

TROPHIC LEVELS IN COMPLEX FOOD WEBS: THEORY AND DATA

RICHARD J. WILLIAMS AND NEO D. MARTINEZ

Romberg Tiburon Center, Department of Biology,
San Francisco State University, 3152 Paradise Dr., Tiburon, CA 94920
Phone: 415-338-1213, FAX: 415-435-7120
RJW: rich@sfsu.edu; NDM: neo@sfsu.edu

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, USA, the island of St. Martin, a UK grassland, and a Florida seagrass community which appear to be the most trophically complete available 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 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.

INTRODUCTION

The study of food chains and the trophic structure of ecosystems has long been central to ecology (Elton 1927, Lawton 1989, 1995, Wilbur 1997). Food chains depict the paths through a food web that organic energy travels along beginning with basal species and ending with assimilation by a species of interest. A species' trophic level 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 and are at trophic level one while their direct and indirect consumers are at higher levels. Research on trophic levels focuses on patterns common to all ecological systems (Elton 1927, Lindeman 1942, Lawton 1989, 1995, Pimm and Lawton 1978, Pimm 1980, Pimm et al. 1991, Cousins 1987, Yodzis 1989, 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, Hairston and Hairston 1993, 1997, Polis and Strong 1996), and patterns that distinguish species' roles within ecological systems (Power 1990, Cabana and Rasmussen 1994, Brett and Goldman 1997, Pace et al. 1999, Schmitz et al 2000).

Measuring trophic levels is central to this wide range of trophic-level research and food-web research plays a prominent role in this measurement on a species-by-species and whole-system basis (e.g. Pimm et al. 1991, Polis and Winemiller 1996). 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 trophic level" 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' trophic levels. 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) prefer the shorter extreme while Martinez (1991, also see Polis 1991) preferred an intermediate measure we call "chain-averaged trophic level" 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 available 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 trophic level of basal species and non-omnivorous 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 trophic level for these species based on binary webs and independent of energetic flow estimates could greatly increase the scientific productivity of trophic ecologists.

In four food webs, we compare six estimates of trophic level based only on binary link information to the “flow-based trophic level” based on information that quantifies the energy flow through the webs. We studied five additional binary food webs to further evaluate omnivory, limits to trophic levels, and the differences between the estimates based on binary links. Our objectives are to compare recently available trophic data to general theories about trophic levels 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 literature (Tab. 1a) that include 1) relatively many species, 2) empirically derived estimates of the energy flowing through each of the food webs’ links and 3) multiple trophic levels within the habitat described. One describes the food web of the Chesapeake Bay, USA (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 St. Martin (Goldwasser and Roughgarden 1993). The third food web is a UK 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 (Tab. 1b). 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 recent set of 50 Adirondack lake food webs that include only pelagic species (Haven 1992, Martinez 1993), we selected the largest, the Bridge Brook Lake web.

A two-dimensional binary matrix of elements l_{ij} (the 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 non-zero 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 of trophic level (here after referred to as “TL”) that we call “flow-based TL”. This measure is one plus the weighted average of chain lengths from a species to a basal species, where the weighting is given by diet fractions:

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

TL_j is the trophic level of species j , TL_i is the trophic level of the i th resource of species j , and p_{ij} is the diet fraction that species i constitutes in the diet of species j .

Possible estimates of a species’ TL based only on binary link information range

from its shortest food chain at one extreme to the longest food chain at the other extreme (Pimm 1980, 1982). We studied six measures spanning this range:

- 1) Shortest TL; one plus the shortest chain length from a consumer to a basal species.
- 2) Short-weighted TL; the average of shortest TL and prey-averaged TL (see below). This gives a measure biased towards shorter food chains.
- 3) Prey-averaged TL; one plus 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 non-zero link strength $p_{ij} = 1/n_j$, which assumes that a consumer consumes all its prey species equally.

- 4) Long-weighted TL; the average of longest TL (see below) and prey-averaged TL. This gives a measure biased towards longer food chains.
- 5) Chain-averaged TL; one plus the average chain length of all paths from a species to a basal species (Martinez 1991, Polis 1991).
- 6) Longest TL; one plus 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 by only passing through a loop once (Martinez 1991).

Chain-averaged TL assumes energy flow from prey increases with the number of the prey's resources. For example (Fig. 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 equals 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 that each prey plays an equal role in the diet of species 5, one with TL=1 and one with TL=2 resulting in prey-averaged TL=2.5. Other TL measures that weight prey according to trophic level rather than trophic links require *a priori* classification of trophic levels. Especially due to extensive looping (Williams and Martinez 2000), such classification requires an *a priori* choice among TL algorithms that assumes a solution to our analysis before it is conducted. Therefore, we only examined weightings that avoid *a priori* TL classification.

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 maximizes 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, weighting each species equally.

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). 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, figure 1b). We distinguish these two situations and quantify the degree of omnivory of a species by using the standard deviations of the weighed average of the trophic levels 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 standard deviations 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.

RESULTS

Whole Web Results

Results in Table 2a average the measure of TL across all species with more than one chain to a basal species for the four webs with link-flow information. This data compares 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 level for the Chesapeake Bay, St. Martin Island, UK 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 2b average TL measures across all species in the webs and allows different webs to be compared. 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 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.

In three of four webs, the short-weighted TL algorithm slightly underestimates the maximum flow-based TL of species within a web, while the prey-averaged TL algorithm overestimates this quantity in three of four webs. Flow-based TL maxima vary between 3.2 and 4.4 while short-weighted TL maxima vary between 3.4 and 4.3. 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) while showing slightly less 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 Tables 1a and 1b 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% to 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 1a) 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 non-omnivorous 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 prey with higher TL 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 St Martin island web (0.53 levels), *Chlorocytus deschampiae* in the UK grassland web (0.33

levels), and suspension-feeding polychaetes in the St Marks 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 St Martin island web, and a node that includes both Atlantic silverside and bay anchovies (-0.52 levels) in the Florida seagrass web. No species in the UK grassland web consume primarily higher trophic level prey.

Shortest TL gives an absolute lower bound on all species' trophic level. Prey-averaged TL provides an upper bound on flow-based TL for all except five species in the Chesapeake web. For most species in the UK grassland web and for some species in the St. Martin Island web, the bulk of the energy flow is along the shortest path 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. 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 standard deviations of flow-based TLs against the standard deviations of the prey-averaged TLs for the 98 omnivores in the four webs listed in Table 1a. Simple linear regression of the flow-based TL standard deviations (y) of the 98 species as a function of prey-averaged TL standard deviations (x) results in a statistically significant positive relationship that explains almost one half of the variability of flow-based TL standard deviations ($y=0.537x+0.057$, $SE_{\text{slope}} = 0.063$, $R^2 = 0.43$, $P<0.001$). For most species, the prey-

averaged TL standard deviation gives an upper bound on the flow-based TL standard deviation. The most extreme omnivores have flow-based standard deviations of 0.79 in the St Martin web (pearly eyed thrasher and Diptera larva), 0.40 in the UK grassland web (*Eupelmus atropurpureus*), 0.53 in the Chesapeake web (Menhaden) and 0.69 in the Florida seagrass web (Killifishes).

Figure 4 plots prey-averaged TL standard deviations (TL SD) against short-weighted TL for all species in Table 1. Maximum trophic levels are less than 4.3. For most species, TL SD is less than one, 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 above 1.2 indicating prey from very disparate trophic levels (e.g., figure 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). Prey-averaged TL and short-weighted TL address this challenge 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, Martinez and Lawton 1995, Haunzinger and Morin 1998). In contrast, chain-averaged TL (Martinez 1991, Polis 1991) 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 rarely addressed in the literature. 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 found it most accurate among the 34 omnivores in the St. Marks web. We also note that the 98 omnivores include a wide range of aquatic and terrestrial vertebrates and invertebrates. These observations suggest the general accuracy of short-weighted TL will extend well beyond the data in this study.

Since short-weighted TL is entirely dependent on unweighted binary webs, its accuracy could be affected by variable methodology in food web construction. For example, including unusually rare and often high links could lead to overestimating flow-based TL. This may have happened in the grassland (Table 2a) web constructed during 12 years of painstaking dissection of 164,000 stems of grasses. Alternatively, bias away from rarer links and towards links carrying significant quantities of energy could lead to

overestimates such as in the Chesapeake Bay web (Table 2a). 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) 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 standard deviation 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 are equally consumed provides an approximate upper limit of omnivory that typically remains below 1.0 (Fig 3). On average, flow-based TL standard deviations are about half this upper limit.

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 standard deviations that exceed one (fig. 4). Some of these exceptions occur among organisms that have different diets at different lifecycle stages such as some hyperparasitoids that consume plant material as adults. TL standard deviations usefully distinguish these organisms from other less omnivorous organisms at the same trophic level. Such analyses could also help determine whether omnivores exhibiting ontogenetic trophic

shifts are unusually broad omnivores or whether they are more efficient consumers than similarly omnivorous species whose diets are less tied to ontogeny. Unusually high omnivory may also be due to the common convention of assigning detritus to trophic level 1 (Geadke et al. 1996). Some organisms in the 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 a an unusually broad range of resources (Martinez 1991, 1993b).

The large number of non-omnivorous species and the relatively low degree of omnivory among the other species suggests that the reticulate nature of food webs is constrained in a way that linearizes the trophic interactions of consumers and their biotic resources. Such linearity is consistent with widely observed cascading interactions from consumers at higher trophic levels through to their resource species at lower levels (Pace et al 1999, Schmidt et al. 2000). While highly restricted omnivory is consistent with trophic cascades, such restrictions 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 less 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, Haunzinger 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 trophic levels of 4.3 (Fig 4). This level is well below Elton's (1927) originally postulated limit of 6 and Martinez' (1991) and Polis' (1991) claims of species at levels well over 6 (Tab. 2b). Although the Coachella Valley web includes many parasitoids and hyperparasitoids and has a high level of looping and omnivory, its trophic levels 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, Marcogliese and Cone 1997, Huxman et al. 1995) might increase the maximum trophic levels that occur, the data here do not contain such high trophic level organisms.

Because species at different trophic levels interact in predictably different ways, ecologists measure trophic level with several methods. Enclosure experiments measure species' "effective" trophic level (Paine 1980, Power 1990, Power et al. 1996) based on population dynamics that may cascade down to species at lower levels (Pace et al. 1999,

Schmidt et al. 2000). Isotopic and gut-content analyses measure trophic levels that predict how biomagnification extends up trophic levels concentrating lipophilic toxic substances at higher levels (Cabana and Rasmussen 1994). 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' trophic levels and omnivory, and therefore roles within ecological systems. The narrow bracket between shortest TL 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 more labor-intensive analyses.

Our analyses accept the structural food-web convention of treating detritus as a non-consuming basal species (Geadke et al. 1996). Rather than including uniquely dead organic matter within an 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 to the second TL (Geadke 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 trophic level of the source of the detritus. 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 microbial detritivores as the base of food chains of live organisms, 2) simplifies food web construction, and 3) excludes ecologically and evolutionarily incongruous forms of biomass.

CONCLUSION

We present new data and analyses that support and develop the scientific basis of trophic levels. Our new methods for measuring trophic level enable more rigorous analyses of larger and more complex food webs than previously possible. Our findings support historically claimed limits to trophic levels and reject more contemporary challenges to the limits, meaning, and use of trophic levels. Specifically, our data and analyses directly and rigorously incorporate trophic elements thought to severely challenge the trophic-level concept. These elements, including omnivory, cannibalism, mutual predation, long chain lengths, and high species diversity, are quantitatively integrated into the calculation of species' trophic levels. In general, the challenges these elements present appear to have been overstated since they leave many species unaffected and are quantitatively constrained among affected species. Additional research, especially on comprehensive webs with 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 and experimental manipulations of species.

ACKNOWLEDGEMENTS

Support was provided by National Science Foundation Grants 9950461 and 9905446 to NDM. The comments of Jennifer Dunne, Mark Newman, and several reviewers greatly improved an earlier version of the manuscript. The research was partially conducted during visits to the Santa Fe Institute by NDM and RJW.

REFERENCES

- Adams, S.M., B.L. Kimmel and G.R. Ploskey. 1983. 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.
- Brett, M. T. & Goldman, C. R. 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., 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.
- Carpenter, S.R. and J.F. Kitchell 1993. The trophic cascade in lakes. Cambridge Univ. Press, Cambridge.
- Christian, R. R. and J. J. Luczkovich 1999. Organizing and understanding a winter's

- seagrass foodweb 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, A. J. Kohn, J. H. Lawton, N. Martinez, R. O'Malley, L. M. Page, B. C. Patten, S. L. Pimm, G.A. Polis, M. Rejmánek, T. W. Schoener, K. Schoenly, W. G. Sprules, J. M. Teal, R. E. Ulanowicz, P. H. Warren, H. M. Wilbur, P. Yodzis. 1993. Improving Food Webs. *Ecology* 74:252-258.
- Cousins, S.H. 1987. The decline of the trophic level concept. *Trends in Ecology and 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 interactions 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 and Jackson, London.
- Goldwasser, L. and J. Roughgarden. 1993. Construction of a large Caribbean food web. *Ecology* 74:1216-1233.
- Hall, S.J. and Raffaelli, D., 1991. Food-web patterns: Lessons from a species-rich web. *Journal of Animal Ecology* 60:823-842.
- Hairston, N.G., Sr., F.E. Smith and L.B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421-425.
- 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.
- Hairston, N. G. Jr. and N. G. Hairston Sr. 1997. Does food web complexity eliminate trophic-level dynamics? *American Naturalist* 149:1001-1007.
- 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., Raffaelli, D. & Pike, A. Parasites and food web patterns. *Journal of Animal Ecology* 64, 168-176 (1995).
- Lawton, J.H. 1989. Food webs. Pages 43-78 in J.M. Cherrett, ed. *Ecological Concepts*. Blackwell Scientific, Oxford.
- Lawton, J. H., 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. & Cone, D. K. 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.
- Martinez, N.D. 1993a. Effect of scale on food web structure *Science* 260:242-243.
- Martinez, N. D. 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., Cole, J. J., Carpenter, S. R. and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:483-488.
- Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667-685.
- Pimm, S.L. 1980. Properties of Food Webs. *Ecology* 61:219-225.
- Pimm, S.L. 1982. *Food Webs*. Chapman and 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 Desert food webs: 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 and Hall.
- 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., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., and Paine, R. T. 1996. Challenges in the quest for keystones. *Bioscience* 46, 609-620.
- Schmitz, O. J., Hambäck & Beckerman, A. P. 2000. Trophic Cascades in Terrestrial Systems: A review of the effects of carnivore removals on plants. *Am. Nat.* 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.
- Warren, P.H. 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55:299-311.
- Williams, R. J. & Martinez, N. D. 2000. Simple rules yield complex food webs. *Nature* 404, 180-183.
- Yodzis, P. 1984. The structure of assembled communities. II. *Journal of Theoretical Biology* 107:115-126.
- Yodzis, P. 1989. *Introduction to theoretical ecology*. Harper and Row, Cambridge.

Table 1. Basic properties of food webs. “Species” *S* are taxonomic species or more coarsely lumped species aggregations. Omnivory is the percentage of species that have food chains of at least two different lengths.

a). Basic properties of four food webs with link strength data.

Reference	Name	S	L/S	C	Omnivory (No.)
Baird and Ulanowicz (1989)	Chesapeake Bay	33	2.2	.067	48% (??)
Goldwasser and Roughgarden (1993)	St. Martin Island	44	4.9	.11	59% (??)
Dawah et al. (1995)	UK Grassland	87	1.4	.017	18% (??)
Christian and Luczkovich (1999)	Florida Seagrass	48	4.6	.096	71% (??)

b). Basic properties of five binary food webs.

Reference	Name	S	L/S	C	Omnivory (No.)
Warren (1989)	Skipwith Pond	35	10.9	.31	51% (??)
Hall and Raffaelli (1991)	Ythan estuary	92	4.4	.048	47% (??)
Martinez (1991)	Little Rock Lake	181	13.1	.072	24% (??)
Polis (1991)	Coachella Valley	30	9.7	.32	77% (??)
Havens (1992)	Bridge Brook Lake	75	7.4	.098	16%

Table 2. Web-averaged measures of trophic level.

(a) Measures of trophic level for the four webs listed in Table 1a averaged across only those species with more than one chain to basal species.

	Chesapeake Bay	St. Martin Island	UK Grassland	FL 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

(b) Mean across all species and maximum values of the various measures of trophic level for all webs in tables 1a and 1b. Flow-based TL can only be calculated for the webs with link strength information.

	Flow-based TL		Shortest chain TL		Short-weighted TL		Prey-avg TL		Chain-avg TL	
	Mean	Max	Mean	Max	Mean	Max	Mean	Max	Mean	Max
Chesapeake Bay	2.49	3.85	2.24	3	2.40	3.42	2.56	3.84	2.90	4.87
St. Martin Island	2.45	4.44	2.14	4	2.42	4.28	2.70	4.56	3.33	6.15
UK 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
Skipworth 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	2.58	3.42	3.08	3.97	4.08	7.30
Bridge Brook L.			1.51	3	1.59	3.43	1.65	3.86	1.71	4.82

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.

Figure 1a

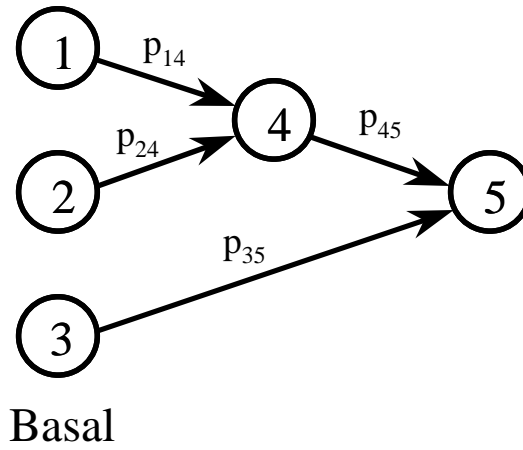


Figure 1b

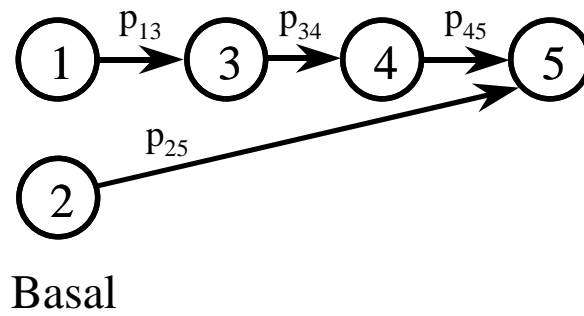


Figure 2. Histograms of differences between flow-based TL and prey-averaged TL, binary-estimated TL and shortest TL for the 98 direct and indirect omnivores in the Chesapeake Bay, St. Martin island, UK grassland and St. Marks estuary food webs.

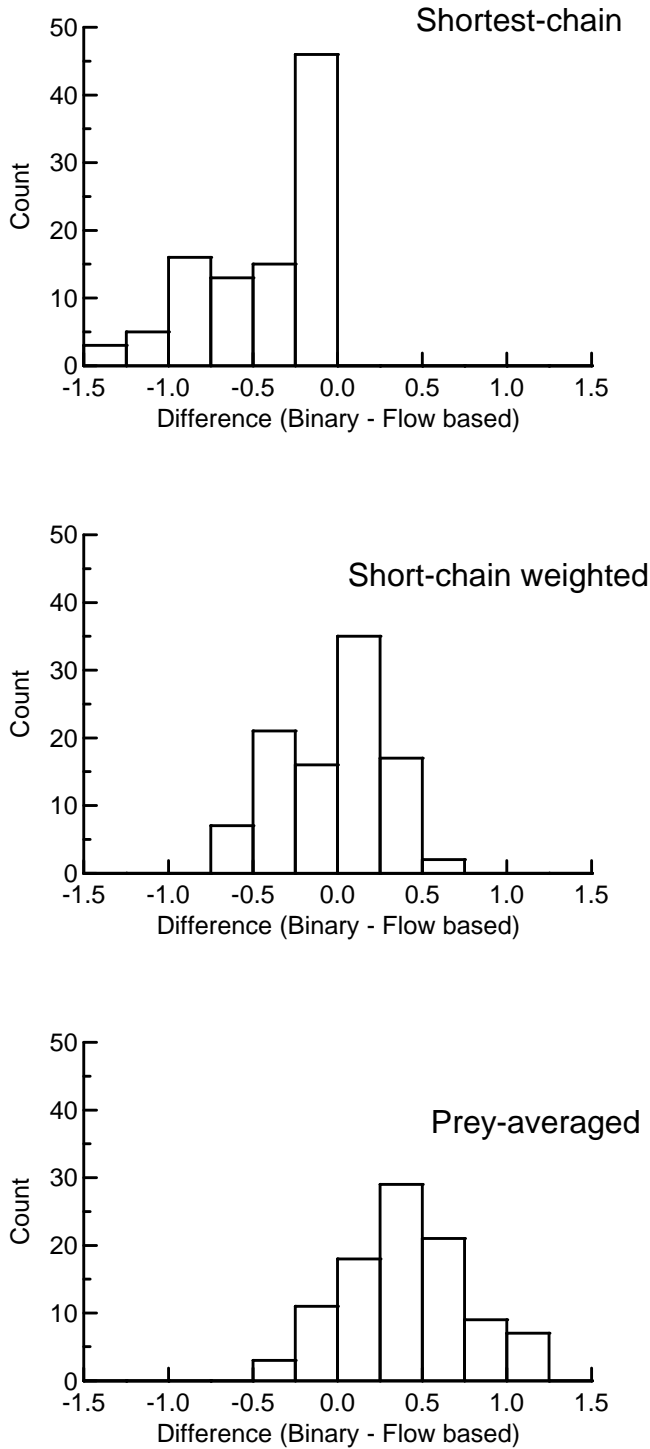


Figure 3. Prey-averaged TL standard deviation vs. flow-based TL standard deviation for the St. Martin island (\square), Chesapeake Bay (Δ), UK grassland (\circ) and Florida seagrass (\diamond) food webs. Solid line illustrates equivalence between the variance measures.

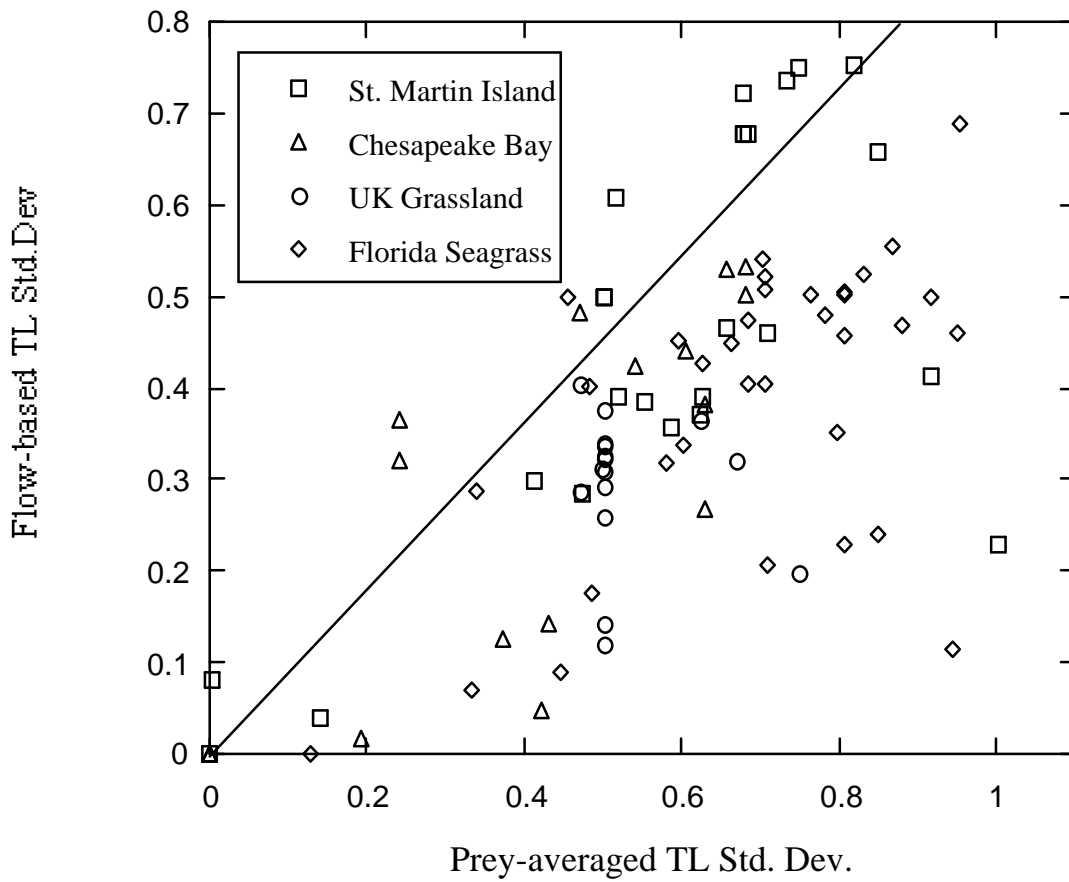


Figure 4. Prey-averaged TL standard deviation vs. short-chain weighted TL for the nine webs listed in Tables 1a and 1b.

