

Comparing methods for building trophic spectra of ecological data

Simone Libralato and Cosimo Solidoro

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The distribution of biomass, production, and catches over trophic levels (TLs) of the foodweb has been shown theoretically and empirically to provide powerful insights into ecosystem functioning and the effects of fishing. One approach for building trophic spectra of ecological data is based on smoothing original data and assuming zeroes when no values are available for a TL (smoothing-based method). An alternative method is proposed, based on the distribution of ecological data according to density functions (dispersion-based method), and a systematic review of the different alternatives is presented. Six different methods for building trophic spectra, i.e. the smoothing-based and five alternative forms for dispersion-based (using normal, lognormal, and Weibull distributions, also including shifted lognormal and Weibull with zero at TL 2), were applied to ecological properties (i.e. production, biomass, and catches) derived for 24 foodweb models to test their relative performance. The smoothing-based method suffers from the lack of consistency with original data and from unrealistic emergent properties, such as transfer efficiency. The analysis demonstrates the advantages of the dispersion-based method for overcoming these issues and shows, using transfer efficiencies estimated from the models (flow-based estimates) as a reference, that the normal density distribution function performs better.

Keywords: ecological indicator, foodwebs, omnivory, transfer efficiency, trophic level.

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S. Libralato and C. Solidoro: *Istituto Nazionale di Oceanografia e di Geofisica Sperimentale—OGS, Borgo Grotta Gigante-Brisciki 42/c, 34010 Sgonico-Zgonik, Italy. Correspondence to S. Libralato: tel: +39 040 2140376; fax: +39 040 2140266; e-mail: slibralato@ogs.trieste.it.*

Introduction

The trophic level (TL) has been a central concept in ecological studies since the seminal work by Lindeman (1942). Originally proposed as the number of energy transfers (levels) from primary producers to a consumer (assigning integer values; i.e. herbivores = 2, consumers of herbivores = 3, etc.), the fractional TL is now computed empirically from information on the diet of a species (Odum and Heald, 1975; Pauly and Watson, 2005). Fractional TL provides insights into energetic pathways (Stergiou and Karpouzi, 2002) and might be used as an empirically based synthetic index for intra- and inter-ecosystem comparisons of species' feeding habits (Badalamenti *et al.*, 2000). Moreover, because TL is positively related to fish size (Jennings *et al.*, 2002a) and fishing is selective with regard to size, there is a relationship between fishing activity and TL. In fact, TL has been suggested as an indicator of fisheries effects on marine communities and has been used successfully in several analyses (Pauly *et al.*, 1998a; Pinnegar *et al.*, 2002; Rochet and Trenkel, 2003; Pauly and Watson, 2005; Piet and Jennings, 2005).

The pyramid of biomasses and production over integer TLs has long been used to represent the ecosystem structure (Lindeman, 1942). More recently, the distribution of ecological properties such as biomass, production, and catches over TLs, termed the trophic spectrum, has been proposed by Gascuel *et al.* (2005) to provide important insights into the ecological effects of exploitation on marine ecosystems. For instance, the shape of biomass data along TLs (the biomass trophic spectrum) has been used as

an indicator of ecosystem structure and functioning (Gascuel *et al.*, 2005), and a modelling approach representing biomass and production as functions of TL (Gascuel *et al.*, 2008; Gascuel and Pauly, in press) highlighted the effects of increasing fishing pressure on the shape of biomass trophic spectra, with distinct, alternate system behaviours resulting when bottom-up or top-down effects dominate.

Notwithstanding recent advances on trophic spectra modelling, the basic study of the trophic spectrum of empirical marine data represents a useful and still novel ecological analysis. The methodology has been used successfully on empirical data on catch (Gascuel *et al.*, 2005), abundance (Bozec *et al.*, 2005), and biomass (Munyandorero, 2006) of marine species, providing information on ecosystem functioning.

Data-based trophic spectrum analyses employ the methodology of Gascuel *et al.* (2005) to obtain a trophic spectrum from ecological data that is based on a seventh-order weighted smoothing of data previously aggregated by fixed TL interval, using zero values for empty intervals (the smoothing-based method).

Here, we compare a set of alternatives for constructing trophic spectra based also on the dispersion of empirical data based on a different density distribution function (ddf; the dispersion-based method) to test capabilities and limitations of different approaches. Using production, biomass and catches taken from a set of 24 well-documented foodwebs, which we assume to be accurate and unbiased, we construct trophic spectra with alternative methods and compare their properties. Our results provide a

basis for discussion of the alternatives and a comparison of their robustness.

Material and methods

Smoothing-based trophic spectra

The data consist of the ecological properties by TL, i.e. biomass, production, and catch, for each consumer of the ecosystem to be analysed. According to Gascuel *et al.* (2005), data are aggregated by fixed TL intervals (0.1 TL), then the trophic spectrum is constructed using a weighted smoothing over a fixed range (0.7 TL). For each TL* interval, therefore, and for each ecological property X, the spectrum assumes a value $\Phi_X(\text{TL} = \text{TL}^*)$ according to a centred seventh-order weighted average:

$$\Phi_X(\text{TL}^*) = \frac{1}{27} \cdot X_{\text{TL}^*-0.3} + \frac{3}{27} \cdot X_{\text{TL}^*-0.2} + \frac{6}{27} \cdot X_{\text{TL}^*-0.1} + \frac{7}{27} \cdot X_{\text{TL}^*} + \frac{6}{27} \cdot X_{\text{TL}^*+0.1} + \frac{3}{27} \cdot X_{\text{TL}^*+0.2} + \frac{1}{27} \cdot X_{\text{TL}^*+0.3} \quad (1)$$

Clearly, at the boundaries of the TL domain (i.e. $\text{TL}^* < \text{TL}_{\min} + 0.3$ and $\text{TL}^* > \text{TL}_{\max} - 0.3$), the weighted average is forced to become asymmetrical (not centred) and of lower order. This smoothing-based procedure will therefore provide unreasonable trophic spectra especially at the lower boundary, i.e. $\text{TL} = 2$, and will lack consistency with input values of ecological properties, i.e. the integral of the trophic spectrum might be different from the sum of the input data for constructing it, implying a loss of information. Hence, the smoothing-based method, although considered robust because no assumption is made about the distribution of original variables (Bozec *et al.*, 2005; Gascuel *et al.*, 2005), is poorly defined at the boundaries of the TL domain analysed. More importantly, this weighted average is applied disregarding the discontinuity of the data, including the zero values in the smoothing (Gascuel *et al.*, 2005). However, zero values may result from the fact that field sampling cannot perfectly resolve all TLs, so zeroes might be considered as unknown values (missing information) rather than the result of empirical evidence, and hence be disregarded from the averaging procedure.

Dispersion-based trophic spectra

An alternative procedure is based on the dispersion of data using opportune ddfs. Original data (production, biomass, or catch) recorded for each *i*th consumer of the ecosystem (X_i) are not discretized to a specific point $\overline{\text{TL}}_i$ of the TL domain, but are distributed over a wider interval assuming that ecological property X_i of the *i*th consumer is distributed around a central value $\overline{\text{TL}}_i$ with a dispersion σ_i^2 .

The $\overline{\text{TL}}_i$ for each consumer (species *i*) is computed based on a widely used definition (Odum and Heald, 1975; Pauly and Watson, 2005), as

$$\overline{\text{TL}}_i = 1 + \sum_{j=1}^n (\text{TL}_j \times \text{DC}_{ji}), \quad (2)$$

where *j* are the *n* prey items of consumer *i*, TL_j their TLs, and DC_{ji} the fraction of each prey in the diet. Dispersion of the $\overline{\text{TL}}_i$ for each species is quantified as the variance of the TLs of its prey (TL_j) weighted by the fraction of each prey item in the diet (DC_{ji}), and it is defined as

$$\sigma_i^2 = \text{OI}_i = \sum_{j=1}^n [\text{TL}_j - (\overline{\text{TL}}_i - 1)]^2 \times \text{DC}_{ji}. \quad (3)$$

This variance is also termed the omnivory index (OI_i) of a given species of $\overline{\text{TL}}_i$ (Christensen *et al.*, 2005).

Different ddfs $X_i(\text{TL})$ have been tested including normal, lognormal, and Weibull distributions. However, only consumers have been included in the trophic spectrum analysis (functional groups with $\overline{\text{TL}}_i \geq 2$), so to test the distributions restricted to the same domain of data, lognormal and Weibull distributions with zero shifted to $\text{TL} = 2$ were also considered. In this way, the dispersion-based method for building trophic spectra was applied using five alternative forms for the ddf (Table 1).

Therefore, given the general form for the ddf, there is a bell-shaped distribution for each consumer and the ensemble of the distributions for the ecosystem overlaps, with virtually no zero values. The trophic spectrum for each ddf is obtained by summing all the distributions over all *N* consumers in the ecosystem:

$$\Phi_X(\text{TL}) = \sum_{i=1}^N [X_i(\text{TL})]. \quad (4)$$

The construction of trophic spectra with the dispersion-based method is presented graphically in Figure 1, using the normal ddf as an example.

For normal and non-shifted lognormal and Weibull distributions (alternative forms 1, 2, and 4), tails falling below $\text{TL} = 2$ were added to values of $\text{TL} > 2$, because no real TL can exist between $\text{TL} = 1$ and $\text{TL} = 2$. This leads to spectra with zero

Table 1. Ddfs used for building trophic spectra based on the dispersion-based method.

Alternatives for dispersion-based method	ddf	Note
(1) Normal	$X_i(\text{TL}) = (X_i/\sqrt{2\pi\sigma_i}) \exp[-(\text{TL} - \overline{\text{TL}}_i)^2/2\sigma_i^2]$	-
(2) Lognormal	$X_i(\text{TL}) = (X_i/\text{TL}\sqrt{2\pi\sigma_i}) \exp[-(\log(\text{TL}) - \overline{\text{TL}}_i)^2/2\sigma_i^2]$	-
(3) Lognormal shifted	$X_i(\text{TL}) = (X_i/[(\text{TL} - 2)\sqrt{2\pi\sigma_i}] \exp[-(\log(\text{TL} - 2) - \overline{\text{TL}}_i)^2/2\sigma_i^2]$	-
(4) Weibull	$X_i(\text{TL}) = X_i(\alpha/\beta^\alpha)(\text{TL})^{\alpha-1} \exp(\text{TL}/\beta)^\alpha$	with $\beta = \overline{\text{TL}}_i$ and $\alpha = (1/\sigma_i)(\overline{\text{TL}}_i/2)$
(5) Weibull shifted	$X_i(\text{TL}) = X_i(\alpha/\beta^\alpha)(\text{TL} - 2)^{\alpha-1} \exp(\text{TL} - 2/\beta)^\alpha$	with $\beta = \overline{\text{TL}}_i$ and $\alpha = (1/\sigma_i)(\overline{\text{TL}}_i/2)$

The ecological property X (biomass, production, catch) of the *i*th consumer is distributed around its central value $\overline{\text{TL}}_i$ with a dispersion σ_i^2 according to the alternative distribution functions reported above. $\overline{\text{TL}}_i$ and σ_i^2 are estimated for each consumer species from dietary habits [see Equations (2) and (3)].

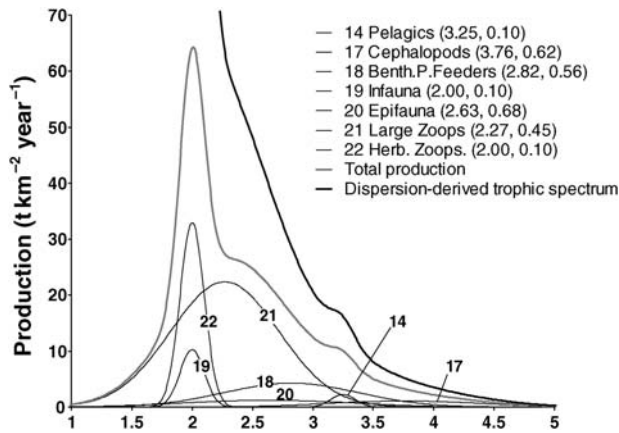


Figure 1. Construction of trophic spectra using the dispersion-based method for the eastern Bering Sea foodweb (NRC, 2003). Trophic spectra for production are built as the sum of productions of all 22 functional groups normally distributed with mean and variance equal to the TL and the OI of the group (in parenthesis), respectively. Only the seven major contributors to total production are reported for reasons of clarity.

values for $TL < 2$, whereas spectra for $TL > 2$ are adjusted to

$$\Phi_X(TL = 2 + \delta)_{\text{adjusted}} = \Phi_X(TL = 2 + \delta) + \Phi_X(TL = 2 - \delta), \quad (5)$$

where $\delta > 0$. This adjustment permits the resulting trophic spectra to be conservative with respect to input data.

Trophic spectra built with the dispersion-based method using the five ddfs were compared with each other and with the smoothing-based methodology proposed by Gascuel *et al.* (2005). The dispersion-based method for building the spectra of production, biomass, and catch over TLs, however, addresses the problems of the discontinuity of variables (zero values) that can influence the results irrespective of the distribution assumed for dispersing the data.

Dataset

The trophic spectrum methods were applied to biomass, production, and catch data used in 24 existing foodwebs built using the Ecopath with Ecosim software package, version 5.1 (www.ecopath.org; Christensen and Walters, 2004). The 24 Ecopath foodwebs, selected because they are well-documented, differ widely in terms of ecosystem type and dimension, period represented, fishing pressure, and number of functional groups employed to describe the ecosystem (Table 2). They also have very different pedigree index, which is a measure of the quality of information used to build the model (Christensen *et al.*, 2005). Biomass, production, and catch (here considered as landings plus discards), TL and OI were obtained for all functional groups of each foodweb and used for trophic spectrum analyses. Most of the information (all catches, but also many biomass and production data) is considered as being raw data, but TL and OI were estimated from the model as reported above. All foodwebs were constructed using biomass wet weight and annual rates; biomasses are expressed in g m^{-2} or t km^{-2} , and flows are in $\text{g m}^{-2} \text{ year}^{-1}$ or $\text{t km}^{-2} \text{ year}^{-1}$.

Comparison of smoothing- and dispersion-based trophic spectra

The consistency of trophic spectrum methods with original data was evaluated by comparing the integral of smoothing- and dispersion-based trophic spectra with the sum of the ecological property for $TL \geq 2$ in the original data.

The transfer efficiency (TE) was used to evaluate the trophic spectra obtained with the alternative methods and forms of ddf. As a measure of the efficiency of energy transfer from one TL to the next, TE varies between 0 and 1 and was originally defined as the ratio between the production of two adjacent integer TLs (Lindeman, 1942). However, trophic spectra imply that properties are continuous in the TL domain, so TE can be calculated over all TL values (including non-integer ones), and an average TE value can be estimated from the slope of continuous trophic spectra for production. This might be done by computing the regression line with the best fit over log-transformed trophic spectra for production (Jennings *et al.*, 2002b). However, alternative ways for computing average TE can be also considered. By log-transforming the production spectrum obtained with the different methods and alternatives, the TEs can be calculated for each interval Δ ($=0.1$ TL) as

$$TE(TL) = \exp\left(\frac{\ln[\Phi_P(TL + \Delta)] - \ln[\Phi_P(TL)]}{\Delta}\right). \quad (6)$$

The average of these estimates provided a synthetic measure, \overline{TE} , characteristic of each foodweb (Pauly and Christensen, 1995; Christensen *et al.*, 2005). Average values of \overline{TE} were estimated both based on smoothing-based (\overline{TE}_S) and dispersion-based (\overline{TE}_D) trophic spectra to be compared with the \overline{TE}_E estimated by Ecopath based on flows of matter in the foodweb (Christensen *et al.*, 2005). Although \overline{TE} is usually reported as an average for $2 \leq TL \leq 4$ (Pauly and Christensen, 1995), we also included estimates for $2 \leq TL \leq 6$ to test trophic spectra over a wider range of the TL domain.

Results

Integrals of the dispersion-based trophic spectra (five alternative forms) do not differ according to the total ecological property of the foodweb, i.e. total catch, total biomass, or total production, because the distribution functions and the eventual adjustment serve to conserve the ecological properties. Conversely, the integrals of spectra built using the smoothing-based method (calculated as reported in Gascuel *et al.*, 2005) are less consistent with regard to original input data (Figure 2). In fact, generally good agreement was observed only when comparing total catches with the integral of smoothing-based trophic spectra for each foodweb (Figure 2a). Notable differences were observed in only three foodwebs, Floreana and Chesapeake Bay (overestimation of total catches in the order of 11.5 and 7.7%, respectively), and Tampa Bay (underestimation of total catches by -10.5%). For total biomass (Figure 2b), the smoothing-based trophic spectra were consistent with total biomass (difference $<1\%$) in only three foodwebs (Azores, Eastern Pacific, and Prince William Sound); underestimated total biomass in 15 cases (maximum -16.8% for the central North Pacific) and overestimated total biomass in six cases (maximum $+10.9\%$ for Georgia Strait). This inconsistency of smoothing-based trophic spectra with original input data was even greater for production (Figure 2c), for

Table 2. Summary of major features of the foodwebs used for comparing trophic spectra.

Number	Foodweb	Ecosystem type and location	Years	Functional groups (living)	Consumers (TL ≥ 2)	Fishing fleets	Pedigree index	Flow-based TE	References
1	Floreana Island, Galapagos	Rocky reefs shallower than 20 m	2000/2001	43 (42)	39	1	0.563	0.131	Okey <i>et al.</i> (2004a)
2	North Central Adriatic Sea	Shelf, 3 miles off the west (or 10 m depth) to 12 miles from the east coast	1990s	40 (37)	36	5	0.657	0.099	Coll <i>et al.</i> (2007)
3	South Catalan Sea	Upper slope from 3 miles or 50 to 400 m depth	1994–2000	40 (37)	36	4	0.666	0.122	Coll <i>et al.</i> (2006)
4	Weddell Sea, Antarctica	Southeast shelf of the Weddell Sea, southern Atlantic Ocean	1980s	20 (19)	18	None	0.357	0.067	Jarre-Teichmann <i>et al.</i> (1997)
5	Azores Archipelago	Small shelf around the islands, seamounts and deep oceanic waters	1997	43 (43)	41	13	–	0.105	Guénette and Morato (2001)
6	Cantabrian Sea	Neritic area of the Cantabrian Sea, from the inner to the outer continental shelf	1994	28 (26)	25	5	0.142	0.381	Sanchez and Olaso (2004)
7	Icelandic fisheries	Shelf area of the northern Atlantic around Iceland	1997	24 (23)	21	14	0.295	0.140	Mendy and Bucharý (2001)
8	Newfoundland	From the coast to the 1000 isobath of the ICES Area 2J3KLNO	1985–1987	31 (30)	29	1	–	0.169	Heymans (2003)
9	Newfoundland	ICES Area 2J3KLNO	1995–2000	45 (44)	43	9	–	0.160	Bundy <i>et al.</i> (2000)
10	Eastern Bering Sea	Temperate shelf and slope down to 500 m	1955–1960	25 (23)	22	7	–	0.170	Trites <i>et al.</i> (1999) and NRC (2003)
11	Central North Pacific	Temperate, open ocean	1990–1998	31 (30)	29	9	–	0.044	Cox <i>et al.</i> (2002)
12	Gulf of Thailand	Tropical shallow coastal area; 10–50 m depth range	1973	40 (39)	37	6	–	0.057	FAO/FISHCODE (2001) and Walters <i>et al.</i> (2005)
13	North Sea	All area from the Faroe Plateau and the Celtic-Biscay Shelf to the Skagerrak	1981	23 (22)	21	1	–	0.116	Christensen (1995)
14	Eastern Pacific	Gulf of Alaska and eastern Aleutian Islands, from 50 to 500 m depth	1963	40 (39)	35	1	–	0.128	Guénette and Christensen (2005)
15	Chesapeake Bay	Temperate, enclosed coastal area	1950s	46 (45)	42	16	0.471	0.126	Walters <i>et al.</i> (2005)
16	Northern Gulf of St Lawrence	NAFO 4SR Divisions, areas shallower than 37 m not included	1980s	32 (31)	30	1	0.651	0.172	Morissette <i>et al.</i> (2003)
17	Georgia Strait	Temperate narrow basin, average depth 156 m	1950s	27 (26)	24	3	–	0.112	Pauly <i>et al.</i> (1998b) and Martell <i>et al.</i> (2002)
18	Faroe Islands	ICES Area Vb: Faroe Plateau and deep pelagic waters	1997	20 (19)	18	8	0.073	0.144	Guénette <i>et al.</i> (2001)
19	Prince William Sound	Cold temperate coastal area in Alaska (USA)	1994–1996	48 (45)	42	3	0.675	0.188	Okey and Pauly (1999)
20	Mid Atlantic Bight, USA	Temperate continental shelf, from intertidal to shelf break at 200 m	1995–1998	55 (54)	51	1	0.415	0.165	Okey (2001)
21	West Florida Shelf, USA	Subtropical shelf area from intertidal zone to 200 m depth	Late 1990s	59 (55)	51	11	0.623	0.117	Okey <i>et al.</i> (2004b)
22	South Atlantic States shelf, USA	Subtropical, continental shelf area, from intertidal area to 500 m depth	1995–1998	42 (41)	37	9	0.528	0.125	Okey and Pugliese (2001)
23	Tampa Bay, FL	Tropical open water estuary	–	52 (51)	48	7	–	0.086	Walters <i>et al.</i> (2005)
24	South Atlantic States shelf, USA	Tropical, continental shelf area, from intertidal area to 500 m depth	1995–1998	98 (94)	88	10	0.499	0.192	T. Okey (unpublished model)

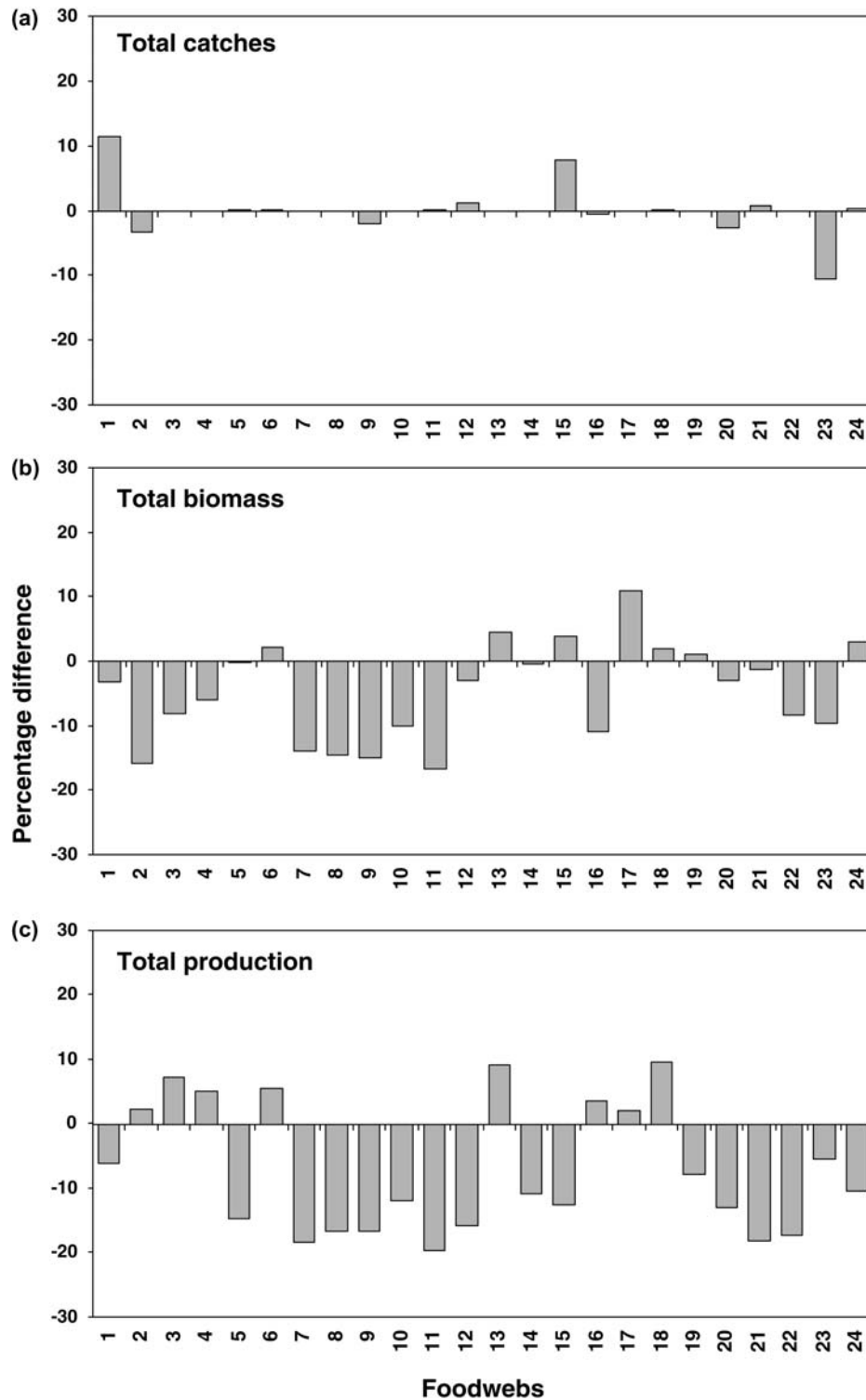


Figure 2. Difference between integral of smoothing-based trophic spectra (X_{tot}') and total value of input data (X_{tot}) for ecological properties (a) catch, (b) biomass, and (c) production for the 24 foodwebs analysed and numbered in Table 2. Differences are reported as percentages, calculated as $(X_{\text{tot}}' - X_{\text{tot}})/X_{\text{tot}}$.

16 foodwebs production was underestimated (maximum -19.6% for the central North Pacific; minimum -5.5% for Tampa Bay), and the other eight foodwebs overestimated it (maximum $+9.5\%$ for Faroe Islands; minimum $+2\%$ Georgia Strait).

Smoothing and alternative dispersion-based trophic spectra obtained for the 24 foodwebs were compared in terms of their shape and tested by comparing their TE estimates with those obtained from original foodwebs. An example of such comparison

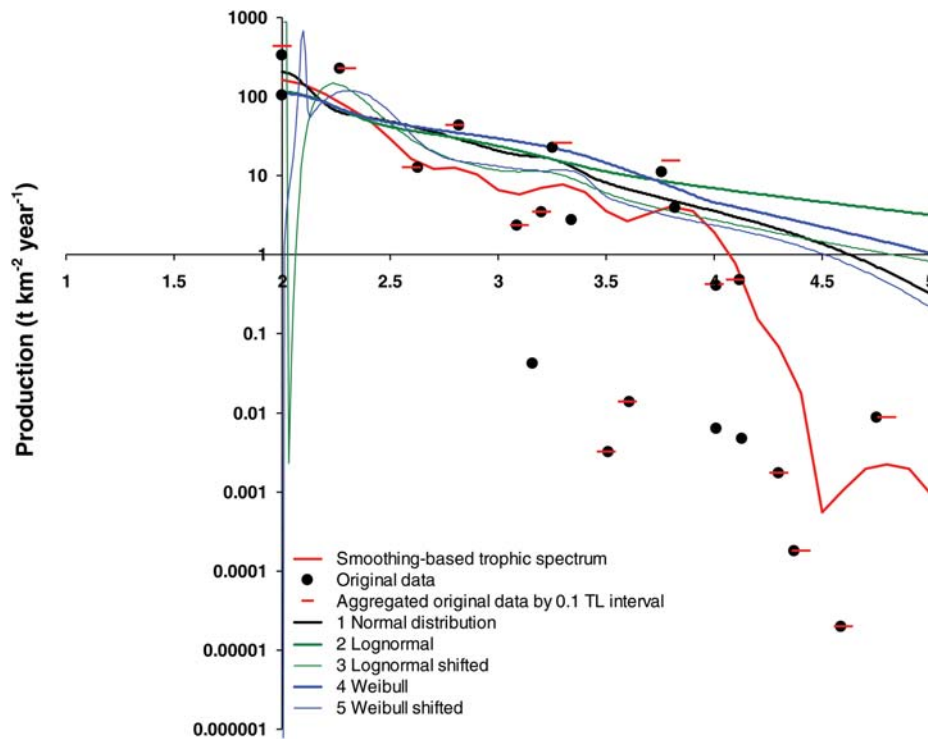


Figure 3. Comparison of different methods for building trophic spectra for production in the eastern Bering Sea (NRC, 2003). The smoothing-derived spectrum is compared with five alternative dispersion-based trophic spectra, each assuming different ddfs for production of consumers (i.e. normal, lognormal, lognormal shifted, Weibull, and Weibull shifted). Original data for the 22 consumer functional groups and data aggregated for the 0.1 TL interval are reported. The y-axis is log-transformed to clarity. Slopes of the alternative spectra permit the calculations of average TE for the foodweb, as listed in Table 3.

is shown in Figure 3, where the production trophic spectra for the eastern Bering Sea foodweb (NRC, 2003) is constructed by employing the different methods (note that logarithmic scaling was used for the y-axis), and original input data are shown. Dispersion-derived trophic spectra are considerably different from smoothing-derived spectra for high values of TL, but these differences have very low absolute values (Figure 3). However, all dispersion-based alternatives are closer to the data than the smoothing-based method for intermediate to low values of TL, where absolute differences are more pronounced. Figure 3 also illustrates the similarity of the behaviour of the dispersion-based trophic spectra, except shifted lognormal and Weibull (alternatives 3 and 5), which show considerable variability for TLs close to 2.

Flow-based synthetic measures of TE, as provided by Ecopath (\overline{TE}_E) for each foodweb, were compared with the average \overline{TE} values estimated based on the smoothing-based and the five dispersion-based trophic spectra, \overline{TE}_S and \overline{TE}_D , respectively, by employing Equation (6). We report the results of such comparison for the eastern Bering Sea foodweb in Table 3, which shows that \overline{TE}_S estimates (0.086 and 0.065, using the range $2 \leq TL \leq 4$ and $2 \leq TL \leq 6$, respectively) are considerably lower than flow-based \overline{TE}_E values (0.170 and 0.162, respectively). Conversely, \overline{TE}_D estimates based on lognormal (0.280, 0.378) and Weibull (0.246, 0.225) distributions overestimate the \overline{TE}_E values for the eastern Bering Sea. The shifting of these two ddfs (alternative forms 3 and 5) produce dispersion-based trophic spectra with \overline{TE}_D averages more consistent with flow-based estimates (Table 3). \overline{TE}_D estimates based on normal ddfs (alternative form 1) were 0.197 for $2 \leq TL \leq 4$ and 0.127 for $2 \leq TL \leq 6$, so showing the

smallest differences with flow-based estimates for both TL ranges (Table 3).

The normal ddf dispersion-based method generally performed better than the alternatives, and only these results (\overline{TE}_D) will be reported compared with the TE for $2 \leq TL \leq 4$ from the smoothing-based method (\overline{TE}_S) for the 24 foodwebs. Regarding all 24 foodwebs, \overline{TE}_E values varied from 0.04 to 0.38 as estimated for the central North Pacific and the Cantabrian Sea, respectively. The mean \overline{TE}_E value among the 24 foodwebs was 0.135.

\overline{TE}_S values from smoothing-based trophic spectra varied from 0.038 (Newfoundland 1995–2000) to 0.225 (Prince William Sound), with a mean of 0.099. \overline{TE}_S values differed significantly

Table 3. Estimates of average TE for the eastern Bering Sea (NRC, 2003) from flow-based (Ecopath) calculations, from smoothing-derived spectra, and from dispersion-derived trophic spectra using alternative ddfs.

Estimates	For $2 \leq TL \leq 4$		for $2 \leq TL \leq 6$	
	\overline{TE}	$\overline{TE} - \overline{TE}_E$	\overline{TE}	$\overline{TE} - \overline{TE}_E$
Flow-based, \overline{TE}_E	0.170	–	0.162	–
Smoothing-based, \overline{TE}_S	0.086	–0.084	0.065	–0.097
Dispersion-based alternatives, \overline{TE}_D				
1 Normal ddf	0.197	0.027	0.127	–0.035
2 Lognormal	0.280	0.110	0.378	0.215
3 Lognormal shifted	0.188	0.018	0.268	0.106
4 Weibull	0.246	0.076	0.225	0.062
5 Weibull shifted	0.233	0.063	0.140	–0.022

Average TE is calculated always for both $2 \leq TL \leq 4$ and $2 \leq TL \leq 6$ ranges.

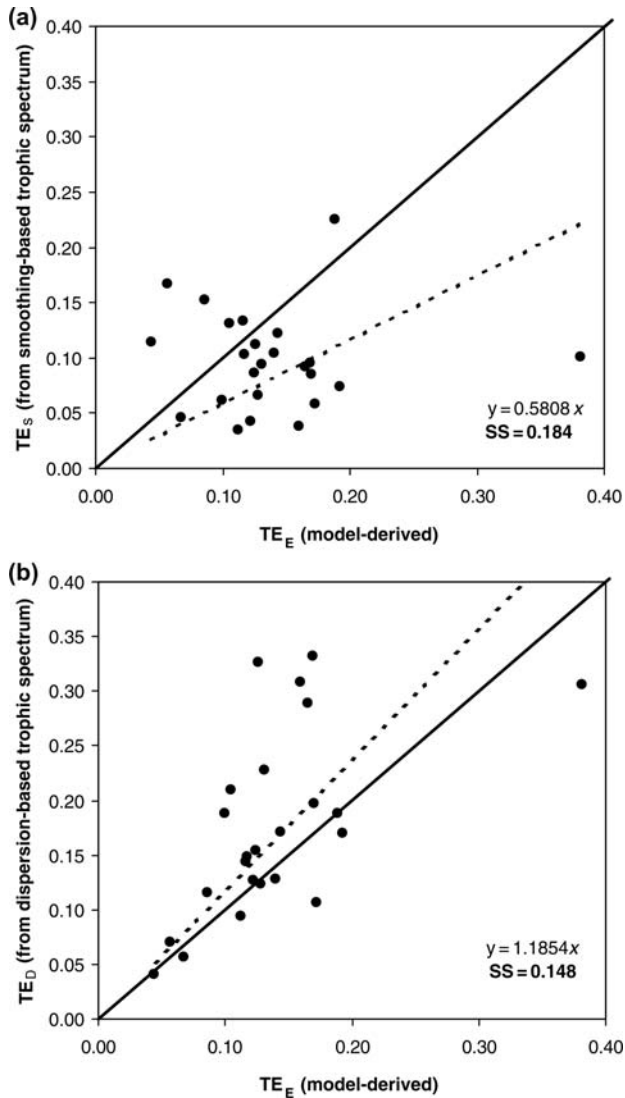


Figure 4. Comparison of average TE (\overline{TE}) for foodwebs estimated based on flows (model-derived \overline{TE}_E) and based on trophic spectra methods. Smoothing-based (\overline{TE}_S) and dispersion-based (\overline{TE}_D) trophic spectra are used in (a) and (b), respectively.

from flow-derived \overline{TE}_E values (Figure 4a; sum of squares of TE differences, $SS = 0.184$), and those estimated based on smoothing-based trophic spectra systematically underestimated the flow-based values (on average \overline{TE} values were underestimated by approximately -0.037).

\overline{TE}_D values estimated based on the dispersion-based trophic spectrum method using normal ddf (Figure 4b) varied from 0.057 (Weddell Sea) to 0.332 (Newfoundland 1985–1987), with a mean of 0.176. \overline{TE}_D estimates were better related to flow-based \overline{TE}_E values ($SS = 0.148$), whereas the average bias was approximately -0.040 . The slope of the regression for \overline{TE}_D against \overline{TE}_E is much closer to 1 than for the \overline{TE}_S vs. \overline{TE}_E regression (1.12 and 0.58, respectively; Figure 4).

Discussion

Trophic spectra of ecological data, i.e. the continuous distribution of biomass, production, and catch across TLs, are increasingly used as a mean for analysing marine ecosystem structure and

functioning. In particular, the effects of exploitation on fish community structure seem to be detectable through trophic spectrum analysis which, therefore, has been used successfully as an ecosystem indicator of fishing impact (Bozec *et al.*, 2005; Moloney *et al.*, 2005). Although the models of trophic spectra might be useful to study and predict the theoretical responses of marine communities to disturbances (Gascuel *et al.*, 2008; Gascuel and Pauly, in press), the analysis of trophic spectra applied directly to ecological data will remain an important tool for detecting erosions in the ecosystem structure. Systematic review of different methods for building trophic spectra is, therefore, useful in increasing the reliability of this type of analysis.

The availability and use of existing foodwebs facilitated the comparison between the trophic spectrum methods using foodwebs as virtual systems: alternative methods for trophic spectrum analysis are therefore compared in terms of their capabilities of representing the virtual system. Moreover, foodwebs permitted comparison of the TE (\overline{TE}), estimated based on web flows and as an emerging property of trophic spectra. The results, although obtained for foodweb outputs, are also valid for empirical data given that production, biomass, catch, TL, and OI are provided for each species or functional group of the system being analysed (Jennings *et al.*, 2002b).

Application of smoothing-based trophic spectra (Gascuel *et al.*, 2005) to a set of 24 foodwebs revealed that this method is not always consistent with respect to the original data. Therefore, properties analysed, i.e. the total value of the ecological property calculated from the spectrum (by integration), does not equal the sum of the original data used as input.

Generally, the trophic spectra of catches from the smoothing-based approach were more consistent with input data than biomass and production spectra, which produced biases as large as 20% (Figure 2). The trophic spectra of catch data were biased relative to the input data in ecosystems with a significant proportion of species of low TL species in the catches (Floreana, Chesapeake Bay, and Tampa Bay). For example, catches of sea cucumbers (TL = 2.06) are $2.922 \text{ t km}^{-2} \text{ year}^{-1}$, and 70% of the total catch in the Floreana rocky reef foodweb (Okey *et al.*, 2004a); adult oysters (TL = 2.09) constitute 10% of the total catch ($1.266 \text{ t km}^{-2} \text{ year}^{-1}$) in Chesapeake Bay; and blue crab (TL = 2.65) represents 9.6% of the total catch ($0.099 \text{ t km}^{-2} \text{ year}^{-1}$) in the Tampa Bay foodweb (Walters *et al.*, 2005). Conversely, the smoothing-based trophic spectrum is accurate when catches are made at a medium–high TL, such as for the central North Pacific (Cox *et al.*, 2002), where target species range from TL = 3.3 (flying squid) to TL = 4.68 (large sharks).

The relatively small bias in the catch spectra and the much larger and more common bias in the biomass and production spectra produced by the smoothing-based approach are attributable to the general absence of low TL functional groups in the catch spectra and the inevitable presence of low TL groups in the other two data types. When ecological data include values for TL close to 2 (lower boundary of the TL domain), the weighted average becomes asymmetrical, so affecting the smoothing-based trophic spectra considerably. This might also explain the difference between the frequency distribution of data and the resulting trophic spectra in applications using empirical data (e.g. Bozec *et al.*, 2005).

The bias of smoothing-based trophic spectra resulted in no correlation with overall model quality, measured in the original foodweb models through the pedigree index, and in weak

correlation with biological resolution, i.e. the number of functional groups used to describe the ecological networks. Although positive bias (integral of spectra larger than input data) was more common for ecological networks with few functional groups and negative bias (integral smaller than total input data) for ecological networks described by many functional groups, the correlation was not significant. Clearly, therefore, the smoothing-based trophic spectra can be corrected for consistency with data by rescaling the spectra so as to obtain the integral of the input total value for the ecological property (total catch, total biomass, total production). Therefore, the lack of consistency with original data could be corrected, but the smoothing results in a modified shape of the trophic spectra, with unavoidable implications.

The smoothing- and dispersion-based trophic spectra differed greatly in shape, and this was also demonstrated in substantial differences in their emerging properties, such as TE. Although the most consistent differences were apparently in the higher part of the TL domain in log scales (Figure 3), these differences involve very low absolute values. Conversely, smoothing- and dispersion-based spectra based on different ddfs show consistent absolute differences in the lower part of the TL domain.

The comparative analysis based on \overline{TE} estimates revealed that the shape of the dispersion-based trophic spectra using normal ddfs gave estimated \overline{TE}_D values that were more similar to those quantified on the flow basis (\overline{TE}_E , Ecopath calculations; Christensen *et al.*, 2005). Conversely, smoothing-based trophic spectra provided \overline{TE}_S estimates that compared poorly with those obtained from flow measurements (\overline{TE}_E), suggesting that the poor definition of smoothing at the boundaries of the TL domain might be a critical issue that can be overcome by employing dispersion-based trophic spectra.

Utilization of normal ddfs and OIs as a measure of dispersion in trophic spectrum analysis might represent two advancements to be evaluated further. Symmetrical distribution of the TL of prey might be a weak assumption, particularly when very few functional group items are represented in the diet of a predator. However, applications using alternative ddfs such as lognormal and Weibull gave poorer results in terms of correct representation of the shape of trophic spectra. Moreover, although normal ddfs call for non-mechanistic adjustments for avoiding properties to be dispersed to unrealistic values ($TL < 2$), dispersion-based methods performed better with the normal form rather than the non-negative ddf (lognormal and Weibull with zero shifted to $TL = 2$).

A weakness in the OI, as a measure of dispersion, is that it only represents the dispersion of prey of a given predator and might be a weak measure of the distribution of energy flow, which is the basis of the trophic spectrum continuum. Gascuel *et al.* (2005) pointed out that the OI might not be a very efficient measure for building trophic spectra because it does not represent a reliable measure of energy dispersion. Despite these considerations, however, our results show that dispersion-based trophic spectra are more consistent with \overline{TE}_E estimates based on flow calculations. It is likely that a better measure of dispersion can be developed, such as one that accounts for (i) errors in the defined diet composition, (ii) dispersion of prey items along TL, and (iii) cascade propagation of this dispersion along the ecological network. By employing OI, the current dispersion-based trophic spectrum method accounts only for the first two sources of variability. Nevertheless, it performed consistently when applied to 24

ecological networks, as measured by the model-derived measures of \overline{TE} , indicating that the construction of trophic spectra benefits from accounting for a dispersion measure, even if roughly estimated.

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