

Longer Food Chains in Pelagic Ecosystems: Trophic Energetics of Animal Body Size and Metabolic Efficiency

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ABSTRACT: Factors constraining the structure of food webs can be investigated by comparing classes of ecosystems. We find that pelagic ecosystems, those based on one-celled primary producers, have longer food chains than terrestrial ecosystems. Yet pelagic ecosystems have lower primary productivity, contrary to the hypothesis that greater energy flows permit higher trophic levels. We hypothesize that longer food chain length in pelagic ecosystems, compared with terrestrial ecosystems, is associated with smaller pelagic animal body size permitting more rapid trophic energy transfer. Assuming negative allometric dependence of biomass production rate on body mass at each trophic level, the lowest three pelagic animal trophic levels are estimated to add biomass more rapidly than their terrestrial counterparts by factors of 12, 4.8, and 2.6. Pelagic animals consequently transport primary production to a fifth trophic level 50–190 times more rapidly than animals in terrestrial webs. This difference overcomes the approximately fivefold slower pelagic basal productivity, energetically explaining longer pelagic food chains. In addition, ectotherms, dominant at lower pelagic animal trophic levels, have high metabolic efficiency, also favoring higher rates of trophic energy transfer in pelagic ecosystems. These two animal trophic flow mechanisms imply longer pelagic food chains, reestablishing an important role for energetics in food web structure.

Keywords: allometric relationships, animal body size, food chain length, one-celled primary producers, production rate, trophic efficiency.

Introduction

An important goal of ecology is to identify dominant factors regulating the structure of food webs (e.g., Cohen 1978; Pimm 1982; Ulanowicz 1997; Pascual and Dunne 2005; Rooney et al. 2007). Food chain length is a key feature of food webs that can be compared across different classes of ecosystems (May 1983; Post 2002). We hypothesize that factors limiting the number of trophic levels constrain overall food web structure. If classes of ecosystems having lon-

ger food chains can be differentiated by the environment that they inhabit or by the sizes and taxa of their organisms, this association between food chain length and size or taxa may lead to inferences about factors regulating food web structure.

Elton (1927) and Hutchinson (1959) postulated that food chain length is limited by trophic energy transfer. They hypothesized that greater flow rates of trophic energy up the food chain should support more trophic levels (see also Lindeman 1942; May 1983). Because the total food energy reaching higher trophic levels should vary monotonically with the input at the base of food webs, longer food chains were predicted for ecosystems with higher primary productivity.

Pimm and Lawton (1977) noted the lack of evidence for this hypothesis, citing a poor observed correlation of ecosystem primary production rates with food chain length. One important counterexample stood out (Pimm and Lawton 1977; May 1983; Cohen 1994): open-water ecosystems have longer food chains but lower mean primary productivity than terrestrial ecosystems. Briand and Cohen (1987) showed that, among 113 food web graphs, ecosystems inhabiting three-dimensional habitats have longer maximum food chains, on average, than those in two-dimensional habitats. Several hypotheses were proposed to explain longer food chains in oceanic, pelagic, or three-dimensional ecosystems (Schoener 1989; Whitehead and Walde 1992; Cohen 1994).

We investigated the role of energetics in pelagic versus terrestrial food webs with five analyses. (1) First, we re-analysed the food chain lengths of 113 food webs to identify the key property of ecosystems that leads to longer maximum food chains. We find longer food chains occur in ecosystems with one-celled primary producers. (2) To provide data to address one hypothesis for why one-celled producers should permit longer food chains, based on the body sizes of organisms at lower animal trophic levels, we gathered body lengths and trophic levels of species from nine pelagic food webs and nine terrestrial webs. (3) To investigate two hy-

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potheses for longer pelagic food chains, comparing the trophic transfer rates of animals in each environment, we constructed a model of food web energetics. (4) We incorporated in the model the allometric dependence of biomass production rate on organism body size. We then computed the rates of trophic energy flow across the lowest three animal trophic levels in these nine pelagic and nine terrestrial webs. Due to negative allometric dependence of production rate on body mass, the much smaller body sizes of pelagic organisms induce greater rates of biomass production at lower animal trophic levels and so provide food more rapidly to a potential fifth trophic level in pelagic ecosystems. Using the model and the data for mean body mass by trophic level, we estimated the relative rates of food production supplied to a fifth trophic level in each environment. (5) Finally, we investigated a second hypothesis for longer pelagic food chains. Pelagic animals at lower trophic levels are nearly always ectotherms, invertebrates or fish. Terrestrial herbivores and carnivores are often endotherms, mammals or birds. Incorporating information about the trophic efficiencies of these two groups of organisms, we showed that pelagic ecosystems at lower animal trophic levels transfer a much higher proportion of trophic energy from primary producers to higher trophic levels.

These five analyses strongly supported both energetic hypotheses (4) and (5) for longer pelagic food chains. By predicting longer pelagic food chains despite lower pelagic primary productivity, these mechanisms vindicate trophic energetics as an important factor in the regulation of food chain length among different classes of ecosystems.

Longer Food Chain Length in Ecosystems with One-Celled Producers

Extending Briand and Cohen (1987), we reconsidered which class of ecosystems supports the longest food chains. Among all 113 food webs of Briand and Cohen (Briand and Cohen 1987; Cohen et al. 1990), and also among the 28 webs in three-dimensional habitats, ecosystems with one-celled plant producers have the longest maximum food chains. By “pelagic” ecosystems, we here mean those based on single-celled primary producers (phytoplankton).

Among these 113 food webs, the 10 ecosystems with longest maximal chains all had single-celled (phytoplankton) primary producers (fig. 1A). Of the 28 three-dimensional webs, the 16 webs with the longest food chains also had single-celled (phytoplankton) primary producers (fig. 1B). In all, about half (56) of the 113 Briand and Cohen webs and 21 of the 28 three-dimensional webs were supported by single-celled plants.

The 10 webs with longest food chains were all aquatic: eight were from pelagic three-dimensional ecosystems (six in oceans and two in lakes). Of the 10 webs with longest

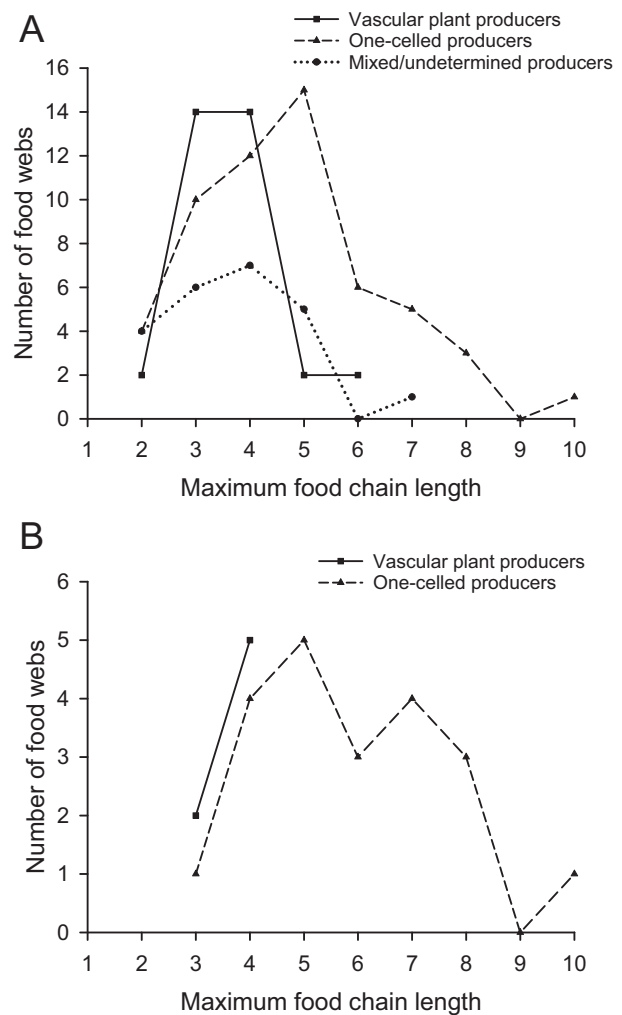


Figure 1: Food web counts versus food chain length by ecosystem type. A, Web frequency versus maximum food chain length among all 113 food webs of Briand and Cohen (1987). Mixed/undetermined producer webs were those for which the plant producer type was diverse or unclear. B, Food web counts versus maximum food chain length among the 28 webs inhabiting three-dimensional (3-D) environments. The seven 3-D ecosystems based on vascular plant producers were forests. There were no mixed/undetermined producer webs among the 3-D webs.

food chains, the two not classified as being from three-dimensional habitats (a Russian bog and a Florida swamp subweb) also had one-celled plants at their base, suggesting that producers being one celled offers a better predictor of longer food chain length.

Statistical testing strongly supported the hypothesis that webs based on one-celled primary producers have longer food chains. A Wilcoxon test for the observed rankings in maximum food chain length of the 56 one-celled producer ecosystems among all 113 webs (fig. 1A) gave $P = .001$, rejecting the null hypothesis of random ordering. Among

the 28 three-dimensional webs identified by Briand and Cohen as having longer food chains, the ecosystems with one-celled primary producers have longer food chains than forests by visual inspection (fig. 1B), and one-celled producer webs among the 28 three-dimensional webs had significantly longer maximum food chains by a Wilcoxon rank test ($P = .002$). The probability of the 10 webs with longest maximal chains having single-celled primary producers by chance alone was $< .0006$.

Mean Body Size: Pelagic versus Terrestrial

To estimate mean body mass by trophic level in pelagic and terrestrial food webs, nine matched pairs of food webs were selected from Briand and Cohen (1987). As the pelagic webs, we chose nine of the 10 webs that had the greatest maximum food chain lengths and that also had exclusively one-celled primary producers. One of these 10 webs, Lake Texoma, had both phytoplankton and benthic vascular plant primary producers and was excluded. Another of the 10 webs with longest food chains, a south Florida swamp, was divisible into two subwebs, one based on algal and the other on vascular plant primary producers; we used only the algal subweb. For each of the nine pelagic webs, a terrestrial web was chosen. We sought to match the number of trophic species as closely as possible between pelagic and paired terrestrial webs. The nine terrestrial webs included one prairie, two desert habitats, and six forests, of which two were tropical rainforests (table 1).

Adult body lengths of all trophic species in these 18 webs were taken from reported values in the literature and on the internet. The trophic level of each trophic species was determined from food web graphs, designating primary producers as trophic level 1, herbivores as trophic level 2, and so on. Six of nine pelagic and two of nine terrestrial webs explicitly indicated principal energy flow pathways in the food web graphs. Where food web diagrams indicated the relative strength of multiple trophic pathways (such as a predator consuming a range of prey species from various trophic levels; e.g., by the width of arrows), the strongest pathways were used to determine food chain length and trophic levels. Otherwise, directed trophic links were used as given. Data of \log_{10} body lengths and their assigned trophic levels for all trophic species in each of the 18 webs are presented in supplementary tables S2 and S3 (tables S1–S3 available online). These data tables also are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.ps1h0> (McGarvey et al. 2016).

Multiple trophic pathways usually connect primary producers to higher animals, and omnivory is common (Williams and Martinez 2004; Thompson et al. 2007), so the assumption that trophic levels are whole numbers (integers) is an approximation. In this study, herbivores and, to a lesser extent, primary carnivores are the principal animal trophic levels of interest, because their body sizes are most different between the two environments, and all trophic energy must pass through these lower animal trophic levels to reach the top of longer food chains. The approximation of integer-

Table 1: Body size statistics and inferred mass-specific production ratios, pelagic over terrestrial food webs, by trophic level (TL)

TL	Quartile range of trophic species lengths (cm)		Geometric mean length, L (cm)	Geometric mean body mass, (g), $M = .02L^3$	Relative biomass-specific production rate, $P/B \propto M^{-1/4}$	Relative P/B ratio by trophic level: pelagic over terrestrial, considering body size alone, $L_{pel}[TL]^{-3/4} / L_{ter}[TL]^{-3/4}$	Cumulative P/B ratio multiplied over animal trophic levels from herbivores, $TL = 2$ to the trophic level $n_{TL} = TL$ of each row, equation (9)
	25%	75%					
Pelagic:							
1	.00094	.019	.0046	1.9×10^{-9}	151	550	...
2	.15	1.5	.36	.0009	5.7	12	12
3	.28	4.8	1.5	.06	2.0	4.8	56
4	1.5	38	8.9	14	.5	2.6	143
5	37	190	82	11,000	.1	.7	100
6	62	290	143	59,000	.06
7	105	360	150	67,000	.06
Terrestrial:							
1	2.8	100	21	180	.27
2	3.3	27	9.6	18	.49
3	5.7	25	12	33	.42
4	16	62	31	580	.20
5	40	59	50	2,600	.14

Note: Body length statistics are from all trophic species across the nine food webs in each environment, by TL.

valued trophic levels is more accurate at these lower animal trophic levels, notably for herbivores (Thompson et al. 2007). Moreover, measuring trophic level according to rates of energy flow along different trophic pathways gives more distinct trophic levels and less smearing by omnivory than does inferring prey-averaged trophic levels from web graph position alone (Williams and Martinez 2004). Using adult body lengths of each trophic species ignores the full distribution of body lengths, including larvae and early juveniles, which typically feed on smaller prey at lower trophic levels than mature adults.

In estimating differences in trophic flow rates between the two environments due to differences in animal body size, we used the geometric mean adult body length by trophic level, aggregated across all nine webs in each environment.

We plotted the distributions of trophic species' \log_{10} body lengths as kernel density functions, with one size-frequency distribution for each trophic level (fig. 2). Pelagic trophic levels were roughly differentiated and ordered by body size (fig. 2A). Pelagic producers ranged in body length from 1 μm

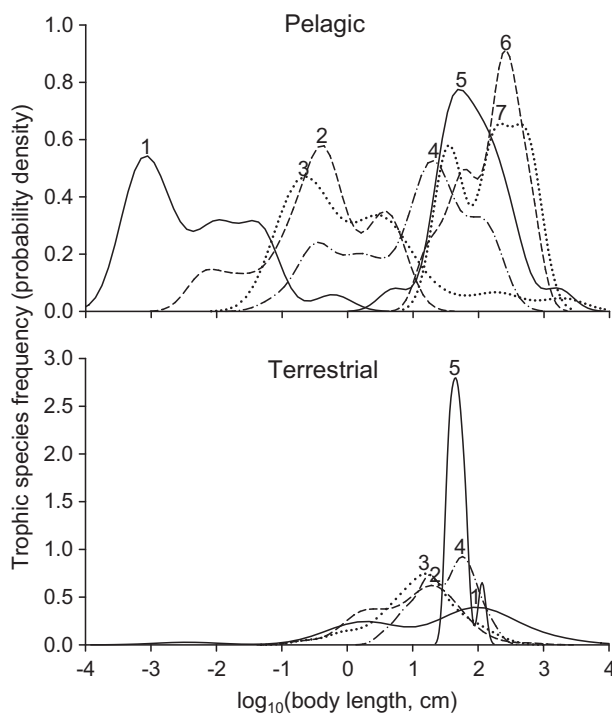


Figure 2: Probability density functions of trophic species versus adult body length, by trophic level, in nine pelagic and nine terrestrial food webs. These size-frequency distributions, which include all trophic species at each trophic level, were generated as kernel density functions of \log_{10} body lengths, using S+ function *density*. A number label indicating the trophic level is positioned above each length distribution mode. Primary producers are shown as trophic level 1, herbivores as trophic level 2, primary carnivores as trophic level 3, and so on.

to about 1 cm (trophic level 1 in fig. 2A), with a geometric mean length of about 50 μm (fig. 3; table 1). Terrestrial plants ranged in size from 1 mm to 10–100 m.

Consuming one-celled primary producers, pelagic herbivores were smaller than their terrestrial counterparts (trophic level 2 in fig. 2A, compared with fig. 2B). In terms of mean \log_{10} length, the difference was more than an order of magnitude (fig. 3). Pelagic primary and secondary carnivores were also smaller than their terrestrial counterparts (trophic levels 3 and 4 in fig. 2; fig. 3).

Though species lengths at each trophic level covered two to three orders of magnitude (fig. 2), mean \log_{10} body lengths were well separated between the two environments at low trophic levels, with statistical differences strengthened by narrow standard errors (fig. 3; table 1). Pelagic herbivores were about 4 mm in length, 26 times smaller in geometric mean body length than terrestrial herbivores (table 1). Primary carnivores and secondary carnivores were estimated to be eight times (1.5 vs. 12 cm) and 3.5 times (9 vs. 31 cm) shorter, respectively.

Using the reported adult body lengths of trophic species (fig. 2), assuming body mass was proportional to the cube of body length, we estimated geometric mean body mass from the mean of \log_{10} body lengths by trophic level in pelagic and terrestrial food webs (fig. 3). Within geometric means, body lengths were weighted equally (not by abundance or relative trophic flow rate). The geometric mean body masses of herbivores, primary carnivores, and secondary carnivores were estimated to be, on average, 20,000, 500, and 40 times less in pelagic than terrestrial ecosystems (table 1).

To verify that our pelagic body masses are consistent with those directly measured in other pelagic ecosystems, we compared our pelagic body mass ranges (table 1) for the first three trophic levels (TL = 1, 2, and 3) with the size-frequency peaks reviewed by Boudreau and Dickie (1992). The 25th and 75th mass percentiles among our nine pelagic webs (lengths for TL = 1 are shown in fig. 2) are 1.6×10^{-11} to 1.4×10^{-7} g. These values agree closely with the range of phytoplankton body masses from about 10^{-11} to 10^{-7} g in Boudreau and Dickie (1992; their fig. 1). For TL = 2, our interquartile range of 7×10^{-5} to 6×10^{-2} g is consistent with body masses of pelagic grazers of approximately 10^{-5} to 10^{-2} g reported by Boudreau and Dickie (1992; second peak, their fig. 1; copepods, their fig. 2). For TL = 3, a similar overlap in body sizes is observed if our body mass range includes quantiles of 10% to 90%.

Trophic Energetic Model

Here we describe a trophic energetic model to estimate biomass production rate by secondary carnivores (TL = 4) as functions of energetic processes at TLs of 4 and lower.

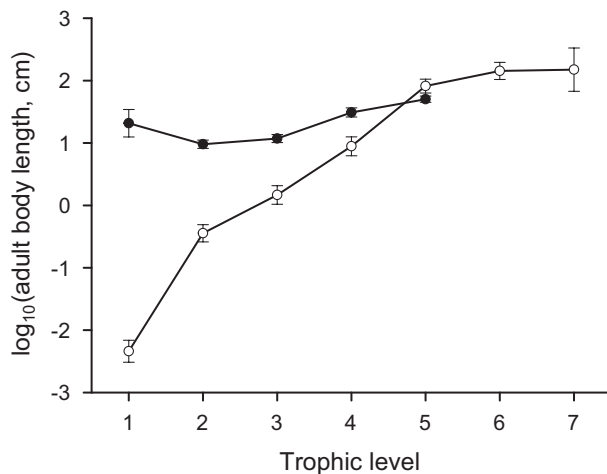


Figure 3: Mean \log_{10} body length versus trophic level in pelagic (open circles) and terrestrial (solid circles) environments. Means by trophic level were taken of all species in the nine pelagic and nine terrestrial webs, respectively. Error bars represent ± 1 standard error of the mean. Raising 10 to the power of the vertical coordinate of the plotted points gives the geometric mean adult body lengths (cm) used in calculations of mass-specific biomass production rates (P/B ; table 1).

Assumptions for Trophic Energetics

Two relationships relevant to trophic energetics are assumed: (1) negative allometric dependence (with $-1/4$ exponent) of production rate on body mass, and (2) dependence of trophic efficiency on metabolic class. To estimate total production rate (P) of biomass (B) by trophic level (TL) as a function of mean animal body size, we assumed that the biomass-specific production rate P/B was proportional to the $-1/4$ power of body mass M (i.e., $P/B \propto M^{-1/4}$) for both pelagic and terrestrial animals. Evidence that the production rate depends allometrically on body mass with exponent $-1/4$ is reviewed by Peters (1983; see chap. 8), Brown et al. (2004), Fenchel (1974), Ernest et al. (2003), and others. Boudreau and Dickie (1989) estimated an allometric dependence of biomass production rate on body mass with a -0.23 exponent, close to $-1/4$, for the entire community of pelagic organisms in an ecosystem. Huryn and Benke (2007) experimentally retested $-1/4$ allometric body size dependence of invertebrate production rate in freshwater streams and found close agreement.

Humphreys (1979) did not find that body mass predicted well the proportion of assimilated food that is allocated to new biomass production (see also McNeil and Lawton 1970; Peters 1983, pp. 142–146). Order-of-magnitude differences in trophic efficiency were evident, however, between broadly different animal taxa when they were classified by metabolic class. Endotherms, for example, are far

less trophically efficient than invertebrates, because they burn a greater share of their assimilated food energy for maintenance.

That production (growth) and respired energy, feeding rate, and metabolism all depend on body mass with the same (approximately $-1/4$ allometric) relationship is consistent with data across a wide range of species (Peters 1983; Brown et al. 2004). This implies that the relative proportions of assimilated energy allocated to production and metabolism are approximately constant with respect to body mass (Nisbet et al. 2000) but can vary between taxa.

In addition to assumptions (1) and (2) above, the trophic energetics model assumes (3) an average rate of primary productivity P_1 ; (4) Boltzmann-Arrhenius temperature dependence; and (5) biomass production rate of predators (at each trophic level) varying in proportion to the biomass production rate of their prey (TL $- 1$), both given in grams of biomass produced \times time $^{-1} \times$ area $^{-1}$.

Modeling Biomass Production Rate by Secondary Carnivores

A model was constructed to compare biomass production rates of pelagic and terrestrial food webs due to differences in animal body size and metabolic category (taxon) while accounting for other factors affecting rates of trophic flow up the food chain. We modeled the biomass production rate of an idealized fourth trophic level in each environment. Secondary carnivores (TL = 4) are the highest trophic level commonly found in terrestrial food webs, whereas a fifth and often higher trophic levels are common in pelagic webs. Each trophic level was aggregated to a single energetic compartment.

The net rate of biomass production by TL = 4 (above what is required for a steady population at TL = 4, including reproduction) equals the rate of prey food supply to a potential tertiary carnivore trophic level (TL = 5). We derive the biomass production rate at TL = 4 as a function of the primary productivity and body size of animals at lower animal trophic levels, TL = 2 through TL = 4. The allometric function of production rate versus body mass used the geometric mean body masses at each trophic level in both environments (table 1). The dependence of production rate by TL on temperature and trophic efficiency was also incorporated. The former was included for use when temperature data are available. Additional details are presented in appendix A (apps. A, B available online).

The total production of biomass can be written as the product of the biomass-specific production (P/B , in units of biomass per unit area per unit time per gram of existing biomass) and the total standing biomass (B , grams per unit area) at each TL:

$$P_{\text{total}}[\text{TL}] = \left(\frac{P}{B}[\text{TL}] \right) \times B[\text{TL}]. \quad (1)$$

Production P and biomass B in $(P/B)[\text{TL}]$ are population totals at trophic level TL.

We assume that production per unit of biomass depends on $M[\text{TL}]$, the geometric mean body mass of animals at trophic level TL, and temperature T (Gillooly et al. 2001; Ernest et al. 2003; Brown et al. 2004, 2007) according to the following:

$$\frac{P}{B}[\text{TL}] = \pi'[\text{TL}] \times \exp\left(\frac{-E}{kT[\text{TL}]}\right) \times M[\text{TL}]^{-1/4}. \quad (2a)$$

The quantities k , E , and T are defined by Brown et al. (2004). The factor $\pi'[\text{TL}]$ accounts for the dependence on variables other than body mass and temperature.

Equation (2a) applies both to an average individual and to the population at each trophic level, because if $N[\text{TL}]$ is the number of individuals per unit area at trophic level TL, then $P_{\text{ind}}[\text{TL}]/M_{\text{ind}}[\text{TL}]$ for individuals applies to all animals at trophic level TL:

$$\frac{P_{\text{ind}}[\text{TL}]}{M_{\text{ind}}[\text{TL}]} = \frac{P_{\text{ind}}[\text{TL}] \times N[\text{TL}]}{M_{\text{ind}}[\text{TL}] \times N[\text{TL}]} = \frac{P}{B}[\text{TL}].$$

A theory relating individual to population levels of production is given by Savage et al. (2004).

The production rate by animals at trophic level TL depends on their food supply rate, namely (ignoring omnivory) the biomass production rate of their prey, $P_{\text{total}}[\text{TL} - 1]$. Taking the dependence to be linear, we expand the factor $\pi'[\text{TL}]$ to include prey biomass production, $\pi'[\text{TL}] = \pi[\text{TL}] \times P_{\text{total}}[\text{TL} - 1]$, giving

$$\left(\frac{P}{B}[\text{TL}] \right) = \pi[\text{TL}] \times P_{\text{total}}[\text{TL} - 1] \times \exp\left(\frac{-E}{kT[\text{TL}]}\right) \times M[\text{TL}]^{-1/4}. \quad (2b)$$

Equation (2b) substituted into equation (1) provides a model of the total biomass production rate $P_{\text{total}}[\text{TL}]$ at trophic level TL as a function of (i) the production rate of prey; (ii) the biomass at trophic level TL; (iii) the temperature $T[\text{TL}]$ of the animals at TL; (iv) the mean body mass $M[\text{TL}]$ of the animals at TL; and (v) a remaining coefficient, $\pi[\text{TL}]$, which includes trophic efficiency of animals at TL:

$$P_{\text{total}}[\text{TL}] = \pi[\text{TL}] \times P_{\text{total}}[\text{TL} - 1] \times \exp\left(\frac{-E}{k \times T[\text{TL}]}\right) \times M[\text{TL}]^{-1/4} \times B[\text{TL}]. \quad (3)$$

Assuming an average primary productivity (grams plant biomass produced per unit time per unit area) of

$P_{\text{total}}[\text{TL} = 1] = P_1$ and applying equation (3), we model the production by herbivores as

$$P_{\text{total}}[\text{TL} = 2] = \pi[\text{TL} = 2] \times P_1 \times \exp\left(\frac{-E}{k \times T[\text{TL} = 2]}\right) \times M[\text{TL} = 2]^{-1/4} \times B[\text{TL} = 2]. \quad (4)$$

Iterating this procedure to the next trophic level, where we substitute the production rate of herbivores for P_1 , the biomass production rate of primary carnivores becomes

$$P_{\text{total}}[\text{TL} = 3] = \pi[\text{TL} = 3] \times \left\{ \pi[\text{TL} = 2] \times P_1 \times \exp\left(\frac{-E}{k \times T[\text{TL} = 2]}\right) \times M[\text{TL} = 2]^{-1/4} \times B[\text{TL} = 2] \right\} \times \exp\left(\frac{-E}{k \times T[\text{TL} = 3]}\right) \times M[\text{TL} = 3]^{-1/4} \times B[\text{TL} = 3]. \quad (5)$$

In the same manner, the production rate at TL = 4 becomes

$$P_{\text{total}}[\text{TL} = 4] = P_1 \times \left\{ \prod_{\text{TL}=2}^4 \exp\left(\frac{-E}{k \times T[\text{TL}]}\right) \right\} \times \left\{ \prod_{\text{TL}=2}^4 \pi[\text{TL}] \right\} \times \left\{ \prod_{\text{TL}=2}^4 M[\text{TL}]^{-1/4} \right\} \times \left\{ \prod_{\text{TL}=2}^4 B[\text{TL}] \right\}. \quad (6)$$

This model of the biomass production rate by secondary carnivores extends previous models to embrace multiple trophic levels. It demonstrates that energetic rates influence production at each of several successive trophic levels multiplicatively. Gillooly et al. (2006, p. 215, below their eq. [7]) also derived a multiplicative relationship. DeBruyn et al. (2007) compared energy transfer over different possible pathways using a model of four trophic species with similar energetic assumptions.

The biomass production rate of secondary carnivores depends on the body masses of animals at the three lowest animal trophic levels according to

$$P_{\text{total}}[\text{TL} = 4] \propto \prod_{\text{TL}=2}^4 M[\text{TL}]^{-1/4}. \quad (7)$$

Assuming body mass varies in proportion to the cube of length ($M = a_{MvL}L^3$), equation (7) can be written in terms of mean adult body length as follows:

$$P_{\text{total}}[\text{TL} = 4] \propto \prod_{\text{TL}=2}^4 L[\text{TL}]^{-3/4}. \quad (8)$$

We assume this relationship applies to both pelagic and terrestrial food webs. The ratio of production rate by secondary carnivores in pelagic (pel) versus terrestrial (ter) environments is

$$A_{\text{BS,pel/ter}}[\text{TL} = 4] = \frac{P_{\text{total,pel}}[\text{TL} = 4]}{P_{\text{total,ter}}[\text{TL} = 4]} \propto \frac{\prod_{\text{TL}=2}^4 L_{\text{pel}}[\text{TL}]^{-3/4}}{\prod_{\text{TL}=2}^4 L_{\text{ter}}[\text{TL}]^{-3/4}}, \quad (9)$$

where the subscript BS indicates that this ratio recognizes only differences in body size.

Relative Production Rates of Secondary Carnivores: Animal Body Size

We use the above model to estimate the impact of body size on the biomass production rates of pelagic relative to terrestrial secondary carnivores. Employing equation (8) and substituting geometric mean body lengths by trophic level, we estimate that pelagic herbivores produce new biomass approximately 12 times faster than terrestrial herbivores (table 1; as a proportion of standing herbivore biomass). Pelagic primary and secondary carnivores, being closer in size to their terrestrial counterparts, had estimated P/B rates 4.8 and 2.6 times greater than terrestrial primary and secondary carnivores (table 1).

At each animal trophic level, if all of the net biomass production is consumed by predators at the next trophic level, then higher rates of biomass production at these three animal trophic levels generate a multiplicatively higher overall rate of trophic energy transfer to trophic level 5 in pelagic, compared with terrestrial, food webs. Considering only differences in geometric mean body mass and substituting these into equation (9), trophic energy is transferred upward across the lowest three animal trophic levels at a rate 143 times faster in the nine pelagic webs than in the nine terrestrial webs (table 1).

Estimating mean body mass by trophic level is critical to estimating the biomass production rate by a pelagic fourth trophic level. To assess the sensitivity of this estimate to which method is used to compute the central tendency of body size by trophic level, and also to the assumed allometric exponent of production rate versus body mass, we repeated this computation using three alternative methods.

First, we computed geometric mean body lengths by trophic level by a two-level mean. At the first level, we took the geometric mean by trophic level within each web individually. At a second level, we took a geometric mean across

webs to estimate overall mean body length by trophic level in each environment. This procedure gives an estimate that pelagic secondary carnivores produce biomass at a rate 53 times the terrestrial rate.

In a second method, we used the medians of species mean adult body lengths by trophic level in place of geometric means, yielding a pelagic production rate at $\text{TL} = 4$ that was 189 times the terrestrial rate. Thus, values of 143, 53, and 189 imply a trophic transfer rate over the lowest three animal trophic levels approximately two orders of magnitude (50–190 times) faster for pelagic, compared with terrestrial, food webs.

Third, we assumed an allometric P/M exponent of $-1/3$ (Banse and Mosher 1980) rather than $-1/4$, implying a body mass-specific production rate that decreases more rapidly with increasing body mass. This change yielded an estimate that the pelagic $\text{TL} = 4$ production rate was 750 times the terrestrial rate.

Assuming the allometric exponent is $-1/4$, the three estimates of 143, 53, and 189 indicate that pelagic secondary carnivores produce biomass two orders of magnitude faster than terrestrial secondary carnivores. This difference results from the smaller size of pelagic animals at lower trophic levels, supporting longer food chains in pelagic webs, all else being equal.

Relative Production Rates of Secondary Carnivores: Animal Trophic Efficiency

We here consider a second hypothesis that may contribute to longer food chains in pelagic than terrestrial ecosystems: pelagic animals at lower trophic levels have higher trophic efficiency. Metabolic (biomass production) efficiency translates into trophic efficiency; a higher proportion of the food consumed by organisms converted to biomass at one trophic level provides more food for their predators. In appendix B, we summarize two other previously proposed hypotheses.

Humphreys (1979; his table 7) estimated that birds and mammals allocate 1.29%–3.14% of their assimilated food to producing new biomass, whereas noninsect invertebrate herbivores and carnivores allocate 20.8% and 27.2% of what they assimilate to new biomass production. Fish allocate approximately 10% of their assimilated food to production (Humphreys 1979). Endotherms generally consume more food biomass per unit time but burn much more for thermal regulation and to support a more energetically expensive nervous system (Lawton 1981; Schmidt-Nielsen 1997).

The ecological implications for biomass production by trophic level of differences in trophic efficiency TE are clear from equation (6). Let us approximate the percentages of assimilated food allocated to producing new biomass by endotherms (birds and mammals), fish, and noninsect invertebrate herbivores and carnivores as 2.5%, 10%, and

25%, respectively. Although insects and other small invertebrates play important roles in terrestrial ecosystems, for this comparison let us consider terrestrial food webs in which mammals and birds dominate as herbivores and carnivores.

We coarsely estimate the order-of-magnitude impact of higher invertebrate trophic efficiencies in pelagic ecosystems using equation (6), writing the ratio of production rate by pelagic over terrestrial tertiary carnivores, analogous to equation (9), as

$$A_{TE,pel/ter}[TL = 4] = \frac{P_{total,pel}[TL = 4]}{P_{total,ter}[TL = 4]} = \frac{\prod_{TL=2}^4 \pi_{pel}[TL]}{\prod_{TL=2}^4 \pi_{ter}[TL]} \quad (10)$$

Equation (10) shows that the accumulated factors of trophic efficiency multiply across trophic levels. To assess whether the second hypothesis of higher pelagic trophic efficiency holds, let us assume, for computational simplicity, that pelagic herbivores are all invertebrates (zooplankton), half the primary carnivores are invertebrates (e.g., krill and calamari) and half are fish, and all pelagic secondary carnivores are fish. For terrestrial systems, we restrict attention to subwebs for which herbivores, primary carnivores, and secondary carnivores are all birds or mammals. For these two idealized food webs, we gauge the difference in expected production at $TL = 4$ from these two environments, assuming these different metabolic classes occur at lower animal trophic levels in each:

$$\begin{aligned} A_{TE,pel/ter}[TL = 4] &= \frac{\prod_{TL=2}^4 \pi_{pel}[TL]}{\prod_{TL=2}^4 \pi_{ter}[TL]} \\ &= \frac{0.25 \times [(0.25 + 0.1)/2] \times 0.1}{0.025 \times 0.025 \times 0.025} \\ &= \frac{0.004}{0.000016} = 280. \end{aligned}$$

Alternatively, when pelagic primary and secondary carnivores are all assumed to be fish,

$$A_{TE,pel/ter}[TL = 4] = 156.$$

Thus, the potential influence of differing metabolic category on trophic efficiencies at lower animal trophic levels gives an advantage in trophic energy transfer rate of approximately two orders of magnitude for pelagic ecosystems. An effect of approximately two orders of magnitude was also inferred from differences in mean body size in the two environments. Ectothermic metabolism and smaller body size in pelagic animals both imply much higher rates of biomass production by pelagic secondary carnivores for food supply to tertiary carnivores at a potential fifth trophic level.

Discussion

The five objectives of this work were (1) to identify ecosystem factors controlling food chain length, (2) to quantify the implications for food web energetics of body size differences between animals at different trophic levels in different ecosystem types in light of allometric body mass dependence of biomass production, (3) to account for the food web energetic implications of variations in metabolic efficiency, (4) to explain longer pelagic food chains in light of (2) and (3), and (5) to demonstrate that the comparison of pelagic and terrestrial ecosystems supports energetics as a significant influence on the length of food chains. Support for (2) and (3) was strong: pelagic trophic flows across the lowest three animal trophic levels were estimated to be two orders of magnitude greater in pelagic food webs. By these mechanisms, the energetic properties of organisms influence the structure of food webs. We elaborate on these outcomes in two subsections below. Other energetic mechanisms potentially acting in pelagic environments are summarized in appendix B.

The theory of pelagic size spectra, initially developed to explain the observations by Sheldon et al. (1972, 1977) that biomass density in the open oceans is nearly constant with increasing body mass, began with models of Kerr (1974) and Sheldon et al. (1977). Yodzis and Innes (1992; also Williams et al. 2007) developed a model of trophic energy dynamics that also incorporates higher food assimilation proportions by carnivores than herbivores. Jennings and Mackinson (2003), Brown et al. (2004), and Gillooly et al. (2006) applied allometric body size dependence and trophic efficiency in models of trophic energy flow. Aquatic and terrestrial ecosystems were compared by Lindeman (1942), Cohen (1994), and Shurin et al. (2006). This study extends these lines of ecological thought to compare trophic flow rates in pelagic and terrestrial ecosystems.

Body Size and Trophic Energy Flow Rates

Eating much smaller plants, pelagic herbivores are approximately four orders of magnitude less massive than terrestrial herbivores (table 1). Allometric scaling of P/M with exponent $-1/4$ implies a rate of biomass production by pelagic herbivores that is approximately one order of magnitude faster than that by terrestrial herbivores. A second order of magnitude difference was estimated for the two lowest levels of carnivores combined. These estimates are robust because (1) the size differences between animals at lower trophic levels are very large (orders of magnitude in body mass) and (2) negative allometric dependence of mass-specific production rate on organism body mass has been empirically confirmed across a wide range of taxa and environments (Fenchel 1974; Peters 1983; Boudreau and Dickie 1989; Brown et al. 2004; Hury and Benke 2007).

These estimates suggest that trophic energetic processes at animal trophic levels can more than compensate for lower pelagic primary productivity. The average primary productivity per unit area of oceans is approximately one-fifth that estimated for terrestrial habitats (Cohen 1994; Polis 1999; app. A), yet pelagic food chains are longer. This counterexample (Cohen 1994) and others (Pimm and Lawton 1977) had earlier cast doubt on energetics being important in determining food chain length. Our estimate that the biomass production rate by secondary carnivores is 50 to 190 times more rapid in pelagic than in terrestrial ecosystems due to smaller pelagic animal body size provides one mechanism by which pelagic food chains can be longer. More than compensating for the lower primary productivity in pelagic ecosystems, it suggests energetic flow rates constrain the number of trophic levels in terrestrial compared with pelagic ecosystems.

As with pelagic ecosystems, by comparison with other environments, Ryther (1969) observed that, among different subclasses of marine pelagic ecosystems, primary productivity was a poor predictor of food chain length. Upwellings, the coastal shelf, and the open ocean have higher to lower average primary productivity but shorter to longer food chains, respectively. And as we found for pelagic versus other environments, longer food chains are associated with smaller primary producers: the longer food chains found in the open oceans are supported by cyanobacteria and small phytoplankton, whereas large phytoplankton (large diatoms) in ocean upwellings support the shortest maximum food chains among these three pelagic ecosystems (Ryther 1969).

Two Hypotheses Supported

We found support for two hypotheses favoring greater biomass production by two orders of magnitude of a potential fourth trophic level in pelagic compared with terrestrial environments: differences at lower trophic levels in mean animal body mass and metabolic class of dominant taxa. Either mechanism is more than sufficient to countervail against the roughly fivefold lower pelagic primary productivity of pelagic ecosystems. Greater biomass production by pelagic secondary carnivores supplies more food to potential tertiary carnivores in pelagic habitats than in terrestrial, permitting them to support a fifth trophic level in ecosystems with one-celled primary producers.

Other Energetic Processes Affecting Pelagic versus Terrestrial Ecosystems

Other consequential differences in the energetics of animals in pelagic and terrestrial environments follow from how heat and light are absorbed and used by life. These

differences include the thermodynamics of water and differing energetics of movement through water compared with air (discussed in app. B). On average, with similar solar energy flux received by pelagic and terrestrial environments at similar latitudes, the effect of temperature differences of a few degrees, as quantified in the Boltzmann-Arrhenius formula, should be small by comparison to the order of magnitude differences observed for body size and trophic efficiency.

We have not considered differences between pelagic and terrestrial food webs in the coefficients of allometric dependence of production rate on body mass. Unlike the allometric exponent, which is consistently about $-1/4$ among a wide range of taxa and body sizes, allometric coefficients vary by taxon (Fenchel 1974; Peters 1983).

Differences in population biomass density at lower animal trophic levels, $B[TL]$, were also ignored. These differences could also be modeled using equation (6) or by more dynamic models (Yodzis and Innes 1992; McCann et al. 1998; Gillooly et al. 2006). However, the standing stock biomass of animals at successive trophic levels is likely to depend strongly on production rate or trophic efficiency, or both, at that and lower trophic levels. This factor of biomass density is not, therefore, independent of the other two.

Conclusion

The use of allometric scaling of production rate versus body size to analyze trophic energetics is an application of the metabolic theory of ecology (Brown et al. 2004). The dependence of production, and thus trophic, efficiency on taxon extends that theory. Here we applied these relationships to explain differing trends of food chain length in different classes of ecosystems. Because allometric body size dependence and trophic efficiency relationships apply across phyla, body sizes, and metabolic types, and even for both animals and plants (Enquist et al. 1998), these energetic relationships can be employed confidently in models of whole food webs (e.g., Kerr 1974; Sheldon et al. 1977; Yodzis and Innes 1992; Brown et al. 2004).

The constraints on trophic energy flow that these energetic relationships impose on food web structure improve the realism of ecosystem models. These relationships enabled us to demonstrate the importance of production rate as a function of body size and of trophic efficiency as a function of metabolic class in influencing the number of energetically viable trophic levels in pelagic and terrestrial food webs. In doing so, we showed that the apparent counterexample of pelagic ecosystems does not refute the hypothesis that food chain length is influenced by food web energetics. On the contrary, the trophic energetics of pelagic food webs at lower animal trophic levels play an important role, by

two mechanisms, in explaining the significantly longer food chains observed in pelagic ecosystems.

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Appendix A from R. McGarvey et al., “Longer Food Chains in Pelagic Ecosystems: Trophic Energetics of Animal Body Size and Metabolic Efficiency”

(Am. Nat., vol. 188, no. 1, p. 76)

Supplementary Methods

Primary Productivity of Terrestrial Compared with Pelagic Environments

In the text, we stated that primary productivity was roughly five times higher in terrestrial than in pelagic environments. This ratio was derived from Cohen’s (1994; his table 1) estimates of net primary production per unit area: 69×10^3 kg carbon $\text{km}^{-2} \text{year}^{-1}$ in oceans and 330×10^3 kg carbon $\text{km}^{-2} \text{year}^{-1}$ on continents. Cohen’s reported estimates (by others) for total terrestrial production of 48–50 Gt C year^{-1} were consistent with a value reported by Foley (1994), who estimates total terrestrial production at 62 Gt C year^{-1} . Polis (1999) reported the same ratio of one-fifth smaller mean productivity for pelagic compared with terrestrial environments.

Converting Body Lengths to Body Mass

To convert the body lengths by trophic species (supplementary tables S2, S3) to body mass (table 1), we assumed a cubic relationship, setting $b_{wvL} = 3$ in $M = a_{wvL} \times L^{b_{wvL}}$. An analysis of 3,929 weight-length relationships among 1,773 fish species (Froese 2006) showed that a mean value for b_{wvL} of 3.03 was statistically supported, but for individual species it ranged from 2.5 to 3.5.

For simplicity, we chose a single plausible value for the weight-length coefficient a_{wvL} . Examining studies of estimated weight-length relationships among species for copepods (Cohen and Lough 1981), freshwater zooplankton (Watkins et al. 2011), and fish (Willing and Pender 1989; Froese 2006), values from about 0.006 to 0.045 were common (in body size units of grams and centimeters). Peters (1983, appendix IIa) found a similar range for these coefficients among diverse taxa. We chose a typical value of $a_{wvL} = 0.02$ for converting geometric mean body length to geometric mean body mass. If one assumes that biomass has a specific mass density equal to that of water, then the values of around 0.02 imply that a living organism typically occupies about 2% of the volume of a cube surrounding it, a cube with length of side equal to the measured body length.

Associativity of Geometric Mean and Allometric Relationships

At each trophic level in the two environments, the (1) geometric mean of body length was computed, and this geometric mean body length was in turn operated on by allometric relationships (2) of body mass to body length, and (3) of P/B to body mass, to estimate P/B (eq. [3]). However, the same result would be obtained if P/B was computed for each trophic species, and geometric means taken of the P/B values at each trophic level. Here we suggest the robustness of the calculations of geometric mean P/B by trophic level is enhanced by the associativity of the geometric mean with the two allometric relationships. The associativity of these three mathematical operations implies that the estimated P/B for each trophic level does not depend on which stage of the computation geometric averaging is done.

We demonstrate this associativity property in the remainder of this section. Mathematical notation is as follows, with the i subscript designating individual trophic species at a given trophic level: (1) the formula for the geometric mean is $\text{geom mean}(\{X_i, i = 1, n\}) = [\prod_{i=1}^n X_i]^{1/n}$, where the input, $\{X_i, i = 1, n\}$, is any vector of n positive length values; (2) the mass-length relationship is $M_i = a_{MvL} \times L_i^3$; and (3) the allometric relationship of P/B versus body mass M is $P/B_i = a_{P/BvM} \times M_i^{-1/4}$.

Substituting for M_i and L_i using the two allometric relationships, we obtain

$$\begin{aligned}
 \text{geom mean}(P/B) &= \left[\prod_{i=1}^n (P/B)_i \right]^{\frac{1}{n}} = \left[\prod_{i=1}^n a_{P/BvM} \times M_i^{-1/4} \right]^{\frac{1}{n}} \\
 &= \left[\prod_{i=1}^n a_{P/BvM} \times (a_{MvL} \times L_i^3)^{-1/4} \right]^{\frac{1}{n}} \\
 &= \left[\{a_{P/BvM} \times (a_{MvL})^{-1/4}\}^n \prod_{i=1}^n (L_i^3)^{-1/4} \right]^{\frac{1}{n}} = a_{P/BvM} \times (a_{MvL})^{-1/4} \left\{ \left[\prod_{i=1}^n L_i \right]^{\frac{1}{n}} \right\}^{-3/4} \\
 &= a_{P/BvM} \times (a_{MvL})^{-1/4} \{\text{geom mean}(L)\}^{-3/4} \\
 &= a_{P/BvM} \times \{a_{MvL} \times (\text{geom mean}(L))^3\}^{-1/4}.
 \end{aligned}$$

Thus, geometric means across species can be taken among sample animal lengths, or among individual computed P/B values, making no difference to the estimated outcome for average P/B at each trophic level.

This associativity applies also to computing geometric mean body mass from a sample of mean body lengths. That is, the same outcome for mean body mass will be obtained for either (1) computing the geometric mean length, and then using that inside the allometric weight-versus-length relationship, or (2) computing a mean weight using the weight-versus-length relationship for each sampled length individually, and then taking their geometric mean of individual weights to estimate the mean weight.

Appendix B from R. McGarvey et al., “Longer Food Chains in Pelagic Ecosystems: Trophic Energetics of Animal Body Size and Metabolic Efficiency”

(Am. Nat., vol. 188, no. 1, p. 76)

Supplementary Discussion

Here we discuss the implications for the production rate body mass hypothesis of three factors: (1) terrestrial food web graphs sometimes omit smaller animals and insects; (2) pelagic food web graphs often omit microbial trophic species; (3) additional differences between terrestrial and pelagic ecosystems may influence trophic energetics. We consider two additional hypotheses for longer pelagic food chains: (4) Schoener’s productive space hypothesis and (5) a size-versus-trophic-level design constraint hypothesis. Finally, (6) we discuss the implications of extending to plant producers the method of comparing P/B in pelagic and terrestrial environments that we applied to trophically lower animals.

Smaller Trophic Species Are Often Omitted from Food Web Graphs

Insects and small detritivores, such as amphipods, are sometimes omitted from published terrestrial food webs (although insects were listed as a trophic species in all nine terrestrial graphs analyzed in this study, and most of these included multiple insect trophic species). The effect of these additional trophic levels is consistent with the small body mass hypothesis for longer food chains, because additional small trophic species in terrestrial food webs imply longer food chains specifically due to the presence of smaller-sized animals in additional trophic levels low on the food chain. Being smaller, they produce biomass for their predators at a more rapid rate, as a multiple of their own body mass. A similar lengthening of food chains at low trophic levels would apply if microbial producers, detritivores, herbivores, and carnivores (protozoa) in the soils were reported in terrestrial food webs. Some of these larger microbial organisms are consumed by arthropods and larvae, further lengthening terrestrial food chains.

Pelagic food webs sometimes also underreport smaller organisms at low trophic positions. The importance of small plankton (Barber 2007), microbial producers, and microbial consumers, sometimes eventually consumed by zooplankton, is increasingly identified in technologically improved field sampling. Microbial organisms also conform to an approximate $-1/4$ -exponent population growth dependence on body mass (Fenchel 1974). Given that their body size is much smaller even than that of grazers of phytoplankton, microbial herbivores grazing on bacteria in pelagic food webs produce new biomass as a multiple of their own body mass at a still faster rate than zooplankton.

Additional Influences on Food Chain Length and Trophic Energetics in Pelagic and Terrestrial Environments

Pelagic food chains are influenced by other differences from terrestrial ecosystems besides animal body size and trophic efficiency. We here note several additional differences between the two environments in animal food web energetics.

Energetic Differences Follow from Animals Living in Different Physical Environments

Physical and biological differences between aquatic and terrestrial environments, which follow in part from the existence of pelagic organisms in a viscous, massive, high-heat-capacity fluid medium, could significantly influence trophic energetics. These include physical differences affecting predator-prey interaction rates: (1) the shorter mean distance to prey in a pelagic three-dimensional environment (Whitehead and Walde 1992), notably when pelagic predators are swimming within a school of prey; (2) the greater ability of terrestrial prey to conceal their presence; and (3) pelagic predators engulfing one or more whole prey organisms at a time. Additional differences affecting organism energy expenditure include (4) swimming versus land propulsion, (5) neutral buoyancy for pelagic organisms, (6) negative buoyancy for dead organisms (and their associated nutrients), and (7) the high specific heat of water.

Schoener's Productive Space Hypothesis

Other hypotheses for longer pelagic food chains can coexist with the body mass production rate and trophic efficiency hypotheses examined in the main text. For example, longer food chains in oceanic ecosystems are consistent with the “productive space” hypothesis of Schoener (1989; Post et al. 2000), wherein total ecosystem production (productivity times habitat area) is a better predictor of food chain length than productivity alone. Longer food chains in open ocean marine ecosystems are predicted by this hypothesis from their much larger habitat area. However, the long chains observed in bog and swamp webs among the 10 Briand and Cohen webs with longest maximum chains are inconsistent with the productive space hypothesis, but being based on one-celled primary producers, they remain consistent with the body size production rate hypothesis.

Related Design Constraint Hypothesis: Smaller Pelagic Plants and Larger Pelagic Top Predators Permit More Trophic Levels between Bottom and Top Trophic Levels in Size-Ordered Food Webs

Unlike animals lower on the food chain, the body lengths of top predators were larger in the nine pelagic webs (fig. 3) than in the matching terrestrial webs. Pelagic environments thus exhibit both larger top predators and much smaller primary producers than terrestrial food webs (figs. 2, 3). We estimated a factor of body size difference between pelagic top predators and phytoplankton primary producers of 4–5 orders of magnitude in geometric mean body length, or 13–14 orders of magnitude in geometric mean body mass (table 1; ratio of body length for pelagic predators over pelagic primary producers: $150 \text{ cm}/0.0046 \text{ cm} = 3.3 \times 10^4$). In terrestrial ecosystems, producers were of similar body size to the animals (table 1). This implies that, between primary producer and top predator, the body size difference is orders of magnitude wider in pelagic food webs.

This observation points to a design constraint hypothesis when predators tend to be larger than their prey. If each trophic link involves a factor of increase in body size, then the much larger difference in body size between top predators and primary producers in pelagic food webs permits more trophic links overall. In particular, much smaller pelagic producers permit additional lower trophic levels of more productive smaller pelagic animals. Our observations of pelagic size ordering (figs. 2, 3) and wide producer-to-top-predator body size ratios (fig. 3; table 1) are consistent with, but do not establish, this design constraint hypothesis, showing there is room in the body size spectrum for additional pelagic trophic levels. Related inferences of smaller predator-prey body mass ratios permitting more trophic levels were proposed by Elton (1927, p. 61) and Barnes et al. (2010).

However, predators are not always larger than their prey in either environment. Insects are often smaller than the plants they eat. Parasites (pelagic and terrestrial) are smaller than their hosts.

P/B Implications for Pelagic versus Terrestrial Plants, Given Their Observed Body Sizes

Primary producers differ in body size between pelagic and terrestrial environments far more than do herbivores. The geometric mean body mass of one-celled pelagic plants was 11 orders of magnitude smaller than that of vascular plants from terrestrial environments (table 1). Enquist et al. (1998) showed evidence that plants, like animals, conform to the $-1/4$ allometric scaling of production as a function of body size. One-celled pelagic producers being approximately 10^{11} times lighter than vascular plants (figs. 2, 3; table 1), under a $-1/4$ scaling, implies a roughly 550-fold advantage in production per gram of standing stock plant biomass (table 1). This very large factor of advantage for pelagic primary production implies that pelagic plants take up nutrients and produce new biomass, as a proportion of existing plant biomass, about two to three orders of magnitude more rapidly than typical-size terrestrial plants, based on the mean lengths we found for primary producers in the two environments.

Our analysis in the main text considered animal, but not plant, energetics in comparing pelagic and terrestrial food chains, taking as given the primary productivity estimates in each environment. Across trophic levels $TL = 2$ through $TL = 4$ combined, we derived a production rate advantage factor for pelagic animals of 140. Multiplying the 550 production advantage factor for pelagic plants by the factor of 140 for herbivores to secondary carnivores would imply an overall advantage in production rate per unit mass of 77,000, four to five orders of magnitude faster biomass production, and thus faster transfer rate from nutrients and sunlight to a potential fifth trophic level.

The allometric dependence of production rate on body mass is based on the same principle by which algae are a generally more productive plant for biofuel production than crops. The much smaller size of one-celled phytoplankton means that, as a proportion of algal biomass present, phytoplankton produce more new biomass per unit time.

Supplementary Tables: Data on trophic levels and body lengths of trophic species in 9 pelagic and 9 terrestrial food webs

Table S1. Summary of the 9 pelagic and 9 matching terrestrial food webs taken from Briand and Cohen (1987). We excluded some ‘species’, particularly detritus and carcasses (consistent with Briand and Cohen according to their numbers of trophic species), larvae and parts of animals or plants (e.g. ‘Salpae’). Where a trophic species was cited as a broad category, e.g. ‘Large insects’, we designated a size range of these organisms, and counted it as a single trophic species.

Reference	Briand & Cohen web number	Briand & Cohen ref number	Number trophic species	Name	Briand & Cohen maximum chain length	Our maximum chain length
Pelagic						
Smirnov (1961)	58	56	17	Sphagnum bog, Russia	7	7
Mackintosh (1964)	30	36	14	Antarctic Seas	7	7
Patten and Finn (1979)	21	30	9	Ross Sea	7	6
Vinogradov and Shushkina (1978)	42	44	15	Upwelling areas, Pacific Ocean	8	4
Hogetsu (1979)	86	82	16	Suruga Bay, epipelagic zone, Japan	6	6
Harris and Bowman (1980)	47	49	27	Swamps, south Florida Terrestrial & pelagic components	5	6
Parin (1970)	41	43	18	Tropical seas, epipelagic zone	8	7
Petipa (1979)	103	98	23	Tropical plankton community, Pacific.	10	4
Sorokin (1972)	71	68	16	Lake Rybinsk, Russia	7	6

Table S1 (continued)

Reference	Briand & Cohen web number	Briand & Cohen ref number	Number trophic species	Name	Briand & Cohen maximum chain length	Our maximum chain length
Terrestrial						
Holm and Scholtz (1980)	98	94	17	Sand dunes, Namib desert, Namibia	5	5
Bird (1930)	24	32	12	Willow forest, Manitoba	4	4
Harrison (1962)	40	42	11	Rainforest, Malaysia	3	3
Bird (1930)	23	32	15	Prairie, Manitoba	4	4
Varley (1970)	27	33	22	Wythan Wood, England	4	4
Twomey (1945)	59	57	29	Trelease Woods, Illinois	4	4
Sharma (1980)	100	96	22	Rajasthan Desert, India	6	5
Bird (1930)	25	32	24	Aspen Communities, Manitoba	4	4
Waide and Reagan (1996)	N/A	N/A	20	Tropical Rainforest, El Verde	N/A	5

Table S2. Average adult body lengths of trophic species in pelagic food webs.

Table S2.1 Sphagnum bog, Russia		
Briand and Cohen (1987) Web No. 58		
Briand and Cohen (1987) Ref No. 56		
B&C mean chain length 4.28		
B&C maximum chain length 7		
Trophic level	Average length (cm)	Species
1		Sphagnum
1	0.00075	Algae
1	0.6	Utricularia
2	0.4	Psectrocladius
2	0.45	Chironomous
2	0.1625	Corynoneura larvae
2	0.525	Cladocera
3	0.5	Ablabesmyia larvae
3	2	Chaoborus larvae
3	2	Odonta larvae
3	2.6	Hemiptera
3	3.85	Coleoptera
3	6	Nematocera imagines
4	1.3	Ants
5	5.1	Spiders
6	15.65	Frogs
6	51.5	Lizards
6	30	Birds
7	35	Birds of prey

Table S2.2 Antarctic seas

Briand and Cohen (1987) Web No. 30

Briand and Cohen (1987) Ref No. 36

B&C mean chain length 5.02

B&C maximum chain length 7

Trophic level	Average length (cm)	Species
1	0.0502	Phytoplankton
2	5	Euphausia superba (krill)
2	0.55	Other herbivorous plankton
3	1.1	Carnivorous plankton
5	64	Birds
4	123	Fish
4	126.75	Squid
3	250	Crabeater seal
5	360	Leopard seal
5	365	Elephant seal
3	1800	Baleen whales
6	545	Smaller toothed whales
5	1650	Sperm whale
7	175	Homo sapiens

Table S2.3 Ross Sea

Briand and Cohen (1987) Web No. 21

Briand and Cohen (1987) Ref No. 30

B&C mean chain length 4.61

B&C maximum chain length 7

Trophic level	Average length (cm)	Species
1	0.0502	Aufwachs
2	7.5	Polychaetes
2	0.35	Copepods
2	1	Amphipods
1	0.0502	Diatoms
2	0.35	Copepods
2	3	Chaetognaths
2	4.5	Euphausids
3	45	Pleurogamma antarcticum
4	127.25	Squid
4	110	Emperor penguin
4	71	Adelie penguin
3	250	Crabeater seal
5	200	Weddell seal
5	200	Ross seal
6	360	Leopard seal
3	2150	Baleen whales
6	675	Toothed whales

Table S2.4 Upwelling areas, Pacific Ocean

Briand and Cohen (1987) Web No. 42

Briand and Cohen (1987) Ref No. 44

B&C mean chain length 4.95

B&C maximum chain length 8

Trophic level	Average length (cm)	Species
1	0.00055	Nanoplankton
1	0.0014	Small phytoplankton
1	0.00605	Medium phytoplankton
1	0.01	Large phytoplankton
2	0.0055	Ciliates
3	0.1	Medium size calanoids
3	1	Juvenile euphausids
3	0.18	Meroplankton
3	0.13	Appendicularians
3	0.13	Doliolids
3	0.1	Small calanoids
4	0.085	Cyclopoids
4	0.25	Calanoids
4	0.3	Small tomopterids
4	0.5	Small colelenterates
4	2	Chaetognaths
4	0.3	Polychaetes
4	20	Anchovy

Table S2.5 Suruga Bay, epipelagic zone, Japan

Briand and Cohen (1987) Web No. 86

Briand and Cohen (1987) Ref No. 82

B&C mean chain length 4.09

B&C maximum chain length 6

Trophic level	Average length (cm)	Species
1	0.0103	Microflagellates
1	0.015	Coscinodiscus
1	0.002	Chaetoceros
1	0.0007	Skeletonema
1	0.00195	Costatum
2	3	Euphausia similis
2	3	Euphausia pacifica
2	0.275	Calanus pacifica
2	0.0975	Palacalanus parrus
3	4.8	Sergia lucens
3	2.5	Engraulis japonica (post-larvae)
3	5	Sagitta nage
3	2.5	Parathemisto gracilis
4	15	Diaphus coeruleus
4	15	Diaphus elucens
4	15	Other myctophids (lanternfishes)
4	9.15	Trachurus japonica (adult)
4	7	Engraulis japonica (adult)
4	9.2	Scomber japonicus (adult)
5	26.75	Todarodes pacificus
5	143.5	Stenella species
6	175	Homo sapiens

Table S2.6 Swamps, south Florida. Terrestrial & pelagic components

Briand and Cohen (1987) Web No. 47

Briand and Cohen (1987) Ref No. 49

B&C mean chain length 4.22

B&C maximum chain length 5

Trophic level	Average length (cm)		Species
	Pelagic subweb	Vascular plant subweb	
1	0.011		Phytoplankton
1		105	Vascular plants
2	0.5		Copepods
2	0.16		Cladocerans
2	1.1		Amphipods
2		91.25	Waterfowl
2		39.5	Marsh rabbits
2		143.25	Deer
2		20	Water rat
3	3.5		Plecopterans
3	5.1		Odonates
3	2.6		Hemipterans
3	10		Crayfish
3	11.25		Cyprinodontids
3	3.8		Mosquitofish
4	3.85		Coleopterans
4	1.4		Dipterans
4	2.6		Hemipterans
4	27.3		Centrarchids
4	140		Snakes
4	16		Turtles
5	90		Bowfin
5	210		Gar
5	100		Pickerel
5	33.3		Hérons
5	25.5		Ibises
5	35.25		Egrets
5	48.25		Raccoons
5	44		Opossums
6	285		Alligators
6	62		Raptors
3		70	Bobcats

Table S2.7 Tropical seas, epipelagic zone

Briand and Cohen (1987) Web No. 41
 Briand and Cohen (1987) Ref No. 43
 B&C mean chain length 5.92
 B&C maximum chain length 8

Trophic level	Average length (cm)	Species
1	0.0502	Phytoplankton
2	1.6	Euphausiids
2	0.5	Copepods
2	0.2	Shrimp
3	20	Flying fish
3	1.55	Hyperiid
3	8.5	Lanternfishes
3	130	Molas
4	25	Chiasmodon (black swallower)
4	30	Snake mackerel
4	140	Squid
4	170	Coryphaena
5	115	Tuna
5	100	Billfish (lancetfishes)
6	270	Marlin
6	250	Medium-sized sharks
7	550	Large sharks

Table S2.8 Tropical plankton community, Pacific

Briand and Cohen (1987) Web No. 103

Briand and Cohen (1987) Ref No. 98

B&C mean chain length 5.59

B&C maximum chain length 10

Trophic level	Average length (cm)	Species
1	0.001	Small phytoplankton
1	0.004	Medium phytoplankton
1	0.0309	Large phytoplankton
2	0.3	Appendicularia (large)
2	0.015	Nauplii of Copepoda
2	0.0075	Appendicularia (small)
2	0.0057	Infusoria
2	0.02	Radiolaria
2	0.035	Copepodita of Copepoda
2	0.15	Calanus (small)
3	0.3	Acartia (large)
3	0.1	Oithona - oncaea (small)
3	0.4	Oithona - oncaea (large)
3	0.325	Centropages
3	0.128	Arcatia (small)
3	0.3	Calanus (large)
3	0.345	Amphipoda
3	0.34	Euchaeta
3	1.15	Euphasia
4	0.35	Pteropoda
4	1.05	Chaetognatha
4	0.33	Ctenophora medusae

Table S2.9 Lake Rybinsk, Russia

Briand and Cohen (1987) Web No. 71

Briand and Cohen (1987) Ref No. 68

B&C mean chain length 5.15

B&C maximum chain length 7

Trophic level	Average length (cm)	Species
1	0.001	Diatom: <i>Melosira italica</i>
1	0.001	Diatom: <i>Asterionella formosa</i>
1	0.0005	Blue-green algae: <i>Aphanizomenon flos-aquae</i>
1	0.0005	Blue-green algae: <i>Anabaena</i> spp.
1	0.0004	Blue-green algae: <i>Microcystis aeruginosa</i>
2	0.055	Protozoa
2	0.1	Rotatoria
3	0.2	<i>Daphnia longispina</i>
3	0.08	<i>Daphnia cucullata</i>
3	0.1	<i>Bosmina coregoni</i>
3	0.525	<i>Leptodora kindtii</i> (planktonic cladoceran)
3	0.525	<i>Polyphemus pediculus</i> (planktonic cladoceran)
3	0.15	<i>Eudiaptomus gracilis</i>
3	0.15	<i>Eudiaptomus graciloides</i>
3	0.15	<i>Heterocope appendiculata</i>
3	0.275	<i>Mesocyclops leuckarti</i>
3	0.275	<i>Mesocyclops orthonoides</i>
3	0.275	<i>Cyclops vicinus</i>
3	0.275	<i>Cyclops kolensis</i>
2	3.45	<i>Isochaetides newaensis</i>
2	4.5	<i>L. hoffmeisteri</i>
2	0.45	<i>Chironomus plumosus</i>
2	0.65	<i>Glyptotendipes</i> spp.
2	0.4	<i>Procladius</i> spp.
2	5.5	<i>Dreissena polymorpha</i> (clam)
4	17.5	<i>Abramis balerus</i> (European bream)
4	20	<i>Osmerus eperlanus</i> (European smelt)
4	20	<i>Alburnus alburnus</i> (bleak)
4	42.5	<i>Abramis brama</i> (bream)
4	30	<i>Rutilus rutilus</i> (roach)
4	40	<i>Blicca bjorkna</i> (silver bream)
5	47.5	<i>Lucioperca lucioperca</i> (pike perch)
5	57.5	<i>Esox lucius</i> (Northern pike)
5	29.5	<i>Pirca fluviatilis</i> (European perch)
6	90	<i>Lota lota</i> (burbot)
6	175	<i>Homo sapiens</i>

Table S3. Average adult body lengths of trophic species in terrestrial food webs.

Table S3.1 Sand dunes, Namib desert, Namibia		
Briand and Cohen (1987) Web No. 98		
Briand and Cohen (1987) Ref No. 94		
B&C mean chain length 3.54		
B&C maximum chain length 5		
Trophic level	Average length (cm)	Species
1	40	Annuals: Monsonia, Stpagrostis, Eragostris
1	100	Perennial: Stipagostis salbulicola
1	100	Perennial: Acanthosicyos horrida
1	100	Perennial: Trianthema hereroensis
2	1.5	Tenebrionidae
2	6.75	Orthoptera
2	1	Curculionidae
2	60	Hare - Lepus capensis
2	120	Oryx gazella
2	1	Aclerda
2	1	Thysanura, Isoptera, other Tenebrionidae
3	2.5	Scarabs
3	13.5	Gerbillius paeba, G. vallinus
3	5	Spiders, solpugids, scorpions
3	8.2	Mole - Eremitalpa granti namibensis
3	50	Aporosaura anchietae - Lacertidae
3	10	Typhlosaurus, lizards
4	160	Snakes - Bitis
4	56	Jackal - Canis mesomelas
4	105.5	Hyaena brunnea
5	34.5	Birds - Tyto alba
5	41	Falco
5	48.5	Corvus
5	34	Bubo africanus
5	40	Bubo asio

Table S3.2 Willow forest, Manitoba

Briand and Cohen (1987) Web No. 24

Briand and Cohen (1987) Ref No. 32

B&C mean chain length 2.7

B&C maximum chain length 4

Trophic level	Average length (cm)	Species
1	100	Salix discolor
2	1.2	Garlerucella decora (beetle, Chrysomelidae)
4	18.75	Redwinged blackbird Agelaius
4	20	Bronze grackle
4	14	Song sparrow
4	13	Maryland yellow throat (Geothlypis trichas), yellow warbler, song sparrow
1	100	Salix petiolaris
1	295	Salix longifolia
3	2	Spiders
2	0.2	Insects, Pontania petiolaridis, collembola
2	0.2	Insects, Disyonicha quinquevitata, collembola
3	8	Rana pipiens
2	1.25	Snails (Vertigo, Succinea, Lymnea)
4	77.33333333	Garter snake (Eutaenia parietalis)

Table S3.3 Rainforest, Malaysia

Briand and Cohen (1987) Web No. 40

Briand and Cohen (1987) Ref No. 42

B&C mean chain length 1.88

B&C maximum chain length 3

Trophic level	Average length (cm)	Species
1	3	Canopy - leaves
2	54.55	Primates: Hylobates
2	61	Primates: Presbytis
2	34	Primates: Nycticebus
2	35.55	Rodents: Ratufa (giant squirrel)
2	24.2	Rodents: Flying squirrels
2	12.75	Rodents: Hapalomys (rat)
2	40	Flying lemur
2	12	Ptilocercus (pen-tail tree shrew)
2	8	Fruit bat
2	16.2	Birds
2	20	Upper air animals: birds and bats, insectivorous, carnivorous birds
3	5.8	Insectivorous bats
3	1.15	Insects
2	595	Elephas
3	265	Didermorcerus (rhino)
3	215	Tapirus (tapir)
3	150	Feral pig (Sus)
3	100	Cervidae (deer)
3	50.5	Tragulus (mouse deer)
3	100	Bos (gaur)
3	120.7	Panthera (tiger and leopard)
3	125	Helarctos (bear)
3	88	Cuon (wild dog)
3	54.5	Hystricidae (porcupine)
3	41	Birds
3	3	Trunk, fruit, flowers
1	54	Macaca (monkeys)
3	47.5	Martes (marten)
3	40	Prionodon (linsang)

Table S3.3 (continued)

Trophic level	Average length (cm)	Species
3	57	Paradoxurinae (civets)
3	80.5	Neofelis (clouded leopard)
3	20.5	Callosciurus (tree squirrels)
3	19	Rattus (tree rats)
3	18.5	Tupaia (tree-shrews)
3	5.5	Bats
3	20	Birds
3	3	Ground - roots, fallen fruit, leaves and trunks (detritus?)
1	70.5	Viverrinae
2	55	Felis (small cats)
2	19	Mustela (stoat)
2	20	Lariscus and Rhinosciurus (ground squirrels)
2	19	Rattus (ground rats)
2	35.5	Rhizomys (bamboo rats)
2	35	Erinaceidae: moonrat
2	14	Erinaceidae: short-tailed shrew
2	7.45	Soricidae (shrews)
2	59	Manis (scaly anteater)
3	12	Birds
2	3.25	Fungi

Table S3.4 Prairie, Manitoba

Briand and Cohen (1987) Web No. 23

Briand and Cohen (1987) Ref No. 32

B&C mean chain length 2.4

B&C maximum chain length 4

Trophic level	Average length (cm)	Species
2	28	Richardson spermophile (ground squirrel)
4	54.5	Marsh hawk (<i>Circus hudsonius</i>)
4	90	Coyote (<i>Canis latrans</i>)
4	52.5	Red-tailed hawk (<i>Buteo borealis</i>)
4	19	Weasel (<i>Mustela</i>)
4	57	Badger (<i>Taxiadea taxus</i>)
2	13	Vole (<i>Microtus</i>)
3	28	13-striped spermophile (ground squirrel)
2	23.5	Pocket gopher (<i>Thomomys</i>)
4	35	Great horned owl
1	80	Agropyron
1	66	Stipa comata, Helianthus scaberrimus
2	1.75	Insects in herb and surface stratum, Diptera, Hermiptera, grasshoppers
3	2.5	Spiders
2	2	Insects in soil stratum, wire worms (<i>Ludius</i> larvae), cutworms, white grubs (<i>Apodius</i> larvae-beetle)
3	22.5	Meadow lark (<i>Strunella neglecta</i>)
3	15	Chipping sparrow (<i>Spizella passerina</i>), clay-coloured sparrow (<i>S. pallida</i>), vesper sparrow (<i>Poecetes confinis</i>) = all sparrows
3	18	Horned lark (<i>Otocoris</i>)
3	28	Upland plover (<i>Bartramia longicauda</i>)
3	47.5	Crow (<i>Corvus brachyrhynchos</i>)
3	8	Frog: <i>Rana</i>
4	77.33333333	Garter snake (<i>Eutaenia parietalis</i>)

Table S3.5 Wythan Wood, England

Briand and Cohen (1987) Web No. 27

Briand and Cohen (1987) Ref No. 33

B&C mean chain length 2.89

B&C maximum chain length 4

Trophic level	Average length (cm)	Species
1	20	Herbs
1	200	Trees and bushes
1	350	Oak trees
2	6	Tortrix, other leaf feeders, earth worms, fungi
2	4	Winter moth <i>Operopthera brumata</i>
2	4	<i>Campaea margaritata</i> , <i>Hemithea aestivaria</i> (moths)
2	0.45	<i>Philontus decorus</i>
2	1.5	<i>Abax parallelipedus</i> (beetles)
2	1.8	<i>Feronia modida</i> , <i>F. melanaria</i> (carabids)
2	0.6	Ladybird beetle: <i>Adalia decempunctata</i>
3	9.1	Voles, mice
3	1	Spider: <i>Linyphia triangularis</i>
3	14	Titmice (the great tit and blue tit)
3	0.45	<i>Cyzenis albicans</i> (Diptera)
3	0.75	Soil insects, mites
4	40.5	Owl (<i>Strix aluco</i>)
4	18.75	Weasels
4	7	Shrews: <i>Sorex</i>
4	9.1	Rats: <i>Clethrionomys glareolus</i>
4	9.25	Rats: <i>Apodemus sylvaticus</i>
4	15	Moles

Table S3.6 Trelease Woods, Illinois

Briand and Cohen (1987) Web No. 59

Briand and Cohen (1987) Ref No. 57

B&C mean chain length 2.379

B&C maximum chain length 4

Trophic level	Average length (cm)	Species
1	2.75	Weed seeds, corn grains, grass seeds, acorns, wild fruits, roots, bark
2	12.5	Deer mice
2	19.5	Cardinal
3	20	Red-headed woodpecker
3	20	Downy woodpecker
2	12.8	Mole
2	55	Rabbit
2	1	Wood borers, weevils
2	15	Brown creeper
3	13	White-breasted nuthatch
3	14	Tufted titmouse
2	20.35	Starling
2	24.5	Robin
2	58.25	Blue jay
2	25.75	Fox squirrel
2	13.3	Junco (junco), tree sparrow (Spizella)
1	1.5	Coleoptera
1	0.525	Diptera larvae
2	3.25	Lepidoptera larvae
2	4	Lepidoptera
1	1.75	Arachnidae
1	0.8	Scale insects
1	1	Miscellaneous insects
1	3	Snails
4	40	Barred owl (Strix)
4	7.5	Shrew

Table S3.7 Rajasthan Desert, India

Briand and Cohen (1987) Web No. 100

Briand and Cohen (1987) Ref No. 96

B&C mean chain length 3.34

B&C maximum chain length 6

Trophic level	Average length (cm)	Species
1	2	Cyperus, Cenchrus, Eleusine (grasses)
1	40	Crotalaria, Zizyphus (herbs-shrubs)
1	100	Prosopis cineraria (trees)
2	1.75	Insects: hoppers, termites, ants, moths, beetles
2	19	Rodents (Rattus, Mus)
2	12.25	Gerbils: Meriones
2	14	Gerbils: Tatera
2	60	Hare
2	24.75	Birds: doves (<i>Streptopalia senegalensis</i>)
2	18	Birds: larks
2	29	Birds: sandgrouse (<i>Pterocles exustus</i>)
2	110	Antelopes: gazelle (<i>Gazella</i>)
2	120	Antelopes: black buck (<i>Antelope</i>)
2	205	Antelopes: nilgai
3	3	Wasps, carpenter ants, tiger beetles, spiders
3	10	Lizards: <i>Acanthodactylus</i> -gekko, <i>Hemidactylus</i>
3	80	Lizards: <i>Varanus</i> spp.
4	66	Snakes: viper <i>Echis carinatus</i>
4	75	Snakes: sand boa <i>Eryx conicus</i>
4	165	Snakes: <i>Phytas</i> , <i>Naja</i>
3	21	Birds: bulbuls (<i>Picnonotus cafer</i>)
3	21	Birds: babblers (<i>Turdoides stiatius</i>)
3	22	Birds: shirke (<i>Lanius excubator</i>)
3	15	Birds: Indian robin (<i>Sexicoloides fulvicata</i>)
3	25	Birds: bee-eater
3	7	Bats: <i>Rhinopoma</i>
3	6.9	Bats: <i>Pipistrellus</i>
3	16	Hedgehog
3	32	Shikra (bird)
5	61	Cat (<i>Felis lybica</i>)
5	65	Dog (<i>Canis familiaris</i>)
5	115	Wolf (<i>Canis lupus</i>)

Table S3.8 Aspen Communities, Manitoba

Briand and Cohen (1987) Web No. 25
 Briand and Cohen (1987) Ref No. 32
 B&C mean chain length 2.16
 B&C maximum chain length 4

Trophic level	Average length (cm)	Species
3	23.5	Birds: baltimore oriole (<i>Icterus galbula</i>)
3	17	Birds: black capped chickadee
3	14	Birds: least flycatcher (<i>Empidonax minimus</i>)
3	15	Birds: warbling vireo, rosebreasted grosbeak (<i>Hedymeles ludovicianus</i>)
2	14.7	Fungus: canker (<i>Hypoxyton pruinaum</i>), white heart rot (<i>Fomes ignarius</i>)
3	20	Hairy and downy woodpeckers (<i>Dryobates</i>)
2	2	Spiders (mature forest)
2	0.75	Insects (mature forest - Diptera is the most abundant)
2	1.35	<i>Dicerca</i> , <i>Saperda calcerata</i> , <i>S. bipuntata</i> (Cerambycid beetle)
2	19.75	Red squirrel (<i>Sciurus</i>)
1	880	Plants: <i>Populus</i>
3	50	Goshawk (<i>Astur</i>)
2	9.1	Redbacked vole (<i>Evotomys</i>)
4	42.5	Coopers and sharpshinned hawks (<i>Accipiter</i>)
3	35	Great horned owl (<i>Bubo occidentalis</i>)
2	44.5	Bird ruffled grouse (<i>Pediocetes</i>)
2	15	Flicker (<i>Coloptes auratus</i>)
2	47.5	Crow
3	12.5	House wren (<i>Tryglodytes aedon</i>)
2	55	Snowshoe rabbit (<i>Lepus</i>)
3	13	Birds: yellow warbler (<i>Dendroica aestiva</i>)
3	12.95	Birds: gold finch (<i>Astragalinus tritis</i>)
3	24.5	Birds: robin (<i>Planesticus migratorius</i>)
1	250	<i>Populus</i> , <i>Symphoricarpos</i> (snow berry), <i>Corylus</i> , <i>Prumus</i>
2	9.1	Red backed vole
2	28	Franklin ground squirrel (<i>Citellus franklini</i>)
2	2.25	Insects (forest edge): <i>Ropolopus</i> (cerambycids)
2	2	Spiders (forest edge)
2	2.25	Snails
3	8	Frog <i>Rana pipiens</i>

Table S3.9 Tropical Rainforest, El Verde

Web not part of the Briand and Cohen (1987) collection

Trophic level	Average length (cm)	Species
1	2000	Leaves (canopy)
1	0.0035	Algae
1	3	Nectar, fruit
2	4.25	Fungi: micorrhizal fungi, Mycena, Psychotria, Favolus
2	7.1	Monophyllus
2	9.65	Brachyphylla
2	9	Artibeus
2	7	Erophylla
2	5.9	Stenoderma
2	4	Snails
3	0.75	Chelicerata: mites, Acari (order Cryptostigmata and Prostigmata), ants
3	6	Chelicerata: Aranea (Pholcidae and Ochyroceratidae)
3	0.25	Miriapoda: Scolopendra
3	0.2	Insecta: Collembola
3	1	Insecta: Homoptera
3	1.75	Insecta: Coleoptera
3	0.8	Insecta: Hemiptera
2	2	Termites
2	8	Earthworms (Oligochaeta)
2	25	Columba
2	30	Zenaida
2	30	Amazona
2	25	Geotrygon
3	2.7	Gekkos
3	8.2	Anguidae
3	19	Rats (Rattus)
2	5	Walking sticks
2	4	Pierid butterfly
2	2	Fulgoroid hoppers
2	3.5	Crickets
2	2.5	Cockroaches
3	18.75	Seiurus

Table S3.9 (continued)

Trophic level	Average length (cm)	Species
3	14	Other birds
3	12.5	<i>A. cuvieri</i>
3	5.8	<i>A. gundlachi</i>
3	4.1	<i>A. stratulus</i>
3	5.5	<i>A. evermanni</i>
4	5	Scorpiones: <i>Tityus</i>
4	3.5	Araneae
3	3.95	<i>Eleutherodactylus</i>
3	5.3	<i>Leptodactylus albilabris</i>
3	5.85	<i>Pteronotus</i>
3	5.25	<i>Eptesicus</i>
3	7	<i>Lasirius</i>
4	22.5	<i>Typhlops plaatycephalus</i>
4	17.7	<i>T. rostellatus</i> and <i>Amphisbaena</i>
4	110	Boidae
4	55.4	Alsophis
4	26.5	<i>Arrhyton</i>
4	42.5	Mongoose
5	52.5	Buteo
5	47.5	Otus