

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

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ABSTRACT: Food web dynamics consist of processes that affect ecosystem structure and functioning. EcoTroph (ET) is a recently developed approach and software for modeling aquatic ecosystems, articulated entirely around the trophic level concept. Here, we used ET to investigate impacts of 2 trophic controls (i.e. foraging arena and top-down controls) on marine ecosystem trophic flows and associated fishing effects. A new version of the ET model accounting for the foraging arena theory was developed. Cross impacts of the 2 trophic controls and different fishing scenarios were analyzed using a virtual ecosystem. Results showed that foraging arena controls decreased the resistance and production of an ecosystem facing increasing fishing mortality. In contrast, the inclusion of top-down controls resulted in a more resistant ecosystem, with a decrease in the kinetics of trophic flows at lower trophic levels (TLs) when the abundance of higher TLs is reduced by fishing. These 2 controls increased the interactions between TLs, and, in part, shaped fishing impacts at the ecosystem scale. Then, we applied ET to 3 real ecosystems which have been previously modeled using Ecopath with Ecosim (EwE). EcoTroph and Ecosim predictions related to changes in fishing effort were compared, and showed that accounting for trophic controls enabled EcoTroph to mimic Ecosim models, and better reflect associated changes in trophic flows. The 3 case studies exhibited different behaviors: while the pelagic ecosystem had strong foraging arena controls but no top-down controls, the other ecosystems were characterized by weaker foraging arena controls but effective top-down controls.

KEY WORDS: Foraging arena · Top-down control · EcoTroph · Ecopath with Ecosim · Ecosystem modeling · Trophic network · Fishing impact

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INTRODUCTION

Human activities are causing unprecedented changes to marine ecosystems, mainly through the direct and indirect effects of fishing (Jackson et al. 2001, Halpern et al. 2008). Despite the fact that main targets are certain size/age groups of selected species, fishing takes place in an ecosystem context with unavoidable repercussions on predators, their competitors, prey, and ultimately the entire ecosystem's trophic network (e.g. Baum & Worm 2009). Thus, it is important to improve our understanding of preda-

tor-prey interactions and impacts of fishing beyond targeted species. However, understanding and predicting consequences of altered trophic interactions is an arduous task (McCann 2007). A great number of food web modeling approaches have been developed (Whipple et al. 2000); and several ecosystem models, such as Ecopath with Ecosim (EwE) (Christensen & Pauly 1992, Christensen & Walters 2004), OSMOSE (Shin & Cury 2001, 2004), Atlantis (Fulton et al. 2011), size spectra (Jennings et al. 2008), linear inverse model (Vézina & Platt 1988, Niquil et al. 2011), and EcoTroph (Gascuel & Pauly 2009, Gascuel

et al. 2011), have been applied to an increasing number of marine ecosystems. Each model type is based on different assumptions and hypotheses, and represents only one of many possible visions of an ecosystem (see reviews in Fulton et al. 2003, Plagányi 2007). Ecosim, the dynamic part of the EwE model, is based on the ‘foraging arena theory’, in which it is assumed that spatial and temporal restrictions in predator and prey activity cause partitioning of each prey population into vulnerable and invulnerable components (see Supplement 2 at www.int-res.com/articles/suppl/m534p017_supp.pdf; Walters & Juanes 1993, Walters et al. 1997, Walters & Korman 1999, Ahrens et al. 2012). Foraging arenas appear common and cover a wide variety of mechanisms in aquatic systems, notably restrictions of distributions in response to predation risk and risk-sensitive foraging behavior (review in Ahrens et al. 2012). The principles of foraging arena theory have been widely used, mainly through the application of Ecosim, to explain and model historical fishing impacts on whole ecosystems (review in Walters & Martell 2004). Several predictions have been made possible to better understand the functioning of trophic networks at different scales, notably that trophic cascades should be common at least in simpler aquatic ecosystems, and surplus production should occur for predators in harvested systems (Ahrens et al. 2012).

Despite numerous insights into trophic functioning, fishing ecosystem effects are still unaccounted for due to a predominant use of single-species assessments in fisheries regulation (Jennings & Kaiser 1998). The scientific community called for the implementation of an ecosystem dimension in fisheries management (e.g. Botsford et al. 1997, Pikitch et al. 2004). This led to the emergence of a new concept, the ecosystem approach to fisheries (EAF), aiming to place fisheries in their ecosystem context, and to emphasize the link between human welfare and ecosystem health (Sainsbury et al. 2000, Sinclair et al. 2002, Garcia et al. 2003). The move toward an EAF calls for scientific support to answer queries by management stakeholders. Ecosystem modeling is an important tool for the evaluation of scenarios and trade-offs, and to explore further the trophic functioning of marine ecosystems (Plagányi 2007). The models needed for EAF practitioners should have the capability of accounting for trophic controls to enhance analyses and predictions of fishing impacts. As a contribution to such efforts, we present here a major improvement to EcoTroph (ET), a recently developed approach and software for modeling aquatic ecosystems, articulated entirely around the trophic

level concept. Many indicators derived from the TL concept are now commonly used by the scientific community, thanks to their ability to reveal ecosystem-level patterns (e.g. Cury et al. 2005, Shannon et al. 2014). ET constitutes a useful model to study impacts of ecological processes on ecosystem trophic flows and fishing impacts through a simple framework. This approach may be viewed as the final stage in the use of the TL metric for ecosystem modeling, since it is not based upon species (as in most ecosystem models; see Plagányi 2007) but trophic levels (see ‘Materials and methods’ and Supplement 1 at www.int-res.com/articles/suppl/m534p017_supp.pdf). It was developed at the same time as the EwE worldwide expansion, and has been incorporated into the EwE plug-in family (Gascuel & Pauly 2009, Gascuel et al. 2009a). ET has been used either in theoretical contexts based on virtual ecosystems (Gascuel & Pauly 2009, Gascuel et al. 2011), or in specific case studies to assess the current fishing impacts at the ecosystem scale in the South African Benguela ecosystem (Gasche et al. 2012), in the Bay of Biscay (Lassalle et al. 2012), or for a worldwide analysis (Tremblay-Boyer et al. 2011), to analyze the effects of marine protected areas on the whole food web (Colleter et al. 2012 [Senegal], 2014 [meta-analysis], Valls et al. 2012 [Mediterranean Sea]), or to estimate meso-pelagic fish biomass in the open ocean (Irigoiien et al. 2014).

EcoTroph current formulation includes top-down controls (see ‘Materials and methods’ and Supplement 1). However, it does not account for behaviors typically predicted by foraging arena theory. In this study, we developed a new ET formulation accounting for foraging arena consumption rate limitations, i.e. an approach to represent how the biomass flow through a TL class that has been reduced by fishing may be limited by the very biomass in that TL class. Cross impacts of ecosystem trophic properties (top-down and foraging arena controls) and fishing impacts were analyzed using a virtual ecosystem. We assessed the changes in trophic flows and the resistance (i.e. the capacity for an ecosystem to remain unchanged at equilibrium when facing fishing pressure, compared to the unexploited state), 2 key aspects that could be impacted by these trophic properties. Finally, ET was applied to 3 real ecosystems which have been previously modeled using Ecopath with Ecosim. We compared EcoTroph and Ecosim predictions considering historical fishing effort changes and different EcoTroph parameterizations. We selected 3 EwE models: 1 EwE model representing a predominantly pelagic ecosystem, the central

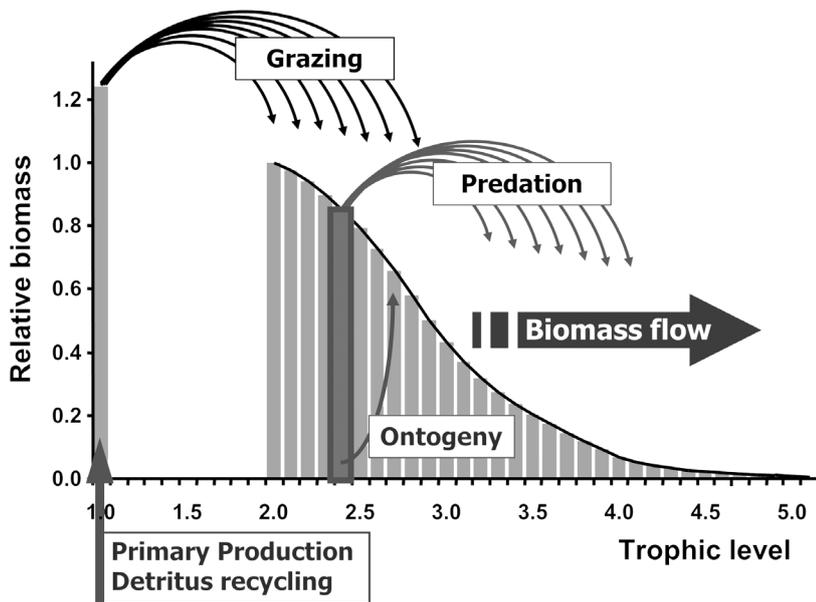


Fig. 1. Diagram of the trophic functioning of an ecosystem according to the EcoTroph model: theoretical distribution of the biomass by trophic level (TL) and trophic transfer processes, given an arbitrary input of biomass (fixed equal to 1 for TL = 2) (adapted from Gascuel & Pauly 2009)

North Pacific Ocean (Cox et al. 2002a,b), and 2 models representing different mixed ecosystems, the Gulf of Thailand (FAO/FISHCODE 2001) in the South China Sea and the Guinean continental shelf (Gascuel et al. 2009b). Patterns associated with foraging arena parameterization were expected to be different considering differences in predator–prey relations in these ecosystem types. This enabled us to discuss theoretical and applied results of foraging arena and top-down controls on ecosystem trophic flows and fishing impacts, but also realism and parameterization of ecosystem models to predict fishing impacts on whole ecosystems.

METHODS

General principles of the EcoTroph model including foraging arena consumption rate limitations

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 ecosystem trophic functioning. Therefore, TL appears as a state variable characterizing each unit of biomass. Against this

background, EcoTroph is an ecosystem approach based on 2 key ideas. The first key idea is that an ecosystem can be represented by the distribution of its biomass across trophic levels. 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 (Fig. 1). Between TL = 1 and TL = 2, the biomass is composed of mixotrophs only; it is usually low and can be 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. As a convention (and based on previous studies; Gascuel & Pauly 2009, Gascuel et al. 2011, Gasche & Gascuel 2013), we consider trophic classes of width $\Delta\tau = 0.1$ TL 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). Trophic spectra can also be built for other parameters than biomass, such as production or catch.

The second key idea behind ET is that the trophic functioning of marine ecosystems is modeled as a continuous biomass flow surging up the food web from lower to higher TLs (Fig. 1). Each organic particle moves more or less rapidly up the food web according to abrupt jumps caused by predation and to continuous processes (ontogenetic 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 (see Supplement 1.1 at www.int-res.com/articles/suppl/m534p017_supp.pdf for a detailed presentation of EcoTroph model equations), the biomass at TL τ (i.e. in the trophic class $[\tau, \tau + \Delta\tau]$, here expressed in tonnes, t) under steady-state conditions is given by:

$$B_{\tau} = \frac{\Phi_{\tau}}{K_{\tau}} \times \Delta\tau \quad (1)$$

where Φ_{τ} is the biomass flow, i.e. the amount of biomass that moves up the food web through the trophic class $[\tau, \tau + \Delta\tau]$ (expressed in t yr^{-1}), and K_{τ} the flow kinetic, which quantifies the speed of the biomass

flow (expressed in terms of the number of TLs crossed per year).

The flow kinetic K_τ depends on the turnover of the biomass. It is one of the parameters that EcoTroph requires as input to define a reference state, on which several simulations of changes in fishing mortality can be done. The reference state is commonly defined as the modeled period for practical case studies (Ecopath models), and the unexploited state for virtual ecosystems (see Supplement 1.2 for a detailed presentation of the EcoTroph parameterization and use). K_τ is estimated for each trophic class using 2 alternative methods depending on input data and studies:

(1) For practical case studies (based on EwE models), $K_{\text{ref},\tau}$ can be derived from the production/biomass (P/B) ratios of an Ecopath model, which defines the reference state. This method is based on the use of P/B ratios as a measure of the speed of the flow (see Supplement 1.1; Gascuel et al. 2008). This is consistent with Allen's relationship ($P/B = F + M$ at equilibrium, where F and M are respectively the fishing and natural mortalities; Allen 1971), and with the fact that the inverse parameter $1/K_{\text{ref},\tau}$ is the mean life expectancy of an organism within the trophic class $[\tau, \tau + \Delta\tau]$. Thus, when mortality changes, the speed of the flow is changing too.

(2) For theoretical studies of ecosystem functioning, or in data-poor situations, an empirical model developed by Gascuel et al. (2008) is used. The P/B ratio and therefore $K_{\text{ref},\tau}$ is expressed as a function of the TL and the mean water temperature.

Predation being an important source of mortality, it is accounted for in simulations using a relationship, called the top-down equation (Eq. 2, see Supplement 1.1), linking the flow kinetic at a TL τ (K_τ) to the biomass (of predators) at TL $\tau + 1$:

$$K_\tau = (K_{\text{ref},\tau} - F_{\text{ref},\tau}) \times \left[1 + \alpha_\tau \times \left(\frac{B_{\text{pred}}^\gamma - B_{\text{ref,pred}}^\gamma}{B_{\text{ref,pred}}^\gamma} \right) \right] + F_\tau \quad (2)$$

where $K_{\text{ref},\tau}$ is the speed of the flow at TL τ in the reference state (which is characterized by a fishing mortality $F_{\text{ref},\tau}$), K_τ is the speed of the flow in any simulated state of the ecosystem (characterized by F_τ), B_{pred} is the biomass of species from TL $\tau + 1$ (i.e. biomass conventionally between TL $\tau + 0.8$ and $\tau + 1.3$), α_τ is a coefficient chosen by the user between 0 and 1 which determines the part of natural mortality at TL τ dependent on predator abundance (called top-down coefficient), and γ is a shape parameter varying between 0 and 1 defining the functional relationship between prey and predators ($\gamma = 0.5$ as a constant

reference value). Eq. (2) enables the model 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 an ecosystem's flow kinetics. This equation also introduces a top-down control in the model, the intensity of which is defined by the α parameter.

As natural losses occur during trophic transfers (through non-predation mortality, respiration, and excretion), the biomass flow Φ_τ 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:

$$\Phi_{\tau+\Delta\tau} = \Phi_\tau \times \exp(-(\mu_\tau + \varphi_\tau) \times \Delta\tau) \quad (3)$$

where μ_τ and φ_τ (expressed TL^{-1}) are, respectively, the mean rate of natural loss and the mean loss rate of biomass flow attributable to fishing over a $[\tau, \tau + \Delta\tau]$ interval. Eq. (3) 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. For practical case studies (based on EwE models), Φ_τ is calculated based on Eq. (1), and the B and K parameters originating in Ecopath (see Supplement 1.2). The value of the φ_τ parameter is computed as the ratio of catch (Y_τ) to production (P_τ) at TL τ ($\varphi_\tau = Y_\tau/P_\tau = Y_\tau/(\Phi_\tau \times \Delta\tau)$), and μ_τ is deduced from previous calculations. Eq. (3) also defines the net transfer efficiency (NTE) between continuous TLs as $\exp(-\mu_\tau)$. Simulations are made assuming that natural loss rates are constant, and that only fishing loss rates change.

However, Eq. (3) does not recognize the fact that the biomass flow, Φ_τ , may be directly limited by the prey biomass at the same trophic level τ , i.e. production is assumed to be purely 'donor controlled'. We developed a foraging arena formulation for Eq. (3) that represents how the biomass flow through a TL class that has been reduced by fishing may be limited by the very biomass flow in that TL class. In fact, the use of the foraging arena theory 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 (see Supplement 2 for a detailed presentation of the inclusion of the foraging arena in EcoTroph). Thus, we included an asymptotic effect to account for foraging arena consumption rate limitations. A consumption limitation modifier H was integrated in

Eq. (3), which modifies $\Phi_{\tau+\Delta\tau}$ using an asymptotic effect scaled relative to the reference biomass flow at trophic level $\tau+\Delta\tau$, $\Phi_{\text{ref},\tau+\Delta\tau}$ (reference situation before simulation):

$$\Phi_{\tau+\Delta\tau} = \Phi_{\tau} \times \exp(-(\mu_{\tau} + \varphi_{\tau}) \times \Delta\tau) \times H_{\tau+\Delta\tau} \quad (4)$$

with H the consumption limitation modifier:

$$H_{\tau+\Delta\tau} = \omega + (1 - \omega) \times \frac{G \times \Phi_{\tau+\Delta\tau} / \Phi_{\text{ref},\tau+\Delta\tau}}{1 + (G - 1) \times \Phi_{\tau+\Delta\tau} / \Phi_{\text{ref},\tau+\Delta\tau}} \quad (5)$$

Eq. (5) assumes that a proportion ω of the biomass flow is due to ontogenetic changes in feeding, and the remaining proportion is dependent on the relative biomass flow rate $\Phi_{\tau+\Delta\tau} / \Phi_{\text{ref},\tau+\Delta\tau}$. The Goodyear (1977) compensation ratio G parameter, coming from the analysis of recruits versus spawning stock biomass (see Walters et al. 2008), is a good proxy for the biomass compensation ratio (Walters et al. 1997, Ahrens et al. 2012). Details on the G parameter and its calculation are provided in Supplement 2 at www.int-res.com/articles/suppl/m534p017_supp.pdf. Ecosim models typically predict G -values of at least 2, and commonly >10 (Walters & Martell 2004, Walters et al. 2008). A low G -value implies a high vulnerability to predation and thus a strong effect of foraging arena controls. We implemented Eq. (4) in EcoTroph equations, and analyzed impacts on trophic flows and the fishing effect of the top-down control (α parameter, Eq. 2), and the foraging arena consumption limitation modifier (ω and G parameters, Eq. 5).

Additionally, the current version of ET (Gascuel et al. 2011, Gasche & Gascuel 2013) is based on 2 distinct kinetics — one for the whole ecosystem biomass and one solely for the biomass accessible to fisheries. The same equations (Eqs. 1–4) 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 unexploited species. Parameters related to the compartment accessible to fisheries are denoted B_{τ}^* , Φ_{τ}^* , K_{τ}^* , φ_{τ}^* , P_{τ}^* or F_{τ}^* . The catch equation (deduced from Eq. 3) applied to the accessible biomass flow is:

$$Y_{\tau} = \varphi_{\tau}^* \times \Phi_{\tau}^* \times \Delta\tau = \varphi_{\tau}^* \times P_{\tau}^* \quad (6)$$

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

where Y_{τ} is the annual catch from the $[\tau, \tau+\Delta\tau]$ trophic class. Detailed equations and simulation procedures are explained in Supplement 1. Equations presented here constitute the core of the ET-Transpose and ET-Diagnosis routines accessible through an R package available on the R Cran (Coll ter et al. 2013), or an EwE plug-in (www.ecopath.org).

Application of EcoTroph to a virtual ecosystem

EcoTroph was first used to simulate a virtual ecosystem facing various exploitation patterns. The virtual ecosystem used as reference state was unexploited ($\varphi_{\text{ref},\tau} = 0$), and had the following characteristics:

(1) Biomass flow: the value of primary production, $\Phi_{\text{ref},1}$, was set at 1000 arbitrary units, such that the biomass flow of the first trophic class considered in the model ($\Phi_{\text{ref},2}$) was equal to 100 using a standard NTE of 10% (see below);

(2) NTE: a unique standard value of $\exp(-\mu_{\tau}) = 0.10$ was used for all trophic levels (Pauly & Christensen 1995);

(3) Flow kinetics: standard flow kinetics were considered, based on empirical equations by Gascuel et al. (2008), for a mean water temperature of 15°C.

Impacts of increasing fishing efforts on biomass were simulated based on several selectivity curves that defined the part of biomass accessible to fisheries. We used 3 logistic curves and 1 additional scenario based on a normal distribution. Each logistic curve was defined by the same selectivity value (S), $S = 1\%$, for $TL = 2$, and by the trophic level where S is equal to 50%, denoted TL_{50} (i.e. ‘trophic level at first capture’, in analogy to the mean length at first capture; Beverton & Holt 1957). The reference scenario referred to a medium trophic level at first catch using $TL_{50} = 3.0$; alternative scenarios corresponded to lower ($TL_{50} = 2.5$) or higher ($TL_{50} = 3.5$) values. An additional scenario was also developed using a selectivity curve based on a normal distribution centered on $TL = 3.0$ ($S = 100\%$) with $S = 1\%$ for $TL = 2$ and 4. Such a curve mimics, for instance, a fishery targeting only small pelagic fishes. All selectivity curves had null values for $TL = 1$. For all trophic levels we used the same fishing mortality F^* applied to the accessible biomass. Thus, the fishing mortality applied to the whole biomass ($F = F^* \times S$) followed a logistic curve (or was centered on $TL = 3$ for the additional scenario). F^* varied between 0 (no fishing) and 1 (strong fishing) in simulations, with $F^* = 0.5$ being considered as the reference scenario.

For each selectivity curve and analysis (see following subsection), we computed different trophic spectra and indices. Impacts on trophic flows were analyzed using the biomass, production, and kinetic trophic spectra. We also assessed the resistance to fishing using indices derived from the biomass and catch trophic spectra. The analysis was separated in 3 parts (Table 1):

Table 1. Detailed parameterization of the 3 different theoretical analyses regarding the fishing scenario (F^* and TL_{50}), top-down (α), and foraging arena (ω and G) controls used in simulations. TL: trophic level

	Fishing scenario		Top-down control	Foraging arena control	
	F^*	TL_{50}	α	ω	G
1. Sensitivity to the foraging arena parameters	{0.5}	{3.0}	Not included	Not included	
			Not included	{0, 0.1, 0.2}	{2, ..., 40}
2. Sensitivity to the exploitation patterns	{0.0, ..., 1.0}	{2.5, 3.0, 3.5, Centered on TL = 3}	Not included	Not included	
			{0.4, 0.8}	Not included	
			Not included	{0.1}	{5, 20}
3. Sensitivity to TL-dependent effects	{0.0, ..., 1.0}	{3.0}	Not included	Not included	
			{0.4, Centered on TL = 3, Exponential decrease, Step decrease}	Not included	
			Not included	{0.1}	{10, Centered on TL = 3, Exponential increase, Step increase}

(1) Sensitivity to the foraging arena modifier parameters. We first tested the sensitivity of EcoTroph predictions to the 2 new parameters of the H modifier, ω and G (Eq. 5). The reference fishing scenario was applied to the virtual ecosystem assuming a null top-down effect (see Table 1). Since trophic flows are mainly the consequence of predation, we supposed ω to be low and tested 3 values ($\omega = 0, 0.1, 0.2$). For G , values ranging between 2 and 40 were applied. We computed the simulated biomass and catch trophic spectra for each combination of parameters, for the unexploited ecosystem, and for the reference fishing scenario without including foraging arena controls.

(2) Sensitivity to exploitation patterns. We then investigated the impact of different theoretical exploitation patterns along with top-down and foraging arena controls. The 4 selectivity curves associated with different F^* (between 0 and 1) were applied. Five EcoTroph parameterizations were set up: one without top-down and foraging arena controls, 2 with top-down but no foraging arena controls, and 2 with foraging arena but no top-down controls (see Table 1). We computed different trophic spectra and ratios to assess impacts on ecosystem trophic flows

and resistance: the biomass, production, and kinetic trophic spectra, B/B^0 and $B_{TL \geq 3.3}/B_{TL \geq 3.3}^0$ ratios (ratios of the total biomass and predator biomass, conventionally referring to $TLs \geq 3.3$, compared to the unexploited state), mean trophic levels of the predator and total biomasses, and mean trophic levels of the predator and total catches.

(3) Sensitivity to TL-dependent effects. The last step of the virtual ecosystem analysis was to consider trophic level-dependent effects for top-down and foraging arena controls. In fact, top-down controls are not constant across trophic levels. They are mainly due to predators, differ between ecosystems, and can lead to trophic cascades (Borer et al. 2005, Baum & Worm 2009, Casini et al. 2009, Andersen & Pedersen 2010). These considerations are also valid for foraging arena controls, but there is no consistent pattern related to trophic levels. Low G -values are usually observed for higher TLs that tend to be more sensitive to fishing, show weaker compensatory response when fished, and forage over wide range habitats (Walters et al. 1997, Ahrens et al. 2012). We tested 4 different scenarios for each type of control (Fig. 2), along with simulation without any control. Cross

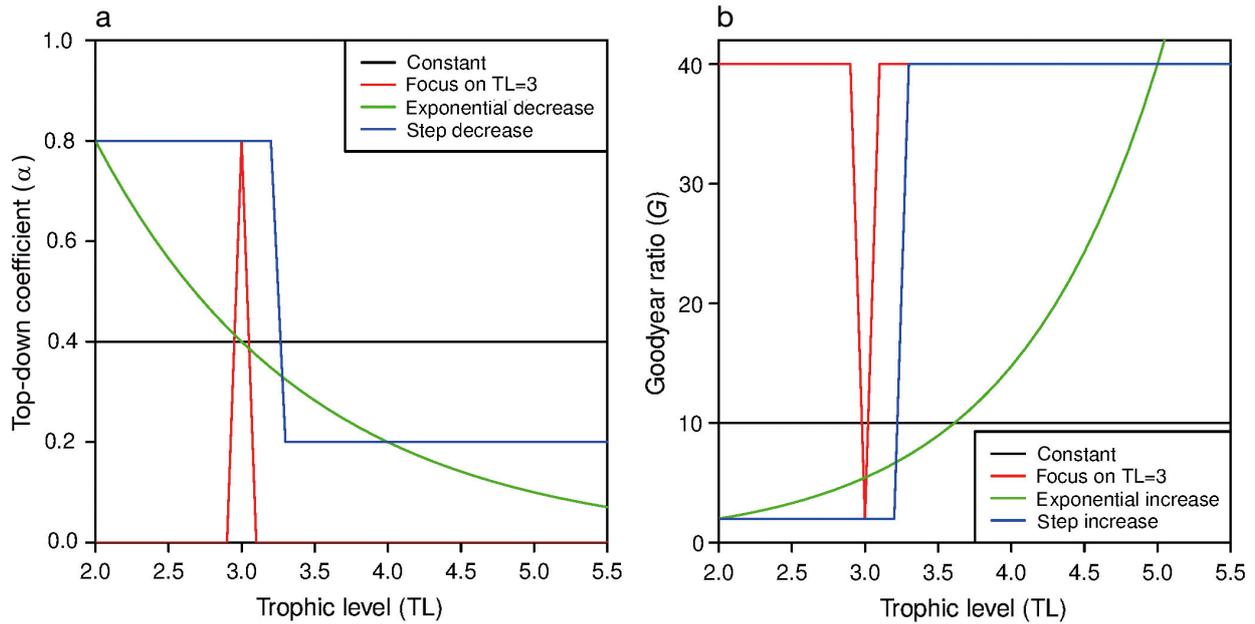


Fig. 2. Four scenarios developed to test the sensitivity to trophic level (TL)-dependent effects for (a) top-down (on the top-down coefficient α) and (b) foraging arena controls (on the Goodyear compensation ratio G)

effects of top-down and foraging arena controls were not analyzed together, but separately following the same design (Table 1): no effect, a constant standard effect across trophic levels, a strong effect for low TLs and weak for high TLs, and a strong effect concentrated on TL = 3 (Fig. 2). We computed the different trophic spectra and ratios used to assess impacts on ecosystem trophic flows and resistance.

Application to case studies

In a second step, EcoTroph was applied to analyze 3 real ecosystems that have previously been modeled using EwE. Three models representing different ecosystem types and patterns of fishing changes were selected: 1 EwE model corresponding to a pelagic environment, the central North Pacific (CN-Pacific; Cox et al. 2002a,b), and 2 models representing mixed environments, the Gulf of Thailand (Go-Thailand; FAO/FISHCODE 2001) and the Guinean continental shelf (CS-Guinea; Gascuel et al. 2009b), since patterns associated with foraging arena parameterization were supposed to be different considering differences in predator-prey relations in these ecosystem types. In fact, low G -values seem to be more common in pelagic environments where trophic interactions are less limited by spatial and temporal separation in prey and predator species. In contrast, high G -values are seen for species that occupy specialized habitats (e.g. reef) and thus have very limited access to the

prey resources that come into those habitats from larger areas (Walters & Martell 2004, Ahrens et al. 2012). But these patterns are not always consistent. Furthermore, each EwE model had previously been developed to simulate different historical fishing effort changes (Table 2):

(1) The CN-Pacific EwE model was developed to assess the trophic impacts of fishing and associated effects on tuna dynamics. The Ecopath model represented the trophic ecosystem during the 1990–1998 period, and has been used to parameterize a dynamic Ecosim model reflecting historical fishing effort changes from 1928 to 1998. This period was separated into 2 components: the ecosystem model was simulated as unexploited from 1928 to 1952, and then fitted on fishing effort data from 1952 to 1998 (Cox et al. 2002a,b).

(2) The Go-Thailand EwE model was designed to study the bio-economic aspects of demersal fisheries. The Ecopath model represented the trophic ecosystem in 1973, and the Ecosim model the 1973–1995 period using historical fishing effort changes. During this period, demersal fisheries' effort increased with the development of the trawl fisheries that greatly impacted resources (FAO/FISHCODE 2001).

(3) The CS-Guinea EwE model was developed to evaluate fishing impacts on the marine Guinean ecosystem. An Ecopath model was developed to represent the whole ecosystem in 1985, when fishing pressure was relatively low, and an Ecosim model to dynamically reproduce the intensification of fishing

Table 2. Parameters of 3 Ecopath with Ecosim (EwE) models used in this study

	EwE models		
	Central North Pacific	Gulf of Thailand	Guinean continental shelf
Reference	Cox et al. (2002a,b)	FAO/FISHCODE (2001)	Gascuel et al. (2009b)
Source	www.ecopath.org (EcopathMSY database)	www.ecopath.org (EcopathMSY database)	Available upon request (Didier.Gascuel @agrocampus-ouest.fr)
Represented year(s) of the base Ecopath model	1990–1998	1973	1985
Simulated year extracted from Ecosim	1951	1995	2004
Associated changes in Ecosim fleets' fishing effort (expressed as effort multipliers) used in EcoTroph simulations	– Domestic longline: 0 – Domestic purse: 0 – Pole and line: 0 – Troll: 0 – Drift net: 0 – Foreign longline: 0 – Foreign purse: 0 – Other: 0 – Turtle egg harvest: 1	– Otter board trawl: 2.412 – Pair trawl: 1.704 – Beam trawl: 0.090 – Pushnet: 1.479 – Purse seine: 1.916 – Other gears: 1.704	– Small scale fishery: 8.967 – Industrial fishery: 5.151

effort and related trophic impacts from 1985 to 2004 (Gascuel et al. 2009b). This model was also used to study the impacts of artisanal fleets and those of industrial fleets separately, but also the interactions and trade-offs when managing both fisheries (Gasche & Gascuel 2013).

These models were selected based on several criteria to ensure homogeneity between Ecosim and EcoTroph procedures. Each Ecosim model was originally parameterized using fishing effort time series and no environmental data as forcing functions, since EcoTroph only accounts for fishing changes. Moreover, no mediation functions were used in Ecosim. Finally, they represented different ecosystem types, and different patterns of fishing changes: simulation of the unexploited state for the CN-Pacific EwE model, strong increase in the fishing effort for the CS-Guinea model, and an increase in demersal fisheries effort for the Go-Thailand model.

Since the 3 EwE models were all available with vulnerabilities by default set to 2 (see Supplement 2 at www.int-res.com/articles/suppl/m534p017_supp.pdf), the Ecosim models were adjusted following a standard methodology (V. Christensen, UBC Fisheries Centre, pers. comm.). We fitted each model to time series using a routine that searches groups' vulnerabilities to reduce the sum of squared residuals compared to the supplied time series of biomass, catches, or mortality. We only searched the groups with time series, since this method seemed more pre-

cautious and avoided searching groups with no information (i.e. no time series) that can lead to unrealistic predictions (Christensen et al. unpubl. data). Then, the annual biomasses, trophic levels, and mortalities (Z) were extracted from the best-fitted Ecosim simulation (coming from the 3 EwE models), and associated trophic spectra were computed. In parallel, we computed for each EwE model an EcoTroph model of the base Ecopath model, and used it to run simulations considering the same changes in fleets' fishing effort for a specific year as in Ecosim (Table 2). These simulations were done using different values of α , ω , and G . We tested all combinations of α ranging between 0 and 1 (steps of 0.1; a null value corresponds to simulations without top-down controls), ω between 0 and 0.3 (steps of 0.1), and G between 2 and 40 (steps of 1), along with the simulations without foraging arena controls. For each simulation, the sum of squared residuals (SSR) by trophic class of the simulated biomass trophic spectra compared to the Ecosim prediction was calculated:

$$SSR = \sum_{\tau=2}^{\tau=5.5} (\log(B_{\tau}^{ET}) - \log(B_{\tau}^{EwE}))^2 \quad (7)$$

where B_{τ}^{ET} , B_{τ}^{EwE} corresponded, respectively, to the biomass of the trophic class $[\tau, \tau + \Delta\tau]$ in the EcoTroph and Ecosim simulations. This enabled us to compare EcoTroph and Ecosim predictions for the 3 EwE models, and to analyze the impacts of ET parameterization.

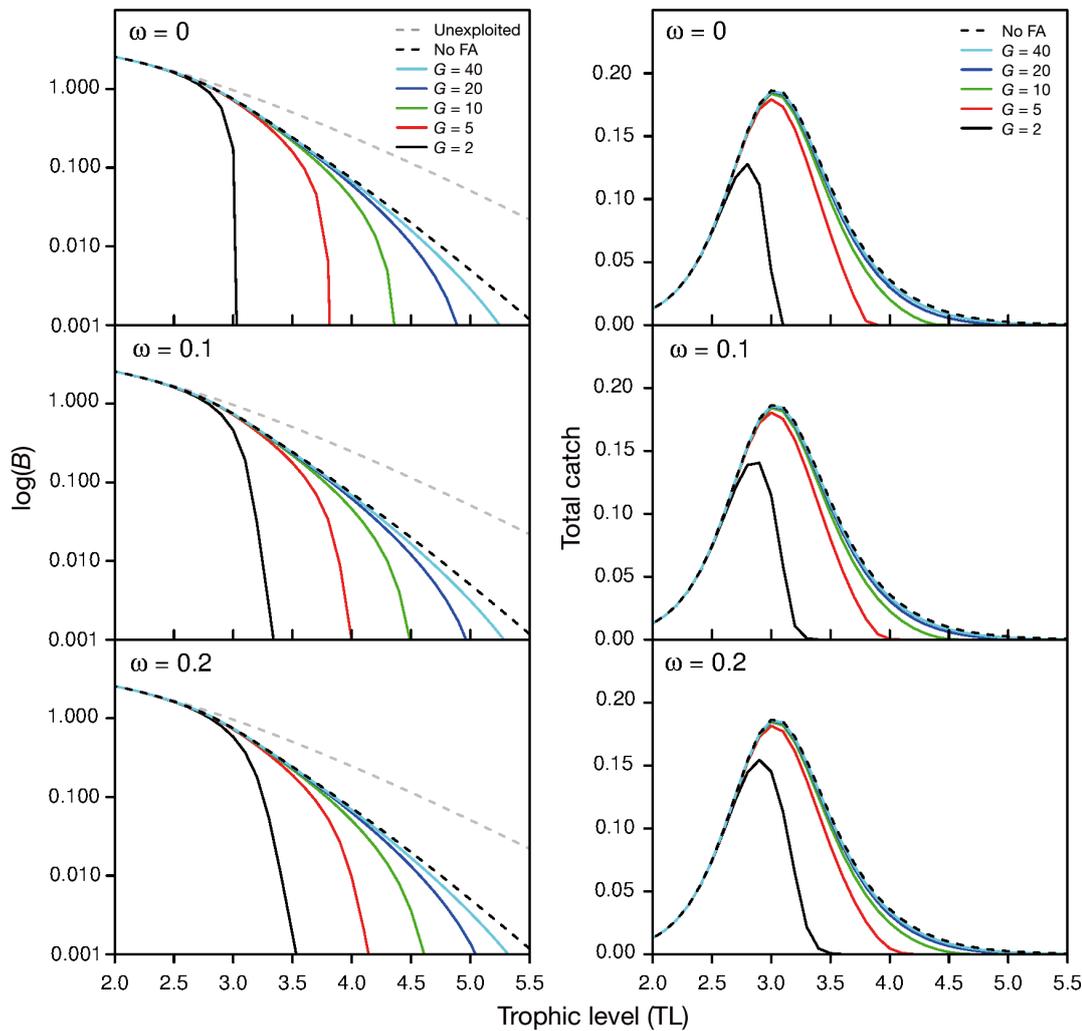


Fig. 3. Biomass (B) trophic spectra (log scale, left column) and catch trophic spectra (right column) simulated using the reference fishing scenario. Solid lines: different simulations including foraging arena controls; black dashed line: the simulation without foraging arena (FA) control; grey dashed line: the unexploited ecosystem

RESULTS

Virtual ecosystem analyses

Analysis of the 2 new parameters of the H modifier, ω and G (Eq. 5), showed that simulations were highly sensitive to G (Fig. 3). Fishing impacts simulated using the reference scenario differed between tested G -values, with a greater impact for low G - and ω -values. The most impacted biomass trophic spectra compared to the unexploited state was observed for $\omega = 0$ and $G = 2$, with a biomass of almost null for TLs ≥ 3 (Fig. 3, left column). This scenario appeared unreasonable; on the other hand, a G -value of 40 caused the model to predict similar impacts to the EcoTroph formulation without foraging arena trophic controls. Differences in fishing impact concentrated on high trophic levels (TLs ≥ 3.5), since TLs between 2 and 3.5 were impacted for the lowest G -values only. Simulated catches remained close, except for G -

values of 2 and 5 which exhibited lower catches due to the high biomass decrease for intermediate and high TLs (Fig. 3, right column).

Furthermore, effects of trophic controls aside, the various exploitation patterns impacted the unexploited ecosystem differently (Figs. 4 & 5, left columns). A fishery scenario targeting a broader part of the ecosystem ($TL_{50} = 2.5$) had greater impact on the relative predator and total biomass (respectively, 80 and 30% decreases compared to the unexploited state for $F^* = 1$) than a fishery scenario targeting only predators ($TL_{50} = 3.5$; respectively, 60 and 10% decreases; Fig. 4, top row). The mean TL of the biomass was also more impacted when the trophic level at first catch was low (Fig. 4, second row). Logically, the scenario centered on TL = 3 showed a greater impact on biomass for TLs around 3 but lower impacts for high TLs (Fig. 5, top row). In fact, the relative predator biomass was slightly impacted, and the mean TL of predator biomass increased due to a greater biomass decrease

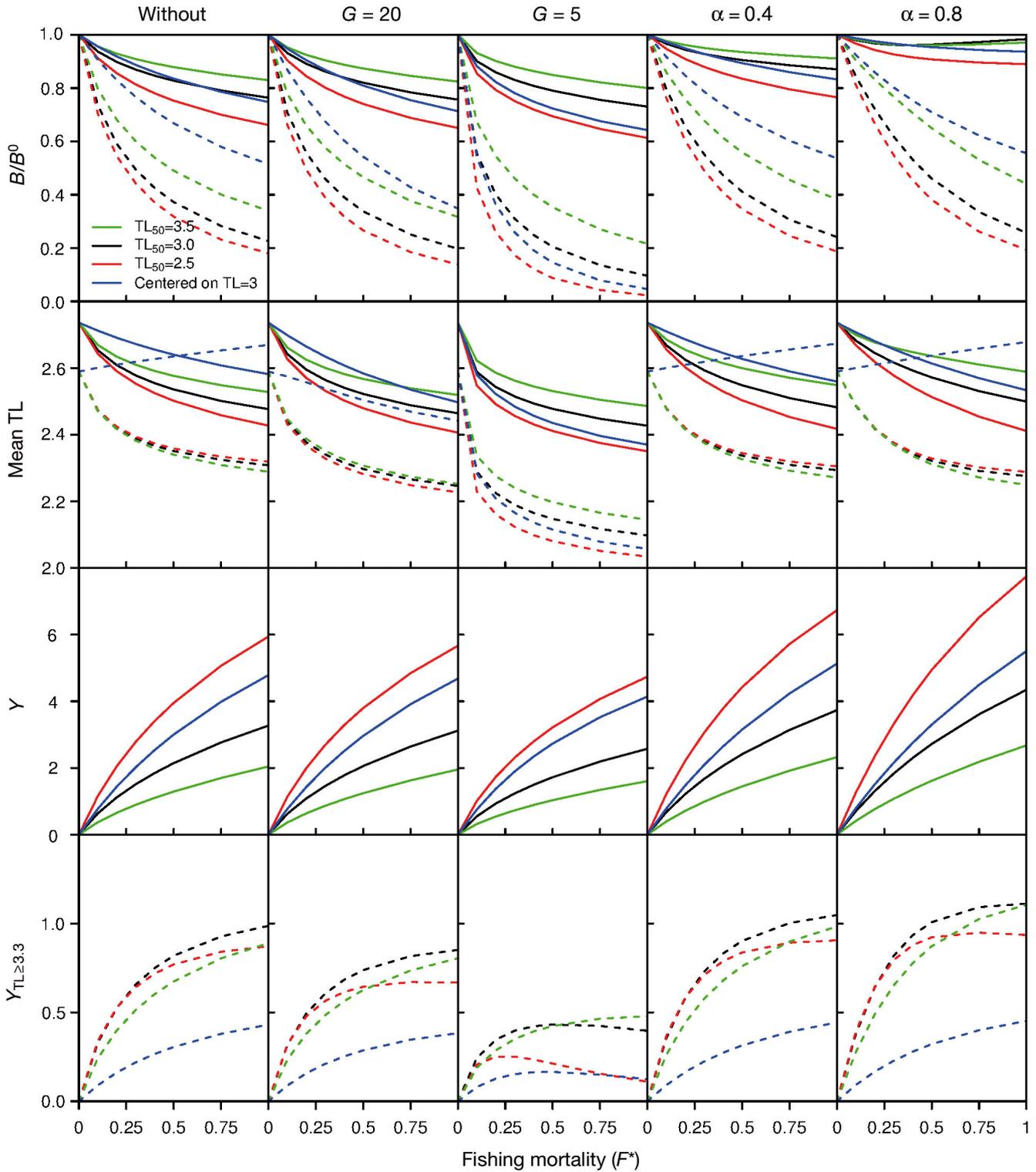


Fig. 4. Value of EcoTroph (ET) outputs as a function of the fishing mortality (F^*) used in simulation: the relative biomass and predator biomass ratios (B/B^0 and $B_{TL \geq 3.3}/B_{TL \geq 3.3}^0$, dashed lines for predator variables), the mean trophic level (TL) of the biomass and predator biomass, the total catch (Y), and the predator catch ($Y_{TL \geq 3.3}$). The left column refers to ET simulations without top-down and foraging arena controls, the subsequent 2 columns refer to ET simulations including only foraging arena controls ($\omega = 0.1$ and $G = 20$ and 5), and the 2 right columns refer to ET simulations including only top-down controls ($\alpha = 0.4$ and 0.8)

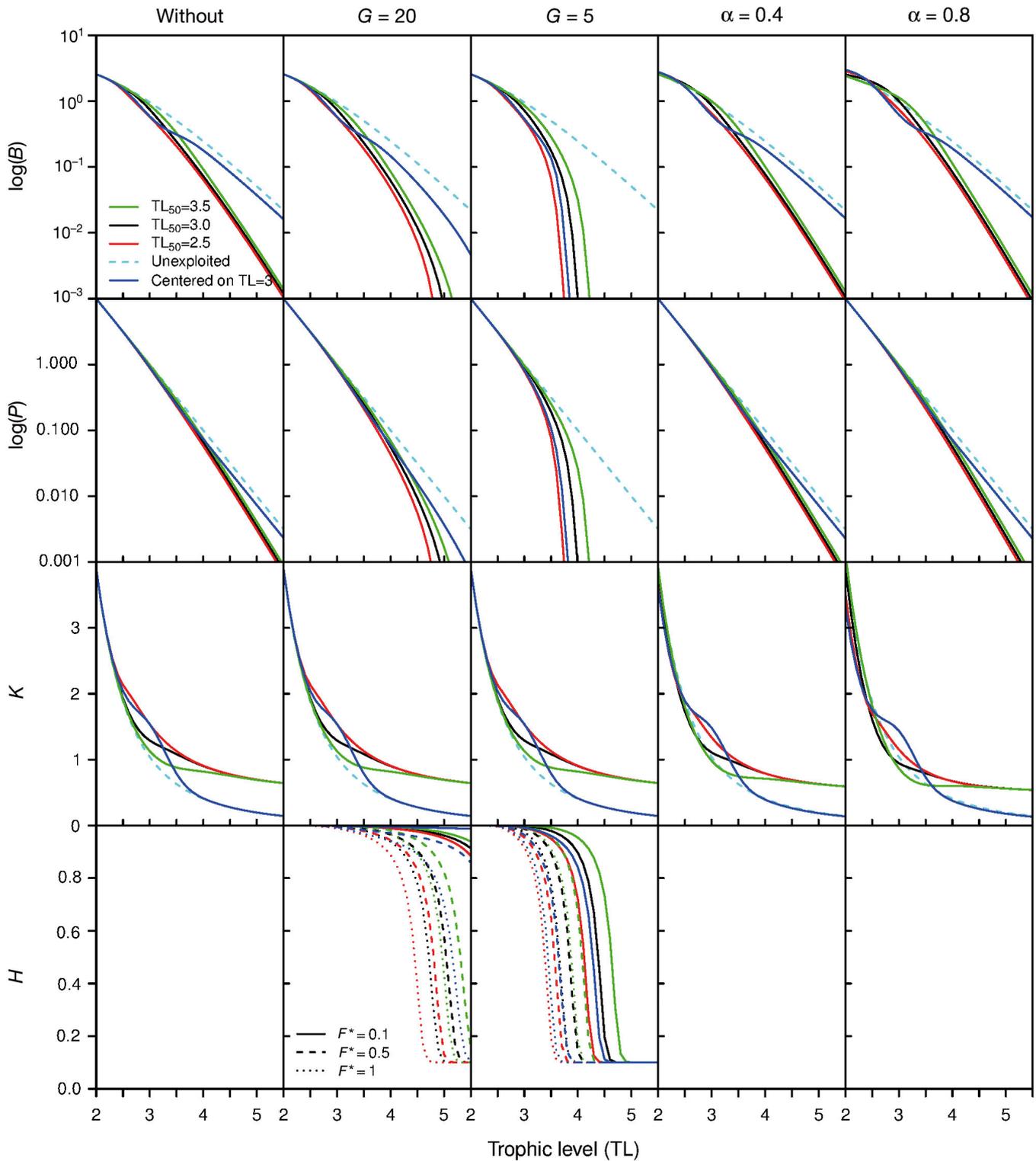


Fig. 5. Trophic spectra of the log biomass (B), log production (P), the kinetic (K , for $F^* = 0.5$), and the H modifier (for $F^* = 0.1, 0.5$ and 1) considering different exploitation patterns and EcoTroph (ET) simulations. The left column refers to ET simulations without top-down and foraging arena controls, the subsequent 2 columns refer to ET simulations including only foraging arena controls ($\omega = 0.1$ and $G = 20$ and 5), and the 2 right columns refer to ET simulations including only top-down controls ($\alpha = 0.4$ and 0.8)

for TLs around 3 (predator biomass starts conventionally at $TL = 3.3$) compared to higher TLs. These results showed that the simulated unexploited ecosystem resisted a fishing scenario targeting only predatory fishes or a specific TL range (additional fishing scenario) better when top-down or foraging arena controls were not taken into account.

Inclusion of foraging arena controls (Figs. 4 & 5, second and third columns) caused the model to predict greater impacts for all the different exploitation patterns. Results showed that decrease in biomass concentrated on high TLs, and were more important considering a strong effect of foraging arena controls (low G -value: $G = 5$; Fig. 5, top row). Overall, this resulted in less resistant ecosystems, as emphasized by greater fishing impacts on the relative biomass and mean TL ratios (compared to the left column, Fig. 4, top and second rows). The fishery scenario targeting a broader part of the ecosystem ($TL_{50} = 2.5$) still had a greater impact than the 2 other scenarios. We observed in all cases lower predator catches and lower total catches, due to lower relative predator biomasses (Fig. 4, third and last rows). The additional fishing scenario biomass trophic spectra showed a strong biomass decrease for high TLs following the fishing impact on TLs around 3.0. This was different from the previous simulation not accounting for foraging arena controls (Fig. 5, top row).

On the other hand, inclusion of top-down controls (Figs. 4 & 5, fourth and fifth columns) caused the model to predict very similar impacts for high TLs compared to the EcoTroph formulation without foraging arena and top-down controls. The relative predator biomass and mean TL remained close, whereas relative biomass increased for high F^* (Fig. 4, top and second rows). These differences showed a greater resistance to fishing impact in terms of total biomass. They were explained by a higher biomass for lower and intermediate TLs due to top-down controls (Fig. 5, top row). In fact, increase in biomass for lower and intermediate TLs resulted from the release in predation caused by the fishing-induced decrease in predator biomass.

EcoTroph simulations showed the impact of top-down and foraging arena controls on the flow kinetic K and the biomass flow (using the production P ; Fig. 5). The H modifier function of TL followed a sigmoid curve and showed greater impacts for higher TLs (Fig. 5, last row). The inflexion point and steepness of the curve were determined by the fishing scenario and mortality we used, the H modifier tending to ω for the highest TLs (see Eq. 4). As a result, foraging arena controls have little impact on the flow

kinetic (Fig. 5, third row), but a strong impact on biomass flow, with important losses of production (Fig. 5, second row). On the other hand, top-down controls directly impacted the flow kinetic but not biomass flow. It introduced a compensatory mechanism for low TLs, exploitation being at least partially compensated for by a release in predation. In parallel, predators benefited from this increase in prey abundance as a feedback effect.

Finally, we considered TL-dependent effects for the top-down and foraging arena controls. The effect of a TL-dependent top-down control (Fig. 2a) appeared to be weak for high trophic levels since biomass trophic spectra were similar for these TL classes. On the contrary, we observed increases in biomass for low and intermediate TLs ($2.3 \leq TL \leq 3.5$), with even greater values compared to the unexploited state (Fig. 6, top row, left column). The amplitude of such increases was determined by the strength and range of the top-down controls: the biomass increase was limited to $TL = 3$ for a top-down effect focusing on that specific TL class, whereas it covered a broader TL range ($2.3 \leq TL \leq 3.3$) using a step increase in α values. Exponential increase and constant scenarios for α values were slightly different, they crossed at $TL = 3$ following both α patterns (see Fig. 2a). More precisely, impacts concentrated on the K -values (flow kinetic) rather than production values (biomass flow) that changed little in the different simulations (Fig. 6, second and third rows, left column). Strong top-down controls for low and intermediate TLs decreased K -values compared to the EcoTroph simulation without top-down controls. Overall, this resulted in similar indices regarding predators' resistance, but strong top-down controls determined more resistant ecosystems in terms of total biomass and associated catches (see Supplement 3 at www.int-res.com/articles/suppl/m534p017_supp.pdf).

In contrast, the effect of a TL-dependent foraging arena control (Fig. 2b) concentrated on intermediate and high trophic levels with important biomass decreases. Biomass trophic spectra (Fig. 6, top row, right column) were similar for low TLs ($2 \leq TL \leq 2.5$) but patterns differed for higher TLs. The different G scenarios determined the amplitude and range of observed biomass decreases. Considering a strong foraging arena control on $TL = 3$ resulted in lower biomasses for $TLs \geq 3$. We observed a decrease in biomass with a step function in G_r . Exponential function and constant scenarios for G -values were slightly different, they crossed at $TL = 4.2$ following both G patterns, with a TL-shift due to the propagating effect of foraging arena controls. More precisely, foraging

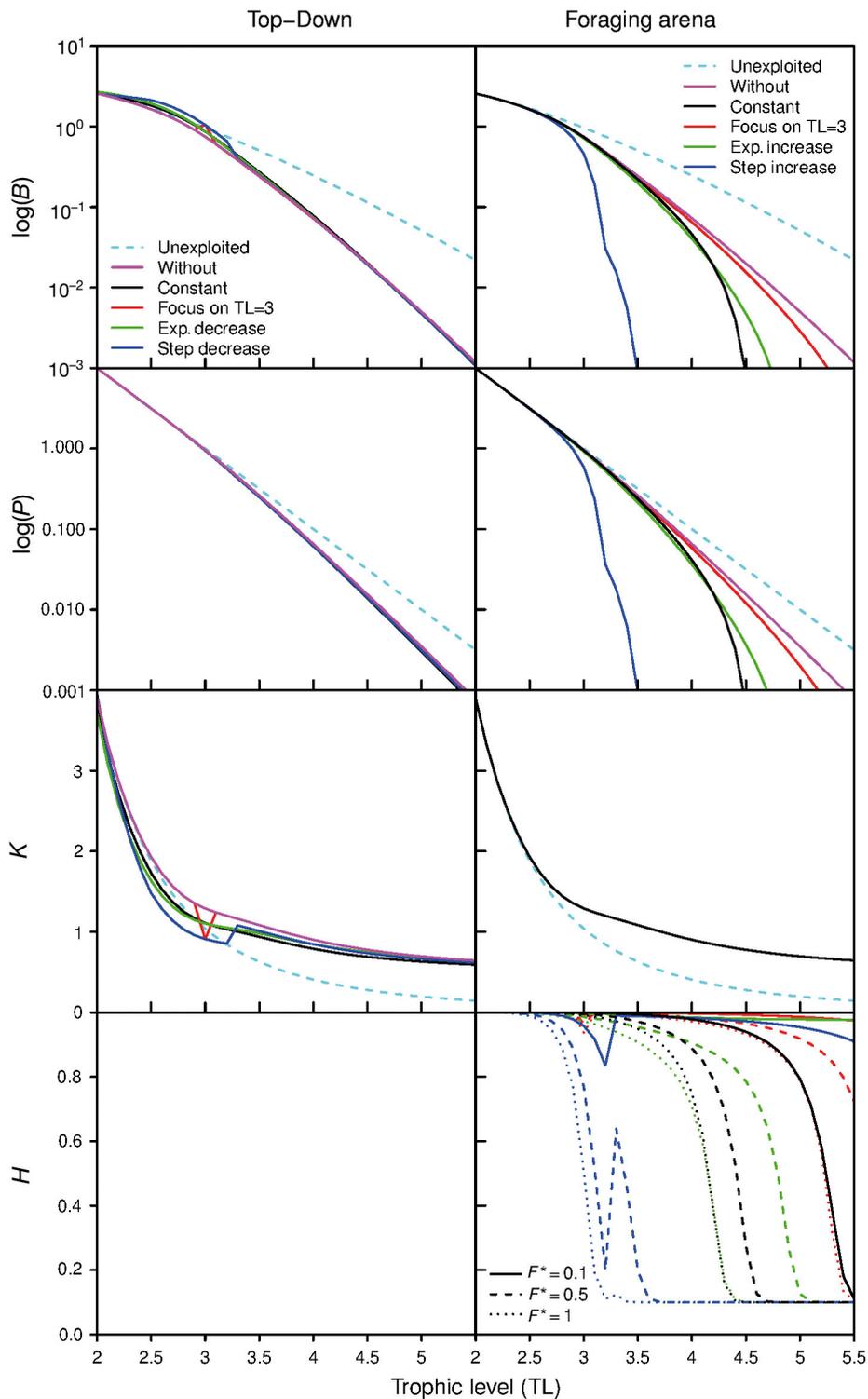


Fig. 6. Trophic spectra of the log biomass (B), log production (P), the kinetic (K , for $F^* = 0.5$), and the H modifier (for $F^* = 0.1, 0.5$ and 1) considering different trophic level (TL)-dependent effects. The left and right columns refer, respectively, to the different EcoTroph simulations with 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 unexploited ecosystem (dashed light blue line), and the simulated exploited ecosystem without foraging arena and top-down controls (purple line) are also represented

arena controls concentrated on the biomass flow (production), with changes determining biomass trends (Fig. 6, second row, right column). As a consequence, we observed different EcoTroph indices showing that strong foraging arena controls determined less resistant ecosystems in terms of total biomass, catches, and predator ratios (see Supplement 3).

Application to case studies

The virtual ecosystem analysis raised questions concerning the ET application to real case studies, and the best parameterization to simulate realistic fishing impacts. Fig. 7 shows that patterns differed between the 3 real ecosystems. The best fit when

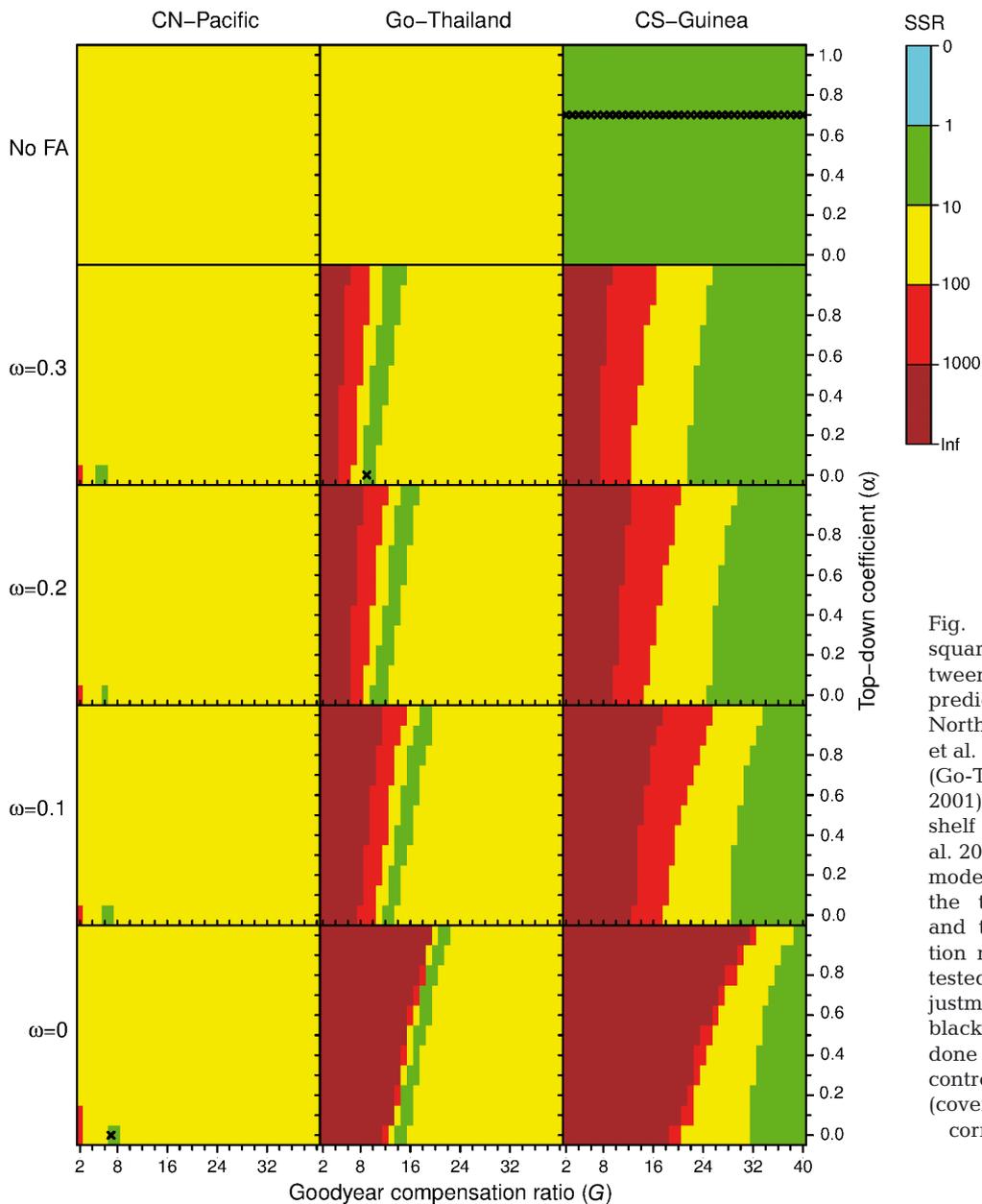


Fig. 7. Plots of the sum of squared residuals (SSR) between Ecosim and EcoTroph predictions for the central North Pacific (CN-Pacific; Cox et al. 2002a,b), Gulf of Thailand (Go-Thailand; FAO/FISHCODE 2001), and Guinean continental shelf (CS-Guinea; Gascuel et al. 2009b) Ecopath with Ecosim models. SSR is a function of the top-down coefficient (α) and the Goodyear compensation ratio (G) for the different tested ω -values. The best adjustment is represented with a black cross. For the simulations done without foraging arena controls, a row of crosses (covering all tested G values) corresponds to 1 simulation

simulating the CN-Pacific in an unexploited state (such as the year 1951 in the Ecosim dynamic model) was obtained for low G -values and no top-down controls ($\alpha = 0$). The lowest SSR values were highly localized, and the best adjustment was obtained for $\omega = 0$, $G = 7$, and $\alpha = 0$. Looking at the 10 best parameterizations (>1727 tested combinations; Table 3), it appeared that the fitting procedure was only slightly sensitive to ω -values but very much more so to G and α values ($5 \leq G \leq 8$, $\alpha = 0$ in all cases). In fact, the Ecosim model predicted a 2-fold biomass increase for TMs ≥ 3.5 compared to the Ecopath model of the recent period (Fig. 8, top row,

left column). The inclusion of foraging arena controls enabled EcoTroph to better reflect this increase in biomass in the unexploited state. However, EcoTroph-tested parameterizations were unable to model such an increase as observed in Ecosim for TMs <5. More precisely, ET was able to better simulate the increase in production in the unexploited state, but unable to simulate a sufficient decrease in kinetics as observed in Ecosim (Fig. 8, second and last rows, left column). Thus, strong foraging arena controls (low G -values) enabled us to better model and understand the increase in production for high TMs.

Table 3. EcoTroph parameters (i.e. ω and G parameters for foraging arena controls, and α for top-down controls) giving the 10 best fits (lower sum of squared residuals [SSR]) compared to Ecosim predictions

	CN-Pacific				Go-Thailand				CS-Guinea			
	ω	G	α	SSR	ω	G	α	SSR	ω	G	α	SSR
1	0	7	0	9.786	0.3	9	0	3.412	Not included		0.7	1.446
2	0.2	6	0	9.817	0.3	10	0.3	4.196	Not included		0.8	1.454
3	0.3	5	0	9.820	0.3	10	0.2	4.291	Not included		0.6	1.460
4	0.1	6	0	9.833	0.3	11	0.5	4.404	Not included		0.9	1.484
5	0.1	7	0	9.844	0.1	12	0	4.510	Not included		0.5	1.496
6	0	8	0	9.878	0.3	11	0.6	4.656	Not included		1	1.535
7	0.3	6	0	9.972	0.3	12	0.8	4.706	Not included		0.4	1.552
8	0.2	7	0	10.011	0.2	12	0.3	4.895	Not included		0.3	1.629
9	0.2	5	0	10.014	0.2	11	0	4.904	Not included		0.2	1.727
10	0.1	8	0	10.044	0.3	12	0.7	4.945	Not included		0.1	1.847

The Go-Thailand case study exhibited a different pattern. In fact, SSR values appeared to be very sensitive to G -values, but much less to α - and ω -values (Fig. 7). The best fit was obtained for $\omega = 0.3$, $G = 9$, and $\alpha = 0$. Looking at the 10 best fits (Table 3), ω -values were found between 0 and 0.3; α , between 0 and 0.8; and G , between 9 and 12. Low G -values caused the model to diverge considerably from the Ecosim prediction. Accounting for foraging arena controls enabled EcoTroph to better predict the decrease in biomass as observed for intermediate and high TLs in Ecosim (Fig. 8, top row, center column). More precisely, it enabled us to better fit the loss of production due to the increase in fishing effort, as observed in Ecosim. However, the EcoTroph- and Ecosim-simulated kinetics were different. The inclusion of constant top-down controls was not sufficient to explain the similar kinetics of Ecosim and Ecopath models observed around TL = 3.6. On the contrary, the increase in kinetics for high TLs (due to the increase in fishing effort) was consistent with EcoTroph predictions (Fig. 8, second and last rows, center column).

Finally, the CS-Guinea model showed a basically common pattern with the Go-Thailand model: SSR values appeared highly sensitive to G -values (and more precisely, inclusion or exclusion of foraging arena controls), but less sensitive to α - and ω -values (Fig. 7). In fact, the best adjustment was obtained assuming no foraging arena and strong top-down controls ($\alpha = 0.7$). The 10 best adjustments all corresponded to an EcoTroph parameterization not accounting for foraging arena controls, and covered all positive α -values ($0.1 \leq \alpha \leq 1$). EcoTroph modeled the decrease in predator biomass, and the inclusion of top-down controls enabled us to understand the relatively similar biomass for intermediate TLs compared to the Ecopath biomass trophic spectra (Fig. 8, top

row, right column). This was due to the fact that the EcoTroph production equation without foraging arena controls was sufficient to explain the loss in production for high TLs (but not for TL = 2.5; see Fig. 8, right column). Constant top-down controls enabled us to better model kinetics for high TLs. This was not the case for the intermediate TLs, since the EcoTroph kinetic equation predicted a decrease that was not observed in Ecosim or the EcoTroph parameterization without trophic controls. Thus, accounting for top-down controls enabled us to better fit kinetic changes caused by the increase in fishing effort, as observed in the CS-Guinea EwE ecosystem model.

DISCUSSION AND CONCLUSIONS

Foraging arena and top-down controls

Ecosystem modeling constitutes an important research area that is still being improved by the inclusion of complex processes and simulation procedures to evaluate fishing impacts. In the present study, results showed that accounting for 2 important trophic mechanisms, top-down and foraging arena controls, can have important consequences on ecosystem models and associated predictions. In fact, inclusion of top-down and foraging arena controls in the EcoTroph ecosystem model impacted trophic flows and the resistance of a virtual ecosystem exposed to different fishing scenarios. This impact differed between fishing scenarios: the stronger and broader the fishing pressure was, the more important effects were on biomass and production and on the resulting impacts of top-down and foraging arena controls. Results emphasized the greater loss of production and resistance when accounting for foraging arena

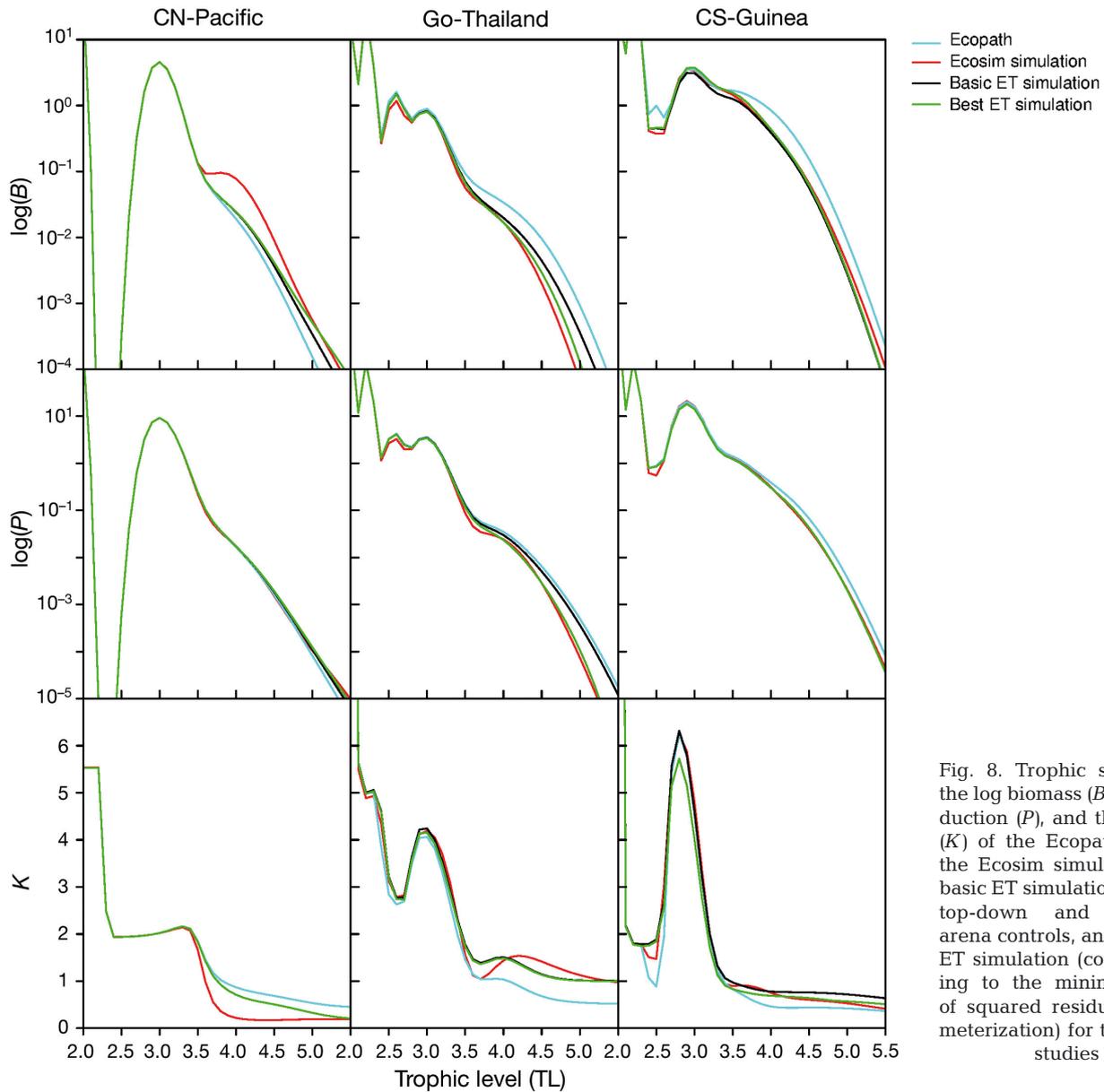


Fig. 8. Trophic spectra of the log biomass (B), log production (P), and the kinetic (K) of the Ecopath model, the Ecosim simulation, the basic ET simulation without top-down and foraging arena controls, and the best ET simulation (corresponding to the minimum sum of squared residuals parameterization) for the 3 case studies

controls. On the other hand, top-down controls affected the kinetics of biomass flows and increased the resistance to fishing impacts. These changes in production and kinetics were also TL dependent, since different scenarios of trophic control affected the TL classes differently.

EcoTroph simulations accounted for the impacts of top-down controls (Eq. 2) on ecosystem trophic flows; the extent to which top-down control occurs is an important element of ecosystem functioning. It may not replace bottom-up control, but occurs simultaneously in real ecosystems (Hunter & Price 1992, Cury et al. 2000, Borer et al. 2005). Since all animals need to eat prey, bottom-up relationships always intervene and were always considered in

the model (Gascuel & Pauly 2009). Conversely, prey are impacted by predator abundance, but this reciprocal relationship may not always apply since prey may experience little predation, depending on their behavior (Walters et al. 1997). When top-down control was considered in our simulations, fishing at a given TL impacted all other TLs by notably inducing a biomass increase at lower TLs. As fishing reduced the biomass of predators responsible for top-down controls, it slowed down prey flows, increasing their survival. Such a pattern has been observed frequently in real ecosystems, and is often considered a major indirect effect of fishing (Goñi 1998, Jennings & Kaiser 1998, Baum & Worm 2009). We showed that top-down controls could limit fishing

impacts on total biomass, even for the highest rates of exploitation, as a result of the increase in prey abundance. In other words, top-down controls could be considered as a compensation mechanism, increasing the overall resistance of ecosystems to fishing. Nevertheless, as fishing pressure increased, the simulated ecosystems changed. Top predators were the most impacted, and the mean TL of the remaining biomass decreased. Such a change constitutes a loss of functional biodiversity (Pauly & Watson 2005). As a consequence, resistance induced by top-down control could be limited, since it vanished when exploitation rates were too high. In such cases, predators disappeared and bottom-up controls became dominant. Therefore, the fishery-induced loss of top predators may change ecosystem trophic controls, the ecosystem becoming more unstable and more dependent on environmental conditions (Jackson et al. 2001, Baum & Worm 2009). Such changes have been observed both in theoretical simulations based on a dynamic version of EcoTroph (Gascuel & Pauly 2009), and in specific ecosystems (e.g. Gascuel et al. 2007). Thus, EcoTroph constitutes a useful tool to study these aspects, since it has the capability to mimic and explain observed changes through the integration of the α parameter. The effect of top-down controls on the trophic class $[\tau + \Delta\tau]$ was determined by α_τ values and changes in biomass due to fishing at TL $\tau + 1$. Different values and functions for this parameter were tested and showed sensitivity regarding fishing impacts and ecosystem indices. We therefore recommend conducting sensitivity analyses when applying EcoTroph to real ecosystems, in order to understand the possible impacts of strong or weak top-down controls on ecosystem functioning.

The analysis also accounted for the impacts of foraging arena controls (Eq. 4) on ecosystem trophic flows in conjunction with fishing impacts. Foraging arenas appear common in aquatic ecosystems and cover a wide variety of mechanisms (see review in Ahrens et al. 2012). Results predicted that including such a trophic control increased the impacts of fishing and resulted in a less resistant ecosystem. In fact, it limited the biomass flow at each TL class compared to the ET formulation without foraging arena controls, where the biomass flow Φ_τ was independent of any reduction effect that fishing may have on that TL class. Furthermore, the inclusion of foraging arena control indicated that exploitation of low TLs could decidedly impact the production and biomass of high TLs, since such control increased the interactions between trophic levels. This was dependent on the

G -value, a lower value resulting in stronger foraging arena controls. This showed that the effect of foraging arena controls propagated through TL classes, i.e. the loss of biomass flow in one TL class affected higher TL classes. This was also consistent with other studies showing that fishing low TL species can have large impacts on other parts of the ecosystem, especially on predators (Smith et al. 2011). It has also been shown that as prey numbers decline the abundances of marine predators become more variable (Plagányi et al. 2014).

As for the top-down control, an important question was the parameterization of this trophic control. We included 2 new parameters, ω and G , having different characteristics. ω was typically assumed to be low, since most biomass does not move to higher TLs simply by organisms changing their diet as they grow. ω -values ranging between 0 and 0.3 were tested, and demonstrated little sensitivity to this parameter. On the contrary, impacts on the biomass flow and related fishing effects were very sensitive to the Goodyear compensation ratio (see Supplement 2 for details on this parameter). Simulations suggested that G should be ≥ 5 to simulate reasonable fishing impacts. Values for this parameter depend on species' behaviors, and Ecosim fitting exercises tend to result in lower G -values for high TLs, i.e. stronger trophic controls corresponding to a high vulnerability to predation. In fact, high TLs tend to be more sensitive to fishing, show weaker compensatory response when fished, and involve a higher vulnerability exchange rate for their prey since they forage over a wider range of habitats (Walters et al. 1997, Ahrens et al. 2012). Low G -values are also more common in pelagic ecosystems, while high G -values are usually observed for species occupying specialized habitats (e.g. reef). When integrated at the ecosystem level, no studies have yet assessed G -values over trophic level classes for different ecosystem types. In this study, we tested different hypothetical values and shapes to gain a preliminary understanding of the impacts of foraging arena control on modeling ecosystem trophic flows and fishing effects. Furthermore, EcoTroph formulation without foraging arena controls assumed the natural losses to be independent of the ecosystem state (i.e. constant μ , see Eq. 3). This is a speculative hypothesis since it has been shown that natural losses can vary over time with changes in environment and fishing effort (e.g. Coll et al. 2009). Inclusion of foraging arena control introduces change in natural losses through the H modifier (Eq. 4) and enables the impacts of fishing on μ to be studied.

Use of EcoTroph to analyze real ecosystems

Integrating top-down and foraging arena controls enabled a better prediction of fishing impacts (increase or decrease in fishing effort) on the 3 real case studies, in relation to Ecosim historical predictions. It was hard to extract general conclusions considering the restricted number of case studies. However, our results were consistent with the basic predictions on G -values. We observed low G -values and no top-down controls for the pelagic CN-Pacific model, whereas the 2 mixed ecosystems (Go-Thailand and CS-Guinea) showed higher G -values and effective top-down controls. More precisely, the Gulf of Thailand adjustment gave G -values between 9 and 12, whereas the Guinean case study exhibited a potential low effect of foraging arena control (high G or no foraging arena control included at all). This was possibly due to the fact that the Gulf of Thailand is a shallow ecosystem (maximum depth is around 80 m), occupied mostly by demersal species (FAO/FISH-CODE 2001) and thus potentially less limited in predator–prey interactions than the Guinean continental shelf (maximum depth around 200 m), which has important demersal and pelagic biomasses occupying specific ecosystem parts (Gascuel et al. 2009b).

A comparison of biomass trophic spectra indicated that EcoTroph simulations without top-down and foraging arena controls corresponded to the trends observed in Ecosim predictions, but with different amplitudes. Inclusion of trophic controls resulted in a better fit to Ecosim predictions. The inclusion of foraging arena controls enabled us to better fit changes in production due to direct and indirect fishing impacts. It caused the ET model to predict more important losses and gains in production with, respectively, increasing and decreasing fishing effort. On the other hand, inclusion of top-down controls seemed to enable a better representation of fishing-induced changes (direct and indirect) in kinetics. This improvement was not sufficient to explain changes observed in the CN-Pacific EwE model, since the return of the biomass to an unexploited state was too strong (for predators) to be simulated by EcoTroph using the tested parameters. Looking at the production and kinetic trophic spectra, it appeared that the main differences between the best ET adjustment and the Ecosim simulation were explained by differences in the flow kinetics. A possible explanation for such differences is the fact that we only tested constant α_r values applied to the different TL classes. The use of different top-down control values for the different TL classes (varying α_r val-

ues) could enable a better adjustment, and is logical considering the different trophic properties between TL classes. This could also be implemented for the foraging arena control to better understand how this control varies between TL classes. Another possible factor is the fact that our EcoTroph results referred to steady-state conditions (ET-Diagnosis routine), whereas Ecosim is dynamically fitted on historical time series. A dynamic version of EcoTroph has also been developed (ET-Dynamic; Gascuel & Pauly 2009, Gascuel et al. 2009a), but it is currently being revised and tested on different case studies. It would be interesting to extend our framework to numerous case studies, with a comparison between Ecosim and ET-Dynamic predictions considering TL-dependent trophic controls. It could enable a better assessment of the shapes and values of α_r and G_r , but also dynamically assess their impacts on ecosystem trophic flows and fishing effects. Furthermore, using EcoTroph in order to analyze ecosystem functioning and fishing impacts on applied case studies does not present any particular conceptual difficulties. This is especially the case when EcoTroph is applied in conjunction with an EwE model.

Finally, trophodynamic models such as EcoTroph and EwE appear to be useful tools to understand and predict changes at the ecosystem scale associated with different fishing scenarios (Coll  ter et al. 2015). EcoTroph relies on a simple structure and standard equations to rapidly provide a much sought-after (by fisheries managers, politicians, scientists) general diagnosis of an ecosystem through interesting indicators and reference levels for fisheries management (see Gasche et al. 2012, Gasche & Gascuel 2013). This broad outlook should be considered as complementary to single-species or species-oriented modeling approaches, as it especially provides a generalized diagnosis of fishing impacts for all trophic levels and the entire biomass of the ecosystem. Furthermore, indices derived from food web models such as Ecopath or EcoTroph (through the use of trophic spectra) have been shown to be useful indicators to assess the ‘good environmental status’ included in the Marine Strategy Framework Directive of the European Union (Lassen et al. 2013, Rombouts et al. 2013). More generally, ecosystem models can be a strategic tool of ecosystem-based management (Sainsbury et al. 2000, Plag  nyi 2007). These models use various kinds of derived indicators to inform the user about the ecosystem’s state and the impacts of fishing or environmental disturbances (e.g. Ulanowicz 1986, Link 2002, Blanchard et al. 2005, Niquil et al. 2012, Shannon et al. 2014). Environmental

impacts can be accounted for in several ecosystem models including Ecopath with Ecosim (see reviews in Fulton et al. 2003, Plagányi 2007). In the present study, we only used EcoTroph as a steady-state model representing mean states of the ecosystem each related to a given set of parameters and drivers, whereas a marine ecosystem is constantly evolving under the influence of climate, anthropogenic influences, and interactions between species. However, it is possible to account for such direct environmental impacts as sea-surface temperature variations (on the flow kinetic; see Gascuel et al. 2008) and for such indirect impacts as changes in primary production (on biomass flow) in EcoTroph. The development of the ET-Dynamic model could help in formalizing and investigating environmental impacts and the way in which they could be integrated into EcoTroph equations (Gascuel & Pauly 2009, Gascuel et al. 2009a). In conclusion, ecosystem models allow for a better understanding of ecosystem properties and trophic functioning. In the present study, results have shown that top-down and foraging arena controls increase interactions between trophic levels and, consequently, the extent of fishing impacts. This result emphasizes the need for an ecosystem approach to fisheries (Garcia et al. 2003) in order to better assess and predict fishing impacts at the ecosystem scale.

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