The trophic-level based ecosystem modelling approach: Theoretical overview and practical uses

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Abstract:

The trophic-level based ecosystem modelling approach is articulated around the idea that an ecosystem can be represented by its biomass distribution across trophic levels (TL). 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.

First, we propose the EcoTroph model, based on simple assumptions and equations, as a theoretical extension of the Ecopath with Ecosim (EwE) approach. 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.

We illustrate the usefulness of the trophic-level based approach through the Guinean ecosystem as a case study, where a fast and strong increase in the fishing pressure occurred over the past 25 years. Biomass estimates from CTSA appear consistent with results of an independent EwE model. Using the diagnostic tools of EcoTroph, we show that increasing fishing efforts led to a three-fold decrease in the biomass of the higher trophic levels, inducing an over-exploitation for these levels and a significant decrease in the mean TL of biomass and catches, which confirm and generalize previous single species assessments. Forecasting suggests that higher yields might be obtained in exploiting lower trophic levels, but this would induce a higher impact on the ecosystem and a degradation of its health.

Keywords: trait-based ecosystem approach, trophic-level, ecosystem modelling, EcoTroph

1 - Introduction

The first step toward what was to become the EcoTroph model for trophic-level based modelling of ecosystems was presented at a conference in France in 2001, whose proceedings were published in the grey literature (Gascuel, 2001). 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). These models, and especially biomass and yield per recruit models (Beverton and Holt 1957), may be regarded as flow models, where fishes move from one year class to the next as a function of their age. Thus, 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 and detritus recycling, which is treated as analogous to 'recruitment' to the system) and moves from one trophic class to the upper ones, 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. A second version, which incorporated biomass flow and flow kinetics equations was then developed as a theoretical representation of ecosystem functioning (Gascuel, 2005). At the same time, an inverse form of the model, called Catch Trophic Spectrum Analysis (CTSA) was proposed as a method for estimating biomass and fishing mortalities at the ecosystem scale, from catch per trophic level (Gascuel and Chassot, 2008, originally presented in 2004).

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) (Polovina 1984; Christensen and Pauly 1992; Walters *et al.* 1997), 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) (Gascuel and Pauly, in press; Gascuel and Pauly, submitted). In fact, within the EwE family of models, EcoTroph may be regarded as constituting the ultimate stage in the use of the trophic level metric for ecosystem modelling, a trait-based model wherein species or the 'functional groups' of EwE as such are subsumed by the trophic levels at which they operate. We must stress that this approach is not a complexification of previous food web modelling effort. On the contrary, 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 a simplified, but potentially very useful caricature.

In the present paper, we propose an overview of this trophic-level based ecosystem modelling approach. First, the theoretical basis of the EcoToph model are briefly presented; through simulation of fishing impact on a virtual ecosystem, we then show that the model is able to mimic the effects of various exploitation patterns on ecosystem biomass expected from theory. Second, the CTSA is introduced and we explain why this method may be seen as a form of 'VPA' (Virtual Population Analysis) applied to ecosystems. Lastly, we illustrate the usefulness of the trophic-level based approach through a specific case study, the Guinean ecosystem.

2 - Method: the EcoTroph model and the CTSA

2.1. Basis of the EcoTroph model

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 (Elton, 1927), where the biomass of each of the various components of ecosystems had to be shoehorned into one of a few integer trophic levels. 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:

$$\tau_j = 1 + \Sigma_j (D_{ij} \cdot \tau_j) \tag{1}$$

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. 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. Additionally, the intra-population variability of the trophic level can be taken into account (and will be in EcoTroph) using a standard deviation around the mean and thus a range of trophic levels for each population. More generally, the trophic level appears as a state variable characterizing each unit of biomass in an ecosystem.

Thus, the first key point of EcoTroph is that it deals with the continuous distribution of the biomass occurring in an ecosystem, as a function of trophic levels (Gascuel, 2005; Gascuel and Pauly, submitted; Fig.1). The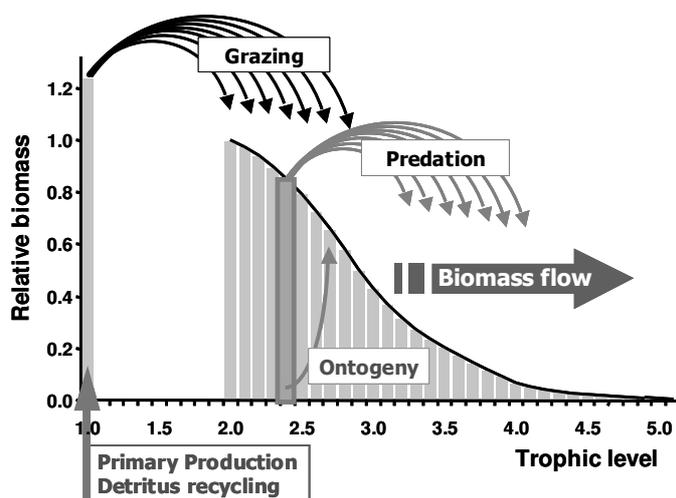 biomass enters the food web at trophic level 1, as generated by the photosynthetic activity of the primary producers, and recycled by the microbial loop. With the exception of semi-autotrophic organisms with small biomasses in some ecosystems (e.g. coral polyps, giant clams, etc.), there is usually no biomass between trophic levels 1 and 2. Herbivorous and detritivorores are at trophic level 2. Then, at trophic levels higher than 2, the biomass is distributed along a continuum of trophic level values. The variability of the diet of the different consumers of an ecosystem should result in all trophic levels being 'occupied'.

Figure 1. Diagram of the trophic functioning of an ecosystem: theoretical distribution of the biomass by trophic level and trophic transfers processes, given an arbitrary input of biomass (from Gascuel and Pauly, submitted.).

As a consequence, the EcoTroph equations are based on a continuous approach and the model aims to simulate

the state variable B(t, τ), i.e., the biomass occurring in the ecosystem at time t, at trophic level τ. A discrete approximation of the continuous distribution is used for mathematical simplification and visual representation (see Fig.1). Conventionally, we consider trophic classes of $\Delta\tau = 0.1$ trophic level, from trophic level 2, corresponding to first-order consumers, to trophic level 5, sufficient to cover all top predators likely to occur in marine systems (Pauly *et al.* 1998; Cortes 1999). We present here a steady state version of the model. Thus, the state variable becomes Bτ, the biomass of the [τ, τ+$\Delta\tau$] trophic class. The resulting bivariate graph (Bτ as a function of τ) represents a key aspect of ecosystem functioning and constitutes what is called a 'biomass trophic spectrum' (Gascuel *et al.*, 2005).

The second key idea of EcoTroph is that the trophic functioning of marine ecosystems can be modelled as a continuous flow of biomass surging up the food web, from lower to higher trophic levels, due to predation and ontogenic processes. As a consequence the biomass Bτ, present at every moment in a given trophic class, can be deduced from two variables:
- The 'biomass flow' $\Phi\tau$ which refers to the amount of biomass that moves up the food web, (expressed in tonnes per year);
- The 'speed of the flow' $\Delta\tau/\Delta t$ which quantifies the velocity of biomass transfers in the food web. (This speed can be expressed in term of the number of trophic levels passed per year).

Thus, the biomass equation is:
$$B\tau = \frac{\Phi\tau}{\Delta\tau/\Delta t} \cdot \Delta\tau \qquad (2)$$

Due to natural losses occurring during trophic transfers (non-predation mortalities, respiration, egestion and excretion), the biomass flow expressed as a function of the trophic level should exhibit a declining trend. 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 expressed as follows:
$$\Phi(\tau+\Delta\tau) = \Phi(\tau) \cdot \exp[-(\mu_\tau + \varphi_\tau) \cdot \Delta\tau] \qquad (3)$$

where μ_τ is the net natural loss rate of biomass flow, and φ_τ is the loss rate of biomass flow due to fishing. Note that the term $\exp(-\mu_\tau)$ is the transfer efficiency (TE) between trophic levels.

The speed of the flow $\Delta\tau/\Delta t$ must be estimated for each trophic class. This can be done using two main alternative methods:
1. Based on analogy with EwE, we showed that the P/B ratio (Production/Biomass) can be considered a practical measure of the speed of the flow (Gascuel *et al.* 2008). Thus, for practical case studies, we can use P/B ratios estimated by field measures of P and B, or from empirical equations, or P/B ratios derived from a previous Ecopath model (see example in §4).
2. When analysing the theoretical functioning of a virtual ecosystem, an empirical model developed by Gascuel *et al.* (2008) is used; it expresses the P/B ratio (and thus the speed of the trophic flow) as a function of the trophic level and the mean water temperature.

In both practical and theoretical cases, an additional equation has to be included in the model, in order to take into account the feedback effect of predators on prey. Indeed, the more predators there are, the faster the prey are likely to be eaten. Therefore, the speed of the flow at trophic level τ partly depends on the abundance at trophic level τ+1. The related equation, detailed in Gascuel and Pauly (in press), introduces a top-down control in the model, while the bottom-up control is implicit in equation (3).

Finally, catches per trophic class and per time unit are deduced from previous equations, as follow:

4

$$Y\tau = \varphi\tau \cdot \Phi\tau \cdot \Delta\tau \tag{4}$$

Nevertheless, for ecological or technological reasons, only a fraction of the ecosystem biomass is usually accessible to fisheries. As a consequence, a selectivity coefficient $S\tau$ must be introduced into the model, expressing the fraction of the biomass $B\tau$ accessible to fishing. This biomass fraction will be referred to as $B^*\tau$ (with $B^*\tau = B\tau.S\tau$) and $\Phi\tau$ is replaced by $\Phi^*\tau$ in equation (4). In the theoretical simulations, a logistic curve is used for $S\tau$, to mimic the increase of accessibilities from low values at low trophic levels to full accessibility at higher trophic levels.

2.2. The Catch Trophic Spectrum Analysis (CTSA)

The trophic-level based models can be viewed as transposition of an age-structured model on an ecosystem scale (Gascuel and Chassot, 2008; Gascuel and Pauly, in press). 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. This analogy allows us to adapt Virtual Population Analysis (VPA; Gulland 1965), and its close relative, Cohort Analysis (Pope 1972), to our needs. Indeed, in analogy with Pope's reasoning, we assume that the catch in interval $[\tau, \tau+\Delta\tau]$ occurs precisely at trophic level $\tau+\Delta\tau/2$. The biomass flow just before and after that trophic level, is equal respectively to:

$$\Phi(\tau)\cdot e^{-\mu\tau \cdot \Delta\tau/2} \qquad \text{, and } \Phi(\tau+\Delta\tau)\cdot e^{\mu\tau \cdot \Delta\tau/2}$$

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

$$\Phi(\tau) = \Phi(\tau+\Delta\tau)\cdot e^{\mu\tau \cdot \Delta\tau} + Y\tau \cdot e^{\mu\tau \cdot \Delta\tau/2} \tag{5}$$

which is equivalent to J.G. Pope's formulation of Cohort Analysis. Thus, Equation (6) 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 reverse form of the flow equation (3), the corresponding fishing flow loss rates φ_τ are calculated:

Catch trophic spectrum analysis requires catches per trophic level $Y\tau$, natural loss rates μ_τ, and coefficients of the top-down equation as inputs. 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 $(\Delta\tau/\Delta t)_\tau$, and fishing mortality F_τ (defined as $F_\tau = Y_\tau/B_\tau$) are estimated from values at level $\tau+\Delta\tau$ using equations (5), (3), (2), and top-down equation respectively. Because B_τ and $(\Delta\tau/\Delta t)_\tau$ are interdependent, the system of equations must be solved iteratively.

3 – Results: simulating virtual ecosystems

3.1 Theoretical impact of fishing on ecosystem biomass

Theoretical simulations illustrate that exploitation affects biomass flow and flow kinetics eventually affecting ecosystem biomass as well (Fig. 2), with total biomass decreasing with increasing exploitation rate. In a 'bottom-up ecosystem', where no feedback effect of predators on preys is considered (Fig. 3, left), only the exploited trophic levels are affected. Increasing fishing pressure decreases the biomass flow, with cumulative effects for the highest trophic levels (even if they are not targeted by fishing). Due to decrease in life expectancy, the higher the fishing mortality, the faster the speed of the flow. The two effects contribute to the decrease of biomass, which is therefore especially strong for the highest

trophic levels. Conversely, in a 'top-down ecosystem' (Fig. 3, right), abundance is changed for all TLs. The fishery-induced decrease in predator abundance leads to a release of predation. This induces a decrease in the speed of the flow for the prey (their life expectancy is increased) and thus an increase of their biomass. Subsequently, predators benefit from this increase and are slightly less affected than in the case of a 'bottom-up ecosystem'.
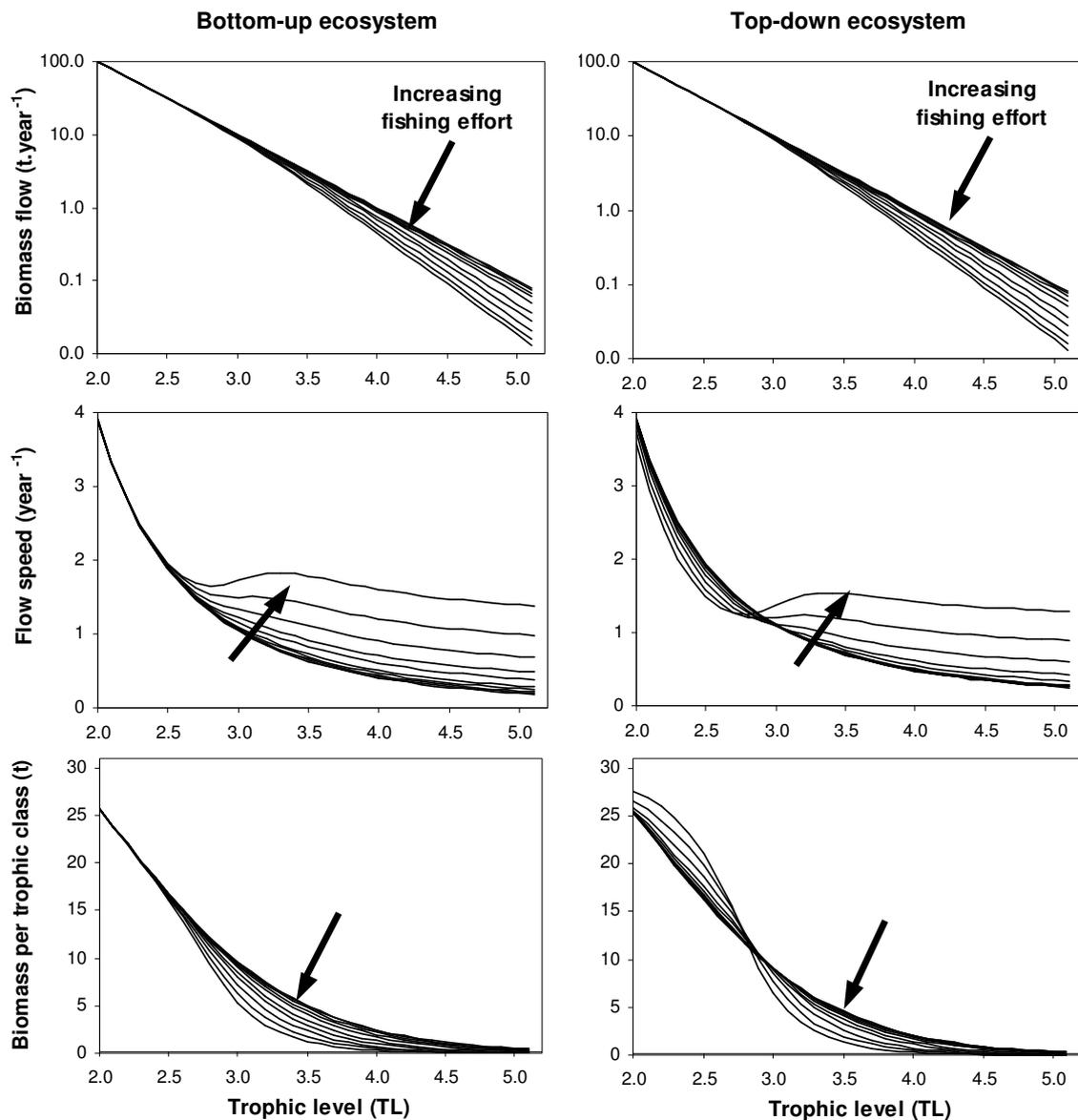

Figure 2 – Impact of increasing fishing mortality on the biomass flow (top), the flow speed (middle) and the biomass trophic spectrum (bottom). Left panels refer to a 'bottom-up ecosystem'; right panels to a 'top-down ecosystem'. The arrows signal increasing fishing mortalities, from F=0 to F=1, using a selectivity curve with a mean TL at first catch τ_{50} equal to 3.

As a consequence, the impact of fishing differs according to the ecosystem control. In a 'bottom-up ecosystem', exploitation has a large impact on total ecosystem biomass, and may lead to strong biomass depletion, especially when the mean trophic levels at first capture is low. For instance, using a selectivity curve $S\tau$ with a trophic level at first catch τ_{50} equal to 2.5, we simulated a reduction in total ecosystem biomass reaching almost 40%. The decrease is especially strong at high trophic levels, because these are affected both by loss of their prey and the direct impact of the catch (For instance, we obtained a reduction in abundance of more than 80 % for trophic levels > 3.5). In a 'top-down ecosystem', the

release of predation compensates, at least partially, for fishing pressure on prey, and thus can induce an increase in their abundance, if the lower trophic levels are not too strongly exploited. 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). 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.
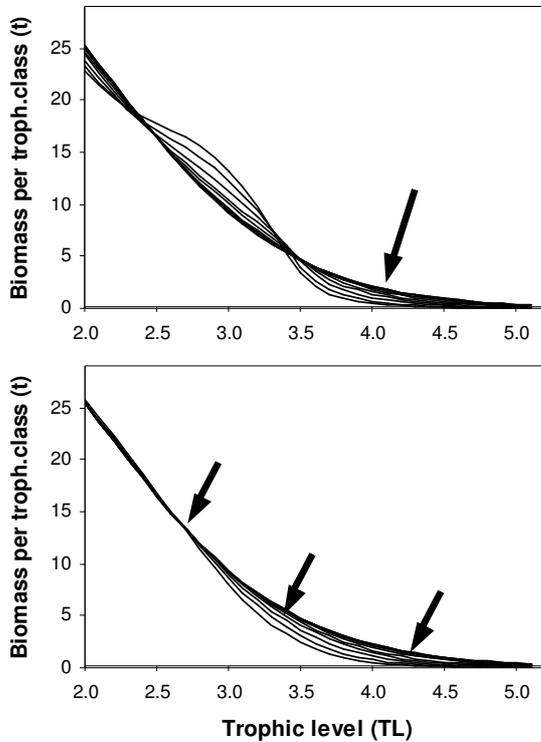

Figure 3. Simulation of a cascade effect (top) and of a more resilient ecosystem (bottom) (arrows indicate the effect of increasing fishing mortality; see text).

Additional insights can be obtained from some 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. 3, 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. 3, 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 minimize the fishing impact and maintain the resilience of exploited ecosystems.

These simulations refer to a given set of values for transfer efficiencies and flow kinetics parameters. Modifying these values does not affect the results substantially. However, it allows us to analyse their influence on the ecosystem response to fishing. Notably, we show that increasing transfer efficiencies leads to higher fishing impact on the total biomass. In this case, the natural loss rates are smaller and a given fishing loss rate induces a higher exploitation rate $\varphi/(\varphi+\mu)$. 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.

3.2. Catch simulation

The catch expressed as a function of exploitation rate is dome-shaped (Fig. 4), with the maximum catch tending toward zero for the highest values of fishing mortality (Note that $E_\Phi = 1$ corresponds to $F = \infty$). 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.

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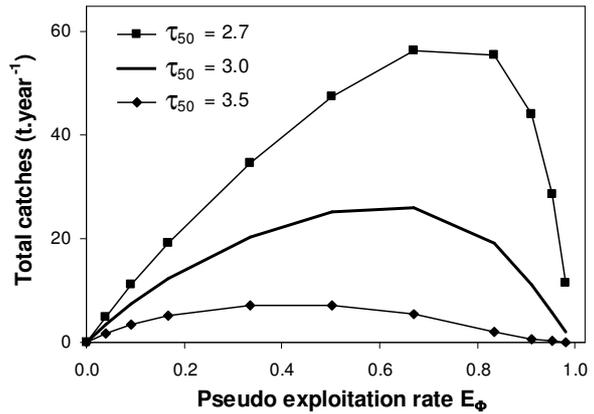

Figure 4. Relationship between catches and fishing intensity expressed as a flow exploitation rate, for three mean trophic levels at first capture

When fishing effort increases, the catch tends to originate increasingly from the low trophic levels (Fig. 5, left), even if these low levels are not specifically targeted. The low trophic levels, indeed, can generate large catches when exploitation rates are strong. 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. 5, right). In the simulation, full exploitation is, for instance, reached with F = 0.2 year^{-1} for trophic level 5, with F = 0.3 year^{-1} for trophic level 4.5, and with F = 0.8 year^{-1} for trophic level 3.5. This higher sensitivity of high trophic levels is a major characteristic of ecosystem functioning. As a consequence fishing strongly affects the mean trophic level of the catch, and of the residual biomass in the ecosystem, leading all the way to the disappearance of the predators. Of course, this phenomenon is a manifestation of the 'fishing down marine food webs' (Pauly *et al.*, 1998).
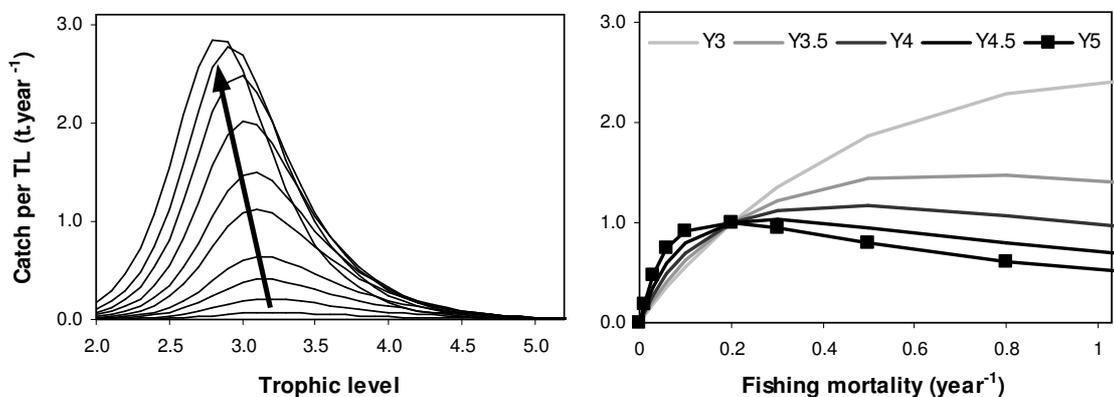

Figure 5 – Simulation of catch trophic spectra (left; arrow indicates increasing fishing mortality) and catch by trophic class (right; values Yτ are standardized for 1 for F = 0.2 year^{-1}) ('Bottom-up ecosystem'; τ_{50} = 3.0)

3.3. Testing the CTSA on simulated date

We used simulated data (i.e. simulated catches based on an EcoTroph model using a given set of parameters) to test the CTSA. 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}.
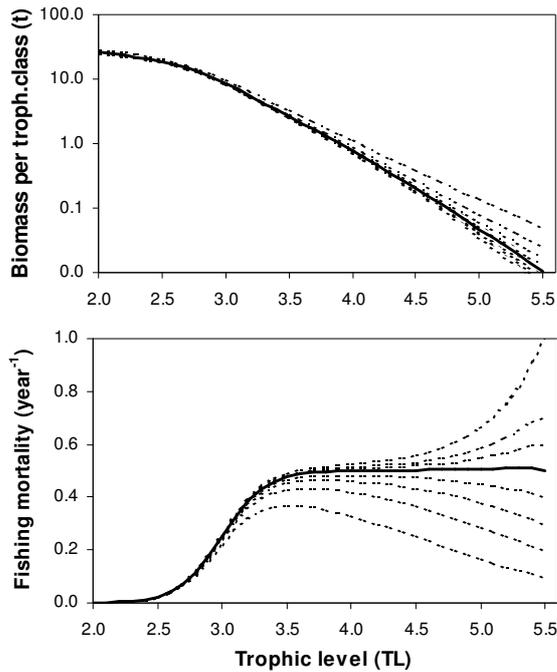
Figure 6 – Illustrating that the convergence properties CTSA are similar to those of cohort analysis. Top: biomass estimates; middle: fishing loss rate estimates; bottom: fishing mortality estimates (see text).

As expected, using the 'true value' of the terminal fishing mortality, 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, and the fishing mortality (Fig. 6). 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.

We also 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. Additional sensitivity analyses were conducted (not shown here), using as input catch data simulated with non standard parameters. Of course, the estimates resulting from the CTSA appear sensitive to the tested parameters (the mean transfer efficiency, the flow kinetics and the intensity of top-down controls). The biomass estimates at low trophic levels were especially affected by parameters changes. However, we concluded that, if the shape of the biomass distribution or the absolute value of biomass at trophic level 2 were estimated independently (for instance by direct methods), then CTSA could be calibrated and should provide reliable estimates.

4 - Applying EcoTroph to a real ecosystem: A Guinean case study

A first attempt to apply EcoTroph to a real ecosystem is presented here, based on data from the Guinean shelf, where a fast and strong increase in the fishing pressure occurred over the past 25 years. Data on catch and scientific surveys 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 (Gascuel *et al.,* in prep.). In a first step, two Ecopath models were built, for 1985 and 2004 respectively. Models take into account 34 ecological groups, including 24 fish groups defined accordingly to their ecology (especially their diet) and to data availability (see the groups list Tab. 1 in annex). Parameters required by these models (mainly P/B, Q/B and diet, see Tab. 1) were estimated based on a previous Ecopath model (Guénette and Diallo, 2004) and on complementary *ad hoc* procedures detailed in Gascuel et al. (in prep.). Our aim here

is not to analyse these Ecopath models or the detailed functioning of the Guinean ecosystem, but to illustrate the usefulness and pertinence of a complementary EcoTroph approach.

First, EcoTroph is used only as a tool for the graphical representation of the two Ecopath models (Fig. 7). The biomass per trophic group and the catch per fishery can be represented as a distribution over trophic levels, assuming that the distribution (of the biomass or catch) of a trophic group around its mean trophic level follows a lognormal curve. The Biomass Trophic Spectrum is the curve obtained by summing all biomasses. This representation provides a very synthetic overview of an ecosystem and may help users to think at that scale. For the Guinean ecosystem, we observe, between 1985 and 2004, a global decline in the biomass of the various trophic groups (Fig. 7 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. 7 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.
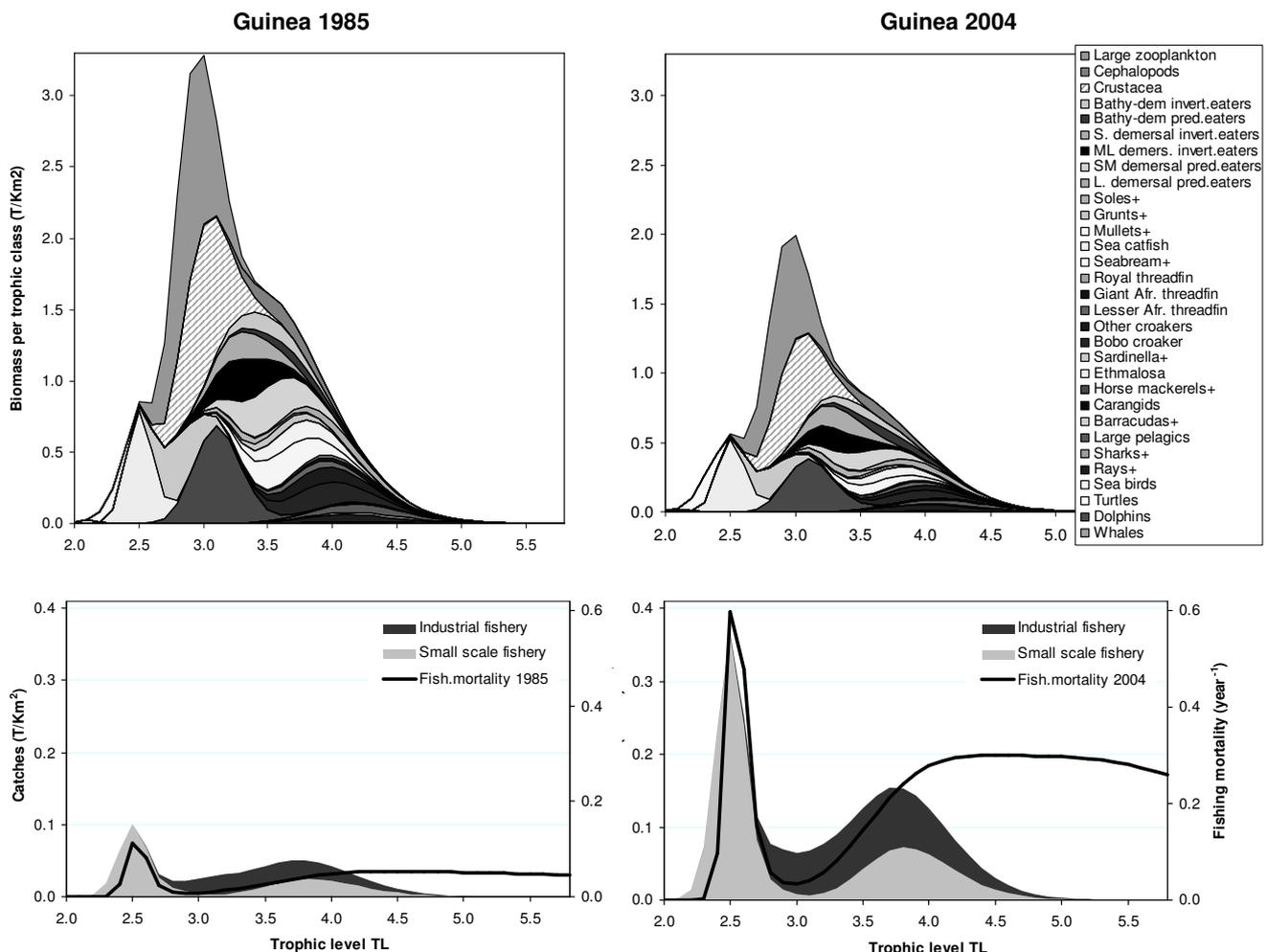

Figure 7 - A representation of the two Guinean Ecopath models, for 1985 (left) and 2004 (right), as interpreted by EcoTroph: biomass distribution by Ecopath group and trophic levels (top; small zooplankton and detritus were removed for clarity); catch per fishery and aggregate fishing mortality, by trophic level.

Secondly, EcoTroph provides diagnostic tools for assessing the impact of fishing on the Guinean ecosystem. Starting with the 'current' situation (i.e., 2004), we simulated changes in the fishing pressure by using multipliers ranging from 0 to 5 of the fishing mortality applied to the whole ecosystem. In this case study, the shapes of the biomass and catch trophic spectra are irregular (Fig. 8 top). This contrasts with results obtained using the virtual ecosystem with constant values of the parameters μ or φ, and a monotonous empirical function of flow kinetics. Nevertheless, fishing effects in this specific case appears consistent with the theoretical schemes previously established (compare, instance comparison figures 5 and 8).

Particularly interesting is that the current fishing effort led to a decrease in abundance, compared to the unexploited ecosystem (multiplier equal to 0, Fig. 8, bottom left), which is consistent with estimates from scientific surveys. For instance, the model predicted a 3-fold decrease in biomass of higher trophic levels, while the decreases observed in the surveys, between 1985 and 2004, were estimated to be 2 to 3-fold, depending on the groups considered.

The decrease in abundance of these high trophic levels induces their over-exploitation (Fig. 8, bottom right) and a significant decrease in the mean TL of both the total biomass and the catches. These results confirm and generalize previous single species assessments (Gascuel et al., 2004; Sidibé *et al.,* 2004). Forecasting suggests that higher yields might be obtained by exploiting lower trophic levels, but this would induce a higher impact on ecosystem and a qualitative degradation of the ecosystem health.
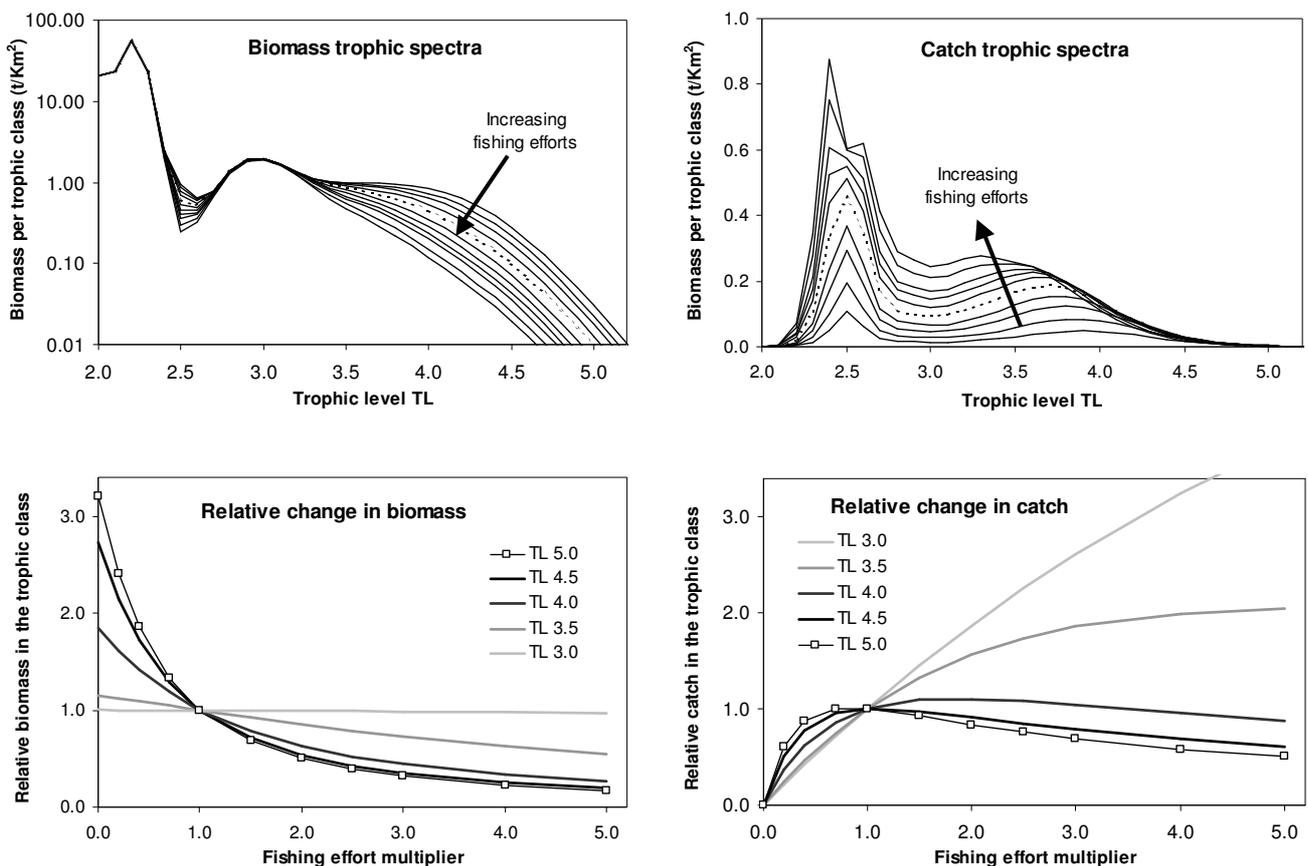

Figure 8 - Simulation of impact of increasing fishing effort on biomass (right) and catches (left) of the Guinean ecosystem. Top panels refer to biomass and catch trophic spectrum, where dashed lines represent the 'current' (i.e. 2004) situation. In the bottom panels, the relative values of biomass and catch for the trophic classes are expressed as a function of the multiplier of the current fishing mortality..

Finally, the CTSA was used as a stand-alone routine to estimate the biomass of the Guinean ecosystem, independently of any Ecopath model or surveys data. The 2004 catch trophic spectrum, built from catches and mean TL per group, was used as input. We assumed a mean trophic efficiency equal to 8 % for all TLs (higher than 2) and used the empirical model of flow kinetics of Gascuel et al. (2008) with a mean water temperature of 28 °C. As outputs, the CTSA provides estimates of the current biomass, and of unexploited biomass (Fig. 9).

Given the use of a mean efficiency and a monotonous regular flow kinetic model, the biomass trophic spectrum estimates from CTSA exhibit a regular shape, quite different f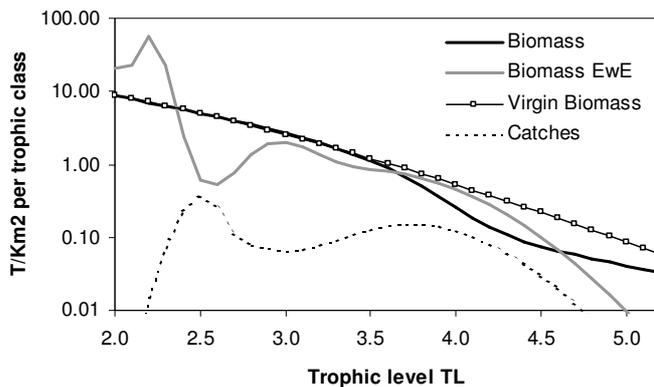rom those obtained from survey data or the Ecopath model. Nevertheless, the CTSA estimates appear consistent with results of the Ecopath model mentioned previously. Biomasses are of the same order of magnitude, and their decrease due to fishing is once again estimated at around 3-fold for the high trophic levels. Diagnoses based on the CTSA estimates (not shown) are very close to the previous ones and thus still consistent with the knowledge derived from single species assessments.

Figure 9 - Biomass trophic spectrum estimated from the CTSA applied to the 2004 catch data (see text); comparison with independent Ecopath estimate

5 - Conclusion

Overall, we found that taking into account a few simple, trophic-level related processes appears sufficient to simulate the biomass distribution patterns and responses to fishing pressure observed in real ecosystems. The best argument for the trophic-level based model presented here is that it appears to be a useful tool for understanding ecosystem functioning in both ecological and fisheries contexts. It provides the theoretical basis to explain the distribution of biomass of an ecosystem over its various trophic levels, and the impact of fishing on this distribution. For example, it provides consistent relationships between parameters (e.g. catches versus fishing mortalities); it shows that slower flow implies slower biomass regeneration, which causes (usually large) high-trophic level species to be intrinsically more vulnerable to fishing, and it mimics, finally, the decline under exploitation of the mean trophic level of catches now known as 'fishing down marine food webs' (Pauly *et al.,* 1998).
The model also explains more complicated patterns. Notably, it suggests that cascade effects can only occur with particular fishing patterns, strictly and strongly targeting the highest trophic levels. It suggests that, when top-down control occurs, applying a low fishing mortality to a wide range of trophic levels may be the best way to maintain the resilience of exploited ecosystems. It shows, more generally, that low transfer efficiencies, fast transfers and strong top-down controls may contribute to the resilience of marine ecosystems in the face of fishing.

We also presented here a first application of the trophic-level based approach to an actual ecosystem. This test appears very successful, its result being consistent with those of EwE models. By concentrating on biomass flow as a quasi-physical process, this approach allows aspects of ecosystem functioning to be explored which are complementary to EwE. Of course, EcoTroph, based only on trophic levels, is a caricature of the functioning of real

ecosystems. At the same time, we must not forget that in the face of the actual complexity of evolved (and evolving!) ecosystems, all attempts at reducing them to equations and models are equally vain. The question, thus, is one of utility, i.e., how useful (or informative) a model is, relative to the time and other resources invested in its construction. These resources, in the case of EcoTroph are minimal, especially when, as we suggest here, EcoTroph is used as a complement, rather than an alternative to other approaches.

EcoTroph is now available as a plug-in module of EwE Version 6 (Christensen and Lai, 2007), and a users' guide will be available shortly (Gascuel and Pauly, in press).

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Table 1 - Biomass, catch, natural mortality (M; year^{-1}), fishing mortality (F year^{-1}), production/biomass ratios (P/B = F+M; year^{-1}), consumption/biomass (Q/B; year^{-1}) and production/consumption (P/Q) of functional groups in the 1985 and 2004 Guinean shelf ecosystem models[a] (EE, the ecotrophic efficiency, is the proportion of the total mortality caused by predation and fishing)

| Functional groups | Component species | 1985 model | | | | | 2004 model | | | | Common parameters | | |
		Biom. (t·km^{-2})	P/B (yr^{-1})	EE (-)	Landings (t·km^{-2}·yr^{-1})	F (yr^{-1})	Biom. (t·km^{-2})	P/B (year^{-1})	Landings (t·km^{-2}·yr^{-1})	F (yr^{-1})	P/Q (-)	M (yr^{-1})	Q/B (yr^{-1})
1 Whales	Mainly *Balaenoptera physalus*	0.031	0.020				0.031	0.020					4.65
2 Dolphins	Mainly *Globicephala melas* and *Physeter macrocephalus*		0.070	0.15				0.070					12.12
3 Turtles	*Caretta caretta*		0.150	0.20				0.150					3.50
4 Sea birds	Various shore birds		0.300				0.001	0.300					85.66
5 Rays+	Mainly *Raja miraletus*	0.678	0.289		0.013	0.019	0.386	0.356	0.036	0.086	0.10	0.27	7.99
6 Sharks+	Various coastal sharks		0.270	0.40	0.009			0.405	0.010	0.135	0.10	0.27	4.33
7 Large pelagics	*Ablennes hians, Albula vulpes, Pomatomus saltatrix*, etc.		0.640	0.80	0.032	0.107		0.850	0.094	0.312		0.54	6.60
8 Barracudas+	*Sphyraena guachancho, S. barracuda, S. sphyraena*		0.602	0.80	0.007	0.100		0.920	0.030	0.421	0.10	0.50	9.51
9 Carangids	*Caranx* spp, *Selene dorsalis*, etc.		0.800	0.70	0.007	[b]		1.000	0.033	0.200	0.10	0.80	9.46
10 Horse mackerels+	*Decapterus punctatus, Scomber japonicus*, etc.		0.640	0.80	0.073	0.106		0.700	0.115	0.167	0.10	0.53	10.25
11 Ethmalosa	*Ethmalosa fimbriata*		0.860	0.95	0.261	0.215		1.420	0.946	0.779	0.10	0.65	13.51
12 Sardinella+	*Sardinella aurita, S. maderensis, Engraulis encrasicolus*		1.390	0.95	0.047	0.231		2.110	0.196	0.959		1.15	12.04
13 Bobo croaker	*Pseudotolithus elongatus*	1.253	0.369		0.062	0.049	0.509	0.633	0.260	0.313	0.25	0.32	10.09
14 Other croakers	*Pseudotolithus senegalensis, P. senegallus, P. typus, P. epipercus, P. moori*	0.869	0.414		0.073	0.084	0.259	0.474	0.134	0.144	0.25	0.33	8.42
15 Lesser Afr. threadfin	*Galeoides decadactylus*	0.350	0.390		0.019	0.053	0.197	0.475	0.078	0.085	0.25	0.39	10.52
16 Giant Afr. threadfin	*Polydactylus quadrifilis*	0.221	0.450		0.010	0.047	0.054	0.428	0.028	0.028	0.20	0.40	5.57
17 Royal threadfin	*Pentanemus quinquarius*	0.125	0.550		0.019	0.153	0.068	0.411	0.011	0.011	0.25	0.40	11.70
18 Seabream+	*Dentex angolensis, D. canariensis, Pagellus bellottii bellottii, Pagrus caeruleostictus, Sparus auratus*, etc.	1.410	0.530		0.043	0.031	0.479	0.650	0.108	0.150	0.25	0.50	9.00
19 Sea catfish	*Arius gigas, A. heudelotti, A. lastiscutatus, A. parkii*	0.957	0.253		0.041	0.043	0.462	0.573	0.218	0.363	0.25	0.21	8.00
20 Mullets+	*Acanthurus monroviae, Aluterus schoepfii, Liza dumerili, Mugil bananensis*, etc.	0.213	0.609		0.014	0.064	0.415	0.597	0.056	0.052	0.25	0.55	13.00
21 Grunts+	*Pomadasys incisus, P. jubelini, P. perotaei, P. rogerii, Lethrinus atlanticus*	0.387	0.286		0.018	0.046	0.094	0.293	0.039	0.053	0.25	0.24	9.04
22 Soles+	*Cyanoglossus canariensis, C. senegalensis, Dicoglossa cuneata*, etc.	0.273	0.761		0.035	0.128	0.284	0.750	0.105	0.118	0.25	0.63	11.04
23 L. demers.l piscivores	*Ephippion guttifer, Argyrosomus regius, Epinephelus aenus, Epinephelus itajara, E. goreensis, Lutjanus dentatus, Trichiurus lepturus, Zeus faber*, etc.	0.557	0.390		0.020	0.036	0.514	0.434	0.045	0.077	0.20	0.36	7.24
24 SM demer. piscivores	*Arnoglossus imperialis, Citharus lingualata, Priacanthus arenatus, Scorpaena angolensis*, etc.	1.849	0.835		0.005	0.003	0.772	0.844	0.018	0.012	0.25	0.83	11.90
25 ML dem. Invertivores	*Balistes carolinensis, B. vetula, Bothus poda, Pseudupeneus prayensis*	1.544	0.730		0.006	0.004	0.853	0.781	0.043	0.056	0.25	0.72	10.32
26 S. dem. Invertivores	*Antigonia capros, Brachydeuterus auritus, Chaetodipterus goreensis, Drepane africana*, etc.	1.029	1.070		0.009	0.009	0.849	1.070	0.027	0.026	0.25		9.60
27 Bathydem piscivores	*Gephyroberyx darwinii, Merluccius senegalensis,*		0.760	0.80	0.001			0.429	0.005		0.25	0.43	6.10

	Pontinus kuhlii etc.							
28 Bathydem invertivores	*Pterothrissus belloci, Synagrops bellus, Trigla lyra*	0.370	0.90	0.001		0.004	0.25	4.70
29 Crustacea	Shrimps and crabs	2.500	0.80	0.013		0.037		20.00
30 Cephalopods and other mollusks	*Octopus vulgaris, Illex, Haliotis, Cymbium*, etc.	2.500	0.90	0.069		0.155		10.00
31 Benthos		1.800						25.00
32 Large zooplankton		10.000	0.80					
33 Small zooplankton		40.000	0.60				0.20	
34 Primary producers		84.000			49.000			
35 Detritus					290.00			

a) see Guénette and Diallo [2004] for details; b) negligible