



Institut de recherche
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Mémoire de fin d'études Spécialisation halieutique d'Agrocampus Ouest

Cross-modelling of the Southern-Benguela ecosystem: sensitivity and relevance of a modélisation with EcoTroph

Présenté par :

Gasche, Loïc

Soutenu le :

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Introduction

It is now commonly accepted that overfishing can be a main source of perturbations in marine ecosystems (Goñi, 1998), impacting the whole food web through direct and indirect interactions. Confronting this reality, the European Parliament stated in one of its reports in early 2009 that “Controlling fishing effort should take account of the various species, the various types of fishing gear and the assessed impact of catches on stocks of each species”. To assess this impact ecosystem models can be used as tools allowing the simulation of various fishing scenarios. Several models are being applied to a constantly increasing number of marine ecosystems, each model being based on a certain number of assumptions and hypotheses and representing just one of many possible visions of an ecosystem. These models use various kinds of indicators to tell the user about the ecosystem’s state and the impacts of fishing. Trophodynamic indicators have first been defined in the form of trophic levels (TLs) by Lindeman in 1942 and modified in 1975 by Odum and Heald. They are now widely used, thanks to their ability to reveal ecosystem-level patterns (Cury et al., 2003). The trophic spectrum, which represents the distribution of biomass, catch or production by trophic level, may be seen as a new evolution of this indicator, enabling the structure and functioning of marine ecosystems to be represented (Gascuel et al., 2005; Gascuel et al., 2008). One of the main assets of trophic spectra is that they are sensitive to changes in ecosystem structure and so allow a good observation of the effects of fishing on the ecosystem. EcoTroph (Gascuel 2005; Gascuel and Pauly, 2009) is a trophic level-based model using trophic spectra to represent marine ecosystems and being able to leave aside the notion of species. EcoTroph (ET) models marine ecosystems as flows of biomass from low to high trophic levels, defined by their intensity and their speed. EcoTroph largely uses outputs of other models and is now a part of the Ecopath with Ecosim (EwE) software. EcoTroph has already been extensively applied to the Guinea ecosystem to assess the impacts of fishing on the latter (Gascuel et al., 2009).

Here we apply EcoTroph to the southern Benguela ecosystem, one of the world’s four great eastern boundary upwelling ecosystems. Because of its biological and commercial importance, this ecosystem has been deeply studied and results have been synthesized into ecosystem models, in particular: Ecopath (Shannon et al., 2003; Watermeyer and al, 2008; Shannon et al., 2008) and Osmose (Travers et al., 2006; Vergnon et al., 2008; Travers et al., 2009; Travers et al., 2010; Travers and Shin, 2010). Outputs of both modeling approaches can be used in EcoTroph. Ecopath (Polovina, 1984; Christensen and Pauly, 1992) with Ecosim (EwE) is a non-opportunistic, non-spatial model representing marine organisms (mostly gathered by species) across various trophic classes being linked together by means of a diet table. Osmose is a spatial individual-based model based on the principle that predation is opportunistic (Shin and Cury, 2001; Shin and Cury, 2004). Osmose was originally a high trophic levels model but it is now forced by a biogeochemical model of plankton so as to represent the biology of species across the whole food chain. Both models take top predators such as marine mammals and birds into account; they also both represent fishing mortality.

The first goal of this study is to represent the Southern Benguela ecosystem using EcoTroph and to assess the impact of fishing on the ecosystem. This study allows us to gather more information about EcoTroph’s functioning and its sensitivity to inputs and parameters, which can be useful considering this model’s ability to use data from various other models. Applying EcoTroph to one ecosystem with data from two different models allows us to make comparisons between results obtained with the two sets of data. These comparisons are interesting in the sense that they can help us better validate results from the two models and therefore the hypotheses at the base of each model. Besides, similar results obtained with different models suggest robustness across models in terms of the conclusions that can be drawn, and may be seen as more likely to be close to reality. On the other hand differences are interesting in the sense that they provide us with new questions to be answered and highlight model sensitivities and constraints. Comparisons have already been made of the

results given by EwE and Osmose applied to the southern Benguela ecosystem (Shin et al., 2004; Travers et al., 2010) and have shown great similarities in results obtained. Shin et al. (2004) underline differences between the two models with respect to two pelagic species (Horse mackerel and Chub mackerel), Osmose highlighting the indirect effects of fishing on these species. Travers et al. (2010) mainly show that Osmose suggests species recover more quickly and more completely from a period of highly increased fishing effort, largely due to their more opportunistic feeding strategies than species modeled in EwE.

An important part of this study is an analysis of EcoTroph's sensitivity to the parameters coming from one or the other model. Based on an EcoTroph (ET) model of the Southern Benguela, we answer the following two questions: What is the impact of fishing on the trophic functioning of the Benguela ecosystem? What is the influence of each input model and of the parameterization on the results given by EcoTroph? Attempts at a back-simulation of a pristine state and comparisons with a model for the ecosystem's pristine state can give us interesting insights on EcoTroph's functioning and ability to simulate. Further we attempt to fit the simulated model to the pristine ET-Ecopath by changing the accessibility of species in EcoTroph. This approach gives us interesting informations about how fisheries have modified the ecosystem's properties since the start of exploitation.

Finally we use a modified EcoTroph model to simulate increases in fishing efforts targeting only a few species in the ecosystem. Two scenarios are simulated, corresponding to those used in Travers et al. (2010), and results obtained using ET are compared with those of the previous Osmose-EwE study. This new version of EcoTroph has never been used before and this part of the study is seen as an exploratory work that will need to be extended and validated through other comparisons.

Models mentioned before will be presented more completely below and details will be given about EcoTroph's input parameters. Subsequently, results obtained will be presented and discussed. We will conclude by discussing the potential role of EcoTroph in giving us a better understanding of marine ecosystems and of the effects of fishing.

1) Ecological and Scientific context

1.1) The Southern Benguela ecosystem

1.1.1) Location



Figure 1 : Location of the Benguela upwelling system and of two other major eastern boundary upwelling systems

The Benguela ecosystem is located off the western coast of Angola, Namibia and South-Africa (Figure 1). This ecosystem is divided in two parts: the Northern Benguela off Angola and Namibia and the Southern Benguela off South Africa. Basically the Southern Benguela ecosystem extends from the Orange River (the north-western boundary between Namibia and South-Africa) to East London on the Indian Ocean (Figure). In reality the two ecosystems are fairly independent from one another because of a strong upwelling cell near Lüderitz (Namibia) which causes them to evolve differently.

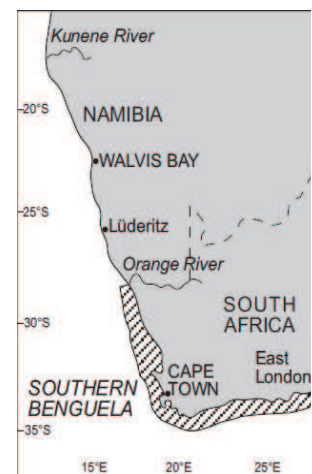


Figure 2 : Location of the Southern Benguela ecosystem, corresponding to the modelled area (from Shannon et al., 2008)

1.1.2) An upwelling ecosystem

The Benguela upwelling ecosystem is one of the world's four most important eastern boundary upwelling systems. Cold nutrient-rich water from depth is upwelled and reaches the surface because of the action of the wind near the coast. Winds blowing from South to North (in the Southern Hemisphere) cause surface water to move westward because of the Coriolis force (Eckman spiral). Near a coast this movement causes deep water to be upwelled to the surface. The Southern Benguela ecosystem distinguishes itself from other ecosystems for two reasons:

- Intrusion of warm water at its southern boundary due to the Agulhas Current which terminates the western boundary current of the Indian Ocean, and the existence of a warm water shallow bank area in the south, bordering the true upwelling area on the west coast.
- A pulsed seasonal upwelling due to the south-easterly winds that blow during summer.

Because of their richness in nutrients upwelling ecosystems have very high primary production that can support high fish biomass, although the fish production / primary production ratio fluctuates from one upwelling to another. For example the Benguela ecosystem has the highest primary production of all upwelling systems but its fish production is rather low when compared to that of the Humboldt ecosystem (Shannon et al., 2008). Upwelling ecosystems are also characterized by high small pelagic fish biomass that impacts both biomass of plankton and of predators. In the Southern Benguela the dominating small pelagic species are anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*), and commercially important predator is hake (*Merluccius capensis* and *Merluccius paradoxus*). Because of these high fish biomasses, upwelling ecosystems have historically sustained numerous fisheries and can be important sources of income for some countries.

1.1.3) Exploitation

Human exploitation of the Benguela ecosystem can be divided in 4 eras: aboriginal (before 1652), preindustrial (1652-1910), industrial (1910-1975) and postindustrial (after 1975) (Griffiths et al., 2004). The aboriginal period is characterized by low levels of mostly intertidal exploitation, the preindustrial period by an intense exploitation of a few large and accessible species, the industrial period by a massive increase in catches due to technological development and the postindustrial period by improved resource management and a stabilization of catches. Extraction rates peaked at over 1.3 million t.yr⁻¹ in the 1960s and have subsequently declined by more than 50%. Populations of whales, seals, pelagic and demersal fish are recovering from historical overexploitation. On the other hand populations of inshore stocks, particularly abalone, rock lobster and inshore linefish remain severely depressed.

Since the 1970s (roughly the beginning of the postindustrial era) South Africa has managed its marine resources cautiously. Indeed, apart from rock lobster and several species of linefish catches that have shown marked declines, catches overall have remained relatively stable in the Southern Benguela. The Northern Benguela ecosystem has undergone a shift in its species because of overexploitation combined with unfavourable environmental conditions. After peaking in the late 1960s and sustaining levels of around 0.5 million tons between 1970 and 1980, catches of small pelagic species in the Northern Benguela have dwindled to current levels of less than 100 000 tons. Catches of rock lobster have decreased even more dramatically in the same period.

1.2) Ecopath

Ecopath with Ecosim (EwE) is a widely used food web model based on Polovina's (1984) initial mass-balance model and extended and fully described by Walters et al. (1997). Species are aggregated into groups in terms of size, feeding and mortality parameters which means that a group can comprise of one species, various species, or on the contrary only

one particular stage of development of one species. Each group is attributed a specific diet based on scientific observations. These diets result in fractional trophic levels for predators above trophic level 2, that can be calculated as: $\tau_i = 1 + \sum_j (D_{ij} \cdot \tau_j)$ where D_{ij} is the proportion of prey j in the diet of consumer i and τ_j the mean trophic level of prey j . Groups are linked by trophic flows, described by Winberg's balanced energy equation: Consumption = Production + Respiration + Unassimilated food. In Ecopath relationships between groups are described by a set of linear equations, so that the production of a group (i) is balanced by the sum of (a) predation on that group by other groups, (b) exports by means of fishing or emigration from the system and (c) other sources of mortality.

By re-expressing this equation, a balance for each interaction of prey group (i) with predator group (j) is computed:

Production by (i) = $B_i \times P/B_i$

Predatory losses of (i) = $\sum_j (B_j \times Q/B_j \times DC_{j,i})$

Other losses of (i) = $(1 - EE_i) \times B_i \times P/B_i$

Where (i) is a prey group, j is a predator group (i), B_i is the biomass of group (i), P/B_i is the production of group (i) per unit biomass, Q/B_j is the consumption of group (i) per unit biomass, $DC_{j,i}$ is the proportion of prey group i in the diet of predator group j , and EE_i is the EcoTrophic efficiency of group(i) (i.e. the proportion of the total production of group (i) that is consumed by predators or lost from the ecosystem (e.g. as catch). So for box (i):

$B_i \times P/B_i \times EE_i - \sum_j (B_j \times Q/B_j \times DC_{j,i}) - Ex_i - F_i \times B_i = 0$

Where Ex_i is the export of (i) by emigration and F_i the fishing mortality applied to group (i), $F_i \times B_i$ thus corresponding to Y_i the catch of group (i). Once required inputs of B , P/B , consumption/biomass (Q/B), EE (one of which may be estimated by the model), unassimilated food, diet and catch are supplied, a mass balance model can be created by balancing the flow of production between groups (Christensen et al. 2005).

In the Ecopath model the Southern Benguela ecosystem extends from the Orange River to East London, boundaries that are relatively close to those used in Osmose, thus facilitating comparisons. The modeled area extends offshore to the 500m isobaths and covers 220000 km². The first Ecopath model used in this study includes 32 groups and covers the 1990-1997 period (Shannon et al., 2003). An Ecopath model of the "pristine" ecosystem (Watermeyer et al., 2008) was used so as to make comparisons with a simulated pristine model made with EcoTroph using the 1990-1997 Ecopath model.

1.3) Osmose

Osmose is a multispecies, dynamic model structured by size and age (Shin and Cury, 2000). Osmose is individual-based, each individual being a school of fish of the same species with the same size and the same physiological and morphological characteristics. Osmose is a spatialized model where each fish school is distributed according to specific density maps that depend on species age and season.

The Osmose model is organized into a hierarchy as each school belongs to a cohort, belonging to a species, included in the whole community. Predation is opportunistic: there are no pre-established trophic links between species.

Plankton production and carrying capacity:

Osmose's biomass of non piscivorous fish was limited in the first version of the model by the ecosystem's carrying capacity, which stood for the amount of phytoplankton available for these fish. An excess in the non piscivorous fish biomass led to an explicit mortality applied to it at the beginning of each time step. The Osmose model we use in this study is forced by a phytoplankton model (Travers et al., 2009). Fish feed on plankton like on any other prey and can undergo starvation mortality if not enough plankton is available.

Fish life cycle:

Osmose explicitly models life cycles.

Three different natural mortalities are applied at the beginning of each time step, respectively to larval schools, to fish schools inside the modeled area and to fish schools outside the

modeled area. Larval mortality is applied only during the first month of life of fish schools and takes into account both physical and biological factors influencing the survival of larvae. As these factors are not well known or well documented they are used to calibrate the model. Natural mortality applied to fish schools stands for sources of mortality that are not explicit in the model, for example predation from predators that are not included in the model. Natural mortality applied to fish schools outside the modeled area is especially important for migratory species. Natural mortality M reduces the abundance N of fish schools according to the equation: $N_{s,t+\Delta t} = N_{s,t} \cdot e^{-M \cdot \Delta t}$

Predation mortality is applied only if there is a matching relation in size between a predator and its potential prey. Indeed the feeding spectrum restrains each predator to prey on fish schools or plankton groups within a relative size range. If there is more than one school of possible prey in the cell, the predator uniformly eats the available prey according to their relative abundance. For each fish school, predation efficiency is calculated as the ratio between the ingested biomass per unit of time and the maximum ingestion rate. Predators can only prey on fish school with which they share the same cell of the grid. Each fish school can move from one cell to another at each time step, each school moving to the adjacent cell with the highest biomass of prey.

For each species growth is represented thanks to a discretised Von Bertalanffy growth model. The growth rate is adjusted according to the amount of food ingested by each fish school during each time step. In Osmose a fish is estimated to need 3,5g of food per gram of body weight per year in order to grow and develop (Shin and Cury, 2004). An estimated annual ration of 2,01g of food per gram of body weight per year is needed for fish maintenance in the model (Shin and Cury, 2004). Thus a critical ratio $\xi_{crit} = 0,57$ is defined as the ratio between the annual maintenance ration and the annual mean ration and is chosen as the critical threshold under which starvation occurs. If the predation efficiency of a school is above this critical threshold its growth rate increases linearly with its predation efficiency. If the predation efficiency of a school is under ξ_{crit} the school will not grow in length and starvation mortality will be applied to it. Starvation mortality increases linearly when predation efficiency decreases.

Fishing mortality applies at each time step and is homogeneously distributed over the cells of the model grid. Fishing mortality can vary from one year to another but only applies to schools older than the recruitment age provided as input. The equation describing fishing mortality is similar to that of natural mortality, with F replacing M .

Spawning occurs seasonally for each mature fish of every species. Egg production is calculated from the spawning biomass of adults and the relative fecundity, assuming that females account for 50% of each species. Egg production for each school also depends on the food intake, increasing linearly when the predation efficiency is above ξ_{crit} .

This Osmose model is applied to the Southern Benguela ecosystem by modeling 10 fish species and 1 crustacean species, chosen for their commercial importance and/or in terms of biomass : euphausiids (*Euphausia lucens*), anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), round herring also called redeye (*Etrumeus whiteheadi*), horse mackerel (*Trachurus trachurus capensis*), shallow water Cape hake (*Merluccius capensis*), deepwater Cape hake (*Merluccius paradoxus*), snoek (*Thyrsites atun*), silver kob (*Argyrosomus inodorus*), lanternfish (*Lampanyctodes hectoris*) and lightfish (*Maurolicus muelleri*).

The modeled area extends from the Orange River (28.2°S–16°E) to Cape St Francis (37.5°S–24.4°E), thus including the southern Benguela west of South Africa and the major part of the Agulhas Bank on the South Coast. The time step is 2 weeks. The modeled period (1990-1997) as well as the fishing mortalities are the same as those adopted in Ecopath.

So as to allow comparisons with Ecopath, a modified Osmose model was set up: plankton were added to the Osmose model, using on the one hand groups and trophic levels from the literature and on the other hand biomass from Ecopath. As P/B ratios are not directly provided by Osmose ratios used are those used in the Ecopath model, summarized in Shannon et al. (2003).

2) Modeling the ecosystem with EcoTroph

2.1) Method

2.1.1) EcoTroph:

EcoTroph (ET) is a trophic level-based model using trophic spectra to represent marine ecosystems (Gascuel & Pauly, 2009; Gascuel et al., 2009). Trophic spectra are a graphical representation of the continuous distribution of the ecosystem biomass (or production, or consumption by predators, or catches) across trophic levels. EcoTroph needs biomass, catches, production, consumption and trophic level of each species to run. As these data are not all available from direct scientific observations, they can also be obtained from other models. Thus, EcoTroph can be seen more as complementary than as an alternative to other models; one of its main assets being its ability to leave aside the notion of species. EcoTroph models marine ecosystems as flows of biomass from low to high trophic levels. Biomass enters the ecosystem at trophic level 1, generated by the photosynthetic activity of primary producers and recycling by bacteria that form a part of the microbial loop. A β coefficient chosen by the user between 0 and 1 determines the intensity of the biomass input control, 0 meaning that all the biomass comes from primary producers and 1 that it all comes from recycling. Thus herbivorous and detritivores are at trophic level 2, but biomass from trophic level 1 can also be consumed by species at trophic levels higher than 2. EcoTroph's representation of the ecosystem stops at trophic level 6 which is deemed high enough to cover most top predators. This trophic level-based model is built using two equations, one for biomass flow and the other for flow kinetics, from which biomass at trophic level τ (B_τ) can be calculated, as: $B_\tau = \frac{\Phi_\tau}{\Delta_\tau/\Delta_t} \cdot \Delta_t$, where Φ_τ is the mean biomass flow passing through the trophic class $[\tau, \tau + \Delta_t]$ and Δ_τ/Δ_t is the mean speed of the flow through that class. Biomass flows through trophic levels by means of two processes: predation of predators on their prey and ontogeny, as ontogeny can be associated, for some species, with increases in trophic levels. The distribution of the ecosystem biomass per trophic classes of 0,1 is a discrete approximation of a continuous distribution. Biomass outputs can occur at each trophic level undergoing fishing mortality and natural mortality other than predation. These outputs (e.g excretion and egestion, loss of energy by respiration) and the various sources of mortality are the cause for the decline in the biomass flow per trophic level curve. These output parameters are calculated on the reference state of the ecosystem, which corresponds to the modeled period (1990-1997 in this study that we improperly call the current period). The biomass flow per trophic class can be calculated as: $\Phi(\tau + \Delta_t) = \Phi(\tau) \cdot \exp([-(\mu_\tau + \phi_\tau) \cdot \Delta_t])$ where μ_τ is the natural loss rate and ϕ_τ the fishing loss rate. When attempting simulations these parameters are important because simulations are made under the hypothesis that natural mortality is constant and that only fishing mortality changes. This equation also defines the transfer efficiency (TE) between trophic levels, $\exp(-\mu_\tau)$. The speed of the flow Δ_τ/Δ_t can be expressed as the ratio between production and biomass $\Delta_\tau/\Delta_t = \left(\frac{P}{B}\right)_\tau$ coming from Ecopath. The previous equation shows that any cause of mortality has an influence on the flow kinetic of a species. Predation mortality being an important source of mortality, top-down control is introduced in the model. It allows the model to take into account indirect effects of fishing on the ecosystem when performing simulations. This is accomplished by means of a relationship linking the kinetics at a trophic level τ , and therefore the biomass flow, to the biomass of predators at trophic level $\tau+1$, based on Allen's relationship:

$$\left(\frac{P}{B}\right)_\tau = F_{\tau+1} + M_\tau$$

A coefficient α chosen by the user between 0 and 1 determines the part of natural mortality at trophic level τ that is due to predation mortality (and thus linked to top-down control). As a result the P/B ratio per trophic class can be recalculated, as:

$$\left(\frac{P}{B}\right)_{\tau} = \alpha_{\tau} \cdot M_{resf,\tau} \cdot \left(\frac{B_{pred}}{B_{pred,ref}}\right)^{\gamma} + (1 - \alpha_{\tau}) \cdot M_{resf,\tau} + F_{\tau} , \text{ where } \gamma \text{ is a shape parameter.}$$

Fishing, reducing the life expectancy of its target species, can be the cause of important accelerations in the ecosystem's flow kinetics; but as it also affects predator species responsible for top-down control and reduces their biomass the effects of fishing can become more complex.

2.1.2) Application to the Southern Benquela : building of a first standard model

i. Building a trophic spectrum

A first EcoTroph model was created, based on the 1990-1997 Ecopath model described previously. This Ecopath model represents 32 groups, some comprising more than one species and some representing a particular stage of development of one species.

The first step is to build spectra, representing the distribution of the ecosystem biomass across trophic levels. For each Ecopath group, the biomass is spread across trophic levels around the group's mean trophic level. According to the empirical method proposed in the EcoTroph plugin for EwE, each group has its own distribution of biomass across trophic levels. These curves are density probability log-normal functions centered on each species' mean trophic level and their standard deviation can either be empirically defined or chosen as the species' omnivory index given by Ecopath. When all these curves are put together they are referred to as a Smoothing function: Smooth 1 when standard deviations are empirically defined and Smooth 2 when based on the omnivory index. EcoTroph's sensitivity to the choice of the smoothing function and to other parameters mentioned above is one of the main aspects of the work done in this study.

Here we use a theoretical standard deviation as EcoTroph's smoothing function's standard deviation (Figure 1b). This theoretical standard deviation is calculated for each trophic level τ as: $\sigma = \lambda \cdot \ln(\tau - 0,05)$. The result is a continuous distribution of biomass across all trophic levels, biomass from different groups contributing more or less to various adjacent trophic levels (Figure 1c). The trophic spectrum corresponds to the sum of all biomass for every trophic level represented in the model. Thus the result is only one curve where species cannot be differentiated anymore, giving a simplified view of the ecosystem (Figure 1d). As Ecopath also provides P/B ratios a production trophic spectrum can also be built from which the $(P/B)_{\tau,ref}$ can be deduced. We use the same approach to build the catch trophic spectrum from which the fishing mortality trophic spectrum ($F=Y/B$) and the fishing loss rate trophic spectrum ($\phi=Y/P$) that can be used to perform simulations.

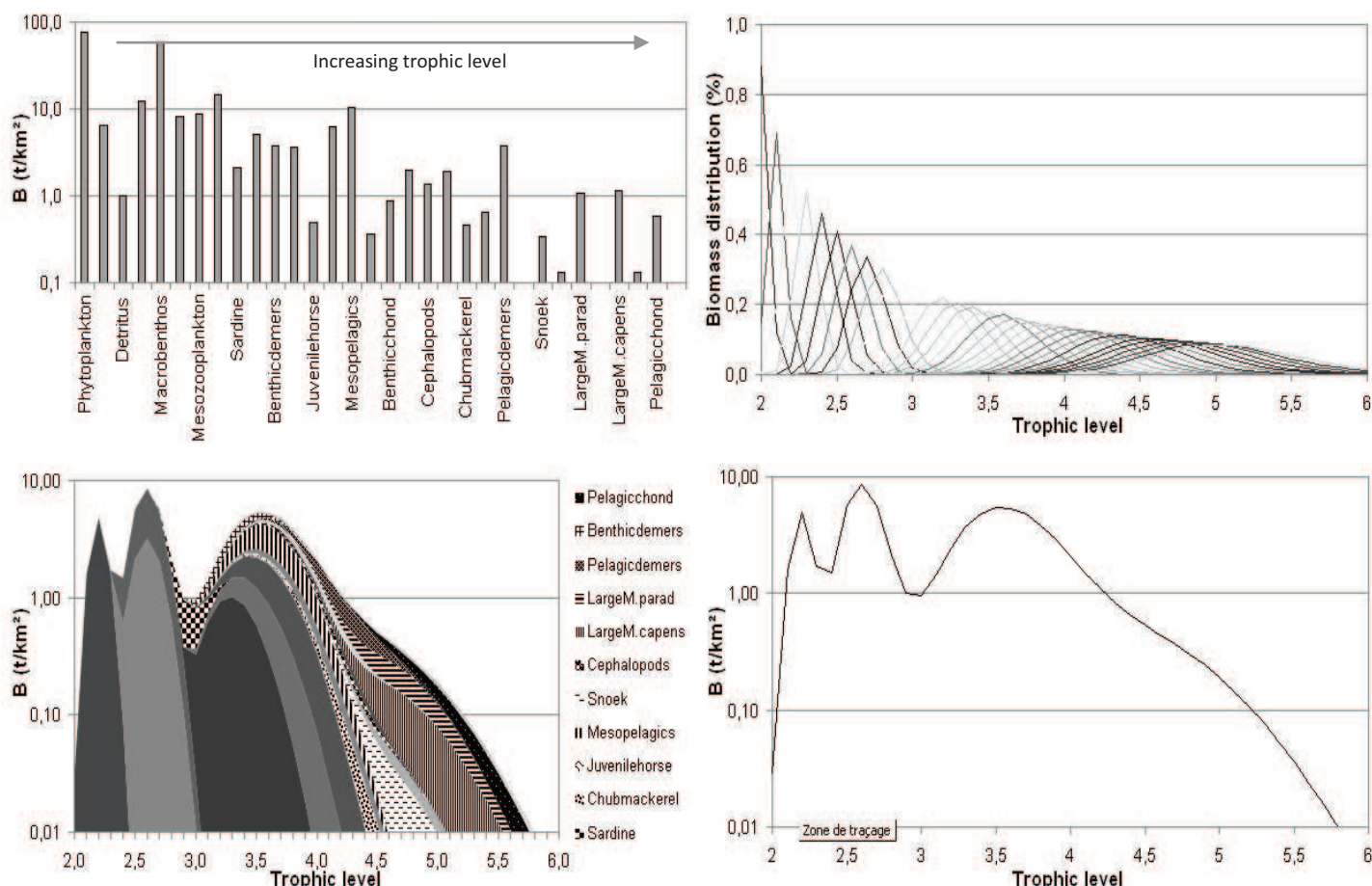


Figure 1 : Stages of the building of a trophic spectrum. Biomasses per species (a)(top left) are spread for each species by a smoothing function the shape of which depends on the mean trophic level of the species (b)(top right). Biomasses per trophic level per species (c)(bottom left) are summed for each trophic level, resulting in a biomass trophic spectrum (d)(bottom right)

ii. Choosing accessibilities and other parameters

EcoTroph does not model one flow but two: one for total biomass and one for the fraction of biomass which is accessible to fisheries. In other words the model is based on the assumption that one part of the biomass cannot be fished, for ecological or technological reasons. Thus the accessible part of the biomass is defined by means of an accessibility to fisheries parameter for each species. This parameter corresponds to the proportion of this species that would be caught under the hypothesis of an infinite fishing effort. This parameter also takes into account whether a species is directly targeted by fisheries or not. Therefore a group composed of a few target species and a lot of non-target species will have a lower accessibility than a

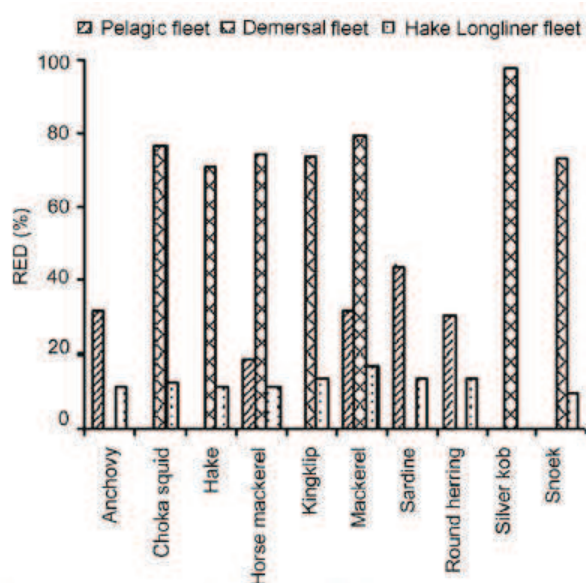


Figure 2 : Ratio of fished area and distribution area by species for pelagic and demersal fleets (average 1985-2001) (Fréon et al., 2005)

group containing only target species. Our main criterion when fixing accessibilities for the groups was the ratio between the fished area of a species and the distribution area of this species within the ecosystem (Figure 2). We assumed that this ratio corresponds to the fraction of the species that would be caught if the fishing effort was infinite. Then values obtained were corrected to take into account the fact that only some species of a group or some stages were targeted. According to available literature corrections were also made for deep species or species living in areas limiting fishing so as to try to be as close as possible to reality.

Regarding top-down and biomass input controls values of $\alpha=0,5$ and $\beta=0,1$ have been chosen, in an attempt to be as close as possible to the ecosystem characteristics. These values have been chosen because the Southern Benguela ecosystem is an upwelling ecosystem, characterized by wasp-waist control (Cury 2000) and very high phytoplankton biomass (and therefore biomass recycling was deemed not to have much importance).

iii. Simulations

Various fishing pressures are then simulated, using fishing effort multipliers ranging from 0 to 5, so as to have better insights on the current state of the ecosystem and on the effects of fishing on the latter. The current fishing mortality is calculated as the Catch / Biomass ratio, either for the accessible part of the ecosystem or the whole ecosystem. Fishing mortality F is calculated for each 0.1 trophic level class, which gives a trophic spectrum of the fishing effort. For each 0.1 TL class the current fishing mortality is multiplied by an effort multiplier ranging between 0 and 5, values between 0 and 1 corresponding to decreases in the fishing effort and values above 1 to increases in the fishing effort. Values chosen are : 0; 0.2; 0.4; 0.7; 1; 1.5; 2; 2.5; 3; 3.5; 4; 5. Modifying F changes the P/B calculated in the top-down control equation of EcoTroph and the catch. As production and biomass are back-calculated using the P/B ratio the whole image of the ecosystem is modified when F changes.

In a second step, an EcoTroph model is set up based on a pristine Ecopath model of the Southern Benguela. This model is compared with the simulated pristine model elaborated from the 1990-1997 ET-Ecopath model by reducing the fishing mortality to 0. We expect that setting the fishing mortality to 0 would not be enough to simulate the pristine state of the ecosystem. Therefore, we track down differences between the pristine model and the simulated pristine model by comparing biomasses, accessible biomasses and speed of biomass flows (P/B). The goal of these comparisons is to try to understand which parameters of the ecosystem may have been modified by fishing. To address this question we modify some parameters such as the accessibility to fisheries and make comparisons between the pristine and the simulated state.

iv. Sensitivity analyses

Sensitivity analyses are performed on both the current state of the ecosystem (trophic spectra) and on the simulated states. During a sensitivity analysis we modify only the tested parameter, within a realistic range of values, all other parameters remaining constant. We look at the effects of these changes on the simulated biomass and catch trophic spectra. In particular we compare the rate of variation of the parameter with that of biomasses and catches: If the rate of variation of the results is higher than that of the parameter they are very sensitive to this parameter; if not they are not.

So as to do the sensitivity analysis we set up four different representations of the Southern Benguela ecosystem, as shown in Figure 3:

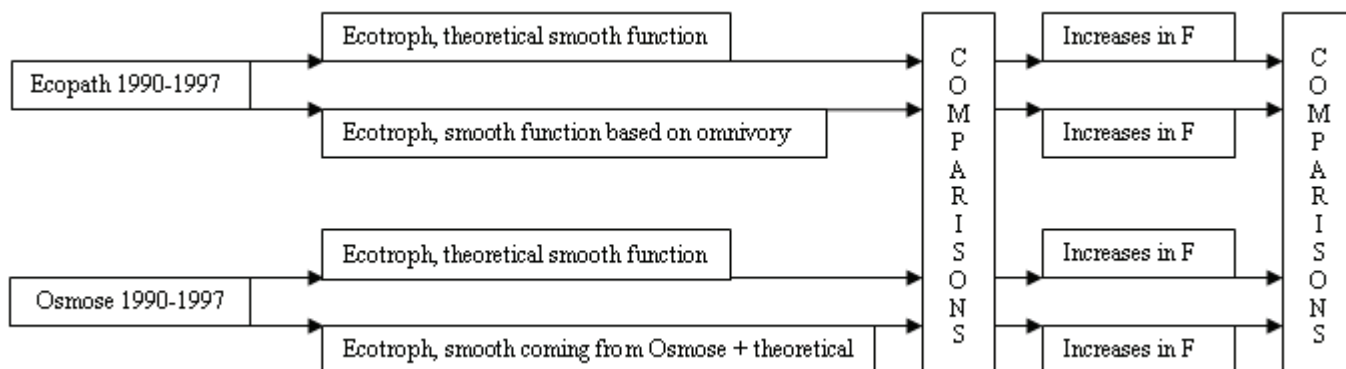


Figure 3 : Representations of the ecosystem set up for the sensitivity analyses

From the 1990-1997 Ecopath model we first build an EcoTroph model for simulations, using the theoretical smooth function to represent the distribution of the biomass of each Ecopath group around its mean trophic level (Figure 1b). This kind of smoothing function is based on the idea that the standard deviation of the density probability curve increases with the mean trophic level to which they correspond, according to the equation: $\sigma = \lambda \ln(\tau - 0,05)$. τ is the trophic level, σ is the standard deviation and λ is a width parameter chosen by the user, the value of 0.07 being proposed as default value (Gascuel et al., 2009). A sensitivity analysis to λ is performed, λ evolving between 0.04 and 0.115 with 0.015 increments. The two smoothing functions obtained with those extreme values are presented in Figure 4, a low value of λ corresponding to sharp peaks and a high value of λ to wide curves.

The second model elaborated is based on a different smoothing function, also suggested as an option of the EcoTroph plugin: the standard deviation of each smoothing function no longer depends on the mean trophic level of the group but is equal to the omnivory index of this group, as provided by Ecopath. The omnivory index measures the variability between trophic levels of preys of a group and is here used

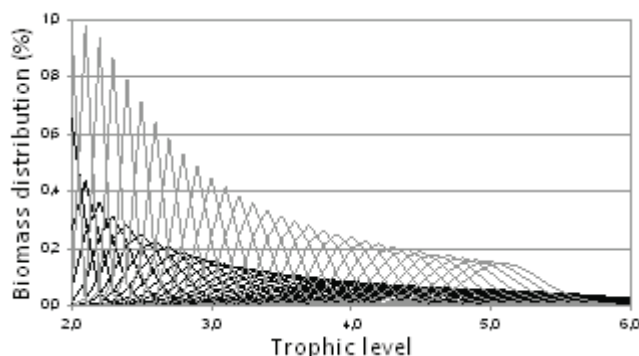


Figure 4 : Aspects of Smooth 1 for two different λ parameters: $\lambda=0.04$ (grey) and $\lambda=0.115$ (black). Each curve corresponds to a trophic level class so some species can have the same curve and some curves may correspond to no species in this ecosystem

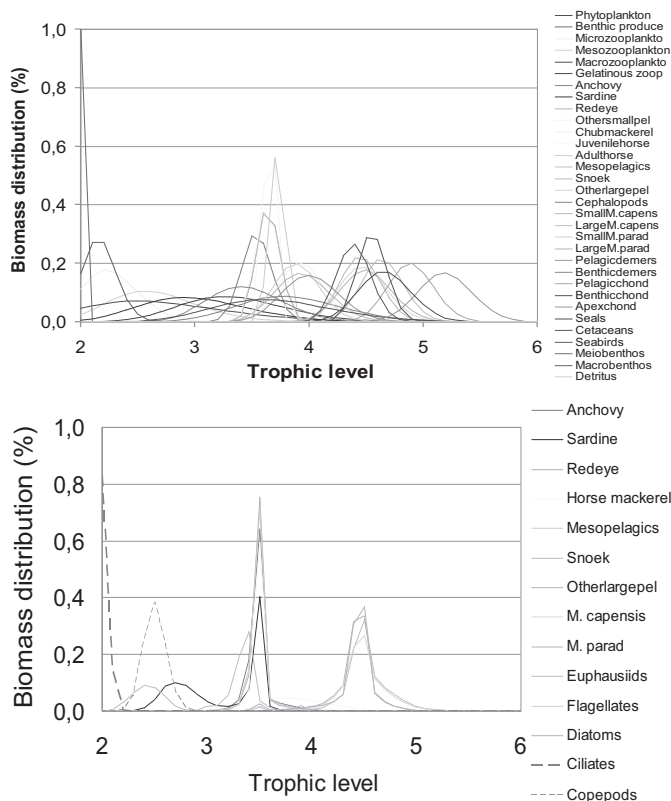


Figure 5 : Shape of smoothing function Smooth 1(a) Smooth 2 and (b) Smooth Osmose. Each curve corresponds to a species. Ciliates and copepods were added to the initial Osmose model and their curves follow the same equation as in Smooth 1

as a proxy of the variability between individuals within a group. This approximation can be questioned and will be discussed later. As shown in Figure 5a, using the omnivory index as σ drastically modifies the aspect of the smoothing functions.

Then two other models are put together, using as inputs values from the Osmose model. The first model uses mean trophic levels, biomass, catches from Osmose but with the theoretical smoothing functions previously detailed. Planktonic groups, being needed in EcoTroph but not directly modelled by Osmose, are introduced in the model using data coming from Osmose's forcing model and Ecopath. The second model uses biomass distributions from Osmose (Figure 5b). Indeed, Osmose, being an individual-based model representing life cycles, gives its own distribution function across trophic levels for each species. Planktons were also introduced in this model by means of biomasses from the forcing model and theoretical smoothing functions.

For each model, trophic spectra are compared so as to answer the question: What is the influence of the smoothing functions on the representation of the ecosystem? Then we simulate changes in the fishing effort to evaluate the effect of the smoothing function and of the input model on results obtained, regarding the fishing impact on the ecosystem biomass and the amount of simulated catches.

Table 1: Parameters used in the model, standard value and units

Variable	Parameter definition	Value or Formula	Units
B	Biomass	-	tonne.km ⁻²
B*	Accessible biomass	-	tonne.km ⁻²
C	Catch	-	tonne.km ⁻² .an ⁻¹
S	Selectivity	B*/B	-
P	Production	P/B.B	tonne.km ⁻² .an ⁻¹
F	Fishing mortality	Y/B	y ⁻¹
F*	Accessible fishing mortality	Y/B*	y ⁻¹
M	Natural mortality	exp(-μ)	y ⁻¹
μ	Natural loss rate of biomass	LN(P _T /P _T +Δ _T)/Δ _T -φ	TL ⁻¹
φ	Fishing loss rate of biomass	Y/P	TL ⁻¹
φ*	Accessible fishing loss rate of biomass	Y/P*	TL ⁻¹
σ	Standard deviation of the smoothing function	λ*LN(TL-0,05)	-
λ	Parameter modifying the value of σ with the Smooth1 function	0,07	-
β	Coefficient of biomass input control	0,1	-
α	Coefficient of top-down control	0,5	-

Sensitivity analyses to α (intensity of the top-down control) and β (intensity of the biomass input control) are also performed. The α parameter evolves between 0 and 1 with 0.1 increments and the β parameter evolves between 0 and 0.5 with 0.1 increments as well. Sensitivity to the accessibility of fish to fisheries is also tested. First, accessibilities between 0 and 1 are tested for anchovy (a small pelagic species) and for *M.capensis* (a demersal predator), with 0.1 increments. Then accessibility of all species is made to evolve between -50% and +10%, by 10% steps.

Results obtained are presented and commented on in the following part and their limitations subsequently considered.

2.2) Results

2.2.1) The current state of the ecosystem:

According to the EcoTroph model based on Ecopath 1990-1997 the biomass of the ecosystem is 147.7 tonnes per square kilometer, accessible biomass is 12.2 tonnes per square kilometer and catch is 2.8 tonnes per square kilometer.

Biomass at high trophic levels depends on biomass at lower trophic levels, thus the decreasing trend in biomass we observe on **Erreur! Source du renvoi introuvable.** 8 is logical. Two peaks in biomass can be observed: around trophic level 2.5 and 3.5 (Figure 6). Biomass at trophic levels close to 2.5 corresponds to various kinds of zooplankton. The gap at trophic level 3 comes from the fact that only one species has a mean trophic level around 3 in this ecosystem: sardine (TL=2.99). On the other hand biomass is high at trophic level 3.5 approximately; this is one of the main characteristics of upwelling ecosystems that are structured by small pelagic species. As these small pelagic species mostly feed on zooplanktons, their high biomass can easily be explained by the high biomass at trophic level 2.5: a high biomass of prey supports a high biomass of predators. Accessible biomass is null at low trophic levels because plankton are not targeted by fisheries in the Southern Benguela. The difference between total biomass and accessible biomass remains high for fished low trophic levels because of the low accessibility of small pelagic species in our model. Indeed selectivity (the B^*/B ratio) is below 0.3 for all trophic levels under 4, which is close to the value of the accessibilities we chose for small pelagics in this ecosystem. Accessibilities of small pelagics are low because they are only fished in a small fraction of their distribution area. The difference between biomass and accessible biomass decreases with increasing trophic levels because of the higher accessibility to fisheries of high trophic level species. Selectivity reaches a maximum of approximately 0.6 around trophic level 4.8, which means that in this ecosystem at least 40% of the total biomass at one trophic level is not accessible to fisheries.

The catch curve roughly has the same shape as the accessible biomass curve, with more important oscillations showing that not all trophic levels are targeted with exactly the same intensity. Small pelagics represent the greatest part of the catch but high trophic level species still represent an important part of it too.

Two parameters can give more details about fishing in this ecosystem: fishing mortality F and fishing loss rate ϕ . F is the catch / biomass ratio while ϕ is the catch / production ratio. These two parameters can give two different images of the same ecosystem. For example in an ecosystem with high biomass of high trophic level fish with low productions F could tell us that only a fraction of biomass is targeted while ϕ might show that too much is being fished already in comparison with what is produced: F would “hide” a situation of overexploitation and only detect it once the stock has been depleted. On the other hand some low trophic level species with short life cycles can produce each year more than their total biomass; in this case looking at F would lead to heavy underexploitation while ϕ would allow knowing to what extent what is produced is exploited. Thus F should be viewed as an indicator of which

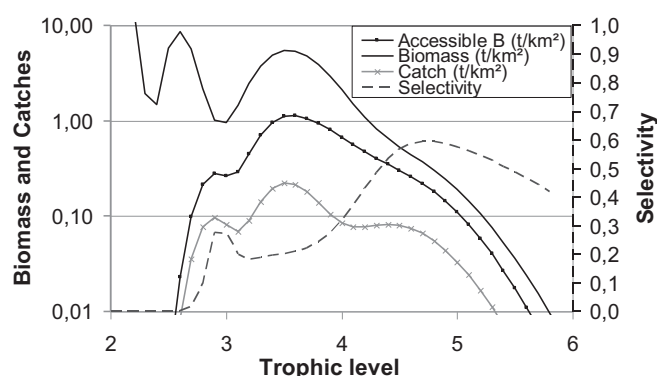


Figure 6 : Biomass (without planktons), Accessible biomass, Catches of the ecosystem and Selectivity (B^*/B).

trophic levels are targeted by fishing while ϕ is an indicator of the impact of fishing on the ecosystem.

We can observe that fishing mortality and fishing loss rate are rather similar to one another in this ecosystem (Figure 7). Fishing mortality reaches a maximum of 0.18 at trophic level 4.8 and fishing loss rate reaches approximately 0.25 at trophic level 4.9. These values are more than 3 times higher than those of small pelagic species but they nonetheless remain small, giving the image of an ecosystem that is far from intensive exploitation. They show that even if small pelagics account for the most important part of the catch it is predatory fish that are mainly targeted by fishing. We can also notice that for trophic levels below 4.4 fishing mortality is slightly higher than fishing loss rate, whereas above 4.5 fishing loss rate becomes higher than fishing mortality. This can be explained by the duration of species life cycles: species with low trophic levels tend to have short life cycles and high productions that may be higher than their biomass, which results in low ϕ that can even be lower than F . On the contrary high trophic level species have long life cycles and low productions making them more likely to have high ϕ and anyway ϕ that are higher than their F . The decrease in fishing loss rate at trophic level 4 is an exception due to the presence of the cephalopods group. The high production/biomass ratio of this group is the main cause for low fishing loss rates around trophic level 4; this effect may even be strengthened by the presence of small hakes that also have a high P/B ratio. Indeed the cephalopod group is made of mostly predator species and has a trophic level of 3.8, but these species only have a one year life cycle resulting in a very high production. Accessible fishing mortality and accessible fishing loss rate are higher because catch are compared to accessible biomass and accessible production instead of total biomass or production. They follow the same tendencies as the other two curves with low values for small pelagics and high values for predator species. One difference is that accessible fishing mortality reaches its maximum around trophic level 2.9 (corresponding to sardine) whereas even if fishing mortality peaks around this trophic level its values are smaller than at high trophic levels. This could be due to the fact that, in this model, small pelagics such as sardine have been attributed accessibilities to fisheries that are globally smaller than those given to high trophic level species, resulting in relatively (and possibly unrealistically) low accessible biomass and thus high fishing mortalities for small pelagics. As sardine is the species fished with the smallest trophic level values of F and ϕ below 2.9 only come from the smoothing of sardine's biomass and catches along trophic levels and can be seen as modelling artifacts. Accessible fishing loss rate reaches its maximum of 0.41 around trophic level 5, underlying the fact that fishing has a lot more impact on high trophic level species than on low trophic level species.

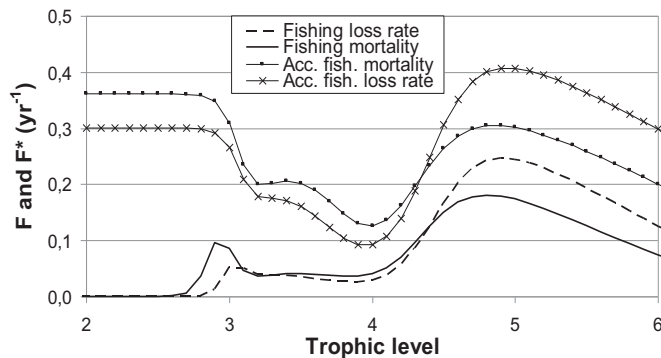


Figure 7 : Fishing loss rate and fishing mortality for total biomass and accessible biomass

2.2.2) Simulations of changes in the effort multipliers

i. Fishing impact on biomass

The first thing we observe on Figure 8 when running the simulations is that the effect of fishing on the ecosystem's biomass only starts being noticeable from trophic level 4. Increasing fishing efforts decreases

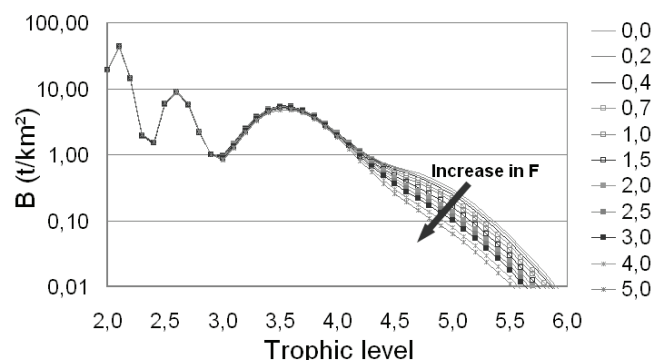


Figure 8 : Simulated biomass trophic spectra for effort multipliers ranging between 0 and 5

biomass but we do not observe any collapse in biomass, the decrease looking rather linear when effort multipliers increase.

To gather more information we can focus on some specific trophic levels of the ecosystem and observe how their biomass evolves when fishing efforts are modified.

We can see that when fishing effort increases some trophic levels are affected much more than others (Figure 9). Here we can say that the higher the trophic level the more strongly biomass decreases when fishing effort increases (with an exception: biomass at trophic level 3 decreases a little more than biomass at trophic level 3.5). Biomass of trophic level 5, which is the most affected by fishing, has already been reduced by more than one third in comparison with a situation with no fishing. In short we can say that the impact of fishing is noticeable above trophic level 4.5, where biomass is decreased by about 20% in comparison with the pristine state, but negligible below trophic level 4.5.

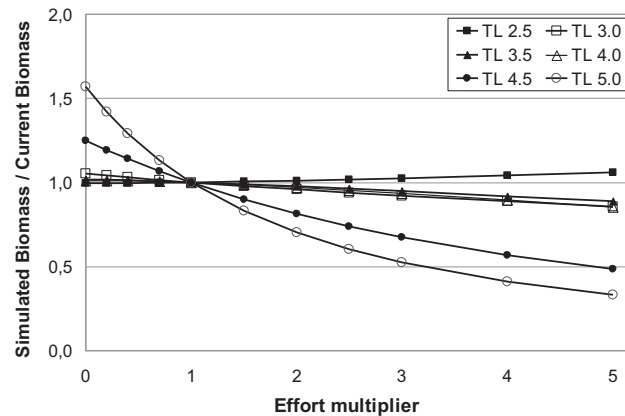


Figure 9 : Simulated biomass / Current biomass ratios at six 0.1 trophic level classes of the ecosystem (e.g TL 2.5 corresponds to the [2.5;2.6[class)

Current biomass at trophic level 5 would be reduced by 30% if the fishing effort were doubled and by 60% if it were multiplied by 5. However high these values may look, a doubling in fishing efforts is not likely to happen in the Southern Benguela ecosystem and higher multipliers are even less likely to be invoked in reality. Besides, a decrease in total biomass by 60% is considered to be the threshold for overexploitation; therefore we can say that the Southern Benguela ecosystem is moderately exploited and is not likely to be overexploited at current (1990-1997) biomass levels, even if increases in fishing efforts occur. Trophic levels 3 to 4 are far less sensitive to fishing and their biomass only decrease a little when the effort increases. There are two reasons why the decrease is far smaller for these trophic levels: first they undergo small fishing mortalities, because most of the fish biomass at these low trophic levels is not targeted by the fishery. Indeed, even if sardine and anchovy are rather strongly targeted, redeye, round herring and mesopelagic fish are not targeted in spite of their high biomasses. This means that even when high multipliers are applied across these trophic levels their absolute F_s remain, and so the impact of fishing on these trophic levels looks deceptively small. Second these trophic levels take advantage of the relaxing of top-down control by high trophic levels, whose biomass is decreased. Indeed, as there is approximately 1 trophic level between a predator and its prey, trophic levels 3 to 4 see a part of the increased fishing mortality they undergo compensated by a decrease in their predation mortality. Top-down effects propagate through the food chain and are the reason why an increase in fishing efforts causes biomass at trophic level 2.5 to slightly increase: species at this trophic level benefit from reduced predation mortality by fish at trophic level 3.5 and, as they are mostly not fished, the result is a decrease in global mortality and therefore an increase in biomass.

The trophic level of total biomass is very little affected by fishing with a decrease of less than 0.05 trophic level between the pristine state and the current state. Empirically it is said that there is a strong impact of fishing on the ecosystem when the trophic level of the ecosystem is reduced by more than 0.1 trophic levels (in 10 years), which is not the case here.

Trophic levels of accessible biomass and catches are more impacted than biomass by an increase in effort multipliers, with current trophic levels being approximately 0.1 trophic level lower than in the pristine state (Figure 10). The trophic level of catches decreases more strongly than that of the accessible biomass, with higher trophic levels at low multipliers and lower trophic levels at multipliers between 1 and 5. This can be explained by the low fishing mortality of low trophic level species. Indeed, as F is high for high trophic level species, catches of these species tend to reach a maximum and to increase less quickly or stagnate. On the contrary catches of small pelagic species will increase linearly with the increase of fishing mortality without reaching a maximum. Therefore the proportion of small pelagic fish in the catch will progressively increase, dragging the trophic level of the catch towards that of small pelagics, hence the decrease in trophic levels observed.

ii. Simulated catches

The observation of the evolution of catches gives results that are slightly different from those given by the analysis of the evolution of biomass.

Globally, the more the fishing effort increases the more catches increase (Figure 11). Catches do not increase linearly with the increase in fishing efforts multiplier. Indeed for low fishing multipliers a small increase in the effort causes a high increase in the catch. On the contrary at high effort multipliers an increase in the fishing effort only causes a very small increase in the catch. There is even a limit, around trophic level 4.4, above which we observe that the maximum catch is no longer obtained for the highest fishing effort multiplier, but for much smaller multipliers. This means that in the case of an increase in the fishing effort there is a risk of overexploitation of high trophic level species. For example the

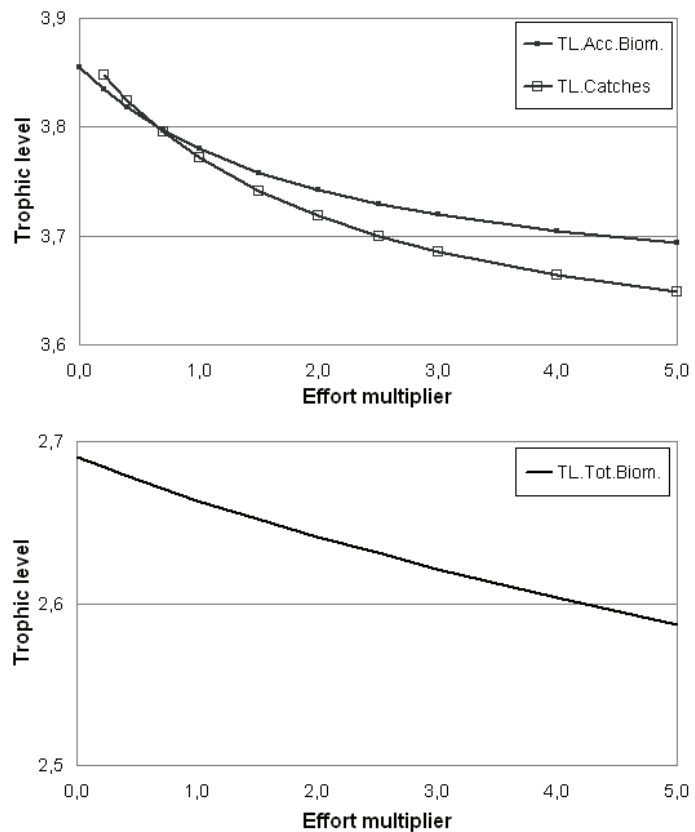


Figure 10 : Evolution of the trophic level of the Accessible biomass and of Catches (top) and of Total biomass (bottom) with the effort multiplier.

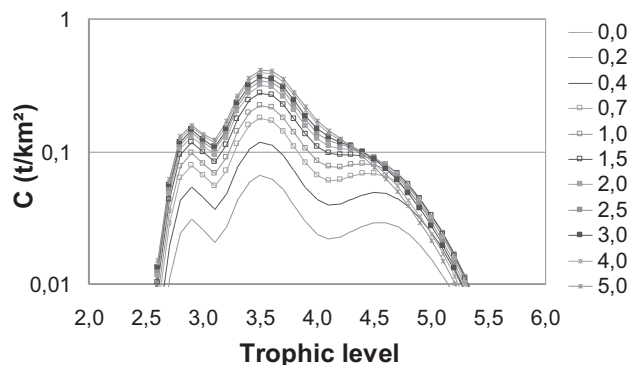


Figure 11 : Simulated catch trophic spectra for effort multipliers ranging between 0 and 5

simulation shows us that the Maximum Sustainable Yield (MSY) for trophic level 4.5 would be reached for a doubled effort multiplier.

The global pattern of the catch slowly evolves when fishing effort increases because catches of high trophic level species reach their maximum earlier than catches of other species that keep on increasing. Therefore the three-peak curve we observe at low effort multipliers progressively turns into a two-peak curve when effort increases, with small pelagic fish greatly dominating the catch.

As we did for biomass we can focus on only some trophic levels of the ecosystem to better look at the effects of an increase in the fishing effort on the catch.

Differences in the evolution of the catch with the increase of the effort multiplier are very important between the various trophic levels (Figure 12a). We can notice that trophic level 5 is currently fully exploited and that catches of trophic level 4.5 could only be increased by about 10% by a doubling in the fishing mortality. Catches of other trophic levels do not reach a maximum within the range of fishing effort multipliers tested. It is to be noticed that the most important relative increase takes place for trophic level 4, even if absolute catches at trophic level 3.5 are far higher than absolute catches at trophic level 4. This stronger increase for trophic level 4 may come from the fact that for most trophic levels the fishing mortality is a mix of high fishing mortalities from strongly exploited commercial species and low fishing mortalities from other species; whereas for trophic level 4 fishing mortality comes from the mix of rather low F from a variety of moderately fished species. For example trophic levels 3.5 and 3.6 are comprised of anchovy that is rather heavily targeted (for this ecosystem) and mesopelagics that are almost not caught in spite of their high biomass, with other moderately fished groups. In the case where only a fraction of the species of a trophic level are fished and the others are not, when the fishing effort multiplier increases only fished species will contribute to the increase in the catch. As these species already have high fishing mortalities the increase in their catch will be moderate, resulting in an even more moderate increase in the catch at this trophic level. On the contrary if all the species of a trophic level are moderately fished the increase in the fishing multiplier will cause the catch of every species to increase strongly, causing a relatively greater increase for that trophic level. We can add that trophic level 4 has the lowest accessible fishing mortality, which can directly be seen as the greatest potential to increase catches as it is the ratio of what is fished versus what can be fished.

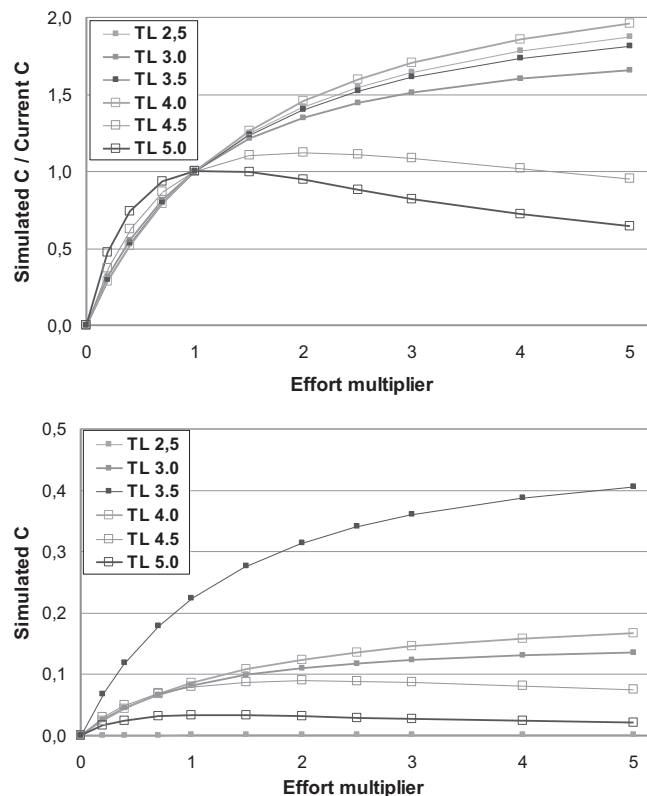


Figure 12: (a) Simulated catch / Current catch ratios at six 0.1 trophic level classes of the ecosystem (e.g TL 2.5 corresponds to the [2.5;2.6[class) and (b) Simulated catch at six 0.1 trophic level classes of the ecosystem

Figure 12b confirms that catches at trophic level 3.5 are far higher than catches at other trophic levels. They are for example about 2.5 times higher than catches at trophic level 4, which are the second highest. As we said before catches are dominated by small pelagic

species and there is a clear distinction between these species and their predators: catches of small pelagics keep on increasing for any effort multiplier whereas catches of predators reach a maximum for rather small multipliers and then decrease.

iii. Simulation of the pristine state

A pristine ecosystem is simulated, starting from the current ecosystem and setting the fishing mortality to zero. In fact, two models of the ecosystem can be used: the previous model of the 1990-1997 period and a model for the 2000-2003 period (Figure 13a). These simulated pristine ecosystems can be compared to the EcoTroph model derived from a pristine Ecopath model built with the oldest data available (Figure 13b).

The two current EcoTroph models are very similar to one another at high trophic levels but differ a lot from one another at low trophic levels (Figure 13a). The biggest difference can be observed around trophic level 3 where biomass decreases a lot according to the 1990-1997 model and does not decrease much in the 2000-2003 model. On the contrary the 90-97 model simulates a smaller decrease in biomass than the 00-03 model at trophic level 2.4. We can notice that for trophic levels below 4 the simulated pristine states do not differ from the present states (Figure 13b). At trophic levels above 4 simulated biomasses are above present biomass. The 1990-1997 model is very close to the pristine model at low trophic levels and only differs from the latter because of lower values at trophic levels 2.4 and 3 in the pristine state. On the contrary the 2000-2003 model differs a lot from the pristine model at trophic level 3. Present biomasses are smaller than pristine biomass at high trophic levels but simulation of the pristine state increases these biomasses. The result is that the simulated pristine model elaborated from the 90-97 Ecopath model reproduces very well biomasses from the pristine ET-Ecopath model whereas the 2000-2003 model cannot reproduce the pristine biomass correctly. Therefore the only model commented in the rest of the study is the pristine model simulated from the 1990-1997 model.

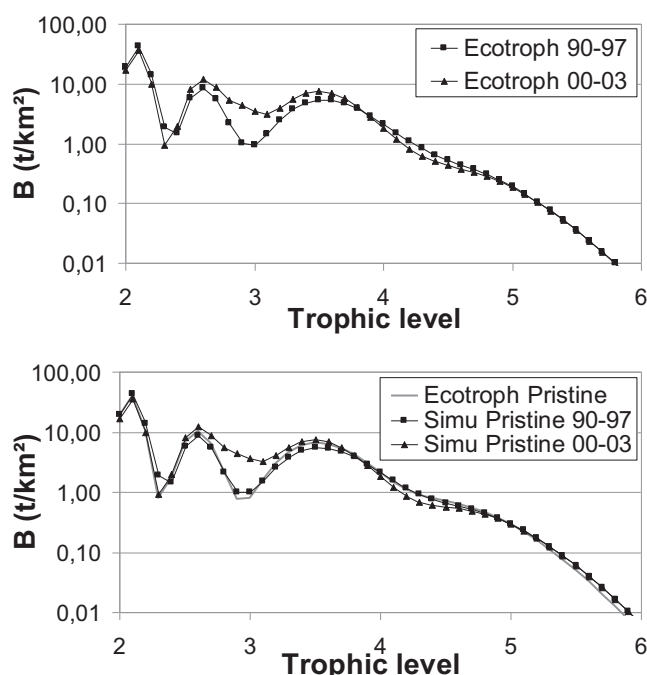


Figure 13 : Biomasses per trophic level given by the current EcoTroph models (a), by the pristine EcoTroph model and the simulated pristine models (b)

The simulated biomass is rather close from the pristine biomass for trophic levels between 3.5 and 5, which include most commercial species of the ecosystem (Figure 14). Two peaks can be observed where the simulated biomass is significantly different from the pristine biomass. These differences in simulations come from the 90-97 model used for the simulation, which

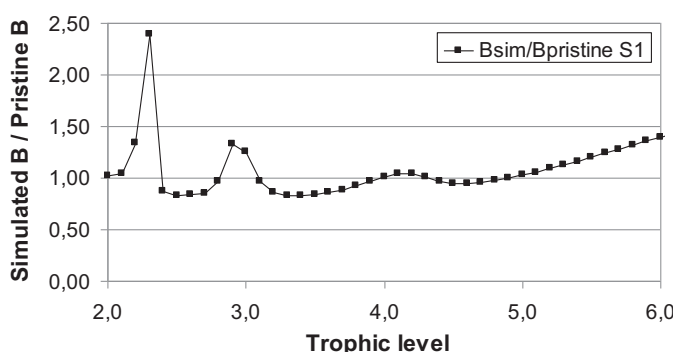


Figure 14 : Ratio of the pristine biomass simulated from the 1990-1997 ET-Ecopath model and the pristine biomass

represents higher biomass of sardine and zooplankton than the pristine model. These higher biomasses are the result of environmental forcing and not of fishing and therefore cannot be much modified by turning the fishing effort to 0. The influence of environmental forcing stands out much more in the 2000-2003 model where biomasses of both sardine and anchovy are far higher than biomasses of these species in the 90s or in the pristine era. Environmental appears to drive decadal oscillations of the biomasses of anchovy and sardine, which are the dominant (in terms of biomass) small pelagic fish species in the Southern Benguela. This is why back-simulations of a pristine state are likely to be wrong, depending on the state of the ecosystem they use as an initial model.

The simulated pristine ecosystem reproduces pristine biomass well but discrepancies are bigger when looking at other parameters of the ecosystem. The simulated flow kinetic is below the pristine flow kinetic at high trophic levels (Figure 15a). In fact, it appears that present and pristine speeds are almost identical at high trophic levels. It seems normal that the simulated pristine speed of the flow is under the present speed, as fishing increases this speed by shortening life cycles of fished species. What looks abnormal is the fact that the speed of the flow in the pristine model is the same as in the present model. This may be a choice of the modeller of the pristine state who, lacking data to estimate the speed of the flow in the pristine state, fixed it at the level of the present speed.

Simulated pristine production (Figure 15b) also is below the pristine production, but this time current production is different from pristine production.

If the pristine model overestimates P in comparison with the simulated model then it underestimates the impact of fishing on this ecosystem. This can easily be observed when looking at the accessible biomass trophic spectrum (Figure 15c). Indeed the pristine model strongly underestimates pristine accessible biomass (that is to be seen as the fraction of biomass that would be fished if the ecosystem was exploited) at all trophic levels, confirming that this model underestimates the effects of fishing.

Because of these observations we can say that the pristine model has been adjusted with data on biomass but that the flow kinetic has not been corrected (or not enough) when setting-up the model, resulting in underestimated production/biomass ratios and productions. If this assumption is true EcoTroph could be an asset when creating pristine models, allowing the correction of pristine productions

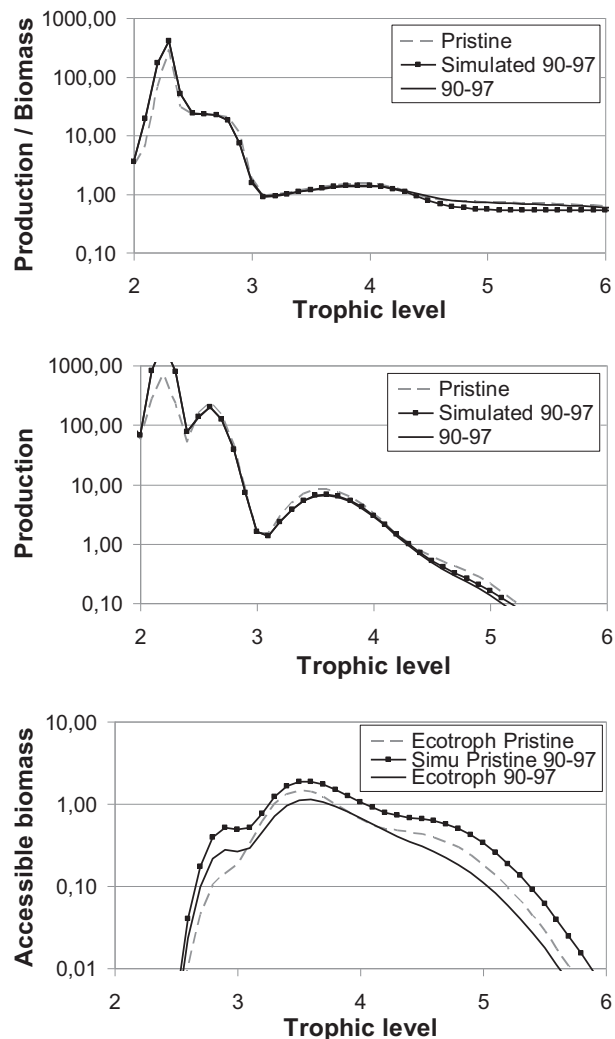


Figure 15 : Production / Biomass ratio (a), Production (b), Accessible biomass (c) trophic spectra for the current state, the pristine state and the simulated pristine state

2.2.3) Sensitivity analyses:

i. Sensitivity to the smoothing function and the input model

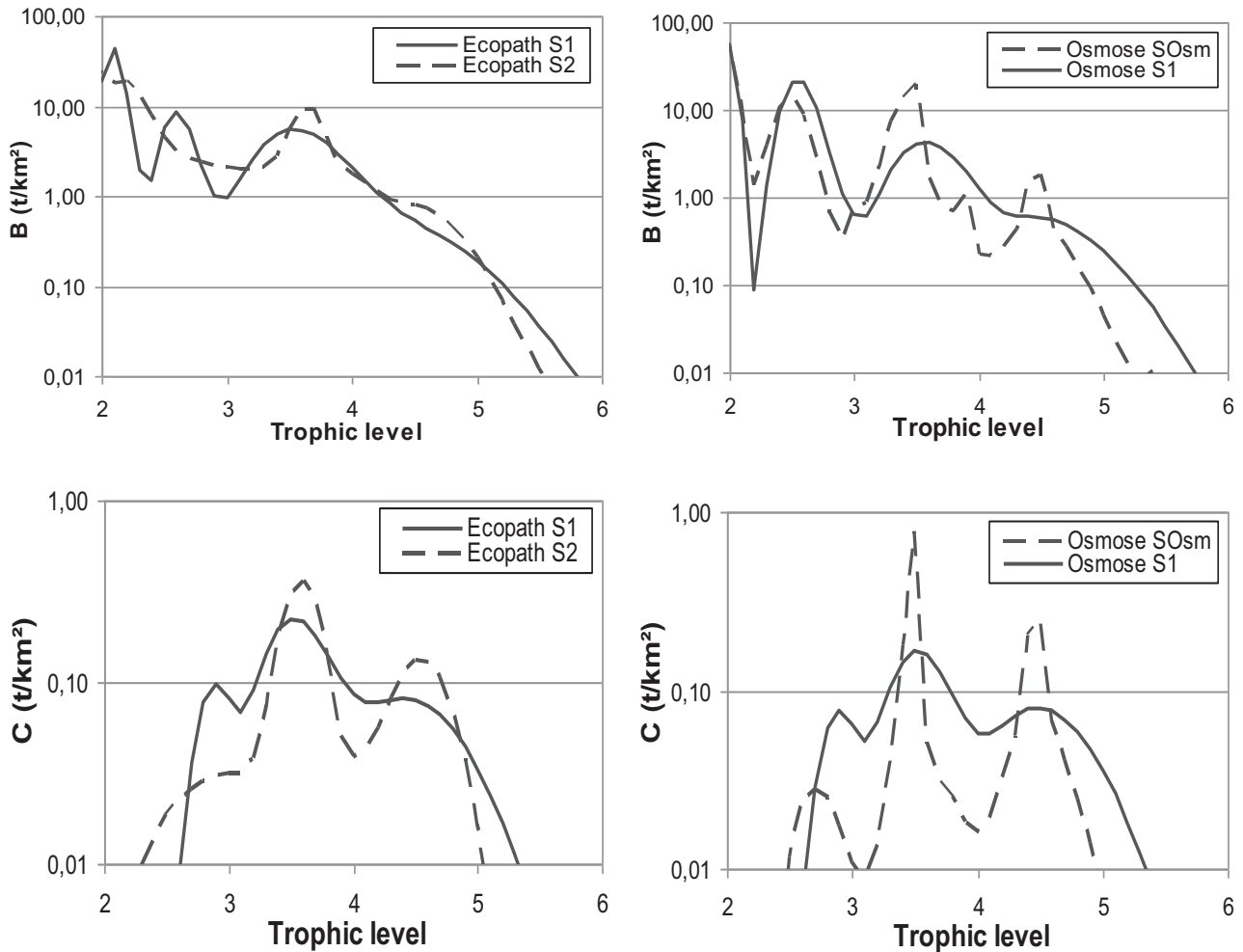


Figure 16 : Impact of the smoothing function on (a) the biomass trophic spectrum obtained with ET-Ecopath, (b) biomasses given by ET-Osmose, (c) the catch trophic spectrum given by ET-Ecopath and (d) the catch spectrum obtained with Osmose

Starting from the Ecopath standard model the smoothing function 2, based on the omnivory index, smoothes the biomass spectrum much more than the smoothing function 1, based on the empirical model of biomass distribution around the mean trophic level of each group (Figure 16a). One peak around trophic level 3.5 is an exception and is higher for Smooth 2 than for Smooth 1. Despite an increased smoothing by Smooth 2 the biomass trophic spectrum made with Smooth 2 ends at a lower trophic level than the spectrum made using the Smooth 1 function. This may partly be due to the fact that Smooth 2 puts more biomass around trophic level 4.5 while Smooth 1 tends to spread this biomass across more trophic levels. This difference in biomass trophic spectra directly comes from differences in the shapes of the smoothing functions. Using Smooth 2, some species around trophic level 4.5 have narrow repartition curves, which mean that biomasses will be more concentrated at these levels, creating a peak in the spectrum.

The biomass spectrum built from the Osmose model (Figure 16b) using the empirical Smooth 1 function appears to be close to the spectrum built from Ecopath, both graphs showing a decreasing trend and peaks at trophic levels 2.5 and 3.5. For Osmose the spectrum built with

Smooth 1 peaks less than the spectrum built with the smoothing function coming from Osmose (and completed with Smooth 1 for low trophic level planktons). Globally spectra from Osmose are less smoothed than spectra from Ecopath. One result similar to what we observed with Ecopath is the fact that Smooth 1 spreads the trophic spectrum towards higher values than the other smooth does.

Looking at catches (Figure 16c,d), patterns we can observe in both graphs are rather similar, with three peaks in catches. Osmose in particular, through its biomass and catch trophic spectra shows an ecosystem that seems to be structured by trophic levels 2.5, 3.5 and 4.5. This is due to the fact that in Osmose Copepods and Euphausiids at trophic level 2.5 (and 3.5 for some Euphausiids) are at the base of the food chain, allowing high biomasses of their predators at trophic level 3.5 and of their predators' predators at trophic level 4.5. Indeed we can see in the diet tables from Osmose that only Sardine mainly feeds on Ciliates (at trophic level 2) while other species mostly feed on Copepods and to a smaller extent on Euphausiids. Peaks in the Osmose smoothing function are very narrow and contribute to the particular shape of the spectrum. Indeed the ecosystem is structured around three trophic levels, which means that a predator will feed on prey close to 1 trophic level below him, resulting in a small omnivory index.

When simulating changes in the fishing effort, the choice of the smoothing function does not have much impact on the simulated biomass (Figure 17a). As we said before biomass is higher in the Et-Osmose model than in the ET-Ecopath model. For both Ecopath and Osmose models biomass decreases a bit more strongly with the Smooth 1 function than with the other smoothing functions. The slope of the curve of biomass is rather similar between the two models built with Smooth 1, which means that the estimated impact of fishing is the same between the two models. The difference between the two curves is far more noticeable for the Osmose model. Indeed when using the smoothing function coming from Osmose total biomass does not decrease when the fishing effort is increased. This could be due to a decrease in the intensity of top-down control because of the decrease in the predator biomass: an important decrease in predator biomass would result in the decrease of predation mortality on lower trophic levels (small pelagics) that could maybe compensate the increase in the fishing mortality. This is made possible by the particular aspect of the fishing loss rate and fishing mortality curves: fishing loss rate ϕ is almost constant and above 0.15 for trophic levels

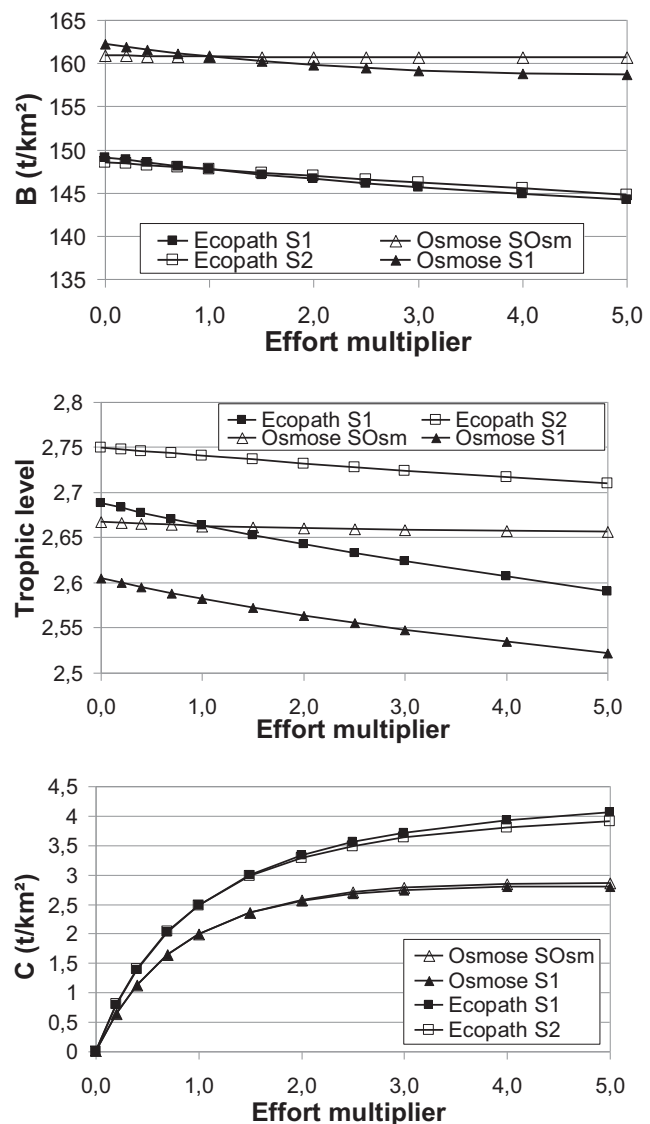


Figure 17 : Simulated biomasses (a), trophic levels (b) and catches (c) for ET-Osmose and ET-Ecopath, with two smoothing functions for each model

between 4.3 and 6. On the contrary ϕ only evolves between 0 and 0.01 for trophic levels between 2 and 3.9. Therefore when the fishing effort is multiplied for small pelagic species it is so small that the increase in catches (and so the decrease in biomass) is very small. Besides when the fishing effort is multiplied the increase is far greater for predators whose biomass is more heavily impacted. Thus the decrease in predators' biomass may propagate down the food web by means of top-down control, resulting in an increase in small pelagics' biomass that could compensate for the decrease due to fishing of all species. For the same smoothing function the trophic level of the total biomass of the ecosystem is higher for Ecopath than for Osmose (Figure 17b). Trophic levels evolve in the same way for the Smooth 1 function, resulting in a 0.03 trophic levels decrease between the pristine state and the current state. In Ecopath trophic levels obtained with Smooth 2 don't decrease as much as those obtained with the other smooth. As biomass before, the trophic level of the ecosystem remains almost constant when the smoothing function coming from Osmose is used. The slight decrease in the trophic level of the ecosystem confirms that fishing has a low impact on this ecosystem. Results obtained for catches are rather close to those obtained for biomass (Figure 17c). It is worth noticing that, while modelling lower biomasses than Osmose, Ecopath models higher catches. For both models the choice of the smoothing function does not have much impact on the predicted catches. The Osmose model is less "optimistic" than the Ecopath model in terms of catches: catches in Osmose reach their maximum when multiplied by 4 while catches in Ecopath still are on an increasing trend when multiplied by 5. Ecopath's "optimism" could partly be explained by its higher number of species at large and of top predators in particular.

We can say that the choice of the smoothing function has a moderate impact on the results but nevertheless has to be carefully made as it does affect not only the absolute value of a parameter but also the way this parameter evolves when fishing efforts are increased. On the contrary, a major point highlighted by this sensitivity analysis is that the choice of the input model has much impact on the absolute values of the parameters but does not influence much the way these parameters evolve when doing simulations

ii. Sensitivity to user-defined parameters

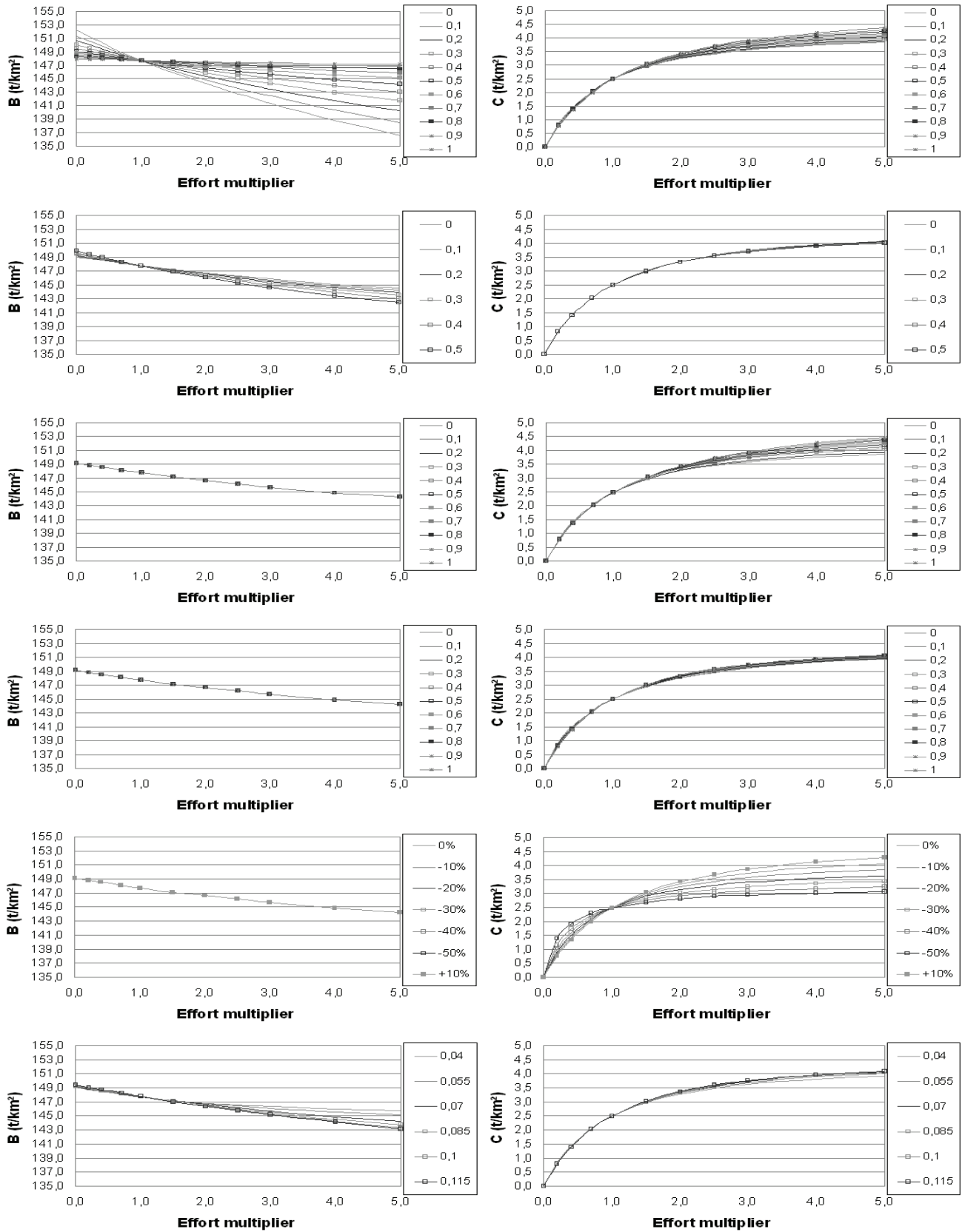


Figure 18 : Sensitivity analysis of biomass and catch to six parameters of the model, from the top to the bottom: top-down control (α) (a) and (b), Biomass recycling (β) (c) and (d), Accessibility of anchovy to fisheries (e) and (f), Accessibility of hake to fisheries (g) and (h), Global accessibility to fisheries (i) and (j) and width of the curves in Smooth 1 (λ) (k) and (l)

The only parameter tested to which total biomass is rather sensitive is the intensity of top-down control (α) (Figure 18a). The higher the top-down control the less biomass is impacted by an increase in the fishing effort. However, making α evolve between its minimum (0) and its maximum (1) possible values only modifies total biomass by 10 tonnes per square kilometre (roughly 7% of total biomass) when fishing mortality is multiplied by 5. Therefore we can say that the choice of the α parameter does not have much impact on the final results.

Catches are especially affected by modifications in the total accessibility of species to fisheries (Figure 18j). The higher the accessibility to fisheries, the higher catches at effort multipliers higher than 1 but the lower catches at multipliers below 1. However catches do not appear to be overly sensitive to the accessibility because reducing the accessibility by 50% only reduces catches by 25% (from 4 t/km² to 3 t/km²) when the fishing mortality is multiplied by 5.

2.3) Discussion

2.3.1) Building EcoTroph from Ecopath and Osmose

There are huge differences between Ecopath and Osmose, especially when looking at their structure and at the hypotheses on which they are based. To summarise up it can be said that Ecopath is a non-spatialized steady state model based on defined diets for each species whereas Osmose is a spatialized stochastic model representing life cycles where predation is opportunistic. In spite of these differences these two models were used as inputs in EcoTroph and their results compared, allowing us to highlight and to discuss other differences coming from choices made when applying the model to the Benguela ecosystem. The first critical point lies in the number of species modelled: 32 species for Ecopath and only 10 for Osmose. However these 10 species were selected because of their importance in terms of catches and biomass, reducing the gap between the models. EcoTroph making abstraction of the notion of species a difference in the number of groups is not a major drawback. Other modelling choices have been made in order to allow the comparison of these models that introduce biases in our results. Our first choice comes from the fact that EcoTroph is based on the idea that biomass flows from low to high trophic levels and therefore has to be initiated at low trophic levels. Osmose, being a high trophic level model is forced for low trophic levels by another model. To create an ET-Osmose model we had to add four species to the initial model whose biomasses, provided by the forcing model, are far higher than those given by Ecopath. These biomasses having no distribution curve we attributed them theoretical curves identical to those used in Smooth 1, and thus in reality the Smooth Osmose is only partially provided by the Osmose model. Another bias that was necessary to make comparison possible is the use of identical P/B ratios in ET-Ecopath and ET-Osmose. For Ecopath these ratios are based on field observations found in the scientific literature. These ratios can not be easily provided by Osmose and we chose to use the same ratios we used in Ecopath for all the groups we modelled in Osmose. The use of identical P/B ratios underlines the fact that the models do not represent the ecosystem in the same way. Indeed production, calculated as $B \cdot P/B$, is seven times higher in Osmose than in Ecopath. This is due to the fact that we apply high biomasses (provided by the forcing model) and high P/B ratios (provided by Ecopath) to low trophic levels in Osmose, resulting in very high productions that can be seen as a (necessary) modelling artefact. If P/B ratios had been retrieved from Osmose they would probably have partly compensated the high biomasses from the forcing model. We can also add that as groups in Ecopath are different from those in the forcing model P/B values attributed to low trophic levels are even more likely to be wrong. In spite of these biases and artifacts results given by the two models are rather similar and provide us with globally similar diagnoses of the impact of fishing on this ecosystem. This stresses EcoTroph's ability to represent an ecosystem with various sources of information and shows its rather low sensitivity to modelling choices.

2.3.2) Influence of the environmental forcing

The influence of environmental forcing stood out much in our attempt at back-simulations of a pristine state of the ecosystem. Indeed biomass of anchovy was multiplied by more than 5 and biomass of sardine by more than 6 between the 1990-1997 model and the 2000-2003 model. This emphasizes the combination of two phenomena: A well-known decadal oscillation between anchovy and sardine, resulting in an oscillation in total biomass of small pelagics (because biomass of anchovy is higher and changes more than that of sardine)(Fréon et al., 2005(b)). Another phenomenon is the unusual constantly increasing trend followed by the biomass of sardine since the 1980's because of good environmental conditions that, in combination with the decadal oscillation, led to the extremely high biomasses of small pelagics observed in the early 2000's. Interestingly our EcoTroph models show that the decadal oscillation in the biomass of small pelagics is not linked to changes in the primary production or in the biomass of high trophic level species. This highlights the fact that this oscillation is due to changes in transfer efficiencies linked to environmental conditions. The importance of this natural phenomenon is the reason why attempts at back-simulations of pristine states give results that differ from one another, depending on the present model chosen and on how environmental conditions evolved since the pristine state. In fact when we try to simulate the pristine state of the ecosystem with EcoTroph we only simulate one of the states of the decadal oscillation. Besides we saw before that total biomass is very little affected by increases in fishing efforts in this ecosystem, with biomass above trophic level 4 being the only one affected. Thus we can even question the use of models applied to the Benguela ecosystem, especially in order to determine the amount of catches allowed to fisheries. It seems that only models accurately taking into account the effects of the environment on the ecosystem (for example under the form of a forcing function like in Ecosim) have a chance to give accurate results. Indeed, even if fishing currently has a rather low impact on the whole ecosystem, the interactions between fishing and environmental forcing are not taken into account in our EcoTroph model even though they could be a real threat to this ecosystem. Indeed a high fishing effort on high trophic level species combined with bad environmental conditions (i.e causing low recruitments or high mortality) could deplete biomass of these species enough to affect the recruitment of the following years. If repeated this combination of events could lead to the overexploitation and even the disappearance of species. Therefore a system linking annual environmental conditions to an allowed amount of catches could be more efficient than a fixed amount of catches and safer than the use of the boundaries (or absence of boundaries for some species) fixed by our model (Fréon et al., 2005 ;Rothschild B. and Shannon L. J., 2004). Higher catches could be allowed when environmental conditions are good (at least for low trophic level species that are not threatened by overexploitation) and reduced in case of bad conditions. This could give a higher income to local fisheries or allow more boats to exploit some stocks if clear relationships were to be found between environmental conditions and fish biomasses.

2.3.3) EcoTroph's ability to simulate changes

EcoTroph is a steady state balanced model based on equations linking together the different parameters of the ecosystem. On the contrary a marine ecosystem is constantly evolving under the influence of climate, anthropogenic influences, and interactions between species. Therefore EcoTroph only represents mean states of the ecosystem each related to a given set of parameters, including the fishing intensity. It has to be kept in mind that any one model is only one way among others to see an ecosystem, based on various hypotheses chosen by the modeller. In this context EcoTroph's goal is not to provide with definitive solutions but rather to provide decision makers with a new and more global vision of the ecosystem that can be combined with other sources of information. In the context of decision making EcoTroph can be an asset in the sense that it answers the question: What would be the mean state of the ecosystem if the fishing effort was modified, other parameters remaining constant? This can be a useful piece of information in the context of the elaboration of fishing

policies, allowing partly anticipating the long-term effects of these policies (when a new form of equilibrium has been reached).

EcoTroph's main asset, its ability to generalize and simplify the pieces of information we have about the ecosystem, can be seen as its main flaw when trying to predict changes. First EcoTroph is not spatialized, putting aside the fact that fish densities fluctuate a lot within the ecosystem, that fish move and that fisheries only exploit a part of the ecosystem trying to target areas where fish is more abundant. As a consequence the overexploitation of a specific area or the exploitation of sensitive area such as spawning grounds can not be detected by EcoTroph. Second, EcoTroph leaves aside the notion of species, which can be a handicap when trying to set up fisheries management policies. Indeed in this moderately exploited ecosystem the main risk is not that of a global shift but that of the overexploitation of a particular species. In this case looking at the whole ecosystem could even be a mistake because the general good state of the ecosystem could hide the overexploitation of a species. In Short EcoTroph has the flaws of its qualities: it provides a much sought-after (by fisheries managers, politicians, scientists) global diagnosis on an ecosystem but this wide vision cannot show every detail of the ecosystem's changes.

This possible disappearance of species can be linked with the issue of the use of smoothing functions that can cause problems when attempting simulations. Indeed as catches and biomasses are spread over trophic levels the mix can occur at one trophic level between a species with relatively high catches and low biomass and a species with no catches and a high biomass. The fishing mortality calculated for this trophic level will be multiplied to calculate the simulated biomass and production, which results in multiplying fishing mortalities on species that are not fished and cause errors to appear in the simulated total biomasses and productions. Catches and the parameters concerning the accessible part of the ecosystem are calculated with the accessible fishing mortality and therefore do not suffer from the same problem. A future development of EcoTroph could be the introduction of a non accessible part of biomass that could be reunited with the accessible part of biomass after doing simulations so as to obtain an unbiased total biomass of the ecosystem. One other solution would be to keep species in the model for the simulations so that non-targeted species remain non-fished.

3) Simulation of changes in the ecosystem fishing pattern

The current version of EcoTroph allows simulations where the same effort multiplier is applied to all trophic levels. Such simulators refer to a given fishing pattern (the current one) defining which trophic levels are targeted. Here, we develop a new version of the EcoTroph model where the fishing mortality can be changed species by species. The main difference with the previous version of EcoTroph is that when the user multiplies F he can now do it species by species. This enables making simulations of changes in the ecosystem fishing pattern.

3.1) Methods

For each simulation the fishing mortality of each trophic class is calculated as:

$$F_{tot,\tau} = \frac{Y_{tot,\tau}}{B_{tot,\tau}} = \sum_{i=1}^N mE_i \times \frac{Y_{i,\tau}}{B_{i,\tau}} = \sum_{i=1}^N mE_i \times F_{i,\tau}$$

Where mE_i is the fishing effort multiplier applied to species i , N the number of species modelled, $Y_{i,\tau}$ the amount of catch of species i at trophic level class τ and $B_{i,\tau}$ the biomass of i at class τ . The accessible fishing mortality trophic spectrum is obtained thanks to a similar equation where biomass is replaced by accessible biomass. Then these simulated

fishing mortalities are used in EcoTroph's usual equations to calculate kinetic, biomass, production and catch.

Two scenarios are built, corresponding to scenarios already simulated with Ecosim and Osmose models of the Southern Benguela (Travers et al., 2010). The first scenario corresponds to a doubling in the fishing mortality of small pelagic species (i.e sardine, anchovy and redeye) and the second scenario to a doubling in the fishing mortality of hakes (large *M. capensis* and large *M. paradoxus*). Results obtained with EcoTroph are first analyzed for each scenario, so as to underline differences in the observed impacts on the ecosystem between the two scenarios. Then results, and in particular biomass per trophic level, were compared with results obtained with Ecosim and Osmose by Travers et al. (2010). Here 0.1 trophic level classes are not used anymore, but classes of 1 trophic level instead. Thus biomass for a trophic level corresponds here to the sum of all biomasses between TL and TL+1 (TL+1 theoretically being excluded). Results obtained with EcoTroph are plotted against results obtained with the other two models so as to allow comparisons. Then a sensitivity analysis of the results to various parameters is performed, not so much to track changes in values but changes in the general patterns of biomass obtained.

3.2) Results

3.2.1) Simulations:

i. Fishing mortality

An increase in F on different groups of species has very different effects on the fishing mortality trophic spectrum (Figure 19). Trophic level 4 can be seen as an approximate limit between the changes in F brought by each scenario: doubling the fishing mortality on small pelagics does not have much impact on the F spectrum above trophic level 4 while doubling F on hakes does not really impact the spectrum below trophic level 4. Trophic level 4 being a hinge trophic level seems to be rather natural as this ecosystem is structured by two groups of species, respectively at trophic levels 3.5 and 4.5. Doubling fishing mortality on some species results in a global increase of the fishing mortality that can be calculated. For example doubling F on small pelagics corresponds to a 1.6 multiplier applied to all species while doubling F on hakes corresponds to a 1.2 global multiplier.

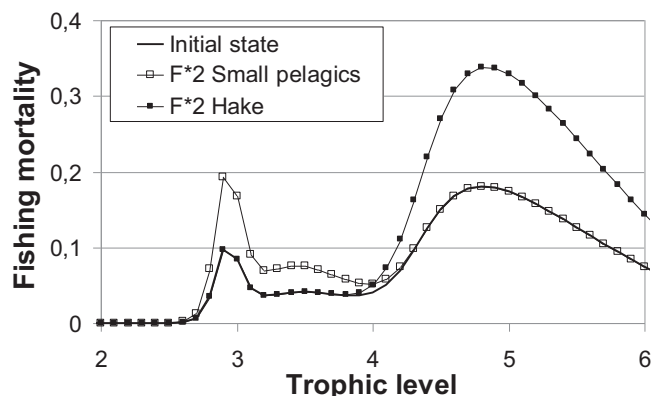


Figure 19 : Fishing mortality trophic spectra for the initial state, the small pelagics scenario and the hakes scenario

ii. Catches

In terms of catches two patterns appear when looking at the two different scenarios:

Doubling the fishing mortality on small pelagic species does not double catch of these species but has a far less important effect, with catches increasing by one third at best (Figure 20). This increase in the fishing mortality of small pelagics causes a significant decrease in catches of their predators, around

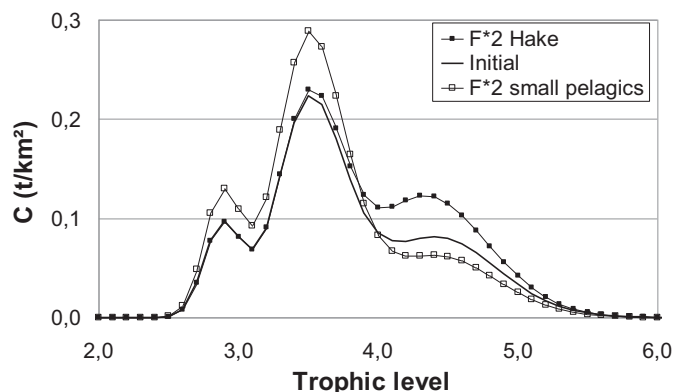


Figure 20 : Catch trophic spectra for the initial state, the small pelagics scenario and the hakes scenario

trophic level 4.5. This is due to the bottom-up control of high trophic level biomass by lower trophic level biomass. This raises one of the most important problems of the exploitation of low trophic level species: it may provide high biomasses of fish but impacts the whole food chain, reducing the biomass of predators even if they are not targeted. This can have serious consequences because predators are historically the most heavily targeted species and thus often already heavily depleted. Besides, predators are often high economic value species and a reduction in their number can heavily impact fisheries that target them. Another problem to be taken into account is that some high trophic level species (such as marine mammals) are protected species and thus reducing their biomass could be a great problem. Doubling the fishing effort on hakes increases their catches by 50% at best, which still is a higher increase than that observed for the small pelagics scenario. In this scenario we can observe that the increase in catches of hakes slightly increases the catch at trophic level 3.5 because of top-down effects.

iii. Accessible biomass

Increasing fishing mortality on small pelagics reduces accessible biomass at all trophic levels (Figure 21). On the other hand increasing fishing mortality on hakes only causes a decrease in biomass around trophic level 4.5 and even causes a slight increase in accessible biomass at trophic level 3.5 because of top-down effects. The effects of an increased fishing mortality seem to be much more important when this increase targets small

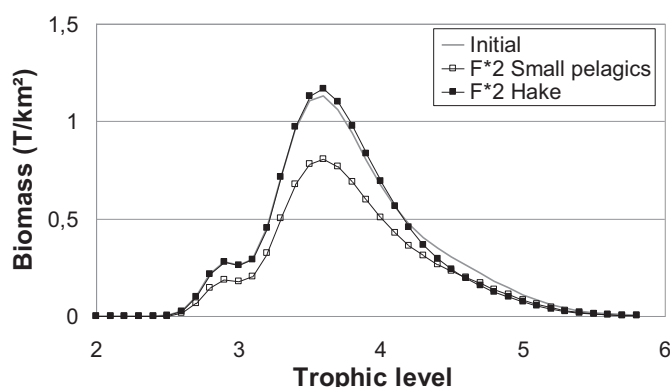


Figure 21 : Accessible biomass trophic spectra for the initial state, the small pelagics scenario and the hakes scenario

pelagics: accessible biomass is reduced by about 30% between trophic level 3 and trophic level 4, with smaller reductions for other trophic levels. When hakes are targeted accessible biomass is reduced only between trophic levels 4.2 and 5.2 and by no more than 25%. An interesting point is that doubling the fishing effort on small pelagics impacts accessible biomass above trophic level 4.5 almost as much as a doubling in the fishing effort multiplier on adult hakes (whose mean trophic levels are 4.50 and 4.64 depending on the species). These results clearly show that fishing small pelagics is far from being harmless for the ecosystem and on the contrary is a bigger threat than the increase in the fishing mortality of hakes. These results can be seen as a complement to results obtained when simulating global increases in the effort multiplier: We show that even if biomasses of small pelagics are little impacted by increased fishing efforts, increases in their catch have to be very careful because they have great impacts on the whole food chain. We also explain why biomasses of predators are so much reduced when simulating a global increase in F : they undergo both the direct effects of fishing and a strong bottom-up control by small pelagics.

These results may partly come from the choice of the species in each scenario: the 3 species of small pelagics chosen represent almost all fished small pelagics in this ecosystem and have a pivotal role because they feed most higher trophic level species and thus changes in their biomass are likely to propagate in the food chain.

iv. Comparisons with Ecosim and Osmose:

For the small pelagics scenario differences between Osmose and Ecosim are not very important according to Travers et al. (2010), except for trophic level 5 where the B_{sim}/B ratio was a few percents higher for Osmose. Especially, Osmose and Ecosim follow the same trend, with a decrease in biomass at trophic levels 2 and 4 and an increase in biomass at trophic levels 3 and 5 (Figure 22a). In Travers et al., the decrease in biomass at trophic level 2

is explained by the strong decrease in the biomass of sardine whose trophic level is 2.8 whereas their trophic level is 2.99 in our study. According to Travers et al. biomass at trophic level 3 increases even if anchovy and redeye are heavily fished because of compensations by other species that take advantage of reduced competition with anchovy and redeye. The decrease in biomass at trophic level 4, mostly due to Silver kob and also to hakes in Osmose, is harder to explain. It could be understood in Ecosim where diets are initially fixed and evolve with changing prey abundances, but since predation is opportunistic in Osmose we could expect an increase in biomass at trophic level 4 in reaction to an increase in biomass at trophic level 3. EcoTroph (with the theoretical smoothing function Smooth 1) does not show the same patterns at all, with an increase in biomass at trophic level 2 and decreases at other trophic levels. This pattern can be explained by Top-down and Bottom-up controls only: fishing decreases biomass at trophic level 3 (besides a good part of the biomass of sardine is above trophic level 3 in our model), therefore biomass at trophic level 2 increases in response to reduced predation on this trophic level by trophic level 3. Less biomass means less food for trophic level 4 which exerts bottom-up control of biomass at trophic levels 4 and 5.

For the hake scenario patterns observed look more similar between EcoTroph and the other two models (Figure 22b). In this scenario, as in the previous one, looking at trophic level 5 does not have much meaning for Ecosim and Osmose, given the fact that it only comprises of one species (pelagic-feeding chondrichthyans).

By comparison, in EcoTroph trophic level 5 gathers more species because of the smoothing functions and could be seen as more interesting to study. In the small pelagics scenario either EcoTroph or Osmose predicts the most important change in absolute value, and this is also true for the hake scenario. In this scenario the simulated biomass/initial biomass ratio is much lower than in the first scenario at trophic levels 4 and 5. This is rather surprising because in

Osmose a decrease in the biomass of one species can be compensated by other species and predation is opportunistic, therefore biomass could be expected to be less sensitive to fishing. Biomasses at trophic levels 4 and 5 decrease because of the increased fishing effort on hakes. Biomass at trophic level 3 increases for Osmose and EcoTroph as the result of a top-down control whereas biomass at this trophic level decreases only slightly in Ecosim. Biomass at trophic level 2 is very lightly impacted by changes in the fishing mortality of hakes. In EcoTroph biomass decreases at this trophic level as a result of top-down effects while biomass increases in the two other models.

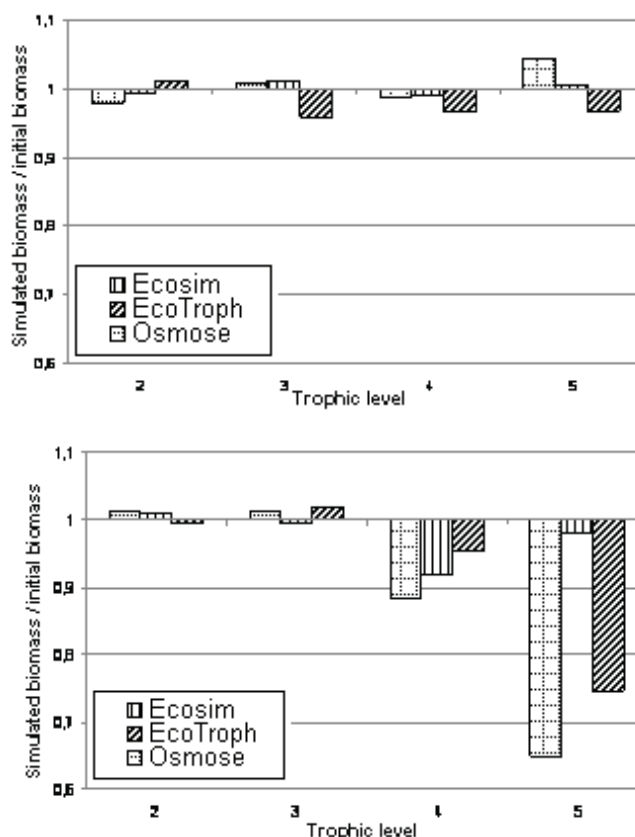


Figure 22 : Comparison of the simulated biomass/initial biomass ratios per trophic class for the small pelagics scenario (a) and the hakes scenario (b)

3.2.2) Sensitivity analysis:

Full sensitivity analysis have been performed but only summarized results are presented here

i. Sensitivity to top-down control

For the small pelagics scenario, biomass at trophic level 3 decreases which is logical because it is the trophic level undergoing fishing. Because of bottom-up control biomasses of predators at trophic levels 4 and 5 are also reduced, but their biomass ratio increases towards 1.

The top-down parameter has two effects (Figure 23a):

- It reduces the impact of fishing on biomass, especially for the trophic levels where the fishing effort is increased but also for higher trophic levels that benefit from an increase in the biomass of their prey. This agrees with the previous sensitivity analysis performed that also showed that a high top-down control limited the effects of fishing on the ecosystem.

- The role of the TopD parameter can especially be observed at trophic level 2 where biomass decreases a bit without top-down control (trophic class 2 being a little exploited because of the spreading of catches of small pelagics across trophic levels) but increases when TopD is given a value of 0.5. The increase in biomass at trophic level 2 will be noticeable for any value of TopD, only the ratio of biomasses will change. The increase in biomass at trophic level 2 is due to the decrease in biomass at trophic level 3 under the effects of fishing; less predators meaning higher biomasses for trophic level 2.

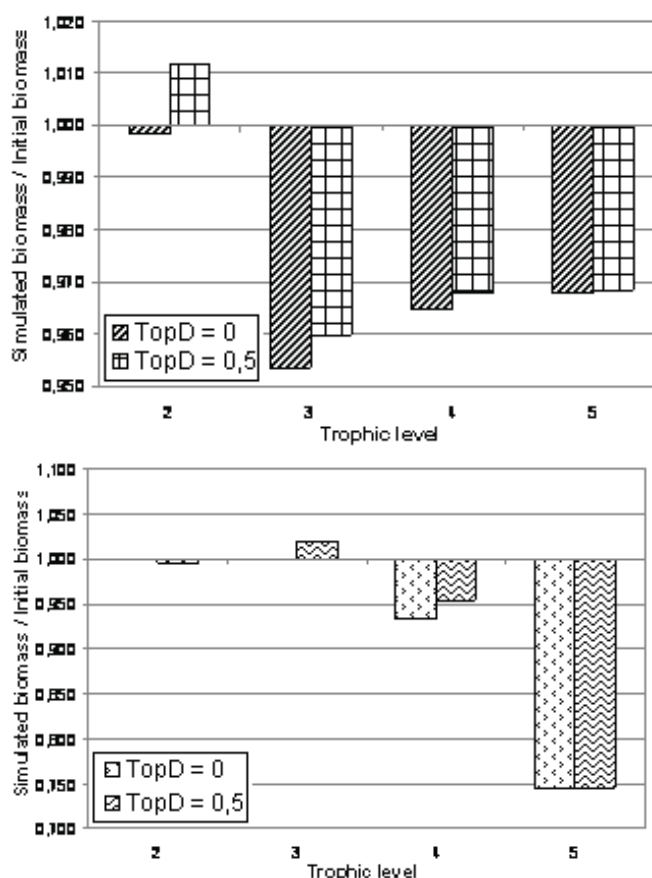


Figure 23 : Sensitivity analysis to top-down control on the small pelagics scenario (a) and on the hakes scenario (b)

For the hakes scenario (Figure 23b) the effects of top-down control are the same as for the small pelagics scenario: it reduces the effects of fishing on biomass and causes these effects to propagate downwards in the food chain. As hakes are high trophic level species the propagation of the effects of fishing down the food chain is clearer and exhibits a trophic cascade effect: a decrease in biomass at trophic level 4 causes an increase at trophic level 3 and then again a smaller decrease at trophic level 2. The effects of the top-down control are progressively dampened when the trophic level decreases.

ii. Sensitivity to the smoothing function

As in the first part of this study two smoothing functions can be used, Smooth 1 corresponding to the theoretical smoothing function and Smooth 2 to the smoothing function based on the omnivory index.

In the small pelagic species scenario we can observe that with Smooth 2 the simulated biomass is always closer to the initial biomass than with Smooth 1 (Figure 24a). Simulated total biomass differs by a few percents between Smooth 1 and Smooth 2 for each trophic level. Total biomass of the ecosystem is not modified by the smoothing function so differences observed only result from the way each species is smoothed. One of the main differences between Smooth 1 and Smooth 2 concerns plankton. Indeed these low trophic level species have very narrow repartition curves in Smooth 1 and are therefore likely to belong only to class "2" (corresponding to trophic levels 2 to 3) whereas they have wide repartition curves in Smooth 2 and belong to classes "2" and "3". This means that with Smooth 2 the increase in biomass planktons experience because of the decrease in biomass of their predators does not appear entirely in class "2" but also contributes to reducing the decrease in biomass at class "3".

Apart from far greater differences in biomass ratios, the situation is identical for the hake scenario (Figure 24b): simulated biomass is far closer from initial biomass for Smooth 2 than for Smooth 1. This can partly be explained by wider repartition curves for Smooth 2 than for Smooth 1. Indeed, if we increase the width of the curves in Smooth 1 (Figure 25) by

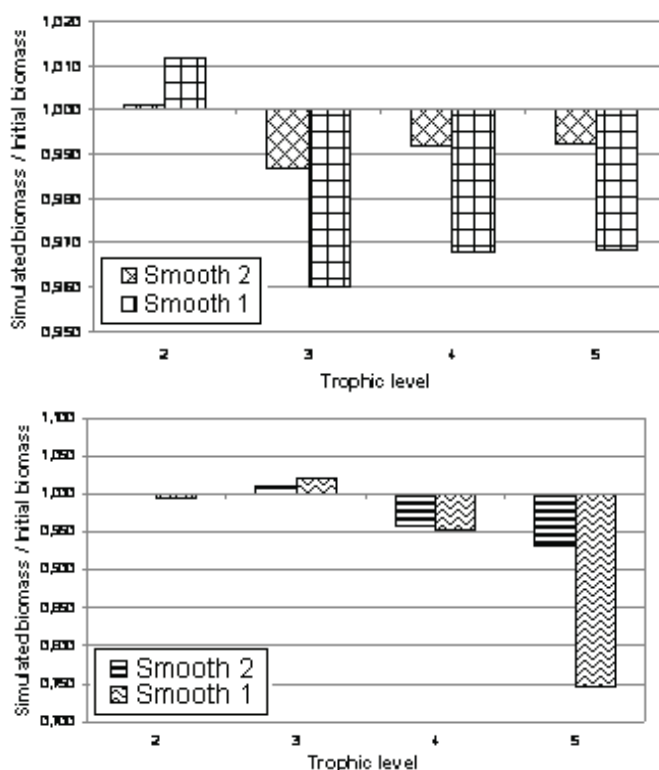


Figure 24 : Sensitivity analysis to the smoothing function on the small pelagics scenario (a) and on the hakes scenario (b)

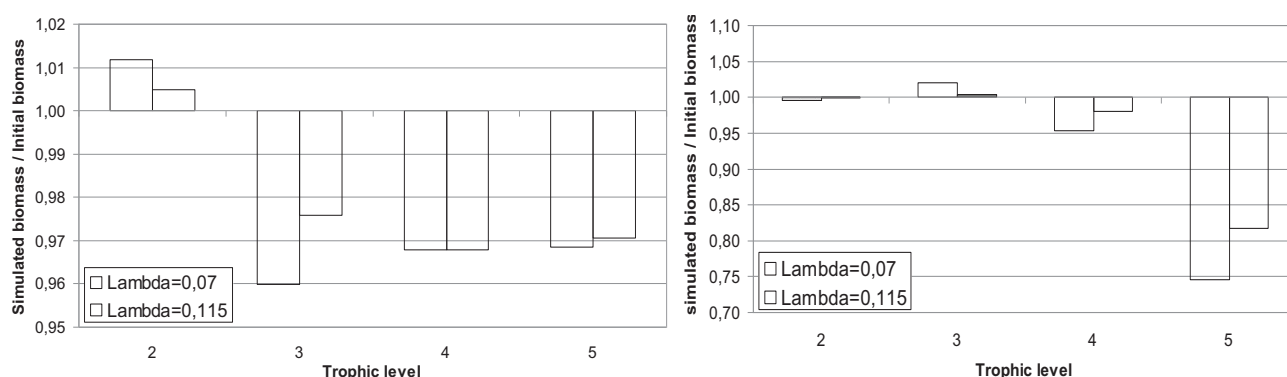


Figure 25 : Sensitivity analysis to the value of the lambda parameter (width of Smooth 1 curves) for the small pelagics scenario (a) and for the hakes scenario (b)

increasing the λ parameter (see Figure 4 for the shape of the functions) the simulated biomass gets closer to initial biomass (thus looking more like biomass obtained with Smooth

2). However increasing λ does not reproduce results obtained with the smoothing function 2, especially at low trophic levels where results are more alike those obtained with $\lambda = 0.07$. We can say that when using the Smooth 2 function users can expect to have simulated biomasses that do not differ much from initial biomasses. This is to be taken in consideration as it could be the cause of an overestimation of simulated biomass, especially at high trophic levels where the need for precise estimations would be the more important. Indeed the overestimation of simulated biomasses can lead to an underestimation of the effects of fishing and even, in some extreme cases, hide situations of possible overexploitation. These observations could lead to the use of new values of the λ parameter in Smooth 1 in an attempt to make Smooth 1 closer to Smooth 2 and to reality.

3.3) Discussion

3.3.1) Choice of the smoothing function

In the first part of this study we see that results given by Smooth 2 are very close to those given by Smooth 1. In the second part however differences are more important between simulations made with the two smoothing functions and therefore the question of the choice of the smoothing function has to be tackled with. In the second part of our work we see that Smooth 2 has a tendency to underestimate the effects of fishing on the ecosystem when compared with Smooth 1. Even if this underestimation may be this ecosystem model's own particular characteristic we can recommend great caution when using Smooth 2, especially because an underestimation is what has to be avoided at any cost when managing stocks. Another element against the use of Smooth 2 is the hypothesis upon which it is based. Indeed the omnivory index is used as a proxy of the variability in trophic levels between predators but is in fact an estimate of the variability of prey of these predators, which is not proved to be linked to the variability within predators. Indeed if all predators of an Ecopath group eat a wide range of prey but in the same proportion they will have exactly the same trophic level, and thus there will be no variability between them in spite of a high diversity in prey. Another problem when using Smooth 2 is that the omnivory index is an output from Ecopath that is directly determined by the diet table of the model. The diet table is in turn created by the modeller from whatever information is available in the literature about the diet of each species. Therefore if the diet of a species has not been deeply studied for the period under consideration and across the full extent of the species' geographical distributions the diet table may to be inaccurate, resulting in wrong omnivory indexes and eventually wrong smoothing functions in Smooth 2. A last problem is that a group often comprises of more than one species (and more than one ontogenic stage) which means that the diet of this group and its omnivory index are only approximations. The best solution would be to have estimates of the intra-group variability coming directly from the field; this implies the development of diets observation systems. Facing all these difficulties we recommend that EcoTroph users make a first run of the model using Smooth 1 before attempting to use Smooth 2.

3.3.2) possible developments of the study

Results given by the 3 models can be rather similar or rather different, depending on the scenario studied. Therefore we cannot determine whether one model is better than the others when attempting to simulate changes in fishing efforts. This is the reason why an interesting addition to this study would be the comparisons its results with real data so as to acquire a new point of view on the models. For example fitting the models to time series, using Ecosim or the dynamic version of EcoTroph (Gascuel et al., 2009), and then comparing simulations with those obtained in this study could help determine if one model gives more reliable informations than the others. If so, this model could be used as a standard on which to preferably base diagnoses concerning the Benguela ecosystem and comparisons with other models.

Conclusion

Modelling with EcoTroph

- ➡ EcoTroph is not very sensitive to parameterization: a wide range of values have been tested for parameters we deemed to be important and variations in results are small.
- ➡ The most critical point when parameterizing the model is the choice of the accessibility to fisheries of each species for which pieces of information are scarce and needs to take into account various aspects of the fisheries.
- ➡ The use of the theoretical smoothing function (Smooth 1) is advised for a first run of EcoTroph on an ecosystem.
- ➡ Even if predicted absolute values for biomass and catch are different from one model to another, trends are rather similar when doing simulations and thus we can have useful informations about how the ecosystem would evolve under increased fishing mortalities.

The Southern Benguela ecosystem

- ➡ According to our model the Southern Benguela ecosystem is not overexploited, but fully exploited for apex predators (around trophic level 5).
- ➡ The environmental forcing seems to be far more important in terms of biomass than fishing for small pelagics (but fishing is the only parameter we can control).
- ➡ Conversely biomass at trophic levels higher than 4 seems to be significantly controlled by fishing.
- ➡ Increasing the fishing effort on small pelagics reduces their biomass but also seems to cause a significant decrease in the biomass of their predators.

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Appendices

I. Choice of the interval in the smoothing function

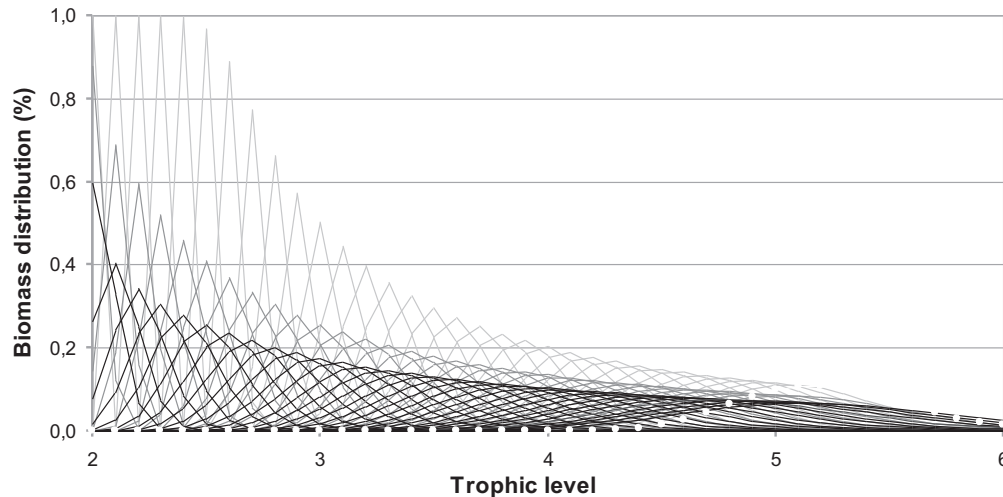
An interval has been implemented in the probability density functions of the repartition curves:

$$f(x) = \frac{1}{(x - \Delta TL) \times \sigma_{LN} \times \sqrt{2\pi}} \times \exp \left[-\frac{(\ln(x - \Delta TL) - \ln(\mu - \Delta TL))^2}{2 \times \sigma_{LN}^2} \right]$$

Functions for Smooth 1 and Smooth 2 are identical, apart from the fact that σ_{LN} is replaced in

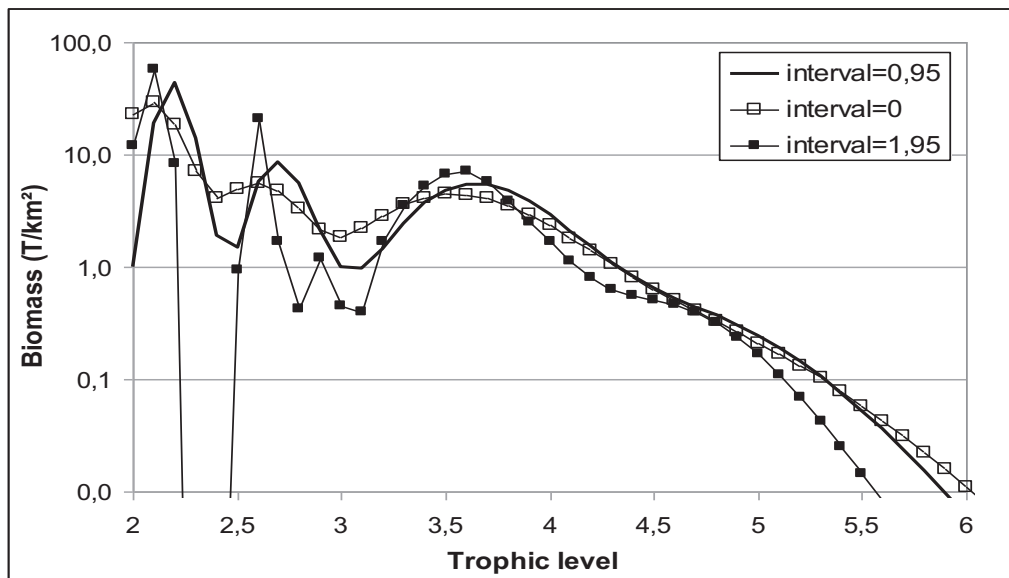
Smooth 2 by $\frac{\sigma_{LN}}{\mu}$ so as to approximate a normal curve with a log-normal curve.

This interval represents the fact that our representation of the ecosystem begins at trophic level 2 while the probability density function used starts at 0. The simplest way to compensate this difference would be to withdraw 2 to values of “x” and “μ” in our formula to translate the function to the right. In fact the correct value to withdraw would be 1.95 because a smoothing function corresponds to a 0.1 trophic level class and is applied at the middle of this class (e.g the first smoothing function, corresponding to class [2;2.1[would be calculated for trophic level 2.05). But with a $\Delta TL=1.95$ the smoothing function obtained is too sigmoid, with very narrow functions for a lot of low trophic levels and a rather sudden widening. Therefore we chose to make a compromise and to use a $\Delta TL=0.95$ that gives a smoothing function we deem to be closer to reality (“reality” corresponding to articles that give informations about the shape of the repartition function of some species, for example: Chassot et al., 2008) . With this ΔTL the smoothing function ranges between 1 and the infinite. This seems to be acceptable as there is little biomass between trophic levels 1 and 2 and the way it is smoothed does not matter much in our diagnosis.



Appendix I-I : Aspect of Smooth 1 for $\Delta TL=0$ (light grey), $\Delta TL=0.95$ (grey) and $\Delta TL=1.95$ (black)

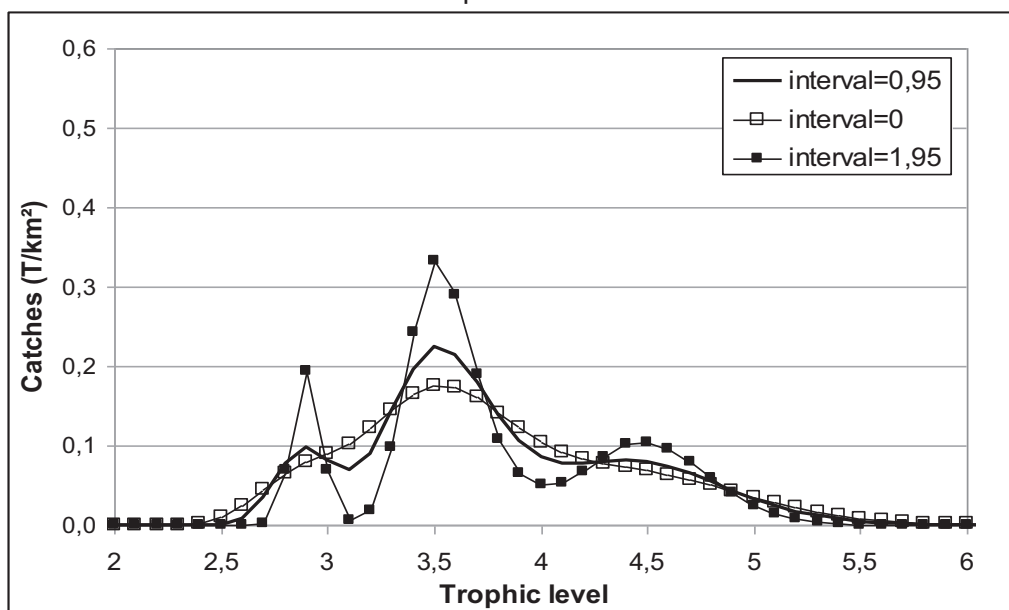
There are important differences between the smoothing function obtained with $\Delta TL=1.95$ and that obtained with $\Delta TL=0.95$, both in the values of the peaks and in the general shape of the functions. Differences are smaller between the function obtained with $\Delta TL=0.95$ and the function where there is no interval.



Appendix I-II : Biomass trophic spectra obtained with the three intervals tested

Differences in the smooth create important differences in the biomass. As before curves obtained with the null ΔTL and $\Delta TL=0.95$ are rather close to one another whereas the curve corresponding to $\Delta TL=1.95$ differs a lot from them. The curves especially differ at low trophic levels where species are almost not smoothed at all with $\Delta TL=1.95$, resulting in sharp peaks in the biomass curve.

Results for catches show the same pattern.



Appendix I-III : Catch trophic spectra obtained with the three intervals tested

II. Influence of the initialisation at trophic level 1

Because of the smoothing function the model gives an accessible biomass and an accessible production to trophic level 1, which is irrelevant as species at trophic level 1 are not fished. This is all the more irrelevant as in Smooth 1 these values of accessible P and B at TL 1 come from high trophic level species because of their wide smoothing functions. Accessible production serves to calculate accessible fishing loss rate and accessible natural loss rate while accessible biomass is used to calculate accessible fishing mortality. Accessible natural loss rate is one of the parameters linking accessible flows between trophic levels. If we manually turn B^* and P^* at trophic level 1 to 0 (or if the smoothing function does not spread P^* and B^* enough) then μ^* can't be calculated and accessible biomass at trophic levels higher than 1 can't be calculated either, resulting in other problems in the model. To try to avoid this problem the model should be initialized at the lower trophic level where there is an accessible biomass and an accessible production. But this limit changes from one input model to another and from one smoothing function to another and so is difficult to define. Therefore we chose to define trophic level 2 as the lower limit of our model as it can theoretically include some small pelagics feeding exclusively on trophic level 1 planktons and that are targeted by fisheries. Having a P^* at trophic level 2 and a $\mu^* P^*$ at higher trophic levels can be calculated.

Appendix II-I : Values of accessibilities to fisheries for species in the Southern Benguela

Group name	Accessib-ility to fisheries (proportion)
Phytoplankton	0
Benthic produce	0
Microzooplankton	0
Mesozooplankton	0
Macrozooplankton	0
Gelatinous zoop	0
Anchovy	0,3
Sardine	0,45
Redeye	0,3
Othersmallpel	0,4
Chubmackerel	0,3
Juvenilehorse	0,15
Adulthorse	0,2
Mesopelagics	0
Snoek	0,7
Otherlargepel	0,8
Cephalopods	0,4
SmallM.capens	0,3
LargeM.capens	0,8
SmallM.parad	0,4
LargeM.parad	0,7
Pelagicdemers	0,5
Benthicdemers	0,5
Pelagicchond	0,3
Benthicchond	0,3
Apexchond	0
Seals	0
Cetaceans	0
Seabirds	0
Meiobenthos	0
Macrobenthos	0
Detritus	0

