencies of 0.101 for the California Current, 0.062 for the South China Sea and 0.082 for the Sea of Japan (see Fig. A5). These ecosystem-specific TE estimates are generated from the mean TL/total catch data of three cells, and can be made more reliable by using data from more cells in the ecosystem. Despite the fact that they are preliminary, these estimates occur in the region of the TE expected for ecosystems and support the view that TE is not constant amongst global marine ecosystems. They demonstrate the usefulness of the method presented here to derive approximations of ecosystem-specific TE.

Lastly, the key assumption behind the method is that the proportion of production extracted by fishing is the same for all exploited trophic levels, and it is likely that this assumption is not always met in practice. However, the method can be made robust to violations of this assumption by accounting for the relationship between trophic level and the proportion of production exploited, which can be estimated using data from Ecopath models. This theme will be explored by one of us (L.T-B.) and the results presented in a forthcoming publication.

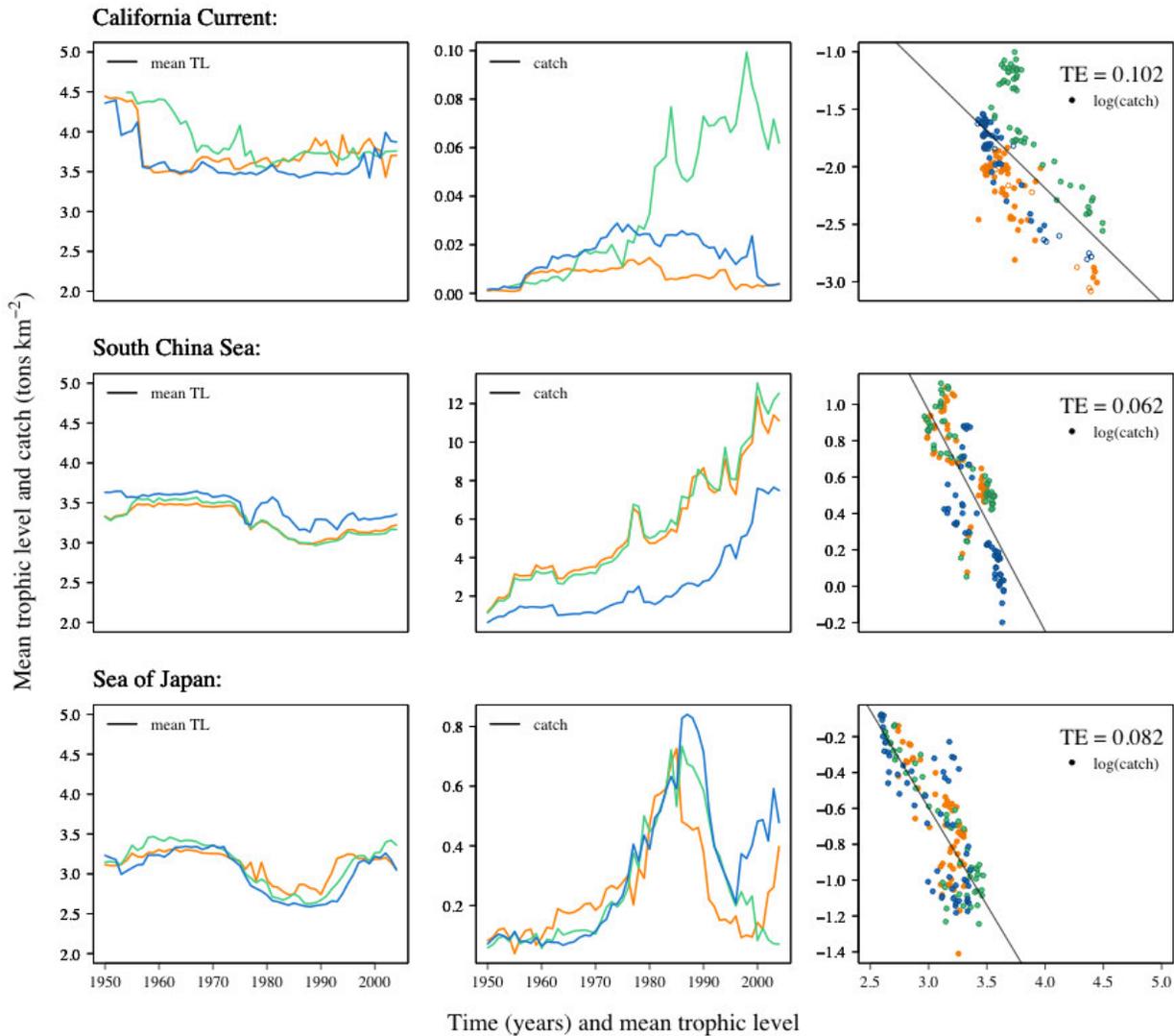


Figure A5 - Estimation of TE from time-series of mean TL of the catch and log(catch) for three LMEs (three cells/LME, one color for each cell). The left and center panels show time series of mean TL and total catch; the right panels show the regression lines fitted through to the plot of mean TL vs. log(total catch). Points that were not used in for the regression (because of high variations in their TL; see text) are shown as open dots.