EcoTroph: a simple model to assess fishery interactions and their impacts on ecosystems

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The EcoTroph model leaves aside the notion of species, and models the functioning of marine ecosystems as flows of biomass from low to high trophic levels, so as to quantify easily the impacts of fishing at an ecosystem scale. In this paper, based on two case studies we present a new development of the EcoTroph model that is devoted to the analysis of fishery interactions and impacts of fleet segments on ecosystems. First, deriving an EcoTroph model from an Ecopath model of the Guinea ecosystem, the impacts of the artisanal fishery are distinguished from those of the industrial fishery. It appears that these fisheries do not always compete for the same fish groups but that they both strongly impact the ecosystem and moderately impact one another. Then, an EcoTroph model of the Southern Benguela ecosystem is set up, also based on a pre-existing Ecopath model. Two scenarios are simulated: a doubling in the fishing mortality of small pelagics and a doubling in the fishing mortality of hake. An increase in fishing mortality of small pelagics causes a strong decrease in biomass at all trophic levels of the ecosystem, confirming the pivotal role of these "wasp-waist" species in this ecosystem.

Keywords: Ecopath, ecosystem modelling, EcoTroph, fishery interactions, fishing impact, Guinea, management scenario, small pelagics, Southern Benguela.

Introduction

Models are increasingly used to improve our understanding of marine ecosystem functioning and address applied questions in the field of fishery management (Walters and Martell, 2004). In particular, the recognition that the impact of fishing extends well beyond the targeted species lets fishery scientists develop new ecosystem models, as key tools for the implementation of ecosystem-based fishery management.

One of these models is EcoTroph (Gascuel, 2005; Gascuel and Pauly, 2009), a minimum-realistic ecosystem model which provides a simplified overview of ecosystem functioning and facilitates simulations of changes in fishing mortality. EcoTroph uses trophic spectra to represent marine ecosystems, leaving aside the notion of species and modelling marine ecosystems' functioning as flows of biomass from low to high trophic levels (TLs). In the past few years, EcoTroph's applications have shifted from theoretical contexts based on virtual ecosystems (Gascuel and Pauly, 2009; Gascuel et al., 2011) to specific real case studies to assess the

current fishing impacts at the ecosystem scale (Tremblay-Boyer et al., 2011; Gasche et al., 2012; Lassalle et al., 2012) or to analyse the effects of marine protected areas (MPAs) on the whole foodweb (Colleter et al., 2012; Valls et al., 2012).

However, EcoTroph's simulation abilities remained limited, allowing modellers only to simulate a global change in the fishing pressure using the same effort multiplier for all TLs. We therefore developed a new version of the EcoTroph model where fishing mortality can be changed either for each fleet segment operating in the ecosystem or for each functional group of the foodweb. This considerably increases the number of possible simulations and allows users to simulate management scenarios closer to reality. Indeed, the model can now be used to assess the specific impact of each fleet segment on the foodweb and to investigate relationships between fisheries as well as their joint effect on the ecosystem.

Here, using the Guinean and the Southern Benguela ecosystems as case studies, we demonstrate that this simple model can be used

to simulate complex changes in the dynamics of fisheries. Simulations by fleet segments are presented through an application to the Guinean ecosystem where the interactions between artisanal and industrial fisheries are a key aspect of fishery management. Then the EcoTroph model is applied to the Southern Benguela upwelling ecosystem to simulate two hypothetical fishing scenarios. This case study especially highlights the strong influence of the exploitation of small pelagic species on the whole foodweb as well as on other fisheries. Both these applications to real ecosystems give us valuable insights into the key mechanisms driving ecosystem reactions to fishing that could be of great use in an ecosystem approach to fishery management.

Material and methods
General principles and major equations of the EcoTroph model

EcoTroph is a TL-based model using trophic spectra to represent marine ecosystems (Gascuel, 2005; Gascuel and Pauly, 2009). Trophic spectra are graphical representations of the continuous distribution of the ecosystem biomass (or production, or consumption by predators, or catch, etc.) across TLs (Gascuel *et al.*, 2005). Conventionally, this continuous distribution is approximated by a distribution in trophic classes whose width is $\Delta\tau = 0.1$ TL.

EcoTroph models marine ecosystem functioning as flows of biomass from low to high TLs. Biomass enters the ecosystem at TL 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. A value of 0 means that all the production at TL 1 comes from primary producers, while a value of 1 indicates that all production comes from recycling (and thus depends on the total ecosystem biomass). There is usually no biomass between TLs 1 and 2, herbivores and detritivores being at TL 2. Then, at TLs >2, the biomass is distributed along a continuum of values of TL, the diet variability of the various consumers resulting in all fractional TLs being filled. Conventionally, EcoTroph's representation of the ecosystem stops at TL 6, which is deemed high enough to cover all top predators.

Despite its apparent simplicity and representation of the ecosystem as flows of biomass, EcoTroph falls into the "whole ecosystem models" category as defined in Plagányi *et al.* (2007). Indeed, EcoTroph attempts to take into account all TLs in the ecosystem and is commonly based on Ecopath (Christensen and Walters, 2004) outputs possibly representing tens of trophic groups. Nonetheless the notion of species quickly disappears from EcoTroph as trophic spectra are built summarizing all the information available at the species (or trophic group) level with one curve per output variable. EcoTroph only models top−down and bottom−up effects of fishing along the food chain, with no spatial, temporal, or environmental variations, mostly using common stock assessment equations. Therefore, this model could also correspond to the "extensions of single-species assessment models" (ESAMs) category. It is our opinion that the EcoTroph approach is one of the simplest available when trying to model the effects of fishing at the ecosystem

level. Thus we chose in this paper to refer to EcoTroph as a minimum-realistic ecosystem model, even if these terms are partly antagonistic.

Biomass flows through TLs by means of two processes: predation of predators upon their prey; and ontogeny (as ontogeny can be associated, for some species, with increases in TLs). Gascuel *et al.* (2008) showed that even if characterized by abrupt jumps at the level of organisms (according to predation events), this flow can be modelled in a continuous way at the ecosystem scale. Therefore, ecosystem functioning is considered a non-conservative flow of biomass moving through TLs, using the usual equations of fluid dynamics. In steady-state conditions, the biomass at TL τ (i.e. in the trophic class $[\tau, \tau + \Delta\tau[$, expressed here in tonnes) is calculated as:

$$B_r = \frac{\phi_\tau}{K_\tau} \cdot \Delta\tau \qquad (1)$$

where Φ_τ is the mean biomass flow passing through the trophic class $[\tau, \tau + \Delta\tau[$, obtained from Equation (2) below and expressed in t year^{-1}. The flow kinetics K_τ is the mean speed of the biomass flow through that class [obtained from Equation (4)], which quantifies the velocity of biomass transfers through the foodweb (in TL year^{-1}, the number of TLs crossed per year).

Losses in the biomass flow occur at each TL undergoing fishing mortality, natural mortality other than predation, and losses from metabolism (e.g. excretion and egestion, loss of energy by respiration). Thus, the biomass flow Φ_τ decreases according to TLs and can be calculated as:

$$\phi_{\tau+\Delta\tau} = \phi_\tau \cdot \exp\left[-(\mu_\tau + \phi_\tau) \cdot \Delta\tau\right] \qquad (2)$$

where μ_τ is the natural loss rate (encompassing non-predation natural mortality and metabolic losses) and φ_τ the fishing loss rate. The value of the φ_τ parameter in the current state (i.e. the last one observed, used to build the model; see below) is computed as the catch over production ratio at TL $\tau[\varphi_{\text{cur},\tau} = (Y/P)_{\text{cur},\tau}]$, and μ_τ as:

$$\mu_\tau = ln\left(\frac{P_\tau}{P_\tau + \Delta_\tau}\right)/\Delta_\tau - \varphi_\tau \qquad (3)$$

Simulations are made under the hypothesis that natural loss rates are constant and that only fishing loss rates change.

The biomass flow Equation (2) implies that the biomass flow occurring at one TL (and therefore the related biomass) depends on the flow at lower TLs. In other words, it implicitly introduces a bottom−up control of prey on predators in the model. This equation also defines the net transfer efficiency (TE) between TLs as $\exp(-\mu_\tau)$.

The speed of the biomass flow K_τ depends on the turnover of the biomass. Gascuel *et al.* (2008) showed that 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 is changing 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 flow kinetics at a TL τ (K_τ) to the biomass of predators at TL $\tau + 1$:

$$K_\tau = \left(K_{\text{ref},\tau} - F_{\text{ref},\tau}\right) \cdot \left[1 + \alpha_\tau \cdot \frac{B_{\text{pred}}{}^\gamma - B_{\text{ref,pred}}{}^\gamma}{B_{\text{ref,pred}}{}^\gamma}\right] + F_\tau \quad (4)$$

where $K_{\text{cur},\tau}$ is the speed of the flow at TL τ in the current state (which is characterized by a fishing mortality $F_{\text{cur},\tau}$); K_τ is the speed of the flow in any state of the ecosystem (characterized by F_τ); B_{pred} is the predator biomass of species from TL $\tau + 1$ (i.e. biomass conventionally between TL $\tau + 0.8$ and $\tau + 1.3$); α is a co-efficient chosen by the user between 0 and 1 which determines the part of natural mortality at TL τ that is dependent on predator abundance; γ is a shape parameter varying between 0 and 1 defining the functional relationship between prey and predators. A value of $\gamma = 1$ 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. 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 targeted species, can be the cause of notable accelerations in the ecosystem's flow kinetics. This equation also introduces a top–down control in the model, whose intensity is defined by the α parameter. Because it reduces the biomass of predators responsible for top–down control, fishing can slow down prey flows, increasing their life expectancy.

In the last version of EcoTroph (Gascuel *et al.*, 2011), two distinct compartments may be considered within the ecosystem: one where biomass is accessible to fisheries and one where it is not. The same Equations (1)–(4) are used either for the whole ecosystem or for the accessible part only. Parameters differ from one compartment to the other (and are noted B_τ^*, Φ_τ^*, K_τ^* or F_τ^* for the accessible part), 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 TLs where the rate of turnover (and thus the flow kinetics K_τ) is for instance much higher for large zooplankton than for pelagic finfish.

Finally, the catch equation used for simulations is deduced from Equation (2) applied to the accessible biomass flow (Gascuel *et al.*, 2011):

$$\begin{aligned} Y_\tau &= \varphi_\tau^* \cdot \Phi_\tau^* \cdot \Delta_\tau = \varphi_\tau^* \cdot P_\tau^* \\ Y_\tau &= F_\tau^* \cdot B_\tau^*, \quad \text{with :} \\ \varphi_\tau^* &= K_\tau^* \cdot F_\tau^* \end{aligned} \quad (5)$$

where Y_τ is the annual catch from the $[\tau, \tau + \Delta\tau[$ trophic class.

Building an EcoTroph model

To run, EcoTroph needs as inputs estimates of the current biomass, catch, production, and mean TL for all species or groups present within the studied ecosystem. If these data are all available from direct scientific observations, EcoTroph can be used as a stand-alone model. Otherwise, missing data can be obtained from other models such as an Ecopath model. In both cases, the first step in setting up an EcoTroph model is to derive trophic spectra representing the current distribution of the ecosystem biomass (and production and catch) across TLs. Thus, the biomass of each functional group is distributed on a range of TLs according to a density probability log-normal function

centred on the group mean TL and whose standard deviation measures within-group variability in TLs. The trophic spectrum is the single curve corresponding to the sum of biomass (or production or catch) for all groups (for more details about trophic spectra, see Gascuel *et al.*, 2009a; Gasche *et al.*, 2012).

The current kinetic trophic spectrum is deduced from biomass and production trophic spectra [$K_{\text{cur},\tau} = (P/B)_{\text{cur},\tau}$] either for the all groups or for accessible groups only. In this process, the accessibility to fisheries has to be defined for each trophic group, allowing for the calculation of the current accessible biomass and production trophic spectra ($B_{\text{cur},\tau}^*$ and $P_{\text{cur},\tau}^*$). This accessibility parameter theoretically corresponds to the proportion of the group's biomass that would be caught under the hypothesis of infinite fishing effort (Gascuel and Pauly, 2009). It takes into account the proportion of target and non-target species within the group, and the ratio between the fished area and the whole distribution area of the species.

Running simulations to assess fisheries interactions

Simulations in EcoTroph are based on changes applied to the fishing mortality trophic spectrum. The previous version of EcoTroph allowed for simulations where a unique fishing mortality multiplier was applied to all TLs, resulting in a general increase or decrease in the values of the fishing mortality across all TLs. Here, we develop a new version of the EcoTroph model where fishing mortality can be changed fleet by fleet, or trophic group by trophic group, therefore allowing for simulations of changes in the ecosystem fishing pattern. Simulations performed fleet by fleet are quite similar to those previously performed with EcoTroph, except that total fishing mortality now is the combination of fishing mortalities coming from a set of different fisheries. Changes in the fishing mortality trophic spectrum allow for simulations of changes in selectivity or targeting such that there is an increase or decrease in mortality applied to some groups.

For each simulation, the fishing mortality applied to each trophic class is derived from the current situation as:

$$F_\tau^* = \sum_g mE_g \cdot F_{cur,g,\tau}^* = \sum_g mE_g \cdot \frac{Y_{cur,g,\tau}}{B_{cur,\tau}^*}, \quad (6)$$

in the case of fleet by fleet simulations

$$F_\tau^* = \sum_i mE_i \cdot F_{cur,i,\tau}^* = \sum_i mE_i \cdot \frac{Y_{cur,i,\tau}}{B_{cur,\tau}^*}, \quad (6')$$

in the case of group by group simulations

Where: mE_g and mE_i are multipliers of the accessible fishing mortality applied, respectively, to fleet g or to trophic group i; $F_{cur,g,\tau}^*$ and $F_{cur,i,\tau}^*$ are the current partial accessible fishing mortalities related to the fleet g or to the trophic group i; $Y_{cur,g,\tau}$ and $Y_{cur,i,\tau}$ are the current catch of the fleet g and trophic group i, respectively, at trophic class τ; and $B_{cur,\tau}^*$ is the current accessible biomass of the trophic class τ.

Finally, the new version of EcoTroph also provides the ability to run simulations by fleet and by group at the same time, Equations (6) and (6′), thus becoming:

$$F_\tau^* = \sum_g \sum_i mE_{g,i} \, F_{cur,g,i,\tau}^* = \sum_g \sum_i mE_{g,i} \cdot \frac{Y_{cur,g,i,\tau}}{B_{cur,\tau}^*} \quad (7)$$

Values of fishing mortality multipliers between 0 and 1 correspond to decreases in the fishing mortality, and values above 1 to increases in the fishing mortality.

These simulated fishing mortalities are used in EcoTroph's usual equations to calculate biomass flow kinetics, biomass, production, and catch. Modifying the initial $F_{\mathrm{cur},\tau}$ (and $F^*_{\mathrm{cur},\tau}$) changes the current flow kinetics $K_{\mathrm{cur},\tau}$ (and $K^*_{\mathrm{cur},\tau}$) into the simulated K_τ and K^*_τ calculated in the top–down control equation of EcoTroph [Equation (4)]. Biomass flow Φ_τ and Φ^*_τ are calculated from the biomass flow Equation (2), and biomass B_τ and B^*_τ are back-calculated from Equation (1), modifying the whole image of the ecosystem. Finally total catches are deduced from the accessible biomass by means of Equation (5), while partial catch of fleet g is calculated from the simulated partial mortality due to this fleet. As biomass (B_τ or B^*_τ) and kinetics (K_τ or K^*_τ) are interdependent, the system of equations needs to be solved iteratively, starting each simulation with the current values of $K_{\mathrm{cur},\tau}$ and $K^*_{\mathrm{cur},\tau}$ as initial values. Then B_τ and B^*_τ can be estimated from Equations (1) and (2), and K_τ and K^*_τ from Equation (4). These last two steps are repeated until K and B estimates stabilize (i.e. when computed values do not vary by more than 10^{-6} between two consecutive iterations). Note that the model does not allow users to identify which species or groups represent which amount of a given trophic class, as all trophic groups are pooled together. Thus, it is not possible to calculate biomass or catch per species or trophic group (but only per trophic class), except if a trophic class is linked to only one trophic group.

Study sites and previous ecosystem models

In order to test the method, changes in the fishing pattern were simulated within two African ecosystems, where previous Ecopath and EcoTroph models have been developed (Shannon et al., 2003; Gascuel et al., 2009b, 2011; Gasche et al., 2012). Each application illustrates a new feature of the new version of the EcoTroph model. In the Guinean case study, where there has been a strong increase in fishing pressure over the past 25 years, we analysed interactions between artisanal and industrial fisheries, both targeting a wide range of species. The Guinean model refers to the continental shelf of the Guinean Exclusive Economic Zone (EEZ) between the coast and the 200 m isobath (Figure 1). This shelf is one of the largest of the Central-East Atlantic, with distance between the coast and the 200 m isobath $\sim$ 104 nautical miles (193 km) in the north. It is characterized by a high productivity and large inflows of continental nutrients. The total area of the studied zone is an estimated 42 969 km². The initial Ecopath model (Gascuel et al., 2009b) refers to year 2004 and includes 35 functional groups, of which 24 were fish groups defined based on their ecology (especially their diet) and available fisheries data. This classification is especially aimed at discriminating fished species, as each commercial category regularly representing > 1% of the catch of the small-scale fishery or of the industrial fishery is identified as a separate functional group. Data on catch and from scientific surveys were provided by the Guinean institute CNSHB (Centre National des Sciences Halieutiques de Boussoura). The required model-parameter estimates (mainly P/B, Q/B, and diet) were obtained from an earlier balanced Ecopath model (Guénette and Diallo, 2004), using complementary ad hoc procedures detailed in Gascuel et al. (2009b).

In the Southern Benguela ecosystem, we equated the set of fisheries to a mixed fishery and simulated increases in the fishing mortality of some specific groups of trophic classes, corresponding on the one hand to small pelagics, and on the other hand to two groups of hake.
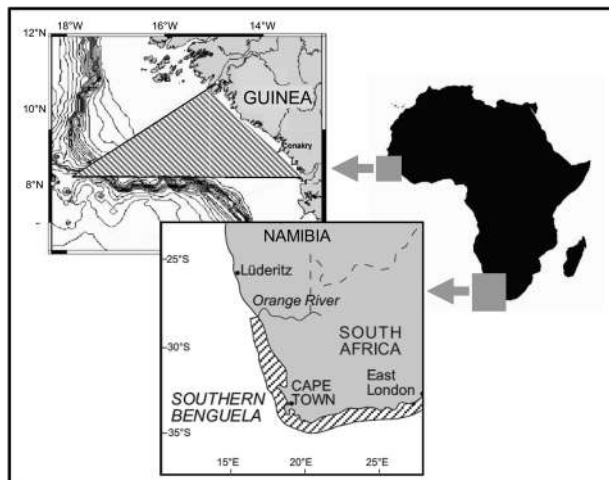
The Southern Benguela ecosystem is one of the world's four most important eastern boundary upwelling systems (Hutchings et al., 2009) and extends from the Orange River (the northwestern boundary between Namibia and South-Africa) to East London on the Indian Ocean, with a total modelled area of 220 000 km² (Figure 1). The Ecopath model from Shannon et al. (2003) has been set up for the 1990–1997 time period and has 32 groups so as to include all the major components of the ecosystem, and especially small pelagics. Indeed, because of their richness in nutrients such upwelling ecosystems have a very high primary production that can support a high fish biomass (Shannon et al., 2008), and in particular a high small pelagic fish biomass that impacts biomasses both of plankton and of predators (Cury et al., 2000). In the Southern Benguela, the dominating small pelagic species are anchovy (Engraulis encrasicolus), sardine (Sardinops sagax), and redeye round herring (Etrumeus whiteheadi), whereas Cape hake (Merluccius capensis) and Deep-water Cape hake (M. paradoxus) are commercially important predators. Extraction rates strongly increased since the beginning of the 20th century to peak at > 1.3 million t year^{-1} in the 1960s and have subsequently declined by > 50% (Griffiths et al., 2004). Since the 1970s, South Africa has managed its marine resources cautiously, allowing overall catches to remain relatively stable (Griffiths et al., 2004).

Applying EcoTroph to the Guinean and Southern Benguela ecosystems

EcoTroph-specific parameters, accessibilities, and top–down (α) or biomass input (β) controls, were obtained from the previously published versions of the model (Gascuel et al., 2011; Gasche et al., 2012) and set accordingly to ecosystem characteristics (Table 1). For instance, upwelling ecosystems such as the Southern Benguela are known to be characterized by very high phytoplankton biomass. Therefore, biomass recycling was deemed not to have much importance in this ecosystem and the related β parameter was set to a low value of 0.1. Conversely, the Guinean shelf ecosystem is characterized by large intertidal areas (mangroves) inducing higher importance of biomass recycling in the food chain, and the β parameter was set equal to 0.2. All of these EcoTroph parameters are based on expert knowledge and remain highly uncertain. Thus, sensitivity analyses of the new model have been performed, but results do not differ from those obtained from the elasticity analyses presented in Gasche et al. (2012), and will therefore not be discussed in this paper.

For the Guinea ecosystem, where the matter of competition between national and foreign fleets is a key question for fishery management, we focused on the study of the interactions between the small-scale fishery and the industrial fishery (mainly due to foreign fleets), and their joint impacts on the ecosystem. This leads to the building of isopleth graphs for biomass, catch, or mean TLs that show how they evolve for fishing mortality multipliers ranging from 0 to 3 for the small-scale fishery on the one hand, and the industrial fishery on the other hand. As the Guinea ecosystem is already strongly exploited, these fishing mortality multipliers were deemed sufficient to encompass the range of possible effects of changes in the fishing mortality. On such isopleth graphs, the current situation corresponds to the fishing mortality multiplier 1 for each fishery.

For the Southern Benguela ecosystem, two scenarios are built, corresponding to scenarios already simulated with the Ecosim and OSMOSE models of Southern Benguela (Travers *et al.*, 2010). We use these scenarios to test EcoTroph's ability to simulate changes in a fishery's fishing pattern, alternatively increasing fishing mortality on different trophic groups. 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 hake (large Cape hake and large Deep-water Cape hake). These scenarios were used in Travers *et al.* (2010) to compare outputs from the Osmose and the Ecosim models. We add outputs from EcoTroph to this comparison, so as to determine whether results

Figure 1. Location of the two case studies (striped areas): the Guinean shelf ecosystem (from Gascuel *et al.,* 2009b) and the Southern Benguela ecosystem (from Shannon *et al.,* 2008), corresponding to the modelled areas.

Table 1. Parameter values used in the two models.

	Guinean ecosystem	Southern Benguela ecosystem
		Continued

from this simple model can to some extent supplement or replace results from more complex models.

Results
Fishery interactions in the Guinean ecosystem
Ecosystem fishing patterns
Small-scale and industrial fisheries do not exhibit the same current fishing pattern and thus are not exploiting the Guinean ecosystem in the same way (Figure 2). The small-scale fishery is using a large

variety of gears (seines, lines, traps, etc.) and is mainly targeting an abundant and very coastal pelagic fish, the bonga shad (*Ethmalosa fimbriata*), as well as higher TL demersal groups, such as croakers (*Pseudotolithus* spp.), threadfins (*Polydactylus* spp.)**,** and seabreams (for the detailed specific composition of these trophic groups, see Gascuel *et al.*, 2009b). The importance of the bonga shad for the small-scale fishery is clearly noticeable in Figure 2a, with a peak in catches around TL 2.5. The industrial trawl fishery does not fish the bonga shad but is targeting intermediate TLs, especially small pelagics such as horse mackerels (*Trachurus* spp.**)** and sardinella (*Sardinella aurita*), and the same demersal and high TL species as the small-scale fishery.

Fishing loss rates (equal to the catch over production ratio; Figure 2c) indicate that the small-scale fishery has a lower impact on the bonga shad than could be expected from catches (Figure 2a) and from fishing mortalities (equal to the catch over biomass ratio; Figure 2b). Indeed, even if $\sim 60\%$ of the biomass of bonga shad is caught each year by the small-scale fishery, it amounts to 35% of the annual production at TL 2.5 (and 44% of the total production of bonga shad). The industrial fishery's impact on small pelagics appears to be very low, due to the very large biomass of these stocks and their high productivity. In contrast, for higher TL species, the catch over production ratio is high and always higher than the catch over biomass ratio, indicative of long-lived species with low production rates. Looking at the total fishing loss rate, we can note that higher TL species (with a TL between 4 and 4.5) experience the highest fishing pressure: $\sim 40\%$ of the yearly production of each of these TLs is fished; with almost the same values of fishing loss rates for the two individual fisheries. The cumulative effects of both fisheries across a wide range of TLs indicate very strong impacts of fishing on some species belonging to these TL classes. Indeed, some emblematic species of this area on which the small-scale fishery depends a lot have very high fishing loss rates. For example, the fishing loss rate for the bobo croaker (*Pseudotolithus pseudotolithus*) is 0.62 and that of sea catfish (*Arius* spp.) is 0.69, which leaves little room for an economically viable increase in their catches.

Catch simulations
The "current" (2004) total annual catch is equal to 2.8 t km^{-2} (Figure 3a), with 1.2 t km^{-2} for the industrial fishery and 1.6 t km^{-2} for the small-scale fishery. Total catch increases strongly when the fishing effort increases, but the higher the fishing mortality, the harder it is to increase the catch for both fisheries. We know from theoretical EcoTroph simulations that catches will reach a maximum for a certain total fishing mortality and decrease afterwards, because of ecosystem overexploitation (Gascuel and Pauly, 2009; Gascuel *et al.*, 2011). Isopleths tend to horizontality when increasing the fishing mortality for both fisheries. This means that the higher the fishing mortality, the lower the impact of the small-scale fishery on the total catch and the greater the impact of the industrial fishery. The industrial fishery, in its "current" state and structure, also has a greater influence on total catch when increasing fishing efforts than the small-scale fishery. For instance, the total catch reaches 3.5 t km^{-2} if the industrial fishing effort is doubled and only 3.2 t km^{-2} when doubling relates to the small-scale fishery (the other fleet remaining constant).

Catches per fishery highlight fleet interactions (Figure 3c and e). Indeed catch isopleths for the small-scale fishery are not perfectly vertical (especially for high F multipliers for the small-scale fishery), underlining an impact of the industrial fishery.
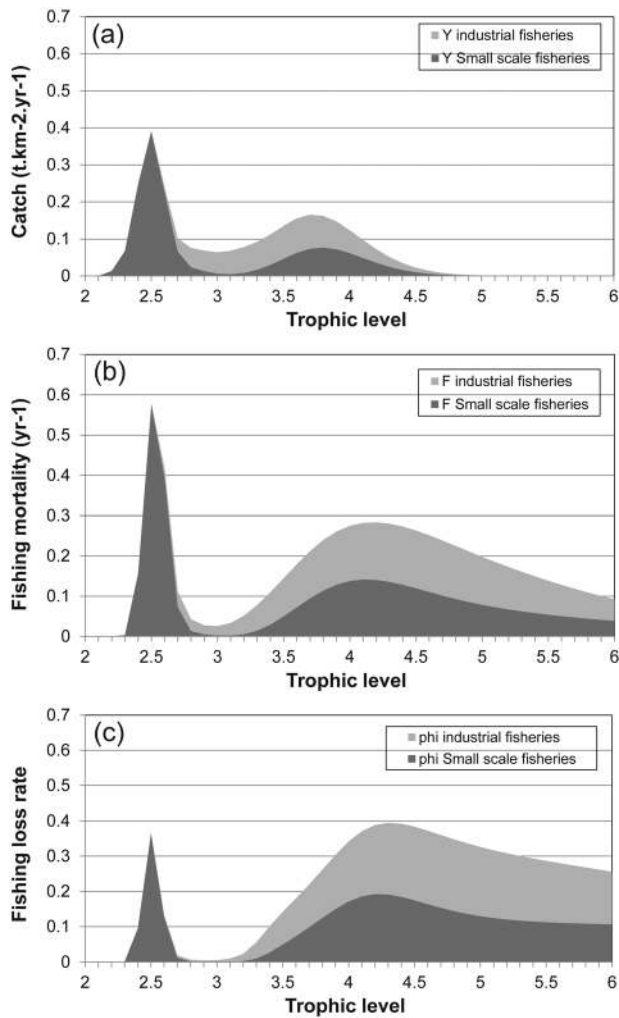
Figure 2. Current fishing pattern in the Guinean ecosystem.
(a) Fishing mortality; (b) fishing loss rate.

Nevertheless, in the current state, this impact of the industrial fishery on the small-scale fishery remains rather low. In the absence of the industrial fishery, the artisanal catch would be increased by ∼ 13%. Such an increase would alternatively be achieved with a 25% increase in fishing mortality of the small-scale fishery. Competition increases with the fishing pressure, and the higher the fishing mortality for the small-scale fishery, the higher the impact of the industrial fishery on the catch of the small-scale fishery.

The industrial fishery is more impacted by the small-scale fishery than the small-scale fishery is impacted by the industrial fishery (Figure 3e). Indeed, in the absence of the small-scale fishery, the industrial catch would be 40% higher, which would also be achieved by a 65% increase in the current fishing mortality of the industrial fishery. This impact of one fishery on the other comes from the fact that both are in competition for some species in the ecosystem: they partly target the same high TL species. The lower sensitivity of the small-scale fishery can be explained by its large catches of fish of TL 2.5, with the core species, the bonga shad, not being targeted at all by the industrial fishery. In contrast, a larger part of the industrial fishery catches is also targeted by the small-scale fishery, especially high TL groups.

Gascuel *et al.* (2009b) estimated that fishing intensity increased by 3% per year since 1997 for both the industrial and the small-scale fishery. Our EcoTroph model represents year 2004, thus a 3% yearly increase would correspond to a 30.5% increase in fishing effort in 2013 compared with 2004. This increase in the fishing effort would lead to a 13% increase in the catch of the artisanal fishery and to a 15% increase for the industrial fishery. This increase especially concerns catch of low TL groups for both fisheries, with no increase in catch for TLs > 4.

The current mean TL of the total catch in this ecosystem is equal to 3.21 (Figure 3b), with a higher TL for the industrial fishery (3.52; Figure 3f) than for the small-scale fishery (3.0; Figure 3d). Thus, when the fishing mortality of the small-scale fishery is increased, the proportion of its catch in the total catch increases and therefore the mean TL of the total catch decreases (Figure 3b). When only industrial F is increased, the model predicts a decrease in mean TL of the catch for both fisheries (Figure 3d and f), while it remains almost constant for the whole catch because the proportion of industrial landings is increased. A 30.5% increase in the fishing effort, corresponding to a hypothetical steady-state 2013 situation, would only moderately impact the TL of the catch, with a <0.1 decrease in the TL of the catch for both fisheries.

It is worth noting that the TL of the catch of the small-scale fishery is mostly impacted by the industrial fishery, especially when the fishing mortality of the small-scale fishery is high (isopleths tend to get more horizontal when fishing mortality increases for the small-scale fishery increases). This comes from competition between the two fisheries for species of TL >3.5. An increase in the catch of these species for the industrial fishery will reduce the biomass of these species available to the small-scale fishery, and therefore their share in its catches, resulting in a decrease in TL of the catch of the small-scale fishery. Starting from the current situation, this competition implies that the mean TL of the small-scale fishery's catch may vary from 2.85 to 3.10, depending on the industrial fishery. When industrial fishing mortality is high, the catch of the small-scale fishery is dominated by bonga shad. In contrast, if it is low, then the small-scale fishery catches more demersal predators and the TL of its catch is ∼ 3.1. In other words, the impact of the industrial fishery on the small-scale fishery is quantitatively low (in terms of catch) but qualitatively high (in terms of TL and therefore in terms of catch composition).

These two fisheries, with their different histories and exploitation patterns, do not react to an increased fishing mortality in the same way. For the industrial fishery, increasing the fishing mortality for either or both fisheries will result in fishing down the foodweb, i.e. a decrease in the trophic level of the catch. This decrease in TL is the result of both high fishing mortalities applied to high TL species and rather low mortalities applied to very productive small pelagic species. In contrast, increasing the fishing effort for the small-scale fishery results in a small increase in the TL of its catch, While an increased competition with the industrial fishery causes a decrease in the TL of the catch of the small-scale fishery. This is because the bonga shad (whose TL is 2.5) will be overexploited more quickly than higher TL groups around 3.7 in the case where the small-scale fishery is the only one to increase its fishing effort.

Most of these results can be explained by the spatial extension and gears used by these two fisheries. The small-scale fishery is mainly using nets, small purse-seines, lines, and traps. Pirogues are able to target demersal finfish and especially high valuable
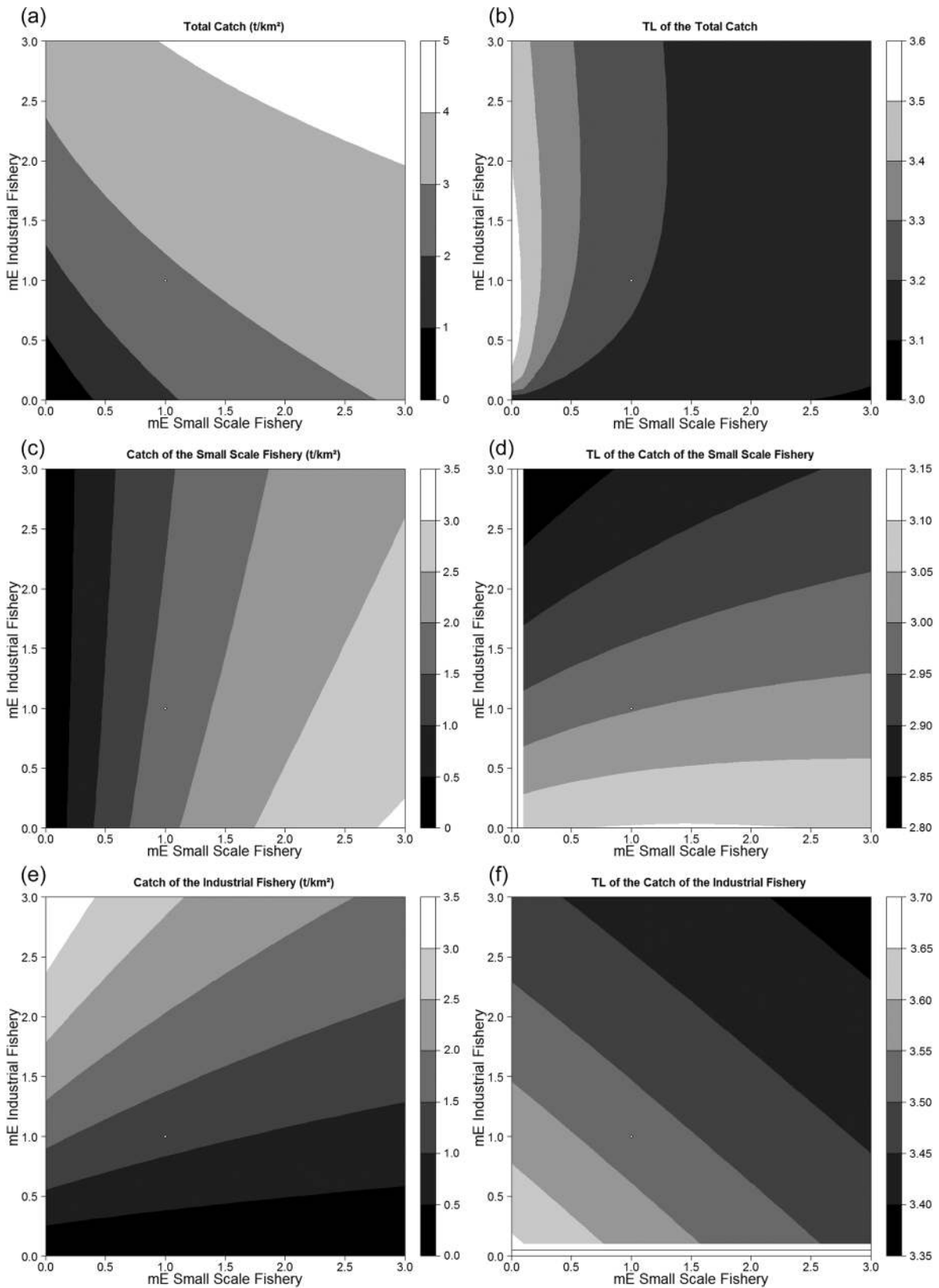
Figure 3. Simulations of catches and trophic levels in the Guinean ecosystem: (a) total catch (in t year^{-1} km^{-2}), (c) catch of the small-scale fishery, (e) catch of the industrial fishery. Trophic level of the total catch and of the catch of each of the two simulated fisheries (b, d, and f). Each parameter is simulated for fishing effort multipliers ranking from 0 to 3, for the small-scale fishery (x-axis) and the industrial fishery (y-axis).

species such as croakers, threadfins, or sea catfish. They also target the estuarine and very coastal bonga shad, which are living mainly on grounds whose depth is < 5 m and thus accessible only to small boats. Conversely, the industrial fishery is targeting species such as sardinella and horse mackerel using large pelagic trawls, but also shrimps or cephalopods (*Octopus vulgaris*) using bottom trawls. The two fisheries are competing for the demersal finfish located on the whole continental shelf. The small-scale fishery developed in Guinea in the 1980s, and motors grew more powerful during the 1990s (Gascuel *et al.*, 2009b), increasing the area available for exploitation for these boats. This caused an increase in fishing mortality on all stocks, but especially on those that were shared with the industrial fishery. Therefore, shared stocks of high TL species quickly underwent high fishing loss rates, and the small-scale fishery had little room for development in this situation as most of its target stocks were fished at high levels. In contrast, the industrial fishery had (and still has in our model) access to more stocks of little exploited pelagic and demersal invertebrates, and therefore had a higher potential for an increase in its catch.

Impact on the ecosystem

Total animal biomass (TL $\geq$2) is currently ~146.4 t km^{-2}, while it is estimated at ~149.8 t km^{-2} without any fishing. Thus it is little affected by fishing, as it mostly consists of unexploited low TL species such as zooplankton or benthos. In the same way, mean TL of the ecosystem biomass is 2.3 and is little affected by changes in fishing mortality. The small-scale fishery has a bit more impact on total biomass than the industrial fishery (Figure 4a) due to higher catch and to the high exploitation rates of its main targets, including the bonga shad, croakers, and sea catfish (~85% of its catch). In contrast, the industrial fishery is targeting a wide range of pelagics, as well as cephalopods and shrimps. These species are characterized by low exploitation rates.

Current biomass accessible to fisheries is equal to 11.3 t km^{-2} and was estimated to be equal to 18.7 t km^{-2} in the unexploited state (multipliers equal to zero for both fisheries, Figure 4c). In other words, biomass accessible to fishing has been reduced by more than one-third in this ecosystem since the onset of fishing. Increasing the fishing effort for both fisheries to hypothetical 2013 levels (+30.5%), accessible biomass would be reduced to 10.2 t km^{-2}, a 10% additional decrease. The small-scale fishery impacts accessible biomass more than the industrial fishery and is responsible for ~75% of the decrease predicted by the model between the unexploited state and the 2004 situation. However, at the same time, this small-scale fishery has much less impact on the trophic level of the accessible biomass than the industrial fishery (Figure 4d). Indeed, increasing the fishing effort for the industrial fishery amounts to removing most high TL groups while leaving most small pelagics in the ecosystem. As small pelagics have lower TLs and because they remain plentiful in the environment, they drag down the TL of the accessible biomass. In contrast, the small-scale fishery already strongly fishes the low TL bonga shad in addition to some higher TL species. We can infer that removing these various groups from the ecosystem, without depleting any given TL, has balanced impacts on the trophic diversity of the part of the ecosystem that is accessible to exploitation. This causes a much lower decrease in the mean TL of accessible biomass. This also explains why the lowest simulated TLs for the accessible biomass are reached for high industrial fishery effort and low small fishery effort: in this case, the industrial fishery

removes the high TL species while low TL species (in particular bonga shad) are not fished and stay in the ecosystem.

This ecosystem does not appear to be globally overexploited, but the fraction that is accessible to fisheries has undoubtfully been strongly modified by fishing, in terms of biomass as well as TL. High TL pelagic and demersal species are particularly impacted by fishing as most of them undergo the cumulative effects of both fisheries. Indeed, the model indicates that the biomass of TLs >4 is divided by two compared with the unexploited state. This reduction agrees with results from surveys undergone since the early 1980s (Gascuel *et al.*, 2007).

One of the methods to decrease the impact of the industrial fishery on high TLs would be to increase fishing mortality selectively on little fished small pelagic groups and to decrease mortality applied to some predatory species. However, as suggested by Cury *et al.* (2000) and Bakun (2006), these species can apply a wasp-waist control on other populations within the ecosystem and be the source of major shifts, and should therefore be managed carefully. This question is tackled in more detail in the next subsection.

Species interactions in the Benguela ecosystem
Fishing pattern and catch simulation

Previously we simulated competition between two fisheries each characterized by a fixed fishing pattern (only global changes in the fishing effort). Here we equate the ecosystem's complex set of fisheries to a single mixed fishery and then look at changes in the fishing pattern of that simulated fishery based on two simple scenarios: (i) a doubling in the fishing mortality of three small pelagic species (anchovy, sardine, and redeye at TLs 3.54, 2.99, and 3.64, respectively) and (ii) a doubling in the fishing mortality of the two groups of hake (TL = 4.50 for Deep-water Cape hake and TL = 4.64 for Cape hake) of the ecosystem. These scenarios aim at better understanding of key ecosystem dynamics and do not correspond to realistic management options given the current state of the ecosystem. Indeed, the Southern Benguela ecosystem is still recovering from past overexploitation, with Cape hake spawning biomass being at ~ 50% of its pre-exploitation level but Deep-water Cape hake still being at < 10% of its pre-exploitation level (Rademeyer *et al.*, 2008).

Trophic spectra corresponding to these scenarios can be compared with the base spectrum (Figure 5). In terms of fishing mortality, it appears that the effects of a doubling in fishing effort applied to a given group do not propagate much more than 0.5 TL away from the mean TL of this group in our model. Indeed, our fishing mortality multipliers do not modify the spectrum below TL 2.5 or above TL4 in the small pelagics scenario, and almost no changes can be observed below TL 4 in the hake scenario. This may be highly dependent on choices made when defining smoothing functions for each trophic group.

In terms of catches, two patterns appear when looking at the two different scenarios (Figure 5b). Doubling the fishing mortality on small pelagic species has little direct effect, the catch of these groups increasing by one-third at best. This increase in fishing mortality of small pelagics causes some decrease (up to 25%) in the catch of their predators, around TL 4.5. This is due to the bottom–up control of high TL biomass by lower TL biomass. This may have notable consequences as it suggests that the South African purse-seine fishery (targeting small pelagics; Rademeyer *et al.*, 2008) can have direct impacts on the catch of demersal trawlers. Therefore, the hypothetical choice to favour the
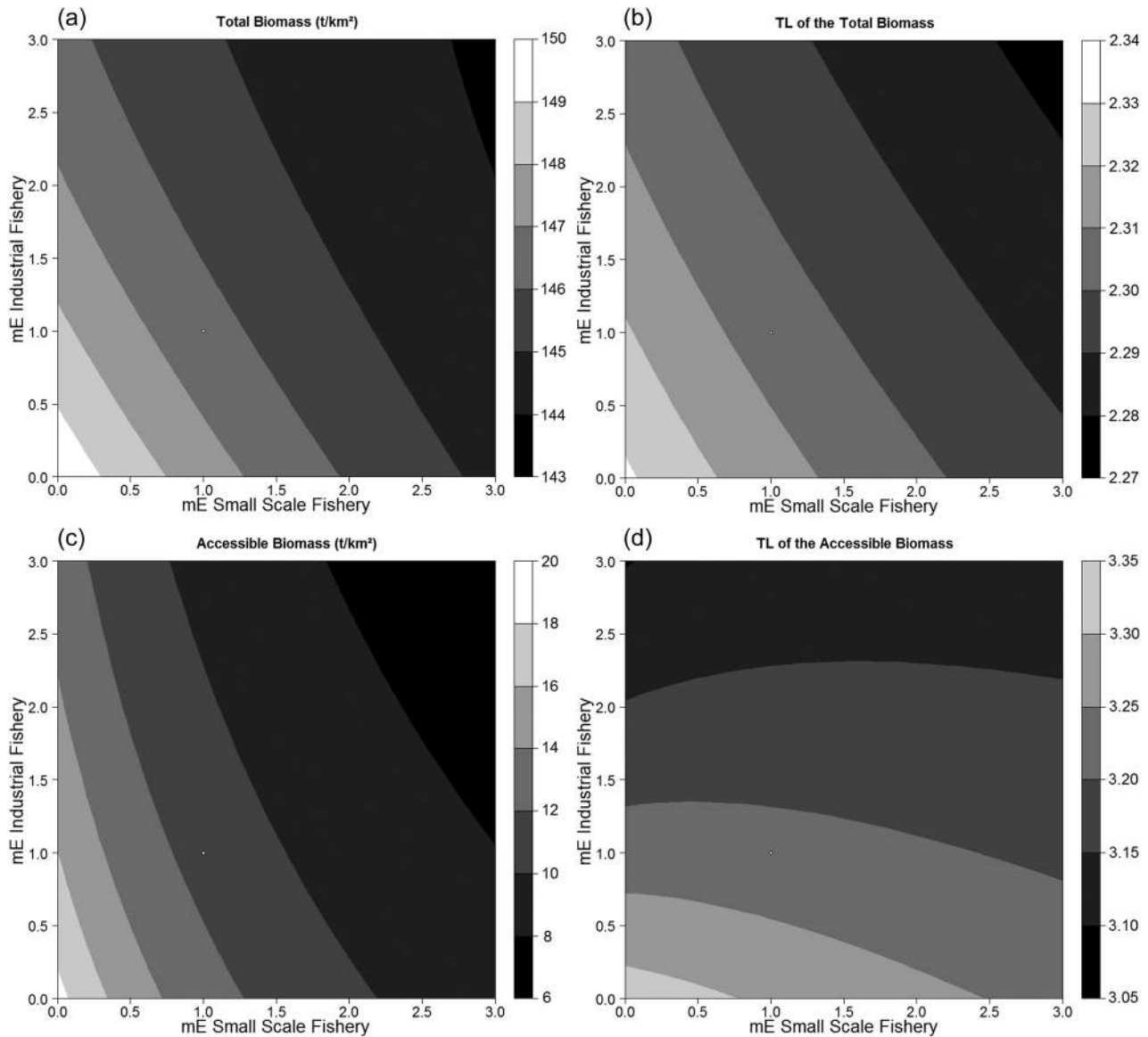
Figure 4. Simulations of the fishing impact on the Guinea ecosystem biomass (a, c) and on the mean trophic level of biomass (b, d). The accessible biomass is defined as the biomass of all species currently fished that is accessible to fishing.

pelagic fishery to the detriment of the demersal fishery would be a highly political one, with potentially deep social consequences. Indeed, the trawl fishery was identified as the most secure employment of all South African sectors, whereas employment in the pelagic fishery is less stable and more risky due to fluctuations in total allowable catches and greater fixed operating costs (de Young *et al.*, 2012). Notwithstanding its stability, the deep-sea hake industry is also the fishery with the largest wage bill on the west and southwest coasts (de Young *et al.*, 2012).

Doubling the fishing effort on hake increases their catch by 50% at best, which still is a higher increase than that observed for the small pelagics scenario. In this scenario, the increase in hake catches is predicted to result in a slight increase in catch at TL 3.5 (+ 2%), because of a release in predation linked to top–down effects, but not at lower trophic levels (e.g. TL 3.0). Thus, our simple simulations tend to indicate that increasing the fishing effort on hake could have positive consequences for the

local fishing industry with much less detrimental side effects than an increase in the catch of small pelagics.

Impact on the accessible biomass

Increasing fishing mortality on small pelagics reduces accessible biomass at all TLs (Figure 5c). This result agrees with those of Walters *et al.* (2005) and Shannon *et al.* (2009) who showed by means of Ecosim models that a decrease in small pelagic fish abundance is likely to have marked effects on both higher and lower TLs of the foodweb. On the other hand, increasing fishing mortality on hake only causes a slight decrease in biomass around TL 4.5 and even causes a very slight increase in accessible biomass at TL 3.5 because of top–down effects. Thus, the effects of an increased fishing mortality vs. the current level seem to be much more important when this increase targets small pelagics: accessible biomass is reduced by ∼ 30% between TL 2.8 and TL 4.8, with smaller reductions for other TLs. As a comparison, model

simulation of a collapse in small pelagic fish in Shannon *et al.* (2009) suggests severe declines in large pelagic fish (48% reduction in biomass), cetaceans (27%), seals (17%), and birds (33%), whose mean TL is within a 4.4–4.7 range in our model. Evidence of strong competition between the purse-seine fishery and birds for small pelagics can also be found in Okes *et al.* (2009). When hake are targeted, accessible biomass is reduced only between TLs 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 TL 4.5 almost as much as a doubling in the fishing effort multiplier on adult hake. 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 catches may have great impacts on the whole food chain. We also illustrate the vulnerability of predatory species to fishing: in an ecosystem with developing fisheries, they would have to bear the double burden of an increased direct fishing effort and of a reduced availibility of their prey. With both of these factors possibly having a high impact, this may lead to quick collapses in population abundances.

Comparison with other models of the Southern Benguela ecosystem

Results obtained with EcoTroph for the Southern Benguela case study are compared with those obtained with Osmose and Ecosim (Travers *et al.*, 2010). When simulating a doubling in the fishing effort applied to small pelagics (Figure 6a), biomass in trophic class 3 decreases by 4% in EcoTroph as the three small pelagic groups belong to this class. This relatively small decrease can be explained by the fact that this trophic class is also made up of other non-targeted small pelagic species with high biomasses (in particular mesopelagic fish) that act as a buffer against strong variations of total biomass. EcoTroph results exhibit a strong bottom–up effect, with decreases in biomass for classes 4 and 5 almost as strong as that observed for targeted class 3. Results for trophic class 5 for all three models have to be treated with great care as it only consists of one trophic group (and some smoothed biomasses from class 4 in EcoTroph). Simulated biomass obtained with EcoTroph for trophic class 2 is higher than the initial biomass because of the decrease in biomass of potential predators from trophic class 3 that causes a slackening in top–down control from this class.

Ecosim and Osmose predict an increase in biomass at trophic class 3, probably because some groups in this trophic class benefit from the decreased competition from anchovy, sardine, and redeye. The issue when comparing these three models is that in EcoTroph, sardine belongs to class 3 while class 2 only comprises benthos and zooplankton, whereas in the other two models sardine belongs to trophic class 2 with benthos and zooplankton. As this difference could be one of the causes of the differences observed between models, we pooled trophic classes 2 and 3 and plotted the obtained biomass ratio (Figure 6b). Therefore, biomass ratios for trophic class 2–3 take into account both the direct effects of fishing and the indirect effects of top–down control. These combined effects have no noticeable impact on biomass when using the Ecosim model and a limited negative impact in both Osmose and EcoTroph.

When simulating a doubling in the fishing effort applied to hake, all three models predict a decrease in biomass for trophic class 4, ranging from ∼ 5% in Ecotroph to 11% in Osmose (Figure 6c). EcoTroph predicts a strong top–down effect that
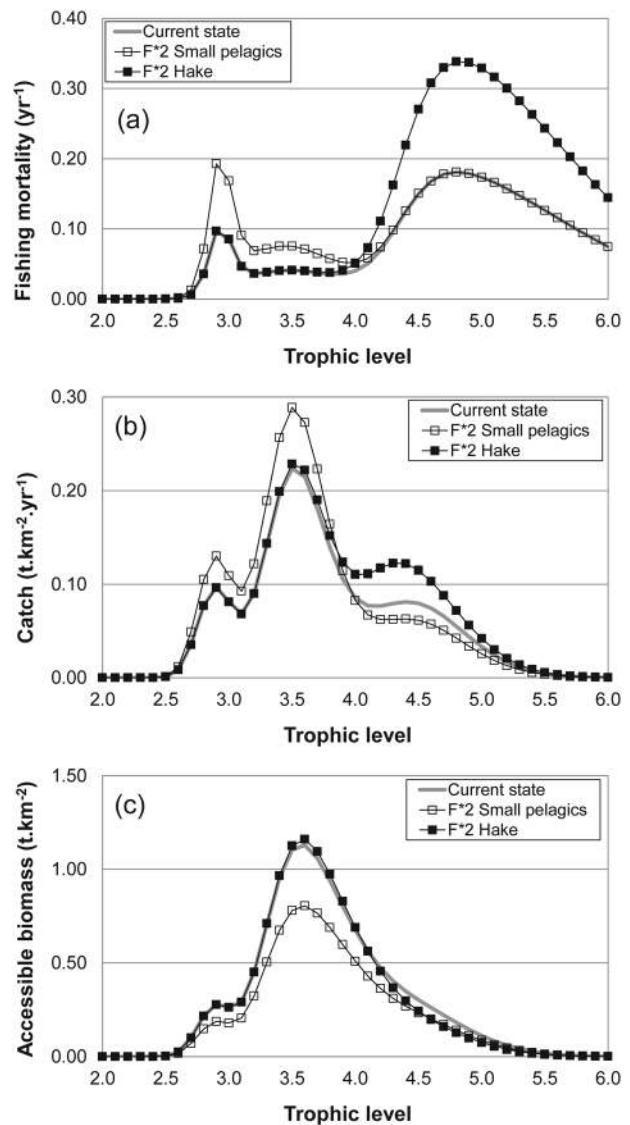
Figure 5. Simulation of a fishing pattern change in the Benguela ecosystem. Fishing mortality trophic spectra for the initial state, the small pelagics scenario, and the hake scenario (a). Catch trophic spectra for the initial state, the small pelagics scenario, and the hake scenario (b). Accessible biomass trophic spectra for the initial state, the small pelagics scenario, and the hake scenario (c).

impacts classes 3 (positively) and 2 (negatively). The other two models also predict a top–down effect, but with slightly different impacts on biomass. In Osmose, the positive impact on biomass observed for both class 2 and class 3 could be explained by the ability of trophic class 4 fish to feed on both these classes in this model (opportunistic predation).

Discussion

In this paper we showed that the EcoTroph model can provide useful answers to some commonly asked questions in fishery management. In the Guinean case study, we tackled the question of the level of impact of industrial fisheries on artisanal or small-scale fisheries. We found that the impact of the industrial fishery on the small-scale fishery is moderate in terms of biomass caught

but significant in terms of decrease in the TL of the catch, due to a competition for demersal high TLs. In contrast, the small-scale fishery has a stronger impact in terms of biomass but a very limited impact on the ecosystem's mean TL because of the exploitation of a wider range of TLs. These particular impacts of each fishery are mainly linked to the gears they use, but also to their ability to exploit the very coastal and estuarine resources including the abundant bonga shad. The small-scale fishery heavily targets a few species, all of them except the bonga shad being high TLs, while the industrial fishery moderately fishes a greater number of species spanning a wide range of TLs (between 2.7 and 4.7). Our simulations showed that the most impacted groups in this ecosystem are those undergoing the combined effects of both fisheries and highlight the need for discussions between stakeholders and managers if these stocks are to be preserved in the long run. Results concerning Guinea further suggested that exploiting a wider range of TLs induces a higher impact on the whole ecosystem biomass (and on its accessible part as well) but a lower decrease in mean TL of the ecosystem and thus in trophic biodiversity. From a theoretical point of view, this should ensure a higher stability in the whole foodweb, as predators are known to have a regulatory role. From a practical point of view, it should be noted that the exploitation of forage fish (i.e. low TL) species usually does not replace the exploitation of their predators but adds to it. In that case, due to the bottom–up controls underlined above, the reduction in biomass of high TLs is increased and the impact on the ecosystem is even greater, as shown in the Benguela case study.

When studying the Southern Benguela ecosystem, we tried to determine whether some parts of the fishery could be developed, and with which impacts on the fish stocks. Our results indicated that increasing the fishing effort on small pelagic species in the Southern Benguela would be to the detriment of high TL species and of fisheries targeting them, with noticeable decreases in accessible biomass and catch. A general result from our models was that low TL species are key species in the sense that they greatly influence their ecosystem through predator–prey relationships. These results seem consistent with those of previous studies by Cury *et al.* (2000) and Shannon *et al.* (2009), and raise one of the most important problems of the exploitation of low TL species: it may provide high catches but impacts the whole food chain, reducing the biomass of predators even if they are not directly targeted. Therefore, choices are to be made between fisheries with high but often irregular catches of low value small pelagics and demersal fisheries with higher value fish, more stable yields, but lower production and catch. As predators are not only commercial fish species but also birds and cetaceans with their own environmental and indirect commercial value, it becomes apparent that a balance has to be found between all these ecosystem components. The first step towards this balance may be to leave enough food in the ecosystem to avoid reaching thresholds where lack of energy might hamper reproduction and growth of key species, possibly by means of explicit protection of forage fish species as suggested by Walters *et al.* (2005) and Cury *et al.* (2011).

As stated previously, EcoTroph is a simple model based on a limited number of equations and hypotheses that tries to provide a minimum realistic representation of an ecosystem as well as a quick and easy way to simulate changes in the fishing mortality applied to this ecosystem. The new development of the EcoTroph model presented herein is part of this approach and allows for the simulation of an almost infinite number of scenarios
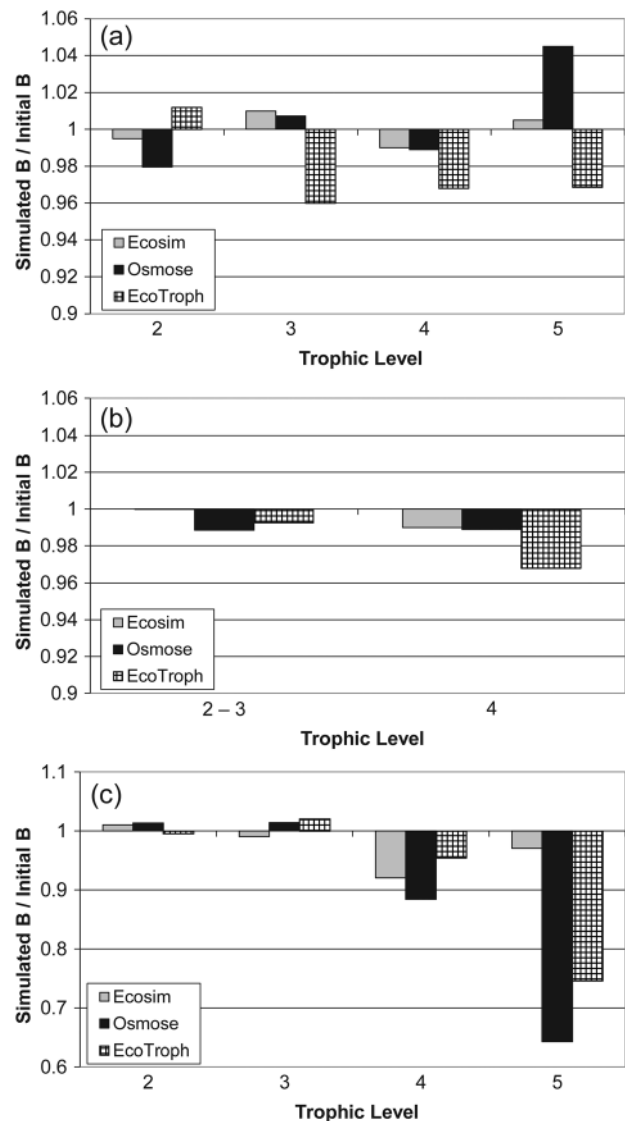
Figure 6. Comparison of results obtained with EcoTroph with results obtained with Ecosim and Osmose (from Travers *et al.,* 2010) for the Southern Benguela ecosystem. The small pelagics scenario corresponds to graphs a and b, and the hake scenario to graph c. Trophic class 2 corresponds to trophic levels from 2 to 2.9, class 3 to TLs from 3 to 3.9, etc.

without greatly increasing model complexity or introducing new equations in the model. The model is available as an R package on http://sirs.agrocampus-ouest.fr/EcoTroph/ (Colleter *et al.,* 2013), or as an EwE plug-in on http://www.ecopath.org/plugins.

EcoTroph provides a new simple and very synthetic view on ecosystem functioning. Analysing the ecosystem effects of fleet interactions based on more complex ecosystem models such as EwE, Osmose, ISIS-Fish, or Atlantis is usually a difficult task. Here, we proposed simple graphical representations such as catch, biomass. or TL isopleths as tools to analyse fishery interactions. Potential EcoTroph users have to keep in mind that EcoTroph results are rather straightforward and based on interactions between the direct impacts of fishing on an ecosystem and the indirect reactions caused by top–down and bottom–up control. This could easily be seen in our comparison of

EcoTroph results with those of Osmose and Ecosim: EcoTroph easily obtained the big picture, with results that were coherent with those of other models, but was unable to capture smaller variations that could be explained by spatial interactions, species competition, or changes in the species composition of a given TL. Nonetheless, EcoTroph was set up to study ecosystem trends and to help users to think differently, in a more synthetic way, about the ecosystem aspect of fisheries. We hope it will be useful to modellers as a simple and easy to use tool to aggregate information about ecosystems and study major ecosystem trends through various simulated scenarios.

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