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Journal of Marine Systems

journal homepage: [www.elsevier.com/locate/jmarsys](http://www.elsevier.com/locate/jmarsys)

# Global assessment of the fishing impacts on the Southern Benguela ecosystem using an EcoTroph modelling approach

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## ARTICLE INFO

### Article history:

Received 8 April 2011

Received in revised form 8 July 2011

Accepted 28 July 2011

Available online 28 August 2011

### Keywords:

Ecosystem indicators

Trophic modelling

EcoTroph

Fishing impact

Overfishing

Southern Benguela

## ABSTRACT

We show that the EcoTroph model based on trophic spectra is an efficient tool to build ecosystem diagnoses of the impact of fishing. Using the Southern Benguela case study as a pretext, we present the first thorough application of the model to a real ecosystem. We thus review the structure and functioning of EcoTroph and we introduce the user to the steps that should be followed, showing the various possibilities of the model while underlining the most critical points of the modelling process. We show that EcoTroph provides an overview of the current exploitation level and target factors at the ecosystem scale, using two distinct trophic spectra to quantify the fishing targets and the fishing impact per trophic level. Then, we simulate changes in the fishing mortality, facilitating differential responses of two groups of species within the Southern Benguela ecosystem to be distinguished. More generally, we highlight various trends in a number of indicators of the ecosystem's state when increasing fishing mortality and we show that this ecosystem is moderately exploited, although predatory species are at their MSY. Finally, trophic spectra of the fishing effort multipliers  $EMS_Y$  and  $E_{0.1}$  are proposed as tools for monitoring the ecosystem effects of fishing.

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## 1. Introduction

It is now commonly accepted that overfishing can be a main source of perturbations in marine ecosystems (Gislason et al., 2000; Goñi, 1998; Heithaus et al., 2008; Jackson et al., 2001), impacting the whole food web through direct and indirect interactions. To assess the ecosystem effects of fishing models can be used as tools facilitating the simulation of various fishing scenarios. Several ecosystem models, such as Ecopath with Ecosim (EwE) (Christensen and Walters, 2004; Walters et al., 1997), OSMOSE (Shin and Cury, 2000, 2004a), and Atlantis (Fulton et al., 2004), have been 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 inform the user about the ecosystem's state and the impacts of fishing. Here we propose EcoTroph (ET), a trophic-level based ecosystem model, as a new tool to build synthetic diagnoses of fishing impacts at the ecosystem scale.

Trophodynamic indicators were first defined in the form of trophic levels (TLs) by Lindeman (1942) and modified in 1975 by Odum and Heald. Many indicators have been derived from the TLs and are now commonly used by the scientific community, thanks to their ability

to reveal ecosystem-level patterns (Cury et al., 2003 and Cury et al., 2005). New indicators can be derived from the trophic spectrum, which represents the distribution of biomass, catch or production across trophic levels (Gascuel et al., 2005). One of the main assets of trophic spectra is that they are sensitive to changes in ecosystem structure and so potentially enable tracking of the effects of fishing on the ecosystem. EcoTroph (Gascuel, 2005; Gascuel and Pauly, 2009) uses trophic spectra to represent marine ecosystems, leaving aside the notion of species and modelling the functioning of marine ecosystems as flows of biomass from low to high trophic levels. The model can be used as a standalone application, especially in data poor environments, or, taking as input the outputs of other models such as Ecopath with Ecosim, the EcoTroph model can provide a new and more synthetic view of the system.

Until now, EcoTroph has mainly been used in theoretical contexts, based on virtual ecosystems (Gascuel and Pauly, 2009) and only preliminary results have been presented regarding the application of EcoTroph to a specific case study (Gascuel et al., 2009, 2011). Here we present the first complete application of EcoTroph to a real case study, applying the model to the Southern Benguela ecosystem, one of the world's four great eastern boundary upwelling ecosystems.

Because of its biological, scientific and commercial importance, the Benguela ecosystem has been deeply studied and main trophic processes have been modelled. In particular for the southern Benguela, Ecopath (Christensen and Pauly, 1992; Polovina, 1984) models for several periods have been constructed (Osman, 2010; Shannon

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et al., 2003; Shannon et al., 2008; Watermeyer et al., 2008) and OSMOSE (Shin and Cury, 2001, 2004b) models for the 1990s have been developed (Shin et al., 2004; Travers, 2009; Travers et al., 2006, 2010; Travers and Shin, 2010; Vergnon et al., 2008; Yemane et al., 2009). Outputs of both modelling approaches can be used as inputs in EcoTroph. The first goal of the present study is to test the ability of EcoTroph to represent the Southern Benguela in a consistent way and to assess the impact of fishing on this ecosystem. This study allows us to bring to light a certain number of interesting indicators provided by EcoTroph and to document the performance of EcoTroph. It also provides an opportunity for testing the sensitivity of EcoTroph to inputs and parameters.

## 2. Material and methods

### 2.1. The EcoTroph model

EcoTroph (ET) is a trophic level-based model using trophic spectra to represent marine ecosystems (Gascuel, 2005; Gascuel and Pauly, 2009). It is based on non-integer trophic levels (TLs): primary producers and detritus are assigned a TL of 1 and TLs of consumers are calculated based on  $1 + \text{mean TL of prey items}$  (weighted by the contribution of each prey group in the diet of the consumer in question). Trophic spectra are a graphical representation of the continuous distribution of the ecosystem biomass (or production, or consumption by predators, or catch, etc) across trophic levels. Here, this continuous distribution is approximated by a distribution in classes whose width is conventionally  $\Delta\tau = 0.1$  TL. This representation results from the hypothesis that all individuals in a trophic group are not identical and therefore do not share the same trophic level but on the contrary occupy a range of trophic levels around the group's mean trophic level. To run, EcoTroph needs as inputs: biomass, catch, production, consumption and mean trophic level of each species or group. Usually, these data are not all available from direct scientific observations, but they can be obtained from other models. Thus, EcoTroph can be seen more as a complementary model 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 ecosystem functioning 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  $\beta$  coefficient chosen by the user between 0 and 1 determines the intensity of the biomass input control, 0 meaning that all the production at trophic level 1 comes from primary producers and 1 that it all comes from recycling (and thus depends on the total ecosystem biomass). As a predator is at least one trophic level above its prey there is usually no biomass between trophic levels 1 and 2. Herbivores 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. Conventionally, EcoTroph's representation of the ecosystem stops at trophic level 6 which is deemed high enough to cover all top predators. In the last version of EcoTroph (Gascuel et al., 2011) two distinct compartments are considered within the ecosystem: one where biomass is accessible to fisheries and one where it is not. For each compartment the same equations are used, but with different parameters, taking into account the fact that exploited species usually do not have the same characteristics as the unexploited ones. This is especially the case at low or intermediate trophic levels where the rate of turnover (and thus the flow kinetics) is for instance much higher for large zooplankton than for pelagic finfish.

Biomass flows through trophic levels by means of two processes: predation of prey by their predators and ontogeny, as ontogeny can be associated, for some species, with increases in trophic levels (Pauly et al., 2001). Gascuel et al. (2008) showed that even if characterised by abrupt jumps at the level of organisms (owing to predation

events), this flow can be modelled in a continuous way at the ecosystem scale. Therefore, the ecosystem functioning is considered as a non conservative flow of biomass moving through trophic levels, using general equations of fluid dynamics (see Appendix B for equations).

Biomass outputs occur at each trophic level undergoing fishing mortality, natural mortality other than predation, and losses from metabolism (e.g. excretion and egestion, and loss of energy by respiration). The biomass flow equation implies that the biomass flow occurring at one trophic level (and therefore the related biomass) depends on the flow at lower trophic levels. In other words, it implicitly introduces a bottom-up control of prey on predators in the model.

The speed of the biomass flow  $K_\tau$  depends on the turnover of the biomass. Gascuel et al. (2008) showed it can be estimated from an Ecopath model as  $K_\tau = (P/B)_\tau$ . This is consistent with Allen's relationship ( $P/B = M + F$  at equilibrium) and with the fact that the inverse parameter  $1/K_\tau$  is the mean life expectancy of an organism within the trophic class  $[\tau, \tau + \Delta\tau]$ . Thus, when the mortality changes, the speed of the flow changes too. Predation mortality being an important source of mortality, it is taken into account in the model by means of a relationship, called the top-down equation, linking the kinetics at a trophic level  $\tau$  (and therefore the biomass flow) to the biomass of predators at trophic level  $\tau + 1$ . This equation allows the model to take into account indirect effects of fishing on the ecosystem when performing simulations. Fishing, reducing the life expectancy of its target species, can be the cause of important accelerations in the ecosystem's flow kinetics. This equation also introduces a top-down control in the model, whose intensity is defined by the  $\alpha$  parameter. Because it reduces the biomass of predators responsible for top-down control, fishing can slow down flows of prey through the food web. Thus, it induces some indirect effects that may be more complex than anticipated.

### 2.2. Building an EcoTroph model: the Southern Benguela example

#### 2.2.1. Study site and previous ecosystem models

The Southern Benguela ecosystem off South Africa extends from the Orange River (the north-western boundary between Namibia and South-Africa) to East London on the Indian Ocean (Fig. 1). It is fairly independent from the Northern Benguela off Namibia, because of a strong upwelling cell near Lüderitz which caused the two ecosystems to evolve differently (Hutchings et al., 2009). The Southern Benguela ecosystem has a small primary production when compared to other major upwelling systems and its average fish production only supports moderate catches when compared to that of the Humboldt ecosystem (Carr, 2002; Moloney et al., 2005; Shannon et al., 2008). The dominating small pelagic species are anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and redeye round herring (*Etrumeus whiteheadi*), whereas Cape hake (*Merluccius capensis* and *Merluccius paradoxus*) are commercially important predators (we use the term "predators" for high trophic level species; see Shannon et al. (2004) for more details about modelled species).

Total catch of all species confounded strongly increased since the beginning of the 20th century to peak at over 1.3 million  $\text{t yr}^{-1}$  in the 1960s and have subsequently declined by more than 50% (Griffiths et al., 2004). Since the 1970s South Africa has managed its marine resources cautiously, allowing overall catches to remain relatively stable in the Southern Benguela (Griffiths et al., 2004). 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.

Here our model is based on a 1990–1997 Ecopath model of the Southern Benguela by Shannon et al. (2003), which was comparable to an OSMOSE model of the same period (Shin et al., 2004), selected as a means of performing sensitivity analyses to EcoTroph model inputs. The Ecopath model represents 32 functional groups, some comprising more than one species and some representing a particular stage of development of one species. OSMOSE is a spatialized

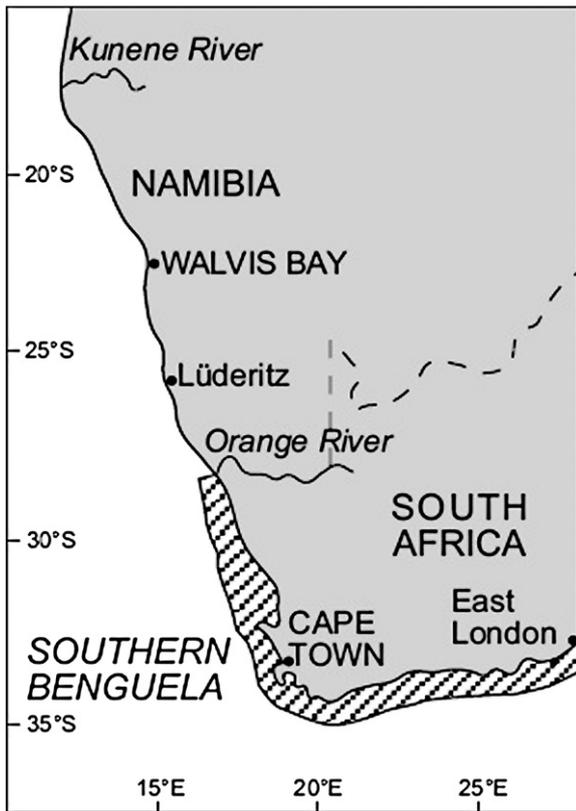


Fig. 1. Location of the Southern Benguela ecosystem, corresponding to the modelled area (from Shannon et al., 2008).

individual-based model explicitly representing life-cycles, based on very different hypotheses from those of Ecopath. The biggest difference is that in OSMOSE predation is opportunistic, which means that a group can potentially eat any other group provided fish prey are in the correct size spectrum, whereas diets are initially fixed for each group in Ecopath. Here we use the version of the OSMOSE model set up by Travers et al. (2009), which corresponds to the 1990s reference period and only comprises of 10 groups chosen because of their importance in terms of biomass and catch.

### 2.2.2. Building a trophic spectrum

The first step in applying EcoTroph to a specific case study is to build trophic spectra, representing the distribution of the ecosystem biomass across trophic levels. For each group, Ecopath provides a biomass and a mean trophic level (Fig. 2a). This biomass is spread across trophic levels around the group's mean trophic level. According to the empirical method proposed in Gascuel et al. (2009) and implemented in the EcoTroph plugin for EwE (<http://ecopath.org/plugins/ecotroph>), each group has its own distribution of biomass across trophic levels. These curves (Fig. 2b) are density probability log-normal functions centred on each species' mean trophic level and their standard deviation is theoretically defined. When all these curves are put together they are referred to as a smoothing function. For each trophic class  $\tau$  the theoretical standard deviation ( $\sigma$ ) is calculated as  $\sigma_{\tau} = \lambda \cdot \ln(\tau - 0.05)$  in an attempt to reproduce the increase in the omnivory of fish species with trophic levels. The  $\lambda$  coefficient is user-defined and allows modifications of the width of the curves in the smoothing function. The result is a continuous distribution of biomass across all trophic levels (Fig. 2c), biomass from different groups contributing more or less to various adjacent trophic levels. The trophic spectrum corresponds to the sum of all biomasses for every trophic level represented in the model. Thus the result is a single curve

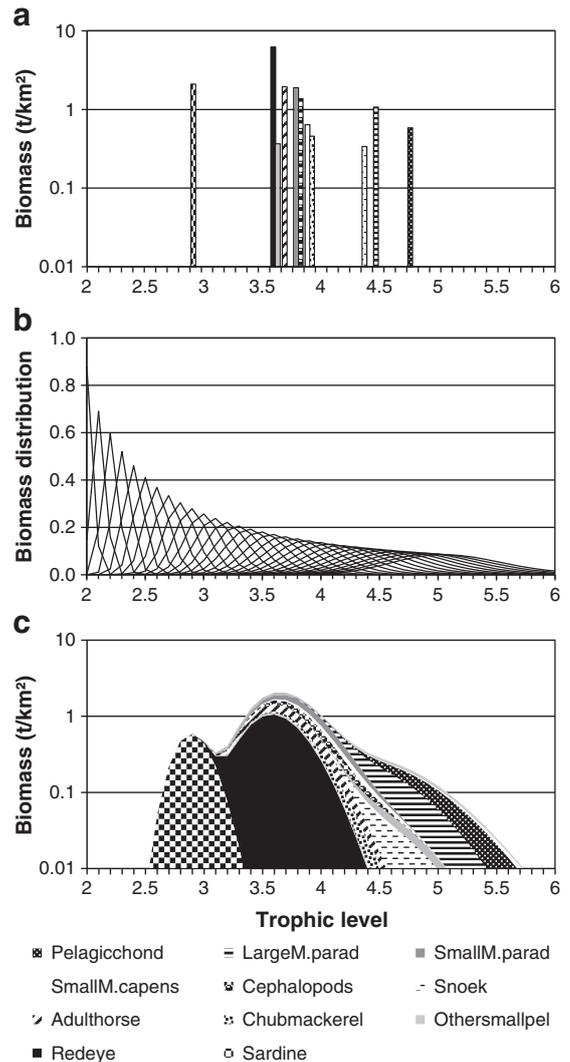


Fig. 2. Steps for building a trophic spectrum. Biomasses per Ecopath group (a) are spread across trophic levels by a smoothing function whose shape depends on the mean trophic level of the group (b). Biomasses per trophic level per group (c) are summed for each trophic level, resulting in a biomass trophic spectrum (not all 32 groups modelled are represented for the sake of clarity).

where species cannot be differentiated anymore, giving a simplified view of the ecosystem. As Ecopath also provides P/B ratios and thus the production of each group, 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 ( $\varphi=Y/P$ ) can be obtained and used to perform simulations. These two parameters  $F$  and  $\varphi$  give two different images of the exploitation of the ecosystem and will be interpreted in more detail below.

### 2.2.3. Choosing accessibilities and other EcoTroph parameters

The accessibility to fisheries parameter corresponds to the proportion of a species or group that would be caught under the hypothesis of an infinite fishing effort. Thus, this parameter takes into account whether a species is 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 group containing only targeted species. In a first step, the accessibility of each group is defined as the ratio between the fished area of a group and the distribution area of this group within the ecosystem. We assumed that this ratio

corresponds to the fraction of the species that would be caught if the fishing effort was infinite. In our case study, these ratios were obtained from Fréon et al. (2005) and Drapeau et al. (2004). Subsequently, values obtained were corrected to take into account the fact that only some species of a model group or some stages of a species were targeted. According to available literature (Payne and Crawford, 1989), corrections were also made for deep species or species living in areas limiting fishing in an attempt to be as close as possible to reality. From these accessibility parameters, trophic spectra are deduced regarding the accessible biomass ( $B^*$ ), the accessible flow ( $\Phi^*$ ) and the speed of the accessible flow in the reference state ( $K^*_{ref}$ ).

Finally, EcoTroph simulations require the top-down and biomass input controls parameters,  $\alpha$  and  $\beta$  respectively, to be defined. Values of  $\alpha = 0.5$  and  $\beta = 0.1$  have been empirically chosen, in an attempt to reflect the functioning of the Southern Benguela ecosystem. Indeed, it is widely accepted that upwelling ecosystems tend to be characterised by wasp-waist control (Cury et al., 2000) of predators and prey via small pelagic groups, contrary to other ecosystems where top-down or bottom-up controls can be observed. But since wasp-waist control is likely to be complemented by some top-down and bottom-up control between groups in the southern Benguela (e.g. Shannon et al., 2008), an intermediate value of  $\alpha$  has been chosen for all groups ( $\alpha$  may vary between 0 and 1). Theoretically the top-down parameter should be different for each 0.1 trophic level class. However, because of the lack of information about this parameter and in an attempt to facilitate simulations this parameter was defined as constant across trophic levels. This assumption is unlikely to be true and sensitivity analyses to the intensity of the top-down control have been performed to try to underline the effects of this assumption on results obtained. Upwelling ecosystems are also characterised by very high phytoplankton biomasses at the base of the trophic web. Therefore biomass recycling was deemed not to have much importance in this ecosystem and was set to a low value of 0.1.

### 2.3. Running simulations of changing fishing efforts and sensitivity analyses

#### 2.3.1. Simulations

Various fishing pressures were simulated, so as to have 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 ( $F^*$ ) or the whole ecosystem ( $F$ ). For each 0.1 TL class the current fishing mortality was modified during simulations, using a user-defined effort multiplier ( $mE$ ) ranging between 0 and 5, values between 0 and 1 corresponding to decreases in the fishing mortality and values above 1 to increases in the fishing mortality. The 0 value has a particular importance as it stands for an ecosystem with no fishing. Therefore, our simulations of an “unfished” ecosystem are based on the strong hypothesis that only fishing mortality changed but that other ecosystem parameters remained constant over time, as our simulations are all based on the EcoTroph model of the “current” ecosystem. Modifying  $F$  (resp.  $F^*$ ) changes the flow kinetics  $K$  (resp.  $K^*$ ) calculated in the top-down control equation of EcoTroph (Appendix B.3). Biomass flow  $\Phi$  (resp.  $\Phi^*$ ) is calculated from the biomass flow equation (Appendix B.2) and biomass  $B$  (resp.  $B^*$ ) is back-calculated using the actualised  $K$  (resp.  $K^*$ ) and  $\Phi$  (resp.  $\Phi^*$ ) (Appendix B.1), modifying the whole image of the ecosystem when  $F$  changes. Finally catches are deduced from the accessible biomass as  $Y = mE \cdot F^* \cdot B^*$ . Various indicators can be derived from catches. The MSY (maximum sustainable yield) is one of these indicators and can be defined as the maximum fish biomass that can sustainably be extracted from the ecosystem every year.  $E_{MSY}$  is the fishing effort allowing this level of catch (precisely it is a fishing mortality, that can be assimilated to a fishing effort under the hypothesis that both are linearly linked). It is obtained by means of numerous simulations of fishing mortality

multipliers and by selecting the one giving the maximum catch (and could therefore be written  $mE_{MSY}$  to be consistent with the previous notation  $mE$ ). There are two reasons why this method can be used here: we know that catch as a function of fishing mortality has only one maximum, and the EcoTroph model is a balanced model (any simulated level of catch can be sustained indefinitely). Therefore, for each trophic level, the effort multiplier giving the highest catch is  $E_{MSY}$ . We chose the  $E_{0.1}$  notation by analogy with the classical reference point  $F_{0.1} \cdot E_{0.1}$  is the fishing mortality multiplier for which the slope of the catch per trophic level as a function of effort becomes inferior to a tenth (0.1) of the slope at the origin. Here, simulations were performed for fishing effort multipliers ranging from 0 to 5 by 0.1 increments. We therefore compared the slope of the catch curve between the two adjacent effort multipliers (e.g. 3 and 3.1) with the slope between effort multipliers 0 and 0.1. By calculating the ratio between these slopes, we determined for each trophic level the multiplier at which the ratio becomes lower than 0.1.

#### 2.3.2. Sensitivity analyses of biomass and catch to parameterisation and model used as input

Sensitivity analyses have been performed on both the current state of the ecosystem (trophic spectra) and on the simulated states. The tested parameters are modified one by one, within realistic ranges of values, all other parameters remaining constant. We looked at the effects of these changes on the simulated biomass and catch trophic spectra. In particular we compared the rate of variation of the parameter with that of biomass and catch: if the rate of variation of the results is higher than that of the parameter, model results are considered sensitive to this parameter. The tested parameters are the following:

- The  $\lambda$  parameter, used to define the intra-groups variability in TLs (0.07 being proposed as default value in Gascuel et al., 2009).  $\lambda$  has been made to evolve between 0.04 and 0.115 with 0.015 increments, a low value of  $\lambda$  corresponding to sharp peaks and a high value of  $\lambda$  to wide curves in the smoothing function.
- The  $\alpha$  parameter, defining the intensity of the top-down control, has been made to evolve between 0 and 1 with 0.1 increments. The same value for this parameter is assigned across all groups in the model, because of our modelling hypothesis.
- The  $\beta$  parameter, defining the intensity of biomass recycling, has been made to evolve between 0 and 1 with 0.1 increments, but results are presented up to 0.5 only because higher values of  $\beta$  are very unlikely to be found in marine ecosystems.
- Accessibility of fish to fisheries has also been tested. Accessibility of all species was made to evolve between  $-50\%$  and  $+10\%$ , by 10% steps.

So as to explore the sensitivity of EcoTroph to the input model, we set up a new representation of the Southern Benguela ecosystem based on results provided by the OSMOSE model from Travers et al. (2009), in place of the Ecopath model from Shannon et al. (2003). OSMOSE provides to EcoTroph species biomass and distributions of trophic levels of 10 modelled species which emerge from size-based opportunistic predation. In addition, OSMOSE is a high trophic level model forced by a biogeochemical model for representing the plankton communities (Travers et al., 2009). Thus, to create an ET-OSMOSE model (i.e. an EcoTroph model using OSMOSE as input), we added the four plankton groups that force the OSMOSE model, assuming their biomass distribution over trophic levels is identical to those used in ET-Ecopath (the EcoTroph model built using Ecopath as input). Results obtained from both the ET-Ecopath and the ET-OSMOSE models, in the current state and when performing simulations, have been compared so as to determine the importance of the choice of the input model for EcoTroph simulations.

### 3. Results

#### 3.1. Current state of the ecosystem

According to the EcoTroph model, based on the Ecopath model for the 1990–1997 period, the total biomass of the ecosystem is  $231.2 \text{ t km}^{-2}$  with trophic level 1 included and  $147.7 \text{ t km}^{-2}$  for animals only (TLs > 2). Accessible biomass is  $12.2 \text{ t km}^{-2}$  and catch is  $2.5 \text{ t km}^{-2} \text{ yr}^{-1}$ .

##### 3.1.1. Biomass and catch trophic spectra

In ecosystems, biomass at high trophic levels depends on biomass at lower trophic levels, thus producing a global decreasing trend of the biomass trophic spectrum (Fig. 3). Two peaks in biomass can be observed: around trophic levels 2.5 and 3.5. Biomass at trophic levels close to 2.5 corresponds to various kinds of zooplankton. Trophic level 3.5 comprises of small pelagic species and mesopelagic species. Predatory species such as hakes and snoek have a trophic level around 4.5. 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 around 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 zooplankton, their high biomass can easily be explained by the high biomass at trophic level 2.5. Accessible biomass is null at low trophic levels because these levels only aggregate zooplanktons, which 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 this ecosystem. Indeed selectivity (the  $B^*/B$  ratio) is below 0.3 for all trophic levels under 4. Accessibilities of small pelagics are low because these species are only fished in a small fraction of their distribution area or/and several small pelagic species are only lightly targeted. The difference between biomass and accessible biomass decreases with increasing trophic level 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 trophic spectrum roughly has the same shape as the accessible biomass trophic spectrum, with more important oscillations showing that not all trophic levels are targeted with the same intensity. Small pelagics represent the greatest part of the catch but high trophic level species cannot be neglected.

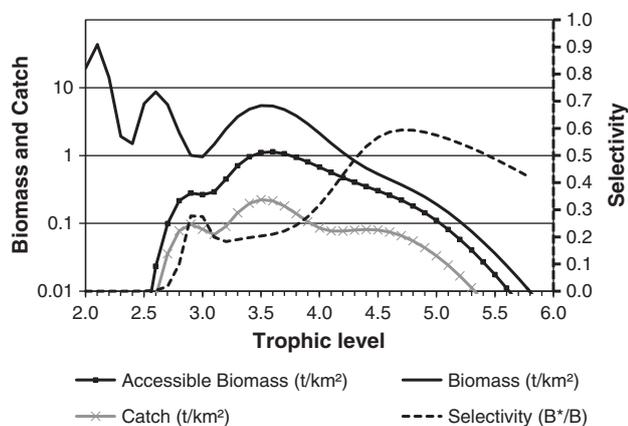


Fig. 3. The trophic structure of the ecosystem: trophic spectra of biomass, accessible biomass, catch and selectivity ( $B^*/B$ ) for animals in the Southern Benguela ecosystem.

##### 3.1.2. Fishing mortality and fishing loss rate

Two parameters provide a synthetic overview of the ecosystem exploitation: fishing mortality and fishing loss rate. Fishing mortality measures the probability of one fish being caught and the fishing mortality spectrum reflects which trophic levels are currently targeted in the ecosystem. Here, fishing mortality reaches a maximum of  $0.18 \text{ yr}^{-1}$  at trophic level 4.8 (Fig. 4), showing that fisheries mainly target predatory species such as hakes, snoek or other large pelagics and remove every year about a sixth of the total biomass of these species. The curve shows a small peak at trophic level 3, corresponding to the trophic level of sardine, underlining the fact that this small pelagic species is more targeted than the others (whose trophic level is rather around 3.5).

The fishing loss rate measures the proportion of the production caught each year and the corresponding trophic spectra reflects the level of impact of fishing on the ecosystem. The fishing loss rate reaches approximately  $0.25 \text{ yr}^{-1}$  at trophic level 4.9. This value is more than 5 times higher than those of small pelagic species but it nonetheless remains small. In other words our results suggest that less than 5% of the production of small pelagics is fished every year while a quarter of the production of predators is fished in the same period of time. Even if small pelagics account for the most important part of the catch, it is predatory fish that are mainly targeted by fishing in the Southern Benguela and that are more impacted by fisheries at 1990s levels of fishing. The decrease in fishing loss rate at trophic level 4 is an exception due to the presence of the cephalopods group (and to a lower extent of small hakes) that is characterised by very high production.

#### 3.2. Simulation of changes in fishing pressure

##### 3.2.1. Impact on ecosystem biomass

Increasing fishing mortality changes the shape of the biomass trophic spectrum, with an “erosion” of the spectrum around trophic level 5 (Fig. 5). When the fishing effort increases some trophic levels are affected much more than others (Fig. 6a). The higher the trophic level the more strongly biomass decreases when fishing mortality increases. The impact of fishing is noticeable above trophic level 4, where biomass is decreased by about 20% in comparison with the unexploited state, but negligible below trophic level 4. Biomass of trophic level 5, which is the most affected by fishing, had in the 1990s already been reduced by more than one third in comparison with a situation with no fishing. Compared to the current (1990s) state, biomass at trophic level 5 would be reduced by 30% if the fishing mortality was doubled and by 60% if it was multiplied by 5. Trophic levels 3 to 4 are far less sensitive to fishing and their biomasses only decrease a little when the effort increases.

However, a different picture emerges at the level of accessible biomass (Fig. 6b), with far clearer tendencies. The accessible biomass of all groups appears to have been deeply depleted since the onset of

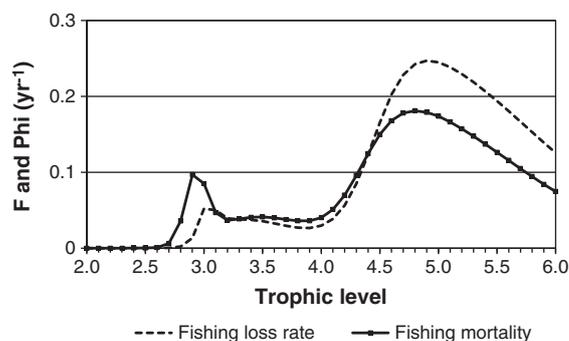


Fig. 4. Exploitation patterns at the ecosystem scale: fishing loss rate and fishing mortality for the total biomass.

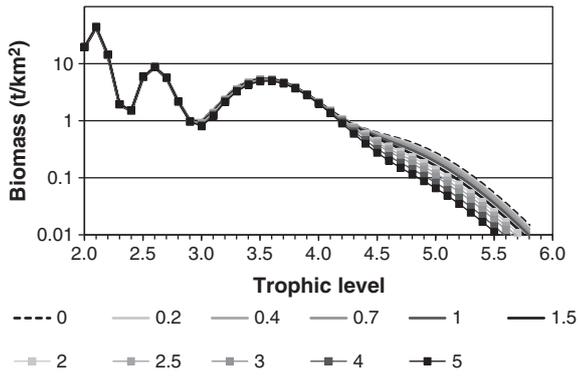


Fig. 5. Simulated biomass trophic spectra for effort multipliers ranging between 0 and 5.

fishing: accessible biomass of groups at trophic level 3 has been decreased by 30%, that of TL4.5 has been more than halved and accessible biomass at TL5 has been divided by three. Accessible biomass also is far more sensitive than total biomass to increases in the fishing effort:  $B^*$  at TL4.5 and TL5 would be halved by a doubling in the fishing effort while  $B^*$  at other trophic levels would be reduced by 25%. Simulations suggest that fishing favours non-fished species that take advantage of a decrease in the biomass of their fished competitors.

### 3.2.2. Impact on catch

Globally, the more the fishing mortality increases the more the catch increases (Fig. 7). For low fishing multipliers a small increase in the mortality causes a high increase in the catch. On the contrary at high effort multipliers an increase in the fishing mortality 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 mortality multipliers, but

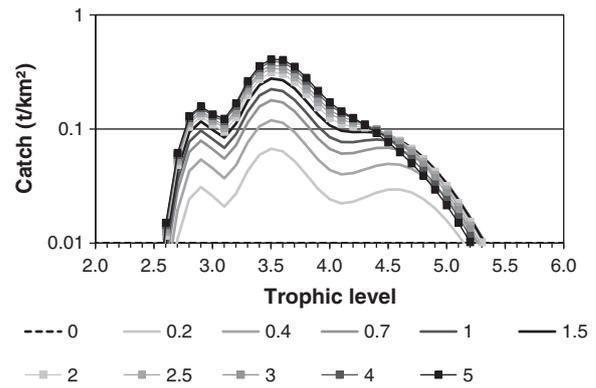


Fig. 7. Simulated catch trophic spectra for effort multipliers ranging between 0 and 5.

for much smaller multipliers. This means that in the case of an increase in the fishing mortality there is a risk of overexploitation of high trophic level species.

In the current situation the total catch is  $2.5 \text{ t km}^{-2}$ . The increase in the total catch with fishing mortality is not linear (Fig. 8a) and will eventually reach a maximum before decreasing. The total catch keeps on increasing for each fishing mortality multiplier simulated, even if we can infer that the value of  $4 \text{ t km}^{-2}$  that is reached for a multiplier of 5 is close to the maximum total catch possible in this ecosystem.

We can notice that trophic level 5 is currently fully exploited and that catch at trophic level 4.5 could only be increased by about 10%, by a doubling in the fishing mortality, before decreasing (Fig. 8b). Catches at other trophic levels do not reach a maximum within the range of fishing mortality multipliers tested and catch of small pelagics can be increased by about one third by a doubling of the fishing mortality. It is to be noted that the most important relative increase takes place for trophic level 4 (because of cephalopods), even if the absolute catch at trophic level 3.5 is far higher.

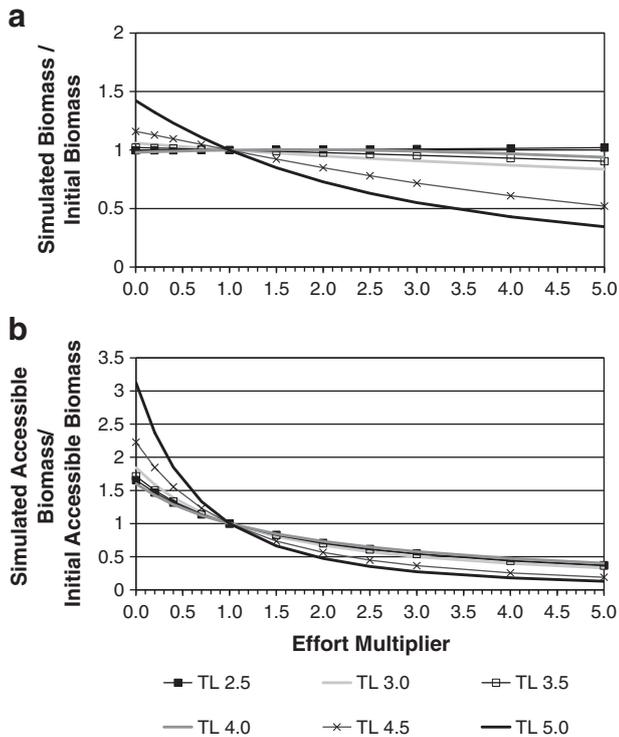


Fig. 6. (a) Simulated relative biomass of six different trophic level classes of the ecosystem and (b) simulated relative accessible biomass.

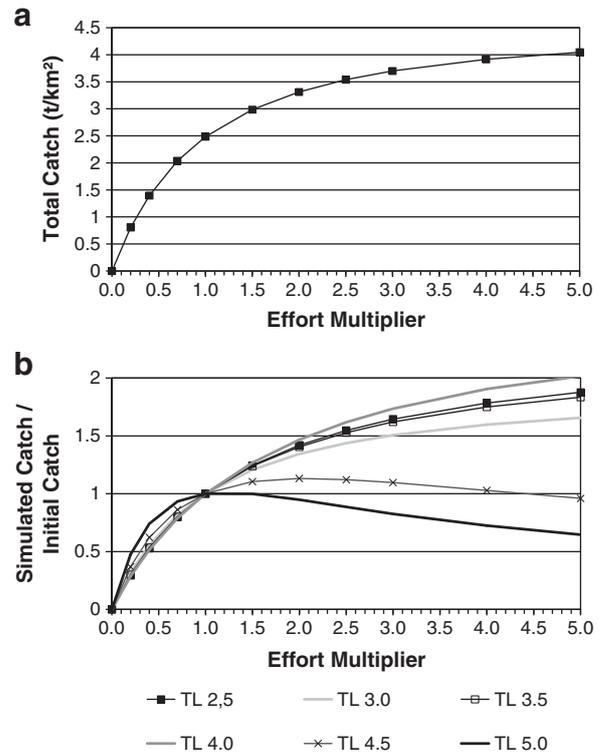


Fig. 8. Simulated total catch (a) and simulated relative catch per trophic level classes (e.g. TL 2.5 corresponds to the [2.5;2.6] class) (b).

### 3.2.3. Ecosystem indicators

A useful reference level for determining the level of exploitation of the ecosystem is the  $E_{MSY}$  (Fig. 9), meaning the fishing mortality multiplier at which the Maximum Sustainable Yield (MSY) would be reached. As the catch of the low trophic levels are still below the MSY within the range of fishing mortality multipliers tested, the  $E_{MSY}$  is provided by EcoTroph simulations from TL = 4.2 only. Fig. 9 shows that the ecosystem is not overexploited but that species at trophic level 5 and above are very close to full exploitation. Trophic level 4.5 is interesting to look at as it includes some of the ecosystem's most economically important predator species such as hakes and snoek. It appears that fishing mortality on this trophic level could be doubled according to the  $F_{MSY}$  indicator, but with only a small increase in the catch.

Because the production function can be very flat around  $E_{MSY}$ , a more conservative reference level has also been used.  $E_{0.1}$  is the fishing mortality multiplier at which the slope of the catch-per-fishing-mortality-multiplier curve becomes inferior to a tenth of the slope at the origin of the curve. This indicator is commonly used in single species assessment as defining the limit of full exploitation. Simulations show that  $E_{0.1}$  is reached in the current state at trophic level 4.7 and the fishing mortality already is beyond  $E_{0.1}$  for trophic levels above 4.8. Interestingly, while the  $E_{MSY}$  is not within the range of multipliers tested for small pelagics  $E_{0.1}$  reaches rather low values in comparison for those species:  $E_{0.1} = 2.5$  at TL 3, corresponding to the trophic level of sardines and  $E_{0.1} = 3$  at trophic level 3.5, corresponding to most other small pelagics and in particular anchovy. This shows that the catch of small pelagics can increase rather significantly until these multipliers are reached. In this ecosystem, the highest value of  $E_{0.1}$  is reached at trophic level 4, confirming that this trophic level has the greatest potential of increase in catch. Values of  $E_{MSY}$  and  $E_{0.1}$  show that the Southern Benguela ecosystem is moderately exploited and could be overexploited at "current" (1990–1997) biomass levels only if very large increases in fishing efforts occurred. These optimistic results have to be linked with the work choices that were made: groups were aggregated by integral trophic levels and both fished and non-fished species were considered. Other choices may have given a different picture of the ecosystem. Besides, a clear pattern appears and underlines the need for more detailed observations: predatory species are fully exploited in terms of catch in the Southern Benguela ecosystem whereas catch of small pelagic species could increase significantly, their high biomass being the reason why the ecosystem as a whole appears only moderately exploited.

A strong decrease in total biomass is considered to be the threshold for overexploitation. For instance, in a Fox single-species production model biomass of one stock has been decreased by 63% when  $F = F_{MSY}$ . To verify the relevance of results given by our model we plotted the accessible biomass loss at  $E_{0.1}$  per trophic level (Fig. 10). Accessible biomass is reduced by about 70% when the  $E_{0.1}$  is reached for small pelagic species, with a maximum of 72% at trophic level 4

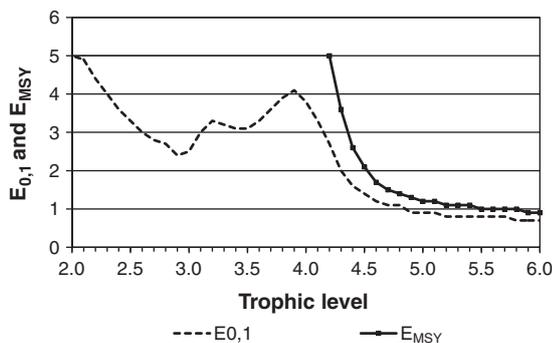


Fig. 9. Indicators of the current status of the ecosystem: fishing effort multipliers  $E_{MSY}$  and  $E_{0.1}$  per trophic level in the Southern Benguela.

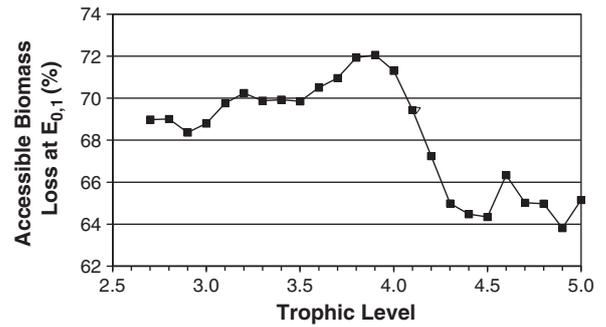


Fig. 10. Trophic spectrum of the accessible biomass loss rate at  $E_{0.1}$  in the Southern Benguela ecosystem (in % compared to the unfished state of the ecosystem).

which mostly comprises of cephalopods. There is a sharp decrease in the level of the threshold in terms of accessible biomass between TL4 and TL4.5, underlining the fact that the ecosystem is made of two different groups of species. Indeed, from TL4.5 onwards overexploitation is reached for a decrease in accessible biomass of about 65%, confirming the fact that high trophic level species are more easily overexploited than low trophic level species.

Trophic levels of accessible biomass and catch are impacted by an increase in fishing mortality multipliers, with current trophic levels being approximately 0.07 TL lower than in the unexploited state (Fig. 11). The trophic level of catch decreases more strongly than that of the accessible biomass. This can be explained by the fact that the catch of predatory species is already at its maximum and therefore their proportion in the catch decreases when  $F$  increases, dragging the trophic level of the catch towards that of small pelagics.

### 3.3. Sensitivity analyses

#### 3.3.1. Sensitivity to the model used as input

The biomass spectrum built from the OSMOSE model (Fig. 12a) appears to be close to the spectrum built from Ecopath, both graphs showing peaks at trophic levels 2.5 and 3.5 approximately. The spectrum built from OSMOSE is less smooth than the spectrum built from Ecopath.

Looking at catch (Fig. 12b), patterns observed in both graphs are rather similar too, with three distinct peaks. 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 are dominant prey groups at the base of the food chain. These peaks also appear in the spectrum obtained with Ecopath but are far less important, with catch fluctuating around 0.1 t km<sup>-2</sup> for most trophic levels. The spectrum in OSMOSE starts and stops at lower trophic levels than that obtained with Ecopath, underlining

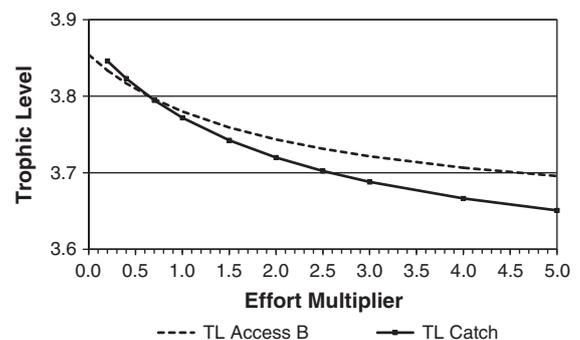


Fig. 11. The impact of fishing on the mean trophic level of the accessible biomass and of catch: results of EcoTroph simulations in the Southern Benguela ecosystem.

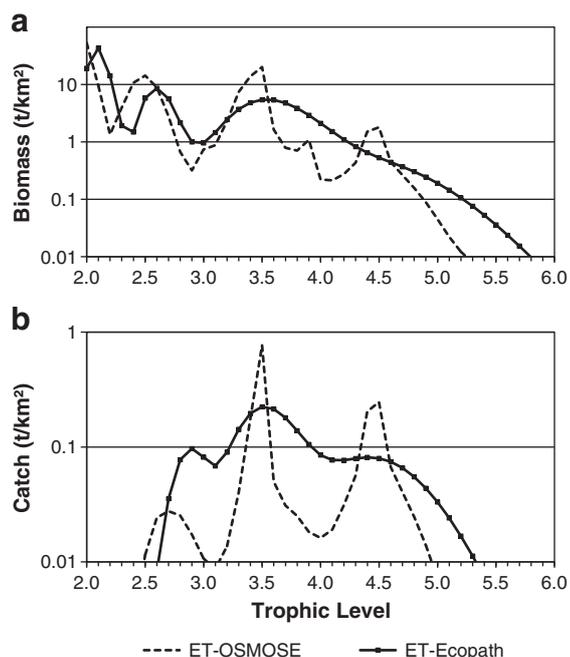


Fig. 12. Using EcoTroph as a tool to compare the ET-Ecopath and ET-OSMOSE models of the Southern Benguela ecosystem: (a) the biomass trophic spectra, (b) the catch trophic spectra.

different modelling choices, such as the number of groups and their emergent trophic level. The fact that peaks obtained with OSMOSE are very narrow compared to those obtained with Ecopath can be explained by the fact that less species diversity is represented in OSMOSE, hence the marked depressions at trophic levels 3 and 4. It could, rather paradoxically, be strengthened by the fact that predation is opportunistic in this model. Indeed if all predators can eat all species in the ecosystem provided they are small enough they will have much diversified diets but these diets will be very similar from one predator to another, resulting in very similar trophic levels for all predatory species. A smaller species diversity is also the reason why the biomass trophic spectrum stops earlier with the OSMOSE model. Indeed in OSMOSE the groups with the highest trophic levels are hake groups, and in particular *M. capensis* at TL 4.64. In Ecopath, the highest trophic level is 5.2 and there are two groups of sharks and two groups of marine mammals with trophic levels higher than that of *M. capensis*.

The accessible biomass predicted by EcoTroph is very similar whether Ecopath or OSMOSE is used for input (Fig. 13), with a slightly stronger decrease using OSMOSE because this model only comprises of fished species. In both cases EcoTroph suggests that accessible

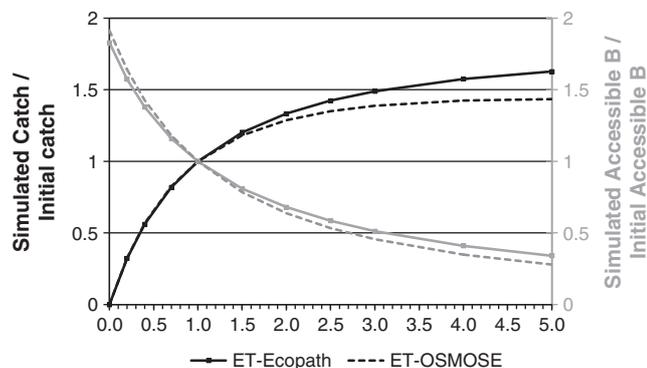


Fig. 13. Sensitivity analysis to the model used as input performed on catch (black) and accessible biomass (grey).

biomass in the Southern Benguela ecosystem has already been reduced by 40% since the onset of fishing and would be reduced by approximately one third by a doubling in the fishing mortality.

The use of the OSMOSE model for parameterising EcoTroph provides slightly less “optimistic” results in terms of catch than when using the Ecopath model (Fig. 13): catch in OSMOSE reaches its maximum when fishing mortality is multiplied by 4 while catch in Ecopath is still increasing when fishing mortality is multiplied by 5. This difference can be explained by the choice of the species in OSMOSE. Indeed, only 10 species are modelled in OSMOSE that have been chosen especially for their importance in terms of biomass and catch. On the contrary, Ecopath models many species, spanning commercially important and largely unfished species whose catch can be greatly increased in comparison with the current situation.

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 running simulations. Thus, the global diagnosis provided by EcoTroph at the ecosystem scale appears little sensitive to the model used as input.

### 3.3.2. Sensitivity to user-defined parameters

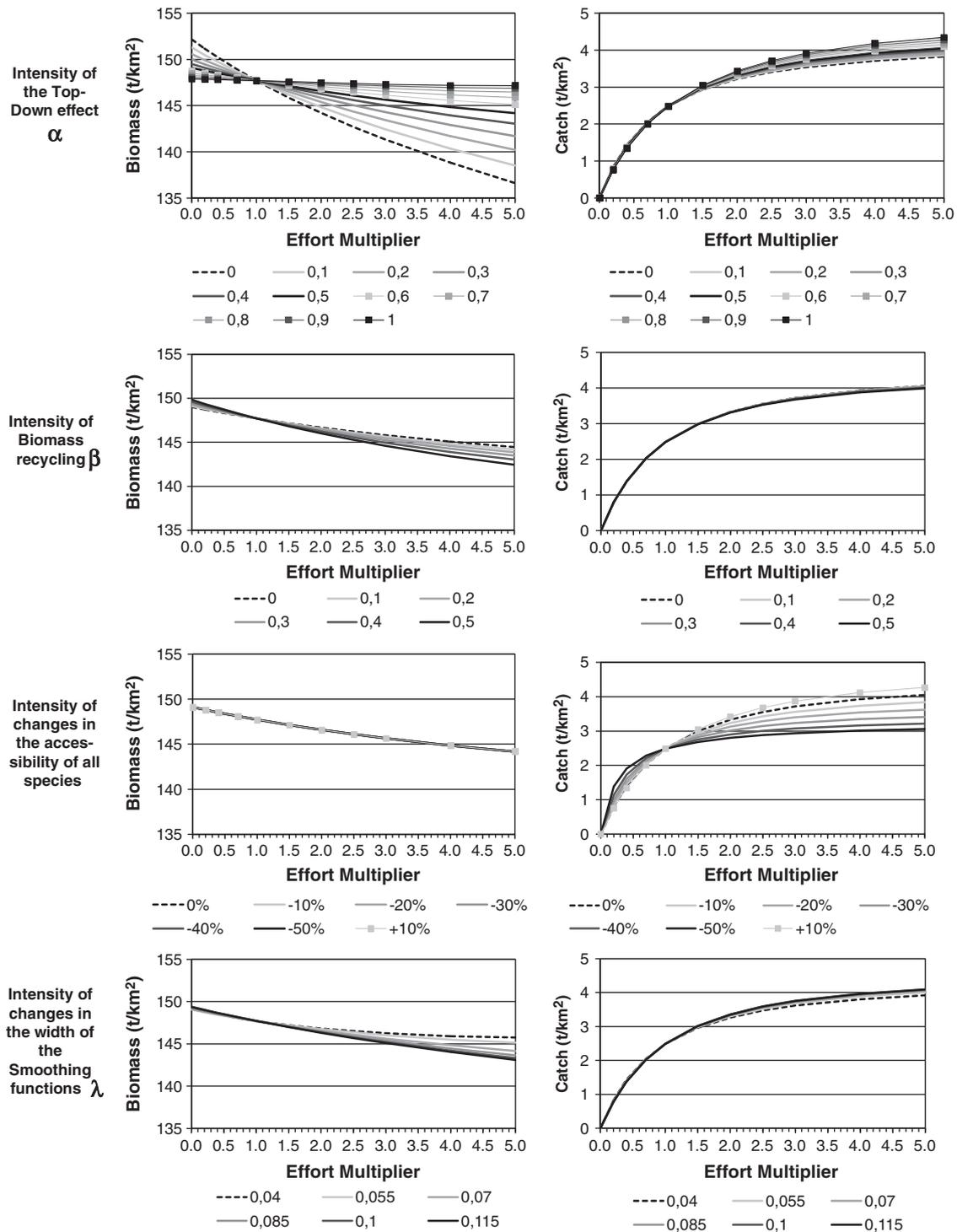
The intensity of top-down control ( $\alpha$ ) is the only parameter tested to which total biomass was shown to be sensitive (Fig. 14, top-left). Nevertheless, making  $\alpha$  evolve between its minimum (0) and its maximum (1) possible values only modifies total biomass by  $10 \text{ t km}^{-2}$  (roughly 7% of total biomass) when fishing mortality is multiplied by 5. Therefore the choice of the  $\alpha$  parameter does not actually have a large impact on the global results, an increase in  $\alpha$  only slightly decreasing the impact of fishing on biomass.

Total accessibility of species to fisheries is the parameter most affecting the catch. The higher the accessibility to fisheries, the higher the catch (at least for effort multipliers over 1). However catches do not appear to be overly sensitive to the accessibility parameter because reducing the accessibility by 50% only reduces catches by 25% (from  $4 \text{ t km}^{-2}$  to  $3 \text{ t km}^{-2}$ ) when the fishing mortality is multiplied by 5.

## 4. Discussion

### 4.1. Tools for a global ecosystem diagnosis on the fishing impact

The Southern Benguela ecosystem could be seen as moderately exploited when initially considered in its entirety but some results given by EcoTroph urge us to be more careful. When looking at fishing mortality  $F$  and fishing loss rate  $\phi$  it is easy to notice that these two indicators can give two different images of the same ecosystem. In the case of high trophic level fish with low production rates  $P/B$ , a low  $F$  indicates that a small fraction of biomass is targeted while  $\phi$  might show that too much is being fished relatively to what is produced:  $F$  could conceal a situation of overexploitation and only allow its detection once the biomass of the stock has been significantly reduced. 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  $F$  only would erroneously guide management towards underexploitation of the resources. Thus the fishing mortality  $F$ , defined as the ratio  $Y/B$ , should be viewed as an indicator of which trophic levels are targeted by fishing, while the fishing loss rate  $\phi$  defined as the ratio  $Y/P$  is an indicator of the actual impact of fishing on the ecosystem. In other words, a fishing mortality of  $0.3 \text{ yr}^{-1}$  has a stronger impact on predatory species such as hake than on prey species such as anchovy. This EcoTroph modelling study shows that total biomass of the ecosystem is not very sensitive to increases in fishing mortality. This is because a very large part of the ecosystem, especially low trophic levels, is not exploited at all. The cause for this absence of exploitation can be monetary: too low market prices or no market for a species will prevent its exploitation.



**Fig. 14.** Sensitivity analysis of biomass (left) and catch (right) to the main EcoTroph parameters: top-down control ( $\alpha$ ), Biomass recycling ( $\beta$ ), Global accessibility to fisheries and width of the curves in the smoothing function ( $\lambda$ ).

The other parameter reducing exploitation possibilities is the accessibility of fish groups to fisheries. Here we have shown the need for a focus on the accessible fraction of the ecosystem, that greatly changes the image we have of it. In particular we have shown far stronger decreases in accessible biomass than in biomass, identifying potential local overexploitation of parts of the stock of each species. We underline another kind of potentially harmful effect of fishing: the higher the fishing mortality, the stronger the relative decrease in the biomass of targeted commercial species. This means that fishing modifies the balance between species in the ecosystem and tends to

favour non-fished species that take advantage of the decrease in biomass of their fished competitors. In some extreme cases this could lead to a sudden shift in the composition of the ecosystem, such as has been observed in the Northern Benguela (Heymans et al., 2004).

#### 4.2. Modelled states VS real states: a difficult comparison

This paper is largely based on simulations of changes in the fishing mortality applied to the Southern Benguela ecosystem and on the calculation of various indicators from the results of these simulations.

Therefore one naturally wonders about our model's ability to make realistic predictions, and one straightforward way to get this piece of information would be to compare our predictions to past states of the ecosystem. However, in spite of the simulation of a hypothetical un-fished state of the ecosystem based on many hypotheses, no such comparisons were performed in this paper. The first reason why we did not perform these comparisons is that our model is based on a "current" set of parameters. Therefore, as we do not know how these parameters have been impacted by human activities since the onset of fishing it is difficult to represent past states of the ecosystem, and the modelling error would probably increase as we would try to model further in the past. This makes our simulation of an un-fished state a very bold attempt given the little information we have and this is the reason why we analyse this simulation more in terms of possible trends than in terms of values. Another reason why we chose to model the un-fished state is that it is a balanced state. Indeed, the second reason why comparing past states with model results is difficult is that EcoTroph is a balanced model. This means that EcoTroph simulations have to be compared to balanced states of the ecosystem. The issue in the Southern Benguela ecosystem is that fishing effort and catches have been increasing during most of the 20th century, to peak at the beginning of the 1970s and subsequently decrease (mostly because of government regulations) until the present days. Therefore this ecosystem has known no balanced states in recent history with which to compare our results. Even if the Southern Benguela ecosystem is not currently in such a state, we can infer that it is as close to it as it has been since the beginning of the 20th century. Indeed, fishing effort series seem to be stabilising for many fisheries after times of more or less erratic fluctuations (Shannon et al., 2008). Two aspects of the Southern Benguela ecosystem would add to the difficulty of simulating past states: it is strongly environmentally-driven, with high biomasses of planktons and pelagic species, and the dominance in terms of biomass of small pelagic species regularly shifts between anchovy and sardine. Modelling past states of an ecosystem is a very demanding task requiring a lot of data and many hypotheses, and can be the topic of a paper by itself as did Watermeyer et al. (2008) on the Southern Benguela ecosystem.

#### 4.3. EcoTroph with Ecopath and OSMOSE

There are huge differences between Ecopath and OSMOSE, especially when looking at their structure and at their underlying hypotheses. Ecopath is a non-spatialised steady state model based on defined diets for each species (contrary to Ecosim where diets can evolve dynamically), whereas OSMOSE is a spatialised, size-based 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 were compared, providing interesting insights in the modelling of the trophic structure and functioning of the studied ecosystem. Importantly, EcoTroph's ability to make abstraction of the notion of species allows for comparison between such heterogeneous models. While the number of species or groups considered in both cases is very different (32 groups for Ecopath and only 10 for OSMOSE), biomass and catch spectra show that the same global trophic structure is in fact considered in both models. The 10 species included in OSMOSE were selected because of their importance in terms of catch and biomass, reducing the gap between the models. At the same time, comparison using EcoTroph also highlights some differences, and especially a smoother distribution of the biomass (and catch) over trophic levels for the Ecopath model (compared of far more model groups) than for the OSMOSE model. Regarding the diagnosis based on inputs from these two models, modelling choices have been made in order to facilitate comparisons between EcoTroph model results stemming from each of the other two models. The major one 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 could not be easily provided as an output from OSMOSE and we chose to use the same ratios as used in Ecopath. Assuming such identical P/Bs based on the scientific literature, both input models provide us with identical diagnoses of the impacts of fishing on this ecosystem overall, illustrating EcoTroph's adaptability and robustness to the choice of the input model. This adaptability could make EcoTroph a useful tool allowing integrating various sources of knowledge in one single modelling process. More generally, EcoTroph can be used as a powerful framework for comparing various models, owing to its ability to underline differences in modelling choices and hypotheses.

#### 4.4. The EcoTroph modelling tool—conclusion

Throughout this article we have attempted to highlight EcoTroph's abilities and applications, and its possible contribution to the improvement of steady-state ecosystem modelling as we currently know it. However, any one model is only one imperfect way amongst others to view an ecosystem, and EcoTroph's limits, resulting from the model's structure and modelling choices and hypotheses, should always be considered before attempting simulations or when reading results.

Firstly, in the present study we only used EcoTroph as a steady state model representing mean states of the ecosystem each related to a given set of parameters and drivers, whereas a marine ecosystem is constantly evolving under the influence of climate, anthropogenic influences, and interactions between species. A dynamic version of EcoTroph has been developed (Gascuel and Pauly, 2009) but was not applied here.

Secondly, EcoTroph is not spatialised, thus it does not account for the fact that fish densities fluctuate a lot within the geographic extent of the ecosystem, that fish move and that fisheries only exploit part of the ecosystem targeting areas where fish are more abundant. This means that EcoTroph provides a spatially averaged diagnosis that for instance would not assist in spatial management deliberations.

Finally, EcoTroph leaves aside the notion of species, which can also be an obvious limitation when trying to set up fisheries management policies. In a moderately exploited ecosystem such as the Southern Benguela, the major risk is not that of an overall shift but more that of overexploitation of a particular species. In this case, considering the ecosystem as a whole could even be misleading because the general good state of the ecosystem could hide the overexploitation of single species. However, the user can always refer to the groups' mean trophic levels used as inputs to check which species represent the bulk of the biomass at any trophic level, making the abstraction of the notion of species more a modelling trick than a relative limit of the model.

In short, EcoTroph has the limits imposed by its qualities: it relies on a simple structure and standard equations to quickly provide a much sought-after (by fisheries managers, politicians, scientists) general diagnosis of an ecosystem through interesting indicators and reference levels (fishing mortality and loss rates, accessible biomass,  $E_{0,1}$ ,  $E_{MSY}$ ). This broad outlook should be considered as complementary to single-species or species-oriented modelling approaches, as it especially provides a generalised diagnosis of fishing impacts for all trophic levels and the entire biomass of the ecosystem. EcoTroph thus appears as a new tool which could contribute in the future to a better understanding of ecosystem functioning and thus to the scientific information base necessary for the development of an Ecosystem Approach to Fisheries Management.

#### Acknowledgements

The authors would like to thank K. Watermeyer for providing EwE modelling data and information about the Southern Benguela ecosystem and M. Travers for providing OSMOSE modelling data.

## Appendix A. Variables used in this paper

**Table 1**  
Parameters and variables of the EcoTroph model, values and units.

Variable	Parameter definition	Value or formula	Units
B	Biomass	–	t km <sup>-2</sup>
B*	Accessible biomass	–	t km <sup>-2</sup>
Y	Catch	–	t km <sup>-2</sup> yr <sup>-1</sup>
S	Selectivity	B*/B	–
P	Production	K.B or $\Phi \cdot \Delta\tau$	t.km <sup>-2</sup> yr <sup>-1</sup>
F	Fishing mortality	Y/B	yr <sup>-1</sup>
F*	Accessible fishing mortality	Y/B*	yr <sup>-1</sup>
K	Flow kinetic	P/B	$\tau$ yr <sup>-1</sup>
K*	Accessible flow kinetic	P/B*	$\tau$ yr <sup>-1</sup>
$\mu$	Natural loss rate of biomass flow	$\text{LN}(P_T/P_T + \Delta\tau)/\Delta\tau - \phi$	$\tau^{-1}$
$\phi$	Fishing loss rate of biomass flow	Y/P	$\tau^{-1}$
$\phi^*$	Accessible fishing loss rate of biomass flow	Y/P*	$\tau^{-1}$
$\sigma$	Standard deviation of the smoothing function	$\lambda \cdot \text{LN}(\tau - 0.05)$	–
$\lambda$	Parameter modifying the value of $\sigma$ with the smoothing function	0.07	–
$\beta$	Coefficient of biomass input control	0.1	–
$\alpha$	Coefficient of top-down control	0.5	–

## Appendix B. Main equations in EcoTroph

In steady state conditions,  $B_\tau$  the biomass at trophic level  $\tau$  (i.e. in the trophic class  $[\tau, \tau + \Delta\tau]$ ), expressed for instance in tonnes, is calculated as:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \cdot \Delta\tau \quad (\text{B.1})$$

where:  $\Phi_\tau$  is the mean biomass flow passing through the trophic class  $[\tau, \tau + \Delta\tau]$  (expressed for instance in tonnes/year), and  $K_\tau$  is the mean speed of the biomass flow through that class, which quantifies the velocity of biomass transfers through the food web (in TL/year, the number of trophic levels crossed per year).

Thus, the biomass flow  $\Phi_\tau$  decreases according to trophic levels and can be calculated as:

$$\Phi_{\tau+\Delta\tau} = \Phi_\tau \cdot \exp[-(\mu_\tau + \phi_\tau) \cdot \Delta\tau] \quad (\text{B.2})$$

where  $\mu_\tau$  is the natural loss rate (encompassing non predation natural mortality and catabolic losses) and  $\phi_\tau$  the fishing loss rate. When attempting simulations these parameters are important because simulations are made under the hypothesis that natural loss rates are constant and that only fishing loss rates changes.

This equation also defines the transfer efficiency (TE) between trophic levels as  $\exp(-\mu_\tau)$ .

The top-down equation, links the kinetics at a trophic level  $\tau$  (and therefore the biomass flow) to the biomass of predators at trophic level  $\tau + 1$ :

$$K_\tau = \left[ K_{\text{ref},\tau} - F_{\text{ref},\tau} \right] \cdot \left[ 1 + \alpha \cdot \frac{(B_{\text{pred}}^\gamma - B_{\text{pred,ref}}^\gamma)}{B_{\text{pred,ref}}^\gamma} \right] + F_\tau \quad (\text{B.3})$$

where  $K_{\text{ref},\tau}$  is the speed of the flow at trophic level  $\tau$  in the reference state (which is defined by the Ecopath model and characterised by a fishing mortality  $F_{\text{ref},\tau}$ ),  $K_\tau$  is the speed of the flow in any state of the ecosystem (characterised by  $F_\tau$ ),  $B_{\text{pred}}$  is the predator biomass of species at trophic level  $\tau$  (i.e. biomass conventionally between TL

$\tau + 0.8$  and  $\tau + 1.3$ ),  $\alpha$  is a coefficient chosen by the user between 0 and 1 which determines the part of natural mortality at trophic level  $\tau$  that is dependent on the abundance of predators,  $\gamma$  is a shape parameter varying between 0 and 1 defining the functional relationship between prey and predators. A value of 1 for  $\gamma$  results in a linear effect of the abundance of predators on the flow kinetics, while a smaller value would reflect non linear effects due to predators' competition.

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