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The trophic spectrum: theory and application as an ecosystem indicator

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Trophic spectra represent the distribution of biomass, abundance, or catch by trophic level, and may be used as indicators of the trophic structure and functioning of aquatic ecosystems in a fisheries context. As a theoretical background, we present a simple ecosystem model of biomass flow reflecting predation and ontogenetic processes. Biomass trophic spectrum of total biomass can be modelled as the result of three major factors and processes: trophic efficiency, transfer kinetics, and extent of top-down control. In the simulations, changes in the spectrum highlight fishing impacts on trophic structure and reveal some functional characteristics of the underlying ecosystem. As examples of potential applications, three case studies of trophic spectra are presented. Catch trophic spectra allow description of structural differences among European fishing areas and periods. Abundance trophic spectra of coral-reef fish assemblages display different trophic signatures, characterizing different reef habitats in New Caledonia and highlighting fishing effects in a marine protected area context. Biomass trophic spectra of demersal resources off Northwest Africa show a shift in ecosystem structure that can be attributed to the rapid increase in fishing pressure during the past few decades. Off Senegal, total biomass remained fairly constant, suggesting a strong top-down control linked to fisheries targeting high trophic level species. Off Guinea, exploitation rates are spread over a wider range of trophic levels, and the total biomass of demersal resources tended to decrease. The trophic spectrum is concluded to be a useful indicator describing and comparing systems in time and space, detecting phase shifts linked to natural or anthropogenic perturbations, and revealing differences in ecosystem functioning.

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Introduction

General consensus has emerged among fisheries scientists that trophodynamics represent a major aspect of ecosystem functioning (Cury et al., 2003). Trophic level (TL) has become a key concept in many ecosystem models, providing a suitable ecosystem indicator of fishing impact (Pauly et al., 1998, 2000). The TL concept, however, may be elaborated further for the description of ecosystem functioning (Winemiller and Polis, 1996). Based on such an approach, we introduce the trophic spectrum of the total consumer biomass, defined as the biomass distribution by trophic class (in steps of 0.1 from herbivores and detritivores to top predators, i.e. TL = 2−5) as an indicator of trophic structure. Alternatively, a total commercial catch spectrum or an abundance trophic spectrum (in terms of number of individuals) may be derived, based on the community sampled by a survey gear.

The theoretical basis of the biomass trophic spectrum, and expected changes therein, is described by focusing on a simple model of biomass flows. This is followed by three case studies constructing trophic spectra for different ecosystems, then by a discussion of the usefulness of trophic spectra for comparing structure of aquatic ecosystems, to monitor trends and to detect phase shifts, and to highlight ecosystem effects of fishing.

Methods

Simulation model

The biomass trophic spectrum of total consumers by trophic class can be considered to be the result of three processes: (i) input of biomass at TL = 2 (i.e. production of primary consumers through grazing and recruitment of early-stage larvae feeding on phytoplankton); (ii) transfer of biomass from one TL to the next (i.e. predation and ontogenetic changes in TL during the life history of organisms); (iii) loss of biomass at all TLs as a consequence of fishing mortality, all natural mortality other than predation, and respiration and digestive inefficiencies (egestion and excretion). Therefore, given a certain biomass at TL = 2, the shape of the biomass trophic spectrum can be modelled to investigate the impact of fishing.

The foodweb is constructed to allow for increments in TL of 0.1. Steady state biomass and biomass flows for each trophic level are modelled in two steps, one for biomass transfer and one for biomass flow kinetics (for notations see Table 1). Biomass (B) is transferred from TL = τ to TL = $\tau + \Delta\tau$, with losses caused by natural (other than predation) and fishing mortality according to:

$$\Phi(\tau + \Delta\tau) = \Phi(\tau)\exp(-[\varphi_\tau + \mu_\tau]\Delta\tau) \quad (1)$$

To allow for bottom-up or top-down controls, we assume that the rate of natural loss is related to the relative predator abundance in the unexploited situation (Bv):

$$\mu_\tau = (1 - \alpha)\mu v_\tau + \alpha\,\mu v_\tau(B_{\tau+1}/Bv_{\tau+1}) \quad (2)$$

Therefore, when predator abundance decreases relative to the unexploited situation, transfer efficiency increases, depending on α. If bottom-up control is assumed, $\alpha = 0$.

B is transferred faster at low TL because of higher metabolic rates. Then, to model biomass flow kinetics, we assume that the time required by a unit of biomass to transit from one TL to the next follows a logistic curve. This implies a relationship between trophic level (τ) and time (t), with the form:

$$\tau = a\,\ln[\exp(b\,t) - 1] + c \quad (3)$$

The biomass present in the interval (τ; $\tau + \Delta\tau$) under steady state conditions (B$_\tau$) and the catch in this interval during a unit of time (Y$_\tau$) follow accordingly from:

$$B_\tau = \int \Phi(\tau)(dt/d\tau)d\tau \approx (\Delta t/\Delta\tau)$$
$$[\Phi(\tau) - \Phi(\tau + \Delta\tau)]/(\mu_\tau + \varphi_\tau) \quad (4)$$

$$Y_\tau = [(\Delta t\,\varphi_\tau)/(\mu_\tau + \varphi_\tau)][\Phi(\tau) - \Phi(\tau + \Delta\tau)] \quad (5)$$

The model is used first to explore the range of parameter values leading to realistic results by analysing the effect of transfer efficiency (e$^{-\mu v_\tau}$) and flow kinetics on the biomass trophic spectrum in the unexploited situation. Next, the effect of fishing on biomass and yield is explored for bottom-up and top-down control (α parameter in Equation (2)). We assume a standard selectivity curve by trophic level (S$_\tau$), considering that fishers mainly target TL > 3 (Table 1).

Construction of empirical trophic spectra

The construction of trophic spectra for the case studies is based on aggregated data by species (biomass, catch, abundance) in combination with estimates of species TL (based on gut contents, isotope analyses, or modelling results). Because TL may vary among individuals of a given species (for instance, with size), it is appropriate to spread the biomass of a species over a range of TL around the mean, according to the intraspecific variance. Because this variance is generally unknown, we use a pragmatic approach and apply a weighted smoothing

Table 1. The model of biomass flow: parameter definitions and values used in the simulations (TL: trophic level; subscript τ refers to TL interval [τ; $\tau + \Delta\tau$]; ci: constant during interval).

Notation	Parameter definition	Values used in simulations
$\Phi(\tau)$	Biomass flow at TL = τ	$\Phi(2) = 100$; $\Phi(\tau \neq 2)$ estimated by Equation (1)
B_τ	Biomass in (τ, $\tau + \Delta\tau$) interval	Estimated by Equation (4)
Bv_τ	Unexploited biomass	Estimated by Equation (4)
Y_τ	Yield per unit of time	Estimated by Equation (5)
μ_τ	Natural loss rate (ci)	Determined by Equation (2)
μv_τ	Natural loss rate unexploited (ci)	Exploring values from e$^{-\mu v_\tau} = 0.1$ to 0.3
φ_τ	Fishing loss rate (ci)	Exploring value $\varphi_\tau = mf\,S_\tau\,\mu v_\tau$, with mf = 0 to 2
α	Coefficient of top-down control	0 for bottom-up; 0.8 for top-down
a, b, c	Coefficients of time−TL relationship (Equation 3)	Empirical values corresponding to a range of realistic curves (cf. Figure 1)
S_τ	Selectivity coefficient by TL	Logistic curve

over a range of TL of 0.7, after first aggregating all species information by classes of 0.1TL.

Results

Simulations

The value of the transfer efficiency (TE) in the unexploited system has a direct effect on the biomass trophic spectrum. For a fixed biomass flow at TL = 2, a low TE leads to a predominance of biomass at low TLs, whereas high biomasses of top predators imply high TEs (Figure 1a, b).

Flow kinetics also influence the spectrum by inducing biomass accumulation in TL characterized by slow transfer (Figure 1c, d). Therefore, for a given biomass flow, slow transfers imply high biomass, and vice versa. This phenomenon becomes particularly clear by simulating a declining flow at intermediate TL only, representing for instance species that suffer little predation.

Exploitation does not affect transfer kinetics, but it does impact the biomass flow and the biomass trophic spectrum (Figure 2). The higher the exploitation rate, the lower the total biomass, and therefore changes in the spectrum clearly reflect the ecosystem impact of fisheries. Under bottom-up control, all exploited TLs are affected (Figure 2a), but the decline is strongest for higher TLs, because the effects of losses of prey are added to those of catches. Under top-down control, a decline in predator abundance leads to a release from predation, compensating to some extent for fishing pressure on higher TLs, and potentially inducing an increase in biomass of the lower, less exploited TLs (Figure 2b). Overall, top-down control tends to stabilize total biomass and so appears to induce resilience to exploitation.

The trophic spectra of catches depend on the TL selectivity curve and the biomass trophic spectrum. In the simulations, catches at low TL are small, because these are targeted less by fishers (Figure 2c, d). The peak shifts to a lower TL when exploitation increases, and overexploitation is only observed in the higher TL when fishing pressure is greater. Top-down control allows for bigger catches at an intermediate TL than bottom-up control, because of the release from predation.

Comparison and evolution of European fisheries

Trophic spectra of the catches were used as a descriptive tool in comparing European fisheries by region and
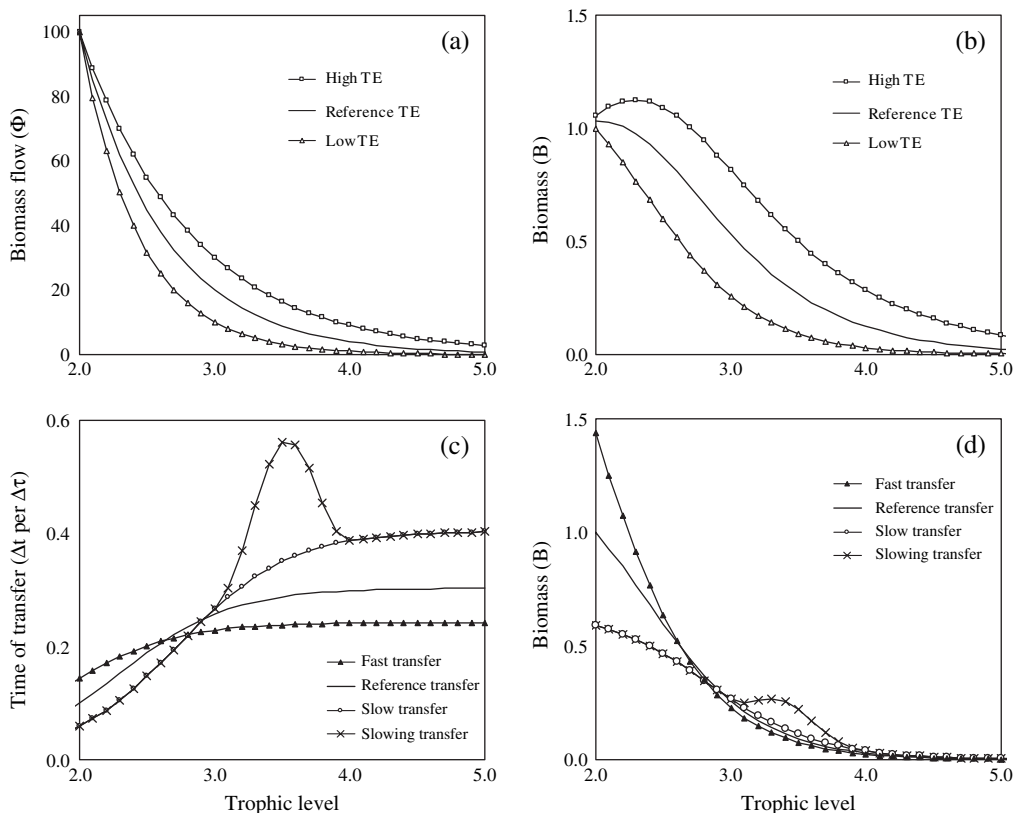

Figure 1. Modelling results for an unexploited system: (a) biomass flows simulated with different transfer efficiencies (low TE = 0.1, reference TE = 0.2, high TE = 0.3) for reference values of transfer kinetics; (b) corresponding biomass trophic spectra; (c) simulation of different transfer kinetics (different values of empirical parameters in Equation (3)) for reference value of TE (line with crosses: a declining flow inducing biomass accumulation); (d) corresponding biomass trophic spectra.
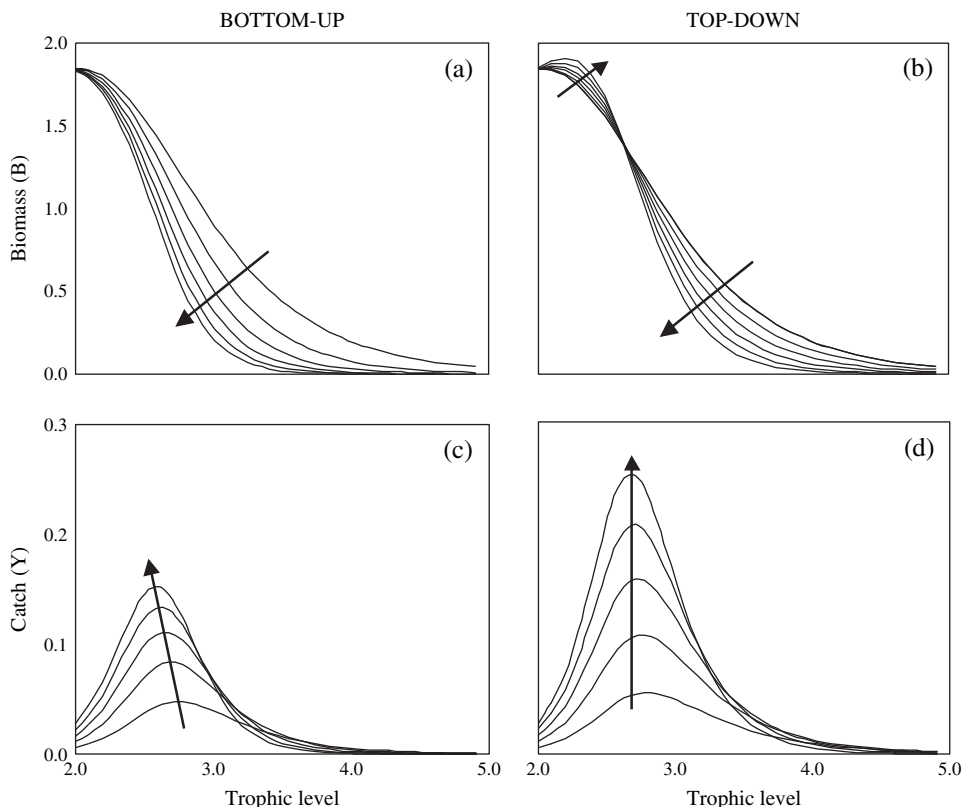
BOTTOM-UP　　　　　　　　　　TOP-DOWN

Figure 2. The impact of fishing on biomass (top) and catch (bottom) trophic spectra for bottom-up (left) and top-down (right) control (arrows indicate the effects of increasing fishing pressure).

investigating temporal trends. Catch data were extracted from the ICES database using FishstatPlus software (FAO, 2000). We selected species that accounted for at least 1% of the total catch in any ICES Subdivision. Trophic levels were derived from FishBase (Froese and Pauly, 2000). Surface areas correspond to the continental shelf boundaries (limited by the 1000 m isobath). European waters were split into nine "ecosystem fisheries units" (Chassot *et al.*, 2002) and a mean trophic spectrum of the catch (average 1992–2001) was plotted for each unit. In addition, trophic spectra were plotted by 7-year time frames over the period 1973–2001, to illustrate changes observed in the Irish Sea.

The catch trophic spectra reveal large differences between areas (Figure 3). Notably in the northern areas (Faroe Islands, northern North Sea, North Sea, West of Scotland & Ireland), most of the yield is concentrated in a narrow TL range (500–1000 kg km^{-2}). In contrast, the Celtic Sea, Irish Sea, and Bay of Biscay have much lower yields spread over a large TL range (2.1 for shellfish to >4.0 for tunas and some gadoids). The spectra may reflect differences in the underlying ecosystem structure as well as exploitation patterns. They suggest different strategies of exploitation, and a different trophic structure and functioning in the selected areas.

The Irish Sea data reveal a decreasing trend in mean TL of the catch since 1973 (Figure 4a). The trophic spectra display three modes, corresponding to three commercially important trophic groups: the high and intermediate groups (mainly represented by gadoids and small pelagics, respectively) show a consistent decline since the 1970s, whereas the yield of the low TL group (blue mussel, scallops, whelk) has increased (Figure 4b). This temporal analysis of the trophic spectrum allows tracking the development of a "fishing down marine foodweb" effect.

Trophic signatures of coral-reef fish assemblages

Trophic spectra of coral-reef fish abundance were used to investigate possible links between habitat and trophic structure in the southwest lagoon of New Caledonia (Figure 5). Since the late 1980s, the fish community at 360 sampling stations has been censused using scuba along belt transects of 500 m^2, encompassing 527 species of reef-dwelling fish (Figure 5). TL was estimated from local gut content analyses (of some 100 species), from FishBase information (340 species), and from congeneric analogies when no
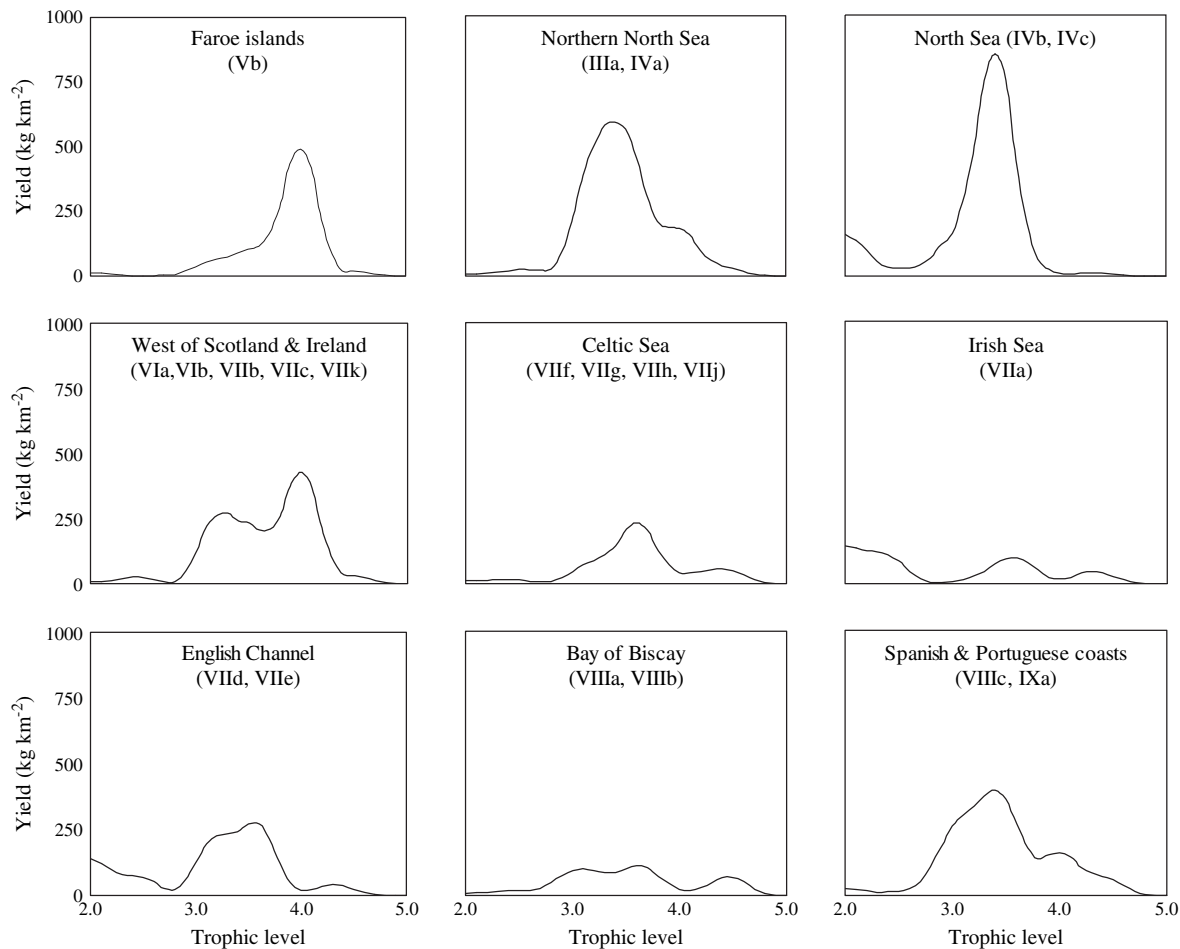
Figure 3. Catch trophic spectra for nine European fishing areas (average 1992−2001).

information was available (some 80 species). A trophic spectrum of fish abundance (number of individuals) was estimated for each station. Stations were grouped according to three major types of habitat defined in the lagoon:

fringing reefs along the mainland coast, inner lagoon reefs, and barrier reefs. Trophic spectra were averaged (geometric mean) by habitat type, and a confidence interval of the mean was estimated by bootstrapping.
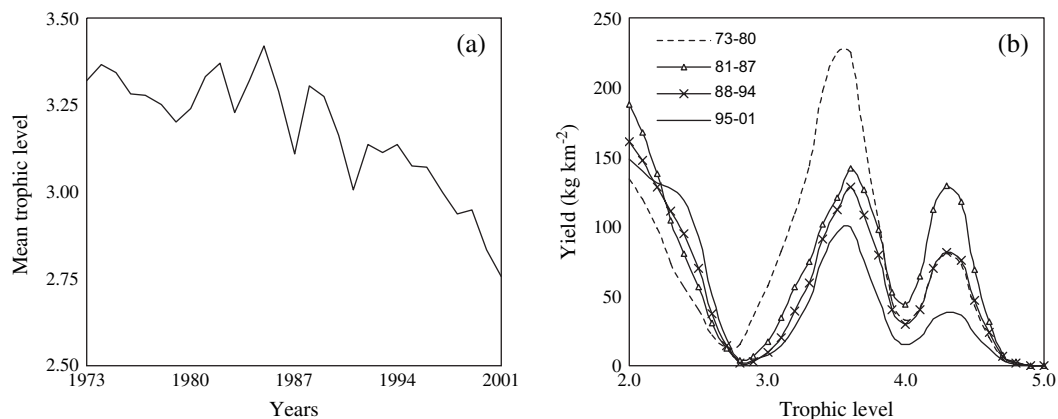

Figure 4. Evolution of (a) mean trophic level of catch (1973−2001) and (b) catch trophic spectra by 7-year period, for the Irish Sea.
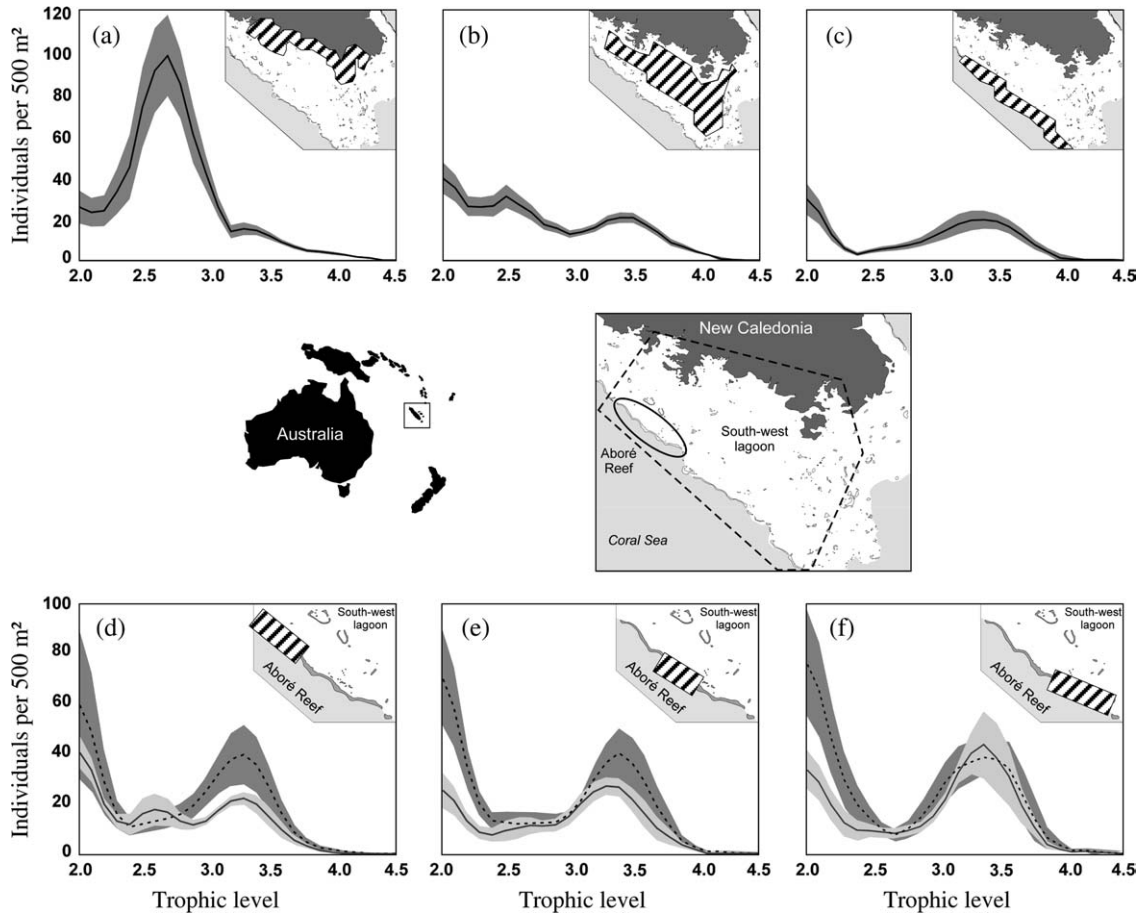
Figure 5. Mean abundance trophic spectra of coral-reef fish assemblages in the southwest lagoon of New Caledonia (grey: bootstrap confidence interval of the geometric mean). Top: habitat-related spectra for (a) fringing reefs, (b) inner lagoon reefs, and (c) barrier reefs. Bottom: spectra in three sections of Aboré Reef, before (dotted line) and 2 years after (solid line) the opening of the protected areas (d and e) to exploitation, (f) remaining protected.

Mean trophic spectra exhibited consistent changes between the three defined habitats (Figure 5a−c). Trophic spectra of the fringing reefs were characterized by a peak abundance for TLs ranging from 2.5 (omnivores with mixed diet of benthic algae and sessile invertebrates) to 3 (zooplankton feeders). A similar pattern has been observed in the fringing reefs of two urbanized bays of the southwest lagoon (Bozec *et al.*, 2003). The peak decreased progressively when moving from the coast to inner lagoon reefs and to the barrier reef, where herbivores (TL = 2) and predators of mobile invertebrates (TL = 3.2−3.6) dominated the fish community. Total abundance was higher on fringing reefs, reflecting the fact that omnivores and zooplankton feeders often live in large schools. The narrow confidence limits indicate that trophic spectra exhibit a well-defined shape by habitat type, suggesting that they represent reliable trophic signatures of the foodweb structure of the community. The gradual change with distance to the coast suggests that the spectrum may be considered an indicator of trophic state, influenced by environmental conditions.

To illustrate the potential indicator function of trophic spectra in a fishery context, we also investigated fishing effects on the fish assemblages of Aboré Reef, a marine protected area located on the barrier reef (Figure 5d−f). In 1993, two reef sections were opened to exploitation, while a third remained closed, allowing a before−after-control−impact evaluation. Trophic spectra show that the abundance of herbivores tended to decrease after exploitation commenced, even in the zone that remained protected. Predators of mobile invertebrates (TL = 3.2−3.5) also decreased, but they remained fairly constant in the protected zone. This may reflect a fishing effect, because herbivorous and carnivorous species are both targeted in coral-reef fisheries.

Fishing impact on West African demersal resources

Senegalese and Guinean fisheries have been characterized by a marked increase in fishing effort during the past three decades. Indices of abundance derived from trawl surveys were used to build biomass trophic spectra to investigate fishing impacts on demersal resources of both countries (Laurans *et al.*, 2004).

Off Senegal, 18 bottom-trawl surveys have been conducted covering the entire continental shelf during the periods 1971−1974 and 1986−1995. Biomass trophic spectra (based on 254 species and FishBase values of TL) were averaged by 5-year period (Figure 6a). Since the 1970s, total biomass of demersal resources has remained fairly constant, but trophic spectra clearly show that biomass in the higher TL range has decreased, while that in the lower range has increased. This evolution suggests a top-down effect and some resilience to increasing fishing pressure.

Demersal catches are on record since 1981 for both artisanal and industrial fisheries. Trophic spectra of the catches highlight a continuous decline in yield for the higher TL (Figure 6b), representative of strongly over-exploited species (Gascuel *et al.*, in press). Until 1995, the yield from lower TLs was relatively stable, supporting the top-down effect suggested above. Subsequently, these yields have also decreased, suggesting that the maximum resilience of the ecosystem may have been reached. The ratio of catch and biomass trophic spectra shows that Senegalese fisheries are "trophically selective" in mainly targeting the highest TL (Figure 6c).

Off Guinea, 26 coastal bottom-trawl surveys have been conducted since 1985. At that time, coastal demersal sciaenid resources were considered to be almost unexploited (Domain *et al.*, 2000). The decline in total biomass is linked to an increase in fishing pressure (Figure 6d). The pattern is reversed, however, if compared with that off Senegal: higher TL species have increased and mid-range biomass values have decreased markedly. The decrease appears particularly strong for TL classes around 4, without inducing any biomass increase at a lower TL. This may reflect a weaker top-down control than off Senegal. Because catch statistics are only available from 1995, they do not allow investigation of long-term trends, but the ratio of the two spectra for the last 5-year period (Figure 6e) indicates that the fishery targets a wider range of TLs, but not the higher TLs. This may explain why no increase in abundance of prey is observed off Guinea, and why there is no indication of resilience.

Discussion

Predation is a key process in structuring biological communities (Martinez, 1995). Moreover, a key to improving our understanding of ecosystem functioning lies in the analysis of energy flows (Pahl-Wostl, 1997; Cury *et al.*, 2003). Our theoretical model combines these two considerations through the analysis of biomass flows from the lower to the upper TL. In such an approach (initially proposed by Gascuel, 2002), species are not grouped into compartments according to their position in the foodweb, but ecosystem biomass is distributed along a continuum of TL values. More accurately, the model is based on the use of fractional TL, as defined by Odum and Heald (1975) and Adams *et al.* (1983). TL classes are thus used as an approximation of the continuous distribution. This differs from the mass-balance Ecopath/Ecosim model (Polovina, 1984; Christensen and Pauly, 1992; Walters *et al.*, 1997), which relies on the allocation of biomass in discrete trophic groups. Using just a few basic equations, the model shows that the distribution of ecosystem biomass through TLs is the result of biomass flow characterized by transfer speed and transfer efficiency.

Biomass entered the system only at TL 2, thus neglecting the biomass of carnivorous larvae and assuming that they account for small inputs only. All biomasses at TL > 2 are directly derived from lower levels by predation or ontogenic processes. Although this approximation might be corrected by including inputs of biomass attributable to recruitment, such a complication should not modify the global dynamics of the model, and the shape of the trophic spectrum and the qualitative impact of fishing would not be expected to change markedly. Similarly, the recycling of detritus is usually recognized as having a great influence on ecosystem dynamics, so the relationships between flow loss and detritus, and between detritus and secondary production might be included in the model. Once again, we do not expect that this would modify the qualitative results. Variations in secondary production are not considered in the model. At this developmental stage, the model can be used only to explore the main factors affecting the steady state shape of trophic spectra.

Another limitation lies in the uncertainty about the appropriate range of parameter values. Indeed, suitable values are largely unknown, and parameterization is necessarily empirical. Despite this uncertainty, the model shows that biomass at each TL depends on three major characteristics of ecosystem dynamics: transfer efficiency (TE), flow speed, and the extent of top-down control. Consequently, the associated parameters are of interest in modelling ecosystems. TEs have long been recognized as essential parameters of ecosystem functioning (Lindeman, 1942), and have been studied intensively by many (e.g. Pauly and Christensen, 1995; Jennings *et al.*, 2002). In contrast, transfer kinetics remain largely neglected in research programmes. The model results indicate that transfer kinetics represent a key characteristic that allows conversion of biomass flows into biomass present at each TL, and might help to build a general theory on ecosystem functioning.
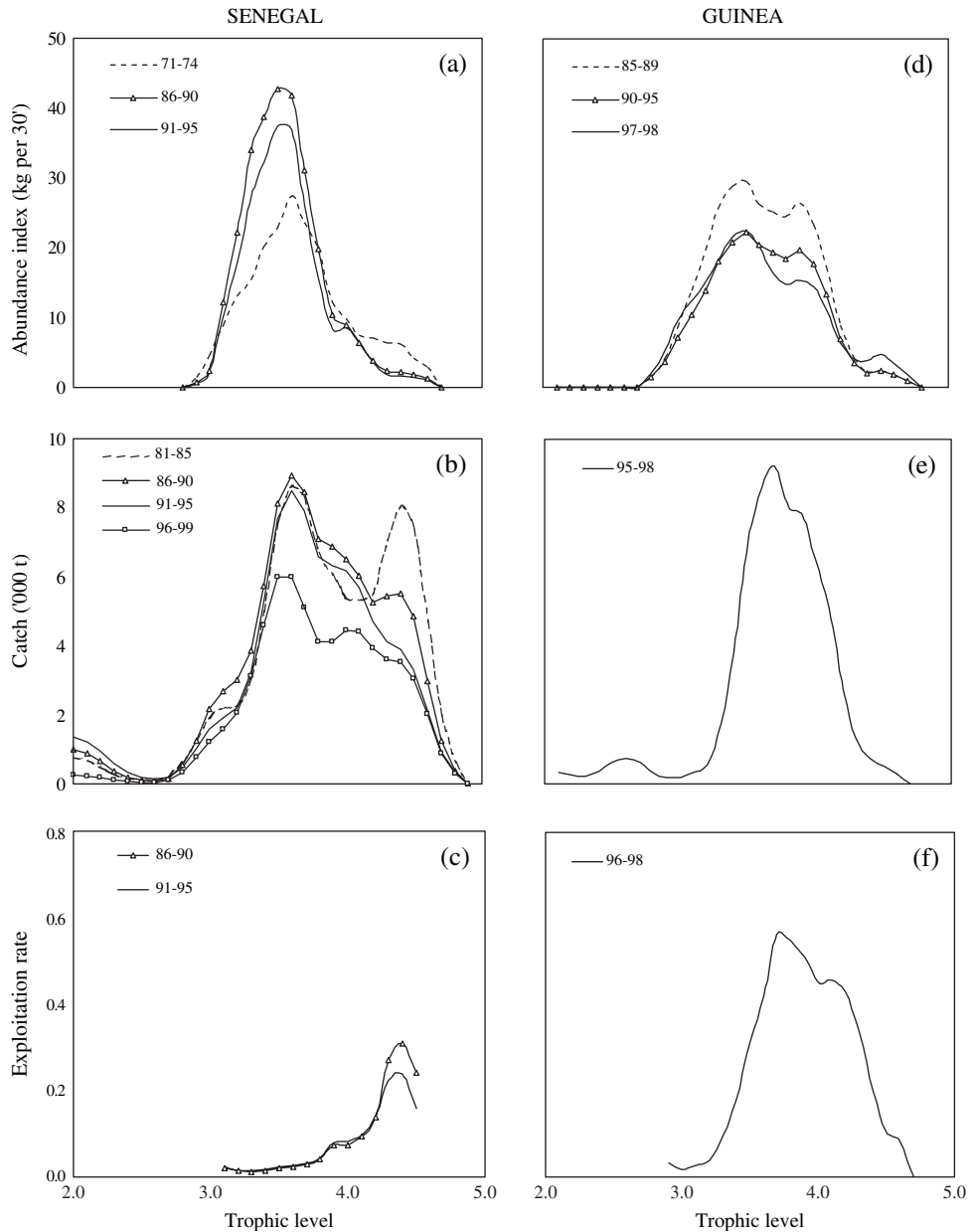
Figure 6. Biomass (top), catch (middle), and exploitation rate (bottom) trophic spectra for Senegalese (left) and Guinean (right) demersal resources.

As a graphic representation of biomass distribution across TLs, the biomass trophic spectrum appears to be a continuous generalization of the trophic "pyramid of numbers" (Elton, 1927), which is usually built by discrete TL integers (Lindeman, 1942). Following Odum (1959), pyramids based on numbers, biomass, and energy have been used extensively, in terrestrial as well as marine ecology. Our model based on biomass flow formalizes and underpins the theoretical basis of such pyramids. Notably, it facilitates understanding of why "pyramids of energy"

(which correspond to flow representation) must exhibit decreasing values with TL, while "pyramids of biomass" may be inverted at some TL (Odum, 1959), because of slow transfer kinetics of transfers, followed by biomass accumulation.

In practice, trophic spectra may be built using TLs directly estimated from diet data (Adams *et al.*, 1983; Cortès, 1999; Froese and Pauly, 2000), or from the analysis of stable isotope ratios (Vander Zanden *et al.*, 1997; Post, 2002; McCutchan and Lewis, 2003). The latter appear to

yield more accurate estimates (Vander Zanden and Rasmussen, 1996; Pinnegar *et al.*, 2002), but comparative analyses have shown strong correlations between estimates obtained with different methods (Vander Zanden *et al.*, 1997; Kline and Pauly, 1998; Davenport and Bax, 2002). Nevertheless, improving the estimates of trophic parameters by crossing the different approaches remains a major challenge, because reliable estimates of trophic level that take into account intraspecific variability in time and space are essential in interpreting the ecosystem effects of fishing.

The weighted smoothing technique provides a pragmatic approach to spread biomass or catches of a species along a range of fractional TL, according to the expected variability in diet at a population level. This results in a constant, symmetrical distribution among all species. Some authors have proposed measuring TL variability with an "omnivory index" (Levine, 1980; Froese and Pauly, 2000; Pauly *et al.*, 2000), but this index is a measure of the TL range of prey covered in the diet of a given predator, not a measure of the TL variability among predators, which would be required to improve the trophic spectrum estimated. Nevertheless, the moving average technique is a conventional smoothing method, and the differences observed among spectra in the case studies are probably not dependent upon the smoothing technique used. Indeed, the choice of weights and ranges used in smoothing should have no effect on the qualitative results obtained.

Focusing on TL appears to be a promising way of analysing and modelling marine ecosystems and their associated fisheries. Following the work of Kerr (1974), there has been a focus on length-structured ecosystem models and analysis of size spectra (reviews by Bianchi *et al.*, 2000; Shin *et al.*, 2005). Length is a key parameter in investigating trophic relationships among fish and building comprehensive predator—prey models. Therefore, the trophic-level-based approach should be seen as complementary rather than alternative in such analyses. Length and TL are correlated at the community level (Jennings *et al.*, 2001). Length is an essential factor determining ecosystem dynamics, whereas TL may appear rather as an emergent result of these dynamics, providing an *a posteriori* metric of the trophic processes involved.

Trophic spectra provide a key tool in the TL-based approach. Spectra may be plotted for biomass, numerical abundance, catches, or exploitation rate, and can be estimated for the entire ecosystem or for subsystems. Other trophic spectra may be anticipated, perhaps expressed in terms of species diversity or price of fish products. The use of TL has introduced an important new quantitative metric for ecosystem analysis, because it appears to present an explanatory variable for many parameters in both ecological and fisheries contexts.

The case studies illustrate the potential of using the trophic spectrum as an ecosystem indicator. Impacts of fishing are shown in the spectra for African demersal resources and Caledonian coral-reef communities. More generally, the case studies show that trophic spectra may provide useful trophic signatures to compare ecosystems, to analyse trends, and to detect shifts in trophic structure, as well as to highlight the ecosystem effects of fishing. The spectra synthesize complex information contained in various types of data in a clear and simple graphical way, as well as allowing curve-tracking of structural and functional ecosystem properties.

While qualitative interpretation is easy, appropriate methods for testing whether the differences observed are significant would greatly enhance the quantitative interpretation. For instance, a confidence interval could be determined by a bootstrap procedure in the case study of coral-reef fish assemblages. Linear models (Laurans *et al.*, 2004) or multivariate analyses (Bozec *et al.*, in press) are other statistical methods that may be applied. Nevertheless, the current use of trophic spectra remains largely descriptive because no summary statistic has been derived or evaluated, so no reference value can be defined. To assess the impact of fishing, it would help if the biomass trophic spectrum in, or close to, the virgin situation could be defined. This is generally not possible, because collection of time-series data mostly started long after the onset of exploitation (Myers and Worm, 2003). Nevertheless, a reference spectrum may be estimated in the case of recently initiated fisheries (such as in West Africa) or using theoretical approaches (Jennings and Blanchard, 2004) and ecosystem modelling. In addition, metrics with corresponding target or limit reference points need to be developed. For instance, spectrum slope, spectrum range, number of modes, and relative amplitude among them might offer suitable starting points. Although ideally response time to perturbations should be short, this would be dependent on the TL impacted by the fishery, and long time-series may be needed to investigate response time empirically. More comparative studies and meta-analysis should help to better understand perturbation effects on the structure of ecosystems.

Acknowledgements

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