

*The following supplements accompany the article*

# **Including foraging arena and top-down controls improves the modeling of trophic flows and fishing impacts in aquatic food webs**

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Supplement 1 – The EcoTroph model and its use.

Supplement 2 – Integrating foraging arena consumption rate limitations in the EcoTroph model.

Supplement 3 – Value of EcoTroph outputs as a function of the fishing mortality ( $F^*$ ) used in simulation.

## Supplement 1

### Supplement 1.1. EcoTroph core principles and equations.

TLs characterize the position of organisms within trophic networks (Lindeman 1942, Odum & Heald 1975). They may change during ontogeny (Pauly et al. 2001), and vary in time and space as the function of encountered prey organisms. However, for any ecosystem state, the TL of each organism or the mean TL of each species results from the ecosystem trophic functioning. Therefore, TL appears as a state variable characterizing each unit of biomass.

EcoTroph is an ecosystem approach based on two key ideas. The first key idea is that an ecosystem can be represented by the distribution of its biomass across trophic levels (TLs). This distribution is called the biomass trophic spectrum (Gascuel et al. 2005). The biomass enters the food web at TL=1, as generated by the photosynthetic activity of primary producers and recycling by the microbial loop (see Figure 1). Between TL=1 and TL=2, the biomass is composed of mixotrophs only, i.e., of organisms that are simultaneously primary producers and first-order consumers, such as e.g., giant clams. Their biomass is usually low, and is conventionally split between biomasses at TL=1 and 2. Then, at TLs>2, the biomass is composed by heterotrophic organisms with mixed diet and fractional TLs resulting in a continuous distribution of biomass along TLs.

The second key idea is that the trophic functioning of marine ecosystems is modeled as a biomass flow surging up the food web from lower to higher trophic levels (see Figure 1). Each organic particle moves more or less rapidly up the food web according to abrupt jumps caused by predation and to continuous processes (ontogenic changes in TLs). All particles jointly constitute a biomass flow modeled as a continuous model (Gascuel et al. 2008). Based on the traditional equations of fluid dynamics, the biomass flow  $\Phi(t, \tau)$ , i.e., the quantity of biomass moving up through TL  $\tau$  at every moment  $t$ , is expressed as:

$$\Phi(t, \tau) = D(t, \tau) \times K(t, \tau) \quad (S1)$$

where  $\Phi(t, \tau)$  is expressed in  $t \cdot \text{year}^{-1}$ ,  $D(t, \tau)$  is the density of biomass at TL  $\tau$  (expressed in  $t \cdot \text{TL}^{-1}$ ), and  $K(t, \tau) = d\tau/dt$  is the flow kinetic, which quantifies the velocity of biomass transfers in the food web (expressed in term of the number of TLs crossed per year, i.e., in  $\text{TL} \cdot \text{year}^{-1}$ ). Under steady-state conditions, Eq. (S1) becomes:

$$D(\tau) = \frac{\Phi(\tau)}{K(\tau)} \quad (S2)$$

A discrete approximation of the continuous distribution  $D(\tau)$  is used for mathematical simplification and visual representation (see Figure 1). Thus, the continuous distribution of the biomass across TLs is approximated using narrow classes  $[\tau, \tau + \Delta\tau[$ . As a convention (and based on previous studies; Gascuel & Pauly 2009, Gascuel et al. 2011), trophic classes of width  $\Delta\tau = 0.1$  TL were considered to be an appropriate resolution, and a range starting at TL=2 (corresponding to the first-order consumers), up to TL=5.5 (with calculations performed up to TL=7), an appropriate range to cover all top predators likely to occur in marine systems (Pauly et al. 1998, Cortés 1999). Therefore, mean values  $D_\tau$ ,  $\Phi_\tau$ , and  $K_\tau$  over the trophic class  $[\tau, \tau + \Delta\tau[$  are considered. Thus, Eq. (S2) becomes:

$$D_\tau = \frac{\Phi_\tau}{K_\tau} \quad (S3)$$

Under steady-state conditions, the biomass (in tonnes) present at any moment within the trophic class  $[\tau, \tau + \Delta\tau[$  is:

$$B_\tau = \int_{\tau}^{\tau + \Delta\tau} D(\tau) \times d\tau = D_\tau \times \Delta\tau \quad (S4)$$

So, according to Eq. (S3), the biomass  $B_\tau$  is expressed as:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \times \Delta\tau \quad (\text{S5})$$

Moreover, the biomass flow  $\Phi(\tau)$  is a density of production at TL  $\tau$ . Therefore, the production of a trophic class  $[\tau, \tau+\Delta\tau[$  is:

$$P_\tau = \int_\tau^{\tau+\Delta\tau} \Phi(\tau) \times d\tau = \Phi_\tau \times \Delta\tau \quad (\text{S6})$$

Production is commonly expressed in  $\text{t}\cdot\text{year}^{-1}$ . In fact, it implicitly refers to the conversion of biomass eaten at TL  $\tau-1$ , into predator tissues whose mean TL is  $\tau$ . Therefore, in a TL-based approach such as EcoTroph, production has to be expressed in  $\text{t}\cdot\text{TL}\cdot\text{year}^{-1}$ , i.e. tonnes moving up the food web by 1 TL on average during 1 year. This ensures consistency in the units used.

As natural losses occur during trophic transfers (through non-predation mortality, respiration, and excretion), the biomass flow  $\Phi_\tau$  is a decreasing function of TL. Biomass removal by fisheries can be considered as an additional diversion of one part of the trophic flow that bolsters this negative natural trend. Therefore, from one trophic class to the next, the biomass flow is calculated as:

$$\Phi_{\tau+\Delta\tau} = \Phi_\tau \times \exp(-(\mu_\tau + \varphi_\tau) \times \Delta\tau) \quad (\text{S7})$$

where  $\mu_\tau$  and  $\varphi_\tau$  (expressed in  $\text{TL}^{-1}$ ) are, respectively, the mean rate of natural loss and the mean loss rate attributable to fishing over a  $[\tau, \tau+\Delta\tau[$  interval. Eq. (S7) implies that the biomass flow at a given TL depends on the flow from lower TLs. In other words, it implicitly introduces a bottom-up control of prey on predators in the model. Eq. (S7) also defines the net transfer efficiency (NTE) between continuous TLs as  $\exp(-\mu_\tau)$ .

The speed of the biomass flow  $K_\tau$  (flow kinetic) depends on the turnover of the biomass, and is defined using mean values per trophic class. It is deduced from Eqs. (S5) and (S6):

$$K_\tau = \left(\frac{P}{B}\right)_\tau \quad (\text{S8})$$

Under equilibrium assumption, Allen (1971) demonstrated that  $P/B=Z$ , with  $Z$  the total mortality. Here too, the production implicitly refers to one TL jump in the food web, and unit consistency requires rewriting Allen's equation as:

$$\frac{1}{\Delta\tau = 1} \left(\frac{P}{B}\right) = Z, \text{ and hence } K_\tau = (F_\tau + M_\tau) \quad (\text{S9})$$

where the term  $(\Delta\tau=1)$ , useful only for unit consistency, is omitted, and where  $F_\tau$  and  $M_\tau$  are respectively the usual fishing and natural mortalities (in  $\text{year}^{-1}$ ).

Starting from a reference state, Eq. (S7) may be used to simulate the biomass flow for various fishing patterns defined by their fishing loss rates  $\varphi_\tau$ . Predation being an important source of mortality, a top-down control effect is introduced into the model assuming that a fraction  $\alpha_\tau$  of the natural mortality  $M_\tau$  depends on predator abundance as follows:

$$M_\tau = \alpha_\tau \times M_{ref,\tau} \times \left(\frac{B_{pred}}{B_{ref,pred}}\right)^\gamma + (1 - \alpha_\tau) \times M_{ref,\tau} \quad (\text{S10})$$

where the subscript 'ref' indicates the reference state and  $B_{pred}$  is the biomass of predators (conventionally equal to the biomass of the  $[\tau+0.8, \tau+1.3[$  trophic class; Gascuel et al. 2009). The coefficient  $\alpha_\tau$ , i.e., the top-down coefficient varies between 0 and 1 and determines the part of natural mortality at TL  $\tau$  dependent on predator abundance. The coefficient  $\gamma$  is a shape parameter varying between 0 and 1 and defines the functional relationship between prey and predators. A value of 1 results in a linear effect of the abundance of predators on the flow

kinetics; a smaller value would turn the equation into a non-linear relationship akin to Holling's type II. The top-down equation is deduced from Eqs. (S9) and (S10):

$$K_{\tau} = (K_{ref,\tau} - F_{ref,\tau}) \times \left[ 1 + \alpha_{\tau} \times \left( \frac{B_{pred}^Y - B_{ref,pred}^Y}{B_{ref,pred}^Y} \right) \right] + F_{\tau} \quad (S11)$$

Starting with the reference state of the ecosystem, where the flow kinetics  $K_{ref,\tau}$  is known (see Supplement 1.2), Eq. (S11) enables to simulate  $K_{\tau}$  for various changes in the fishing patterns, and to account for indirect impacts of fishing on the ecosystem when performing simulations. Fishing, reducing the life expectancy of targeted species, can be the cause of notable accelerations in ecosystem's flow kinetics. Note that Equation (S11) requires an estimate of predator biomass, which is based on Eq. (S5). As this last equation reciprocally includes flow speed, the solution must involve an iterative procedure, starting with the reference values of  $K_{ref}$  estimating K for a given F, then estimating B, and iterating until K and B estimates stabilize.

Additionally, the current version of ET (Gascuel et al. 2011, Gasche & Gascuel 2013) is based on two distinct compartments, one accounting for the whole ecosystem biomass and one solely for the biomass accessible to fisheries. The same equations (Eqs. (S5), (S7), and (S11)) are used for both compartments, but their parameters differ since they take into account the fact that exploited species usually do not have the same characteristics as the unexploited ones. Parameters of the accessible part of the biomass are noted  $B_{\tau}^*$ ,  $\Phi_{\tau}^*$ ,  $K_{\tau}^*$ , or  $F_{\tau}^*$ . Thus, a selectivity coefficient  $S_{\tau}$  is defined as the fraction of the ecosystem biomass accessible to fisheries. It can be estimated in the reference state ( $S_{ref,\tau} = B_{ref,\tau}^*/B_{ref,\tau}$ ), based on field observations or from a theoretical model (see Supplement 1.2). These parameters allow simulation of the accessible biomass flow for any value of the accessible fishing loss rate  $\varphi_{\tau}^*$ . The computations are initialized for secondary producers (if no fishing at TL=1, otherwise initialized at TL=1) by:

$$\Phi_2^* = \Phi_{ref,2}^* \times \frac{\Phi_2}{\Phi_{ref,2}} = \Phi_2 \times S_{ref,2}$$

And then

$$\Phi_{\tau+\Delta\tau}^* = \Phi_{\tau}^* \times \exp[-(\mu_{\tau}^* + \varphi_{\tau}^*) \times \Delta\tau] \quad (S12)$$

The accessible biomass is simulated from:

$$B_{\tau}^* = \frac{\Phi_{\tau}^*}{K_{\tau}^*} \times \Delta\tau \quad (S13)$$

where  $K_{\tau}^*$  is the kinetic of the accessible flow, deduced from the reference state  $K_{ref,\tau}^*$  (see Supplement 1.2) based on Eq. (S11).

Finally, catches per time unit (in  $t \cdot \text{year}^{-1}$ ) are derived from earlier equations. They can be expressed either as the integration over time of instantaneous catches  $dY/dt$ , or as the integration over TLs of the catch densities  $dY/dt$ , leading to:

$$Y_{\tau} = \int_{t=0}^1 \frac{\varphi_{\tau}^*}{\varphi_{\tau}^* + \mu_{\tau}^*} \times [\Phi^*(\tau) - \Phi^*(\tau + \Delta\tau)] \times dt \quad (S14)$$

or

$$Y_{\tau} = \int_{s=0}^{\Delta\tau} \varphi_{\tau}^* \times \Phi^*(\tau + s) \times ds \quad (S15)$$

Eq. (S14) indicates that catches are equal to the fraction of flow loss attributable to the fishery, whereas Eq. (S15) stems from the definition of the fishing loss rate. Integration of Eqs. (S14) or (S15) both lead to the catch equation, which can be expressed, after simplification as:

$$Y_{\tau} = \varphi_{\tau}^* \times \Phi_{\tau}^* \times \Delta\tau = \varphi_{\tau}^* \times P_{\tau}^* \quad (\text{S16})$$

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

where  $F_{\tau}^*$  is the fishing mortality of the accessible biomass,  $P_{\tau}^*$  the production of the accessible biomass, and  $Y_{\tau}$  is the annual catch from the  $[\tau, \tau+\Delta\tau[$  trophic class. Equations presented here constitute the core of the ET-Transpose and ET-Diagnosis routines (see Supplement 1.2) accessible through an R package available on the R Cran (Coll  ter et al. 2013), or an EwE plugin ([www.ecopath.org](http://www.ecopath.org)).

### Supplement 1.2. EcoTroph parameterization and use

Throughout this article, EcoTroph was used to analyze two kinds of ecosystems: virtual ecosystems, and case studies modeled using Ecopath (see ‘Methods’ section). As explained in Supplement 1.1, the EcoTroph model requires as input data several parameters by trophic class: two of the three parameters  $B_{\text{ref}}$ ,  $K_{\text{ref}}$ , and  $\Phi_{\text{ref}}$  (the remaining one is calculated using the two others),  $Y_{\text{ref}}$  the catches (or either  $F_{\text{ref}}$  or  $\varphi_{\text{ref}}$ ), and the selectivity  $S$ . These data define the reference state, on which several simulations of changes in fishing mortality can be done.

The reference state for a virtual ecosystem usually refers to an unexploited state. It is commonly defined using an arbitrary  $\Phi_{\text{ref},1}$  and an associated net transfer efficiency to derive  $\Phi_{\text{ref},\tau}$  for each trophic class (see ‘Methods’ section). The speed of the biomass flow  $K_{\text{ref},\tau}$  is estimated for each trophic class using an empirical model developed by Gascuel et al. (2008). The P/B ratio and therefore  $K_{\text{ref},\tau}$  is expressed as a function of the TL and the mean water temperature. Lastly, theoretical fishing patterns, i.e.,  $F_{\tau}$  or  $\varphi_{\tau}$ , and  $S_{\tau}$ , are defined to simulate different fishing impacts.

The reference state for real case studies is usually derived from an Ecopath model. It is computed by converting Ecopath data referring to functional groups into data referring to trophic classes. For each Ecopath group, the biomass is distributed across TLs assuming that this distribution follows a lognormal curve, defined by the TL of the trophic group in question as a mean, and a standard deviation, which is a measure of the TL variability within the group (conventionally defined according to an empirical model; see Coll  ter et al. 2013). The biomass trophic spectrum is the curve obtained by summing the biomass of all functional groups across TLs. The same procedure can be applied to the catch of the functional groups or their production (calculated for each group as  $P=P/B*B$ ) to create respectively a catch or production trophic spectrum.  $K_{\text{ref},\tau}$  can be derived from the production/biomass  $(P/B)_{\tau}$  ratios of each trophic class. Since EcoTroph is based on two distinct compartments (one accounting for the whole ecosystem biomass and one solely for the biomass accessible to fisheries), simulations required setting up the accessibility to fishers of each trophic group in the Ecopath model, a parameter that has been theoretically defined as the proportion of a species or group that would be caught under the hypothesis of an infinite fishing effort (Gascuel & Pauly 2009). This parameter takes into account whether a species is targeted by fisheries or not. Therefore a trophic group composed of a few target species and a lot of non-target species will have a lower accessibility than a group containing only targeted species (see Coll  ter et al. 2013). This enables to calculate the parameters  $B_{\tau}^*$ ,  $\Phi_{\tau}^*$ ,  $K_{\tau}^*$ , or  $F_{\tau}^*$  related to the biomass accessible to fisheries.

Starting from these reference states, Eqs. (S5), (S7), and (S11) enable the calculation of biomasses, productions, etc... at the equilibrium for each trophic class and various fishing patterns defined by their fishing loss rates  $\varphi_{\tau}$ . As these equations are interrelated, the solution must involve an iterative procedure, starting with the reference values of  $K_{\text{ref}}$  and  $\Phi_{\text{ref}}$ , estimating  $K$  and  $\Phi$  for a given  $F$ , then estimating  $B$ , and iterating until  $K$ ,  $\Phi$ , and  $B$  estimates stabilize. Effects of fishery mortality changes at an ecosystem scale include biomass and kinetic changes, but also impacts on the mean trophic levels of the catch and of the total biomass (Gascuel & Pauly 2009, Coll  ter et al. 2013).

Two ET routines (also available as R-functions; see Coll  ter et al. 2013) are used. ET-Transpose enables the conversion of data referring to functional groups (extracted from Ecopath) into data referring to trophic classes in order to create trophic spectra. These data represent the current distribution of biomass  $B_\tau$ , production  $P_\tau$ , catches  $Y_\tau$ , fishing mortality  $F_\tau$  ( $F_\tau=Y_\tau/B_\tau$ ), or fishing loss rate ( $\varphi_\tau=Y_\tau/P_\tau$ ) across TLs, as well as  $B_\tau^*$ ,  $P_\tau^*$ ,  $Y_\tau^*$ ,  $F_\tau^*$ , and  $\varphi_\tau^*$  the equivalent parameters for the accessible part of the ecosystem. ET-Diagnosis is used to simulate the effect of different fishery mortality scenarios on trophic spectra coming from ET-Transpose. Different effort multipliers are applied to the initial fishing mortalities. For instance, a null effort multiplier corresponds to a fishery closure ( $F=0$ ), and allows users to rebuild an estimate of the unexploited status of the studied ecosystem.

## Supplement 2

EcoTroph is based on a continuous representation of trophic flows. This differs from the EwE approach where biomass is split between various trophic boxes. However, homologies between EwE and ET help understand aspects of both models. In EwE, each box generates during each time unit a biomass production ( $P$ ) at trophic level  $\tau$ , of which a part  $Q$  is consumed by predators, whose production occurs on average at trophic level  $\tau+1$  (Figure S1). Thus, the production  $P(\tau+1)$  constitutes a trophic flow transferred from level  $\tau$  to level  $\tau+1$ . Furthermore, trophic flows appear to be the consequence of two processes: predation ( $M_2$ ), by which biomass is transferred from a prey to a predator, and growth, through which the predator converts the biomass of trophic level  $\tau$  into its own biomass, on average at trophic level  $\tau+1$ . Losses occur due to four processes during these transfers: catches ( $Y$ ), non-predation mortality ( $M_0$ ), excretion ( $U$ ) and respiration ( $R$ , see Figure S1). The first of these four processes is accounted for in ET Eq. (S7) using the fishing loss rate parameter  $\varphi_\tau$ , which is related to fishing mortality  $F_\tau$ . The three others are implicit in the natural loss rate parameter  $\mu_\tau$ . Thus, in both models, the ecosystem is represented as a trophic flow moving from lower to upper trophic levels, with losses due to non-predation mortality, catches, excretion and respiration.

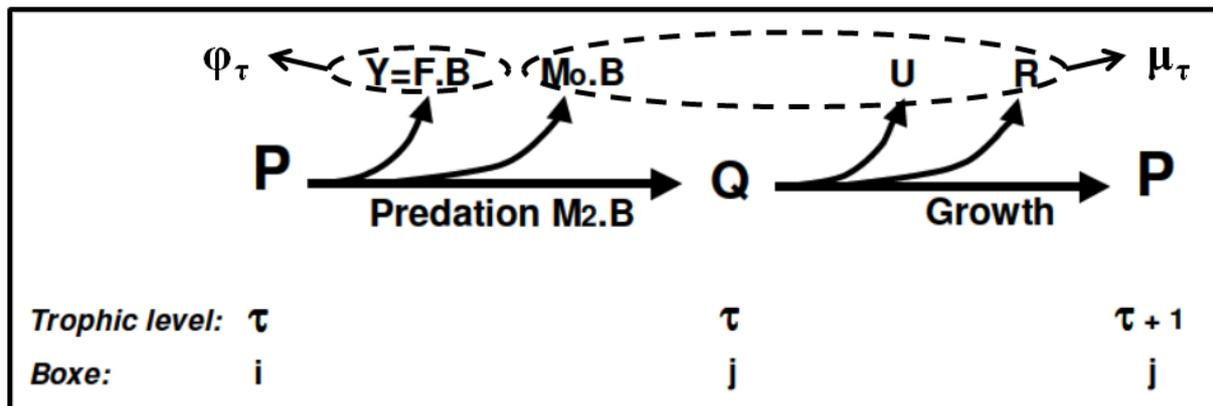


Figure S1 – Schematic representation of the conceptualization of biomass flow in EwE: the production  $P$  of the prey  $i$  at trophic level  $\tau$  is split into three parts: predation ( $M_2.B=Q$ ), losses due to non-predation mortality ( $M_0.B$ ) and fisheries catches ( $F.B=Y$ ). Of the amount  $Q$ , only a small fraction is transferred by the predator  $j$  from trophic level  $\tau$  to  $\tau+1$ , due to losses connected with excretion ( $U$ ) and respiration ( $R$ ). These processes are integrated into  $\varphi_\tau$  and  $\mu_\tau$  EcoTroph parameters (adapted from Gascuel et al. 2009).

However, there is a large difference between the underlying logic of these two models. The Ecosim dynamic model is based on the foraging arena theory: spatial and temporal restrictions in predator and prey activity cause partitioning of each prey pool  $B_{prey}$  as having an

available component,  $V$ , and an unavailable (safe) component,  $B_{prey} - V$ , to each predator pool  $B_{pred}$ , at any moment in time (Figure S2). Prey organisms alternate between these two components at rates  $v$  and  $v'$  (called vulnerabilities) with a flux rate:  $v \times (B_{prey} - V)$  to the available one, and a flux rate:  $v' \times V$  to the unavailable one. Finally, it assumes that biomass flow rate  $Q$  from prey to predator satisfies the mass-action relationship:  $Q = a \times V \times B_{pred}$ , with 'a' the predator rate of search for the prey pool (see Figure S2; Walters & Juanes 1993, Walters et al. 1997, Walters & Martell 2004, Ahrens et al. 2012).

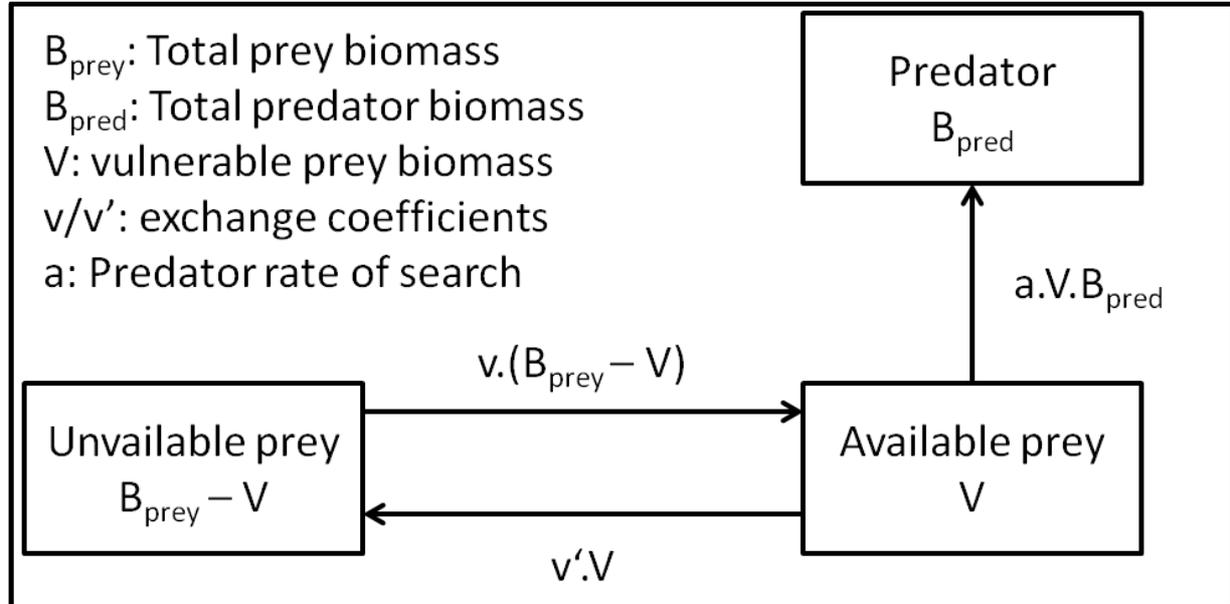


Figure S2 – Foraging arena approach used in Ecosim to simulate dynamic change in biomass flow between the unavailable and available components of the prey pool, and the predator pool (adapted from Walters et al. 1997).

Therefore, the foraging arena model for  $Q$  recognizes that prey and predator behaviors may severely limit consumption rates:

$$Q = \frac{a \times v \times B_{prey} \times B_{pred}}{v + v' + (a \times B_{pred})} \quad (S17)$$

Dividing Eq. (S17) by predator biomass  $B_{pred}$  enables the calculation of the instantaneous food-intake rate of prey per predator, i.e.,  $Q/B_{pred}$ . This last element can be much higher at low predator biomass than the natural rate whether or not there is any increase in prey biomass.

In contrast, ET Eq. (S7) predicts an exponential decline in production with an increasing TL. The current formulation permits top-down control effects (Eq. S11), and assumes a bottom-up loss of biomass flow due to harvesting and natural loss (Eq. S7). However, Eq. (S7) does not recognize the fact that the biomass flow,  $\Phi_\tau$ , may be directly limited by the prey biomass at the same trophic level  $\tau$ , i.e., production is assumed to be purely 'donor controlled'. Thus, it does not admit that production at  $TLs \geq 2$  is actually a proportion of consumption, i.e.,  $P = e \times Q$ , where food conversion efficiency 'e' is typically around 0.5-0.6. The use of Eq. (S17) in models like EwE causes their predictions to diverge in a very fundamental way from EcoTroph predictions, since these models predict severe limits on compensatory increase in productivity as predator biomasses are reduced.

Any attempt to incorporate nonlinear interaction rates as in Eq. (S17) into Eq. (S7) leads to a highly nonlinear differential equations system that has no analytical solution. In Eq. (S17),  $Q$  is predicted to increase asymptotically as  $B_{pred}$  increases, toward the maximum flow rate

$Q_{max} = v \times B_{prey}$  with the steepness of this increase determined by the ‘a’ parameter (see detailed calculations in Walters & Martell 2004, Ahrens et al. 2012). Thus, we included such an asymptotic effect to account for foraging arena consumption rate limitations and approximate analytical solutions. We integrated a consumption limitation modifier H in Eq. (S7), which modifies  $\Phi_{\tau+\Delta\tau}$  using an asymptotic effect scaled relative to the reference biomass flow at trophic level  $\tau+\Delta\tau$ ,  $\Phi_{ref,\tau+\Delta\tau}$  (Figure S3).

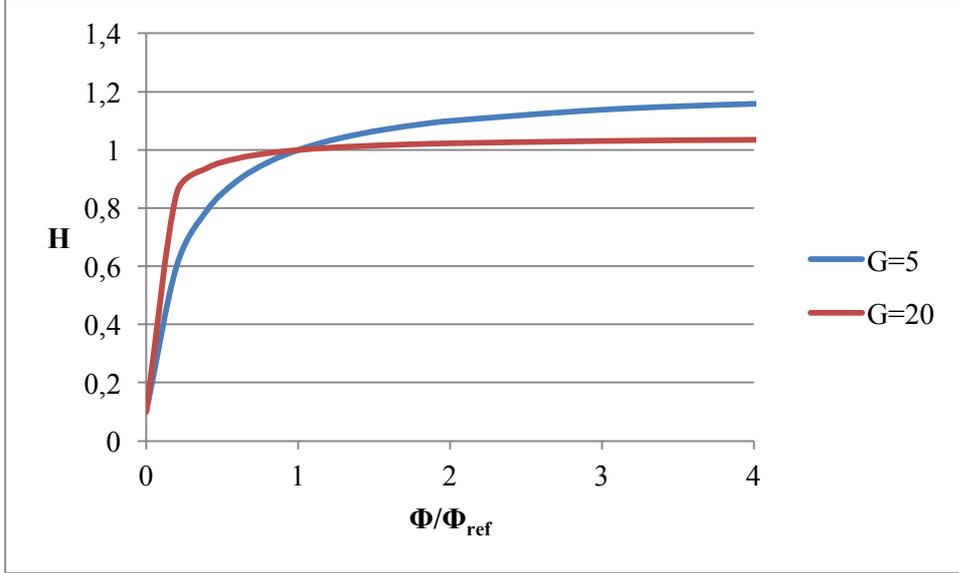


Figure S3 – Value of the H modifier as a function of the ratio  $\Phi/\Phi_{ref}$  for  $G=5$  and  $20$ .

H, the consumption limitation modifier (Eq. 5), is of the same form as Eq. (S17). It assumes that a proportion  $\omega$  of the biomass flow is due to ontogenetic changes in feeding, and the remaining proportion is dependent on the relative biomass flow rate  $\Phi_{\tau+\Delta\tau}/\Phi_{ref,\tau+\Delta\tau}$  and the Goodyear compensation ratio G. G is a parameter coming from the analysis of recruits vs. spawning stock biomass (see Walters et al. 2008), and it is a good proxy for the biomass compensation ratio, i.e., the maximum possible relative increase in  $Q/B_{pred}$  when  $B_{pred}$  is greatly reduced (Walters et al. 1997, Ahrens et al. 2012).

In fact, the Goodyear (1977) compensation ratio is originally defined using the plot of recruits vs spawning stock biomass. The compensation ratio is the ratio of the slope of the plot near zero spawning stock biomass (maximum recruits per spawner biomass) to the recruits/spawner biomass at the unfished equilibrium. It measures how much juvenile survival rate increases from the unfished to nearly extinct spawner biomass. To get this plot for a multi-stanza species in an Ecosim model, you have to fish the stock down to a low level, and then let it recover to the unfished level. As a consequence, there is no simple way to calculate this without doing Ecosim runs specifically set up to expose the stock-recruit relationship. In fact, there is no explicit recruitment-numbers accounting in ecosystem dynamics models. The quantity corresponding to the compensation ratio is the population ‘r’ value, the maximum surplus production per biomass at low biomass (with surplus production equal to zero at unfished equilibrium) (Walters & Martell 2004). In Ecosim, surplus production is defined as:  $(e \times Q) - (M \times B_{pred})$ , with  $M = M_2 + M_0$  (non fishing mortality rate, see Figure S1). Thus, surplus production per biomass is defined as:  $e \times Q/B_{pred} - M$ . Q basically varies as defined in Eq. (5), so  $Q/B_{pred}$  approaches  $aB_{prey}/2$  as  $B_{pred}$  approaches zero. This means that ‘r’ is given approximately by:  $e \times a \times B_{prey}/2 - M$ , assuming  $B_{prey}$  does not increase much as  $B_{pred}$  decreases (the most common situation).

The predator search rate ‘a’ is given by:  $a = 2 \times k \times (Q^0/B_{prey}^0) / [B^0 \times (k - 1)]$

where 'k' is the input vulnerability ratio of maximum prey mortality rate ( $Q/B_{prey}$ ) to Ecopath base prey mortality rate  $Q^0/B_{prey}^0$ . Thus, 'r' depends negatively on 'k': as 'k' approaches 1, 'a' approaches infinity, and so does 'r'. As 'k' increases toward infinity, 'r' decreases substantially. The bottom line is that, in biomass dynamics using the foraging arena equation,  $1/k$  is a good proxy for the biomass 'compensation ratio' G. More precisely, G should be approximately equal to  $2k/(k-1)$ . The most common vulnerability exchange multiplier values that come from fitting time series data are in the range 1.1-10, roughly implying G values between 20 and about 2 respectively.

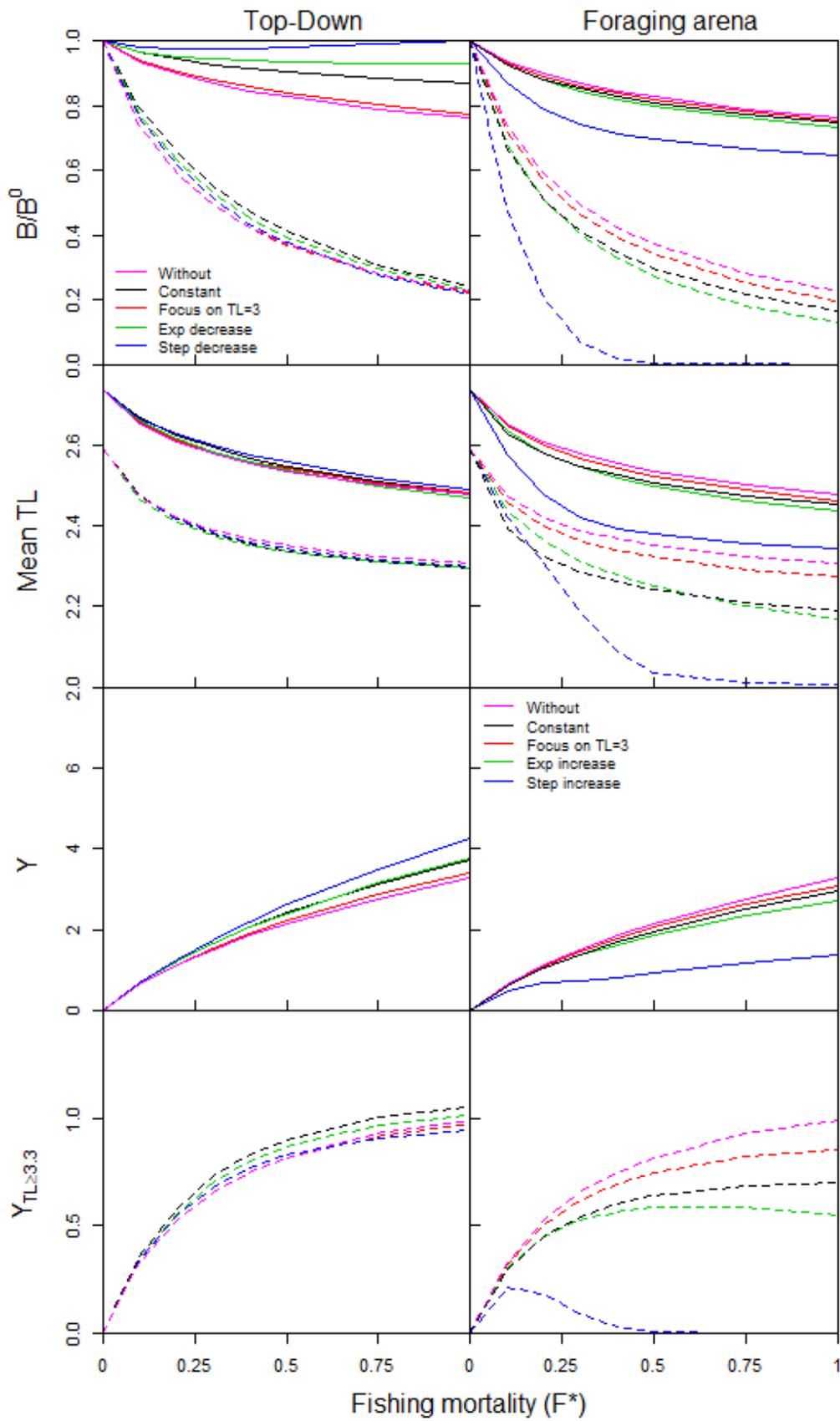


Figure S4 – Value of EcoTroph outputs as a function of the fishing mortality ( $F^*$ ) used in simulation: the relative biomass and predator biomass ratios ( $B/B^0$  and  $B_{TL \geq 3.3}/B_{TL \geq 3.3}^0$ , dashed lines for predator variables), the mean trophic level of the biomass and predator biomass, the total catch ( $Y$ ), and the predator catch ( $Y_{TL \geq 3.3}$ ). The left and right columns refer respectively to the different EcoTroph simulations with varying top-down and foraging arena control scenarios. The different TL-dependent effects are represented using black for scenarios where controls are constant over TLs, red where controls focus on TL=3, green where controls exponentially increase over TLs, and blue where controls step increase with strong controls for high TLs only. The simulated exploited ecosystem without foraging arena and top-down controls (purple line) was also represented

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