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Didier Gascuel[1]*, Sylvie Guénette[1], and Daniel Pauly[2]

[1]Université Européenne de Bretagne, UMR Agrocampus ouest / INRA Ecologie et Santé des Écosystèmes, 65 rue de Saint Brieuc, CS 84215, 35042 Rennes cedex, France
[2]University of British Columbia, Fisheries Centre, Sea Around Us Project, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada

*Corresponding Author: tel: +33 223 485534; fax: +33 223 485535; e-mail: didier.gascuel@agrocampus-ouest.fr.

A trophic-level (TL)-based ecosystem modelling approach is presented, where ecosystem functioning is modelled as a flow of biomass up the foodweb through predation and ontogenetic processes. The approach, based on simple equations derived from fluid dynamics, provides insights into ecosystem functioning and the impact of fishing. A virtual ecosystem is simulated and the model shown to be capable of mimicking the effects of various exploitation patterns on ecosystem biomass expected from the theory. It provides the theoretical basis to explain complex patterns, such as cascading effects, maximum sustainable ecosystem yield, and fishing down the foodweb. The utility of the TL-based approach as a practical tool for determining fishing impacts in specific ecosystems is illustrated using the Guinean ecosystem as a case study, showing how current fishing effort levels led to full exploitation of higher TLs, confirming and generalizing previous single-species assessment results. Finally, catch trophic spectrum analysis is presented to show that it provides reliable biomass estimates when catches per TL and primary production are known.

Keywords: ecosystem modelling, EcoTroph, fishing impact, Guinea, resilience, trophic level, top-down control.

Introduction

Developing models that represent the trophic functioning of marine ecosystems is obviously a key to improving the implementation of an ecosystem approach to fisheries management. Fishing causes significant reductions in the abundance of targeted and non-targeted species, affecting their prey, predators, and competitors, then via the trophic web, the entire ecological community, with consequences depending on the type and intensity of trophic interactions (Jennings and Kaiser, 1998; Hall, 1999). Therefore, trophodynamic models need to make it possible to analyse, quantify, and forecast the impacts of fishing, and more generally human activities, on targeted resources as well as on other biological components of marine ecosystems.

One of the standard tools for ecosystem modelling is the Ecopath with Ecosim (EwE) software, developed since the mid-1990s at the University of British Columbia (Christensen and Pauly, 1992; Walters *et al.*, 1997). The model has been used worldwide for many case studies, in ecosystems of various sizes and characteristics, and contributing to a significant improvement of our knowledge of ecosystem functioning (Pauly *et al.*, 2000; Christensen and Walters, 2004). In EwE, ecosystem biomass is distributed among various trophic boxes, each including species or stages with similar production, diet, and predators. The model allows the standing biomass in each box, as well as the trophic flows between them and towards fisheries, to be quantified.

More recently, the EcoTroph model has been proposed as a simplified representation of ecosystem functioning (Gascuel, 2005; Gascuel and Pauly, 2009). Within the EwE family of models, EcoTroph may be regarded as the ultimate stage in the use of the trophic level (TL) concept for ecosystem modelling, wherein species and Ecopath functional groups are subsumed into their TLs. The EcoTroph model, by concentrating on trophic flow as a quasi-physical process, allows theoretical aspects of ecosystem functioning to be explored as a complement to EwE modelling (Gascuel and Pauly, 2009). Using equations from a preliminary version of EcoTroph, catch trophic spectrum analysis (CTSA) was developed as a method for estimating biomass and fishing mortality at an ecosystem scale, from data of catch per TL (Gascuel and Chassot, 2008).

Application of earlier versions of the EcoTroph model to real case studies led to optimistic diagnoses compared with single-species assessments. It turned out that the model was too simplistic, because it assumed the same flow kinetics equation for fishable and non-fishable biomasses. Here, we introduce two distinct flow kinetics equations: one for the whole and one for the fishable biomass, and we propose an overview of the TL-based ecosystem modelling approach. The aim was to demonstrate that such an approach, based on few assumptions and simple equations derived from fluid dynamics, provides a simplified and useful description of ecosystem functioning and the impact of fishing, theoretically and practically.

After briefly introducing the theoretical basis of the EcoTroph model, we show, through simulations of fishing impacts on a virtual ecosystem, that the model can mimic the effects of various exploitation patterns on ecosystem biomass expected from the theory. In terms of the CTSA, this method is shown to

be seen as a form of VPA (virtual population analysis) applied to ecosystems. Then, using the Guinean ecosystem as a practical case study, we demonstrate the utility of the TL-based approach to providing a diagnosis on fishing impact at the scale of an ecosystem.

The EcoTroph model and CTSA

Basis of the EcoTroph model

TLs characterize the position of organisms within foodwebs. Initially (Elton, 1927; Lindeman, 1942), ecosystems were represented as trophic pyramids, the biomass of each component of ecosystems being shoehorned into a few integer TLs: 1 for primary producers and detritus, 2 for the first-order consumers, 3 for their predators, etc. In reality, most consumers feed on different prey items, each with its own TL. As a result, these consumers have fractional TLs (Odum and Heald, 1975; Adams *et al.*, 1983), which can be calculated from

$$\tau_i = 1 + \sum_j (D_{ij}\tau_j), \tag{1}$$

where D_{ij} is the proportion of the prey j in the diet of consumer i, and τ_j is the mean TL of prey j.

The TL of an organism may change during ontogeny (Pauly *et al.*, 2001) and may also vary in time and space as the function of the prey fields it encounters. However, for any ecosystem state, the TL of each organism or the mean TL of each species emerges as the result of the trophic functioning of the ecosystem. TL therefore appears as a state variable characterizing each unit of biomass. As for species, each population is distributed across a range of TLs, according to the variability between individuals.

The first key idea of the EcoTroph model is that it deals with the continuous distribution of the biomass in an ecosystem as a function of continuous TL (Gascuel, 2005; Gascuel and Pauly, 2009). The biomass enters the foodweb at TL 1, generated by the photosynthetic activity of primary producers, and recycled by the microbial loop (Figure 1). There is no biomass between TLs 1 and 2, all animals being at a TL equal to (for herbivores and detritivores) or higher than 2. Then, at TLs >2, the biomass is distributed along a continuum of values of TL, the diet variability of the
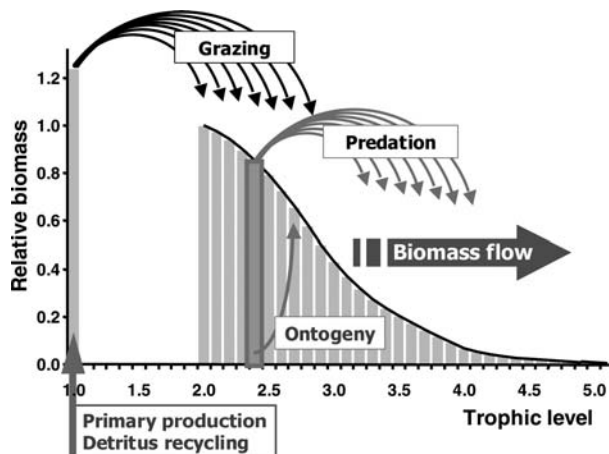
Figure 1. Diagram of the trophic functioning of an ecosystem: theoretical distribution of biomass by TL and trophic transfer processes, for an arbitrary biomass input (from Gascuel and Pauly, 2009).

various consumers usually resulting in all fractional TLs being filled. The resulting graph, i.e. the biomass distribution, expressed as a function of τ, represents a key aspect of ecosystem functioning and constitutes what is called a biomass trophic spectrum (Gascuel *et al.*, 2005).

The second key feature of the EcoTroph model is that the trophic functioning of marine ecosystems is modelled as a continuous flow of biomass surging up the foodweb, from lower to higher TLs, through predation and ontogenic processes. Each organic particle moves more or less rapidly up the foodweb according to continuous processes (ontogenic changes in TLs) and abrupt jumps caused by predation. All particles jointly constitute a biomass flow which is considered together using a continuous model (Gascuel *et al.*, 2008).

Based on the traditional equations of fluid dynamics (see the Appendix for a detailed presentation of the EcoTroph model equations), the density of biomass at TL τ (expressed in tonnes per TL) under steady-state conditions is expressed as

$$D(\tau) = \frac{\Phi(\tau)}{K(\tau)}, \tag{2}$$

where $\Phi(\tau)$ is the biomass flow, which refers to the amount of biomass that moves up the foodweb through TL τ (expressed in tonnes per year), and $K(\tau)$ is the speed of flow, which quantifies the velocity of biomass transfers in the foodweb (expressed in term of the number of TLs crossed per year).

A discrete approximation of the continuous distribution $D(\tau)$ is used for mathematical simplification and visual representation (Figure 1). As a convention (and based on preliminary tests), we consider trophic classes of width $\Delta\tau = 0.1$ TLs to be an appropriate resolution, and a range starting with TL 2 corresponding to the first-order consumers, up to TL 5, an appropriate range to cover all top predators likely to occur in marine systems (Pauly *et al.*, 1998; Cortés, 1999). Hence, the model state variable becomes B_τ, the biomass (in t) present at every moment under steady-state conditions in the $[\tau, \tau + \Delta\tau]$ trophic class. Equation (2) becomes

$$B_\tau = \int_\tau^{\tau+\Delta\tau} D(\tau)d\tau = \Phi_\tau \frac{\Delta\tau}{K_\tau}, \tag{3}$$

where Φ_τ and K_τ are the mean biomass flow (in t year^{-1}) and the mean speed of the flow (in TL year^{-1}) within the $[\tau, \tau + \Delta\tau]$ trophic class, respectively. Equation (3) indicates that biomass per trophic class, B_τ, can be deduced from two parameters: the biomass flow Φ_τ and the speed of the flow K_τ. Note that $1/K_t$ is the mean time spent by the biomass within a trophic class; it may be interpreted as the mean life expectancy of organisms, before leaving the trophic class as a result of mortality (including predation) or ontogeny.

As natural losses occur during trophic transfers (through non-predation mortality, respiration, and excretion), the biomass flow $\Phi(\tau)$ expressed as a function of TL is a decreasing function. Adding to this negative natural trend, exploitation by fisheries can be considered a diversion of one part of the trophic flow. Therefore, within a trophic class, the biomass flow equation is

$$\Phi(\tau + \Delta\tau) = \Phi(\tau)\exp[-(\mu_\tau + \varphi_\tau)\Delta\tau], \tag{4}$$

where μ_τ is the mean rate of natural loss of biomass flow within the

trophic class, and φ_τ is the mean rate of loss of biomass flow attributable to fishing. Integration of Equation (4) leads to an expression of the mean biomass flow Φ_τ within the $[\tau, \tau + \Delta\tau]$ trophic class [Equation (A6)]. Note that the term $\exp(-\mu_\tau)$ defines the transfer efficiency (TE) between continuous TLs. Equation (4) also implies that the biomass flow Φ_τ at a given TL (and therefore the corresponding biomass B_τ), depends on the flow from lower levels. In other words, Equation (4) implicitly introduces bottom-up control of prey on predators into the model.

The speed of flow K_τ must be estimated for each trophic class. First, this is done for a reference state (usually the current state), using the following two alternative methods.

(i) For practical case studies, $K_{\text{ref},\tau}$ can be derived from the production/biomass (P/B) ratios of an Ecopath model which defines the reference state (see the Guinean example below). This method is based on the use of the P/B ratio as a measure of the speed of flow (Gascuel *et al.*, 2008; see Appendix).

(ii) For theoretical studies of ecosystem functioning, or in data-poor situations where neither an Ecopath model nor field data are available, an empirical model developed by Gascuel *et al.* (2008) can be used; it expresses the P/B ratio and therefore $K_{\text{ref},\tau}$ as a function of TL and mean water temperature.

In a second step, the speed of flow for a given simulated state is calculated from the reference state using the top-down equation

$$K_\tau = [K_{\text{ref},\tau} - F_{\text{ref},\tau}]\left[1 + \alpha_\tau \frac{B_{\text{pred}}^\gamma - B_{\text{ref,pred}}^\gamma}{B_{\text{ref,pred}}^\gamma}\right] + F_\tau. \quad (5)$$

This equation takes into account the effect of fishing on flow kinetics K_τ and the effect of predators on prey. Indeed, fishing reduces the life expectancy of individuals; animals spend less time in their trophic class and hence the speed of flow is increased, according to the term of fishing mortality F_τ. As for predation, the more predators there are, the faster prey are likely to be eaten. Therefore, the speed of flow at TL τ depends partly on the abundance of predators, referred to as B_{pred}. As a consequence, Equation (5) introduces top-down control into the model. The coefficient α_τ defines the intensity of this control and may vary between 0 (no top-down control) and 1 (all natural mortality M_τ depends on predator abundance). The coefficient γ is a shape parameter varying between 0 and 1, defining the functional relationship between prey and predators.

Equations (3), (4), and (5) are used to calculate the biomass trophic spectrum B_τ for any simulated fishing pattern. Finally, catches per trophic class and per time unit are derived from previous equations, as follows:

$$Y_\tau = \varphi_\tau \Phi_\tau \Delta\tau \quad \text{or} \quad Y_\tau = F_\tau B_\tau, \quad (6)$$

where F_τ is the usual fishing mortality (year^{-1}), defined as the ratio Y_τ/B_τ and equal to $\varphi_\tau K_\tau$ [from Equations (3) and (6)]. To account for the fact that only a fraction of ecosystem biomass is usually accessible to fisheries, a selectivity coefficient S_τ estimated from field observations or from a theoretical selectivity function (see below) is added to the model. Hence, B_τ and Φ_τ are replaced by

the accessible biomass B_τ^* and the accessible biomass flow Φ_τ^* in Equation (6) (see detail in the Appendix).

In the previous version of the EcoTroph model (Gascuel and Pauly, 2009; Gascuel *et al.*, 2009a), it was assumed that the flow kinetics are similar whether or not the biomass was accessible. This assumption is unlikely to hold in reality, especially for the lowest TLs where catchable species, often the biggest ones, such as forage fish or shrimps, exhibit slower kinetics than, for instance, zooplankton, although they may share the same TL of ~2.5. Here, this aspect of the model was improved, using two distinct kinetics of trophic transfer to characterize the speed of flow in the reference state, one for the entire biomass ($K_{\text{ref},\tau}$), and the other for the accessible biomass only ($K_{\text{ref},\tau}^*$). The procedure used to define these two kinetics is described below.

Applying the EcoTroph model to a virtual ecosystem and the Guinean shelf ecosystem

The EcoTroph model was applied first to a virtual ecosystem, to analyse the theoretical impact of fishing on biomass and catch trophic spectra. Here, the unfished ecosystem is defined as the reference state using a standard set of parameter values (Table 1). For each TL, the speeds of flow $K_{\text{ref},\tau}$ and $K_{\text{ref},\tau}^*$ are calculated based on two empirical equations proposed by Gascuel *et al.* (2008), one for the flow kinetics of the overall biomass and the other for fish assumed to represent the accessible biomass kinetics (Table 1). A logistic curve was used for S_τ to mimic the increase in accessibility to fishing starting from a low value at low TLs to full accessibility at higher levels. This curve was characterized by a TL at first catch (τ_{50}, the TL for which $S_\tau = 50\%$). We then simulated the effect of increasing fishing mortalities and analysed the sensitivity of the model outputs (catch and biomass, by TL or for the whole ecosystem) to two main parameters, the strength of top-down controls (α_τ) and the TL at first catch (τ_{50}).

Next, the EcoTroph model was applied to the Guinean shelf ecosystem, where there has been a rapid and strong increase in fishing pressure over the past 25 years. Two Ecopath models, built for 1985 and 2004, respectively (Gascuel *et al.*, 2009b), were used. The models included 35 functional groups, of which 24 were fish groups defined based on their ecology (especially their diet) and available fisheries data. Data on catch and from scientific surveys were provided by the Guinean institute CNSHB (Centre National des Sciences Halieutiques de Boussoura). Based on catch reconstructions (*sensu* Zeller *et al.*, 2007) and generalized linear modelling procedures applied to the survey data, catches and biomass per trophic group were estimated for the period 1985–2004. The required model-parameter estimates (mainly P/B, Q/B, and diet) were obtained from an earlier balanced Ecopath model (Guénette and Diallo, 2004), using complementary *ad hoc* procedures detailed in Gascuel *et al.* (2009b). In the current paper, the aim is not to analyse these Ecopath models or the detailed functioning of the Guinean ecosystem, but to illustrate the utility and appropriateness of the complementary EcoTroph modelling approach.

Biomass and catch trophic spectra were built assuming for each Ecopath functional group a lognormal distribution (of biomass or catch) around the mean TL of the group (as estimated by Ecopath). The trophic spectrum is the curve obtained by summing all functional groups (see procedure in Gascuel *et al.*, 2009a); it provides a synthetic view of the underlying Ecopath model, allowing for instance global comparisons between the Guinean shelf ecosystem state in 1985 and 2004.

Table 1. Notation, definition, and values or origin of parameters used in EcoTroph model simulations or in testing the method.

Notation	Parameter	EcoTroph		CTSA
		Virtual ecosystem	Guinean ecosystem	Virtual ecosystem or Guinea
–	Reference state	Unfished	Current	Current
Φ_2	Biomass flow at TL 2	100	Ecopath[a]	CTSA[b]
$e^{-\mu}$	Trophic efficiency	10%	From Equation (4)	5 or 10%
$F_{\mathrm{ref},\tau}$	Current fishing mortality	–	From Equation (6)	CTSA[b]
F_τ	Simulated fishing mortality	$F = 0$ to 2	$mF_{\mathrm{ref}} = 0$ to 5	–
τ_{50}	TL at first catch	2.7, 3.0, 3.5	–	–
S_τ	Selectivity	Logistic[c]	Ecopath[a]	–
Φ_τ	Current biomass flow	–	Ecopath[a]	CTSA[b]
Φ_τ	Simulated biomass flow	From Equation(4)	From Equation (4)	–
$K_{\mathrm{ref},\tau}$	Flow kinetics for the total biomass	Empirical Equation (1)[d]	From Equation (3)	Empirical Equation (1)[d]
$K^*_{\mathrm{ref},\tau}$	Flow kinetics for the accessible biomass	Empirical Equation (2)[e]	From Equation (3)	Empirical Equation (2)[e]
α	Coefficient of top-down control	0 or 0.6	0.2	0.2
B_τ	Current biomass	–	Ecopath[a]	CTSA[b]
B_τ	Simulated biomass	From Equation (3)	From Equation (3)	–
Y_τ	Current catch	–	Ecopath[a]	Input data[f]
Y_τ	Simulated catch	From Equation (6)	From Equation (6)	–

[a]Input parameter from the Guinean Ecopath model (Gascuel *et al.*, 2009b).
[b]Parameters not input, but the results of CTSA.
[c]Logistic equation with asymptote 1.0, conventional value $S_\tau = 0.01$ for $\tau = 2.0$, and a slope defined by the TL at first catch (where $S_\tau = 0.5$).
[d]Input values from the empirical equation proposed in Gascuel *et al.* (2008) for all organisms: $K_\tau = 20.2\ \tau^{-3.26} \exp(0.041\ \theta)$, where θ is the mean water temperature (15 and 28°C, for the virtual and the Guinean ecosystems, respectively).
[e]Input values from the empirical equation proposed in Gascuel *et al.* (2008) for finfish: $K^*_\tau = 2.31\ \tau^{-1.72} \exp(0.053\ \theta)$, where θ is the mean water temperature (see above).
[f]Catch trophic spectrum: (i) simulated for the virtual ecosystem using EcoTroph and the default parameters of the virtual ecosystem, with $F = 0.5$ year^{-1} and $\tau_{50} = 3.0$; (ii) built for the Guinean ecosystem, from catch statistics and mean TLs per ecological group, using the smoothing procedure described in Gascuel *et al.* (2009b), with the option within-group variability = omnivory index.

The EcoTroph model was also used as a diagnostic tool to assess the impact of fishing on the Guinean ecosystem. Starting from the current situation (i.e. 2004, used as the reference state), the trophic efficiency, speed of flow and current fishing mortality were calculated from the biomass, production, and catch trophic spectrum using the inverse forms of Equations (4), (3), and (6), respectively (Table 1). Accessible biomass or flow and the related selectivity and flow kinetics were also deduced from the 2004 Guinean shelf Ecopath model, taking into account only groups fished at the time. The impact of fishing on ecosystem biomass and catches was assessed by starting with the current situation and applying a range of fishing mortality multipliers (from 0 to 5).

Catch trophic spectrum analysis

TL-based models can be viewed as a transposition of an age-structured model onto an ecosystem scale. Indeed, classical biomass and yield-per-recruit models (Beverton and Holt, 1957) may be considered as flow models, where fish move from one year class to the next as a function of their age. The EcoTroph model was initially built using the same logic and equations, with biomass entering the ecosystem at TL 1 (as primary production and detritus recycling, which were treated as analogous to recruitment to the system), then moving from one trophic class to the next (Gascuel, 2001). Of course, this reinterpretation involved some modifications of key equations, the major one being the replacement of the time (age) dimension by TL; additional equations were also introduced, notably to link the flow Φ_τ and the biomass B_τ [Equation (3)] or to take into account the feedback effects caused by top-down control [Equation (5)].

This analogy was used to adapt VPA (Gulland, 1965), and its close relative cohort analysis (Pope, 1972), to the needs here. Indeed, in analogy with Pope's reasoning, we assumed that the catch in the interval $[\tau, \tau + \Delta\tau]$ occurs precisely at the midpoint of the trophic class, i.e. at $\tau + \Delta\tau/2$. The biomass flow just before and after that midpoint of the trophic class are then $\Phi(\tau)\exp(-\mu_\tau \Delta\tau/2)$, and $\Phi(\tau + \Delta\tau)\exp(\mu_\tau \Delta\tau/2)$. The difference between these two values is equal to the catch of the trophic class over a unit of time. From this, we deduce

$$\Phi(\tau) = \Phi(\tau + \Delta\tau) \exp(\mu_\tau \Delta\tau) + Y_\tau \exp\left(\frac{\mu_\tau \Delta\tau}{2}\right), \qquad (7)$$

which is equivalent to Pope's (1972) formulation. Therefore, assuming the steady-state conditions, Equation (7) allows us to back-calculate biomass flow, its value at TL τ being deduced from the value at TL $\tau + \Delta\tau$ and from the observed catch Y_τ. Furthermore, the corresponding fishing flow loss rates φ_τ and fishing mortalities F_τ are calculated using the reverse form of the flow equation [Equation (4)].

In summary, CTSA requires as inputs the catches per TL Y_τ, values for TE, flow kinetics in the reference state, and the coefficients of the top-down equation. Also, as in cohort analysis, computations must be initialized for the highest TL with an estimate of terminal fishing loss. Then, for each TL τ, biomass flow Φ_τ, fishing flow loss φ_τ, biomass B_τ, flow kinetics K_τ, and fishing mortality F_τ are estimated recursively from values at level $\tau + \Delta\tau$ using Equations (7), (4), (3), (5), and (6), respectively. As B_τ and K_τ are interdependent, the system of equations needs to be solved iteratively.

The CTSA method was first tested on simulated catches using as input the theoretical catch trophic spectrum resulting from EcoTroph simulations and standard parameter values from Table 1. The convergence of the CTSA for biomass and fishing mortality estimates was investigated, with computations initialized using different values of terminal fishing mortality (from 0.2 to 1.0 per year). We also explored the sensitivity of the method, using as input catch data simulated with non-standard parameter values for TE, flow kinetics, and intensity of top-down controls (right column in Table 1).

Next, we applied the CTSA method to the Guinean case study. For that, the current (i.e. 2004) Guinean catch spectrum was the only observed data used as input. Flow kinetics, TE, and intensity of top-down controls were all assumed to be equal to the standard empirical values in Table 1. We therefore explored the ability of the method to provide reasonable estimates of ecosystem biomass and fishing mortality relative to earlier Ecopath-derived estimates.

Results
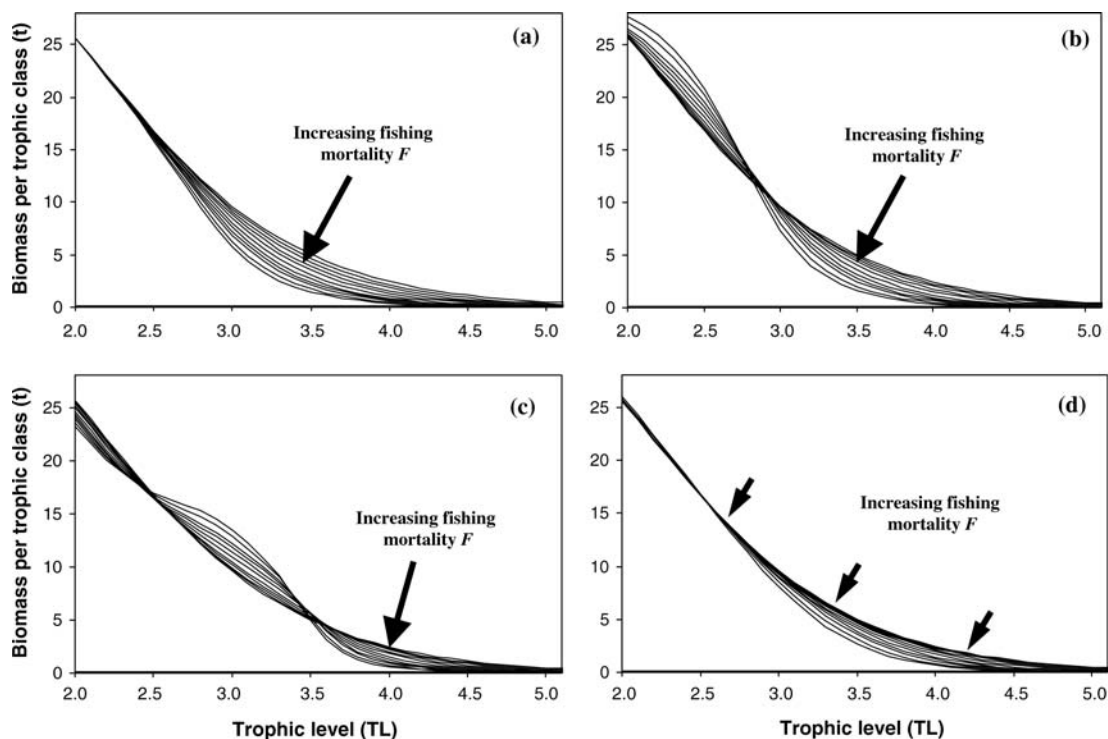### Theoretical impact of fishing on ecosystem biomass
The use of the current modified version of the EcoTroph model, including two distinct flow kinetics for accessible and inaccessible biomasses, did not modify the basic results obtained in terms of the behaviour of the model and the theoretical impact of fishing on ecosystems described in detail in Gascuel and Pauly (2009). The main modelling results are summarized here, focusing on the impact of increasing fishing mortality and various fishing patterns on the biomass trophic spectrum of the simulated ecosystem.

Increasing fishing pressure resulted in a decrease in biomass flow. In addition, the model took into account the effect of fishing mortality on the life expectancy of organisms and hence on their flow kinetics. Eventually, the two effects cumulate and contribute to a decrease in biomass per trophic class (Figure 2). This decrease is particularly strong at high TLs, because these are affected by both the loss of prey and the direct impact of fishing.

In a bottom-up ecosystem with no feedback effect of predators on prey, only the exploited TLs were influenced by fishing (Figure 2a). Exploitation had a great impact on the entire ecosystem and led to biomass depletion. Using the standard selectivity curve S_τ (i.e. with $\tau_{50} = 3.0$), we simulated a reduction in total ecosystem biomass reaching 25%, with a >85% decrease for predators (conventionally defined as all TLs >3.5; Pauly and Watson, 2005).

In a top-down ecosystem, fishing changed the abundance at all TLs (Figure 2b). The fishery-induced decrease in predator abundance led to a release of predation, which induced a decrease in the flow speed of the prey (whose life expectancy increased) and hence an increase in prey biomass. Additionally, predators benefited from the increase in their prey and were slightly less affected than in the strictly bottom-up-driven ecosystem scenario.

In a top-down controlled ecosystem, additional insights can be obtained from changing the fishing patterns. Targeting only high TLs ($\tau_{50} = 3.7$) resulted in a cascade effect caused by a decrease in top predators, which induced an increase in prey biomass at intermediate TLs, whereas the prey of the prey decreased (Figure 2c). Conversely, low selectivity, simulating a fishery targeting a large range of TLs, led to fairly constant biomass values for all

Figure 2. Theoretical impact of increasing fishing mortality on the biomass trophic spectrum (i.e. the biomass distribution over TLs) in a theoretical virtual ecosystem. Arrows indicate the effect of increasing fishing mortality, from $F = 0$ to $F = 1$ year^{-1}. (a) Bottom-up ecosystem ($\alpha = 0$); (b–d) top-down ecosystem ($\alpha = 0.6$). In (a) and (b), the TL at first catch τ_{50} is equal to 3, allowing for comparison of the fishing impact in a bottom-up and a top-down ecosystem. In (c), a cascade effect is simulated, using a high TL at first catch ($\tau_{50} = 3.5$), and (d) illustrates a more sustainable fishing pattern, with a wide range of TLs targeted ($\tau_{50} = 2.5$), inducing a low impact on the ecosystem.

prey, the predation release by top predators being more or less compensated for at intermediate and low TLs (Figure 2d). This suggests that, where there is top-down control, applying a low fishing mortality to a wide range of TLs may be a way to minimize the fishing impact on exploited ecosystems.
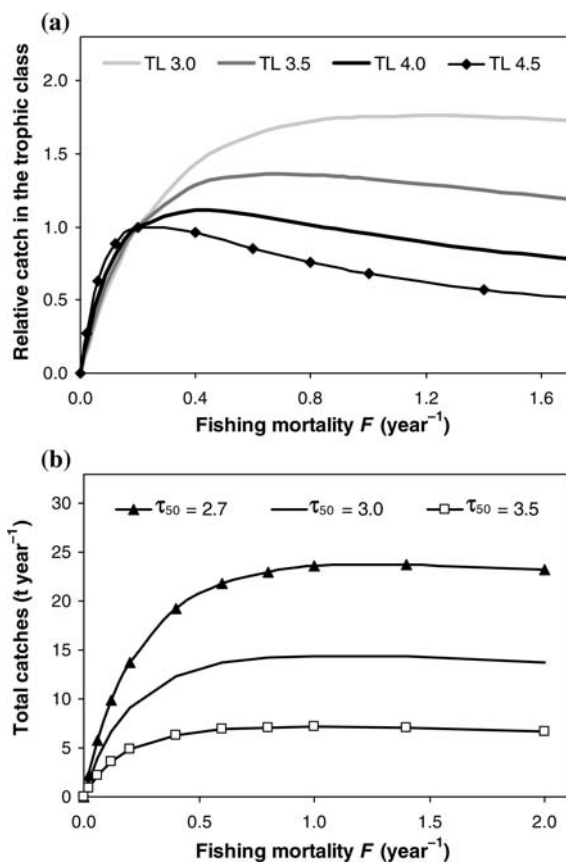
Theoretical catch simulations

The theoretical simulations underscored the fact that low TLs, characterized by high productivity, can generate large catches when exploitation rates are strong (Figure 3a). Conversely, high TLs were more sensitive to fishing and the first to be overexploited when fishing effort increased. In our simulation with flow kinetics for a temperate ecosystem, full exploitation was reached with $F_{MSY} = 0.25$ year^{-1} for TL 4.5, with $F_{MSY} = 0.4$ year^{-1} for TL 4.0, and with $F_{MSY} = 0.7$ year^{-1} for TL 3.5. This greater sensitivity of high TLs resulted from the decrease in the flow kinetics as a function of TL. Hence, when fishing effort increased, predators tended to disappear and the catch increasingly originated from the lowest targeted TLs. Therefore, the residual biomass in the ecosystem and the mean TL of the catch decreased, leading to fishing down marine foodwebs (Pauly *et al.*, 1998).

Simulations showed that total catches, expressed as a function of fishing mortality, exhibited a curve that was very flat, but with a maximum value identifying something akin to maximum


Figure 3. Theoretical simulations of (a) relative catches by trophic class (each curve referring to one trophic class), illustrating the greater sensitivity of high TLs to overexploitation (simulations for a bottom-up ecosystem and $\tau_{50} = 3.0$; values of Y_τ are standardized to 1 for $F = 0.2$ year^{-1}); (b) relationship between total ecosystem catch and fishing mortality for three mean TLs at first capture.

sustainable ecosystem yield (MSEY; Figure 3b). High fishing mortalities resulted in a decrease in total ecosystem catch, the model mathematically tending to zero for a fishing mortality equal to infinity. The value of F_{MSEY} depended on the exploitation pattern, and the higher the mean TL at first capture, the more easily overfishing occurred. In the simulations, overexploitation arose from $F_{MSEY} = 1.0$ on when targeting only high TLs ($\tau_{50} = 3.5$), and from $F_{MSEY} = 1.3$ when targeting also lower TLs ($\tau_0 = 2.7$). Additionally, for a given value of F, the lower the TL at first catch the higher the catch, because low TLs are characterized by large biomass and fast turnover. In this case, however, the fishing impact on the ecosystem was higher, especially for the accessible part of the biomass.

The fact that the production function at the ecosystem scale was characterized by a very flat curve around the maximum yield is also important. Large catches were derived for a wide range of fishing mortalities, because of the replacement of high TLs by low TLs when fishing pressure increased. Such simulations may represent the situation observed for many fisheries in the world, where the total catch (all species) remained more or less constant over decades, while the fishing pressure increased continuously. As species are overexploited (and sometime collapse), new ones are caught, often at lower TLs. Conversely, the flat curve implies that catches close to MSEY (and probably of high profitability) were observed with moderate levels of fishing mortality. The value of $F_{0.1}$, conventionally used to define the limit of full exploitation, was estimated at 0.5 and 0.7 year^{-1}, for $\tau_{50} = 3.5$ and 2.7, respectively.

Testing the CTSA on simulated data

Estimates based on simulated data show that the CTSA method retained the well-known convergence property of classical cohort analysis (Figure 4). As expected, using the true value of terminal fishing mortality, the CTSA routine led to estimates of ecosystem biomass per trophic class, fishing loss rate and fishing mortality equal to the input data used for simulation. A single value of terminal fishing mortality (the "correct" one) allowed us to estimate a curve with constant values for high TLs, linked to the logistic shape of the selectivity curve. For other values, convergence was observed and the relative error in estimated F decreased with decreasing TL. Biomass estimates also converged, leading to estimates for TL 2 which were relatively independent of terminal fishing mortality. We also observed, in analogy to cohort analysis, that the higher the fishing mortality, the faster was the convergence. In other words, the more intensively exploited the ecosystem, the more reliable the estimates from CTSA will be.

Sensitivity analyses showed that CTSA estimates were significantly affected by the values of the input parameters (Figure 5).

(i) The extent of top-down control had the least impact on the estimates (Figure 5c). Using a mean parameter ($\alpha = 0.4$) for CTSA computations when in reality the system was completely bottom-up ($\alpha = 0$) or top-down driven ($\alpha = 0.6$) resulted in a relative error in fishing mortality estimates up to 25%. At the same time, however, biomass flow estimates were close, with relative errors <5%.

(ii) Transfer kinetics had a significant effect on fishing mortality and biomass estimates but, because of the structure of the EcoTroph model, they did not affect the estimates of biomass flow (Figure 5b). Assuming a flow kinetics model based on a mean water temperature of 15°C while the true
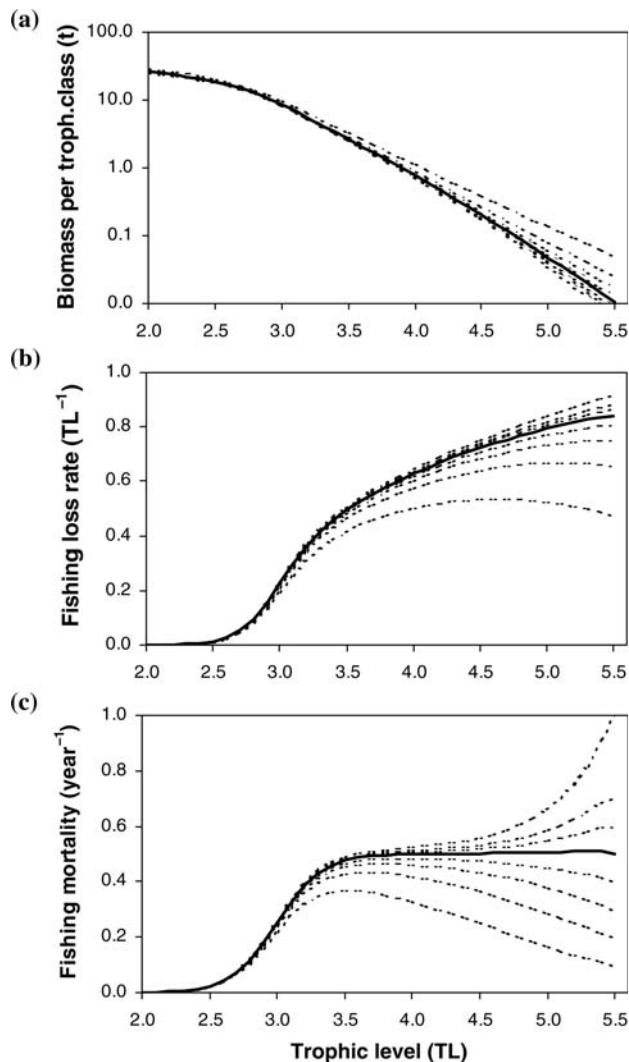
Figure 4. Illustration of the convergence properties of CTSA for lower TLs based on simulated data: (a) biomass estimates, (b) fishing loss rate estimates, and (c) fishing mortality estimates. Solid lines refer to the true values of the parameters and to estimates based on the "correct" terminal fishing mortality, and dotted lines refer to estimates based on erroneous input values for terminal fishing mortality.

values were 5 or 25°C induced a relative estimation error of ~50% for fishing mortality and biomass estimates.

(iii) TE had the greatest impact on CTSA estimates (Figure 5a). Assuming TE of 10% while the true value was 7 or 15% induced relative errors >100% for the three parameters estimated. The absolute errors were particularly high for low TLs where there was no exploitation and where, therefore, the flow and biomass estimates depended heavily on the assumed TE.

Finally, biomass estimates were very sensitive to the input parameter values for CTSA computations. Conversely, this means that if the shape of the biomass distribution or the absolute value of biomass or biomass flow at TL 1 or 2 were available as independent estimates (for instance primary production estimates from remote-sensing imagery), the CTSA could be calibrated and should provide reliable estimates for higher TLs.

Guinean case study

The synthetic representation of the Guinean Ecopath model using the EcoTroph model clearly highlighted the global decline in the biomass of the various trophic groups between 1985 and 2004 (Figure 6, top), whereas catches and fishing mortality increased fivefold (Figure 6, bottom). The decrease in biomass was especially pronounced at the highest TLs. Indeed, in recent years, groups of TLs >4 targeted by both fishing fleets (industrial and small-scale) experienced heavy fishing pressure and were submitted to the highest fishing loss rates. Conversely, low TL groups (i.e. mainly the Bonga shad *Ethmalosa fimbriata*) were exploited only by the small-scale fishery, with moderate fishing mortality and very low fishing loss rates.

EcoTroph was also used to assess the impact of fishing on the Guinean ecosystem (Figure 7). In contrast to the simulated ecosystem, based on constant values for the loss rates μ or φ and a monotonic empirical function of flow kinetics, the shapes of the biomass and catch trophic spectra were irregular (Figure 7a and b). Nevertheless, fishing effects in that specific case appeared consistent with the theoretical simulations (compare especially Figures 2 and 3 with Figure 7).

Interestingly, the results showed that current levels of fishing effort led to a decrease in abundance compared with the unexploited ecosystem (multiplier equal to zero; Figure 7c), consistent with estimates from scientific surveys. Indeed, the model highlighted a threefold fishing-induced reduction in the current biomass of higher TLs, whereas estimates based on demersal surveys decreased two- to threefold between 1985 and 2004, depending on the groups considered, year 1985 being considered close to the virgin state in this ecosystem (Gascuel *et al.*, 2004, 2007).

The decrease in abundance of higher TLs indicated their full exploitation (Figure 7d) and induced a significant decrease in the mean TL of both total biomass and catches. These results confirm and generalize previous single-species assessments (Gascuel *et al.*, 2004; Sidibé *et al.*, 2004). Forecasts suggest that higher yields might be obtained by exploiting lower TLs, but this would induce a greater impact on ecosystem biomass and a stronger decrease in mean TL (see theoretical simulations).

Finally, CTSA was used as a stand-alone routine to estimate the current and the unexploited biomass of the Guinean ecosystem, independently of any Ecopath model or survey data (Figure 8). Assuming a mean TE and a monotonous regular-flow kinetic model, the biomass trophic spectrum resulting from CTSA had a regular shape, somewhat different from those obtained from survey data or the Ecopath model. Nevertheless, the CTSA estimates appeared consistent with the results of the Ecopath model. Biomasses were of the same order of magnitude, and the decrease caused by fishing was also estimated at about threefold for the higher TLs. Diagnoses based on the CTSA estimates (not shown) were close to the results based on trophic spectra built from the Ecopath model, so still consistent with the knowledge derived from single-species assessments.

Discussion
Revised EcoTroph model

In the present version of the EcoTroph model, we relaxed the assumption of single flow kinetics for both accessible and inaccessible biomasses. Using the same mean flow kinetics for the whole biomass, as in the previous EcoTroph version (Gascuel and
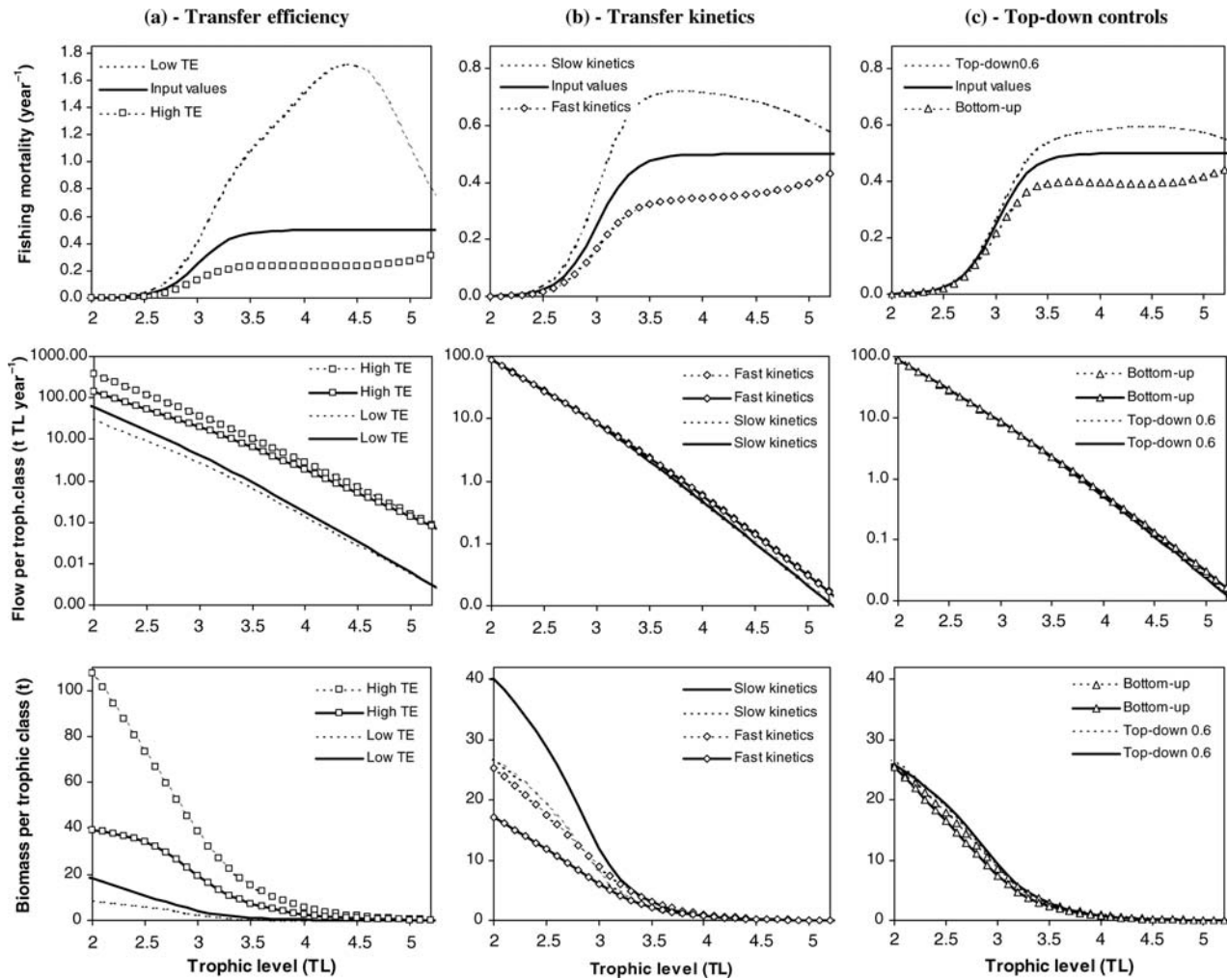
Figure 5. Sensitivity analysis of CTSA estimates (fishing mortalities, biomass flow, and biomass per trophic class) to the three main input parameters: mean TE, flow kinetics, and the intensity of top-down controls. Solid lines refer to the true values (based on non standard input parameters), and dotted lines are the estimates based on the standard (and hence erroneous) parameters. Note that the true values of fishing mortality were the same for all simulations (top row), whereas the true values changed between simulations (middle and bottom row).

Pauly, 2009), led to an overestimate of turnover and hence to an overestimate of the potential catches at low TLs. Using an empirical equation initially proposed only for finfish (Gascuel *et al.*, 2008) for the whole accessible biomass is still not totally satisfactory, although it improves the realism of estimates compared with previous results, especially for F_{MSEY} values at the ecosystem scale, or the values of F_{MSY} for each trophic class. Estimates of F_{MSY} equal to 0.25 and 0.4 year^{-1} for TLs 4.5 and 4.0, respectively, are in the same range as real values observed in European waters for many fish stocks (gadoids, anglerfish, flatfish, etc.; ICES, 2009).

When an Ecopath model is available, such as in the Guinean case study, flow kinetics can be derived directly from the model, for the whole biomass or for the exploited groups only, i.e. for the accessible biomass. Then, the subsequent EcoTroph analysis inherits all the assumptions used in the Ecopath model and simulations, and diagnoses only refer to a given pattern of exploitation, defined by the currently exploited groups and referring to steady-state conditions. In the case study here, such an approach led to very realistic diagnosis on ecosystem exploitation state, whereas first attempts to use the model with a unique flow kinetics

equation resulted in inconsistent estimates, especially for low TLs (unpublished results).

Top-down control and ecosystem resilience

Here, theoretical simulations focused on the effects of bottom-up and top-down controls on ecosystem resilience in conjunction with fishing. Although the extent to which top-down control occurs is an important element of ecosystem functioning (Hunter and Price, 1992; Sala *et al.*, 1998; Cury *et al.*, 2000, 2003), it may not replace bottom-up control but occur simultaneously in real ecosystems. Predators always depend on their prey, because all organisms need to eat. Hence, bottom-up relationships always intervene and are always considered in the model. Conversely, prey is impacted by predator abundance, but this reciprocal relationships may not always apply, because certain (potential) prey may experience little predation, depending on their behaviour (Walters *et al.*, 1997).

When top-down control was considered in the model, fishing at a given TL impacted all other levels and notably induced a biomass increase at lower TLs. Such increases have often been
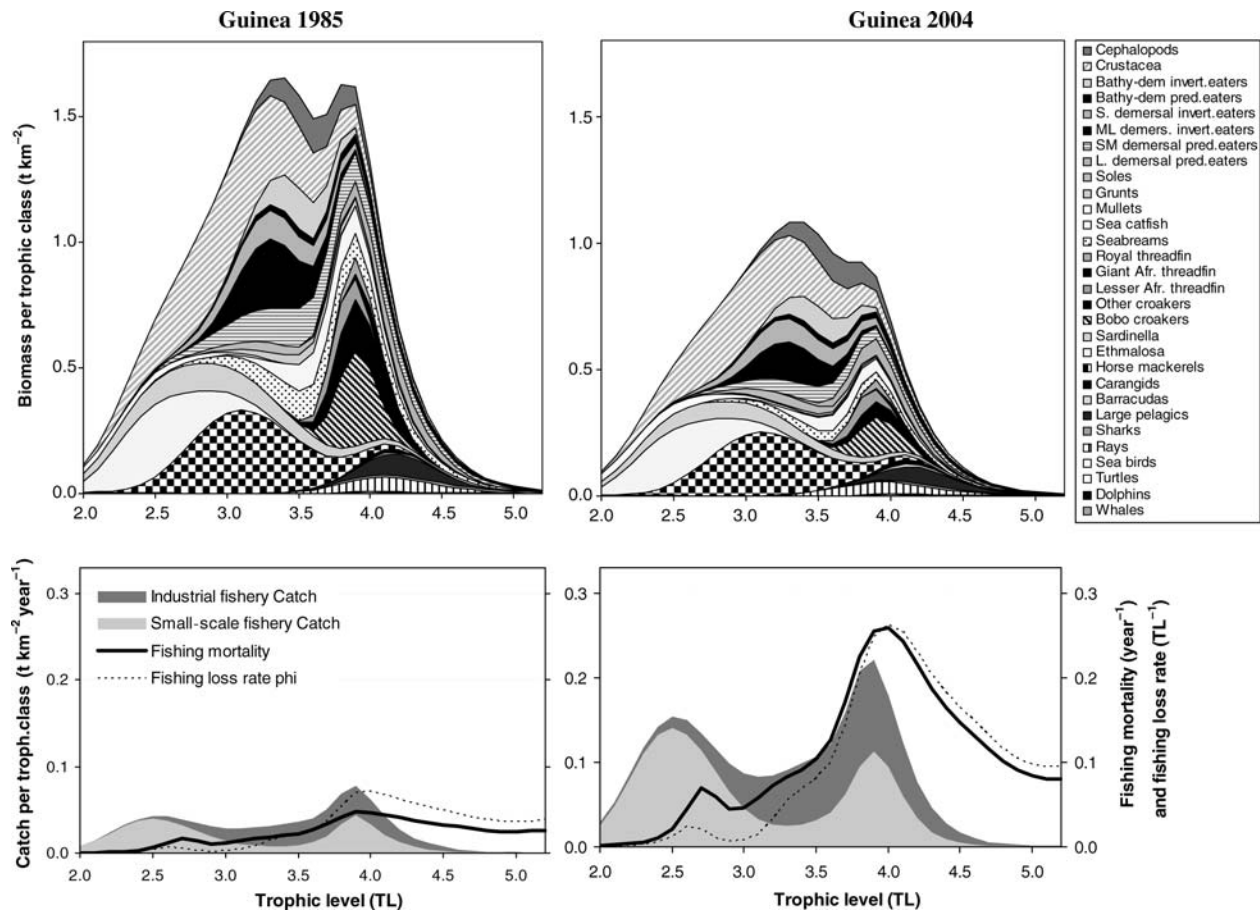
Figure 6. Representation of two Guinean Ecopath models, for 1985 (left) and 2004 (right), as interpreted by the EcoTroph model: (top) biomass distribution by Ecopath group over TLs (small zooplankton and detritus were removed for clarity; group names refer to the dominant species); (bottom) catch per fishery, fishing mortality, and fishing loss rate by TL.

observed in real ecosystems and are generally considered a major indirect effect of fishing (Goñi, 1998; Jennings and Kaiser, 1998; Hall, 1999). In West Africa for instance, rapid increases in fishing pressure in recent decades led to severe overexploitation of upper TL species and are responsible for an increase in the abundance of species at lower TLs, such as octopus and penaeid shrimp (Caverivière, 1994; Laurans *et al.*, 2004; Gascuel *et al.*, 2005). Conversely, fisheries-induced cascade effects, involving increasing biomass at intermediate TLs and a decrease for lower TLs, are more difficult to observe in real ecosystems (Pace *et al.*, 1999; Pinnegar *et al.*, 2000; Cury *et al.*, 2003). The EcoTroph model suggests that such cascade effects can only be found if there are top-down controls for all TLs and with certain fishing patterns, strictly and strongly targeting the highest TLs (Figure 2c).

As a result of the increase in prey abundance, top-down control led to limited fishing impacts in total biomass, even for the heaviest rates of exploitation. In other words, top-down controls can be considered a compensation mechanism, increasing the overall resilience of ecosystems to fishing. Nevertheless, as fishing pressure increases, the ecosystem is changed. Top predators are the most affected, and the mean TL of the remaining biomass decreases. Such a change constitutes a loss of functional biodiversity (Pauly and Watson, 2005). As a consequence, resilience induced by

top-down control is limited, and it vanishes when exploitation rates are too high. In that case, predators disappear and bottom-up controls become dominant. Therefore, the fishery-induced loss of the top-predation functions may change global ecosystem controls, the ecosystem becoming more unstable and more dependent on environmental conditions. Such changes have been observed both in theoretical simulations based on a dynamic version of EcoTroph (Gascuel and Pauly, 2009) and in specific ecosystems. For instance, we have observed a significant correlation between the total demersal biomass estimated for Mauritania from surveys and the intensity of annual upwelling, the correlation only occurring in recent years, after the ecosystem has been over-exploited and the demersal biomass severely depleted (Gascuel *et al.*, 2007).

Gascuel and Pauly (2009) showed that increasing TEs lead to greater fishing impact on total biomass, because of the change in biomass distribution: high TEs lead to high predator abundance, which are most affected by fishing. As for flow speed, ecosystems characterized by high flow speed appear to be less sensitive to fishing pressure because biomass regeneration is faster, more readily compensating for fisheries removals. Finally, the theoretical simulations have shown that low TEs, fast transfers, and strong top-down controls may contribute to the resilience of fished marine ecosystems.
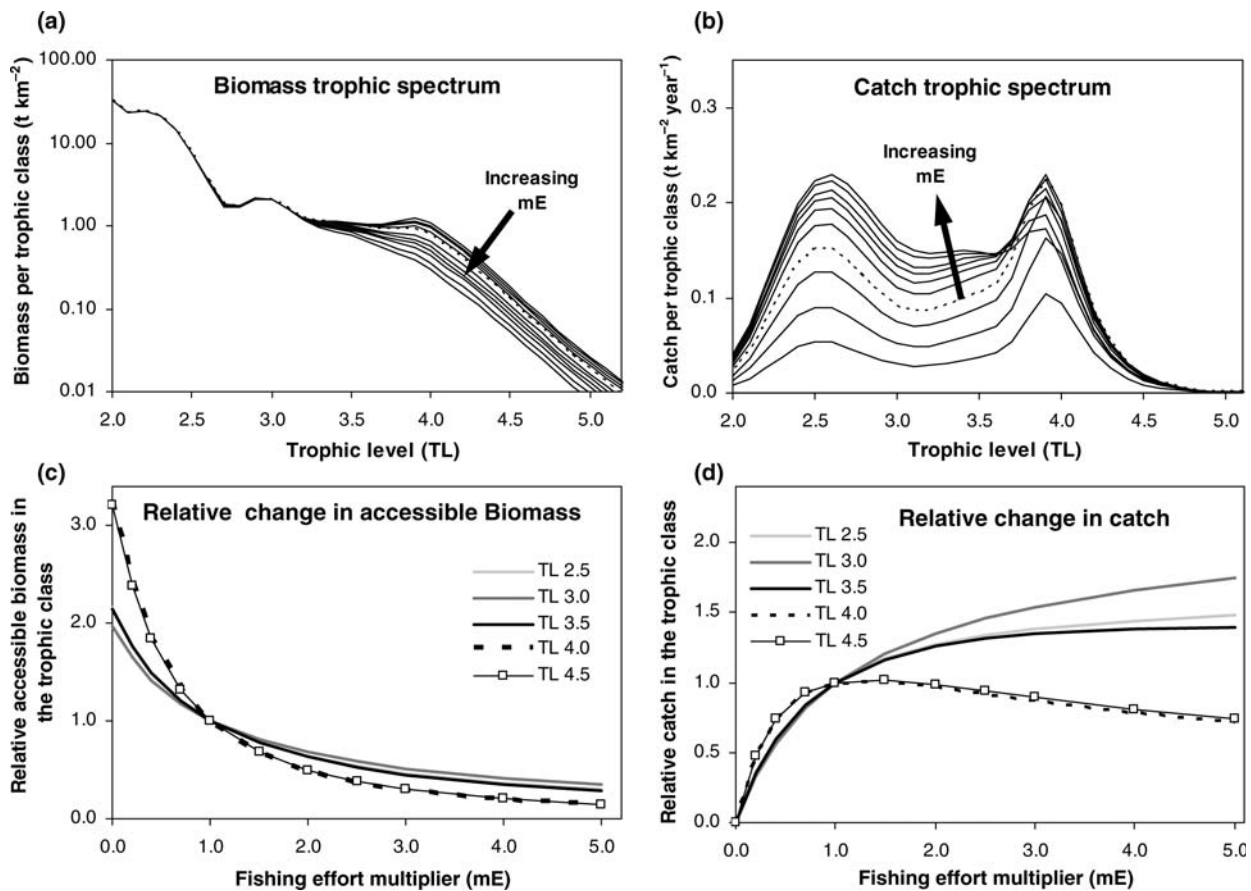
Figure 7. Simulations of the impact of increasing fishing effort on (a) biomass and (b) catches of the Guinean ecosystem. The top panels refer to the biomass and the catch trophic spectrum, where dashed lines represent the current (i.e. 2004) situation. In the bottom panels, the relative values of biomass and catch for the trophic classes are expressed as a function of the fishing mortality multiplier. Results highlight the strong impact of the current fishing effort (mE = 1) on the biomass of higher TLs (compared with the unexploited state, mE = 0); production functions show that higher TLs are fully exploited.
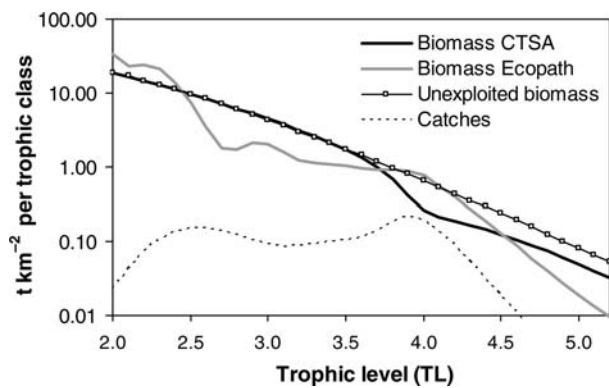
Figure 8. Biomass trophic spectrum estimated from CTSA applied to the 2004 catch data for the Guinean shelf (see text), compared with the independent Ecopath estimate.

The CTSA: an ecosystem-scale VPA

CTSA appears to be a useful tool, especially for data-poor situations. It allows the reconstruction of the state of whole ecosystems and only requires data on total catches per species or group, along with estimates of the mean TL of each species or group.

Subsequently, EcoTroph can be used as a stand-alone method, without the need for an Ecopath model. In the absence of other data, the mean TL per group can be obtained from FishBase or SeaLifeBase and computations performed using reasonable values for TE (usually 10%; Pauly and Christensen, 1995) and for the top-down coefficient. In addition, empirical models proposed by Gascuel et al. (2008) can be used to define flow kinetics in the current state of the ecosystem. Our sensitivity analyses illustrate how poor input estimates for some of the CTSA input parameters lead to great uncertainty in output estimates. Hence, sensitivity analyses need to be performed. However, the simulations also suggested that CTSA can provide reliable estimates if the value of primary or secondary production (or biomass) can be estimated independently.

Finally, CTSA and VPA applied to single species share similarities in methods and limitations. In VPA, fishing mortalities and estimated of stock biomass depend heavily on natural mortality M, which is often poorly estimated. Only experience and comparative analyses between periods or stocks can confirm (or correct) the reliability of the M values used. Application of CTSA to the Guinean ecosystem showed that results are coherent with current understanding, but more work is needed, with detailed case studies and comparisons, for users to gain experience with input parameter values.

EcoTroph: a theoretical and practical tool

From the 1950s, fisheries management was essentially based on single-species approaches using relatively simple models of the dynamics of exploited populations, i.e. the holistic model of Schaefer (1954) and the analytical models of Beverton and Holt (1957). These models are both theoretical and practical. For instance, Schaefer's surplus-production model, nowadays perceived as simplistic, is still used widely both to illustrate theoretical concepts, such as optimum fishing effort or maximum sustainable yield, and to estimate their values in specific fisheries. In the same way, the ecosystem representation provided by the EcoTroph model constitutes a simplified caricature, allowing for both theoretical simulations (e.g. illustrating the generic effect of changing the TL at first catch on the ecosystem production function) and for evaluation of specific ecosystems. Note that the results presented here only refer to steady-state conditions, although a dynamic version of EcoTroph has also been developed (Gascuel and Pauly, 2009).

Compared with EwE, the EcoTroph model is not only a simplification, but also provides practical diagnostic tools and allows theoretical aspects of ecosystem functioning to be explored. Conversely, Ecopath and more particularly Ecosim provide a more comprehensive representation of ecosystem state and function. Obviously, though, information on groups or species is needed because ecosystem-based fisheries management cannot be based on trophic classes only. Hence, EcoTroph should be used as a stand-alone application only in data-poor situations where it can be useful for a first overview of various ecosystem aspects. In all other cases, EcoTroph should be used more as a complement than as an alternative to other approaches. In this sense, EcoTroph is complementary to approaches such as size-spectrum theory (Benoît and Rochet, 2004; Andersen *et al.*, 2009), helping scientists to think at the ecosystem scale. EcoTroph is now available as a plug-in module of EwE Version 6 (Christensen and Lai, 2007), which was designed to accommodate extensions of this nature (a detailed users' guide is available online; Gascuel *et al.*, 2009a).

To conclude, although the EcoTroph model is based solely on TLs and is a caricature of the functioning of real ecosystems, it allows exploration of theoretical aspects by concentrating on biomass flow as a quasi-physical process. Overall, we found that taking into account a few simple, TL-related processes appeared sufficient to simulate biomass distribution patterns and the responses to fishing pressure in real ecosystems. The best argument for the TL-based model presented here is that it appears to be a useful tool for understanding ecosystem functioning in both theoretical and practical contexts. For example, it allows users to estimate consistent relationships between parameters, e.g. catches or biomass vs. fishing mortalities. It provides the theoretical basis for explaining the greater sensitivity of high TLs to over-fishing. It explains more complicated patterns, such as fishing down marine foodwebs or cascading effects, and clarifies the impact of flow kinetics or top-down controls on ecosystem resilience.

A first application of the TL-based approach to a real ecosystem has also been presented and the test appeared to be successful, its results consistent with partial single-species approaches and with those of more complex EwE models. Obviously, however, the TL-based approach has now to pass the acid test of being applied to several ecosystems.

References

Adams, S. M., Kimmel, B. L., and Ploskey, G. R. 1983. Sources of organic matter for reservoir fish production: a trophic-dynamics analysis. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1480–1495.

Allen, K. R. 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada, 28: 1573–1581.

Andersen, K. H., Farnsworth, K. D., Pedersen, M., Gislason, H., and Beyer, J. E. 2009. How community ecology links natural mortality, growth, and production of fish populations. ICES Journal of Marine Science, 66: 1978–1984.

Benoît, E., and Rochet, M-J. 2004. A continuous model of biomass size spectra governed by predation, and the effects of fishing on them. Journal of Theoretical Biology, 226: 9–21.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fishery Investigations, London, Series II, XIX. 533 pp.

Caverivière, A. 1994. Le poulpe (*Octopus vulgaris*) au Sénégal: une nouvelle ressource. *In* L'évaluation des Ressources Exploitables par la Pêche Artisanale Sénégalaise, pp. 245–256. Ed. by M. Barry-Gérard, T. Diouf, and A. Fonteneau. ORSTOM éditions, Paris. Colloques et Séminaires, 2.

Christensen, V., and Lai, S. 2007. Ecopath with Ecosim 6: the sequel. Sea Around Us Newsletter, 43(September-October): 1–4.

Christensen, V., and Pauly, D. 1992. The ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61: 169–185.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science, 56: 707–717.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., and Verheye, H. M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science, 57: 603–618.

Cury, P., Shannon, L. J., and Shin, Y-J. 2003. The functioning of marine ecosystems. *In* Responsible Fisheries in the Marine Ecosystems, pp. 103–123. Ed. by M. Sinclair, and G. Valdimarsson. Oxford University Press, Oxford, UK.

Elton, C. 1927. Animal Ecology. Macmillan, New York. 207 pp.

Gascuel, D. 2001. Un modèle écosystémique structuré par niveau trophique: approche théorique de l'impact de la pêche sur la biomasse, la production halieutique et la dynamique des écosystèmes marins exploités. *In* Halieutique: complexité et Décision, Actes du 5ème Forum Halieumétrique, Lorient, juin 2001, pp. 87–110. Association Française d'Halieumétrie, Agrocampus Ouest, Rennes.

Gascuel, D. 2005. The trophic-level based model: a theoretical approach of fishing effects on marine ecosystems. Ecological Modelling, 189: 315–332.

Gascuel, D., Bozec, Y., Chassot, E., Colomb, A., and Laurans, M. 2005. The trophic spectrum: theory and application as an ecosystem indicator. ICES Journal of Marine Science, 62: 443–452.

Gascuel, D., and Chassot, E. 2008. Exploring catch trophic spectra analysis: a method to estimate fishing rates and biomass at the ecosystem level. *In* Reconciling Fisheries with Conservation. Proceedings of the Fourth World Fisheries Congress, pp. 1059–1072. Ed. by J. L. Nielsen, J. J. Dodson, K. Friedland, T. R. Hamon, J. Musick, and E. Vespoor. American Fisheries Society Symposium, 49.

Gascuel, D., Guénette, S., Diallo, I., and Sidibé, A. 2009b. Impact de la pêche sur l'écosystème marin de Guinée, modélisation EwE 1985/2005. Fisheries Centre Research Reports, 17(4). Fisheries Centre University of British Columbia, Vancouver. 60 pp. www.fisheries.ubc.ca/publications/reports/report17_4.php.

Gascuel, D., Labrosse, P., Meissa, B., Taleb Sidi, M. O., and Guénette, S. 2007. Decline of demersal resources in North-West Africa: an analysis of Mauritanian trawl survey data over the past 25 years. African Journal of Marine Science, 29: 331–345.

Gascuel, D., Laurans, M., Sidibé, A., and Barry, M. D. 2004. Diagnostic comparatif de l'état des stocks et évolutions d'abondance des ressources démersales dans les pays de la CSRP. *In* Pêcheries Maritimes, Écosystèmes et Sociétés en Afrique de l'Ouest: un Demi Siècle de Changement, pp. 205–222. Ed. by P. Chavance, M. Ba, D. Gascuel, J. M. Vakily, and D. Pauly. Actes du Symposium International, Dakar (Sénégal), Juin 2002. Bruxelles, Office des Publications Officielles des Communautés Européennes. 532 pp. Collection des Rapports de Recherche Halieutique ACP-UE 15.

Gascuel, D., Morissette, L., Palomares, M. L., and Christensen, V. 2008. Trophic flow kinetics in marine ecosystems: toward a theoretical approach to ecosystem functioning. Ecological Modelling, 217: 33–47.

Gascuel, D., and Pauly, D. 2009. EcoTroph: modelling marine ecosystem functioning and impact of fishing. Ecological Modelling, 220: 2885–2898.

Gascuel, D., Tremblay-Boyer, L., and Pauly, D. 2009a. EcoTroph: a trophic-level based software for assessing the impact of fishing on aquatic ecosystems. Fisheries Centre Research Reports, 17(2). Fisheries Centre, University of British Columbia, Vancouver. 82 pp. http://www.fisheries.ubc.ca/node/366.

Goñi, R. 1998. Ecosystem effects of marine fisheries: an overview. Ocean and Coastal Management, 40: 37–64.

Guénette, S., and Diallo, I. 2004. Exploration d'un modèle préliminaire de l'écosystème marin de Guinée. *In* Pêcheries Maritimes, Écosystèmes et Sociétés en Afrique de l'Ouest: un Demi Siècle de Changement, pp. 328–346. Ed. by P. Chavance, M. Ba, D. Gascuel, J. M. Vakily, and D. Pauly. Actes du Symposium International, Dakar (Sénégal), Juin 2002. Bruxelles, Office des Publications Officielles des Communautés Européennes. 532 pp. Collection des Rapports de Recherche Halieutique ACP-UE 15.

Gulland, J. A. 1965. Estimation of mortality rates. Annex to the Report of the Arctic Fisheries Working Group, Hamburg, January 1965. International Council for the Exploration of the Sea, 1965/3.

Hall, S. J. 1999. The Effects of Fishing on Marine Ecosystems and Communities. Blackwell Science, London. Fish Biology and Aquatic Resources Series, 1. 274 pp.

Hunter, M. D., and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology, 73: 724–732.

ICES. 2009. Report of the ICES Advisory Committee, 2009. ICES Advice, Book 11. 71 pp.

Jennings, S., and Kaiser, M. J. 1998. The effect of fishing on marine ecosystems. Advances in Marine Biology, 34: 201–352.

Kot, M. 2001. Elements of Mathematical Ecology. Cambridge University Press, Cambridge, UK. 453 pp.

Laurans, M., Gascuel, D., Chassot, E., and Thiam, D. 2004. Changes in the trophic structure of fish demersal communities in West Africa in the three last decades. Aquatic Living Resource, 17: 163–174.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, 23: 399–418.

Odum, W. E., and Heald, E. J. 1975. The detritus-based food web of an estuarine mangrove community. *In* Estuarine Research, pp. 265–286. Ed. by L. E. Cronin. Academic Press, New York.

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution, 14: 483–488.

Pauly, D., and Christensen, V. 1995. Primary production required to sustain global fisheries. Nature, 374: 255–257; Erratum in Nature, 376: 279.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. C. 1998. Fishing down marine food webs. Science, 279: 860–863.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57: 697–706.

Pauly, D., Palomares, M. L., Froese, R., Sa-a, P., Vakily, M., Preikshot, D., and Wallace, S. 2001. Fishing down Canadian aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences, 58: 51–62.

Pauly, D., and Watson, R. 2005. Background and interpretation of the Marine Trophic Index as a measure of biodiversity. Philosophical Transactions of the Royal Society of London, Series B, 360: 415–423.

Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M-L., Hereu, B., *et al.* 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation, 27: 179–200.

Pope, J. G. 1972. An investigation into the accuracy of virtual population analysis. Research Bulletin International Commission for the Northwest Atlantic Fisheries, 9: 65–74.

Sala, E., Boudouresque, C. F., and Harmelin-Vivien, M. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos, 82: 425–439.

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bulletin of the Inter-American Tropical Tuna Commission, 1: 27–56.

Sidibé, A., Gascuel, D., and Domain, F. 2004. Évaluation et diagnostic de quatre stocks de poissons démersaux côtiers en Guinée. *In* Pêcheries Maritimes, Écosystèmes et Sociétés en Afrique de l'Ouest: un Demi Siècle de Changement, pp. 387–392. Ed. by P. Chavance, M. Ba, D. Gascuel, J. M. Vakily, and D. Pauly. Actes du Symposium International, Dakar (Sénégal), Juin 2002. Bruxelles, Office des Publications Officielles des Communautés Européennes. 532 pp. Collection des Rapports de Recherche Halieutique ACP-UE 15.

Walters, C., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7: 139–172.

Zeller, D., Booth, S., Davis, G., and Pauly, D. 2007. Re-estimation of small-scale for U.S. flag-associated islands in the western Pacific: the last 50 years. Fishery Bulletin US, 105: 266–277.

Appendix: Mathematical formulations of the EcoTroph model

A continuous model of biomass flow

Assuming that ecosystem functioning can be modelled as a continuous flow of biomass, moving up through the foodweb (Gascuel *et al.*, 2008), and according to the traditional equations of fluid dynamics (e.g. Kot, 2001), the biomass flow (i.e. the

quantity of biomass moving up through TL τ at every moment t) is

$$\Phi(t, \tau) = D(t, \tau)K(t, \tau), \tag{A1}$$

where $\Phi(t,\tau)$ is expressed in t year^{-1}, $D(t,\tau)$ the density of biomass at TL τ (expressed in t TL^{-1}), and $K(t,\tau) = d\tau/dt$ is the speed of the flow that quantifies the velocity of biomass transfers in the foodweb (in TL year^{-1}). Under steady-state conditions, Equation (A1) becomes

$$D(\tau) = \frac{\Phi(\tau)}{K(\tau)}. \tag{A2}$$

The biomass flow $\Phi(\tau)$ is not conservative and a loss rate is defined as

$$\psi(\tau) = -\frac{1}{\Phi(\tau)}\frac{d\Phi(\tau)}{d\tau}. \tag{A3}$$

This loss rate is split into two terms, one for the natural losses through non-predation mortality, excretion, and respiration, and the other for the losses attributable to fishing. Therefore, integration of Equation (A3) leads to

$$\Phi(\tau + \Delta\tau) = \Phi(\tau)\exp[-(\mu_\tau + \varphi_\tau)\Delta\tau], \tag{A4}$$

where μ_τ and φ_τ (expressed in TL^{-1}) are, respectively, the mean natural loss rate and the mean loss rate attributable to fishing over a $[\tau, \tau + \Delta\tau[$ interval.

Note that these equations are consistent with the general equation of change in the density of biomass over time and TLs (from Kot, 2001):

$$\frac{\delta D(t, \tau)}{\delta t} + \frac{\delta(K(t, \tau)D(t, \tau))}{\delta \tau} = -\xi(t, \tau)D(t, \tau), \tag{A5}$$

which becomes Equation (A3) when assuming steady state and redefining $\xi = \psi K$.

Discrete approximation of biomass and biomass flow

For all TLs higher than 2 (i.e. for animals), the continuous distribution of the biomass across TLs is approximated using narrow trophic classes $[\tau, \tau + \Delta\tau[$, with $\Delta\tau$ conventionally equal to 0.1 TL. We therefore consider mean values D_τ, Φ_τ, and K_τ over the trophic class $[\tau, \tau + \Delta\tau[$. The mean values Φ_τ are derived by integrating Equation (A4):

$$\Phi_\tau = \frac{1}{\Delta\tau}\int_0^{\Delta\tau}\Phi(\tau + s)ds = \frac{1}{\Delta\tau}\left[\frac{\Phi(\tau)\exp[-(\mu_\tau + \varphi_\tau)s]}{-(\mu_\tau + \varphi_\tau)}\right]_0^{\Delta\tau},$$

and therefore

$$\Phi_\tau = \Phi(\tau)\frac{1 - \exp[-(\mu_\tau + \varphi_\tau)\Delta\tau]}{(\mu_\tau + \varphi_\tau)\Delta\tau}. \tag{A6}$$

Equations (A4) and (A6) may be used to simulate the biomass flow for various fishing patterns defined by their fishing loss rates φ_τ.

K_τ is defined directly using mean values per trophic class (see below). Therefore, Equation (A2) becomes

$$D_\tau = \frac{\Phi_\tau}{K_\tau}. \tag{A7}$$

Under steady-state conditions, the biomass (in t) present at any moment within the $[\tau, \tau + \Delta\tau[$ trophic class is $B_\tau = \int_\tau^{\tau+\Delta\tau} D(\tau)d\tau = D_\tau\Delta\tau$, so according to Equation (A7),

$$B_\tau = \Phi_\tau\frac{\Delta\tau}{K_\tau}. \tag{A8}$$

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

$$P_\tau = \int_\tau^{\tau+\Delta\tau}\Phi(\tau)d\tau = \Phi_\tau\Delta\tau. \tag{A9}$$

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

Flow kinetic and top-down equation

From Equations (A8) and (A9), we deduce

$$K_\tau = \left(\frac{P}{B}\right)_\tau. \tag{A10}$$

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

$$\frac{1}{\Delta\tau = 1}\left(\frac{P}{B}\right) = Z, \quad \text{and hence} \quad K_\tau = (F_\tau + M_\tau), \tag{A11}$$

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

A top-down control effect is introduced into the model assuming that a fraction α_τ of the natural mortality M_τ depends on predator abundance as follows:

$$M_\tau = \alpha_\tau M_{\text{ref},\tau}\left(\frac{B_{\text{pred}}}{B_{\text{ref,pred}}}\right)^\gamma + (1 - \alpha_\tau)M_{\text{ref},\tau}, \tag{A12}$$

where the subscript "ref" indicates a 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, using an asymmetric interval akin a lognormal distribution; see Gascuel *et al.*, 2009a). The coefficient α_τ varies between 0 and 1 and defines the intensity of the top-down control that affects TL τ. The coefficient γ 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 Equations (A11) and (A12):

$$K_\tau = (K_{\text{ref},\tau} - F_{\text{ref},\tau}) \left[1 + \alpha_\tau \frac{B_{\text{pred}}^\gamma - B_{\text{ref,pred}}^\gamma}{B_{\text{ref,pred}}^\gamma} \right] + F_\tau. \quad \text{(A13)}$$

Starting with a reference state of the ecosystem, where the flow kinetics $K_{\text{ref},\tau}$ is known (see text), Equation (A13) allows us to simulate K_τ for various changes in the fishing patterns. Note that Equation (A13) requires an estimate of predator biomass, which is based on Equation (A8). 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.

Accessible biomass and catches

The selectivity coefficient S_τ is defined as the fraction of the ecosystem biomass accessible to fisheries. It can be estimated in the reference state ($S_{\text{ref},\tau} = B_{\text{ref},\tau}^* / B_{\text{ref},\tau}$), based on field observations or from a theoretical model (e.g. a logistic curve). Then, the net natural loss rate of the accessible biomass flow is derived from the inverse of Equation (A4):

$$\mu_\tau^* \approx \ln\left(\frac{\Phi_{\text{ref},\tau}^*}{\Phi_{\text{ref},\tau+\Delta\tau}^*} \right) \frac{1}{\Delta\tau} - \varphi_{\text{ref},\tau}^*, \quad \text{(A14)}$$

where $\Phi_{\text{ref},\tau}^* = \Phi_{\text{ref},\tau} S_{\text{ref},\tau}$ and $\varphi_{\text{ref},\tau}^* = \varphi_{\text{ref},\tau} / S_{\text{ref},\tau}$ are, respectively, the accessible biomass flow and the fishing loss rate of the accessible biomass flow, in the reference (and known) situation. Note that the term μ_τ^* may exhibit negative values because it results from the balance between real losses in the biomass flow and gains attributable to the transition of biomass flow from the inaccessible to the accessible state (see discussion in Gascuel and Pauly, 2009).

These parameters allow simulation of the accessible biomass flow, for any value of the fishing loss rate φ_τ^*. The computations are initialized for secondary producers (TL = 2) by

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

and

$$\Phi_{\tau+\Delta\tau}^* = \Phi_\tau^* \exp[-(\mu_\tau^* + \varphi_\tau^*)\Delta\tau]. \quad \text{(A15)}$$

The accessible biomass is simulated from

$$B_\tau^* = \Phi_\tau^* \frac{\Delta\tau}{K_\tau^*}, \quad \text{(A16)}$$

where K_τ^* is the kinetic of the accessible flow, deduced from the reference state $K_{\text{ref},\tau}^*$ (see text) based on Equation (A13).

Finally, catches per time unit (in t 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 $dY/d\tau$, leading to

$$Y_\tau = \int_{t=0}^{1} \frac{\varphi_\tau^*}{\varphi_\tau^* + \mu_\tau^*} [\Phi*(\tau) - \Phi*(\tau + \Delta\tau)] dt \quad \text{(A17)}$$

or

$$Y_\tau = \int_{s=0}^{\Delta\tau} \varphi_\tau^* \Phi*(\tau + s) ds. \quad \text{(A17a)}$$

Equation (A17) indicates that catches are equal to the fraction of flow loss attributable to the fishery, whereas Equation (A17a) stems from the definition of the fishing loss rate. Integration of Equation (A17) or (A17a) leads to the catch equation, which can be expressed, after simplification based on Equation (A6), as

$$Y_\tau = \varphi_\tau^* \Phi_\tau^* \Delta\tau$$

or

$$Y_\tau = F_\tau^* B_\tau^* \quad \text{with} \quad F_\tau^* = \varphi_\tau^* K_\tau^*, \quad \text{(A18)}$$

where F_τ^* is the fishing mortality of the accessible biomass.