Food webs are more than the sum of their tritrophic parts

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Many studies have aimed to understand food webs by investigating components such as trophic links (one consumer taxon eats one resource taxon), tritrophic interactions (one consumer eats an intermediate taxon, which eats a resource), or longer chains of links. We show here that none of these components (links, tritrophic interactions, and longer chains), individually or as an ensemble, accounts fully for the properties of the next higher level of organization. As a cell is more than its molecules, as an organ is more than its cells, and as an organism is more than its organs, in a food web, new structure emerges at every organizational level up to and including the whole web. We demonstrate the emergence of properties at progressively higher levels of structure by using all of the directly observed, appropriately organized, publicly available food web datasets with relatively complete trophic link data and with average body mass and population density data for each taxon. There are only three such webs, those of Tuesday Lake, Michigan, in 1984 and 1986, and Ythan Estuary, Scotland. We make the data freely available online with this report. Differences in web patterns between Tuesday Lake and Ythan Estuary, and similarities of Tuesday Lake in 1984 and 1986 despite 50% turnover of species, suggest that the patterns we describe respond to major differences between ecosystem types.

body mass | community ecology | food chain | population density | trophic link

Trophic cascades and tritrophic interactions have long been studied. Community-level trophic cascades involve trophic levels (1, 2). Species-level trophic cascades (3) involve interactions among a few species (4, 5) and have been documented in many systems (6, 7). Tritrophic interactions occur by diverse mechanisms (8–11), can cross ecosystem boundaries (12, 13), and matter practically, for example in management of marine fisheries (14) and biological control of crop pests by using consumers of pests (15).

Species-level tritrophic interactions (henceforth tritrophic interactions) have rarely been examined within a larger food web (henceforth web). Some studies that did so counted the commonness of a tritrophic interaction motif by using only web topological structure (16, 17). The stability of tritrophic interactions has been investigated as a function of ratios of consumer body mass to resource body mass in each trophic link (henceforth link) and of the numbers of predators and prey of each species (18), although the dynamical model of that study was not tested by dynamic data, and measurements of population density were not considered.

Webs with the average body mass (M) and population density (N) of each species or other taxon (henceforth M,N-webs) (19–26) reveal previously unrecognized features of web structure (27, 28) and connect body mass (29) and metabolism (30) to webs (31). We analyzed links, tritrophic interactions, and food chains in M,N-webs from Tuesday Lake, Michigan, in 1984 and 1986 and Ythan Estuary, Scotland. These three examples are all of the M,N-webs we know where the links, average body masses, and population densities are based on direct observations in situ, and the data are publicly available. This paucity of directly observed, appropriately organized, publicly available M,N-webs seems shocking after more

than a century of scientific ecology, limits the possibility of empirically based generalization and indicates the great need for more such M,N-webs from varied habitats to be published.

We used statistics on link length, link angle, and between-angle of tritrophic interactions. Intuitively, the length of a link from resource R (eaten) to consumer C (eater) is the number of orders of magnitude of difference in body mass plus the number of orders of magnitude of difference in population density between R and C. The angle or slope of a link measures the rate of change in biomass, population productivity and population consumption from R to C. The between-angle of a tritrophic interaction from R to intermediate taxon I to C measures the acceleration (rate of change in the rate of change) in biomass, population productivity and population consumption from R to I to C. Definitions are specified in detail below.

Two models that treated a trophic link as independent of other trophic links in a tritrophic interaction or food chain were rejected. Our statistics and modeling revealed that links appearing in tritrophic interactions differed systematically from random links, that food chains were more than compositions of overlapping tritrophic interactions, and that some features of communities were not wholly accounted for by food chains. At each higher level of structure, new properties emerged. These results support a holistic quantitative approach to understanding food webs, however informative reductionist study of components may be. These results matter practically because they suggest that the larger food web context may affect efforts to manipulate links, tritrophic interactions, and longer chains within webs.

Results

Definitions. *Link statistics.* Taxa were plotted on ($\log(M)$, $\log(N)$) coordinates (base-10 logarithms throughout) (Fig. 1 *A–C*). In all three webs, the log population density $\log(N)$ of taxa decreased approximately linearly with increasing log body mass $\log(M)$, confirming the existence of an approximately allometric (or power law) relationship between population density and body mass with negative exponent (31, 32). Linear regression coefficients and confidence intervals are given in Table S2. In Tuesday Lake 1984 and 1986 (Fig. 1 *A* and *B*), the three classes of basal, intermediate, and top taxa were clearly separated by average body mass. In Ythan Estuary (Fig. 1*C*), by contrast, these three groups intermingled much more as a function of body mass. Thus food chains in Ythan Estuary started or stopped in the middle of the range of M, whereas those in Tuesday Lake generally began at small M and ended at large M.

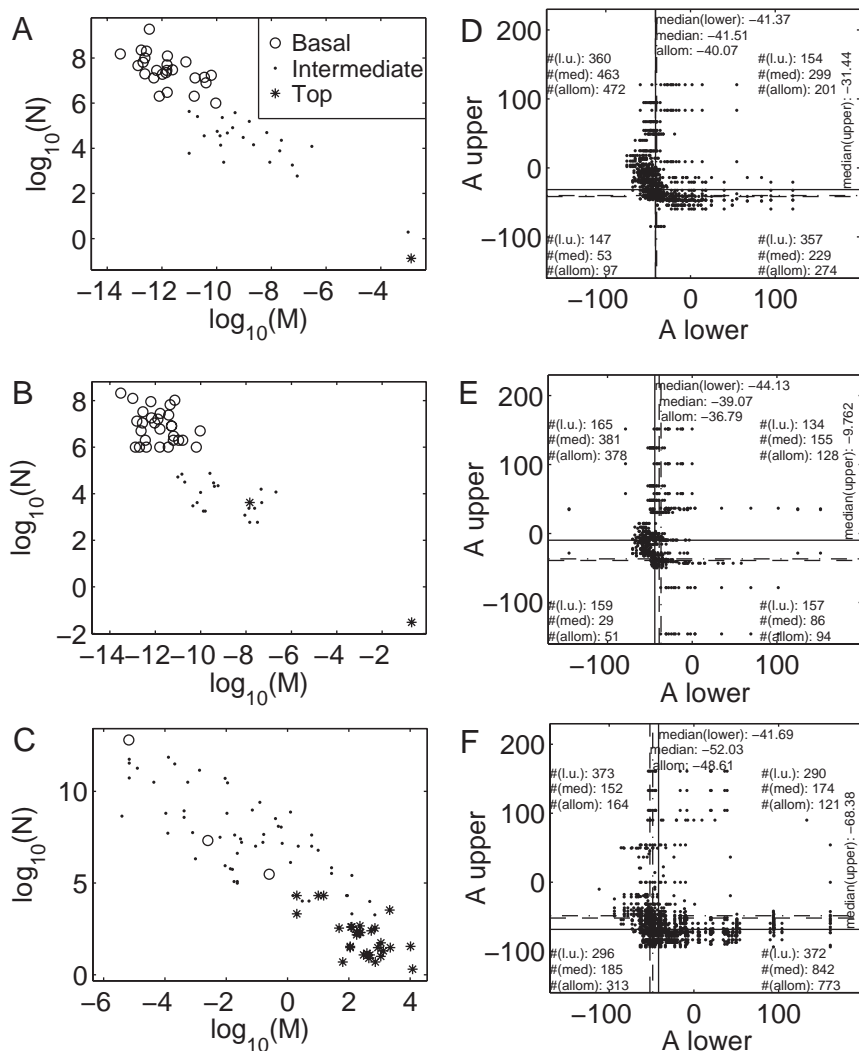The l_1 distance (henceforth distance) between two taxa a and b

Fig. 1. Properties of food webs in Tuesday Lake 1984 (*A* and *D*), Tuesday Lake 1986 (*B* and *E*), and Ythan Estuary (*C* and *F*). (*A*–*C*) Log population density N declines approximately linearly as a function of increasing log average body mass M of taxa. Trophic links were omitted for clarity, but food generally flowed from upper left toward lower right, because consumers were generally less abundant and had larger average body mass than the resource taxa they consumed. In Tuesday Lake (*A* and *B*), basal, intermediate, and top taxa were distinct with high, intermediate, and low population density. In Ythan Estuary (*C*), basal and top taxa spread to the middle of the body mass distribution. Numbers, means, and standard deviations of log(*M*) and log(*N*) of taxa in each category are in Table S1. Linear regression coefficients are in Table S2. (*D*–*F*) Upper angle A_{upper} was a horseshoe-shaped function of lower angle A_{lower} of 2-chains. Vertical and horizontal lines represent median lower and upper angles for all 2-chains (solid line), median angle of all links (dashed line), and allometric angle (dash-dotted line). Counts of data points in each quadrant refer to quadrants formed by medians of lower and upper angle [#dots(l.u.)], median angle of all links [#dots(med)], and allometric angle [#dots(allom)].

was defined as $|\log(M_a) - \log(M_b)| + |\log(N_a) - \log(N_b)|$ (27). The first term $|\log(M_a) - \log(M_b)| = |\log(M_a/M_b)|$ is the absolute log body mass ratio, the number of orders of magnitude of difference in body mass. The second term $|\log(N_a) - \log(N_b)| = |\log(N_a/N_b)|$ is the absolute log density ratio, the number of orders of magnitude of difference in population density. The distance between two taxa a and b measures the square-block or Manhattan-grid distance between a and b when they are plotted on (log(*M*), log(*N*)) coordinates. This distance is preferred to Euclidean distance because the square-block distance has a direct biological interpretation: the l_1 distance is the number of orders of magnitude of difference between two taxa in body mass and in population density.

Viewing a link as a vector (R, C) from resource R to consumer C, the length of a link (or link length) was defined as the distance from R to C (using the definition of distance in the previous paragraph). The angle of a link (or link angle) was the counterclockwise angle to the link from a horizontal arrow starting from R and pointing right parallel to the positive log(*M*)-axis, and took values in the interval $[-180°, 180°]$ (Fig. 2*A*)]. (The angle is not defined when $M_R = M_C$ and $N_R = N_C$, as in cannibalism, for example.) If the link angle equaled $-45°$, then the link had slope -1 because $\tan(-45°) = \tan(-\pi/4 \text{ radians}) = -1$. In this case, the resource biomass $B_R = M_R N_R$ equaled the consumer biomass $B_C = M_C N_C$ because each factor of increase in average body mass from R to C was accompanied by an exactly equal factor of decrease in

population density from R to C. Moreover, if population productivity and population consumption scaled allometrically with M as NM^b, $0 < b < 1$, then in a link with slope $-b$, the population productivity and population consumption of R equaled the population productivity and population consumption of C. Often $b = 2/3$ or $3/4$ is claimed (29, 33). If $b = 2/3$, then, in a link with angle $-33.7° = \arctan(-2/3)$, the value of NM^b for R equals the value of NM^b for C, and the same is true for a link with angle $-36.9° = \arctan(-3/4)$ if $b = 3/4$. Thus the angle or slope of a link revealed the change in biomass, population productivity and population consumption from R to C.

Tritrophic statistics. A 2-chain consisted of three taxa (R, intermediate taxon I, and C), and two links: the lower link (R, I) and the upper link (I, C). When plotted on (log(*M*), log(*N*)) coordinates (Fig. 2 *B* and *C*), the upper link usually appeared below and right of the lower link because as body mass M increased up the typical 2-chain, population density N typically decreased. (Exceptions to this typical case arise when, e.g., C is a parasite smaller in body mass than its host I, but such exceptions were rare in our data; Table S3.) A 2-chain depicted a tritrophic interaction. The 2-span of a 2-chain was defined as the distance from R to C. L_{lower} and A_{lower} denoted the length and angle of lower link (R, I); similarly for L_{upper} and A_{upper}. By the triangle inequality, 2-span $\leq L_{upper} + L_{lower}$. When I fell outside the rectangle described by $M_R \leq M_I \leq M_C$ and $N_C \leq N_I \leq N_R$, the inequality was strict: 2-span $< L_{upper} + L_{lower}$. The difference between the mean of $L_{upper} + L_{lower}$ and the mean 2-span
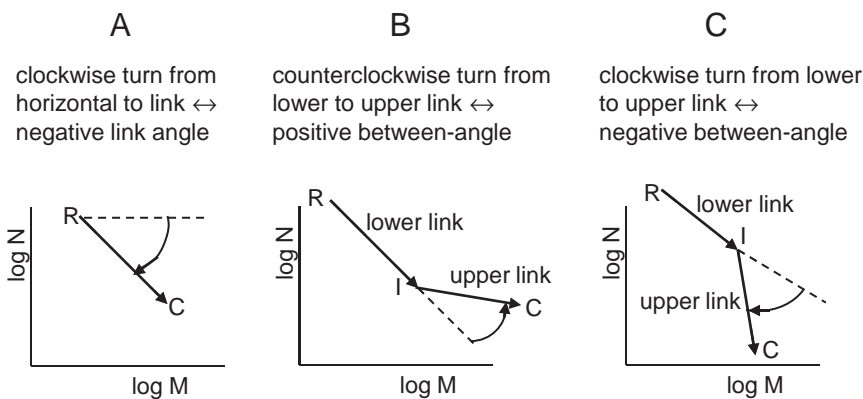
Fig. 2. Definitions of angles. (*A*) Link angle was negative (the typical case) when the link from R to C resulted from a clockwise turn with respect to a horizontal line (dashed line here) starting from R and pointing right parallel to the positive log *M* axis. (*B*) When the upper link (I, C) turned counterclockwise from the lower link (R, I), between-angle was positive. (*C*) When the upper link (I, C) turned clockwise from the lower link (R, I), between-angle was negative. R, resource taxon; I, intermediate taxon; C, consumer taxon.

for all 2-chains measured how much 2-chains departed on average from $M_R \leq M_I \leq M_C$ and $N_C \leq N_I \leq N_R$.

The between-angle of a 2-chain was defined as the angle in the interval $[-180°, 180°]$ from (R, I) to (I, C). Positive angles (Fig. 2*B*) represented a counterclockwise turn from lower to upper link, negative angles (Fig. 2*C*) a clockwise turn. For example, if the lower link had angle $-45°$ and the upper link had angle $-30°$, then the between-angle was $+15°$. The mean and standard deviation of between-angles over all 2-chains measured how log body mass ratios and log population density ratios varied between successive links in 2-chains. As a difference of angles, the between-angle of a 2-chain measured the acceleration (rate of change in the rate of change) in biomass, population productivity and population consumption from R to I to C. (In kinematics, acceleration is the rate of change of velocity, which is the rate of change of position.) A positive mean between-angle signified that biomass, population productivity and population consumption increased faster in the upper link (I, C) than the corresponding measures increased in the lower link (R, I). **Multitrophic statistics.** The allometric slope of a web was defined as the slope of the ordinary linear regression line of $\log(N)$ as a function of $\log(M)$ for all nonisolated taxa. The allometric angle of the web was defined to be the angle between $-90°$ and $90°$ corresponding to the allometric slope, measured from horizontal pointing right. The community span of a web was defined as the range of $\log(M)$ values plus the range of $\log(N)$ values over all nonisolated taxa. The community span was the number of orders of magnitude difference in mass between the largest and the smallest nonisolated taxa plus the number of orders of magnitude difference in population density between the rarest and the commonest nonisolated taxa.

Maximal food chains, those from a basal to a top taxon, hereafter called chains, were enumerated (27) as any chain passing from resource to consumer at each link but not including the same taxon twice (cannibalistic links were not included, and cycles, if present, were not completely traversed). All 2-chains were parts of the enumerated chains. The span of a chain or chain span was defined as the distance between its top and basal taxa. The community span exceeded or equaled the span of every chain. The difference between the community span and the mean chain span measured the degree to which average chains traversed the web in $(\log(M), \log(N))$ space. The count chain length of a chain was defined as the number of links comprising the chain. The sum chain length of a food chain was defined as the sum of the lengths of links comprising the chain. The wiggling of a web was defined as the mean sum chain length divided by the mean chain span. The minimum possible value of a web's wiggling was 1, and the excess over 1 measured the

average changes in direction of links in chains as links progressed from basal to top taxa.

Null hypotheses. We compared statistics from each empirical web, excluding isolated taxa and cannibalistic links, to two null hypotheses. In each empirical web, we enumerated all possible ordered triples, (t_R, t_I, t_C), of three distinct taxa with $M_R \leq M_I \leq M_C$. For each triple, we computed 2-span, between-angle, A_{upper} and A_{lower} as if t_C ate t_I and t_I ate t_R, whether or not these trophic relationships existed. In this way, we produced hypothetical distributions of statistics for all triples in each web under the null hypothesis that 2-chains had only the structure inherited from the observed M and N distributions of taxa and an ordering by body mass. Links with undefined angle and 2-chains with undefined between-angle were excluded (as they were in analyzing data). We also compared webs with simulations of the cascade model, which assumes $M_R \leq M_I \leq M_C$, in *Comparisons with Cascade Model Simulations Plus M and N Distributions* in *SI Text*. More recent models allow for deviations from strict ordering but are not considered here for reasons explained in *SI Text*.

Several measures of a single web were not statistically independent, such as between-angles and link lengths. For example, two link lengths were not independent if a taxon was involved in both links. The lack of independence violated the assumptions of regression and some standard statistical tests. We treated the *P* values from such tests not as probabilities but as descriptive statistics we called nominal *P* values. A result was nominally significant if the nominal *P* value was <5%. The term "nominal" warns that the reported *P* value is vulnerable to the dependence of the underlying measures.

Tritrophic Interactions: Univariate Distributions. *Between-angle, 2-span, A_{upper} and A_{lower}.* In all three webs overwhelmingly, most links had $M_R \leq M_C$ and most 2-chains had $M_R \leq M_I \leq M_C$ (Table S3). Mean between-angle was nominally significantly positive for Tuesday Lake 1984 (mean = 15.83°, *t* test nominal *P* < 0.0001) and for Tuesday Lake 1986 (mean = 31.66°, *t* test nominal *P* < 0.0001), but nominally significantly negative for Ythan Estuary (mean = $-27.46°$, *t* test nominal *P* < 0.0001; Table S1). The positive mean between-angle for Tuesday Lake (both years) indicated that the upper link tended to turn counterclockwise from the lower link, and oppositely for Ythan Estuary (Fig. 3). On average, moving from basal to top taxa, angles of consecutive links in a typical Tuesday Lake (Ythan Estuary) chain had progressively less negative (progressively more negative) values, leading to convexity (concavity) of typical chains on $(\log(M), \log(N))$ coordinates. Link angle increased with resource or consumer log body mass in Tuesday Lake, but decreased in Ythan Estuary (Table S2). In Tuesday Lake, biomass,
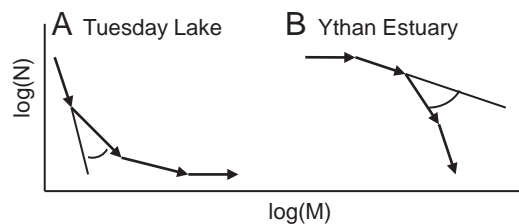
Fig. 3. Typical Tuesday Lake (*A*) and Ythan Estuary (*B*) chains inferred from average between-angles. Tuesday Lake upper links tended to turn counterclockwise from lower links, the opposite of Ythan Estuary.

population productivity and population consumption increased faster in the upper link than the corresponding measures increased in the lower link of tritrophic interactions, whereas the opposite held in Ythan Estuary.

The pronounced positive mean between-angle in Tuesday Lake and the pronounced negative mean between-angle in Ythan Estuary differed from the mean between-angles of hypothetical triples, which were slightly negative (Table S1). For all three webs, comparisons between 2-chains and triples of the distributions of between-angle, 2-span, A_{upper}, and A_{lower} rejected the null hypothesis that distributions were the same with nominal $P < 0.0001$ (Kolmogorov–Smirnov test, Matlab function kstest2).

Standard deviations of between-angle distributions were 52.09° for Tuesday Lake 1984, 61.81° for Tuesday Lake 1986, and 61.15° for Ythan Estuary. Between-angle histograms for webs and triples showed approximately symmetric unimodal distributions.

L_{upper} and L_{lower}. If (hypothetically) 2-chains were pairs of links chosen randomly and independently from all links, one would expect mean(L_{upper}) plus mean(L_{lower}) to be close to twice the mean link length. However, twice the mean link length was greater than the mean of $L_{upper} + L_{lower}$ across all 2-chains (Table 1). Thus 2-chains differed from random pairs of links. Short links were overrepre-

sented in 2-chains. As required from the triangle inequality, mean $L_{upper} + L_{lower}$ across all 2-chains always exceeded mean 2-span.

In all three webs, mean(L_{lower}) > mean(L_{upper}). Histograms of L_{upper} and L_{lower} revealed major differences between these two distributions in Tuesday Lake, but not in Ythan Estuary (Fig. S1). In Ythan Estuary, L_{upper} and L_{lower} distributions were unimodal and similar in shape and location to each other. Tuesday Lake L_{lower} distributions were not radically different from that of Ythan Estuary, but Tuesday Lake L_{upper} distributions were strongly bimodal. Upper links in Tuesday Lake were either very short or very long, for good biological reasons: in (log(M), log(N)) space, zooplankton were close to each other, so upper links where zooplankton ate zooplankton were short; fish were far from zooplankton, so fish eating zooplankton formed long upper links.

Tritrophic Interactions: Bivariate Distributions, Upper Angle Versus Lower Angle. A_{upper} was plotted against A_{lower} and the coordinate plane was divided into quadrants (*Methods*). The general but not universal tendency was for data to fall preferentially in the upper left and lower right quadrants, compared with the other two quadrants (Fig. 1 *D–F*). Data always showed a horseshoe pattern. A_{upper} and A_{lower} were not independent. A lower angle less than the median or allometric angle was, on average, followed by an upper angle greater than the median or allometric angle (Fig. 4*A*), and vice versa (Fig. 4*B*).

The dependence of link angles was partly a consequence of M and N distributions, because the triples reproduced horseshoe patterns in A_{upper} versus A_{lower} (Fig. S2) similar to those in webs (Fig. 1 *D–F*). However, A_{lower} and A_{upper} distributions differed between webs and triples nominally highly significantly (Kolmogorov–Smirnov test; see *Between-angle, 2-span, A_{upper} and A_{lower}* above).

Food Chains. In general, short links were overrepresented in chains: In all three webs, the product of mean count chain length times mean link length exceeded community span (Table 1). On average, chains traversed much more of the range in (log(M), log(N)) space

Table 1. Statistics of links, tritrophic interactions, chains, and webs

Statistic	TL 1984	TL 1986	Ythan
Links and tritrophic interactions			
Mean link length	6.33	5.90	7.29
Mean L_{upper}	5.41	3.43	5.06
Mean L_{lower}	5.99	5.69	6.15
2 × mean link length	12.67	11.79	14.57
Mean 2-span	11.02	8.65	10.51
Mean $L_{upper} + L_{lower}$	11.40	9.12	11.20
2 × mean link length/mean 2-span	1.15	1.36	1.39
Mean $L_{upper} + L_{lower}$/mean 2-span	1.03	1.05	1.07
Community span < mean(count chain length) × mean(link length)			
Mean count chain length	4.84	4.84	4.43
Mean count chain length × mean link length	30.62	28.56	32.31
Community span	20.78	22.66	21.98
Mean count chain length × mean link length/community span	1.47	1.26	1.47
Wiggling of chains			
Mean sum chain lengths	19.96	23.33	16.88
Mean chain span	18.71	20.62	13.18
Mean chain span/community span	0.90	0.91	0.60
Mean sum chain lengths/mean chain span	1.07	1.13	1.28
Mean sum chain lengths/community span	0.96	1.03	0.77
Connectance			
No. of noncannibalistic links	264	236	379
(No. of taxa)^2	2500	2601	8281
No. of trophic links/(number of taxa)^2	0.1056	0.0907	0.0458
No. of trophic links/taxa	5.28	4.63	4.16

TL, Tuesday Lake.

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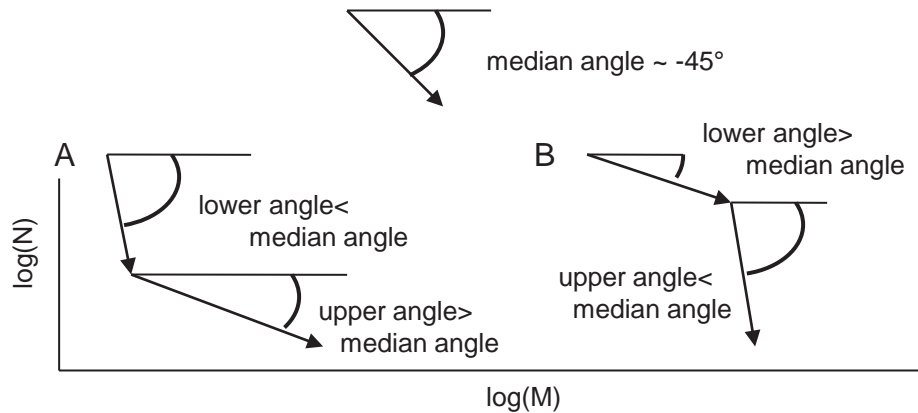
Fig. 4. Upper and lower angle correlated negatively. A lower angle less than the median angle, which was approximately $-40°$ in Tuesday Lake and approximately $-52°$ in Ythan Estuary (for a very rough overall central tendency around $-45°$), was often followed by an upper angle greater than the median angle (*A*), and vice versa (*B*).

in Tuesday Lake than in Ythan Estuary: for Tuesday Lake, mean chain span was 0.90 (in 1984) and 0.91 (in 1986) times community span, whereas Ythan Estuary's mean chain span was 0.60 times community span.

Ythan Estuary chains wiggled slightly more than Tuesday Lake chains: mean sum chain lengths were 1.07 in 1984 and 1.13 in 1986 times mean chain spans in Tuesday Lake and 1.28 times mean chain spans in Ythan Estuary (Table 1). Wiggling compensated for the degree to which chains failed to span the community in Tuesday Lake, but not in Ythan Estuary: in Tuesday Lake, mean sum chain lengths were 0.96 times community span in 1984 and 1.03 times the community span in 1986, whereas in Ythan Estuary, mean sum chain lengths were only 0.77 times community span.

Discussion

In Tuesday Lake, Michigan, in 1984 and 1986, and Ythan Estuary, Scotland, the properties of links did not account for some properties of tritrophic interactions, and the properties of links and tritrophic interactions did not account for some properties of longer chains. Food chains did not account for some properties of webs. Studies of individual links (24, 26–28, 34, 35), tritrophic interactions (14, 16, 18, 38), and food chains remain valuable but insufficient to understand more complex trophic structures.

Comparing observed 2-chains with triples of taxa ordered by average body mass rejected the null hypothesis that 2-chains showed no structure other than that inherited from links, ordering by average body mass, and the distributions of M and N. For triples, the expected between-angle was close to zero, whereas the mean between-angles of 2-chains showed an average positive acceleration of biomass, population productivity and population consumption in Tuesday Lake and an average negative acceleration in Ythan Estuary.

Furthermore, links did not account fully for 2-chains because, in all three webs, mean(2-span) < mean(L_{upper} + L_{lower}) < 2 × mean link length (Table 1). The first inequality means that 2-chains wiggled so strongly that the intermediate taxon I fell outside the rectangle described by $M_R \leq M_I \leq M_C$ and $N_C \leq N_I \leq N_R$. Strict inequality held in all three webs. A strong deviation in the direction of a lower link of a 2-chain from the central value of slope tended to be followed by a compensatory deviation in the direction of the adjacent upper link. The second inequality, mean(L_{upper} + L_{lower}) < 2 × mean link length, arose because, in all three webs, both lower and upper links in 2-chains were on average shorter than the mean link length. This unanticipated finding indicated that links that occurred within fewer 2-chains were longer than those that occurred in more 2-chains. (We clarify this point. Each link occurred in some number of 2-chains. That number may, a priori,

be zero, if the link occurred in no 2-chains, or one 2-chain, or two, etc. Some links occurred in fewer 2-chains than other links. The finding suggests that links that occurred in fewer 2-chains had greater length than links that occurred in relatively more 2-chains.) An unusually long link was found in fewer 2-chains than a short link because a long link had a consumer many orders of magnitude larger and rarer than its resource. Consequently, consumer and resource of that long link were near the outer extremes of the range of average body size and population density, and fewer other taxa were available to form further links.

Despite a 50% turnover of taxa between 1984 and 1986, the mean between-angle remained positive in Tuesday Lake, in contrast to the negative mean between-angle in Ythan Estuary, a qualitatively different ecosystem with respect to type of habitat, size, included taxa, and data resolution. More empirical M,N-webs are needed to examine consistencies or differences in 2-chain structure in relation to habitat.

Links and 2-chains did not account for all properties of chains. For example (Table 1), mean count chain length × mean link length was longer than the community span by 26–47%. These consistent differences challenged the guess of Reuman and Cohen (27) that mean link length approximately equals community span divided by mean count chain length, although the discrepancy is less than an order of magnitude. In addition, mean sum chain lengths exceeded mean chain span by 7–28%. Such inequalities reflected both wiggling and underrepresentation of very long links in chains.

Some differences between webs went beyond what could readily be explained by the differences between communities in links or 2-chains. For example, 2 × mean link length was longer than mean 2-span by 15–39% (Table 1), so the excess of 2 × mean link length over mean 2-span accounted for much or all of the excess of mean count chain length × mean link length over community span (26–47%). By contrast, in 2-chains, mean(L_{upper} + L_{lower}) (the 2-chain version of mean sum chain length) exceeded mean 2-span by 3%, 5%, and 7%, respectively, perhaps not enough to account for the excess (7–28%, Table 1) of mean sum chain lengths over mean chain span.

An unexpected, striking difference between Tuesday Lake and Ythan Estuary was that in Tuesday Lake, mean chain spans covered 90–91% of the respective community spans, whereas in Ythan Estuary, mean chain spans covered 60% of the community span (Table 1). Similarly, the Tuesday Lake mean sum chain lengths were within 4% of the community span, whereas in Ythan Estuary, the mean sum chain length was 77% of the community span. Several factors might contribute to these findings. First, the connectance (links/taxa^2) of Ythan Estuary was approximately half that of either Tuesday Lake web. With fewer links per pair of taxa, mean chain

span in Ythan Estuary might be expected to be relatively smaller than community span. This factor may not be the whole story because the number of noncannibalistic links per taxon of Tuesday Lake in 1986 (namely, 4.63 links per taxon) was intermediate between that of Tuesday Lake in 1984 (5.28) and that of Ythan Estuary (4.16), whereas Tuesday Lake was similar in 1984 and 1986 in the characteristics reviewed above. Another contributing factor may be the clear segregation by average body mass among the three classes of basal, intermediate and top taxa in Tuesday Lake (Fig. 1 *A* and *B*), contrasted to the much greater intermingling of these three groups with respect to body mass in Ythan Estuary (Fig. 1 *C*). It seems difficult to deduce this difference between webs from the differences at the level of single links or 2-chains. Furthermore, community span is sensitive to investigators' choices about which taxa to include in the web at the extremes of body size. Such choices may contribute to the differences involving community span between the Tuesday Lake and Ythan Estuary webs.

When likelihood methods (36) and foraging models (37, 38) for the topology of webs are extended to consider data on body mass and population density such as were analyzed here, they will offer additional modeling approaches that may help explain some of the patterns we report. One optimal foraging model (38) used data on body masses and population densities (allometrically predicted from body masses) to predict correctly 5–65% of links in 15 webs. It remains to be seen whether, in general, using measured population densities would improve the predictive ability of the optimal foraging model and whether a refinement of it can reproduce the empirical patterns we report.

Three ecological conclusions from this analysis are, first, that models that treat links as independent will not accurately represent tritrophic interactions or longer chains. This finding is consistent with the observation in a marine web (14) that strong interactions occur in both links of a 2-chain less often than expected by chance. Second, models that splice overlapping tritrophic interactions to compose chains will fail to reproduce some properties of chains. Third, webs differ in the acceleration of biomass, population productivity and population consumption along typical chains. The reasons for such differences remain to be determined. The multiple levels of structure and heterogeneity among webs observed here constrain and may guide future development of models of M,N-web structure.

Materials and Methods

Data. Webs and M,N-data of Tuesday Lake, Michigan (28) and Ythan Estuary, Scotland (from David G. Raffaelli) are in Dataset S1. In Tuesday Lake, all three fish species in 1984 were removed and replaced by a different fish species in 1985. Data from 1984 and 1986 were analyzed separately. The main connected components of the Tuesday Lake webs had 50 species in 1984 and 51 species in 1986. The Ythan Estuary web had 91 taxa: one mammal, 26 birds, 18 fish, 44 invertebrates, phytoplankton, and macroalgae. Of these, 73 were species; most remaining taxa were genera.

Methods. In bivariate distributions of y versus x where an approximate linear relationship between y and x values appeared plausible (e.g., Fig. 1 *A*–*C*), ordinary-least-squares regression was performed by using Matlab regress (results are in Table S2). The complete set of standard assumptions of linear models was not tested because independence assumptions of the models were already known to be violated. Bivariate distributions were compared visually.

The center of the distribution of angles of all links in a web was measured by the median [denoted median(A)] and by the allometric angle. Mean angle was not used because angle distributions were not symmetric. Median upper (lower) angle [i.e., median(A_{upper}), median(A_{lower})] was used as a central value for the distribution of upper (lower) angles.

For each web, A_{upper} was plotted against A_{lower} for all 2-chains. Plots were divided into quadrants in three ways: with a horizontal line at median(A) and a vertical line at median(A); with a horizontal line at the allometric angle and a vertical line at the allometric angle; and with a horizontal line at median(A_{upper}) and a vertical line at median(A_{lower}). Data points in each of the four quadrants were counted for each method of defining quadrants. When points lay directly on quadrant dividing lines, the points were omitted from quadrant counts.

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Supporting Information

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Comparisons with Cascade Model Simulations Plus *M* and *N* Distributions. We compared webs with simulated predation matrices of the cascade model (1) combined with *M* and *N* values from Tuesday Lake 1984, Tuesday Lake 1986, and Ythan Estuary (treating each web separately). The variant of the cascade model used here selects links (R, C) independently with equal probability from the set of all possible links subject to the constraint that $M_R \leq M_C$ and disallowing cannibalism. We used the cascade model instead of the niche model or other recent models of web topological structure because our purpose was to quantify how much of the structure of 2-chains and longer chains could be explained by a model that assumes independence and equiprobability of links. We are aware of the numerous empirical limitations of the cascade model. Our use of the cascade model is independent of the cascade model's successes or failures, relative to other models, in reproducing aspects of web network structure. Use of other models would not have been appropriate, because other models do not select links independently. In addition, the inequalities $M_R \leq M_I \leq M_C$ had overwhelming empirical support in our webs (Table S3), and the cascade model assumes (2) and other models do not always satisfy these constraints.

Methods. Taxa were ranked by body mass and cascade model parameters were chosen so that the number of taxa and the expected number of links in model predation matrices equaled those in the corresponding webs, ignoring cannibalistic links in the webs because the cascade model does not incorporate cannibalism. Tabulated results for cascade model simulations show means for 5000 simulations. Plots show results of a single simulation. A few taxa in Ythan Estuary had identical *M* values and identical *N* values, causing links in cascade model simulations with undefined angle, and 2-chains with undefined between-angle. These links and 2-chains were necessarily excluded from calculations of mean and other statistics.

We compared statistics for 2-chains (excluding cannibalistic links) with the cascade model with *M* and *N* distributions taken from data. Whereas the cascade model determines which pairs of taxa are possible links based only on the distribution of *M*, the statistics of 2-span, between-angle, A_{upper} and A_{lower} depend on the joint distribution of *M* and *N*. Means and standard deviations of 2-span, between-angle, A_{upper} and A_{lower} distributions were computed for each of 5,000 cascade model simulations; distributions of these statistics were compared with the same statistics from webs to test the null hypotheses of no difference between cascade model distributions and web values.

Results. The cascade model failed to describe several features in which Tuesday Lake differed from Ythan Estuary, such as mean between-angle (positive for Tuesday Lake, negative for Ythan Estuary, approximately equal to 0, on average, for simulations) or the different relation between mean chain span and mean sum chain lengths in relation to community span. These results decisively rejected the null hypothesis that distributions of 2-chains or longer chains could have come from the cascade model, which chooses links independently.

Between-angle and wiggling. Mean between-angles in cascade model simulations were on average similar to those of all triples, namely, close to 0 and slightly negative, on average, in all three webs (Table S1). The largest mean between-angle that occurred in 5,000 cascade model simulations based on Tuesday Lake 1984

M and *N* data was 14.77°; so none of these 5,000 simulations had mean between-angle greater than that of Tuesday Lake 1984 (15.93°). The largest mean between-angle in 5,000 cascade model simulations based on Tuesday Lake 1986 *M* and *N* data was 22.45°, less than the Tuesday Lake 1986 value (31.66°). The smallest mean between-angle that occurred in 5,000 simulations based on Ythan Estuary *M* and *N* data was −21.59°, greater than the Ythan Estuary value (−27.46°). Between-angle histograms for individual cascade model simulations, like those for webs and triples, showed approximately symmetric unimodal distributions.

Link lengths in 2-chains. Cascade model L_{upper} and L_{lower} distributions differed from those of Tuesday Lake and Ythan Estuary in being weighted more heavily toward short values, as observed by Reuman and Cohen (3) (Fig. S1). The cascade model unrealistically allowed short links among phytoplankton, and consumer-to-resource log body mass ratios close to 1 that were not common in nature.

In all three webs and in the cascade model simulations based on Ythan Estuary data, mean(L_{lower}) > mean(L_{upper}) (Table 1). In cascade model simulations using Tuesday Lake *M* and *N* data, mean(L_{upper}) > mean(L_{lower}) on average, contrary to data (Table S5). This result was probably caused by the small number of fish taxa that produced some simulated upper links that were longer in the cascade model than in the web: links between phytoplankton and fish were possible in the cascade model, but were not reported in Tuesday Lake.

2-span and between-angles. Mean 2-span in Tuesday Lake (each year separately) was larger than mean 2-span in 5,000 of 5,000 cascade model simulations based on the same *M* and *N* data. The same was true for Ythan Estuary for 4,986 of 5,000 simulations.

Compared with data, long 2-chains (i.e., 2-chains with large 2-span) in simulations (Fig. S3 *D–F*) had a wider range of between-angles than long 2-chains in real webs (Fig. S3 *A–C*). Because individual taxa were clustered along a line in $\log(N) - \log(M)$ space for both simulations and real webs, only short 2-chains had space for a wide range of between-angles. But the constraint on between-angles in all three webs was stricter than the constraint revealed by the simulations.

Lower and upper angles of 2-chains. Tuesday Lake 1984 mean A_{lower} was smaller than mean A_{lower} for 4,942 of 5,000 simulations. The same was true for Tuesday Lake 1986 for 5,000 of 5,000 simulations, but mean A_{lower} for Ythan Estuary was larger than mean A_{lower} in 4,745 of 5,000 simulations. A_{upper} was larger than the same statistic for 4,998 simulations for Tuesday Lake 1984 and all 5,000 simulations for Tuesday Lake 1986 but was smaller than all 5,000 simulations for Ythan Estuary.

The dependence of the link angles in 2-chains represented by the horseshoe patterns in Fig. 1 *D–F* was apparently partly a consequence of *M* and *N* distributions, because both the cascade model and the set of all triples reproduced A_{upper} versus A_{lower} horseshoe patterns similar to those observed in webs (Fig. S2).

Longer chains. In all three webs (Table 1) and for all cascade model simulations (Table S5), the product of mean count chain length times mean link length always exceeded community span. Mean chain spans were shorter, on average, in cascade model simulations based on Tuesday Lake *M* and *N* data than they were in Tuesday Lake, but longer in cascade model simulations based on Ythan Estuary data than they were in Ythan Estuary. Community spans were necessarily the same in webs and corresponding cascade model simulations, so chains in average cascade model simulations spanned a smaller percentage of the community

span than real chains for Tuesday Lake, but a larger percentage for Ythan Estuary.

Mean sum chain lengths in cascade model simulations based on Tuesday Lake M and N data were, on average, shorter than or similar to mean sum chain lengths in Tuesday Lake, but were longer, on average, in cascade model simulations based on Ythan Estuary data than they were in Ythan Estuary (Table S5). Wiggling in each web was less than the mean wiggling in cascade model simulations (1.07 for the web versus 1.26 for cascade model simulations of Tuesday Lake 1984; 1.13 versus 1.35 for Tuesday Lake 1986; and 1.28 versus 1.41 for Ythan Estuary). Mean count chain lengths were uniformly longer, on average, in cascade model simulations than in corresponding webs.

Grouping of Taxa in Food Webs. In Tuesday Lake, the phytoplankton, zooplankton and fish taxa approximately corresponded to trophic levels along a single energy channel. We could find no equivalent classification for Ythan Estuary, despite considerable efforts. One reason may be the greater taxonomic variety in Ythan Estuary. Tuesday Lake had only aquatic organisms, whereas Ythan Estuary included macroalgae, microbes, invertebrates (such as shrimp and crab), birds, and otters. The broader taxonomic range and terrestrial taxa of high body mass could also have caused the concavity (biomass deceleration) of the Ythan Estuary web (Fig. 3B) if most taxa with a high average body mass were terrestrial animals (e.g., mammals, birds) and if organisms on land were less abundant than organisms of similar body mass in freshwater, as Cyr, Peters, and Downing (4) found.

Methods, Classifications of Taxa, Links, and 2-Chains. To analyze patterns observed in some distributions, Tuesday Lake taxa were classified as phytoplankton (p), zooplankton (z), and fish (f). Links then inherited the classification (resource, consumer) = (p,z), (p,f), (z,z), (z,f), (f,f), although (p,f) was never observed in Tuesday Lake. The set of 2-chains also inherited a classification into the subsets (resource, intermediate, consumer) = (p,z,f), (z,f,f), (z,z,f), (z,z,z), (p,z,z). These classifications were called the PZF classifications. Fish were often top predators, zooplankton were often intermediate, and phytoplankton were always basal.

In Ythan Estuary, we classified taxa as basal (b), intermediate (i) and top (t). We called this grouping the BIT grouping. As for the PZF grouping, the BIT taxon-level grouping implied groupings of links and 2-chains.

Means and standard deviations of link angles, link lengths, log body mass ratios of links, and log population density ratios of links were computed for each link group in each classification, and for all links. The same group statistics were computed for cascade model simulations. For the BIT grouping, the same grouping was used for all simulations, even though a taxon classified as B, I, or T (respectively) may not have been,

respectively, basal, intermediate, or top in a particular simulation.

Results. *Classification of taxa and links.* For Tuesday Lake using the PZF grouping, links between two taxa in the same group were qualitatively different from links between taxa in two different groups. The mean angle of (p,z) links and (z,f) links was more negative than the mean angle of (z,z) links. The standard deviation of link angles was much smaller for (p,z) links and (z,f) links than for (z,z) links. Body mass ratio was smaller for (z,z) links than for (p,z) links and (z,f) links; log population density ratio was close to zero for (z,z) links but was clearly negative and of about the same absolute value as log body mass ratio for (p,z) links and (z,f) links (Table S4 a, c).

These results were reproduced by average cascade model simulations based on M and N data from Tuesday Lake 1984 and 1986 (Table S4 b, d). We present no statistics for (f,f) links because few (f,f) links occurred. Analogous group distinctions for angle, log body mass ratio and log population density ratio statistics were not visible in Ythan Estuary using the BIT grouping because the groups B, I, and T were not separated in $(\log(M), \log(N))$ space as the groups P, Z and F were (Table S4 e, f).

The 2-span versus between-angle. In Tuesday Lake, 2-chains in different groups were qualitatively different. Plots of 2-chains on axes of 2-span versus between-angle showed five groups for 1984 data and four groups for 1986 data (Fig. S3). These groups can be understood as follows. Two-chains in the (p,z,f) group had the biggest 2-span, and had between-angle varying little from 0 (these 2-chains were forced to be approximately straight). These 2-chains appeared at the top of Fig. S3 A and B. Two-chains from the (z,z,z) groups had the shortest 2-span, with between-angles spread over a wide range from $-180°$ to $180°$. These 2-chains appeared at the bottom of Fig. S3 A and B. When a 2-chain stretched across most of Tuesday Lake's $\log(M)$-$\log(N)$ range, it had both a large 2-span and a small-magnitude between-angle. Two-chains with all three taxa within the same group (zooplankton) were necessarily shorter, and were not forced to be straight. Two-chains from the groups (z,f,f), (z,z,f) and (p,z,z) all had intermediate 2-spans, because they spanned two of the three groups in Tuesday Lake. These 2-chains exhibited different trends in between-angle: (z,z,f) 2-chains typically had negative between-angles, (p,z,z) typically had positive between-angles, and (z,f,f) had intermediate between-angles. These patterns were a consequence of the on-average approximately horizontal links occurring among zooplankton on $\log(N)$-versus-$\log(M)$ coordinates.

In Ythan Estuary with the BIT grouping as well as in the cascade model simulations, 2-chain groups in plots of 2-span versus between-angle were much less distinct (Fig. S3 C–F).

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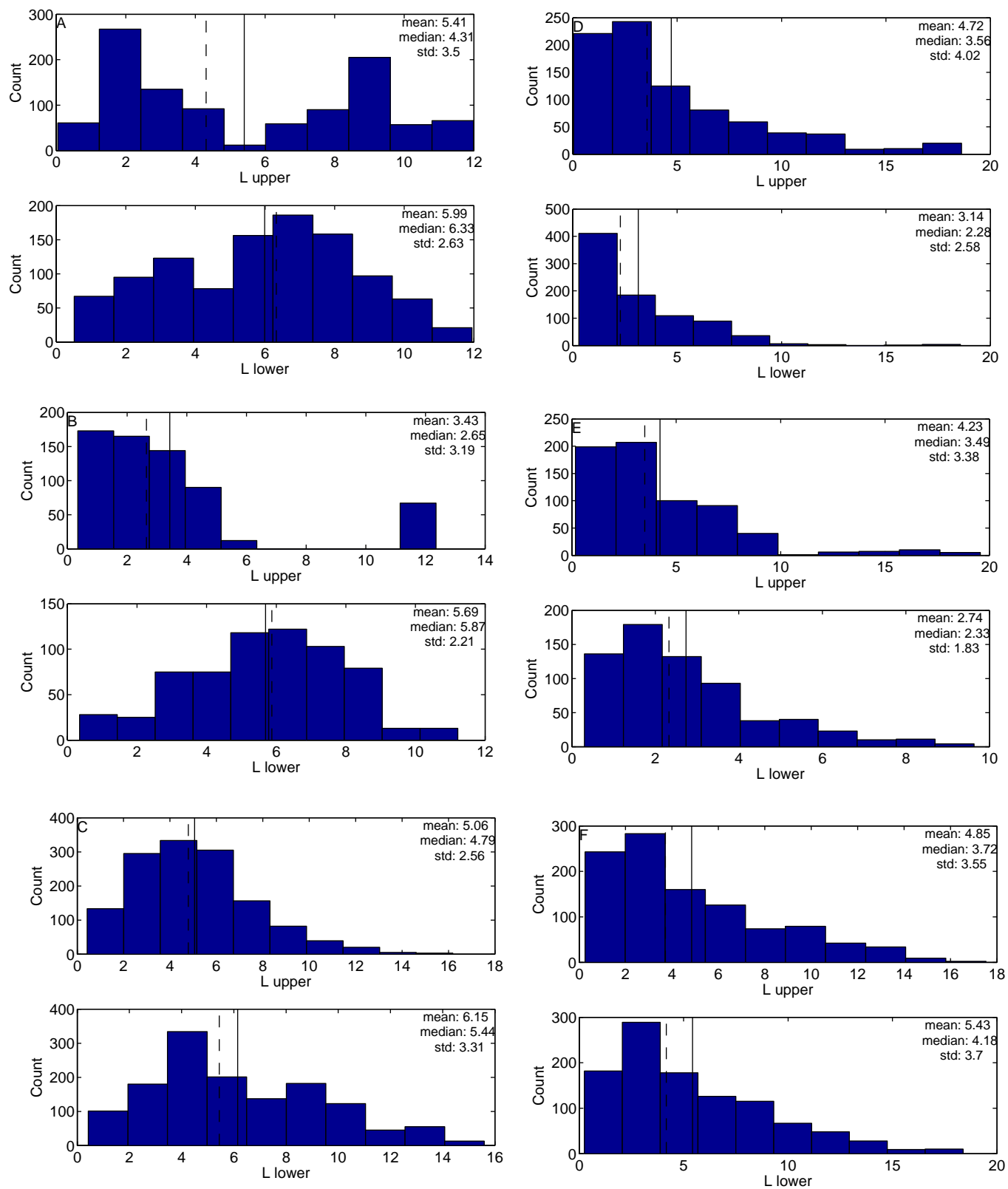
Fig. S1. (*A–C*) Frequency distributions of length of upper link L_{upper} and length of lower link L_{lower} in Tuesday Lake 1984 (*A*); Tuesday Lake 1986 (*B*); Ythan Estuary (*C*). (*D–F*) A cascade model simulation based on *M* and *N* data from Tuesday Lake 1984 (*D*); Tuesday Lake 1986 (*E*); and Ythan Estuary (*F*).
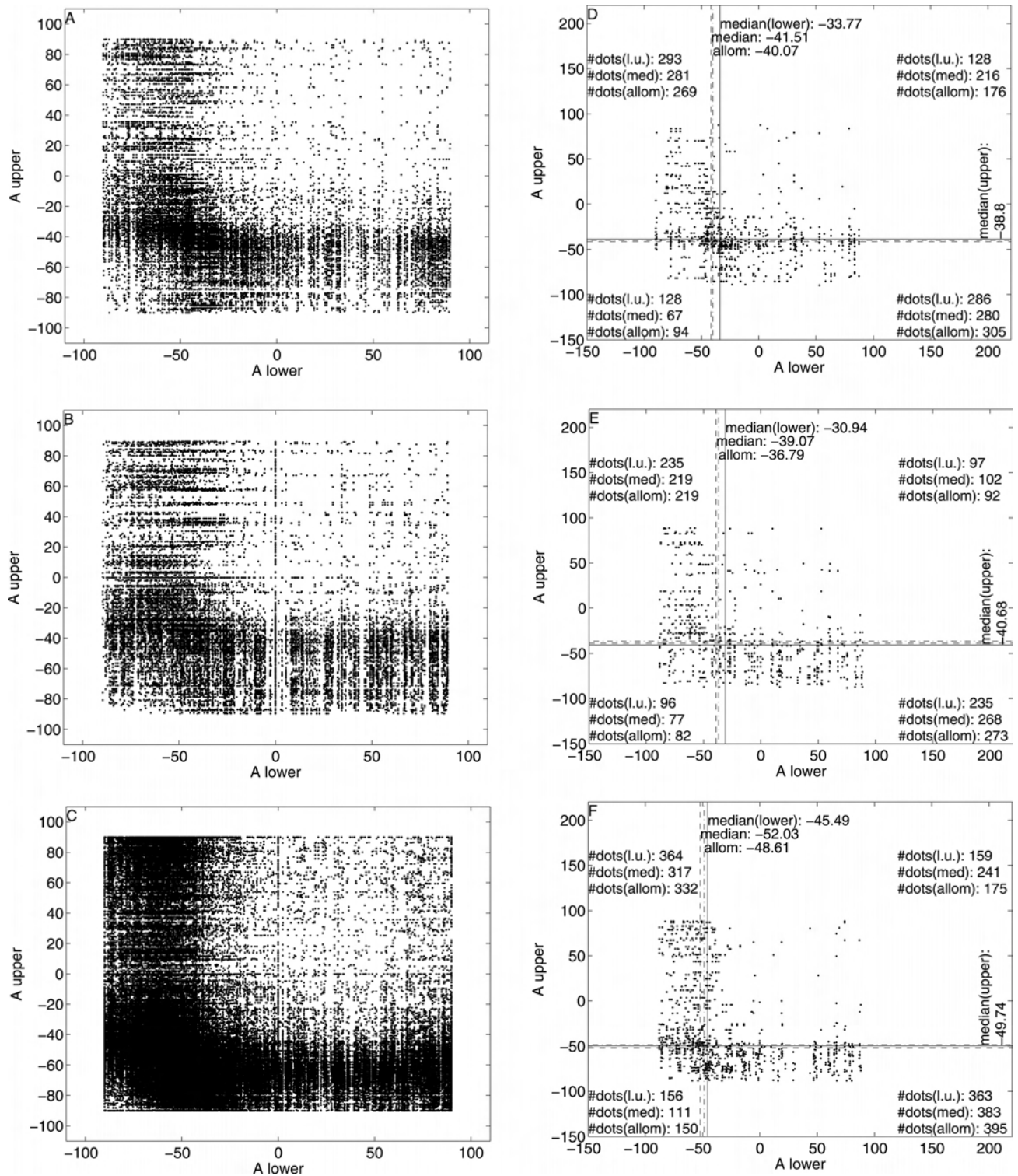
Fig. S2. Plots of the angle of the upper link, A_{upper}, vs. the angle of the lower link, A_{lower}, for all possible triples (*A–C*) and for cascade models simulations (*D–F*) using *M* and *N* data of Tuesday Lake 1984 (*A* and *D*), Tuesday Lake 1986 (*B* and *E*), and Ythan Estuary (*C* and *F*). Results showed the horseshoe pattern seen in webs (Fig. 1 *D–F*). The vertical and horizontal lines (*D–F*) represent the median lower and upper angles for all 2-chains (solid line), median angle of all links (dashed line), and allometric angle (dash-dotted line). Counts of data points in each quadrant refer to quadrants formed by medians of upper and lower angle [#dots(l.u.)], median angle of all links [#dots(med)], and allometric angle [#dots(allom)].
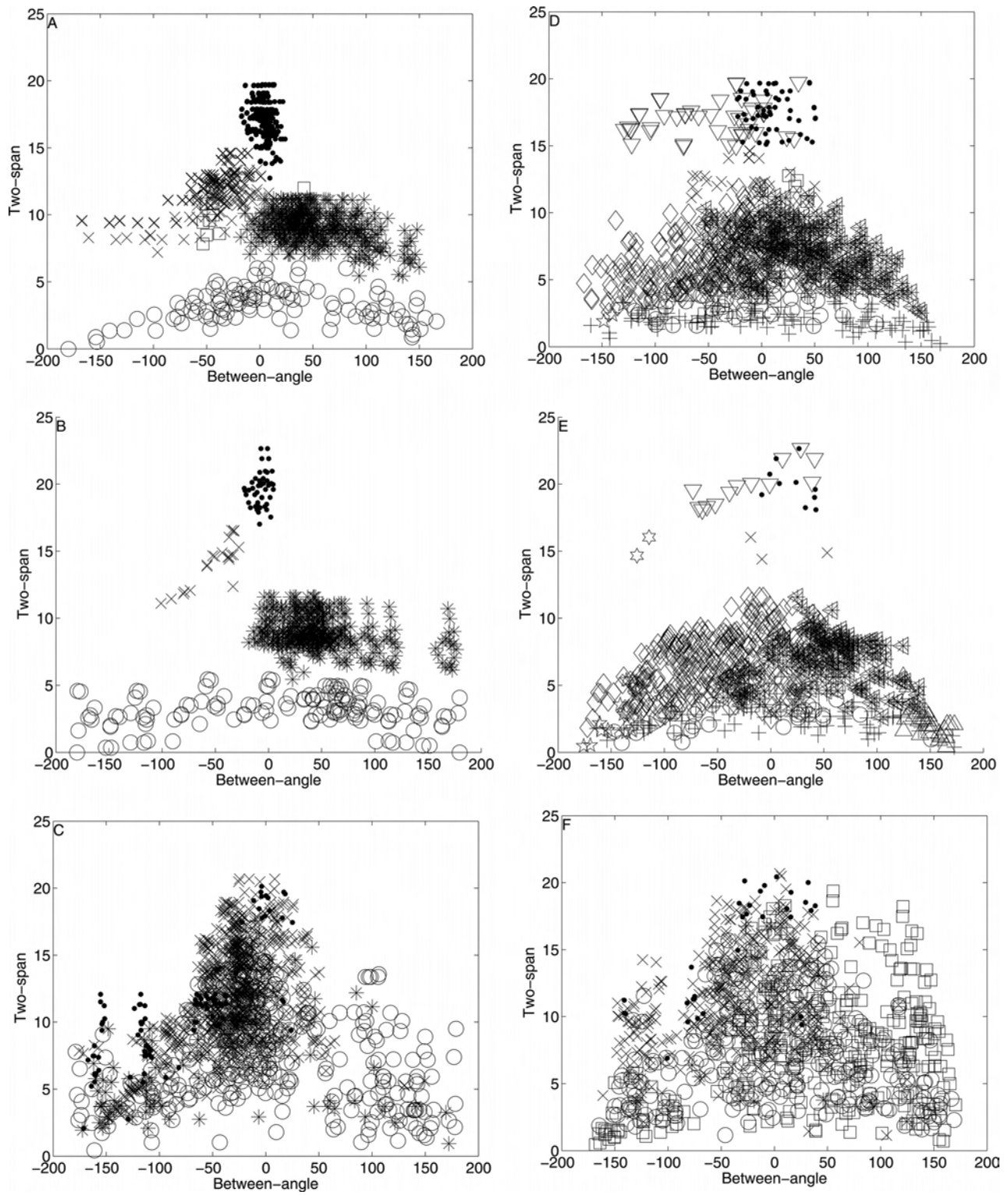
Fig. S3. (*A–C*) 2-span vs. between-angle for Tuesday Lake 1984 (*A*); Tuesday Lake 1986 (*B*); and Ythan Estuary (*C*). (*D–F*) Cascade model simulations based on Tuesday Lake 1984 *M* and *N* data (*D*); Tuesday Lake 1986 *M* and *N* data (*E*); and Ythan Estuary *M* and *N* data (*F*). Markers denote different groups of 2-chains. In *A* and *B*, they are □, (z,f,f); ●, (p,z,f); ×, (z,z,f); ○, (z,z,z); ∗, (p,z,z). In *D* and *E*, they are additionally +, (p,p,p); ◇, (p,p,z); ▽, (p,p,f); △, (p,z,p); ◁, (p,z,z); ▷, (z,p,p); open pentagram, (z,p,z); open hexagram, (z,p,f). In *C*, markers are ●, (b,i,t); ×, (i,i,t); ○, (i,i,i); ∗, (b,i,i). In *F* they are additionally □, which represents 12 categories not occurring in real food webs. Groups clustered for Tuesday Lake data (*A* and *B*), but did not cluster clearly for the corresponding cascade model simulations.

Table S1. Mean and SD of statistics of taxa and 2-chains in data and two null models and number (n) in each category

	Tuesday Lake 1984			Tuesday Lake 1986			Ythan Estuary		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
$\log_{10}(M)$									
Basal	−11.81	0.93	25	−11.84	0.84	29	−2.79	2.29	3
Intermediate	−8.56	2.13	24	−9.03	1.36	20	−1.26	2.18	58
Top	−2.89	0	1	−4.27	5.05	2	2.40	0.89	30
$\log_{10}(N)$									
Basal	7.44	0.73	25	6.89	0.72	29	8.53	3.81	3
Intermediate	4.02	1.53	24	3.85	0.67	20	7.38	2.42	58
Top	−0.88	0	1	1.05	3.64	2	2.06	1.10	30
2-span									
2-chains	11.02	4.42	1,044	8.65	4.22	651	10.51	4.20	1,371
Triples	7.44	4.67	19,648	6.36	4.04	20,825	9.57	4.58	123,182
Cascade	7.45	4.65	908.45	6.37	4.02	710.71	9.62	4.56	1,040.51
Between-angle									
2-chains	15.83	52.09	1,044	31.66	61.81	651	−27.46	61.15	1,371
Triples	−2.94	69.83	19,648	−4.01	75.06	20,825	−2.32	76.98	123,182
Cascade	−3.01	69.40	908.45	−4.02	74.72	710.71	−2.43	76.38	1,040.51
A_{upper}									
2-chains	−17.30	37.92	1,044	−2.10	51.97	651	−54.31	43.93	1,371
Triples	−28.45	40.03	19,648	−24.90	43.32	20,825	−32.90	48.51	123,182
Cascade	−28.57	39.74	908.45	−24.92	43.12	710.71	−33.00	48.07	1,040.51
A_{lower}									
2-chains	−33.47	28.22	1,044	−38.19	28.58	651	−25.27	44.65	1,371
Triples	−25.52	45.93	19,648	−20.89	49.03	20,825	−30.65	47.15	123,182
Cascade	−25.56	45.58	908.45	−20.90	48.76	710.71	−30.60	46.61	1,040.51

M, average body mass; N, population density. Units for Tuesday Lake: M, kg of fresh mass; N, individuals per m^3 of epilimnion. Units for Ythan Estuary: M, g of wet weight; N, individuals in whole estuary. Upper angle, A_{upper} (degrees) and lower angle A_{lower} (degrees) for web 2-chains, all triples of taxa ordered by average body mass regardless of the presence or absence of links, and cascade model simulations. Cascade model values are means over 5,000 simulations of the mean and SD over all 2-chains in each simulation, and n is the average number of simulated 2-chains per simulation.

Table S2. Regression statistics for log population density as a function of log average body mass, link angle as a function of log average body mass of the consumer in the link, and link angle as a function of log average body mass of the resource in the link

Relationship	Slope	Intercept	Lower conf int slope	Upper conf int slope	Lower conf int intercept	Upper conf int intercept	R^2	P	n
Population density (N) − mass (M)									
Fig. 1A Tuesday Lake 1984 $Y = \log(N)$, $X = \log(M)$	−0.84	−2.84	−0.94	−0.74	−3.89	−1.79	0.85	<0.0001	50
Fig. 1B Tuesday Lake 1986 $Y = \log(N)$, $X = \log(M)$	−0.75	−2.34	−0.87	−0.63	−3.62	−1.05	0.76	<0.0001	51
Fig. 1C Ythan Estuary $Y = \log(N)$, $X = \log(M)$	−1.13	5.54	−1.26	−1.01	5.21	5.87	0.78	<0.0001	91
Link angle (A_{link}) − mass of consumer (M_C)									
Tuesday Lake 1984 $Y = \log(A_{link})$, $X = \log(M_C)$	2.15	−18.13	0.68	3.63	−30.10	−6.15	0.0305	0.0044	264
Tuesday Lake 1986 $Y = \log(A_{link})$, $X = \log(M_C)$	7.56	29.02	5.28	9.85	9.90	48.14	0.1534	<0.0001	236
Ythan Estuary $Y = \log(A_{link})$, $X = \log(M_C)$	−7.21	−32.20	−9.98	−4.45	−37.85	−26.56	0.0653	<0.0001	379
Link angle (A_{link}) − mass of resource (M_R)									
Tuesday Lake 1984 $Y = \log(A_{link})$, $X = \log(M_R)$	5.61	27.47	4.17	7.05	11.15	44.79	0.1827	<0.0001	264
Tuesday Lake 1986 $Y = \log(A_{link})$, $X = \log(M_R)$	10.09	82.35	8.14	12.04	59.80	104.90	0.3073	<0.0001	236
Ythan Estuary $Y = \log(A_{link})$, $X = \log(M_R)$	−2.02	−47.40	−3.63	−0.41	−51.49	−43.32	0.0158	0.0143	379

Confidence intervals (conf int) for slope and intercept are nominally at the 95% level. All log = $\log_{10}$.

Table S3. Numbers and percentages of 2-chains and links with each possible ordering of taxa body masses

	Tuesday Lake 1984		Tuesday Lake 1986		Ythan Estuary	
	n	%	*n*	%	*n*	%
2-chains						
$M_R \leq M_I \leq M_C$	1,001	95.88	577	88.63	1,232	89.86
$M_R \leq M_C < M_I$	30	2.87	59	9.06	65	4.74
$M_I < M_R \leq M_C$	12	1.15	10	1.54	68	4.96
$M_I \leq M_C < M_R$	0	0	1	0.15	3	0.22
$M_C < M_R < M_I$	1	0.096	3	0.46	0	0
$M_C < M_I < M_R$	0	0	1	0.15	3	0.22
All 2-chains	1,044		651		1,371	
Links						
$M_R < M_C$	262	99.24	232	98.31	368	97.10
$M_R = M_C$	0	0	0	0	2	0.53
$M_R > M_C$	2	0.76	4	1.69	9	2.37
All links	264		236		379	

Cannibalistic links were ignored.

Table S4. Link statistics, observed and simulated: mean values and SDs of angles, log body mass ratios, log population density ratios, and lengths, for groups of links and all links

(a) TL 1984

	(z,f) links		(z,z) links		(p,z) links		All links	
No. of links	27		69		166		264	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angles	−42.54	5.69	−3.46	31.72	−46.73	8.98	−34.98	26.09
Log M ratios	4.82	0.72	2.16	1.08	3.58	1.12	3.31	1.36
Log N ratios	−4.46	0.91	−0.37	0.80	−3.77	0.96	−2.93	1.81
Link lengths	9.28	1.41	2.90	1.25	7.35	1.77	6.33	2.73

(b) CM TL 1984

	(z,f) links		(z,z) links		(p,z) links		All links	
No. of links	14.14		49.75		114.10		263.70	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angles	−38.86	6.04	−11.68	40.72	−49.10	13.87	−30.30	37.31
Log M ratios	6.13	1.27	1.51	1.04	2.86	1.46	2.66	2.32
Log N ratios	−4.89	0.94	−0.47	1.00	−3.08	1.03	−2.26	2.29
Link lengths	11.02	1.89	2.42	1.34	5.94	2.20	5.15	4.20

(c) TL 1986

	(z,f) links		(z,z) links		(p,z) links		All links	
No. of links	3		68		165		236	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angles	−40.58	2.62	−7.86	42.23	−43.43	10.81	−33.14	29.15
Log M ratios	6.41	0.37	2.10	1.15	3.64	1.16	3.23	1.39
Log N ratios	−5.49	0.30	−0.54	0.86	−3.35	0.86	−2.57	1.57
Link lengths	11.90	0.41	2.97	1.30	6.99	1.59	5.90	2.46

(d) CM TL 1986:

	(z,f) links		(z,z) links		(p,z) links		All links	
No. of links	3.90		38.80		110.22		235.56	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angles	−33.22	3.48	−6.33	40.03	−48.75	15.22	−26.39	40.79
Log M ratios	8.29	1.18	1.57	1.09	2.94	1.50	2.34	2.16
Log N ratios	−5.37	0.58	−0.32	0.87	−3.07	0.94	−1.82	2.04
Link lengths	13.66	1.54	2.34	1.28	6.01	2.04	4.47	3.64

(e) Ythan

	(b,t) links		(i,t) links		(i,i) links		(b,i) links		All links	
No. of links	3		146		214		16		379	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angles	−42.32	2.01	−60.56	12.65	−35.92	34.69	−9.55	58.67	−44.35	32.70
Log M ratios	5.90	0.62	2.92	1.59	3.42	1.93	2.18	1.93	3.20	1.84
Log N ratios	−5.38	0.53	−5.20	2.36	−3.22	2.37	−1.06	3.20	−3.91	2.64
Link lengths	11.28	1.08	8.12	3.67	6.84	3.51	4.84	3.32	7.29	3.64

(f) CM Ythan

	(b,t) links		(i,t) links		(i,i) links		(b,i) links		All links	
No. of links	8.39		152.28		152.94		11.38		378.96	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Angles	−49.80	6.38	−54.96	15.49	−25.52	45.58	−27.60	41.89	−35.74	41.55
Log M ratios	5.17	2.02	3.91	2.14	2.52	1.78	2.98	1.96	2.94	2.12
Log N ratios	−6.44	3.21	−5.54	2.51	−2.09	2.71	−2.80	3.25	−3.38	3.22
Link lengths	11.61	5.15	9.45	4.27	5.31	3.25	6.40	4.22	6.75	4.48

Cascade model (CM) values are means across the 5,000 means (and means of the 5,000 SDs) of 5,000 simulations, using M (average body mass) and N (population density) data from corresponding webs. (a) Tuesday Lake 1984, (b) CM for Tuesday Lake 1984, (c) Tuesday Lake 1986, (d) CM for Tuesday Lake 1986, (e) Ythan Estuary, (f) CM for Ythan Estuary. Statistics for (f,f) and (p,f) links were not included because only two (f,f) links occurred in Tuesday Lake 1984, no (f,f) links occurred in Tuesday Lake 1986, and no (p,f) links occurred. This is also why the sum of the number of links was less than the number of all links for Tuesday Lake 1984. z, zooplankton; p, phytoplankton; f, fish; b, basal taxa; i, intermediate taxa; t, top taxa.

Table S5. Statistics of cascade model simulations of links, tritrophic interactions, chains, and webs

Statistics	Cascade TL 1984	Cascade TL 1986	Cascade Ythan
Links and tritrophic interactions			
Mean link length	5.15	4.47	6.75
Mean L_{upper}	4.83	4.19	4.94
Mean L_{lower}	3.17	2.86	5.71
2 × mean link length	10.12	8.85	13.29
Mean 2-span	7.45	6.37	9.62
Mean $L_{upper} + L_{lower}$	8.00	7.05	10.65
Community span < mean(count chain length) × mean(link length)			
Mean count chain length	5.96	7.25	6.81
Mean count chain length × mean link length	30.18	32.08	45.27
Community span	20.78	22.66	21.98
Mean count chain length × mean link length/community span	1.45	1.42	2.06
Wiggling of chains			
Mean sum chain lengths	20.40	17.34	23.59
Mean chain span	16.21	12.94	16.69
Mean chain span/community span	0.78	0.57	0.76
Mean sum chain lengths/mean chain span	1.26	1.35	1.41
Mean sum chain lengths/community span	0.98	0.77	1.07
Connectance			
No. of noncannibalistic links	263.70	235.56	378.96
(No. of taxa)^2	2,500	2,601	8,281
No. of trophic links/(No. of taxa)^2	0.1055	0.0906	0.0458
No. of trophic links/taxa	5.27	4.62	4.16

Compare with Table 1. TL, Tuesday Lake. For each row, the value indicated in the first column was computed separately for each of 5,000 simulated webs. Each tabulated value is a mean of the corresponding 5,000 simulated values.

Other Supporting Information Files

Dataset S1 (XLS)