

Limits to Trophic Levels and Omnivory in Complex Food Webs: Theory and Data

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ABSTRACT: While trophic levels have found broad application throughout ecology, they are also in much contention on analytical and empirical grounds. Here, we use a new generation of data and theory to examine long-standing questions about trophic-level limits and degrees of omnivory. The data include food webs of the Chesapeake Bay, U.S.A., the island of Saint Martin, a U.K. grassland, and a Florida seagrass community, which appear to be the most trophically complete food webs available in the primary literature due to their inclusion of autotrophs and empirically derived estimates of the relative energetic contributions of each trophic link. We show that most (54%) of the 212 species in the four food webs can be unambiguously assigned to a discrete trophic level. Omnivory among the remaining species appears to be quite limited, as judged by the standard deviation of omnivores' energy-weighted food-chain lengths. This allows simple algorithms based on binary food webs without energetic details to yield surprisingly accurate estimates of species' trophic and omnivory levels. While maximum trophic levels may plausibly exceed historically asserted limits, our analyses contradict both recent empirical claims that these limits are exceeded and recent theoretical claims that rampant omnivory eliminates the scientific utility of the trophic-level concept.

Keywords: trophic level, food chains, omnivory.

The study of food chains and the trophic structure of ecosystems has long been central to ecology (Elton 1927; Lawton 1989, 1995; Wilbur 1997; Post 2002a). Food chains depict the paths through a food web that organic energy travels, beginning with basal species and ending with assimilation by a species of interest. A species' trophic level (TL) indicates the number of times chemical energy is

transformed from a consumer's diet into a consumer's biomass along the food chains that lead to the species. Convention holds that species that eat no other organisms are basal species with $TL = 1$, while their direct and indirect consumers are at higher levels. Research on TL focuses on patterns common to all ecological systems (Elton 1927; Lindeman 1942; Pimm and Lawton 1978; Pimm 1980; Cousins 1987; Lawton 1989, 1995; Yodzis 1989; Pimm et al. 1991; Martinez and Lawton 1995), patterns that distinguish types of systems (Hairston et al. 1960; Ehrlich and Birch 1967; Briand and Cohen 1987; Moore et al. 1989; Carpenter and Kitchell 1993; Hairston and Hairston 1993, 1997; Polis and Strong 1996; Post et al. 2000), and patterns that distinguish species' roles within ecological systems (Carpenter et al. 1987; Power 1990; Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1996; Brett and Goldman 1997; Pace et al. 1999; Vander Zanden et al. 1999; Schmitz et al. 2000), including the role of human exploitation in marine ecosystems (Pauly et al. 1998b, 2002).

Measuring TL is central to this wide range of trophic ecology (Post 2002a). Food-web research plays a prominent role in measuring TL on a species-by-species and whole-system basis (e.g., Pimm et al. 1991; Polis and Winemiller 1996; Vander Zanden and Rasmussen 1996; Post 2002a). Food webs, or "who eats whom" within ecological systems, describe the food chains in these systems. When the food web includes empirical estimates of energy flows through trophic links, "flow-based TL" is measured by computing food-chain lengths and the relative energetic contributions through chains of different lengths (Levine 1980; Adams et al. 1983). Food webs usually lack such flow estimates and more simply characterize flows or "links" between species as present or absent. In this binary situation, various measures of consumers' food-chain lengths have been interpreted as measures of consumers' TL. Pimm (1980, 1982) preferred modal chain length but also identified the extreme measures, the longest and shortest chain to a basal species. Ecologists who argue that most energy flows through the shortest chain to a basal species (e.g., Yodzis 1984; Hairston and Hairston 1993)

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prefer the shorter extreme, while others (e.g., Martinez 1991; Polis 1991; Fussman and Heber 2002) prefer an intermediate measure we call “chain-averaged TL” in which the contribution of each food chain is weighted equally.

Despite the need for webs with link-flow information to address central ecological questions, few published species-rich food webs include estimates of energy flows. In contrast, binary food webs are more abundant and tend to have many more species (Cohen et al. 1990; Williams and Martinez 2000). Adding estimates of energy flows through each link in a binary food web requires a great increase in observation effort (e.g., Cohen et al. 1993; Martinez et al. 1999). This additional effort is unnecessary for establishing the TL of basal species and nonomnivorous consumers whose chains to basal species are all of equal length. However, 16% to 77% of the 625 consumer species in the nine food webs studied here have chains to basal species of various lengths (table 1). Such species include omnivores and their direct and indirect consumers. An accurate measure of TL for these species based on binary webs and independent of energetic flow estimates could significantly increase the scientific productivity of trophic ecologists.

In four food webs, we compare six estimates of TL based only on binary link information to the “flow-based TL” based on information that quantifies the energy flow through the webs. We studied five additional binary food webs to further evaluate omnivory, limits to TL, and the differences between the estimates based on binary links. Our objectives are to compare recently available trophic data to general theories about TL and omnivory while also developing improved approaches for similar endeavors in the future.

Methods

Data and Terminology

We analyzed four of the largest food webs in the primary literature (table 1, pt. A) that include relatively many species, empirically derived estimates of the energy flowing through each of the food-webs’ links, and reasonably resolved basal and other trophic levels within the habitat described. One describes the food web of the Chesapeake Bay, U.S.A. (Baird and Ulanowicz 1989). It focuses on the pelagic portion of the bay emphasizing larger fishes. Another describes an *Anolis*-centered food web on the Caribbean island of Saint Martin (Goldwasser and Roughgarden 1993). The third is a U.K. grassland food web based on endophytic insects found inside the stems of 10 co-occurring grasses (Dawah et al. 1995; Martinez et al. 1999). The fourth is a macroinvertebrate and fish-dominated food web of a Florida seagrass community (Christian and Luczkovich 1999).

We also studied the following five large, high-quality, binary food webs that lack estimates of energy flows (table 1, pt. B). The Skipwith Pond food web (Warren 1989) is a speciose freshwater invertebrate web. The food web from the Ythan Estuary (Hall and Raffaelli 1991) emphasizes birds and fish among invertebrates and primary producers. The food web from the Coachella desert (Polis 1991) is a highly aggregated terrestrial web that is also highly connected. The Little Rock Lake food web (Martinez 1991) is a very large and highly resolved food web that includes both pelagic and benthic species. Among a prominent set of 50 Adirondack lake food webs that include only pelagic species (Havens 1992; Martinez 1993a), we selected the largest, the Bridge Brook Lake web.

A two-dimensional binary matrix of elements l_{ij} (the

Table 1: Basic properties of food webs

Reference	Name	Species ^a	Links per species	Connectance	Omnivory ^b (%)
A. Basic properties of four food webs with link-strength data:					
Baird and Ulanowicz 1989	Chesapeake Bay	33	2.2	.067	48 (16)
Goldwasser and Roughgarden 1993	Saint Martin	44	4.9	.11	59 (26)
Dawah et al. 1995	U.K. grassland	87	1.4	.017	18 (17)
Christian and Luczkovich 1999	Florida seagrass	48	4.6	.096	71 (34)
B. Basic properties of five binary food webs:					
Warren 1989	Skipwith Pond	35	10.9	.31	51 (18)
Hall and Raffaelli 1991	Ythan estuary	92	4.4	.048	47 (43)
Martinez 1991	Little Rock Lake	181	13.1	.072	24 (43)
Polis 1991	Coachella Valley	30	9.7	.32	77 (23)
Havens 1992	Bridge Brook Lake	75	7.4	.098	16 (12)

^a Taxonomic species or more coarsely lumped species aggregations.

^b Omnivory is the percentage of species that have food chains of at least two different lengths. Numbers in parentheses are sample sizes.

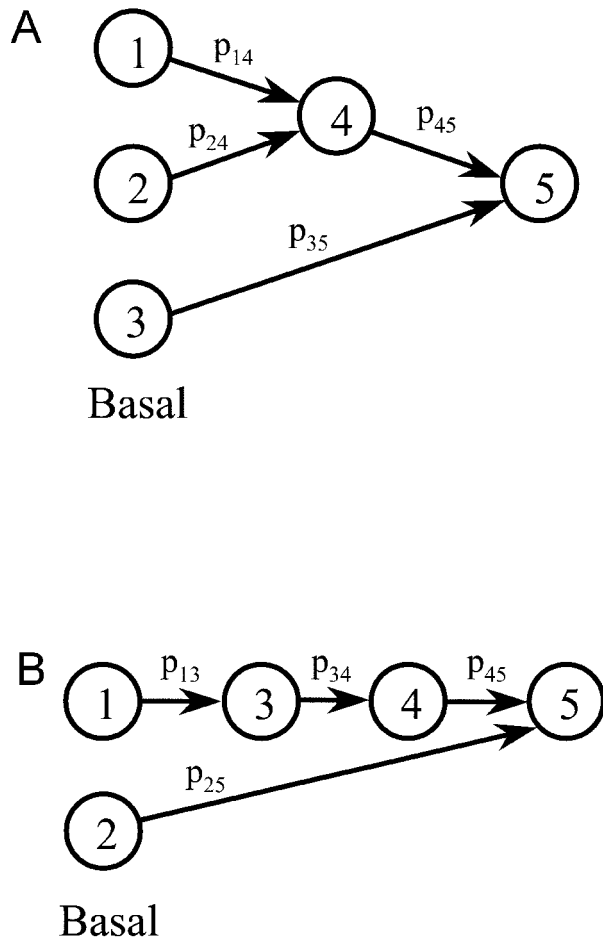


Figure 1: A, Hypothetical food web used to illustrate the effect of multiple pathways to basal species on trophic position measures. B, Hypothetical food web used to illustrate the effect of omnivory on trophic level and trophic-level variance.

connection matrix) with S rows and S columns represents the links in a food web with S species. For column j and row i , l_{ij} is 1 if species j consumes species i and 0 if not. The number of links (L) is the number of nonzero elements in the connection matrix. A food chain is defined as a linked path, excluding loops, from a consuming species to a basal species. Food-chain length is the number of links in that path.

Measures of Trophic Level and Omnivory

For food webs in which each link is weighted according to its relative energetic contribution to the consumer species' diet, Levine (1980) and Adams et al. (1983) defined a measure we call "flow-based TL" used by many subsequent authors (e.g., Winemiller 1990; Pauly et al. 1998a).

This measure is 1 plus the weighted average of chain lengths from a species to a basal species, where the weighting is given by diet fractions:

$$TL_j = 1 + \sum_{i=1}^S TL_i p_{ij}, \quad (1)$$

where TL_j is the TL of species j , TL_i is the TL of the i th resource of species j , and p_{ij} is the fraction that species i constitutes within the diet of species j . A key assumption in our calculations is that empirical diet fractions, measured in terms of gut-content volume, consumption frequency, or biomass estimation, reflect relative energetic contributions to consumers. This assumption is not necessarily met. For example, prey with higher TL may be more readily assimilated than prey with lower TL, which could cause flow-based TL to underestimate true TL. Such discrepancies may be best explored using isotope ratios as discussed below.

Possible estimates of a species' TL based only on binary link information range from the species' shortest food chain at one extreme to its longest food chain at the other extreme (Pimm 1980, 1982). We studied the following six measures systematically spanning this range: (1) Shortest TL is equal to 1 + the shortest chain length from a consumer to a basal species. (2) Short-weighted TL is the average of shortest TL and prey-averaged TL (see below). This gives a measure biased toward shorter food chains. (3) Prey-averaged TL is equal to 1 + the mean TL of all the consumer's trophic resources:

$$TL_j = 1 + \sum_{i=1}^S l_{ij} \frac{TL_i}{n_j}, \quad (2)$$

where n_j is the number of prey species in the diet of species j . This equation is equivalent to equation (1), with each nonzero link strength $p_{ij} = 1/n_j$, which assumes that a consumer consumes all its prey species equally. (4) Long-weighted TL is the average of longest TL (see below) and prey-averaged TL. This gives a measure biased toward longer food chains. (5) Chain-averaged TL is equal to 1 + the average chain length of all paths from a species to a basal species (Martinez 1991; Polis 1991; Fussman and Heber 2002). (6) Longest TL is equal to 1 + the longest chain length from a consumer to a basal species.

Flow-based TL and prey-averaged TL are both computed using the matrix algebra method of Levine (1980) based on summing an infinite geometric series that includes the contributions from all loops. In contrast, the computation of chain-averaged TL maintains tractability in complex food webs by only passing through a loop once (Martinez 1991).

Table 2: Measures of mean trophic level for the four webs listed in table 1 (pt. A) averaged across only those species with more than one chain to basal species

	Chesapeake Bay	Saint Martin	U.K. grassland	Florida seagrass
Flow-based TL	2.92	2.79	3.03	2.75
Shortest TL	2.57	2.36	2.96	2.29
Short-weighted TL	2.79	2.74	3.14	2.79
Prey-averaged TL	3.02	3.11	3.32	3.29
Long-weighted TL	3.92	4.27	3.52	5.03
Longest TL	4.83	5.42	3.72	6.76
Chain-averaged TL	3.51	3.96	3.35	4.41

Chain-averaged TL assumes energy flow from prey increases with the number of the prey's resources. Consider the example in figure 1A. There is one path of length 1, from species 5 to basal species 3, and two paths of length 2, from species 5 to basal species 1 and 2. Chain-averaged TL = 2.67 for species 5, which implicitly assumes that the relative energy flows are $p_{35} = 0.333$ and $p_{45} = 0.667$. In contrast, prey-averaged TL assumes consumption is independent of chain length such that species 5 equally consumes one prey with TL = 1 and another with TL = 2, resulting in prey-averaged TL = 2.5. Other weightings that depend on prey's TL (e.g., 60 : 40 weighting of lower and upper TL prey) require a priori classification of a species' TL before calculating the TL of the species' consumers. This is problematic because extensive looping in binary food webs (Williams and Martinez 2000) creates mutual dependence of prey's TL on consumer's TL. We avoid problematic TL-based weightings either by ignoring prey's TL as the prey-averaged weighting or by employing chain-length-based (e.g., longest or shortest) weighting.

The above procedures calculate TL on a species-by-species basis. We also calculate measures of the average TL of a whole web to compare food webs and the different TL estimates discussed above. When comparing different methods for estimating TL, we average the estimates only for species with more than one food chain. This increases the differences between the methods by eliminating similarities resulting from situations where there is no possibility of differences between the methods (e.g., all methods assign basal species' TL = 1). When comparing webs, we average across all species in the web.

One of the most frequent criticisms of trophic levels is that they inadequately address the role of omnivory (e.g., Lindeman 1942; Darnell 1961; Cousins 1987; Lawton 1989; Polis and Strong 1996; Vander Zanden and Rasmussen 1996). Omnivory can vary in degree from small (e.g., almost entire dependence on prey at one trophic level and very slight consumption of a trophic level one removed) to large (e.g., equal dependence on two different trophic levels that are two levels apart; fig. 1B). We distinguish these two situations and quantify the degree of omnivory

of a species using the standard deviations (SDs) around the weighted average of the TL of the prey species. Levine (1980) discussed this for food webs with link-strength information. Here, we use this measure both for the flow-based TL, which weights the prey using link-strength information, and for the prey-averaged TL of binary food webs, which weights all prey equally. For species 5 in figures 1A and 1B, using equal weighting this calculation yields SDs of 0.7 and 1.4, respectively. This quantifies the observation that species 5 is a more extreme omnivore in figure 1B than in figure 1A, assuming no variation of flows among links reaching each particular species. Goldwasser and Roughgarden (1993) developed a related index of omnivory for whole food webs equal to the SD of each species' chain lengths averaged among all species within the web.

Results

Whole-Web Results

Results in table 2 compare methods by averaging measures of TL across all species with more than one chain to a basal species for the four webs with link-flow information. These data compare the different TL measures based on binary feeding links with the flow-based TL computed using link-flow information. Mean flow-based TL consistently falls between the mean shortest TL and the mean prey-averaged TL. Mean short-weighted TL closely estimates mean flow-based TL, with differences of -0.13 , -0.05 , 0.11 , and 0.04 trophic levels for the Chesapeake Bay, Saint Martin, U.K. grassland, and Florida seagrass webs, respectively. Mean chain-averaged TL consistently overestimates mean flow-based TL by 0.3 to 1.6 levels, while both long-weighted TL and longest TL overestimate the flow-based TL more severely.

Results in table 3 compare webs by averaging TL across all species in the webs. The mean flow-based TL of the four webs with link-flow information stays within 3.2% of 2.5. Mean short-weighted TL is within 4.4% of 2.5 and brackets the mean flow-based TLs, with differences of -0.09 , -0.03 , 0.03 , and 0.03 levels. Mean prey-averaged

Table 3: Mean across all species and maximum values of the various measures of trophic level for all webs in table 1

	Flow-based TL		Shortest TL		Short-weighted TL		Prey-averaged TL		Chain-averaged TL	
	Mean	Maximum	Mean	Maximum	Mean	Maximum	Mean	Maximum	Mean	Maximum
Chesapeake Bay	2.49	3.85	2.24	3	2.40	3.42	2.56	3.84	2.90	4.87
Saint Martin	2.45	4.44	2.14	4	2.42	4.28	2.70	4.56	3.33	6.15
U.K. grassland	2.58	3.20	2.56	3	2.61	3.42	2.67	3.83	2.68	4.00
Florida seagrass	2.47	4.31	2.10	3	2.50	3.91	2.89	4.82	3.78	7.49
Skipwith Pond			2.43	3	2.57	3.36	2.70	3.71	3.32	6.78
Ythan estuary			2.26	4	2.44	4.06	2.62	4.31	3.17	6.50
Little Rock Lake			1.86	3	1.95	3.65	2.03	4.30	2.41	7.79
Coachella Valley			2.07	3	3.09	4.29	4.11	5.63	3.94	7.20
Bridge Brook Lake			1.51	3	1.59	3.43	1.65	3.86	1.71	4.82

Note: Flow-based TL can only be calculated for the webs with link-strength information.

TL overestimates mean flow-based TL by 3%–17% and stays within 7% of 2.7. Mean shortest TL underestimates mean flow-based TL by an average of 11%. Overall, mean trophic levels of these webs show surprisingly little variation.

Results concerning maximum TL were less consistent. In three of four webs, the short-weighted TL algorithm underestimates the maximum flow-based TL of species within a web by less than 0.5 TL. The prey-averaged TL algorithm overestimates this quantity in three of four webs. Flow-based, short-weighted, and prey-averaged TL maxima vary among webs between 3.2 and 4.4, 3.4 and 4.3, and 3.7 and 4.8, respectively. Compared to the four link-weighted webs, the five binary webs show much more variation in mean short-weighted TL (a factor of 1.6) and similar variation in maximum short-weighted TL.

The number of omnivores can be counted in webs with or without link-strength information. The nine webs studied here listed in table 1 range in size from 30 to 181 species for a total of 625 species; of these, 484 are consumers, and the rest are basal species. Direct and indirect omnivores, defined as consumer species with food chains of more than one length, constitute 16%–77% of the species in each web for a total of 231 species. This is 37% of all species and 48% of the consumer species. The four webs with link-flow information (table 1, pt. A) have a total of 212 species, 185 consumer species, and 98 direct and indirect omnivores, or 46% of the total number of species.

Species Results

Species-by-species analyses of the different TL measures refine the whole-web results. Differences between flow-based TL, prey-averaged TL, short-weighted TL, and shortest TL potentially occur only among the 98 direct and indirect omnivores within the four webs with link-flow information. All TL measures considered here are identical

among the remaining 114 nonomnivorous species. Histograms of the difference (Δ) between the flow-based TL and the three binary link-based measures for the 98 omnivores (fig. 2) show that the prey-averaged TL systematically overestimates species' flow-based TL (mean $\Delta = 0.31$ levels). The shortest TL is by definition consistently too small (mean $\Delta = -0.33$ levels), while short-weighted TL gives the closest estimate by far (mean $\Delta = -0.0016$ levels). Short-weighted TL, which preferentially weights the prey with the lowest TL, overestimates TL when higher TL prey make up a very small fraction of the diet. Short-weighted TL underestimates TL when prey are consumed equally and when higher TL prey are preferentially consumed. In concert with the lack of systematic differences between short-weighted TL and flow-based TL, short-weighted TL also has the smallest absolute values of differences (mean = 0.26 levels). This is a little over half the absolute values of shortest TL differences (mean = 0.42 levels) and prey-averaged differences (mean = 0.45 levels).

Differences between short-weighted TL and flow-based TL range from -0.68 levels to 0.53 levels. Only seven of the 98 species have differences less than -0.50 levels, and two have differences greater than 0.50 levels. The largest overestimates in each web occur among *Mya* and oysters in the Chesapeake Bay web (0.17 levels), hummingbirds and grassquit in the Saint Martin web (0.53 levels), *Chlorocytus deschampiae* in the U.K. grassland web (0.33 levels), and suspension-feeding polychaetes in the Florida seagrass web (0.46 levels). Conversely, the largest underestimates in each web occur among weakfish and bay anchovy (-0.56 levels), summer flounder (-0.61 levels), and bluefish (-0.57 levels) in the Chesapeake Bay web, yellow warbler (-0.68 levels) and kestrel (-0.50 levels) in the Saint Martin web, and a node that includes both Atlantic silverside and bay anchovies (-0.52 levels) in the Florida seagrass web. Short-weighted TL does not underestimate the TL of any species within the U.K. grassland web.

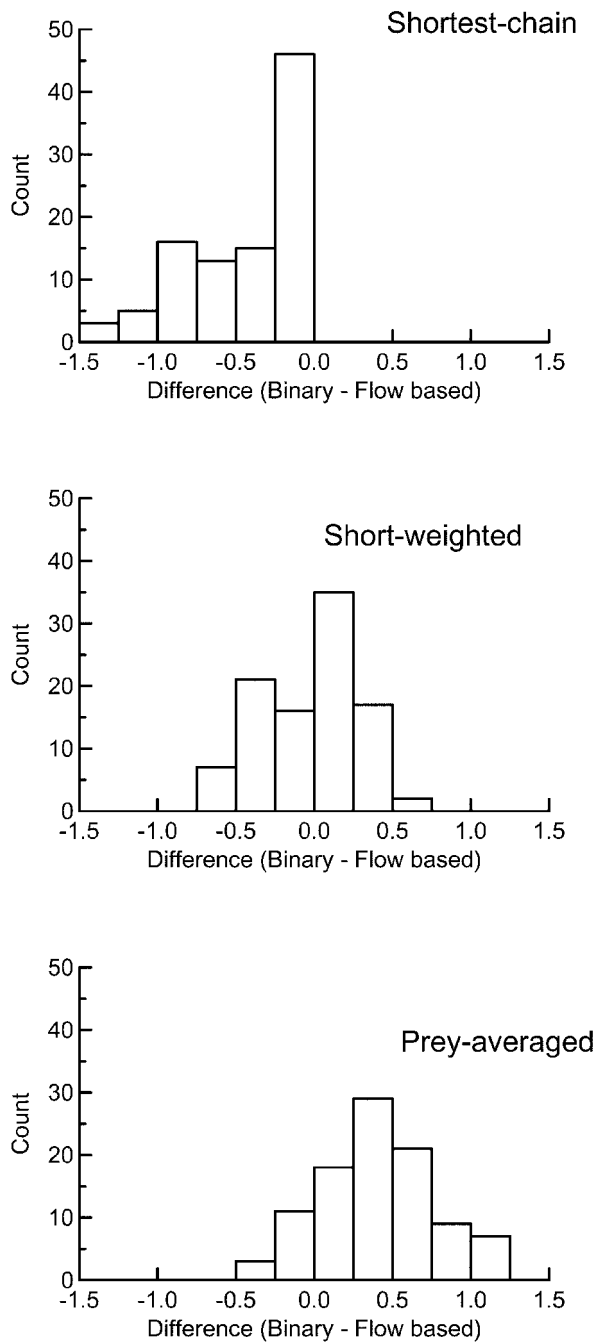


Figure 2: Histograms of differences between flow-based TL and prey-averaged TL and between short-weighted TL and shortest TL for the 98 direct and indirect omnivores in the Chesapeake Bay, Saint Martin, U.K. grassland, and Florida seagrass estuary food webs.

Shortest TL gives an absolute lower bound on all species' trophic levels. Prey-averaged TL provides an upper bound on flow-based TL for all except five species in the Chesapeake Bay web. For most species in the U.K. grassland

web, and for some species in the Saint Martin web, the bulk of the energy flow is along the shortest paths to a basal species. Shortest TL then gives the closest approximation to the flow-based TL, as has been suggested by Yodzis (1984) and Hairston and Hairston (1993). However, for other species, the prey-averaged algorithm gives a more accurate estimate of the flow-based TL, especially in Chesapeake Bay. Because of this range of accuracy, overall the short-weighted TL algorithm is a good compromise and, of the binary measures examined here, gives the most accurate estimate of flow-based TLs.

Figure 3 plots the SDs of flow-based TLs against the SDs of the prey-averaged TLs for the 98 omnivores in the four webs listed in table 1, part A. Simple linear regression of the flow-based TL SD (y) of the 98 species as a function of prey-averaged TL SD (x) results in a statistically significant positive relationship that explains almost one half of the variability of flow-based TL SD ($y = 0.537x + 0.057$, $SE_{\text{slope}} = 0.063$, $R^2 = 0.43$, $P < .001$). For most species, the prey-averaged TL SD gives an upper bound on the flow-based TL SD. The most extreme omnivores have flow-based TL SD of 0.79 in the Saint Martin web (pearly-eyed thrasher and Diptera larva), 0.40 in the U.K. grassland web (*Eupelmus atropurpureus*), 0.53 in the Chesapeake Bay web (menhaden), and 0.69 in the Florida seagrass web (killifishes).

Figure 4 plots prey-averaged TL SD against short-weighted TL for all species in table 1. For most species,

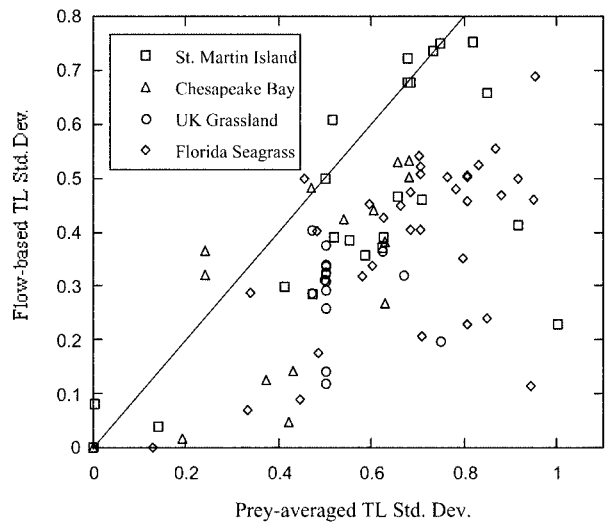


Figure 3: Prey-averaged TL standard deviation versus flow-based TL standard deviation for omnivorous species in the Saint Martin (squares), Chesapeake Bay (triangles), U.K. grassland (circles), and Florida seagrass (diamonds) food webs. The solid line illustrates equivalence between the variance measures.

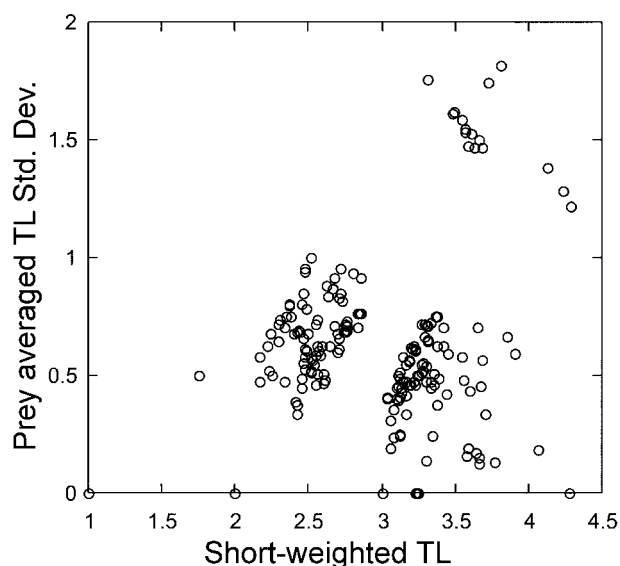


Figure 4: Prey-averaged TL standard deviation versus short-weighted TL for the nine webs listed in table 1.

TL SD < 1, indicating that these species consume prey with similar trophic levels. A number of species, all from the Coachella Valley web (Polis 1991), have a TL SD > 1.2, indicating prey from very disparate trophic levels (e.g., fig. 1B).

Discussion

The concept and scientific utility of trophic levels in complex food webs is challenged (e.g., Polis and Strong 1996) by substantial omnivory and looping, including cannibalism and mutual predation among many species (e.g., Williams and Martinez 2000) and by the huge amount of effort needed to precisely calculate TL based on Levine's (1980; Adams et al. 1983) consideration of relative flows among trophic links in complex food webs (Winemiller 1990; Pauly et al. 1998a, 2002; Martinez et al. 1999). Prey-averaged TL and short-weighted TL address these challenges by rigorously quantifying trophic levels within food webs with no link-strength information. Developing these measures allows us to systematically examine a full range of algorithms for estimating trophic level that effectively incorporate the complexity found in large binary food webs. Short-weighted TL, which is the mean of shortest TL and prey-averaged TL, typically estimates flow-based TL to within a quarter of a trophic level. This should allow short-weighted TL to help expand tests of theory about trophic levels that usually involve measures much less precise than a fraction of a trophic level (Elton 1927; Pimm 1980, 1982; Paine 1992; Hairston and Hairston 1993; Mar-

tinez and Lawton 1995; Kaunzinger and Morin 1998). In contrast, chain-averaged TL (Martinez 1991; Polis 1991; Fussman and Heber 2002) weights all chains equally and considerably overestimates flow-based TL by incorrectly assuming that long food chains convey significant amounts of energy (Hairston and Hairston 1993).

Our results suggest that binary webs in combination with prey-averaged TL and shortest TL can efficiently and effectively inform ecologists about the trophic structure of ecological systems. Additional complete food webs with weighted links are needed to test how broadly this result applies. Such tests would do well to examine whether differences between short-weighted TL and flow-based TL are greater than the measurement error associated with flow-based TL. Such error is a difficult issue only rarely addressed in the literature (Pauly et al. 1998a). Without additional analyses, the general accuracy of short-weighted TL is unclear. We found that short-weighted TL was the most accurate algorithm for the 64 omnivores in three of the webs and then tested and confirmed its success among the 34 omnivores in the Florida seagrass web. We also note that the 98 omnivores include a wide range of aquatic and terrestrial vertebrates and invertebrates. These observations suggest that the general accuracy of short-weighted TL will extend well beyond the data in this study.

Short-weighted TL depends entirely on unweighted binary webs that depend on methodology in food-web construction (e.g., Martinez 1993b). More specifically, including unusually rare links to higher TL prey could lead to overestimating flow-based TL. This may have happened among the parasitoids in the U.K. grassland web (table 2) painstakingly constructed during 12 yr of dissecting 164,000 stems of grasses from several sites around the United Kingdom. Alternatively, bias away from more rare links and toward links carrying significant quantities of energy could lead to underestimates such as in the Chesapeake Bay web (table 2). While more study is required to evaluate such possibilities, our speculations suggest that such methodological variability will have a limited effect.

Omnivory has been asserted to be extreme enough to render the concept of trophic levels misleading (Lindeman 1942; Cousins 1987; Lawton 1989; Vander Zanden and Rasmussen 1996) or even scientifically useless (Polis 1991; Polis and Strong 1996). However, our analyses show that many if not most species within food webs can be assigned to easily measurable discrete trophic levels unaffected by omnivory. The remaining omnivores can be assigned a trophic level indicating the average trophic "distance" that the energy of live organisms travels on its way to being consumed by the omnivore (also see Post et al. 2000). Furthermore, the degree of direct omnivory can be effectively estimated using the SD of the trophic levels of the omnivore's prey. This measure stays below 0.8 among our

analyses that weight consumption according to the flow from each prey. Assuming all prey species are equally consumed provides an approximate upper limit of omnivory that typically remains below 1.0 (fig. 3). On average, flow-based TL SDs are about half this upper limit. Such deviations may be illuminated by examining the variation of isotopic ratios (Post 2002*b*) among individuals within omnivorous populations.

The main exceptions to the relatively low degree of omnivory occur in about half the species in the Coachella desert web (Polis 1991) that have prey-averaged TL $SD > 1$ (fig. 4). Some of these exceptions occur among organisms that have different diets at different life-cycle stages such as some hyperparasitoids that consume plant material as adults. Trophic level SD distinguishes these organisms from other less omnivorous organisms at the same TL. Such distinctions could help determine whether omnivores exhibiting ontogenetic trophic shifts are more trophically general than omnivorous species whose diets are less tied to ontogeny. Unusually high omnivory can be generated by the common convention of assigning detritus to trophic level 1 (Gaedke et al. 1996). Some organisms in the Coachella web, such as golden eagles, consume both carrion (detritus) and high trophic-level prey. Finally, most of the nodes in the Coachella web are highly aggregated groups of species. Aggregating groups of species with disparate diets while maintaining all diet links of the aggregated species (i.e., the maximum linkage criterion of Martinez 1991) artificially creates highly connected species consuming an unusually broad range of resources (Martinez 1991, 1993*b*).

The constraints of many nonomnivorous species plus the limited omnivory among omnivores tends to linearize food webs that would otherwise be more reticulate. Such linearity is consistent with widely observed cascading interactions from consumers at higher trophic levels through to resource species at lower levels (Pace et al. 1999; Schmitz et al. 2000). While highly limited omnivory is consistent with trophic cascades, such constraints do not imply that omnivory is always dynamically unimportant. Dynamic importance does not necessarily correlate with flow or even interaction strength (Paine 1980; de Ruiter et al. 1995; Berlow 1999).

Given this analytical and empirical support for the scientific utility of trophic levels, we can more rigorously address ecological generalities about trophic levels. The most famous of these generalities is that trophic levels are limited to fewer than six (Elton 1927) and food chains are shorter than expected at random (Pimm 1980; Lawton 1989; Yodzis 1989; Williams and Martinez 2000). Classic explanations of such limits include body-size considerations (Elton 1927), thermodynamic efficiency (Lindeman 1942; Hutchinson 1959), and dynamic instabilities that

shorten food chains and reduce omnivory (Pimm and Lawton 1978). Though these mechanisms receive much prominent research (e.g., Bohannan and Lenski 1997; Sterner et al. 1997; Kaunzinger and Morin 1998; Post et al. 2000), the length of food chains and degree of omnivory in ecological systems is still unclear (Lawton 1989). For example, incomplete data may be responsible for the purported shortness of food chains and rarity of omnivory (Lawton 1989; Huxman et al. 1995; Marcogliese and Cone 1997), as suggested by studies that include relatively large fractions of the species within particular habitats (Martinez 1991; Polis 1991; Martinez and Lawton 1995).

Our analyses detect maximal short-weighted TL of 4.3 (table 3). This is well below Elton's (1927) originally postulated limit of 6 and Martinez's (1991) and Polis's (1991) claims of species at levels well over 6 (table 3). Although the Coachella Valley web includes many parasitoids and hyperparasitoids and has a high level of looping and omnivory (Williams and Martinez 2000) that greatly inflates prey- and chain-averaged TL, its short-weighted TLs are limited to a similar degree to the other webs studied here. While it is conceivable that inclusion of parasites of vertebrates that are generally excluded in food webs (Lawton 1989; Huxman et al. 1995; Marcogliese and Cone 1997) might increase the maximum TL, the data here that contain such organisms (e.g., Saint Martin food web) fail to show organisms with short-weighted TL > 5 . Similarly, Pauly et al.'s (1998*a*) analysis of marine mammals' TL finds the highest TL (4.6) in killer whales and speculates that polar bears' TL = 5.0 due to their near exclusive consumption of marine mammals with TL near 4.0. While the maximum prey-averaged TL of 5.6 combined with figure 2 suggests that the Coachella web may have species with TL > 5 , we feel the TL of 5.6 is more likely due to aggregation as discussed above.

Ecologists measure TL with several methods. Enclosure experiments measure species' "effective" TL (Paine 1980; Power 1990; Power et al. 1996*a*, 1996*b*) based on population dynamics that may cascade down to species at lower TL (Pace et al. 1999; Schmitz et al. 2000). Isotopic (Post 2002*b*) and gut-content measures of TL predict how biomagnification concentrates lipophilic toxics at higher levels (Cabana and Rasmussen 1994; Vander Zanden and Rasmussen 1996). Such analyses estimate both the degree and predictability of these top-down and bottom-up interactions (Post et al. 2000) that may be reduced by omnivory diffusing strong linear effects between discrete trophic levels (Strong 1992). Our analyses introduce relatively efficient tools for estimation of species' TL and omnivory and therefore species' roles within ecological systems. The bracket between shortest and prey-averaged TL may accurately predict isotopic composition and contaminant load of species throughout food webs as well as effects of

experimental manipulations. Testing these predictions could demonstrate the ability of structural approaches to complement and extend alternate and more labor-intensive analyses.

Such tests should focus on the large discrepancies between analyses of isotopes and diet compositions (e.g., 1–2 TL; Pauly et al. 1998*a*). Isotopes address the critical issue of assimilation but can be confounded by large variation of analytical assumptions and isotopic ratios at basal trophic level, which can, for example, cause the calculated TL of lake trout in Cayuga Lake to range from 4.1 to 5.9 (Post 2002*b*; also see Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999). Diet composition addresses the critical issue of ecological impact on different trophic levels but is confounded by variation in assimilation efficiencies among diet items, which alters the actual bioenergetic source of a consumer's biomass. Diet fraction, as used in this and other analyses, can be based on volume, mass, or frequency of consumption. Consistently basing a species' diet on a volumetric or mass-based criterion may reduce spurious variability that could otherwise be quite large when, for example, a fish frequently eats small herbivorous zooplankton and rarely eats much larger carnivorous fish. Addressing these issues will inform limitations to our analyses as well as limitations to current definitions of omnivory regarding the distinction between feeding and assimilation.

Our analyses accept the structural food-web convention of treating detritus as a nonconsuming basal species (Gaedke et al. 1996; Pauly et al. 1998*b*). Rather than including uniquely dead organic matter within a food web of live organisms, this convention implicitly includes often-ignored bacterial and fungal detritivores that nourish indirect detritivorous metazoans (Plante et al. 1990). Alternatively, direct detritivores could be assigned the detritus TL + 1 (Gaedke et al. 1996). This alternative presents no challenge to the algorithms described here but would increase trophic levels of direct and indirect detritivores by an amount depending on the original TL of the detrital source. However, this alternative could make food webs empirically intractable due to problems as extreme as considering bacteria that consume fossil oil to be consumers of unidentifiable prehistoric organisms. Since detritus is constituted by dead organisms, their waste, or exfoliates, detritus contributes less directly, if at all, to the reproduction and evolution of the source organism. Therefore, we consider detritus a basal species because it (1) implicitly includes otherwise excluded microbial detritivores as the base of food chains of live organisms, (2) simplifies food-web construction, and (3) normalizes ecologically and evolutionarily incongruous forms of biomass.

Overall, our study suggests that the challenges of omnivory, cannibalism, mutual predation, long chain lengths,

and high species diversity and complexity to the meaning and utility of trophic levels have been overstated. Instead, these challenges leave many species unaffected and are relatively constrained among affected species. Additional research, especially on comprehensive webs with more rigorous empirical estimates of energetic contributions of trophic links, is required to corroborate these findings. Such research may do well to focus on testing trophic-level estimates based on binary food webs with results from isotopic analyses (e.g., Post 2002*b*) and experimental manipulations of species (e.g., Power et al. 1996*a*, 1996*b*).

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Literature Cited

- 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 Science* 40:1480–1495.
- Baird, D., and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59:326–364.
- Berlow, E. B. 1999. Strong effects of weak interactions in ecological communities. *Nature* 398:330–334.
- Bohannon, B. J. M., and R. E. Lenski. 1997. Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. *Ecology* 78:2303–2315.
- Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* 275:384–386.
- Briand, F., and J. E. Cohen. 1987. Environmental correlates of food chain length. *Science* 238:956–960.
- Cabana, G., and J. B. Rasmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372:255–257.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade in lakes*. Cambridge University Press, Cambridge.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, D. M. Dodge, D. Kretchmer, S. He, and C. M. von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876.
- Christian, R. R., and J. J. Luczkovich. 1999. Organizing and understanding a winter's seagrass food web network

- through effective trophic levels. *Ecological Modelling* 117:99–124.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: data and theory*. Springer, Berlin.
- Cohen, J. E., R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. D. Holt, et al. 1993. Improving food webs. *Ecology* 74:252–258.
- Cousins, S. H. 1987. The decline of the trophic level concept. *Trends in Ecology & Evolution* 2:312–316.
- Darnell, R. M. 1961. Trophic spectrum of an estuarine community, based upon studies of Lake Ponchartrain, Louisiana. *Ecology* 42:553–568.
- Dawah, H. A., B. A. Hawkins, and M. F. Claridge. 1995. Structure of the parasitoid communities of grass-feeding chalcid wasps. *Journal of Animal Ecology* 64:708–720.
- de Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269:1257–1260.
- Ehrlich, P. R., and L. C. Birch. 1967. The “balance of nature” and “population control.” *American Naturalist* 101:97–107.
- Elton, C. S. 1927. *Animal ecology*. Sidgwick & Jackson, London.
- Fussman, G. F., and G. Heber. 2002. Food web complexity and chaotic population dynamics. *Ecology Letters* 5: 394–401.
- Gaedke, U., D. Straile, and C. Post-Wahl. 1996. Trophic structure and carbon flow dynamics in the pelagic community of a large lake. Pages 60–71 *in* G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of pattern and process*. Chapman & Hall, New York.
- Goldwasser, L., and J. Roughgarden. 1993. Construction of a large Caribbean food web. *Ecology* 74:1216–1233.
- Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* 142:379–411.
- . 1997. Does food web complexity eliminate trophic-level dynamics? *American Naturalist* 149:1001–1007.
- Hairston, N. G., Sr., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hall, S. J., and D. Raffaelli. 1991. Food-web patterns: lessons from a species-rich web. *Journal of Animal Ecology* 60:823–842.
- Havens, K. 1992. Scale and structure in natural food webs. *Science* 257:1107–1109.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia; or, why are there so many kinds of animals? *American Naturalist* 93:145–159.
- Huxman, M., D. Raffaelli, and A. Pike. 1995. Parasites and food web patterns. *Journal of Animal Ecology* 64:168–176.
- Kaunzinger, C. M. K., and P. J. Morin. 1998. Productivity controls food-chain properties in microbial communities. *Nature* 395:495–497.
- Lawton, J. H. 1989. Food webs. Pages 43–78 *in* J. M. Cherrett, ed. *Ecological concepts*. Blackwell Scientific, Oxford.
- . 1995. Webbing and WIWACS. *Oikos* 72:305–306.
- Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology* 83:195–207.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–418.
- Marcogliese, D. J., and D. K. Cone. 1997. Food webs: a plea for parasites. *Trends in Ecology & Evolution* 12: 320–325.
- Martinez, N. D. 1991. Artifacts or attributes? effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61:367–392.
- . 1993a. Effect of scale on food web structure. *Science* 260:242–243.
- . 1993b. Effects of resolution on food web structure. *Oikos* 66:403–412.
- Martinez, N. D., and J. H. Lawton. 1995. Scale and food-web structure: from local to global. *Oikos* 73:148–154.
- Martinez, N. D., B. A. Hawkins, H. A. Dawah, and B. Feifarek. 1999. Characterization of food-web structure with moderate sampling effort. *Ecology* 80:144–155.
- Moore, J. C., D. E. Walter, and H. W. Hunt. 1989. Habitat compartmentation and environmental correlates of food chain length. *Science* 243:238–239.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14:483–488.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667–685.
- . 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.
- Pauly, D., A. W. Trites, E. Capuli, and V. Christensen. 1998a. Diet composition and trophic levels of marine mammals. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* 55:467–481.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres, Jr. 1998b. Fishing down marine food webs. *Science* 279:860–863.
- Pauly, D., V. Christensen, S. Guénette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson, and D. Zeller. 2002. Towards sustainability in world fisheries. *Nature* 418: 689–695.

- Pimm, S. L. 1980. Properties of food webs. *Ecology* 61: 219–225.
- . 1982. *Food webs*. Chapman & Hall, London.
- Pimm, S. L., and J. H. Lawton. 1978. On feeding on more than one trophic level. *Nature* 275:542–544.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature* 350:669–674.
- Plante, C. J., P. A. Jumars, and J. A. Baross. 1990. Digestive associations between marine detritivores and bacteria. *Annual Review of Ecology and Systematics* 21:93–127.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813–846.
- Polis, G. A., and K. O. Winemiller, eds. 1996. *Food webs: integration of pattern and dynamics*. Chapman & Hall, New York.
- Post, D. M. 2002*a*. The long and short of food-chain length. *Trends in Ecology & Evolution* 17:269–277.
- . 2002*b*. Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* 83:703–718.
- Post, D. M., M. L. Pace, and N. G. Hairston. 2000. Ecosystem size determines food-chain length in lakes. *Nature* 405:1047–1049.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–814.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996*a*. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Power, M. E., M. S. Parker, and J. T. Wootton. 1996*b*. Disturbance and food chain length in rivers. Pages 286–297 in G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of pattern and process*. Chapman & Hall, New York.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155:141–153.
- Sterner, R. W., A. Bajpai, and T. Adams. 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. *Ecology* 78:2258–2262.
- Strong, D. R. 1992. Are cascades all wet? differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747–754.
- Vander Zanden, M. J., and J. B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs* 66:451–477.
- Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rasmussen. 1999. Patterns of food chain length in lakes: a stable isotope study. *American Naturalist* 154:406–416.
- Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55:299–311.
- Wilber, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* 78:2279–2302.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature* 404:180–183.
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60:331–367.
- Yodzis, P. 1984. The structure of assembled communities. II. *Journal of Theoretical Biology* 107:115–126.
- . 1989. *Introduction to theoretical ecology*. Harper & Row, Cambridge.