

Reconciling Fisheries with Conservation: Proceedings of the Fourth World Fisheries Congress



American Fisheries Society Symposium 49

**Jennifer Nielsen, Julian J. Dodson, Kevin Friedland,
Troy R. Hamon, Jack Musick, and Eric Verspoor, editors**

About this CD

This CD contains all papers accepted for publication in the proceedings of the Fourth World Fisheries Congress, held May 2-6, 2004 in Vancouver, BC, Canada. The theme of the Congress was “Reconciling Fisheries with Conservation: The Challenge of Managing Aquatic Ecosystems.”

The **Table of Contents** section is hyperlinked. Clicking on a chapter title in the Contents section will take you to the text of that chapter on the CD.

The **Bookmarks** tab on the left will also help you navigate throughout the document.

PRINTED PROCEEDINGS

The 2-volume printed book of these proceedings has been published by the American Fisheries Society. Ordering information is [HERE](#)

COMMENTS/QUESTIONS

Aaron Lerner

Director of Publications

[American Fisheries Society](#)

5410 Grosvenor Lane

Bethesda, MD 20814 USA

alerner@fisheries.org

Exploring Catch Trophic Spectrum Analysis: A Method to Estimate Fishing Rates and Biomass at the Ecosystem Level

DIDIER GASCUEL* AND EMMANUEL CHASSOT

*Fisheries and Aquatic Sciences Center, Agrocampus Rennes
65 Route de Saint Brieuc CS 84215, 35042 Rennes Cedex, France*

Abstract.—Catch Trophic Spectrum Analysis (CTSA) is based on a model of biomass flow passing through the ecosystem from low to upper trophic levels, according to predation and ontogenic processes. All the biomass of the ecosystem is distributed by fractional trophic classes and moves from one class to another according to its trophic level. The model involves equations of biomass flow and kinetics of transfer. A top-down effect linking prey transfer to their predators abundance is also included in the model. Using CTSA, we show that exploitation rates and biomass present in the ecosystem can be estimated in steady state, from total catches by trophic class. Based on simulated data, sensitivity of such estimates is investigated according to three types of parameters: transfer efficiency, kinetics of transfer and extent of top-down control. Absolute estimates appeared sensitive to these parameters, but relative values were robust. Thus, the method underlines which trophic levels are the most exploited, and displays the distribution of the biomasses in the ecosystem. In order to test the CTSA, it was applied to two European ecosystems: the North sea and the Celtic sea. Using ICES database and trophic levels provided by Fishbase, catch trophic spectra are estimated as 7-year averages since the 1970s. The CTSA underlined different exploitation patterns in both ecosystems. In the Celtic sea, the biomass of top predators remains high and exploitation rates appear globally low and stable over the last two decades. In the North Sea, biomasses seemed to be more affected by exploitation during the last two decades. Simulations showed that total catches could increase with fishing pressure in both ecosystems, notably due to an increase in prey species. Such a shift would imply a decrease in the trophic level of catches and biomasses. Despite the use of empirical relationships and parameters, CTSA appears a useful tool to investigate ecosystem functioning and fishing effects.

Introduction

Ecosystem modeling is obviously recognized as a major task to implement an Ecosystem Approach to Fisheries (EAF). We assisted in the development of many recent ecosystem case studies, using models that generally express trophic flow among various groups

present in the ecosystem. The most popular model used in that way has been the mass-balance Ecopath/Ecosim model (Polovina 1984; Christensen and Pauly 1992; Walters et al. 1997) that relies on the allocation of biomass in discrete trophic groups. Such models appear as useful tools to investigate ecosystem function and to analyze the past effects of fishing (Christensen and Walters 2004). Nev-

* Corresponding author: didier.gascuel@agrocampus-rennes.fr

ertheless, these models do not provide a general theory on fisheries impact on ecosystems. Probably due to their high number of parameters, the models also appear until now as poor tools for forecasts and fisheries management.

We have recently proposed the trophic-level based model as a theoretical representation of ecosystem functioning and impact of fishing (Gascuel 2005). All the biomass of the ecosystem is distributed along a continuum of trophic level values in this model and split into fractional trophic classes. Due to predation and ontogenic processes, biomass moves from one class to the upper ones changing its trophic level. The model is based on biomass flow and flow kinetic equations and allows theoretical investigations of potential harvesting rates and of the impact of fishing on biomass at different ecosystem scales. In this approach, a theoretical catch trophic spectrum is defined as the distribution of yield per trophic level at the ecosystem scale.

In this paper we present a method to apply such a model to real case studies. Catch trophic spectrum analysis (CTSA) is used as a method for estimating exploitation rates and biomass at the ecosystem level. Based on past catches per trophic level, such estimations allow us to simulate consequences of various fishing patterns, in terms of catch and biomass. We first summarize principles and main equations of the trophic-level based model. CTSA is then presented using the reverse form of those equations. The method is tested on simulated data in order to study its sensitivity to the input parameters. As an example of its potential, CTSA is applied to two European ecosystems: the North Sea and the Celtic Sea. Past changes were analyzed and simulations of modified fishing pressure were conducted. We finally discuss the use of some empirical parameters and we address the usefulness of CTSA to model ecosystem exploitation.

Method

The Trophic-Level Based Model

The trophic-level based model (Gascuel 2002 and 2005) expresses the total ecosystem biomass per trophic level, as a result of the biomass flow passing through the ecosystem from lower to upper trophic levels, according to predation and ontogenic processes. Conventionally, the model is structured by trophic classes of $\Delta\tau = 0.1$ range step, from trophic level 2 (secondary producers) to trophic level 5 (top predators).

Under steady state conditions, the biomass B_t present in the trophic class ranging from trophic level τ to trophic level $\tau+0.1$, is expressed as:

$$B_\tau = \int \Phi(\tau) \times \frac{dt}{d\tau} \times d\tau \approx \frac{\Delta t}{\Delta \tau} \times \int \Phi(\tau) \times d\tau \quad (1)$$

with t the time, τ the trophic level,

$$\Phi(\tau) = \frac{dB(t, \tau)}{dt}$$

the biomass flow at trophic level τ , $B(t, \tau)$ the instantaneous biomass at trophic level τ , and Δt the time required by a unit of biomass to go from level τ to level $\tau + \Delta \tau$.

This equation is the key point of the model. It means that the biomass per trophic class is equal to the biomass flow divided by the speed of the flow. Indeed, equation (1) can be rewritten as follows:

$$\frac{B_\tau}{\Delta \tau} = \overline{\Phi(\tau)} \times \frac{\Delta t}{\Delta \tau}$$

where $\overline{\Phi(\tau)}$ is the mean biomass flow in the trophic class, equal to $\frac{1}{\Delta \tau} \times \int \Phi(\tau) \times d\tau$ and $\frac{\Delta t}{\Delta \tau}$ is the speed of the biomass flow through trophic levels.

Subsequently, the model is based on three main assumptions.

1. The biomass flow $\Phi(\tau)$ is assumed to follow a decreasing curve due to natural losses occurring during trophic and ontogenic transfers (non predation mortality, egestion and excretion, dissipation of energy by respiration) and finally to fishing losses (catches):

$$\Phi(\tau + \Delta\tau) = \Phi(\tau) \times e^{-(\mu\tau + \varphi\tau) \times \Delta\tau} \quad (2)$$

with μ_τ the natural loss rate of biomass flow, and φ_τ the fishing loss rate of biomass flow. The natural transfer efficiency between trophic levels corresponds to $e^{-\mu\tau}$.

2. We empirically assume that the time required to go from trophic level τ to trophic level $\tau + \Delta\tau$ follows a logistic curve. This corresponds to fast transfers at low trophic levels, and to slower but equivalent transfers at intermediate or high trophic levels. Such an assumption defines the kinetics of transfers as follows:

$$\frac{\Delta t}{\Delta \tau} = \frac{a}{1 + b \times e^{-c \times \tau}} \quad (3)$$

with a , b and c parameters of the flow kinetics.

3. Bottom-up effects are implicitly included in the model, which takes into account the biomass transfers from preys to predators. In order to also take into account top-down controls, we introduce an additional relationship between the natural loss rate of biomass flow at a given trophic level τ and the biomass of its predators at trophic level $\tau + 1$. We assume that the natural loss rate at trophic level τ is known in the unexploited situation, and that the natural transfer efficiency increases when predator abundance decreases, compared to the unexploited situation. The natural loss rate is then defined as follows:

$$\mu_\tau = (1 - \alpha) \times \mu v_\tau + \alpha \times \mu v_\tau \times \frac{B(\tau + 1)}{Bv(\tau + 1)} \quad (4)$$

with α a coefficient expressing the extent of top-down control, μv_τ and Bv the natural loss rate and the biomass in the unexploited (virgin) situation respectively.

These four equations allow simulation of total biomass and catch per trophic class, for various fishing scenarios (Gascuel 2005). Here, we use them in a reverse form in order to estimate biomass and fishing rates assuming a known catch trophic spectrum.

From Trophic-Level Based Model to Catch Trophic Spectrum Analysis (CTSA)

In usual monospecific models of population dynamics, fishes move from one age to another according to time. In our model it is assumed that all the biomass of the ecosystem is distributed by fractional trophic classes and moves from one class to another according to its trophic level. Thus the trophic-level based model appears as a transposition of age-structured models to the ecosystem scale. Age is “converted” into trophic level, and equation for transfer kinetics (equation 3) expresses the kinetics of the underlying process as growth equation expresses kinetics of growth in a length based mono-specific model. This analogy allows us to use modified version of usual Virtual Population Analysis (VPA) equations.

Thus, according to Pope (1972), we use an approximation considering that all the catch made in interval $[\tau, \tau + \Delta\tau]$ occurs at trophic level $\tau + \Delta\tau/2$. Just before that trophic level, the biomass flow is equal to:

$$\Phi(\tau) \times e^{-\mu\tau \times \Delta\tau/2}$$

just after it is

$$\Phi(\tau + \Delta\tau) \times e^{\mu\tau \times \Delta\tau/2}$$

The difference between this two values is equal to the catch made during the period of time $\Delta\tau$ required to go from τ to $\tau+\Delta\tau$. Hence, the catch made on the interval and for a time unit is:

$$Y\tau = \Delta t \times [\Phi(\tau) \times e^{-\mu\tau \times \Delta\tau/2} - \Phi(\tau+\Delta\tau) \times e^{\mu\tau \times \Delta\tau/2}]$$

And hence:

$$\Phi(\tau) = \Phi(\tau+\Delta\tau) \times e^{\mu\tau \times \Delta\tau} + \frac{Y\tau}{\Delta t} \times e^{\mu\tau \times \Delta\tau/2} \quad (5)$$

This expression is equivalent to Pope equation. It allows back-calculations, the value of biomass flow at trophic level τ being deduced from the value at trophic level $\tau+\Delta\tau$, knowing the catches $Y\tau$. Furthermore, based on equation (2), corresponding fishing flow loss rate is calculated as:

$$\varphi\tau = \frac{1}{\Delta\tau} \times \left[\text{Ln} \left(\frac{\Phi(\tau)}{\Phi(\tau+1)} \right) - \mu\tau \times \Delta\tau \right] \quad (6)$$

In addition, exploitation rate is defined as follows:

$$E\tau = \frac{\varphi\tau}{\varphi\tau + \mu\tau} \quad (7)$$

The catch trophic spectrum analysis (CTSA) requires as inputs: catches per trophic level $Y\tau$; natural loss rates in virgin situation $\mu\nu\tau$; the coefficient of top-down control intensity α ; and parameters of flow kinetics. In addition, as in a typical VPA, calculus must be initialized from the highest trophic level by a value of terminal fishing loss rate.

Then, for each trophic level τ , biomass flow $\Phi(\tau)$, fishing flow loss $\varphi\tau$, exploitation rate $E\tau$, biomass $B\tau$ and natural loss rate $\mu\tau$ are estimated from values at level $\tau+\Delta\tau$ using equations (5), (6), (7), (1), and (4), respectively. Because $B\tau$ and $\mu\tau$ are cross-dependent, the equations must be solved by iterations. At the first step $\mu\tau$ is initialized by $\mu\nu\tau$. For each iteration until convergence, equations lead to

estimate $\Phi(\tau)$, then $B\tau$ and then a new value of $\mu\tau$.

Testing CTSA on Simulated Data

A theoretical catch trophic spectrum was simulated based on the trophic-level based model and using standard arbitrary parameters. We used here an exact form of catch equation coming from equation (2) (Gascuel 2005):

$$Y\tau = \Delta t \times \frac{\varphi\tau}{\varphi\tau + \mu\tau} \times [\Phi(\tau) - \Phi(\tau+1)] \quad (8)$$

Standard natural loss rates in an unexploited situation ($\mu\nu\tau$) and parameters of kinetics of transfers (a, b, c) were chosen in a range of empirical values corresponding to realistic curves (Table 1 and Figure 1a,b). Nonstandard values were used hereafter for sensitivity analyses. In the same way, the coefficient of top-down control intensity (α) was assumed to be equal to 0.6 for catches simulation and a range of values was explored in sensitivity analyses. Catches simulated corresponded to an harvest scenario targeting high trophic levels, with a conventional selectivity curve (Figure 1c) and fishing loss rates equal to natural loss rates for the highest trophic levels ($\varphi\tau = S\tau \cdot \mu\tau$).

Thus, the catch trophic spectrum was simulated (Figure 1 d) for a set of known parameters and for given exploitation rates per trophic level. These simulated data were used as input in CTSA. First, convergence of CTSA in biomass and fishing loss rates estimates was investigated using the set of standard parameters and initializing calculus with different values of terminal fishing loss rate. Secondly, sensitivity of the method was explored using nonstandard values for the three kinds of parameters: natural loss rates (linked to transfer efficiency), intensity of top-down control, and kinetics of transfers.

Table 1. Catch trophic spectrum analysis: parameters definitions and values used in the simulations.

Notation	Parameter definition	Values used in simulations
$B(t, \tau)$	Instantaneous biomass at time t and trophic level τ	
B_{τ}	Biomass in the interval $[\tau; \tau + \Delta \tau]$	Estimated by equation (1)
$B_{V_{\tau}}$	Biomass in the interval $[\tau; \tau + \Delta \tau]$ in the unexploited situation	Estimated by equation (1), with $\varphi_{\tau} = 0$
$\Phi(t)$	Biomass flow at trophic level τ	$\Phi(2) = 100$; $\Phi(\tau \neq 2)$ estimated by equation (2)
μ_{τ}	Natural loss rate of biomass flow, in the interval $[\tau; \tau + \Delta \tau]$	Determined by equation (4)
φ_{τ}	Fishing loss rate of biomass flow, in the interval $[\tau; \tau + \Delta \tau]$	$\varphi_{\tau} = mf \cdot S_{\tau} \cdot \mu_{V_{\tau}}$, with $mf = 0.5$ to 2
Δt	Time required by a unit of biomass to go from level τ to level $\tau + \Delta \tau$	Estimated by equation (3)
a, b, c	Coefficients of the transfer kinetics model (equation 3)	Empirical values corresponding to a range of realistic curves (cf. Figure 1b)
$\mu_{V_{\tau}}$	Natural loss rate of biomass flow in the unexploited situation	Exploring values from $e^{-\mu_{\tau}} = 0.1$ to 0.2
α	Coefficient of top-down control (equation 4)	0 ("bottom-up ecosystem") to 0.8
S_{τ}	Selectivity coefficient by trophic level	Conventional logistic curve (Figure 1c)
E_{τ}	Exploitation rate	Determined by equation (7)
Y_{τ}	Yield per unit of time in the interval $[\tau; \tau + \Delta \tau]$	Estimated by equation (8)

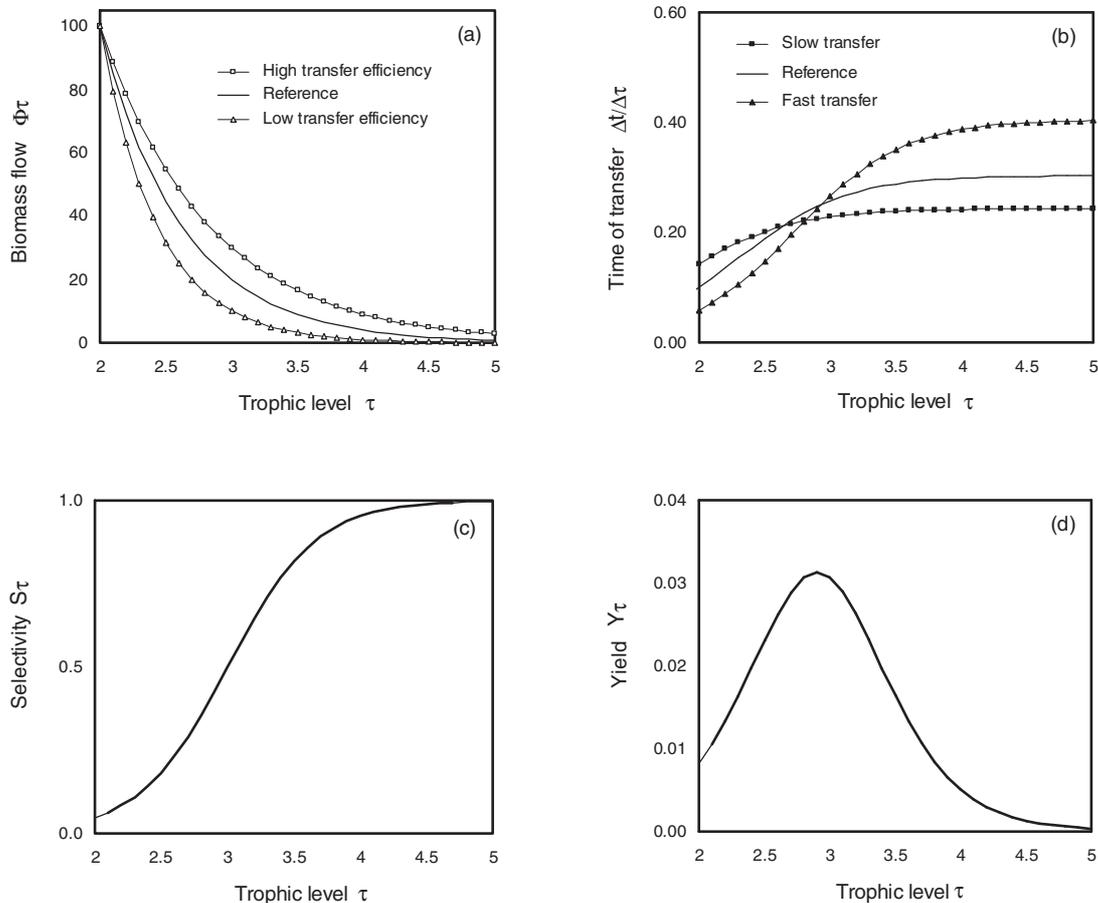


Figure 1. Simulation of the catch trophic spectrum using the trophic-level based model: (a) simulated biomass flows for different values of transfer efficiency; (b) simulated times of transfer required for a unit biomass to pass from τ to $\tau + \Delta\tau$ ($\Delta\tau = 0.1$) for different values of transfer speed; (c) fishery selectivity curve used in the simulations; (d) simulated yield by trophic level in the reference situation.

Example of CTSA Application to Two European Ecosystems

As case studies, CTSA was applied to two European ecosystems, the Celtic Sea and the North Sea. Catch data come from the International Council for the Exploration of the Sea (ICES) database using the FishStatPlus software (FAO 2000). Mean trophic levels τ of each species were extracted from the FishBase database (Froese and Pauly 2000) and were assumed stable from year to year within each study area. Catches were aggregated by τ increments of 0.1. In order to

take into account the intraspecific variability of trophic level, the catch-distribution was smoothed with a weighted moving average technique to spread the catch along an empirical range of trophic levels around the mean (Gascuel et al. 2005). To test the ability of the method to detect long-term changes, four catch trophic spectra were estimated as 7-years averages, from 1973 to 2001 (Figure 2).

Based on CTSA using the set of standard parameters $\{\mu v_\tau, a, b, c, \alpha\}$, exploitation rates and biomass were estimated in both

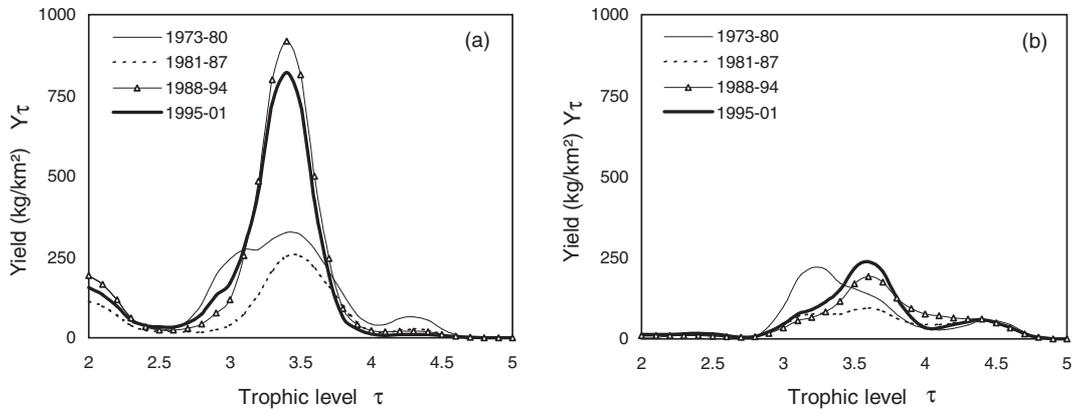


Figure 2. Catch trophic spectra from 1973 to 2001 by 7-year periods for the North Sea (a) and the Celtic Sea (b).

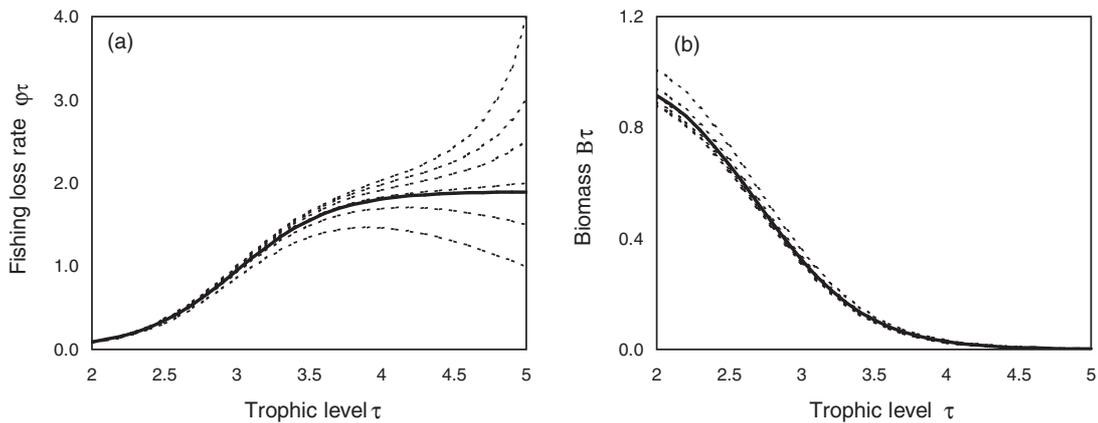


Figure 3. Sensitivity analysis of (a) fishing loss rate ϕ_τ and (b) biomass estimates, according to terminal fishing loss rate (at $\tau = 5.0$).

ecosystems and for each 7-year period. Past changes were thus investigated in the two cases. In addition, simulations were conducted for modified fishing pressures. Here, fishing loss rates of the last known period, considered as the current situation, were used to forecast with fishing effort multipliers equal to 0.5, 1.0 (status quo), and 2.0. Corresponding catches and biomasses per trophic level were estimated by the mean of equations (8) and (1).

Results

CTSA on Simulated Data

Based on theoretical catch trophic spectrum, CTSA provides estimates of fishing loss rates and biomass estimates per trophic level (Figure 3). Logically, using standard parameters leads to output results equal to input data used for catches simulation.

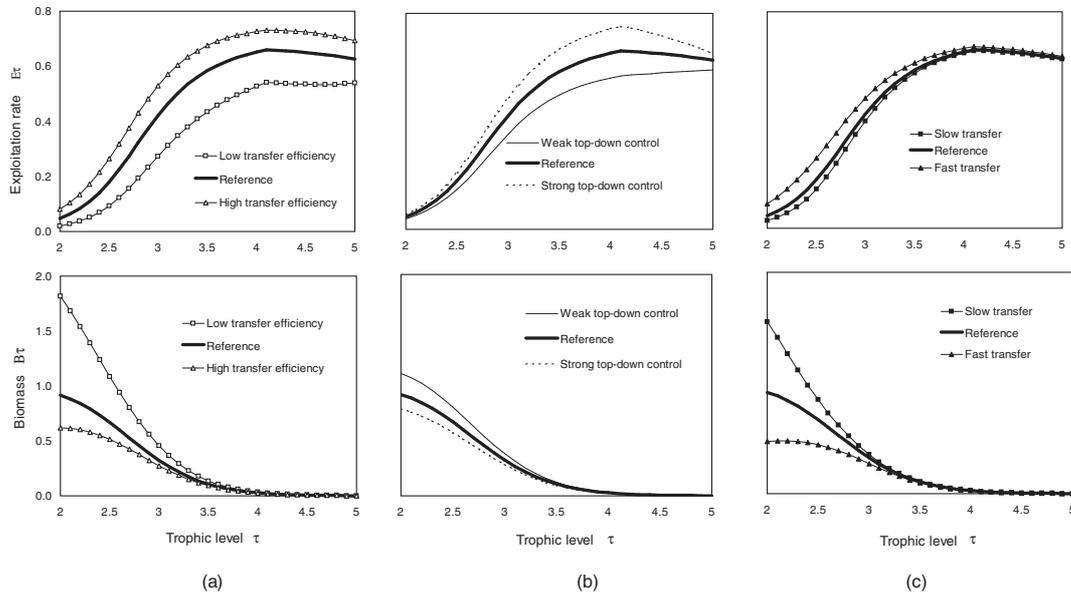


Figure 4. Sensitivity analysis of exploitation rates (top) and biomass estimates (bottom), according to (a) transfer efficiency (b) extent of top-down control, and (c) transfer speed.

Only one value of terminal fishing loss rate (the “true” one) allows us to find a curve with constant rates for high trophic levels (Figure 3a). For other values, convergence property of CTSA is observed. Just as in a common VPA, relative error of fishing loss rates estimated decreases from one trophic level to the previous one, during back-calculation. Biomass estimates also converge in terms of relative error (Figure 3b), but absolute errors increase during back-calculation due to the strong increase of biomass at low trophic levels.

Modeling with input parameters which differ from the standard set of catches simulation, highlights the sensitivity of CTSA estimates (Figure 4). Absolute values of fishing rates and biomass appear sensitive to all parameters. If transfer efficiencies, or top-down control extent, or speed of the biomass flow are overestimated, then fishing rates are overestimated and biomass underestimated. Nevertheless, the shape of the fishing rates curve remains

more or less unaffected and relative values appear robust. It is particularly true for uncertainty due to transfer kinetics (Figure 4c). On the other hand, biomass estimates for low trophic levels are strongly affected by parameters changes. Conversely, if the shape of the biomass distribution, or the absolute value of biomass at trophic level 2, were estimated independently (for instance by direct methods), then CTSA could be calibrated and should provide more reliable estimates.

Application to Two European Ecosystems

Based on CTSA, retrospective analysis shows different distributions of the biomass versus trophic levels τ in the two ecosystems. This analysis also highlights distinct changes in biomass among the 7 year periods considered. The Celtic Sea displays a more stable biomass distribution compared to the North Sea, characterized by high fluctuations between successive periods (Figure 5). Two major modes of trophic levels (3.4/3.8 and 4.3/4.7) were

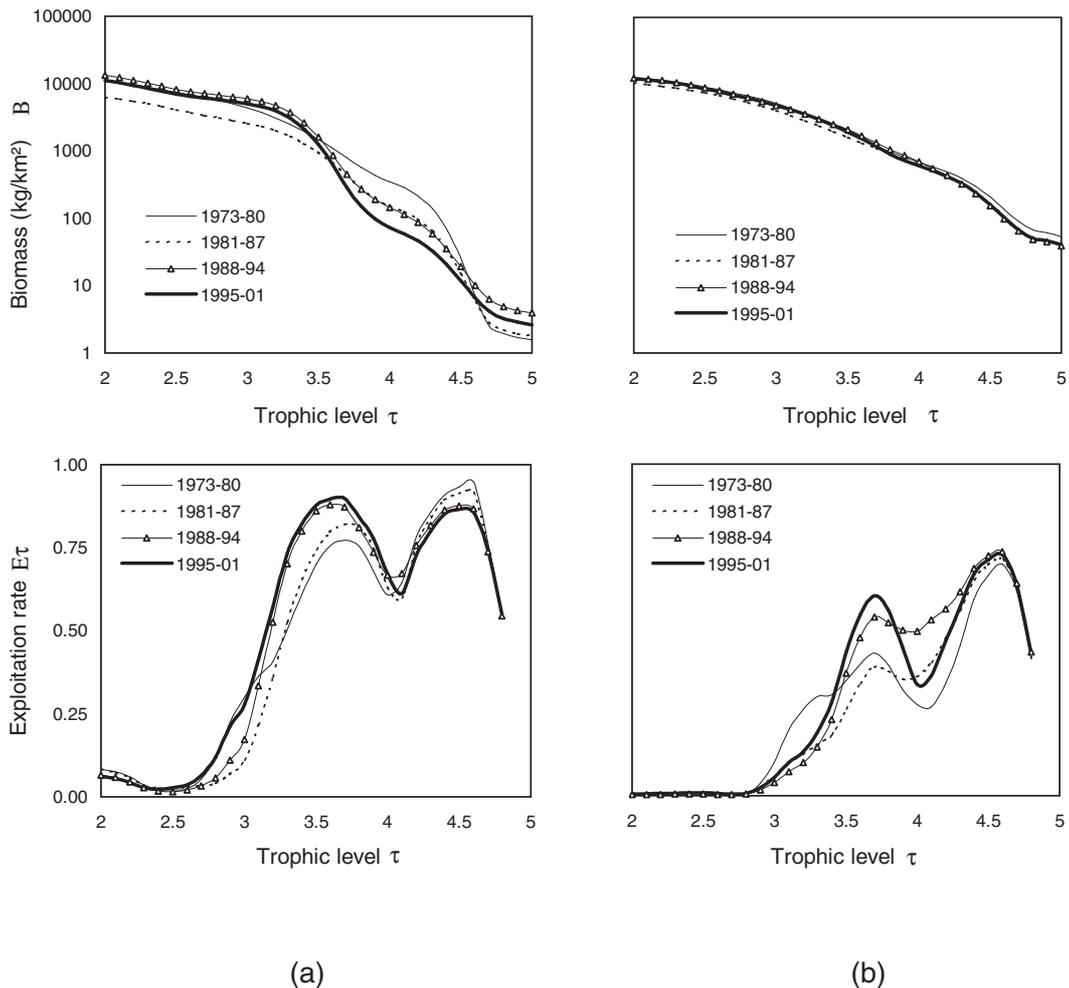
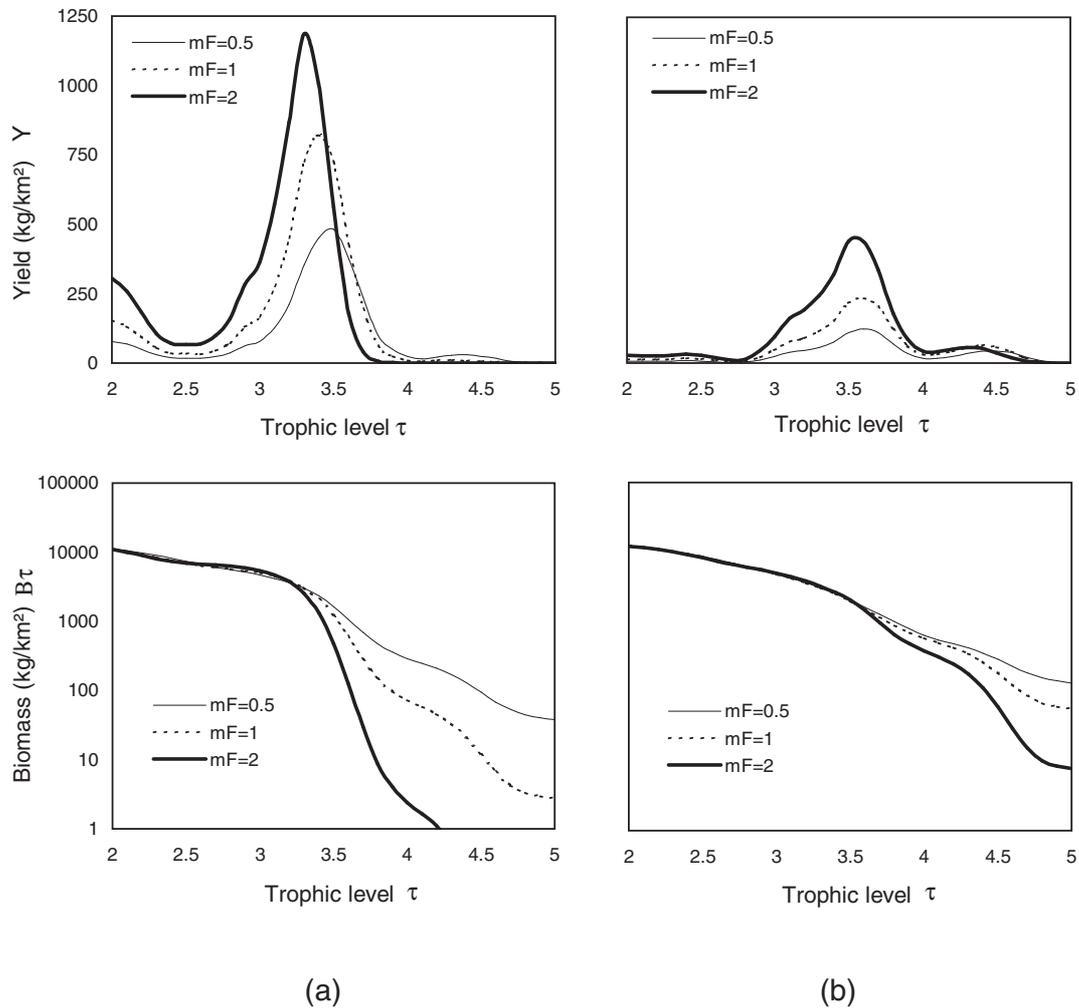


Figure 5. Biomass trophic spectra (top) and exploitation rate spectra (bottom) for the North Sea (a) and the Celtic Sea (b) estimated by retrospective analysis. A log scale is used for the biomass curves.

exploited in both ecosystems, although the North Sea also targets low trophic levels (shellfish) in minor proportions. The North Sea exhibits higher exploitation rates than the Celtic Sea for the range of all levels exploited. Exploitation rates increase in the intermediate trophic levels in both ecosystems while they decrease for the high levels in the North Sea and slightly increase in the Celtic Sea.

Simulations show that total yield could increase with fishing pressure in both ecosystems (Figure 6). The North Sea displays a

higher potential of yield than the Celtic Sea for increasing fishing efforts. Regarding the current fishing pressure applied, the biomass distribution of the North Sea appears highly impacted in the intermediate and high trophic levels for high values of the effort multiplier (Figure 6a), whereas, the distribution in the Celtic Sea seems more stable (Figure 6b). High exploitation rates mainly led to increased yield in intermediate trophic levels, but could drive a strong decline in the high trophic level catches linked to their collapse. This implies a decrease in the mean trophic level of the



catches as well as in the underlying biomass. Actually, the total catch increase results both from the increase in fishing effort and from a biomass increase at intermediate trophic levels released from predation.

Discussion

A Trophic Level-Based Approach

The concept of trophic level was firstly introduced by Lindeman (1942). Odum and Heald (1975) and Adams et al. (1983) defined fractional trophic levels which may be

considered as the metric which expresses the trophic process itself. It not only measures the position of organisms in the food web, but also characterizes each unit of biomass present in an ecosystem. It then could be used to analyze and model transfers of energy through the food web due to predation as well as ontogenic processes. Using this metric in a trophic-level based approach appears to be a promising way to look at the ecosystem from a tropho-dynamic point of view by following biomass flows from low trophic levels to upper ones.

In such an approach, not explicitly taking species into account does not imply that

they have no effects in the ecosystem functioning. Species composition notably determines mean transfer efficiencies per trophic class and flow kinetics, as well as the extent of top-down control. Nevertheless, all parameters except transfer efficiencies are assumed to be constant whatever the ecosystem state. In a sense, they are considered as ecological characteristics of a given ecosystem, independently of changes occurring in trophic classes' species compositions, due to fishing. Only the test of time will be able to indicate in the future if such a simple model is acceptable and useful for ecosystem management, or if more sophisticated models are needed.

Applying the approach to real case studies requires estimates of trophic position for all the species caught in the ecosystems studied. In our case studies we simply use the rough mean trophic levels issued from FishBase. A conventional smoothing technique was applied to spread catches of each species around its mean trophic level. This pragmatic method allowed us to represent the potential variability around these trophic level estimates, but such an approach remains theoretical (Gascuel et al. 2005). Field measures of mean trophic levels and estimates of their corresponding intraspecific variability should improve these types of analyses. Progressively, such measures are becoming more common, based on gut content analysis (Adams et al. 1983; Cortès, 1999; Stergiou and Karpouzi 2002) and stable isotope approaches (e.g., Vander Zanden et al. 1997; Post 2002). The next step in the ecosystem approach to fisheries should include the development of routine estimations of catch trophic levels. This appears to be a key element in ecosystem modeling, in the same way as age estimate can be considered key in monospecific models of population dynamics.

CTSA and Trophic-Level Based Model

Catch Trophic Spectrum Analysis is based on the reverse form of equations used in the trophic-level based model (Gascuel 2005). Such equations simply express the dynamics of the biomass flow passing through the ecosystem according to predation and ontogenic processes. These processes are not explicitly modeled. We just take into account three main characteristics of the ecosystem functioning: the loss of biomass flow during transfers towards high trophic levels; the transfer kinetics measuring the speed of the biomass flow; and the possible existence of top-down effects linking prey transfers to their predators abundance.

The first aspect is well known and transfer efficiencies have been estimated in many ecosystems (Pauly and Christensen 1995; Jennings et al. 2002). In simulations of catch data as well as in case studies, a unique value for all trophic levels ($e^{-\mu\tau} = 0.15$) was used. Improvements in estimates of transfer efficiency should lead to more accurate results.

The kinetics of transfers is less studied and we did not find any estimate of corresponding parameters in the literature. We used here an empirical logistic equation to model the time required by a unit of biomass to go from a trophic level to the upper one. Some authors have analyzed the delay occurring between events of primary production blooms and corresponding abundance peaks for predators. For example, Maury (1998) mentions a 3–6 months lag from primary production to yellowfin tuna *Thunnus albacares* concentration in Atlantic fisheries. According to this, the equation was parameterized in such a way that the time required to go from level 1 to level 4 was equal to 6 months. This value is probably realistic but remains largely unknown. More generally the model used is based on the assumption that the flow speed should decrease

from lower to higher trophic levels, due to decreasing metabolic rates. But this assumption must be confirmed in the future and further investigations are needed to estimate kinetics of transfers.

Because predation is a major cause of natural mortality, top-down control is recognized as an important factor of ecosystem functioning (e.g., Cury et al. 2003). Thus, it has to be included in the model, in order to take into account the impacts of predators on abundance preys. No quantitative expression of this process has been developed until now. Based on the idea that top-down control could act as a partial compensation effect of fishing, we chose to assume that it modifies natural loss rates of biomass flow, and thus transfer efficiencies. Once again, we also used empirical values of the corresponding parameter α . Sensitivity analyses were conducted for a large range of values, from $\alpha = 0$ corresponding to a "bottom-up ecosystem" (prey abundance independent of predators), to $\alpha = 0.8$ corresponding to a very strong top-down control. These analyses highlight that absolute CTSA estimates are sensitive to the top-down control coefficient, but relative and qualitative results appear more robust.

More generally, using empirical equations and parameters implies that we need to consider our results exploratory. Case-studies have been implemented to test CTSA, rather than for their intrinsic quantitative results. The most important result of this analysis was to show that CTSA can lead to exploitation rates and biomass estimates which appear useful to compare ecosystems and analyze changes at the ecosystem scale. We for instance obtain higher potential of yield in the North Sea than in Celtic Sea. This seems consistent with the differences in primary production derived from remote sensing images in these ecosystems (Chassot et al., in press).

Comparing results obtained for case studies with sensitivity analyses led us to conclude that the main uncertainty lies in estimates concerning low trophic levels, which are currently less exploited. Conversely, this means that external data are required for those levels to calibrate CTSA. In the future, results could thus be greatly improved by estimates of primary and secondary production currently available through remote sensing and data assimilation methods and estimates of abundance indices available through scientific surveys.

Finally, the analogy between CTSA and VPA (Gulland 1965) makes it easy to understand and help to solve the equations through the use of well-known approximation methods such as the Pope method (Pope 1972). The essential property of convergence first observed by Jones (1961) is also verified in CTSA. This leads to accurate estimates of fishing loss rates and biomass in the lower trophic levels and can be coupled with sensitivity analyses of terminal fishing loss rates. As in classic stock assessments, projections were conducted for different values of effort multiplier, based on a mean recruitment (here the secondary production) and on constant exploitation pattern regarding the trophic levels targeted. More sophisticated simulations could easily be performed.

Conclusion

Catch trophic spectra analysis (CTSA) appears to be a promising tool to study the evolution of secondary production along the food web and its exploitation by fishermen at different levels of the ecosystem. The model uses simple and well-known equations to represent the biomass dynamics between the different compartments of the web and should help to better understand the effects of fishing on marine ecosystems. The approach presented remains exploratory since some of the

relationships and parameters used are empirical. However, these results should lead to further work in the field of trophic-level based modeling.

Acknowledgments

We thank an anonymous referee and the editor J. Nielsen, for their very useful comments on a previous version of the manuscript.

References

- Adams, S. M., B. L. Kimmel, and G. R. Ploskey. 1983. Sources of organic matter for reservoir fish production: a trophic-dynamics analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1480–1495.
- Chassot, E., F. Mélin, O. Le Pape, and D. Gascuel D. In press. Bottom-up control regulates fisheries production at the scale of eco-regions in the European seas. *Marine Ecology Progress Series*.
- Christensen, V., and D. Pauly. 1992. Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61:169–185.
- Christensen, V., and C. J. Walters. 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., L. Shannon, and Y.-J. Shin. 2003. The functioning of marine ecosystems: a fisheries perspective. Pages 103–123 in M. Sinclair and G. Valdimarsson, editors. *Responsible fisheries in the marine ecosystem*. CAB International, Wallingford, UK.
- FAO (Fish and Agriculture Organization of the United Nations). 2000. Fishstat Plus: Universal software for fishery statistical time series Version 2.3. Fisheries Department, Fishery Information, Data and Statistics Unit, Rome.
- Froese, R., and D. Pauly. 2000. FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna, Philippines.
- Gascuel, D. 2002. 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. Pages 32–33 in A. Biseau, A. Forest, D. Gascuel, and F. Laloë, editors. *Halieutique : complexité et décision*. Ifremer, Lorient, France.
- Gascuel, D. 2005. The trophic-level based model: a theoretical approach of fishing effects on marine ecosystems. *Ecological Modelling* 189:315–332.
- Gascuel, D., Y.-M. Bozec, E. Chassot, A. Colomb, and M. Laurans. 2005. The trophic spectrum: a new ecosystem indicator. Theoretical meaning and practical applications. *ICES Journal of Marine Science* 62:443–452.
- Gulland, J. A. 1965. Estimation of mortality rates. Annex to the Report of the Arctic Fisheries Working Group. Hambourg, janvier 1965. Conseil International pour l'Exploration de la Mer CM 1965/3, Copenhagen.
- Jennings, S., K. J. Warr, and S. Mackinson. 2002. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Marine Ecology Progress Series* 240:11–20.
- Jones, R. 1961. The assessment of the long-term effects of changes in gear selectivity and fishing effort. *Marine Research of Scotland*, H. M. Stationary Office, Edinburgh, Scotland.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–418.
- Maury, O. 1998. Modélisation spatiale en halieutique. Approche par simulateur sous SIG. Application à la modélisation hiérarchique de la population de thons albacore (*Thunnus albacares*) de l'Atlantique tropical. Thèse de Doctorat de l'ENSAR, Agrocampus Rennes, France.
- Odum, W. E. and E. J. Heald. 1975. The detritus-based food web of an estuarine mangrove community. Pages 265–286 in *chemistry, biology and the estuarine system*. Estuarine Research, Volume 1. Academic Press, London.
- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature (London)* 374:255–257.
- Polovina, J. F. 1984. Model of a coral reef ecosystem. I. The ECOPATH Model and its application to French Frigate Shoals. *Coral Reefs*. Springer Berlin, Heidelberg.
- Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *ICNAF Research Bulletin* 9:65–74.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83(3):703–718.
- Stergiou, K. I., and V. S. Karpouzi. 2002. Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries* 11:217–254.
- Vander Zanden, M. J., G. Cabana, and J. B. Rasmussen.

1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Ecology* 54:1142–1158.
- Walters, C., V. Christensen, and D. Pauly. 1997. Structuring dynamics models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 7:139–172.