

On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis

Matías Arim, Francisco Bozinovic and Pablo A. Marquet

M. Arim (marim@bio.puc.cl), Sección Zoología Vertebrados, Facultad de Ciencias, Univ. de la República, Uruguay, Iguá 4225 Piso 9 Sur, Montevideo, Uruguay. – MA, F. Bozinovic and P. A. Marquet, Center for Advanced Studies in Ecology & Biodiversity (CASEB) and Depto de Ecología, Facultad de Ciencias Biológicas, Pontificia Univ. Católica de Chile, Santiago, CP 6513677, Chile. PAM also at: Inst. of Ecology and Biodiversity (IEB), Casilla 653, Santiago, Chile and at: National Center for Ecological Analysis and Synthesis (NCEAS), 735 State Street, Suite 300, Santa Barbara, CA 93101, USA.

Understanding the factors that constrain and drive changes in food chain length represents an open challenge in ecology. Although several explanatory hypotheses have been proposed, no synthesis has yet been achieved. The role of body size has been well-studied in recent years because the hierarchy of trophic connections – in which large animals consume small ones – suggests a positive relationship between trophic position and body size. Empirical evidence, however, supports the existence of both positive and negative associations, and some studies have even reported no significant relationship between trophic position and body size. These results suggest that the relationship may be non-monotonic and driven by several interacting mechanisms. Here, we analyze the effects of energetic limitations and structural constraints on species' trophic positions. We show that the trophic position of small-bodied animals can be limited by their ability to consume large prey, whereas energetic limitations strongly constrain trophic positions for large-bodied animals, with the intensity of this constraint depending on the amount of energy available to top predators. These differences in limiting mechanisms can account for the observed variability in the association between the trophic position of top predators and size. Furthermore, our derivation makes use of the Metabolic theory of ecology and predicts a negative relationship between temperature and the maximum achievable food chain length, providing a mechanistic foundation for the observed reductions in food chain length with temperature.

The question of what determines the length of food chains has been at the core ecological theory for the last 80 years, a time span which has allowed for the accumulation of a wealth of explanations, models, and data, which, however, are not exactly in agreement with each other. The first explanation is known as the Energetic limitation hypothesis (ELH, Elton 1927, Lindeman 1942, Hutchinson 1959, Schoener 1989) and states that the low efficiency associated with the transmission of resources (energy) from one trophic level to the next, limits food chain length by affecting the viability of predators at the top of long food chains. Since the ELH was proposed, alternative explanations, with variable empirical and/or theoretical support, have been accumulating and new patterns have been discovered. Among these alternative explanations are 1)

the Dynamical constraint hypothesis to food chain length, which is based on the observation of a negative relationship between food chain length and population resilience from disturbances (Pimm and Lawton 1977). The existence of a dynamic constraint on food chain length is generally accepted (Pimm 1991, Post 2002), however, the theoretical support for this hypothesis is weak (Post 2002), and has been challenged on methodological grounds (Sternler et al. 1997); 2) the System size hypothesis, whereby predator–prey interactions tend to be more stable in larger environments, which would explain why food chain length increases with system size (Briand and Cohen 1987, Spencer and Warren 1996, Post 2002); 3) the Body size ratio hypothesis, based on the inverse relationship between food chain length and predator–prey differences in

body size (Jennings and Warr 2003); and 4) the Gape limitation hypothesis, which proposes that the major determinant of a predator's potential to occupy upper trophic positions is associated with the its morphological restrictions related to consuming prey (Pimm 1982, Hairston and Hairston 1993). This latter hypothesis points to the existence of a connection between species' trophic positions and their body sizes.

Body size is of paramount importance give its effects on ecological dynamics in general (Brown et al. 2004) and predator-prey interactions in particular (Brose et al. 2006a, Weitz and Levin 2006). Since Elton (1927) noted the effect of body size on the diet of predators, the existence of a body size based hierarchy within trophic connections, where big animals consume small ones, has been widely accepted. Available empirical evidence suggests that this size hierarchy is widespread and represents an important constraint with which predators and prey comply (Vezina 1985, Cohen et al. 2003, Brose et al. 2006b), and is also an assumption made by some of the most popular food web models available (Williams and Martinez 2000). It has been suggested that the size hierarchy in trophic links implies a positive relationship between trophic position and body size (Layman et al. 2005). Although empirical evidence has shown the existence of a positive relationship (Vander Zanden et al. 2000, Cohen et al. 2003, 2005, Cocheret de la Morinière et al. 2003, Swanson et al. 2003, Deudero et al. 2004, Estrada et al. 2006), other studies have shown a negative relationship (Burness et al. 2001) as well as no association between trophic position and size (Vander Zanden et al. 2000, Jennings et al. 2001, Cocheret de la Morinière et al. 2003, Swanson et al. 2003, Deudero et al. 2004, Layman et al. 2005), suggesting that this relationship may be non-monotonic and driven by several interacting mechanisms (Genner et al. 2003). Up to now, however, this relationship and underlying mechanisms remain largely unknown (Cohen et al. 2003), which is surprising considering the historical importance of energetic arguments for explaining food web attributes, such as food chain length, and the direct link between size and energy.

There is little doubt that energy does affect food web structure and function by imposing boundary conditions on individual and population persistence, mediated by the relationship between energetic requirements and environmental resource (i.e. energy) availability (Marquet and Taper 1998, Burness et al. 2001, Cohen et al. 2003, Brown and Gillooly 2003, Brown et al. 2004). The ELH was formulated under a view of ecological communities based on trophic levels. Mathematically, the ELH can be expressed as a function of available resources and their transmission efficiency through the food web as: $R_i = R_0 \times t^P$, where the amount of available energy to sustain a consumer

population i (R_i) is a function of the amount of resources available to the basal level of the food chain (R_0), the transmission efficiency (t) and the species' trophic position (P), formally considered as a discrete value – the trophic level in which the species is observed. When the resources available to a given trophic level are below the minimum amount required for the persistence of at least one consumer population (i.e. $R_i < R_{\min} \forall i$) the trophic level is not viable and the food chain is energetically limited (Elton 1927, Hutchinson 1959).

The ELH does not recognize the complexity of real food webs, which have a large incidence of omnivory and few discrete trophic levels, where individuals present large variations in body size and, consequently, in energetic demands, and with attributes that vary according to habitat and predator and prey types (Cohen et al. 2003, Arim and Marquet 2004, Arim and Jaksic 2005, Brose et al. 2006b). In spite of these limitations, and the fact that notably few empirical studies have been devoted to test the ELH, energy has been shown to be a determinant of food chain length in at least in some systems (Arim et al. 2007). In this paper we propose that the recently formulated Metabolic theory of ecology (MTE, Brown et al. 2004) can help to expand and include at least some aspects of food web complexity into the ELH.

A species' energetic demand depends on its body size (McNab 2002) and temperature (Gillooly et al. 2001, Brown et al. 2004). The potential of a species to satisfy its energetic demands in a given trophic position within the food web, is dependent on the amount of basal resources (Schoener 1989), the efficiency at which these resources flow through the food web to the focal species (Lindeman 1942), and the predator's ability to consume available prey (Pimm 1982, Hairston and Hairston 1993). However, until now, no attempt has been made to merge together, in a single framework, all of the factors that determine the range of trophic positions that a species could occupy. In this article we formally present the connection between a species' trophic position and body size. It is worth noting that our model for the effect of energy limitation on food chain length does not rely on the existence of discrete trophic levels. Instead, it assesses the effect of energy limitation on food webs by considering how energy affects trophic position, thus including greater food web complexity. In addition, it presents an explicit connection between the Metabolic theory of ecology and food web topology. We show that the trophic position of small animals can be limited by their ability to consume large prey. However, energetic limitations will strongly limit the trophic positions of larger animals if no other ecological processes compensate for energy limitation. In addition, we show that temperature, through its effect on

energetic demands, could negativity affect food chain length.

Energetic constraints on trophic position

The basic message we want to convey in this section is that the amount of energy required to maintain a viable population can constrain the maximum trophic position achievable by a consumer (Marquet and Taper 1998, Burness et al. 2001, Marquet et al. 2004), in addition to deriving an explicit equation for this relationship. To do so we need to consider several individual and population attributes and patterns. The energy requirement of one individual is determined by its metabolic rate (B), which scales with body mass (M) as:

$$B = a \times M^{0.75} e^{-E/KT} \quad (1)$$

where E is the activation energy (0.63 electron volts; $1 \text{ eV} = 96.49 \text{ kJ mol}^{-1}$), K is Boltzmann's constant, and T is absolute temperature in Kelvin (Gillooly et al. 2001, Brown et al. 2004). If N_{mvp} is the minimum number of individuals required to ensure long-term population viability (Marquet and Taper 1998), the amount of energy required to maintain this viable population size will be:

$$B_{\text{mvp}} = N_{\text{mvp}} B \quad (2)$$

Since the efficiency of energy transmission through trophic links is typically low (Hairston and Hairston 1993), the amount of energy available for higher trophic positions is limited. Thus, considering that the energy available to the prey is passed on to its predator with transmission efficiency " τ ", a consumer one link apart from the basal resource, R_0 (e.g. an herbivore) will have $R_0 \times \tau$ energy available to sustain its population. Further, assuming a constant efficiency of transmission, a consumer two links apart from the basal resource (e.g. a predator) will have $R_0 \times \tau \times \tau = R_0 \tau^2$, and so on. Hence, the amount of available energy to sustain a consumer population, R_i , is a function of the predator trophic position (P):

$$R_i = R_0 \times \tau^P \quad (3)$$

Trophic position is defined as $P_i = 1 + \sum P_j \times m_{ij}$ where P_j is the trophic position of prey j and m_{ij} is the fraction of consumed food of species i , consisting of prey species j (Winemiller 1990). Thus, in contrast with earlier definitions of the ELH, here we take P to represent a continuous variable that encapsulates several key components of food web complexity (Winemiller 1990). The concept of trophic position is less rigid than trophic level and allows for a better characterization of food web complexity, as it is not blind to phenomena such as omnivory (i.e. eating on more than one trophic level).

Since a consumer population will be viable only if the amount of energy available is larger than the amount required to sustain a viable population, there is a limit to the trophic position of a species population set by the threshold at which the energy demands are greater than the available energy:

$$R_i = R_0 \tau^P \leq B_{\text{mvp}} \quad (4)$$

replacing Eq. 1 in Eq. 2 and inserting this into Eq. 4 and rearranging terms, we can express the relationship between trophic position (P) and body size as:

$$P \leq \frac{\ln\left(N_{\text{mvp}} \frac{a}{R_0}\right) - \frac{E}{KT} + 0.75 \ln(M)}{\ln(\tau)} \quad (5)$$

Equation 5 indicates that the maximum trophic position that a consumer can achieve is a decreasing function of body size and temperature (which at the same time sets metabolic requirements) and an increasing function of the amount of basal resources available and the conversion efficiency.

Morphological constraints on trophic position

In the previous section we showed the effect of energetic constraints and how these predict a negative relationship between trophic position and size. Here we show, however, that morphological constraints, implicit in the existence of feeding hierarchies and which we call "gape limitation," might be more important than energetic constraints for small animals.

The body size of a predator can be considered as equal to the body size of its prey multiplied by a constant:

$$M_{\text{predator}} = r \times M_{\text{prey}} \quad (6)$$

where $r \geq 1$ when the size of the predator is greater than or equal to that of its prey. In each trophic connection body size increases by a factor r from one level to the consumer above it. Therefore r represents the magnitude of the feeding hierarchy, where larger values of r show feeding relationships that are more size structured. If the minimum body size at the base of the food web is M_0 , then the body size of a predator at a given trophic position will be $M_{\text{predator}} = r^P \times M_0$, rearranging terms:

$$P = \frac{\ln\left(\frac{M_{\text{predator}}}{M_0}\right)}{\ln(r)} \quad (7)$$

Equation 7 indicates that the trophic position of a predator will be positively related to the predator's size, and negatively related to the predator-prey body size

ratio and the size of the basal resource. Thus, as r approaches one, P tends to infinity. However, for $r > 1$, P decreases as a consequence of size constraints (Fig. 1). In cases where predators are smaller than the prey, no gape limitation will operate. However, it should be noted that most trophic interactions are size-structured (Cohen et al. 2003, Brose et al. 2006b) and so it is unlikely that the mean difference in predator–prey size is less than one for all the food chains that connect predators with basal resources. Furthermore, the existence of a hierarchy in trophic connections appears to be a necessary condition for food web stability (Brose et al. 2006a).

Since many ecological attributes of an organism are related to its body size (McNab 2002) Eq. 5 and 7 can be used as a starting point from which to explore the connections between size, ecological attributes and trophic position. A final constraint is that the minimum trophic position cannot be less than one for animals – i.e. herbivores or detritivores.

Temperature and food chain length

An interesting result of our explanation is that it allows, for the first time, a theoretical connection between food chain length and temperature (Eq. 5, Fig. 2). The expected increase in metabolic demands with increasing temperature requires an increase in energy consumption,

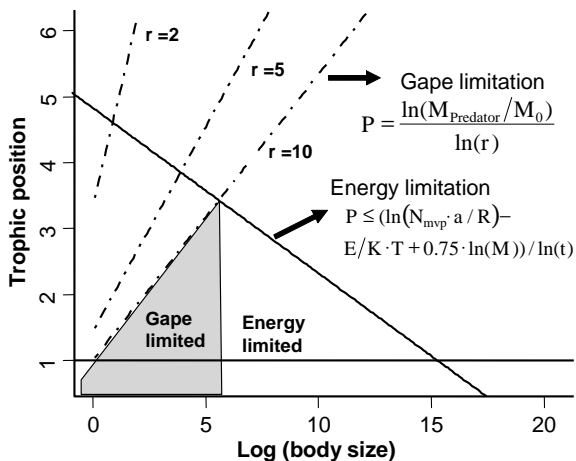


Fig. 1. Possible combinations of body size and trophic position (TP). TP=1 implies an herbivorous organism, TP \geq 2 implies carnivorous species, and non integer trophic positions imply omnivory. The first constraint is gape limitation where larger animals feed on small ones. r is the ratio of predator–prey body sizes; the larger the values of r and basal prey mass M_0 , the greater the probability that a species is gape limited. The second restriction is energy limitation. Larger animals are more prone to be energy limited while small animals tend to be gape limited.

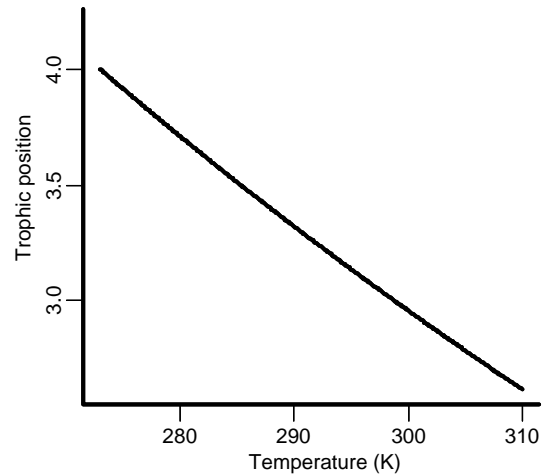


Fig. 2. Predicted effect of temperature on food chain length. Environmental temperature, through its influence on the metabolic demands of animals, increases the amount of energy consumed. This physiological process reduces the energy available to top predators and thereby reduces the length of food chains. Equation 5 allows us to relate the maximum trophic position with temperature: $P \leq (\ln(N_{\text{mvp}} \times a/R_0) - E/K \times T + 0.75 \times \ln(M)) / \ln(t)$.

which results in a reduction in the maximum food chain length achievable. Previous studies have reported a reduction in food chain length with increasing temperature, but researchers were uncertain of the mechanism for this phenomenon (Beisner et al. 1997, Petchey et al. 1999). In microcosm experiments, an increase of 7°C produced a disproportional loss of consumers, reducing the length of food chains (Petchey et al. 1999). Similarly, a three level food chain was unstable at high temperature, 25°C – but stable at low temperature, 18°C (Beisner et al. 1997). This result was explained by the increase in biochemical and physiological rates with temperature, which amplified population fluctuations and resource requirements (Beisner et al. 1997), in agreement with what is expected from the Metabolic theory of ecology (Brown et al. 2004) and our analysis. Finally, it should be highlighted that the trophic position of species constrained by morphology will not be affected by changes in temperature (Fig. 1).

The effect of temperature on food web structure is a promising area of research. Environmental temperature, through its effect on metabolic rates, can have large effects on species interactions and on the structure of ecological systems in general, accounting for seasonal, altitudinal and latitudinal patterns of variation under different scenarios of climate change (Petchey et al. 1999, Allen et al. 2002, Savage et al. 2004). Our analysis is a preliminary step in order to mechanistically connect food web and community structure with temperature.

Model predictions and empirical evidence

As far as we know, there is no dataset which combines all of the information needed to test the model we propose. However, the fact that several predictions from the model are in agreement with reported patterns suggests that it successfully captures some general processes affecting the length of food webs. In particular, our model predicts: 1) an inverse relationship between trophic position and body size for the largest organism in a system, as has been reported by Burness et al. (2001). The opposite is true for the small organisms (Cocheret de la Morinière et al. 2003, Genner et al. 2003, Deudero et al. 2004). 2) Large organisms are energy limited and the range of trophic positions in which they could be observed is positively affected by available energy (Burness et al. 2001). 3) For a range of body sizes that encompass the smallest and largest organisms in a community, a humped pattern of maximum trophic positions is expected. This pattern has only been reported in a single system (Genner et al. 2003). However, the range of body sizes typically studied is relatively narrow in relation to the complete range of body sizes in the system. 4) If no humped pattern is observed for a sufficiently large range of body sizes, other ecological forces should be operating, such as energy subsidies and the coupling of energy channels by large predators within or among food webs (Pace et al. 2004, McCann et al. 2005, Rooney et al. 2006; Fig. 3). 4) Food chain length is inversely related to

mean difference in predator–prey body sizes, as was proposed and empirically demonstrated by Jennings and Warr (2003). 5) Temperature has a negative impact on food chain length for energy limited species, as has been reported by Beisner et al. (1997) and Petchey et al. (1999).

Coda

It should be highlighted that the present analysis focuses on identifying constraints on trophic position in relation to body size. As a consequence, those species for which combinations of trophic position and body size are within the morphospace, but far from the boundaries, could show no restriction. Similarly, it is always possible that other processes (e.g. species interactions) preclude species from attaining the maximum trophic position, dictated only by morphological and energetic constraints. In this sense, considering the relationship between body size and the maximum trophic position for size classes probably represents a better approach than analyzing mean tendencies. One area where more empirical and theoretical research is necessary is on the determinants of minimum population size. Many life history attributes scale with body size and could potentially affect the minimum population size N_{mvp} required to preclude extinction (Charnov 1993). We considered N_{mvp} to be independent of body size as a first approximation, for which there is theoretical (Marquet and Taper 1998, Marquet et al.

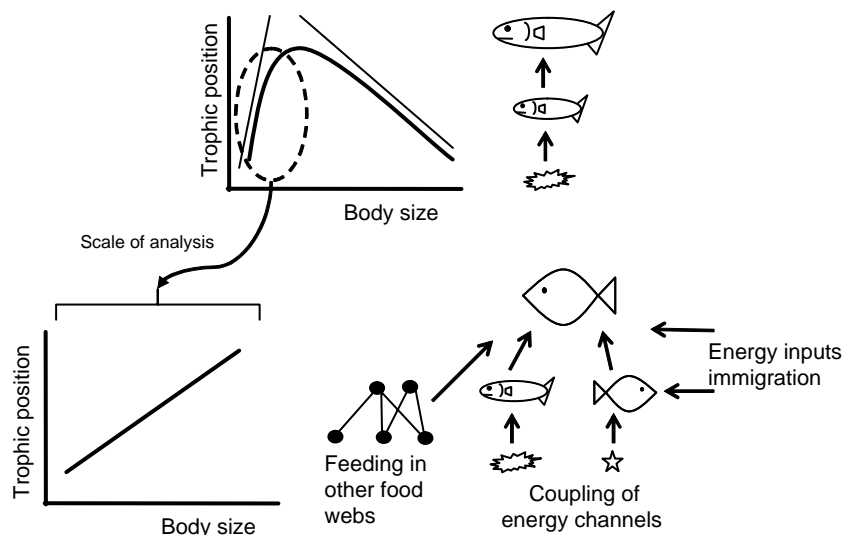


Fig. 3. A potential mechanism that can account for the positive relationship between body size and trophic position. In an isolated system a humped pattern is expected in the food chain structure of trophic connections. Positive associations can originate because of the scale of analysis – when a subset of the species body sizes in the system are analyzed; furthermore, the integration of energy channels within the food web, immigration of individuals to intermediate trophic positions, subsidies, and mobile predators can increase available energy at higher trophic levels.

2005) as well as empirical support (Brown and Maurer 1987, Pimm 1991).

The effects of energy on food chain length have been debated for almost 80 years (Post 2002, Arim et al. 2007). Empirical evidence has shown positive, negative, humped, and U-shaped relationships, as well as no relationships between energy and food chain length (Arim et al. 2007). These contrasting results make it crucial that we understand the conditions under which energy is a limiting factor and the conditions when it is not. Our analysis indicates that, within a single community, the trophic position of small organisms will be more likely to be gape limited, while the trophic position of large organisms will be energy limited. This difference in limiting mechanisms can account for observed changes in the trophic position of top predators in response to changes in available energy and for the observed variability in the relationship between trophic position and size. With our model we hope to advance the theoretical framework for the study and interpretation of observed patterns of associations between trophic position and body size, and in general, to understand the determinants of food chain length.

Acknowledgements – This study was funded by FONDECYT-FONDAP grant 1501-0001 (Programs 1, 2 and 4) to FB, MA and PAM, respectively; Fondo Clemente Estable grant 05-076 to M.A. and ICM P05-002 grant to PAM. Part of this work was conducted while PAM was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (grant no. DEB-0072909), the Univ. of California, and the Santa Barbara campus.

References

- Allen, A. P. et al. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. – *Science* 297: 1545–1548.
- Arim, M. and Marquet, P. A. 2004. Intraguild predation: a significant and widespread interaction. – *Ecol. Lett.* 7: 557–564.
- Arim, M. and Jaksic, F. 2005. Productivity and food web structure: association between productivity and link richness among top predators. – *J. Anim. Ecol.* 74: 31–40.
- Arim, M. et al. 2007. On the relationship between productivity and food chain length at different ecological levels. – *Am. Nat.* 169: 62–72.
- Beisner, B. E. et al. 1997. The influence of temperature and food chain length on plankton predator–prey dynamics. – *Can. J. Fish. Aquat. Sci.* 54: 586–595.
- Briand, F. and Cohen, J. E. 1987. Environmental correlates of food chain length. – *Science* 238: 956–960.
- Brose, U. et al. 2006a. Allometric scaling enhances stability in complex food webs. – *Ecol. Lett.* 9: 1228–1236.
- Brose, U. et al. 2006b. Consumer–resource body-size relationships in natural food webs. – *Ecology* 87: 2411–2417.
- Brown, J. H. and Maurer, B. A. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. – *Am. Nat.* 130: 1–17.
- Brown, J. H. and Gillooly, J. F. 2003. Ecological food webs: High-quality data facilitate theoretical unification. – *Proc. Natl Acad. Sci. USA* 100: 1467–1468.
- Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – *Ecology* 85: 1771–1789.
- Burness, G. P. et al. 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. – *Proc. Natl Acad. Sci. USA* 98: 14518–14523.
- Charnov, E. L. 1993. Life history invariants: explorations of symmetry in evolutionary ecology. – Oxford Univ. Press.
- Cohen, J. E. et al. 2003. Ecological community description using the food web, species abundance, and body size. – *Proc. Natl Acad. Sci. USA* 100: 1781–1786.
- Cohen, J. E. et al. 2005. Body sizes of hosts and parasitoids in individual feeding relationships. – *Proc. Natl Acad. Sci. USA* 102: 684–689.
- Cocheret de la Morinière, E. et al. G. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. – *Mar. Ecol. Prog. Ser.* 246: 279–289.
- Deudero, S. et al. 2004. Spatial variation and ontogenetic shifts in the isotopic composition of Mediterranean littoral fishes. – *Mar. Biol.* 145: 971–981.
- Elton, C. 1927. Animal ecology. – Sidgwick and Jackson, London.
- Estrada, J. A. et al. 2006. Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. – *Ecology* 87: 829–834.
- Genner, M. J. et al. 2003. Isotopic change throughout the life history of a Lake Malawi cichlid fish. – *J. Fish Biol.* 62: 907–917.
- Gillooly, J. F. et al. 2001. Effects of size and temperature on metabolic rate. – *Science* 293: 2248–2251.
- Hairton, N. G. and Hairton, N. G. H. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. – *Am. Nat.* 142: 379–411.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? – *Am. Nat.* 93: 145–159.
- Jennings, S. and Warr, K. J. 2003. Smaller predator–prey body size ratios in longer food chains. – *Proc. R. Soc. Lond. B.* 270: 1413–1417.
- Jennings, S. et al. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. – *J. Anim. Ecol.* 70: 934–944.
- Layman, C. A. et al. 2005. Body size and trophic position in a diverse tropical food web. – *Ecology* 86: 2530–2535.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. – *Ecology* 23: 399–417.
- Marquet, P. A. and Taper, M. L. 1998. On size and area: patterns of mammalian body size extremes across land-masses. – *Evol. Ecol.* 12: 127–139.

- Marquet, P. A. et al. 2004. Metabolic ecology: linking individuals to ecosystems. – *Ecology* 85: 1794–1796.
- Marquet, P. A. et al. 2005. Scaling and power-laws in ecological systems. – *J. Exp. Biol.* 208: 1749–1769.
- McCann, K. S. et al. 2005. The dynamics of spatially coupled food webs. – *Ecol. Lett.* 8: 513–523.
- McNab, B. K. 2002. *The physiological ecology of vertebrates.* – Cornell Univ. Press.
- Pace, M. L. et al. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. – *Nature* 427: 240–243.
- Petchey, O. L. et al. 1999. Environmental warming alters food-web structure and ecosystem function. – *Nature* 402: 69–72.
- Pimm, S. L. 1982. *Food webs.* – Chapman and Hall.
- Pimm, S. L. 1991. *The balance of nature: ecological issues in the conservation of species and communities.* – Chicago Univ. Press.
- Pimm, S. L. and Lawton, J. H. 1977. On the number of trophic levels. – *Nature* 268: 329–331.
- Post, D. M. 2002. The long and short of food-chain length. – *Trends Ecol. Evol.* 17: 269–277.
- Rooney, N. et al. 2006. Structural asymmetry and the stability of diverse food webs. – *Nature* 442: 265–269.
- Savage, V. M. et al. 2004. Effects of body size and temperature on population growth. – *Am. Nat.* 163: 429–441.
- Schoener, T. W. 1989. Food webs from the small to the large. – *Ecology* 70: 1559–1589.
- Spencer, M. and Warren, P. H. 1996. The effects of habitat size and productivity on food web structure in small aquatic microcosms. – *Oikos* 75: 419–430.
- Sterner, R. W. et al. 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. – *Ecology* 78: 2258–2262.
- Swanson, H. K. et al. 2003. Trophic positions and mercury bioaccumulation in rainbow smelt *Osmerus mordax* and native forage fishes in Northwestern Ontario Lakes. – *Ecosystems* 6: 289–299.
- Vander Zanden, M. J. et al. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout *Salvelinus namaycush*. – *Can. J. Fish. Aquat. Sci.* 57: 725–731.
- Vezina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. – *Oecologia* 67: 555–565.
- Weitz, J. S. and Levin, S. A. 2006. Size and scaling of predator–prey dynamics. – *Ecol. Lett.* 9: 548–557.
- Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. – *Nature* 404: 180–183.
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. – *Ecol. Monogr.* 60: 331–367.