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

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Abstract:

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

27

28 **Introduction**

29 Models are increasingly used to improve our understanding of marine ecosystem functioning
30 and address applied questions in the field of fisheries management (Walters and Martell
31 2004). In particular, the recognition that the impact of fishing extends well beyond the
32 targeted species lets fisheries scientists develop new ecosystem models, as key tools for the
33 implementation of ecosystem-based fisheries management.

34 One of these models is EcoTroph (ET) (Gascuel 2005, Gascuel and Pauly 2009), a
35 minimum-realistic ecosystem model which provides a simplified overview of ecosystem
36 functioning and facilitates simulations of changes in fishing mortality. EcoTroph uses trophic
37 spectra to represent marine ecosystems, leaving aside the notion of species and modelling
38 marine ecosystems' functioning as flows of biomass from low to high trophic levels (TLs). In
39 the past few years EcoTroph's applications have shifted from theoretical contexts based on
40 virtual ecosystems (Gascuel and Pauly 2009, Gascuel et al. 2011) to specific real case
41 studies to assess the current fishing impacts at the ecosystem scale (Gasche et al. 2012,
42 Lassalle et al. 2012, Tremblay-Boyer et al. 2011) or to analyze the effects of MPAs on the
43 whole food web (Colleter et al. 2012, Valls et al. 2012).

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

52 Here, using the Guinean and the Southern Benguela ecosystems as case studies, we
53 demonstrate that this simple model can be used to simulate complex changes in the
54 dynamics of fisheries. Simulations by fleet segments are presented through an application to
55 the Guinean ecosystem where the interactions between artisanal and industrial fisheries are
56 a key aspect of fisheries management. Then the EcoTroph model is applied to the Southern
57 Benguela upwelling ecosystem to simulate two hypothetical fishing scenarios. This case
58 study especially highlights the strong influence of the exploitation of small pelagic species on
59 the whole food web as well as on other fisheries. Both these applications to real ecosystems
60 give us valuable insights into the key mechanisms driving ecosystem reactions to fishing that
61 could be of much use in an ecosystem approach to fisheries management.

62

63 **Material and methods**

64 **General principles and major equations of the EcoTroph model**

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

71 EcoTroph models marine ecosystem functioning as flows of biomass from low to high trophic
72 levels. Biomass enters the ecosystem at trophic level 1, generated by the photosynthetic
73 activity of primary producers and recycling by bacteria that form a part of the microbial loop.
74 A β coefficient chosen by the user between 0 and 1 determines the intensity of the biomass
75 input control. A value of 0 means that all the production at trophic level 1 comes from primary
76 producers, while a value of 1 indicates that all production comes from recycling (and thus
77 depends on the total ecosystem biomass). There is usually no biomass between trophic
78 levels 1 and 2, herbivores and detritivores being at trophic level 2. Then, at TLs>2, the

79 biomass is distributed along a continuum of values of TL, the diet variability of the various
80 consumers resulting in all fractional TLs being filled. Conventionally, EcoTroph's
81 representation of the ecosystem stops at trophic level 6 which is deemed high enough to
82 cover all top predators.

83 Despite its apparent simplicity and representation of the ecosystem as flows of biomass,
84 EcoTroph falls into the "whole ecosystem models" category as defined in Plagányi et al.
85 (2007). Indeed, EcoTroph attempts to take into account all trophic levels in the ecosystem
86 and is commonly based on Ecopath (Christensen & Walters, 2004) outputs possibly
87 representing tens of trophic groups. Nonetheless the notion of species quickly disappears
88 from EcoTroph as trophic spectra are built summarizing all the information available at the
89 species (or trophic group) level with one curve per output variable. EcoTroph only models
90 top-down and bottom-up effects of fishing along the food chain, with no spatial, temporal or
91 environmental variations, mostly using common stock assessment equations. Therefore this
92 model could also correspond to the "extensions of single-species assessment models"
93 (ESAM) category. It is our opinion that the EcoTroph approach is one of the simplest
94 available when trying to model the effects of fishing at the ecosystem level. Thus we chose in
95 this paper to refer to EcoTroph as a minimum-realistic ecosystem model, even if these terms
96 are partly antagonistic.

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

$$B_{\tau} = \frac{\Phi_{\tau}}{K_{\tau}} \cdot \Delta \tau$$

105 (1)

106 where Φ_{τ} is the mean biomass flow passing through the trophic class $[\tau, \tau + \Delta \tau]$ (obtained from
 107 eq. (2) below and expressed in tons/year). The flow kinetics K_{τ} is the mean speed of the
 108 biomass flow through that class (obtained from eq. (4)), which quantifies the velocity of
 109 biomass transfers through the food web (in TL/year, the number of trophic levels crossed per
 110 year).

111 Losses in the biomass flow occur at each trophic level undergoing fishing mortality, natural
 112 mortality other than predation, and losses from metabolism (e.g. excretion and egestion, loss
 113 of energy by respiration). Thus, the biomass flow Φ_{τ} decreases according to trophic levels
 114 and can be calculated as:

$$\Phi_{\tau + \Delta \tau} = \Phi_{\tau} \cdot \exp[-(\mu_{\tau} + \varphi_{\tau}) \cdot \Delta \tau]$$

115 (2)

116 where μ_{τ} is the natural loss rate (encompassing non-predation natural mortality and
 117 metabolic losses) and φ_{τ} the fishing loss rate. The value of the φ_{τ} parameter in the current
 118 state (i.e. the last one observed, used to build the model; see below) is computed as the
 119 catch over production ratio at trophic level τ ($\varphi_{cur, \tau} = (Y/P)_{cur, \tau}$), and μ_{τ} as:

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

120 (3)

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

123 The biomass flow equation (2) implies that the biomass flow occurring at one trophic level
 124 (and therefore the related biomass) depends on the flow at lower trophic levels. In other
 125 words, it implicitly introduces a bottom-up control of prey on predators in the model. This
 126 equation also defines the net transfer efficiency (TE) between trophic levels as $\exp(-\mu_{\tau})$.

127 The speed of the biomass flow K_{τ} depends on the turnover of the biomass. Gascuel et al.
 128 (2008) showed that it can be estimated from an Ecopath model as $K_{\tau} = (P/B)_{\tau}$. This is

129 consistent with Allen's relationship ($P/B = M+F$ at equilibrium) and with the fact that the
 130 inverse parameter $1/K_\tau$ is the mean life expectancy of an organism within the trophic class $[\tau,$
 131 $\tau+\Delta\tau]$. Thus, when the mortality changes the speed of the flow is changing too. Predation
 132 mortality being an important source of mortality, it is taken into account in the model by
 133 means of a relationship, called the top-down equation, linking the flow kinetics at a trophic
 134 level τ (K_τ) to the biomass of predators at trophic level $\tau+1$:

$$K_\tau = [K_{cur,\tau} - F_{cur,\tau}] \cdot \left[1 + \alpha_\tau \cdot \frac{B_{pred}^\gamma - B_{pred,cur}^\gamma}{B_{pred,cur}^\gamma} \right] + F_\tau$$

135 (4)

136 where $K_{cur,\tau}$ is the speed of the flow at trophic level τ in the current state (which is
 137 characterized by a fishing mortality $F_{cur,\tau}$); K_τ is the speed of the flow in any state of the
 138 ecosystem (characterized by F_τ); B_{pred} is the predator biomass of species from trophic level
 139 $\tau+1$ (i.e. biomass conventionally between TL $\tau+0.8$ and $\tau+1.3$); α is a coefficient chosen by
 140 the user between 0 and 1 which determines the part of natural mortality at trophic level τ that
 141 is dependent on predator abundance; γ is a shape parameter varying between 0 and 1
 142 defining the functional relationship between prey and predators. A value of $\gamma=1$ results in a
 143 linear effect of the abundance of predators on the flow kinetics, while a smaller value would
 144 reflect nonlinear effects due to predators' competition. This equation allows the model to take
 145 into account indirect effects of fishing on the ecosystem when performing simulations.
 146 Fishing, reducing the life expectancy of targeted species, can be the cause of notable
 147 accelerations in the ecosystem's flow kinetics. This equation also introduces a top-down
 148 control in the model, whose intensity is defined by the α parameter. Because it reduces the
 149 biomass of predators responsible for top-down control, fishing can slow down prey flows,
 150 increasing their life expectancy.

151 In the last version of EcoTroph (Gascuel et al., 2011) two distinct compartments may be
 152 considered within the ecosystem: one where biomass is accessible to fisheries and one
 153 where it is not. The same equations (1) to (4) are used either for the whole ecosystem, or for
 154 the accessible part only. Parameters differ from one compartment to the other (and are noted

155 B_{τ}^* , Φ_{τ}^* , K_{τ}^* , or F_{τ}^* for the accessible part), taking into account the fact that exploited species
 156 usually do not have the same characteristics as the unexploited ones. This is especially the
 157 case at low or intermediate trophic levels where the rate of turnover (and thus the flow
 158 kinetics K_{τ}) is for instance much higher for large zooplankton than for pelagic finfish.

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

161 (5)
$$Y_{\tau} = \varphi_{\tau}^* \cdot \Phi_{\tau}^* \cdot \Delta\tau = \varphi_{\tau}^* \cdot P_{\tau}^*$$

162 or :
$$Y_{\tau} = F_{\tau}^* \cdot B_{\tau}^*, \quad \text{with: } \varphi_{\tau}^* = K_{\tau}^* \cdot F_{\tau}^*$$

163 where Y_{τ} is the annual catch from the $[\tau, \tau+\Delta\tau[$ trophic class.

164 **Building an EcoTroph model**

165 To run, EcoTroph needs as inputs estimates of the current biomass, catch, production and
 166 mean trophic level for all species or groups present within the studied ecosystem. If these
 167 data are all available from direct scientific observations EcoTroph can be used as a
 168 standalone model. Otherwise, missing data can be obtained from other models such as an
 169 Ecopath model. In both cases, the first step in setting up an EcoTroph model is to derive
 170 trophic spectra representing the current distribution of the ecosystem biomass (and
 171 production and catch) across trophic levels. Thus, biomass of each functional group is
 172 distributed on a range of trophic levels according to a density probability log-normal function
 173 centered on the group mean trophic level and whose standard deviation measures within-
 174 group variability in trophic levels. The trophic spectrum is the single curve corresponding to
 175 the sum of biomass (or production or catch) for all groups (see Gasche et al. 2012 and
 176 Gascuel et al. 2009a for more details about trophic spectra).

177 The current kinetic trophic spectrum is deduced from biomass and production trophic spectra
 178 ($K_{cur,\tau} = (P/B)_{cur,\tau}$) either for the all groups or for accessible groups only. In this process, the
 179 accessibility to fisheries has to be defined for each trophic group, allowing for the calculation
 180 of the current accessible biomass and production trophic spectra ($B_{cur,\tau}^*$ and $P_{cur,\tau}^*$). This
 181 accessibility parameter theoretically corresponds to the proportion of the group's biomass

182 that would be caught under the hypothesis of infinite fishing effort (Gascuel and Pauly 2009).
 183 It takes into account the proportion of target and non-target species within the group, and the
 184 ratio between the fished area and the whole distribution area of the species.

185

186 **Running simulations to assess fisheries interactions**

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

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

200 (6)
$$F_{\tau}^* = \sum_g mE_g \cdot F_{cur,g,\tau}^* = \sum_g mE_g \cdot \frac{Y_{cur,g,\tau}}{B_{cur,\tau}^*},$$
 in case of fleet by fleet simulations

201 (6')
$$F_{\tau}^* = \sum_i mE_i \cdot F_{cur,i,\tau}^* = \sum_i mE_i \cdot \frac{Y_{cur,i,\tau}}{B_{cur,\tau}^*},$$
 in case of group by group simulations

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

207 Finally, the new version of EcoTroph also provides the ability to run simulations by fleet and
 208 by group at the same time, eq. (6) and eq. (6') thus becoming:

$$209 \quad (7) \quad F_{\tau}^* = \sum_g \sum_i mE_{g,i} \cdot F_{cur,g,i,\tau}^* = \sum_g \sum_i mE_{g,i} \cdot \frac{Y_{cur,g,i,\tau}}{B_{cur,\tau}^*}$$

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

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

229

230 **Study sites and previous ecosystem models**

231 In order to test the method, changes in the fishing pattern were simulated within two African
 232 ecosystems, where previous Ecopath and EcoTroph models have been developed (Shannon

233 et al., 2003, Gasche et al. 2012, Gascuel et al. 2009b and 2011). Each application illustrates
234 a new feature of the new version of the EcoTroph model. In the Guinean case study, where
235 there has been a strong increase in fishing pressure over the past 25 years, we analysed
236 interactions between artisanal and industrial fisheries, both targeting a wide range of species.
237 The Guinean model refers to the continental shelf of the Guinean Exclusive Economic Zone
238 (EEZ) between the coast and the 200m isobath (Fig.1). This shelf is one of the largest of the
239 Central-East Atlantic, with distance between the coast and the 200m isobath about 104
240 nautical miles (193 kilometers) in the North. It is characterized by a high productivity and
241 large inflows of continental nutrients. The total area of the studied zone is an estimated
242 42 969 km². The initial Ecopath model (Gascuel et al. 2009b) refers to year 2004 and
243 includes 35 functional groups, of which 24 were fish groups defined based on their ecology
244 (especially their diet) and available fisheries data. This classification is especially aimed at
245 discriminating fished species, as each commercial category regularly representing more than
246 1% of the catch of the small scale fishery or of the industrial fishery is identified as a separate
247 functional group. Data on catch and from scientific surveys were provided by the Guinean
248 institute CNSHB (Centre National des Sciences Halieutiques de Boussoura). The required
249 model-parameter estimates (mainly P/B, Q/B, and diet) were obtained from an earlier
250 balanced Ecopath model (Guénette and Diallo, 2004), using complementary ad hoc
251 procedures detailed in Gascuel et al. (2009b).

252 In the Southern Benguela ecosystem, we equated the set of fisheries to a mixed fishery and
253 simulated increases in the fishing mortality of some specific groups of trophic classes,
254 corresponding on the one hand to small pelagics, and to two groups of hake on the other
255 hand.

256 The Southern Benguela ecosystem is one of the world's four most important eastern
257 boundary upwelling systems (Hutchings et al., 2009) and extends from the Orange River (the
258 north-western boundary between Namibia and South-Africa) to East London on the Indian
259 Ocean, with a total modeled area of 220 000 km² (Fig. 1). The Ecopath model from Shannon
260 et al. (2003) has been set up for the 1990-1997 time period and has 32 groups so as to

261 include all the major components of the ecosystem, and especially small pelagics. Indeed,
262 because of their richness in nutrients such upwelling ecosystems have a very high primary
263 production that can support a high fish biomass (Shannon et al., 2008), and in particular a
264 high small pelagic fish biomass that impacts both biomasses of plankton and of predators
265 (Cury et al., 2000). In the Southern Benguela, the dominating small pelagic species are
266 anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and redeye round herring
267 (*Etrumeus whiteheadi*), whereas Cape hake (*Merluccius capensis*) and Deep-water Cape
268 hake (*M. paradoxus*) are commercially important predators. Extraction rates strongly
269 increased since the beginning of the 20th century to peak at over 1.3 million t.yr⁻¹ in the 1960s
270 and have subsequently declined by more than 50% (Griffiths et al., 2004). Since the 1970s
271 South Africa has managed its marine resources cautiously, allowing overall catches to
272 remain relatively stable (Griffith et al., 2004).

273

274 **Applying EcoTroph to the Guinean and Southern Benguela ecosystems**

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

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

297 For the Southern Benguela ecosystem two scenarios are built, corresponding to scenarios
298 already simulated with the Ecosim and OSMOSE models of the Southern Benguela (Travers
299 et al., 2010). We use these scenarios to test EcoTroph's ability to simulate changes in a
300 fishery's fishing pattern, alternatively increasing fishing mortality on different trophic groups.
301 The first scenario corresponds to a doubling in the fishing mortality of small pelagic species
302 (i.e. sardine, anchovy and redeye) and the second scenario to a doubling in the fishing
303 mortality of hakes (large Cape hake and large Deep-water Cape hake). These scenarios
304 were used in Travers et al. (2010) to compare outputs from the Osmose and the Ecosim
305 models. We add outputs from EcoTroph to this comparison, so as to determine whether
306 results from this simple model can to some extent supplement or replace results from more
307 complex models.

308

309 **Results**

310 **Fisheries interactions in the Guinean ecosystem**

311 Ecosystem fishing patterns

312 Small scale and industrial fisheries do not exhibit the same current fishing pattern and thus
313 are not exploiting the Guinean ecosystem in the same way (Fig. 2). The small scale fishery is

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

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

342

343 Catch simulations

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

357 Catches per fishery highlight fleet interactions (Fig. 3c and e). Indeed catch isopleths for the
358 small scale fishery are not perfectly vertical (especially for high F multipliers for the small
359 scale fishery), underlining an impact of the industrial fishery. Nevertheless, in the current
360 state, this impact of the industrial fishery on the small scale one remains rather low. In the
361 absence of the industrial fishery the artisanal catch would be increased by about 13%. Such
362 an increase would alternatively be achieved with a 25% increase in fishing mortality of the
363 small scale fishery. Competition increases with the fishing pressure and the higher the fishing
364 mortality for the small scale fishery, the higher the impact of the industrial fishery on the
365 catch of the small scale fishery.

366 The industrial fishery is more impacted by the small scale fishery than the small scale fishery
367 is impacted by the industrial fishery (Fig. 3e). Indeed, in the absence of the small scale
368 fishery, the industrial catch would be 40% higher, which would correspond to a 65% increase
369 in the current fishing mortality of the industrial fishery. This impact of one fishery on the other

370 comes from the fact that both are in competition for some species in the ecosystem: they
371 partly target the same high trophic level species. The lower sensitivity of the small scale
372 fishery can be explained by its large catches of fish of trophic level 2.5 with the core species,
373 the bonga shad, not being targeted at all by the industrial fishery. On the contrary, a larger
374 part of the industrial fishery catches is also targeted by the small scale fishery, especially
375 high trophic level groups.

376 Gascuel et al. (2009b) estimated that fishing intensity increased by 3% per year since 1997
377 for both the industrial and the small scale fishery. Our EcoTroph model represents year
378 2004, thus a 3% yearly increase would correspond to a 30,5% increase in fishing effort in
379 2013 compared to 2004. This increase in the fishing effort would lead to a 13% increase in
380 the catch of the artisanal fishery and to a 15% increase for the industrial fishery. This
381 increase especially concerns catch of low trophic level groups for both fisheries, with almost
382 no impact of the increase on trophic levels above 4.

383 The current mean trophic level of the total catch in this ecosystem is equal to 3.21 (Fig. 3b),
384 with a higher trophic level for the industrial fishery (3.52; Fig. 3f) than for the small scale one
385 (3.0; Fig. 3d). Thus, when the fishing mortality of the small scale fishery is increased, the
386 proportion of its catch in the total catch increases and therefore the mean trophic level of the
387 total catch decreases (Fig. 3b). When only industrial F is increased, the model predicts a
388 decrease in mean trophic level of the catch for both fisheries (Fig. 3d and 3f), while it remains
389 almost constant for the whole catch because the proportion of industrial landings is
390 increased. A 30,5% increase in the fishing effort, corresponding to a hypothetical steady-
391 state 2013 situation, would only moderately impact the trophic level of the catch, with a less
392 than 0.1 decrease in the trophic level of the catch for both fisheries.

393 It is worth noting that the trophic level of the catch of the small scale fishery is mostly
394 impacted by the industrial fishery, especially when the fishing mortality of the small scale
395 fishery is high (isopleths tend to get more horizontal when fishing mortality increases for the
396 small scale fishery increases). This comes from competition between the two fisheries for
397 species of trophic level above 3.5: an increase in the catch of these species for the industrial

398 fishery will reduce the biomass of these species available to the small scale fishery, and
399 therefore their share in its catches, resulting in a decrease in trophic level of the catch of the
400 small scale fishery. Starting from the current situation, this competition implies that the mean
401 trophic level of the small scale fishery's catch may vary from 2.85 to 3.10, depending on the
402 industrial fishery. When industrial fishing mortality is high the catch of the small scale fishery
403 is dominated by bonga shad. On the contrary, if it is low, then the small scale fishery catches
404 more demersal predators and the trophic level of its catch is about 3.1. In other words, the
405 impact of the industrial fishery on the small scale one is quantitatively low (in term of catch)
406 but qualitatively high (in term of TL and therefore in term of catch composition).

407 These two fisheries, with their different histories and exploitation patterns, do not react to an
408 increased fishing mortality in the same way: for the industrial fishery, increasing the fishing
409 mortality for either or both fisheries will result in fishing down the foodweb, i.e. a decrease in
410 the trophic level of the catch. This decrease in TL is the result of both high fishing mortalities
411 applied to high trophic level species and rather low mortalities applied to very productive
412 small pelagic species. On the contrary, increasing the fishing effort for the small scale fishery
413 results in a small increase in the TL of its catch, and an increased competition with the
414 industrial fishery causes a decrease in the TL of the catch of the small scale fishery. This is
415 because the bonga shad (whose trophic level is 2.5) will be overexploited more quickly than
416 higher trophic level groups around 3.7 in case the small scale fishery is the only one to
417 increase its fishing effort. Most of these results can be explained by the spatial extension and
418 gears used by these two fisheries. The small scale fishery is mainly using nets, small purse-
419 seines, lines and traps. Pirogues are able to target demersal finfish and especially high
420 valuable species such as croakers, threadfins or sea catfish. They also target the estuarine
421 and very coastal bonga shad, which is living mainly on grounds whose depth is less than 5
422 meters and thus accessible only to small boats. Conversely, the industrial fishery is targeting
423 species such as sardinella and horse mackerel using large pelagic trawls, but also shrimps
424 or cephalopods (*Octopus vulgaris*) using bottom trawls. The two fisheries are competing for
425 the demersal finfish located on the whole continental shelf. The small scale fishery

426 developed in Guinea in the 80's and motors grew more powerful during the 90's (Gascuel et
427 al., 2009b), increasing the area available for exploitation for these boats. This caused an
428 increase in fishing mortality on all stocks but especially on those that were shared with the
429 industrial fishery. Therefore shared stocks of high trophic level species quickly underwent
430 high fishing loss rates, and the small scale fishery had little room for development in this
431 situation as most of its target stocks were fished at high levels. On the contrary, the industrial
432 fishery had (and still has in our model) access to more stocks of little exploited pelagic and
433 demersal invertebrates, and therefore had a higher potential for an increase in its catch.

434

435 Impact on the ecosystem

436 Total animal biomass ($TL \geq 2$) is currently about 146.4 t.km^{-2} , while it is estimated around
437 149.8 t.km^{-2} without any fishing. Thus it is little affected by fishing, as it mostly consists of
438 unexploited low trophic level species such as zooplankton or benthos. In the same way,
439 mean trophic level of the ecosystem biomass is 2.3 and is little affected by changes in fishing
440 mortality. The small scale fishery has a bit more impact on total biomass than the industrial
441 fishery (Fig. 4a) due to higher catch and to the high exploitation rates of its main targets,
442 including the bonga shad, croakers, sea catfish (about 85% of its catch). These high fishing
443 efforts become very high when applying multipliers and artificially lead to high catches of
444 these species, strongly impacting biomass. On the contrary the industrial fishery is targeting
445 a wide range of pelagics, as well as cephalopods and shrimps. These species are
446 characterized by low exploitation rates that lead to catches lower than those of the small
447 scale fishery, within the range of fishing effort multipliers simulated here (but with the likely
448 ability to bear much higher multipliers).

449 Current biomass accessible to fisheries is equal to 11.3 t.km^{-2} and was estimated equal to
450 18.7 t.km^{-2} in the unexploited state (multipliers equal to zero for both fisheries, Fig. 4c). In
451 other words, biomass accessible to fishing has been reduced by more than one third in this
452 ecosystem, since the onset of fishing. Increasing the fishing effort for both fisheries to
453 hypothetical 2013 levels (+30.5%), accessible biomass would be reduced to 10.2 t.km^{-2} , a

454 10% additional decrease. The small scale fishery impacts accessible biomass more than the
455 industrial fishery and is responsible for about 75% of the decrease predicted by the model
456 between the unexploited state and the 2004 situation. But at the same time this small scale
457 fishery has much less impact on the trophic level of the accessible biomass than the
458 industrial fishery (Fig. 4d). Indeed, increasing the fishing effort for the industrial fishery
459 amounts to removing most high trophic level groups while leaving most small pelagics in the
460 ecosystem. Small pelagics having lower TLs and remaining plentiful in the environment they
461 drag down the trophic level of the accessible biomass. On the contrary, the small scale
462 fishery already strongly fishes the low TL bonga shad in addition to some higher trophic level
463 species. We can infer that removing these various groups from the ecosystem, without
464 depleting any given TL, has balanced impacts on the trophic diversity of the part of the
465 ecosystem that is accessible to exploitation. This causes a much lower decrease in the mean
466 TL of accessible biomass. This also explains why the lowest simulated trophic levels for the
467 accessible biomass are reached for high industrial fishery effort and low small fishery effort:
468 in this case the industrial fishery removes the high trophic level species while low trophic
469 level species (in particular bonga shad) are not fished and stay in the ecosystem.

470 This ecosystem does not appear to be globally overexploited but the fraction that is
471 accessible to fisheries has undoubtedly been modified by fishing, in terms of biomass as well
472 as trophic level. High trophic level pelagic and demersal species are particularly impacted by
473 fishing as most of them undergo the cumulative effects of both fisheries. Indeed, the model
474 indicates that biomass of trophic levels higher than 4 is divided by two compared to the
475 unexploited state. This reduction agrees with results from surveys undergone since the early
476 80's (Gascuel et al. 2007).

477 One of the methods to decrease the impact of the industrial fishery on high trophic levels
478 would be to selectively increase fishing mortality on little fished small pelagic groups and to
479 decrease mortality applied to some predatory species. However, as suggested by Cury et al.
480 (2000) and Bakun (2006), these species can apply a wasp-waist control on other populations

481 within the ecosystem and be the source of major shifts and should therefore be managed
482 carefully. This question is tackled in more detail in the next subsection.

483

484 **Species interactions in the Benguela ecosystem**

485 Fishing pattern and catch simulation

486 Previously we simulated competition between two fisheries each characterized by a fixed
487 fishing pattern (only global changes in the fishing effort). Here we equate the ecosystem's
488 complex set of fisheries to a single mixed fishery and then look at changes in the fishing
489 pattern of that simulated fishery based on two simple scenarios: (i) a doubling in the fishing
490 mortality of three small pelagic species (anchovy, sardine and redeye at TLs 3.54, 2.99 and
491 3.64 respectively) and (ii) a doubling in the fishing mortality of the two groups of hake
492 (TL=4.50 for Deep-water Cape hake and TL=4.64 for Cape hake) of the ecosystem. These
493 scenarios aim at better understanding key ecosystem dynamics and do not correspond to
494 realistic management options given the current state of the ecosystem. Indeed, the Southern
495 Benguela ecosystem is still recovering from past overexploitation, with Cape hake spawning
496 biomass being at about 50% of its pre-exploitation level but Deep-water Cape hake still being
497 below 10% its pre-exploitation level (Rademeyer et al., 2008).

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

505 In terms of catches, two patterns appear when looking at the two different scenarios (Fig.
506 5b). Doubling the fishing mortality on small pelagic species has little direct effect, the catch of
507 these groups increasing by one third at best. This increase in fishing mortality of small

508 pelagics causes some decrease (up to 25%) in the catch of their predators, around trophic
509 level 4.5. This is due to the bottom-up control of high trophic level biomass by lower trophic
510 level biomass. This may have notable consequences as it suggests that the south-african
511 purse-seine fishery (targeting small pelagics, Rademeyer et al., 2008) can have direct
512 impacts on the catch of demersal trawlers. Therefore the hypothetical choice to favour the
513 pelagic fishery to the detriment of the demersal fishery would be a highly political one, with
514 potentially deep social consequences. Indeed, the trawl fishery was identified as the most
515 secure employment of all South African sectors whereas employment in the pelagic fishery is
516 less stable and more risky due to fluctuations in TAC and greater fixed operating costs (de
517 Young et al., 2012). Notwithstanding its stability, the deep-sea hake industry is also the
518 fishery with the largest wage bill on the West and South-west coasts (de Young et al., 2012).
519 Doubling the fishing effort on hakes increases their catch by 50% at best, which still is a
520 higher increase than that observed for the small pelagics scenario. In this scenario, the
521 increase in hake catches is predicted to result in a slight increase in catch at TL 3.5 (+ 2 %),
522 because of a release in predation linked to top-down effects, but not at lower trophic levels
523 (e.g. TL 3.0). Thus our simple simulations tend to indicate that increasing the fishing effort on
524 hake could have positive consequences for the local fishing industry with much less
525 detrimental side consequences than an increase in the catch of small pelagics.

526

527 Impact on the accessible biomass

528 Increasing fishing mortality on small pelagics reduces accessible biomass at all trophic levels
529 (Fig. 5c). This result agrees with those of Walters et al. (2005) and Shannon et al. (2009)
530 who showed by means of Ecosim models that a decrease in small pelagic fish abundance is
531 likely to have marked effects on both higher and lower trophic levels of the food web. On the
532 other hand increasing fishing mortality on hakes only causes a slight decrease in biomass
533 around trophic level 4.5 and even causes a very slight increase in accessible biomass at
534 trophic level 3.5 because of top-down effects. Thus, the effects of an increased fishing
535 mortality versus current level seem to be much more important when this increase targets

536 small pelagics: accessible biomass is reduced by about 30% between trophic level 2.8 and
537 trophic level 4.8, with smaller reductions for other trophic levels. As a comparison, model
538 simulation of a collapse in small pelagic fish in Shannon et al. (2009) suggests severe
539 declines in large pelagic fish (48% reduction in biomass), cetaceans (27%), seals (17%) and
540 birds (33%), whose mean trophic level is within a 4.4-4.7 range in our model. Evidence of
541 strong competition between the purse-seine fishery and birds for small pelagics can also be
542 found in Okes et al. (2009). When hakes are targeted, accessible biomass is reduced only
543 between trophic levels 4.2 and 5.2 and by no more than 25%. An interesting point is that
544 doubling the fishing effort on small pelagics impacts accessible biomass above trophic level
545 4.5 almost as much as a doubling in the fishing effort multiplier on adult hakes (whose mean
546 trophic levels are 4.50 and 4.64 depending on the species). These results can be seen as a
547 complement to results obtained when simulating global increases in the effort multiplier: we
548 show that even if biomasses of small pelagics are little impacted by increased fishing efforts,
549 increases in their catches may have great impacts on the whole food chain. We also illustrate
550 the vulnerability of predatory species to fishing: in an ecosystem with developing fisheries
551 they would have to bear the double burden of an increased direct fishing effort and of a
552 reduced availability of their prey. Both of these factors possibly being very impacting, this may
553 lead to quick collapses in population abundances.

554

555 Comparison with other models of the Southern Benguela ecosystem

556 Results obtained with EcoTroph for the Southern Benguela case-study are compared to
557 those obtained with Osmose and Ecosim (Travers et al., 2010). When simulating a doubling
558 in the fishing effort applied to small pelagics (Fig. 6a), biomass in trophic class 3 decreases
559 by 4% in EcoTroph as the three small pelagic groups belong to this class. This relatively
560 small decrease can be explained by the fact that this trophic class comprises of other non-
561 targeted small pelagic species with high biomasses (in particular mesopelagic fish) that act
562 as a buffer against strong variations of total biomass. EcoTroph results exhibit a strong
563 bottom-up effect with decreases in biomass for classes 4 and 5 almost as strong as that

564 observed for targeted class 3. Results for trophic class 5 for all three models have to be
565 taken with great care as it only comprises of one trophic group (and some smoothed
566 biomasses from class 4 in EcoTroph). Simulated biomass obtained with EcoTroph for trophic
567 class 2 is higher than the initial biomass because of the decrease in biomass of potential
568 predators from trophic class 3 that causes a slackening in top-down control from this class.
569 Ecosim and Osmose predict an increase in biomass at trophic class 3, probably because
570 some groups in this trophic class benefit from the decreased competition from anchovy,
571 sardine and redeye. The issue when comparing these three models is that in EcoTroph
572 sardine belongs to class 3 while class 2 only comprises benthos and zooplankton, whereas
573 in the other two models sardine belongs to trophic class 2 with benthos and zooplankton. As
574 this difference could be one of the causes of the differences observed between models, we
575 pooled trophic classes 2 and 3 and plotted the obtained biomass ratio (Fig. 6b). Therefore
576 biomass ratios for trophic class 2-3 take into account both the direct effects of fishing and the
577 indirect effects of top-down control. These combined effects have no noticeable impact on
578 biomass when using the Ecosim model and a limited negative impact in both Osmose and
579 EcoTroph.

580 When simulating a doubling in the fishing effort applied to hake all three models predict a
581 decrease in biomass for trophic class 4, ranging from about 5% in Ecotroph to 11% in
582 Osmose (Fig. 6c). EcoTroph predicts a strong top-down effect that impacts classes 3
583 (positively) and 2 (negatively). The other two models also predict a top-down effect, but with
584 slightly different impacts on biomass. In Osmose the positive impact on biomass observed
585 for both class 2 and class 3 could be explained by the ability of trophic class 4 fish to feed on
586 both these classes in this model (opportunistic predation).

587

588 **Discussion**

589 In this paper we showed that the EcoTroph model can provide useful answers to some
590 commonly asked questions in fisheries management. In the Guinean case study we tackled

591 the question of the level of impact of industrial fisheries on artisanal or small scale fisheries.
592 We found that the impact of the industrial fishery on the small scale fishery is moderate in
593 terms of biomass caught but significant in terms of decrease in the trophic level of the catch,
594 due to a competition for demersal high trophic levels. On the contrary, the small scale fishery
595 has a stronger impact in terms of biomass but a very limited impact on the ecosystem's mean
596 trophic level because of the exploitation of a wider range of trophic levels. These particular
597 impacts of each fishery are mainly linked to the gears they use, but also to their ability to
598 exploit the very coastal and estuarine resources including the very abundant bonga shad.
599 The small scale fishery heavily targets a few species, all of them except the bonga shad
600 being high trophic levels, while the industrial fishery moderately fishes a greater number of
601 species spanning a wide range of trophic levels (between 2.7 and 4.7). Our simulations
602 showed that the most impacted groups in this ecosystem are those undergoing the combined
603 effects of both fisheries and put to light the need for discussions between stakeholders and
604 managers if these stocks are to be preserved in the long run. Results concerning Guinea
605 further suggested that exploiting a wider range of trophic levels induces a higher impact on
606 the whole ecosystem biomass (and on its accessible part as well) but a lower decrease in
607 mean trophic level of the ecosystem and thus in trophic biodiversity. From a theoretical point
608 of view, this should ensure a higher stability in the whole food web, as predators are known
609 to have a regulatory role. From a practical point of view, it should be noted that the
610 exploitation of forage fish (i.e. low trophic level) species usually does not replace the
611 exploitation of their predators but adds to it. In that case, due to the bottom-up controls
612 underlined above, the reduction in biomass of high trophic levels is increased and the impact
613 on ecosystem is even greater, as shown in the Benguela case study.

614 When studying the Southern Benguela ecosystem we tried to determine whether some parts
615 of the fishery could be developed, and with which impacts on the fish stocks. Our results
616 indicated that increasing the fishing effort on small pelagic species in the Southern Benguela
617 would be to the detriment of high trophic level species and of fisheries targeting them, with
618 noticeable decreases in accessible biomass and catch. A general result from our models was

619 that low trophic level species are key species in the sense that they deeply influence their
620 ecosystem through predator-prey relationships. These results seem consistent with those of
621 previous studies by Cury et al. (2000) and Shannon et al. (2009) and raise one of the most
622 important problems of the exploitation of low trophic level species: it may provide high
623 catches but impacts the whole food chain, reducing the biomass of predators even if they are
624 not directly targeted. Therefore choices are to be made between fisheries with high but often
625 irregular catches of low value small pelagics and demersal fisheries with higher value fish,
626 more stable yields but lower production and catch. Predators not only being commercial fish
627 species but also birds and cetaceans with their own environmental and indirect commercial
628 value it becomes apparent that a balance has to be found between all these ecosystem
629 components. The first step towards this balance may be to leave enough food in the
630 ecosystem to avoid reaching thresholds where lack of energy might hamper reproduction
631 and growth of key species, possibly by means of explicit protection of forage fish species as
632 suggested by Walters et al. (2005) and Cury et al. (2011). As stated previously EcoTroph is a
633 simple model based on a limited number of equations and hypotheses that tries to provide a
634 minimum realistic representation of an ecosystem as well as a quick and easy way to
635 simulate changes in the fishing mortality applied to this ecosystem. The new development of
636 the EcoTroph model presented in this paper is part of this approach and allows for the
637 simulation of an almost infinite number of scenarios without greatly increasing model
638 complexity or introducing new equations in the model. The model is available as an R
639 package on <http://sirs.agrocampus-ouest.fr/EcoTroph/>, or as an EwE plug-in on
640 <http://www.ecopath.org/plugins>.

641 EcoTroph provides a new simple and very synthetic view on ecosystem functioning.
642 Analysing the ecosystem effects of fleet interactions based on more complex ecosystem
643 models such as EwE, Osmose, ISIS-Fish or Atlantis is usually a difficult task. Here, we
644 proposed simple graphical representations such as catch, biomass or trophic level isopleths
645 as tools to analyse fisheries interactions. Potential EcoTroph users have to keep in mind that
646 EcoTroph results are rather straightforward and based on interactions between the direct

647 impacts of fishing on an ecosystem and the indirect reactions caused by top-down and
648 bottom-up control. This could easily be seen in our comparison of EcoTroph results with
649 those of Osmose and Ecosim: EcoTroph easily got the big picture, with results that were
650 coherent with those of other models but was unable to capture smaller variations that could
651 be explained by spatial interactions, species competition or changes in the species
652 composition of a given trophic level. Nonetheless, EcoTroph was set up to study ecosystem
653 trends and to help users to think differently, in a more synthetic way, on the ecosystem
654 aspect of fisheries. We hope it will be useful to modellers as a simple and easy-to-use tool to
655 aggregate information about ecosystems and study major ecosystem trends through various
656 simulated scenarios.

657

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664

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768 **Table 1 – Parameter values used in the two models**

	Guinean ecosystem	Southern Benguela ecosystem
	Standard values	Standard values
Accessibilities (per Ecopath trophic group)	Empirically defined	Based on literature (1)
Top-down control parameter α	0.4	0.5
Biomass input control parameter β	0.2	0.1

(1) Ratio of the fished area from Fréon et al. 2005 and Drapeau et al. 2004, corrected by the proportion of fished species within the group

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771 **Figure captions**

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

775 Figure 2: Current fishing pattern in the Guinean ecosystem. (a) Fishing mortality; (b) Fishing
776 loss rate.

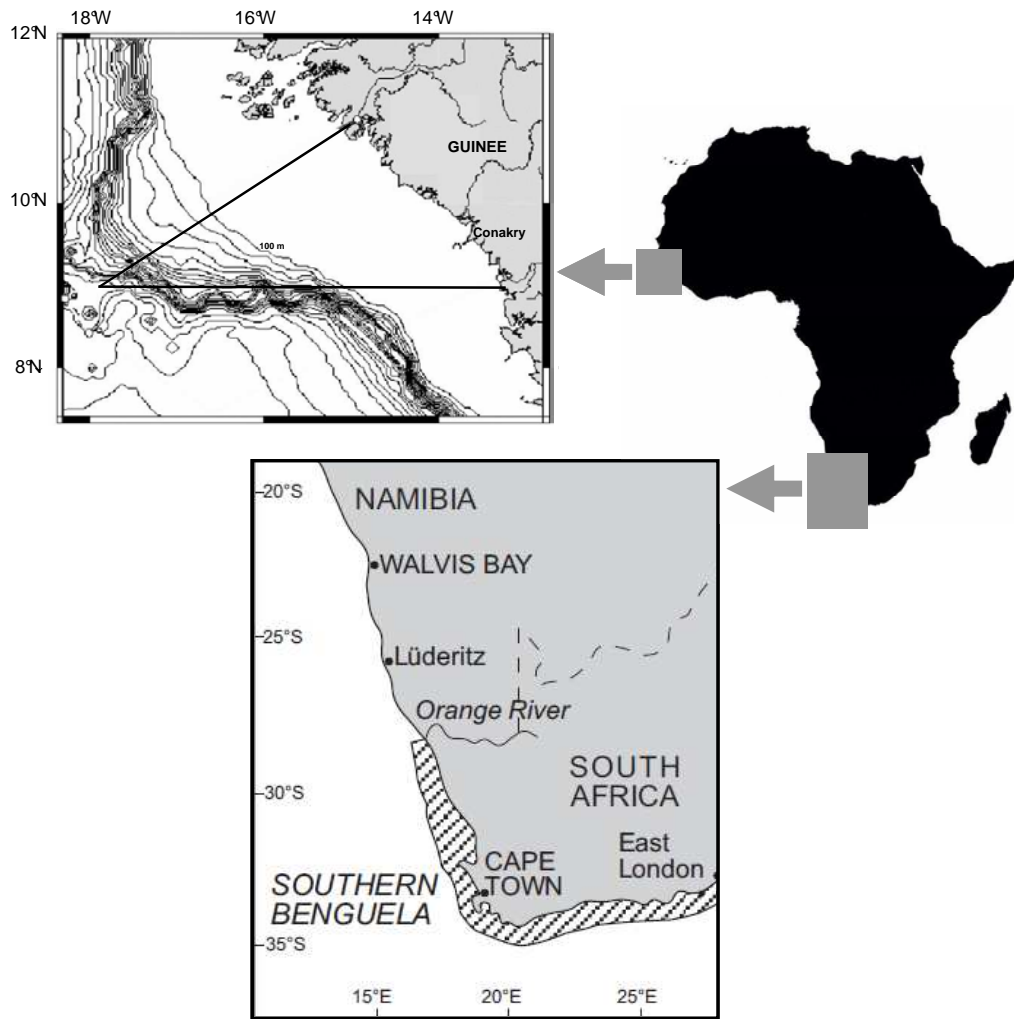
777 Figure 3: Simulations of catches and trophic levels in the Guinean ecosystem: (a) total catch
778 (in $t.y^{-1}.km^{-2}$), (c) catch of the small scale fishery, (e) catch of the industrial fishery.
779 Trophic level of the total catch and of the catch of each of the two simulated fisheries (b,
780 d and f). Each parameter is simulated for fishing effort multipliers ranking from 0 to 3, for
781 the small scale fishery (x axis) and the industrial fishery (y axis).

782 Figure 4: Simulations of the fishing impact on the Guinea ecosystem biomass (a, c) and on
783 the mean trophic level of biomass (b, d). The accessible biomass is defined as the
784 biomass of all species currently fished that is accessible to fishing.

785 Figure 5: Simulation of a fishing pattern change in the Benguela ecosystem. Fishing mortality
786 trophic spectra for the initial state, the small pelagics scenario and the hakes scenario
787 (a). Catch trophic spectra for the initial state, the small pelagics scenario and the hakes
788 scenario (b). Accessible biomass trophic spectra for the initial state, the small pelagics
789 scenario and the hakes scenario (c).

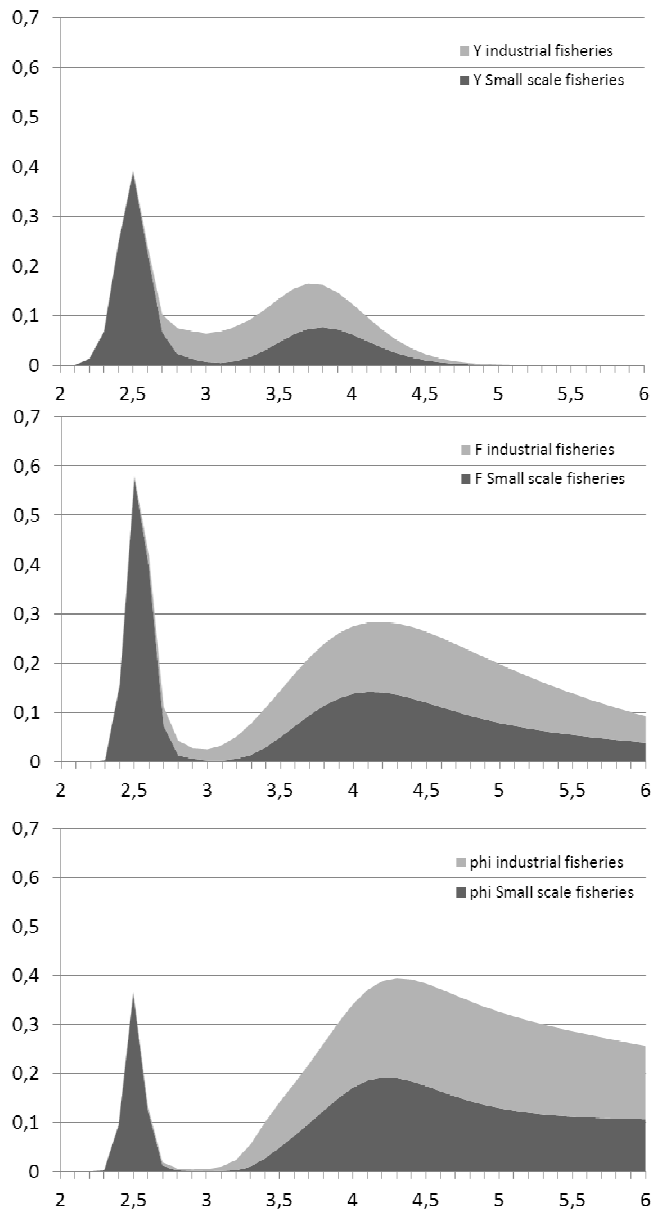
790 Figure 6: Comparison of results obtained with EcoTroph to results obtained with Ecosim and
791 Osmose (from Travers et al., 2010) for the Southern Benguela ecosystem. The small
792 pelagics scenario corresponds to graphs a and b and the hakes scenario to graph c.
793 Trophic class 2 corresponds to trophic levels from 2 to 2.9, class 3 to TLs from 3 to 3.9,
794 etc.

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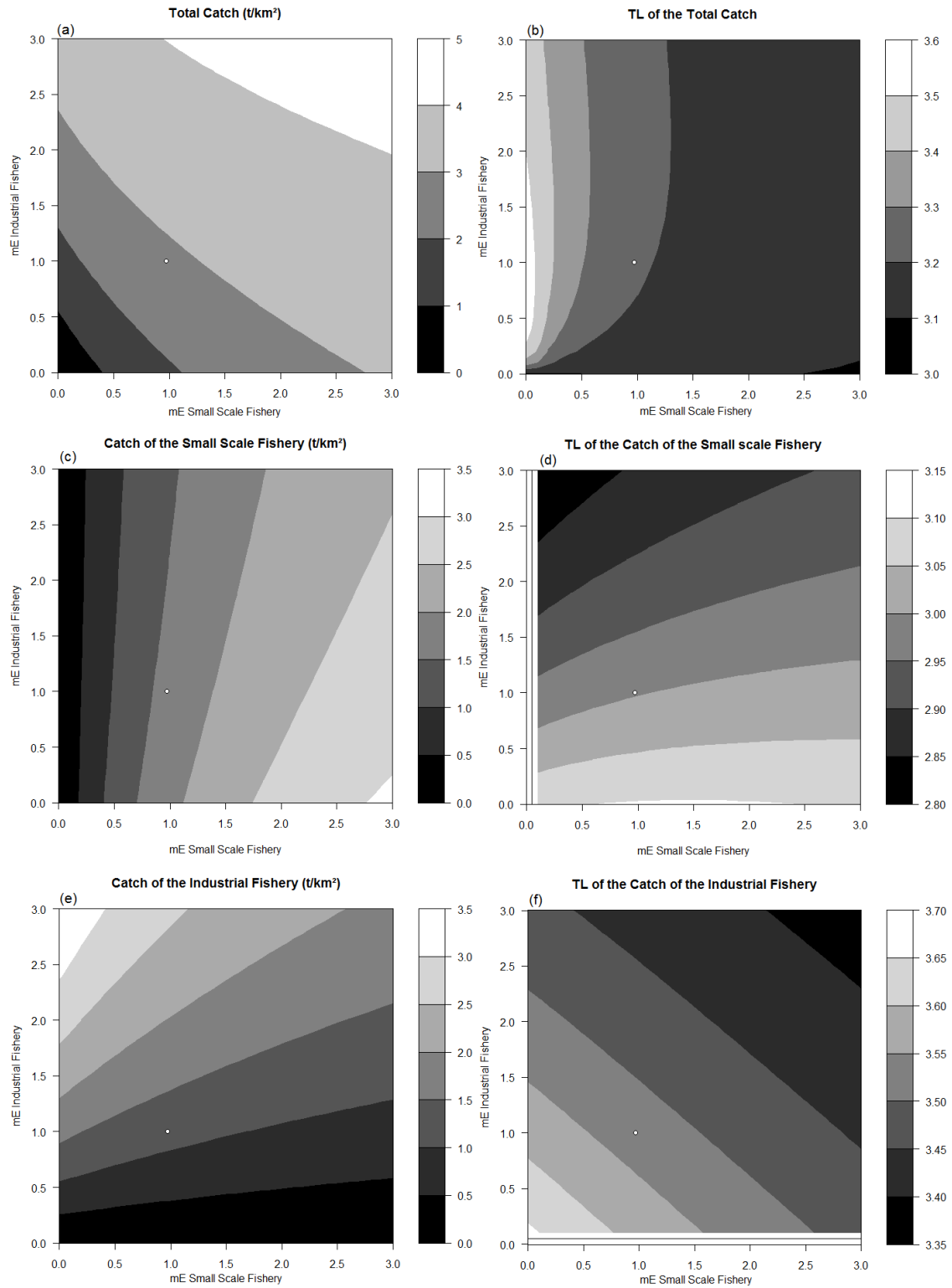
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797 **Figure 1**



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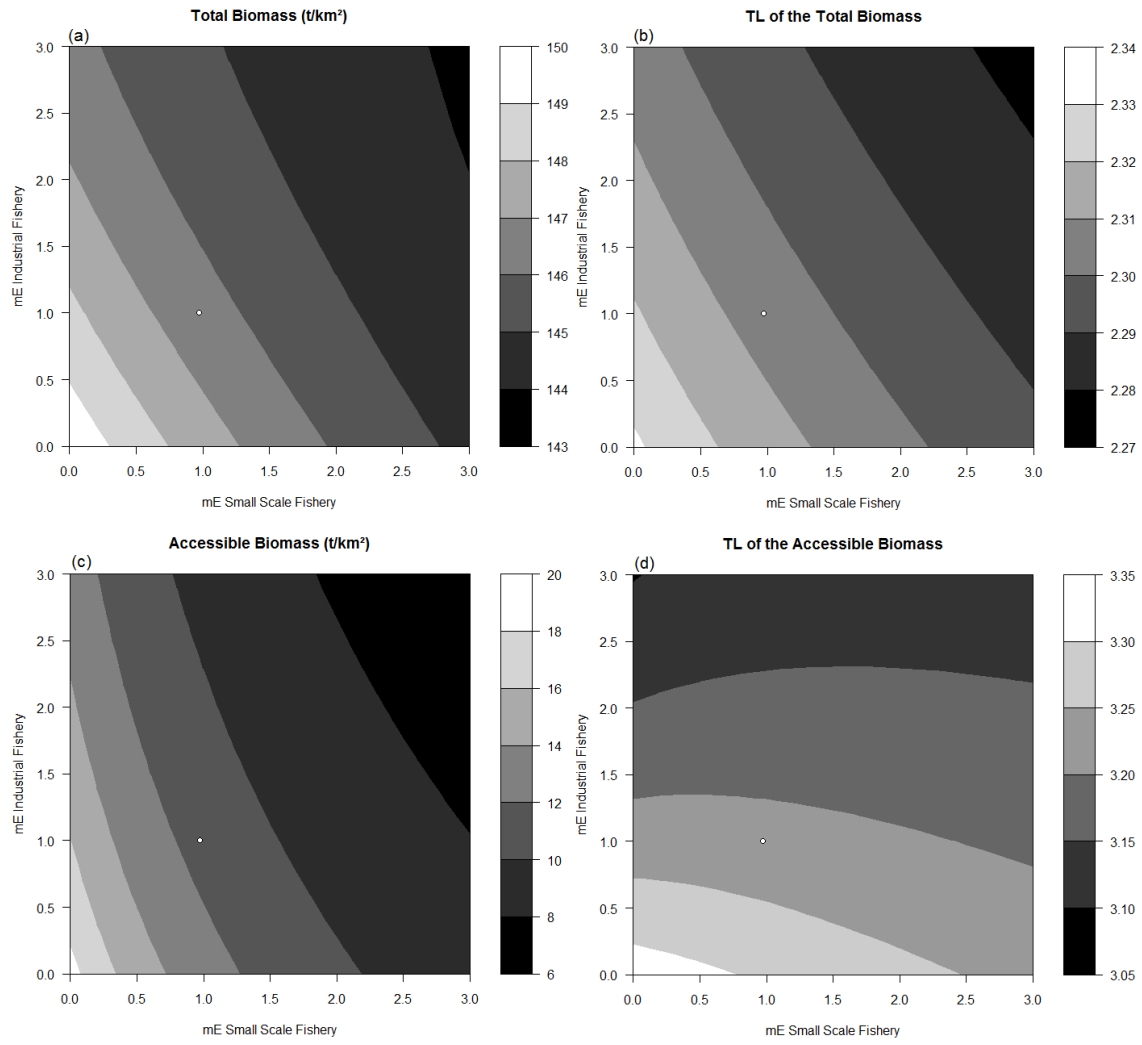
799 **Figure 2**



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801 **Figure 3**

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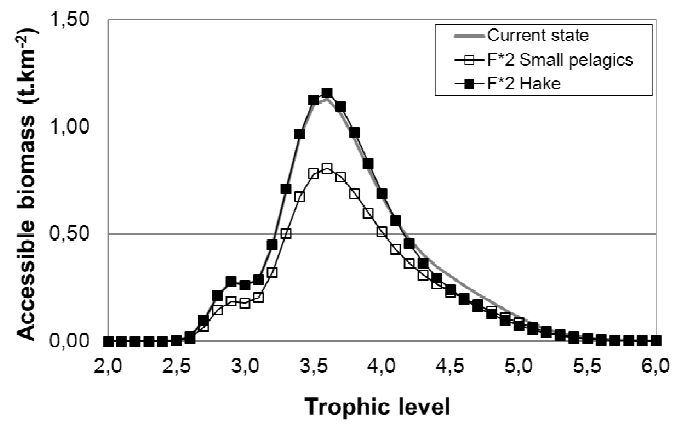
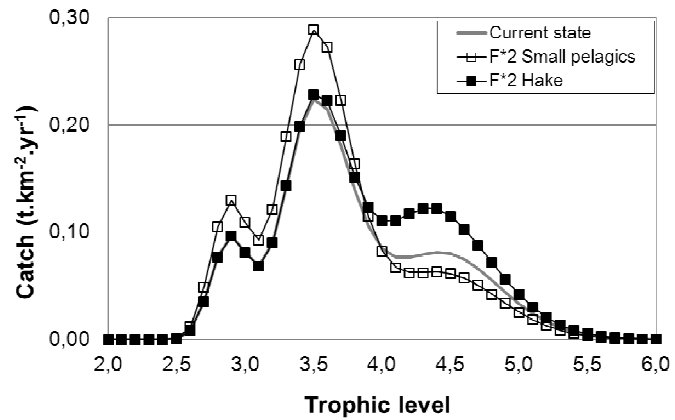
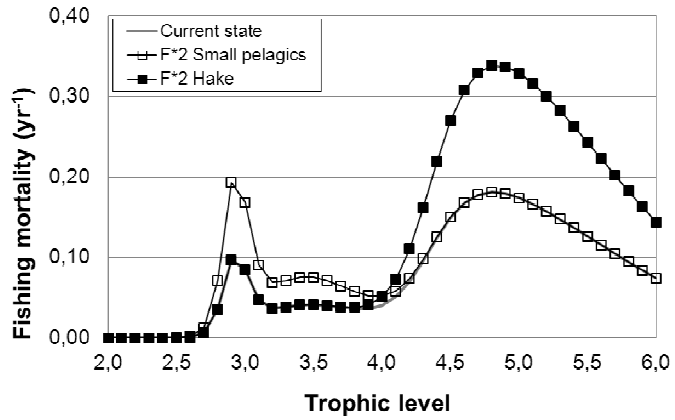


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805 **Figure 4**

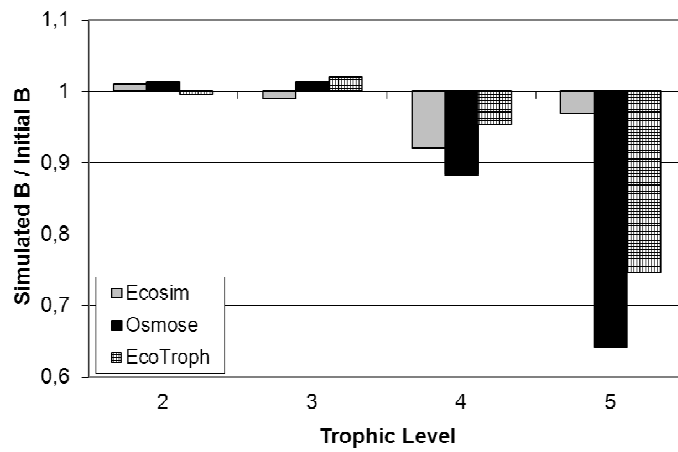
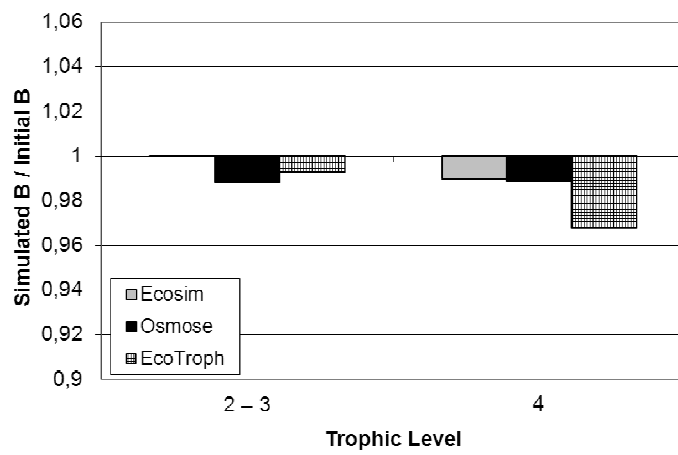
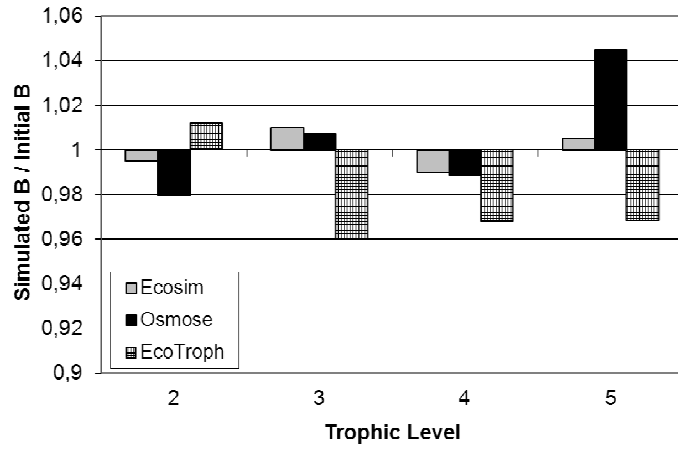
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808 **Figure 5**

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811 **Figure 6**