

CHAPTER SIXTEEN

Body sizes in food chains of animal predators and parasites

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Introduction

Food chains in which animal predators are bigger than their animal prey are called predator chains; those in which the consumers are smaller are called parasite chains (Elton, 1927; Hutchinson, 1959, p. 147). The purpose of this chapter is to display and test empirically some consequences, for predator chains and parasite chains, of assuming that the average mass of a consumer species (predator or parasite) is related to the average mass of its animal resource species (prey or host) by a power law with an exponent less than 1.

In 1858, as part of his development of the theory of evolution, Wallace (1858, p. 54) noted that animal predators are generally larger and less numerous than their prey. Among the many echoes of Wallace's remark, Elton (1927) observed anecdotally that animal predators weigh more than their prey in terrestrial food chains, Hutchinson (1959) analyzed some of the theoretical consequences of predators weighing more than their prey, and Sheldon, Prakash and Sutcliffe (1972) and others posited that marine animal predators outweigh their marine animal prey (see also Humphries, this volume; Woodward & Warren, this volume). Only recently have body sizes been studied empirically in parasite chains (Memmott, Martinez & Cohen, 2000; Leaper & Huxham, 2002) and parasitoid chains (Cohen *et al.*, 2005). The study of parasitoid chains (e.g. Rott & Godfray, 2000; Memmott *et al.*, 2000) appears not to have been considered by Elton (1927) and Hutchinson (1959).

Predator and parasite chains are not the only possibilities observed in nature. Other relations between mass and feeding arise from social hunting and metaphoresis. Among animals that hunt socially (such as wolves and army ants), the aggregate mass of the hunting group may be a more appropriate index of size than the mass of an individual predator. In animals where mass or feeding habit or both change dramatically with the stage of the life cycle (as in many insects and fishes), it is misleading to represent the masses of all stages by a typical adult

mass (Hutchinson, 1959; Cohen *et al.*, 2005). Hutchinson (1959) called a change in diet with changing stage of the life cycle metaphoetesis.

When Christine Müller measured the body lengths of individual aphid hosts and of their parasitoid wasp consumers (Cohen *et al.*, 2005, raw data available online), one nymphal aphid *Capitophorus carduinis* parasitized by a male wasp *Aphidius matricariae* was longer than the wasp when the wasp emerged from its aphid host, while another nymphal aphid *Capitophorus carduinis* parasitized by a male wasp *Aphidius matricariae* was shorter than the wasp when the wasp emerged from its aphid host. Both aphids were found on the same plant species *Cirsium palustre*. Even controlling for the life stage of the aphid, for the sex of the parasitoid wasp, and for the plant, the ordering of body sizes may differ from one consumer–resource pair of individuals to another. This single instance is illustrative of the variability in the relationship of host and parasitoid body length found in many comparable observations.

In most real food webs, predator chains and parasite chains are tightly interwoven because animal predators of almost all sizes support viruses, bacteria and other microscopic and macroscopic parasites. The analysis here of the typical patterns of predator chains and parasite chains makes no claim to cover all kinds of food chains.

The relation between the average masses of animal predator species and the average masses of animal prey species has been approximated empirically as a power law (Schoener, 1968; Peters, 1983, p. 277; Vézina, 1985; Warren & Lawton, 1987). The power law also applies to individual body masses of aphids and parasitoid wasps (Cohen *et al.*, 2005), but the theoretical implications parallel to those derived here for species-average masses remain to be studied.

The analysis below predicts, first, that in predator chains, there is an upper limit to the mass of possible predators and prey; and that this upper limit is independent of the number of trophic links in the chain and independent of the mass of the smallest prey. Conversely, in parasite chains, there is a lower limit to the mass of the smallest host and parasite; this limit is independent of the number of trophic links in the chain and independent of the mass of the largest host.

A second consequence is that, in a predator chain, the ratio of predator mass to prey mass decreases according to a power law, with an exponent one less than that for predators and prey masses, as the trophic level and the mass of the prey increase. (In a single food chain in which no species occurs more than once, the trophic level of a species may be unambiguously defined as the number of links between it and the basal species in the chain; thus the basal species has trophic level 0, its consumer has trophic level 1, and the top species in a chain of n trophic links and $n + 1$ species has trophic level n .) Conversely, in a parasite chain, the ratio of parasite mass to host mass increases as the trophic level of the host increases (and the mass of the host decreases).

This theoretical and exploratory analysis of body sizes and feeding is part of a larger picture that includes numerical abundance (Cohen, Jonsson & Carpenter, 2003).

Theory

Maximal and minimal body masses

Consider a food chain based on an animal (prey or host) of mass M_0 . Let $M_1 = f(M_0)$ be the typical (e.g. geometric mean) mass of a consumer (predator or parasite) of that prey, ignoring variation in the mass of consumers that eat prey of a given mass. Let $M_2 = f(M_1) = f(f(M_0)) = f^2(M_0)$ be the typical mass of a consumer that eats the consumer of typical mass M_1 . The notation $M_2 = f^2(M_0)$ indicates that M_2 results from applying two iterations of f to M_0 ; $f^2(M_0)$ does not denote the square of $f(M_0)$, which would be written $[f(M_0)]^2$. Similarly, $f^{n+1}(M_0) = f(f^n(M_0))$ is the typical mass of a consumer $n + 1$ trophic links above the basal animal of mass M_0 .

When the typical mass Y of predators on animal prey of mass X is a power function

$$Y = f(X) = AX^B, \quad A > 0, \tag{16.1}$$

then by induction (letting \wedge denote exponentiation so that $a \wedge b$ means a^b)

$$f^n(M_0) = M_0^{B^n} \times [A \wedge \left(\sum_{m=0}^{n-1} B^m \right)] = M_0^{B^n} \times A^{(1-B^n)/(1-B)}. \tag{16.2}$$

The equality on the left of Eq. (16.2) is valid for any B . The equality on the right of Eq. (16.2) is valid when $B \neq 1$, since then $\sum_{m=0}^{n-1} B^m = (1 - B^n)/(1 - B)$. Were the consumer's mass directly proportional to the resource's mass according to $Y = AX$, i.e. were $B = 1$, then the mass of the consumer species would change by a factor of A with each additional link in the food chain and then $f^n(M_0) = A^n M_0$. Were $B = 0$, the mass of consumers would be constant and equal to A , regardless of their position in a food chain.

Assume henceforth that $0 < B < 1$, in addition to the previous assumption that $A > 0$. Then according to Eq. (16.1), consumer and resource would have equal body mass $X = f(X)$ when $X = A^{1/(1-B)}$, and this mass is strictly positive. This positivity guarantees that the intersection of the power law Eq. (16.1) with the diagonal line where $Y = X$ lies in the positive quadrant. In this model, a chain is a predator chain or a parasite chain according to whether $M_0 < A^{1/(1-B)}$ or $M_0 > A^{1/(1-B)}$.

With increasing trophic level, the masses of successive consumers approach the finite limit $A^{1/(1-B)} > 0$ (Fig. 16.1a) because the assumption $0 < B < 1$ implies $B^n \downarrow 0$ as $n \uparrow \infty$ and hence

$$\lim_{n \uparrow \infty} f^n(M_0) = A^{1/(1-B)}. \tag{16.3}$$

The limit Eq. (16.3) is a maximum if each consumer has a bigger mass than its resource, as assumed in a predator chain. The limit Eq. (16.3) is a minimum if each consumer has a smaller mass than its resource, as assumed in a parasite chain. The predicted maximal mass of a top predator is independent both of the number of links leading up to that predator and of the mass M_0 of the basal animal prey in the food chain. The predicted minimal mass of a parasite is independent both of the trophic level of that parasite and of the mass M_0 of the basal animal host in the food chain.

The limit $A^{1/(1-B)}$ is very sensitive to the values estimated for A and B . As $B \uparrow 1$, $A^{1/(1-B)} \uparrow \infty$. The values of A and B of course are not known exactly. They are usually estimated by a least-squares fit of the coefficients of the linear relation $y = a + bx$ where $y = \log_{10} Y$ and $x = \log_{10} X$. The parameters are connected by $A = 10^a$ but $B = b$.

For a given value of A , the closer B is to 1, the slower the approach to the limiting size as one proceeds along a food chain from successive resource to successive consumer (Mark Huxham, personal communication, 9 September 1995). So the limit $A^{1/(1-B)}$ may not be closely approached in reality when there are other limitations on food chain length.

According to this model of species-average body mass in food chains, in very long chains, the predators are mostly big, close in mass to the limiting maximum, and the parasites are mostly small, close in mass to the limiting minimum (Fig. 16.1a).

The removal from a predator chain of top predators shifts the size distribution of species-average body masses from one concentrated near the upper maximum to a more widely spaced distribution across the lower portions of the possible range of average body masses. This prediction could be compared with quantitative data on the body size distributions of North American vertebrate species before and after the major extinction of the megafauna and with quantitative data on the body size distributions of marine fauna before and after widespread industrial fishing.

This allometric model of species-average body masses has an implication for predator-parasite cycles. Assume that $M_{t+1} = AM_t^B$ along a predator chain of n links, $t = 0, \dots, n-1$, that the top predator is the starting point for a parasite chain of n links, i.e. $V_0 = M_n > \alpha^{1/(1-\beta)}$ and $V_{t+1} = \alpha V_t^\beta$, $t = 0, \dots, n-1$, with $\alpha > 0$, $0 < \beta < 1$ along the parasite chain. Then it turns out that M_0 can be less than, equal to, or greater than V_n . More generally, dropping the assumption that the predator chain and the parasite chain are of equal lengths, it is still possible for M_0 to be less than, equal to, or greater than V_n , as long as each chain is sufficiently long.

The case where $V_n = M_0$, i.e. where the basal prey of the predator chain weighs the same as the top parasite of the parasite chain, is illustrated numerically in Fig. 16.1b. In this case, if the basal prey and the top parasite were the same

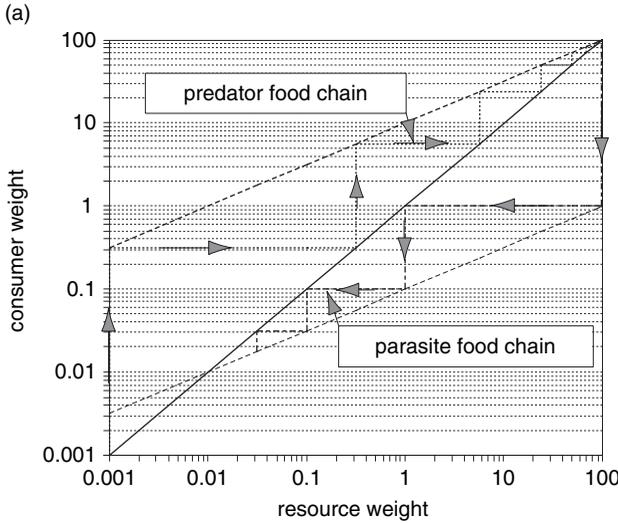


Figure 16.1 (a) Theoretical progression of body masses along a predator chain and a parasite chain. Arrows go from resource to consumer. Body masses are on logarithmic scales. The power-law relation Eq. (16.1) appears as a straight dashed line with slope B ; here, $B = 1/2$ for both predator chain ($A = 10$) and parasite chain ($A = 0.1$). On the solid diagonal line, consumer mass equals resource mass. Predator chains appear above the diagonal; parasite chains appear below the diagonal.

In the predator chain, an arbitrary small basal prey mass is chosen (in this example, $M_0 = 0.001$) and the corresponding predator mass M_1 is found by moving upward to the upper dash line. This predator is the prey of the predator at the next trophic level of the chain. The mass M_1 is located on the abscissa by moving horizontally right to the diagonal line. Then vertical upward motion to the upper dashed straight line gives the mass M_2 of the predator two links above the basal prey. Alternating horizontal right and vertical upward motions intersect the power function (upper dashed straight line) at the masses of successively higher predators in the predator chain. All such trajectories converge where the upper dashed line and the diagonal line intersect.

In the parasite chain, an arbitrary large basal host mass is chosen (in this example, $M_0 = 100$) and the corresponding parasite mass M_1 is found by moving down to the diagonal line. This parasite is the host of the parasite at the next trophic level of the chain. The mass M_1 is located on the abscissa by moving horizontally left to the diagonal line. Then moving down to the lower dashed straight line gives the mass M_2 of the parasite two links above the basal host. All such trajectories converge where the lower dashed line and the diagonal line intersect.

(b) Theoretical masses of species in a predator chain (open bars) and in a parasite chain (filled bars) where the top predator is the basal host, and the top parasite has the same mass as the basal prey. In the predator chain, $M_{n+1} = 10 M_n^{0.5}$ and the upper limit of mass is 100. In the parasite chain, $V_{n+1} = V_n^{0.5}$ and the lower limit of mass is 1. $M_0 = V_{10} = 1.004503$ and $M_{10} = V_0 = 99.55172$.

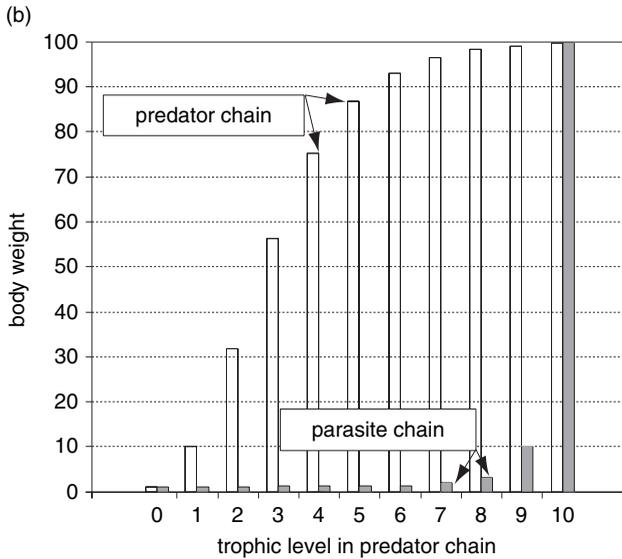


Figure 16.1 (cont.)

species, the predator chain and the parasite chain would be linked in a predator-prey cycle. On the linear scale of mass used in Fig. 16.1b, after the first few trophic levels in both the predator chain and the parasite chain, the consumers are near in mass to the limiting mass.

Predicted value of the exponent

The exponent B may be computed exactly for simple models of the distribution of the pairs (x, y) , where $x = \log_{10} X$ and $y = \log_{10} Y$ are log prey (or host) mass and log predator (or parasite) mass, respectively. Suppose x_{min} is the \log_{10} minimal observed species average mass and x_{max} is the \log_{10} maximal species average mass. The previous theory predicts that $x_{max} = \log_{10}(A^{1/(1-B)})$ but the following calculations hold whether or not that prediction is true.

The slope of any linear relation between y and x will be unaffected if both x and y are replaced by the identical linear transformation of x and y , so no generality is lost by assuming that $x_{min} = 0$ and $x_{max} = 1$. Then each trophic link from resource to consumer may be represented by a dot in a square in the (x, y) plane with lower left corner at the origin $(0, 0)$ and upper right corner at $(1, 1)$. The diagonal of the square is the locus of points where consumer body mass equals resource body mass. Suppose that trophic links are uniformly and independently distributed over this square, and that all links above the diagonal are in predator chains and all links below the diagonal are in parasite chains. Then, in a predator chain, for a given x (between 0 and 1), the expected y is halfway between the diagonal and the upper horizontal edge of the square, that is, $E(y|x) = x + (1/2)(1 - x) = 1/2 + x/2$. Thus the slope of average y as a linear function

of x is predicted to be $B = 1/2$. Similarly, in a parasite chain, for a given x (between 0 and 1), the expected y is halfway between the diagonal and the *lower* horizontal edge of the square, that is, $E(y|x) = x/2$. The slope of average y as a linear function of x is again predicted to be $B = 1/2$.

In the part of this model that pertains to a predator chain, the assumption that each trophic link is uniformly and independently distributed in the triangle above the diagonal follows from the cascade model (Cohen, Briand & Newman, 1990) in the continuous limit (possibly with additional assumptions) of many species of predators and prey. The cascade model assumes that all species are ordered by something interpreted here as body mass, and that each consumer species consumes with equal probability and independently every species smaller than it. (The cascade model does not attempt to describe parasite chains because it was intended to account for food-web data that ignored parasites.) The continuous limit of the joint distribution of prey-to-predator links posited in the cascade model is (possibly with additional assumptions) a two-dimensional distribution of trophic links that is uniform in the upper triangle above the diagonal from (0, 0) to (1, 1) in the unit square in the plane where $x = \log_{10} X$ and $y = \log_{10} Y$, as supposed in the previous paragraph.

For parasite chains, to derive a distribution of trophic links in the (x, y) plane that is uniform over the triangle *below* the diagonal, as supposed above, all that is required is to reverse the ordering by body size in the argument just given for predator chains.

When the pairs (x, y) are not distributed uniformly but lie in a band parallel to the diagonal, the predicted slope B will move from $1/2$ toward 1. Such a band parallel to the diagonal would arise if there were a nearly constant ratio of average body mass between consumer (predator or parasite) and resource. When the pairs (x, y) lie in a band parallel to the x axis (because most predator species are roughly the same size, or most parasite species are roughly the same size), the predicted slope B will move from $1/2$ toward 0.

Ratios and differences of consumer mass and resource mass

Let $R = Y/X = AX^{B-1}$ be the ratio of consumer mass to resource mass in a single trophic link. Then R is a decreasing power-law function of X . The exponent $B - 1$ is negative because $B < 1$. A regression of $\log R$ on $\log X$ is predicted to have a slope exactly one less than the slope of a regression of $\log Y$ on $\log X$, for the same set of data. The ratio R decreases (towards a limit of 1) with increasing trophic level of the prey in predator chains. In parasite chains, because body masses decrease with increasing trophic level, the ratio R increases towards a limit of 1 with increasing trophic level of the host.

The difference in masses behaves in a more complex way than the ratio of masses, as the following analysis shows. Let $D = Y - X = (R - 1)X$ be the difference between the consumer mass Y and the resource mass X in a single

trophic link. (In predator chains, $D > 0$. In parasite chains, $D < 0$.) Because $dD/dX = RB - 1$, the difference D increases with increasing resource mass X if and only if $R > 1/B$. The smaller B is, the bigger R must be for D to increase with X . As $B < 1$, a necessary condition for D to increase with X is that $R > 1$, and this happens only in predator chains. Thus, in predator chains, the difference D in mass between consumer and resource may increase with increasing trophic position (if initially $R > 1/B$); but once $R \leq 1/B$, the difference D will thereafter decrease (towards a limit of 0) with increasing trophic position. By contrast, in parasite chains, where $R < 1$ and $B < 1$, it follows that $RB - 1 < 0$ always; hence with increasing trophic level (and therefore decreasing body mass), D is always increasing (from negative values towards a limit of 0), that is, host mass minus parasite mass is always positive and decreases towards a limit of 0.

Data

The data presented here deal only with food webs (cross-linked food chains), rather than with isolated food chains. The theory is relevant to these food webs in so far as food chains are a first approximation to more complex food webs. First, two examples of data on the masses of animal predators and their animal prey in a particular community will be analyzed. Then some data will be examined from literature surveys of pooled communities of specified habitat types (terrestrial and coastal). A recent database of the masses of consumers and resources (Brose *et al.*, 2005) has been analyzed by Brose *et al.* (2006).

Studies of a well-defined community

Menge *et al.* (1986) described the food web and the masses of the animals of a tropical Panamanian rocky intertidal community. From 31 data points (Fig. 16.2a), hand-read in part from their published graphs, linear regression of \log_{10} masses yielded $a = 2.2334$ (with 95% confidence interval (1.80, 2.67)), and $b = 0.4819$ (with 95% confidence interval (-0.19, 1.15)).

The geometric mean mass Y (kg) of animal predators on animal prey of mass X would be estimated from these data as $Y = 0.1712X^{0.4819}$ and the upper limit in mass $A^{1/(1-B)}$ for the largest predator would be nearly 20.4 kg. The largest observed predator in the data weighed just under 2 kg. The 95% confidence interval for B includes both 0 and 1. If the data satisfy the assumptions of the underlying regression model well enough to justify the conclusion that the asserted confidence interval really has probability 95%, then these data do not specify an allometric relation with sufficient precision to have the predictive upper limit falsified by any finite maximal predator mass.

A simple sensitivity calculation, referred to below as 'the 10% sensitivity range,' confirms a wide range of uncertainty in the upper limit. If the regression intercept $\log A$ and the regression slope B are both replaced by 90% of their estimated values, the maximal predator mass $A^{1/(1-B)}$ is 3.5 kg. If the regression

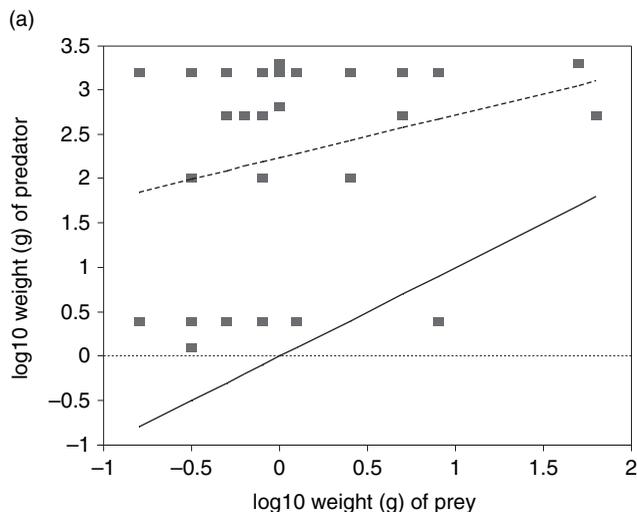


Figure 16.2 (a) Predator masses and prey masses in trophic links of a tropical rocky intertidal food web described by Menge *et al.* (1986). The solid diagonal line indicates where predator and prey masses are equal; all but one of the trophic links fall above this line. The upper dashed line is the regression line: $\log_{10}(\text{predator mass, g}) = 2.2334 + 0.4819 \log_{10}(\text{prey mass, g})$. The regression line is obtained by ordinary least squares using the log-transformed masses; the standard error of the slope coefficient is 0.3268. The data are read from Menge *et al.* (1986); the analysis and figure are original.

(b, c) Prey and predator body mass (kg) in Tuesday Lake in (b) 1984 and (c) 1986, one marker for every trophic link in the unlumped food web. Cannibalistic links are excluded. Dotted line indicates equal prey and predator body mass. The links are coded according to the prey: circles = phytoplankton, squares = zooplankton, stars = fish. For 1984, the regression coefficients were $a = 1.5598$, $b = 0.8445$, with correlation $r = 0.7859$ and 263 trophic links (Jonsson *et al.*, 2005, p. 34). For 1986, the regression coefficients were $a = -1.4108$ and $b = 0.5928$, with correlation $r = 0.6094$ and 233 trophic links.

(d) Regression lines from (b, solid diamonds) and (c, open squares) plotted over the approximate range from the mass of the smallest observed organism to the mass where predator and prey are equal.

Figure 16.2b is reprinted from Cohen *et al.* (2003) with permission from the National Academy of Sciences. Figure 16.2c is reprinted from Jonsson *et al.* (2005), copyright 2005 by T. Jonsson, J. E. Cohen, S. R. Carpenter. Figure 16.2d is original.

intercept $\log A$ and the regression slope B are both replaced by 110% of their estimated values, the maximal predator mass is 169.2 kg. Combining 90% of $\log A$ with 110% of B and vice versa yields a narrower range of uncertainty from 19.0–21.8 kg. When a plausible range of the predicted maximal size is as large as the 10% sensitivity range, from 3.5–169.2 kg, only order-of-magnitude agreement between predictions and observations should be expected, at best.

If seals or sea lions are occasionally part of the rocky intertidal community, the average body mass of those consumers could be compared with the limit

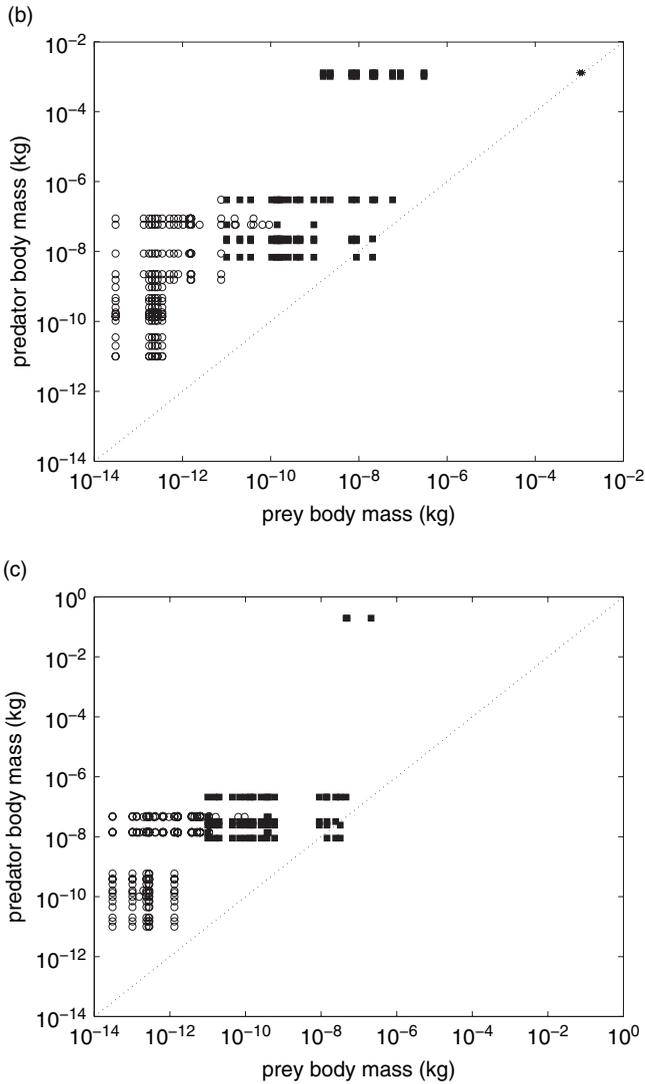


Figure 16.2 (cont.)

predicted here. For example, adult Galápagos fur seal females *Arctocephalus galapagoensis* average about 28 kg in body mass (Horning & Trillmich, 1997). Galápagos fur seal bulls average about 70 kg in body mass (http://www.tamug.tamu.edu/labbb/Galapagos/GFSwork/GFS_work.htm, accessed 27 August 2005).

Cohen *et al.* (2003), Reuman and Cohen (2004), Jonsson, Cohen and Carpenter (2005), Reuman and Cohen (2005), and Cohen and Carpenter (2005) analyzed the community food web, the numerical abundance and the average body size of species in the pelagic community of a small lake, Tuesday Lake, in Michigan. The raw data on the food web, average body mass and numerical abundance by

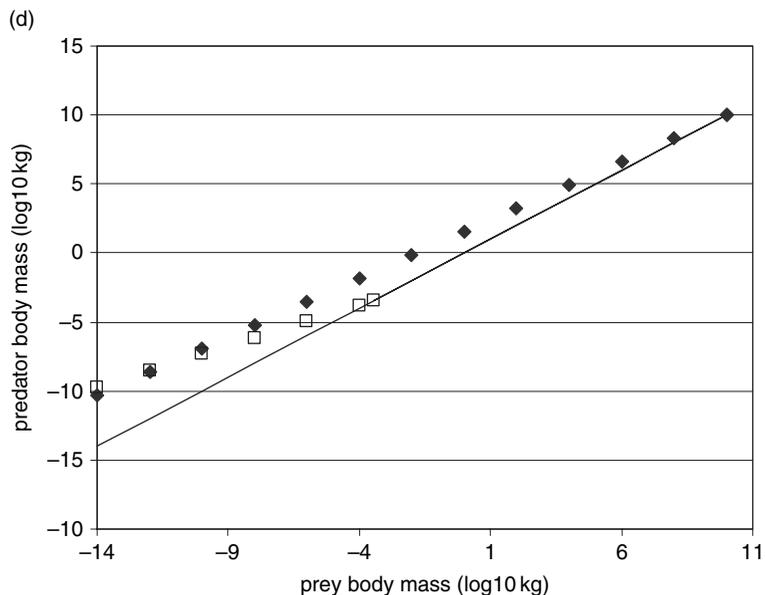


Figure 16.2 (cont.)

species are given by Jonsson *et al.* (2005). Tuesday Lake was intensively sampled during the summers of 1984 and 1986. During the summer of 1985, the three resident species of fishes were largely removed and replaced by a fourth fish species, which consumed the remaining individuals of the original three fish species. In addition to the complete turnover of the fish species present in Tuesday Lake between 1984 and 1986, the other species in the lake also changed dramatically between 1984 and 1986 (Jonsson *et al.*, 2005, p. 23).

Almost all predators had larger average body mass than their prey in 1984 (Fig. 16.2b) and 1986 (Fig. 16.2c). The calculated upper limit in 1984 exceeds 10.7×10^9 kg, far in excess of the largest average species mass observed in 1984, namely, 1.29×10^{-3} kg, or 1.29 g. The upper limit in 1986, 0.34×10^{-3} kg, or 0.34 g, was exceeded by the average body mass, 1.95×10^{-1} kg, of the largest species, the introduced fish *Micropterus salmoides*. The average body mass of this fish also exceeded the upper limit of the 10% sensitivity range. The allometric model of the relationship between predator and prey mass was probably less adequate in 1986 than in 1984: the correlation (on log-log scales) between predator and prey masses dropped notably from 1984 to 1986. Following the complete manipulation of the fish fauna in 1985, the pelagic community may have been observed in 1986 during a transient response to the manipulation. The regression lines before and after the manipulation appear in Fig. 16.2d.

While the predator-prey pairs of Cohen *et al.* (1993) could reasonably be seen as uniformly distributed in the upper triangle of the square in the (x, y) plane, these trophic links were pooled from a variety of different communities. The

predator–prey pairs from Tuesday Lake (Figs. 16.2b, c) and some other individual communities indicate that the pairs (x, y) may sometimes lie in a band parallel to the diagonal (Reuman & Cohen, 2004, p. 857). The non-parasite data from Ythan estuary (Leaper & Huxham, 2002, p. 447) seem to be intermediate between lying in an upper triangle and lying in a band parallel to the diagonal; they are distributed in a wedge shape.

Studies that pool multiple communities

Numerous studies have collected masses of organisms in defined taxonomic groups from scattered published sources and identified trophic links based on reports of feeding habits, without reference to whether the organisms would be likely to occur within a single habitat at any single time (e.g. Schoener, 1968; Peters, 1983; Vézina, 1985; Hansen, Bjórnsen & Hansen, 1994).

Other studies have combined community studies and literature surveys (e.g. Warren & Lawton, 1987; Cohen *et al.*, 1993; Jonsson & Ebenman, 1998a; Brose *et al.*, 2006). Cohen *et al.* (1993) presented two independently collected sets of data on the sizes of animal predators and prey in multiple community food webs. Data set A gave average adult masses of predators and prey in 354 trophic links from 18 community food webs. Data set B gave lengths of prey and predators in 478 trophic links from 30 webs of a compendium of sink, source and community webs. In roughly 90% of the trophic links reported in food webs from terrestrial, coastal, freshwater and marine habitats, the body mass of an animal predator exceeded that of its animal prey. Figure 16.3a compares the estimated regression lines of 109 trophic links from coastal webs in data set A, ten trophic links from coastal webs in data set B, and 31 trophic links from Menge *et al.* (1986). All three regression slopes are less than $1/2$. The predicted largest predator from coastal data sets A and B would weigh, respectively, 0.4 kg (10% sensitivity range 0.2–0.8 kg) and 54.0 kg (10% sensitivity range 11.6–293 kg).

Figure 16.3b compares the estimated regression lines of 48 trophic links from terrestrial webs in data set A, 162 trophic links from terrestrial webs in data set B, and a line hand-fitted to graphed terrestrial data from Vézina (1985). All three regression slopes are greater than $1/2$. The predicted largest predator from terrestrial data set A would weigh 23.8 kg (10% sensitivity range 3.6–247 kg). Because the slope for data set B is so close to 1, the predicted maximal predator mass is meaningless. For the estimates from Vézina's data, the largest predator would weigh 168 kg (10% sensitivity range 13.5–4660 kg). For comparison, the heaviest terrestrial vertebrate predator in Vézina's data is the East African lion (*Panthera leo*), which weighs 160 kg.

The eight empirical regression lines of log predator weight as a function of log prey weight plotted in Figs. 16.2 and 16.3 have slopes ranging from 0.1463 to 0.9443, with median value 0.5489, not far from the predicted value of $1/2$.

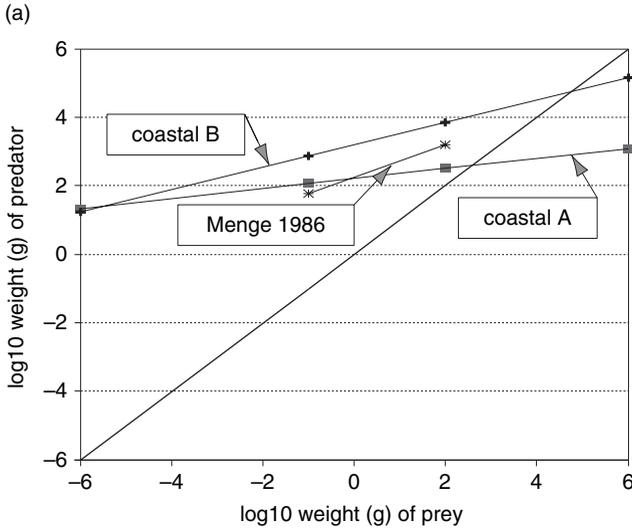


Figure 16.3 (a) Regression lines of predator masses and prey masses in trophic links in three sets of coastal food webs. The regression line for Menge *et al.* (1986) is taken from Fig. 16.2a. The regression lines for coastal A and coastal B are computed from the statistics of Cohen *et al.* (1993, p. 71, Table 2). Lengths reported in data set B were converted to masses, assuming spherical geometry, by $\log_{10}(\text{mass}) = \log_{10}(\pi/6) + 3 \log_{10}(\text{length})$. Although the regression lines for coastal A and coastal B extend to the right of the diagonal line where predator and prey masses are equal, roughly 90% of the data points fell above and to the left of the diagonal. The coastal A regression line is: $\log_{10}(\text{predator mass, g}) = 2.2114 + 0.1463 \log_{10}(\text{prey mass, g})$. The coastal B regression line is: $\log_{10}(\text{predator mass, g}) = 3.1985 + 0.3241 \log_{10}(\text{prey mass, g})$.

(b) Regression lines of predator masses and prey masses in trophic links in three sets of terrestrial food webs. Procedures of Fig. 16.3a apply here. The terrestrial A regression line is: $\log_{10}(\text{predator mass, g}) = 2.1105 + 0.5177 \log_{10}(\text{prey mass, g})$. The terrestrial B regression line is: $\log_{10}(\text{predator mass, g}) = 1.9924 + 0.9443 \log_{10}(\text{prey mass, g})$. Vézina (1985) gave numerically only a range of masses for predators and no masses for their prey. Here a single straight line was fitted by hand to Vézina's graph of the data for insectivores, piscivores and carnivores, and the hand-fitted straight line for the data of Vézina (1985) is: $\log_{10}(\text{predator mass, g}) = 2.19 + 0.58 \log_{10}(\text{prey mass, g})$.

Jonsson and Ebenman (1998a) computed the ratio of predator mass to prey mass for all trophic links for which both masses were known using 768 consumer species (697 trophic species) in 52 community food webs. Their finding that, for most food webs, the higher the trophic level of the predator, the smaller the predator-prey mass ratio, agrees with the theory developed here for isolated food chains if higher trophic level correlates closely with higher body mass. It will be desirable to re-examine this asserted pattern using the data of Brose *et al.* (2005).

Data on parasite and parasitoid food webs and body sizes appear to be scarce. Memmott *et al.* (2000) reported a source food web of a broom community that

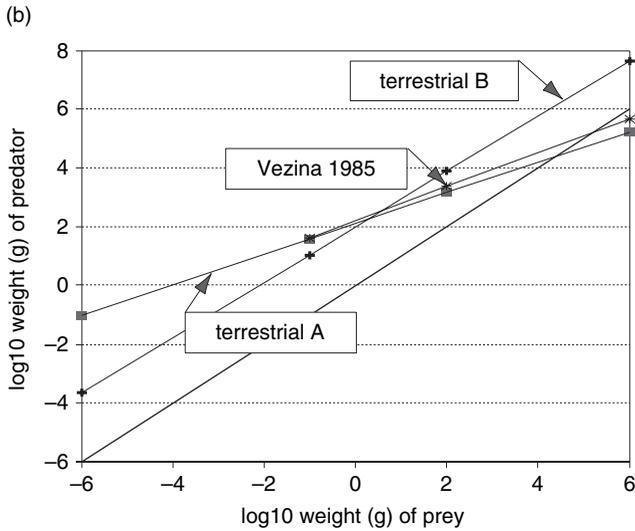


Figure 16.3 (cont.)

contained one plant species, 19 herbivores, 66 parasitoids, 60 predators, five omnivores and three pathogens. They plotted log consumer-species length as a function of log resource-species length with separate symbols for parasitoids, pathogens and predators (their Fig. 7) but they did not report estimates of allometric relations nor list the length data, though they did provide the food-web data. According to Leaper and Huxham (2002), the web reported by Memmott *et al.* (2000) was the first and until 2002 the only published food web to present body masses for both parasites (in fact, they were parasitoids) and other consumers. Leaper and Huxham (2002) calculated but did not publish body masses of 160 of the 171 taxa in the food web of the Ythan estuary: 113 average adult body weights and mean weights for the given life-history stage of the remaining 47 taxa. They reported Pearson's r^2 for \log_{10} consumer and \log_{10} resource body masses for six versions of the web: including non-parasites only, parasites only, and all taxa; and for each group of taxa, with and without distinguishing life stages according to their trophic relations. No regression coefficients of \log_{10} consumer body mass on \log_{10} resource body mass were given. The correlations were positive in all cases and were statistically significantly different from zero at the 0.001 level except for parasites only, disregarding differences among life stages.

Discussion

Hutchinson (1959, p. 147) examined 'the order of magnitude of the diversity that a single food chain can introduce into a community'. It is worthwhile to revisit his influential calculations in the light of data and theory available since he wrote. Hutchinson assumed that 'in general 20 per cent of the energy passing

through one [species] can enter the next [species] in the chain' and that 'each predator has twice the mass (or 1.26 the linear dimensions) of its prey, which is a very low estimate of the size difference between links . . .' This assumption may be represented in the model Eq. (16.1) by putting $A = 2$ and $B = 1$. This model led Hutchinson (1959, p. 147) to envisage the 'ultimate predator' at trophic level 49, with an individual body size 'vastly greater than the volume of the world ocean'. Hutchinson then implicitly assumed that the numerical abundance N , or population size, of each animal species in a predator food chain equals the total energy available divided by the typical body size M , which is tantamount to assuming that the energy consumption of each animal species is directly proportional to its typical body size M . With each increase in the trophic level of species in a predator chain, according to Hutchinson's assumptions, 20% as much energy has to be divided among the organisms each twice as big. The population size therefore is reduced by a factor of $0.2/2 = 0.1$, i.e. decreases by 90%. Consequently, Hutchinson concluded, the population size or numerical abundance N_4 of the fifth animal species will be 10^{-4} times the population size N_0 of the first. In this hypothetical world, food chains cannot be very long.

Hutchinson's assumptions imply an allometric relation between numerical abundance (or population size) and average body mass. Along a trophic link from any species 1 to any species 2, Hutchinson assumes that $M_2 = 2M_1$ (mass doubles) while $N_2 = (1/10)N_1$ (numerical abundance falls by 90%). The slope of the allometric relation between numerical abundance and body mass is then:

$$\begin{aligned} \Delta \log_{10}(N)/\Delta \log_{10}(M) &= [\log_{10}(N_2) - \log_{10}(N_1)]/[\log_{10}(M_2) - \log_{10}(M_1)] \\ &= -\log_{10}(10)/\log_{10}(2) = -3.32. \end{aligned} \quad (16.4)$$

Each step in Hutchinson's argument has been re-examined. Pauly and Christensen (1995) estimated a mean trophic transfer efficiency of 10% (half Hutchinson's estimate of 20%). Rather than doubling with each trophic link, animal body size in a predator chain is more likely to be described by Eq. (16.2) with $A > 0$, $0 < B < 1$, neglecting the substantial variability in the size of predators on prey of a given size. Animal metabolic energy requirements increase approximately in proportion to $M^{3/4}$ rather than to M (Kleiber, 1961). In Tuesday Lake, Michigan, the regression of $\log_{10}(N)$ on $\log_{10}(M)$ had slope -0.8413 (with 99% confidence interval $-0.98, -0.71$) in 1984 and slope -0.7461 (with 99% confidence interval $-0.91, -0.59$) in 1986 (Reuman & Cohen, 2004). These slopes are far from the slope of -3.32 that follows from Hutchinson's assumptions. Cohen and Carpenter (2005) showed that the statistical assumptions underlying linear regression were justified for Tuesday Lake data in regressions of $\log_{10}(N)$ on $\log_{10}(M)$ but not vice versa.

If animal population size were constrained by available energy alone, as Hutchinson supposed, and if the food chain were isolated from all other food chains to or from which energy might be diverted, then, in principle, a better

formula than Hutchinson's for the ratio of the population size or numerical abundance N_n at trophic level n to the numerical abundance N_0 of the basal animal in a predator chain would appear (for the moment) to be:

$$N_n/N_0 = (M_0/M_n)^{3/4} (0.1)^n \quad (16.5)$$

and the slope of the relation between numerical abundance and body mass is predicted by these assumptions to be:

$$\begin{aligned} \Delta \log_{10}(N)/\Delta \log_{10}(M) &= [\log_{10}(N_{n+1}) - \log_{10}(N_n)]/[\log_{10}(M_{n+1}) - \log_{10}(M_n)] \\ &= -3/4 + 1/\log_{10}(M_{n+1}/M_n). \end{aligned} \quad (16.6)$$

For large n , M_0/M_n approaches a constant (less than 1) and the ratio Eq. (16.5) declines by a factor of 0.1 with each increase in trophic level. Apparently by coincidence, this is exactly the behaviour Hutchinson calculated. That is the good news. The rest of the news is bad, and gets worse. For small n , Eq. (16.5) predicts a slower-than-exponential decline, unlike Hutchinson's calculation. For large n , $M_{n+1}/M_n \rightarrow 1$ so $\log_{10}(M_{n+1}/M_n) \rightarrow 0$ and the right side of Eq. (16.6) diverges to infinity, clearly an unrealistic prediction.

Evidently the assumptions stated just before Eq. (16.5) do not hold in the real world. One weak assumption is that the predator chain is energetically isolated from all other food chains. In addition, the population sizes of species, especially species with small body sizes, are often not limited by energy (Blackburn, Lawton & Pimm, 1993; Blackburn & Lawton, 1994). While large-bodied animal species are usually rare, small-bodied animal species commonly have a wide range of population sizes, from abundant to rare. Overall, Hutchinson's argument that a predator chain (and by his off-hand extension, a parasite chain) 'clearly . . . of itself cannot give any great diversity' founders in the face of more recent facts and models.

For three collections of data from coastal communities, $0 < b < 1/2$, while for three collections of data from terrestrial communities, $1/2 < b < 1$. Is this difference true in general? If confirmed by data of better quality from more communities, then a kilogram of resource supports a predator of larger body mass in a terrestrial community than in a coastal community. Why is this?

The starting hypothesis here is that the mass of the consumer (predator or parasite) is related to the mass of the animal resource (prey or host) by a power law with exponent less than 1. This hypothesis is at best an approximation to reality, on both empirical and theoretical grounds (Cohen *et al.*, 1993). Empirically, large predators sometimes eat prey of a wide range of masses while small predators eat prey with a narrower range of masses (as in Figs. 1 and 2 of Cohen *et al.*, 1993). However, in Tuesday Lake, observed trophic links appear to fall in a band above and parallel to the diagonal line where predator mass equals prey mass, rather than in a triangular region in the (x, y) plane (Reuman & Cohen, 2004). Approximating both such relations by a power-law

function ignores the apparent differences between them in how the variance in predator mass changes with the mass of the prey.

The only direct evidence on how well a power-law relation describes body masses in parasite chains is Fig. 1 of Leaper and Huxham (2002, p. 447). Their scatter plots for parasites only in the Ythan estuary provide weak support for the usefulness of a power-law approximation. For log parasite size and log host size of parasites only, without trophospecies $r^2 = 0.015$ was not significant, and with trophospecies $r^2 = 0.125$ was statistically significant but still small.

An approximate power law with exponent less than 1 has been derived theoretically from models of food-web structure, species abundance distributions, and the distribution of biomass across species mass categories (Cohen, 1991, pp. 5–8). Cohen *et al.* (1993) suggested that the logarithm of animal species masses may be approximately normally distributed, and that $E(y|x)$ is the mean of a normal distribution censored below x (i.e. retaining only that portion of the normal distribution to the right of x). Unpublished numerical calculations show that, under this model, $E(y|x)$ is a convex nonlinear function (always with slope less than 1) of x , rather than a strictly linear function as expected by the power-law relation Eq. (16.1). With the observed distribution of body mass reported by Cohen *et al.* (1993, p. 73, their Table 4), the power law approximates reasonably the convex nonlinear function in the range of animal body masses from 10^{-6} g to 10^{+6} g.

Terrestrial vertebrate predators far larger than contemporary top carnivores lived in the past (Burness, Diamond & Flannery, 2001). It would be interesting to determine whether predator and prey masses during the Cretaceous and late Pleistocene are consistent with a power law Eq. (16.1); if so, whether the coefficients A and B had different values from those estimated here; and if so, whether the maximum predator mass at that time could be predicted from the predator–prey body mass relations then in effect.

Jonsson and Ebenman (1998b) suggested that the decrease they observed (Jonsson & Ebenman, 1998a) in the ratio of predator mass to prey mass with increasing trophic level in predator chains has significant consequences for stability in dynamic models of food chains. This suggestion could be extended to parasite chains, and merits further analysis and testing.

The derivation of maximal body mass from the phenomenology of body sizes in trophic links is only one among many possible approaches. Other constraints on maximal body mass include mechanical or design constraints, energetics of food supply and metabolism, land area (for terrestrial consumers), natural selection of life histories and the processes of development (e.g. Bonner, 1988; Yoshimura & Shields, 1995; Burness, Diamond & Flannery, 2001; Gomer, 2001). It remains to be demonstrated whether, and if so how, these approaches are compatible.

To summarize, food chains in which animal predators are bigger than their animal prey are called predator chains. Food chains in which the consumers are

smaller than their animal prey are called parasite chains. If the mass of the consumer (predator or parasite) is related to the mass of the animal resource (prey or host) by a power law with exponent less than 1, then, in predator chains, there is an upper limit to the mass of the largest predator and prey, and in parasite chains, there is a lower limit to the mass of the smallest host and parasite. These limits are independent of the number of trophic links in the chain and independent of the mass of the basal animal species. In a predator chain that obeys this allometric relation of predator and prey masses, the ratio of predator mass to prey mass decreases as the trophic level and mass of the prey increase. In a parasite chain that obeys this allometric relation of predator and prey masses, the ratio of parasite mass to host mass increases as the trophic level of the host increases and the mass of the host decreases. In the data on predator chains here, predator masses generally exceed prey masses. The regression of the logarithm of predator mass on the logarithm of prey mass has slope b less than 1 in all cases. While it is possible to calculate maximal predator sizes from these regressions, estimates of maximal predator size are highly sensitive to uncertainty in the parameters of the regression lines. For three collections of data from coastal communities, $0 < b < 1/2$, while for three collections of data from terrestrial communities, $1/2 < b < 1$. A model of the joint distribution of consumer and resource body masses predicts a slope of $1/2$ for both predator and parasite chains, and specifies conditions under which the slope should deviate up or down from $1/2$. The theory developed here pertains to isolated chains, but all the data are drawn from webs with interconnecting chains. An ideal test of the theory would describe the full frequency distribution of body sizes of each species in a more or less isolated chain, if such can be found in nature. It would also be useful to extend the theory from isolated chains to more complex food webs and to analyze the consequences in the variability of body sizes of both resources and consumers.

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References

- Blackburn, T. M. & Lawton, J. H. (1994). Population abundance and body size in animal assemblages. *Philosophical Transactions of the Royal Society of London Series B*, **343**, 33–39.
- Blackburn, T. M., Lawton, J. H. & Pimm, S. L. (1993). Non-metabolic explanations for the relationship between body size and animal abundance. *Journal of Animal Ecology*, **62**, 694–702.

- Bonner, J. T. (1988). *The Evolution of Complexity*. Princeton, NJ: Princeton University Press.
- Brose, U., Cushing, L., Berlow, E. L. *et al.* (2005). Body sizes of consumers and their resources. *Ecology*, **86**, 2545.
- Brose, U., Jonsson, T., Berlow, E. L. *et al.* (2006). Consumer-resource body-size relationships in natural food webs. *Ecology*, **87**, 2411–2417.
- Burness, G. P., Diamond, J. & Flannery, T. (2001). Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proceedings of the National Academy of Sciences*, **98**, 14518–14523.
- Cohen, J. E. (1991). Food webs as a focus for unifying ecological theory. *Ecology International (International Association for Ecology Bulletin)*, **19**, 1–13.
- Cohen, J. E. & Carpenter, S. R. (2005). Species' average body mass and numerical abundance in a community food web: statistical questions in estimating the relationship. In *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development and Environmental Change – A Volume of Theoretical Ecology*, ed. P. C. de Ruiter, V. Wolters & J. C. Moore. Amsterdam: Elsevier, pp. 137–156.
- Cohen, J. E., Briand, F. & Newman, C. M. (1990). *Community Food Webs: Data and Theory*. *Biomathematics* Vol. 20. Heidelberg, Berlin, New York: Springer-Verlag.
- Cohen, J. E., Pimm, S. L., Yodzis, P. & Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, **62**, 67–78.
- Cohen, J. E., Jonsson, T. & Carpenter, S. R. (2003). Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences*, **100**, 1781–1786.
- Cohen, J. E., Jonsson, T., Müller, C. B., Godfray, H. C. J. & Savage, V. M. (2005). Body sizes of hosts and parasitoids in individual feeding relationships. *Proceedings of the National Academy of Sciences*, **102**, 684–689.
- Elton, C. (1927). *Animal Ecology*. (New impression with additional notes 1935.) New York: Macmillan.
- Gomer, R. H. (2001). Not being the wrong size. *Nature Reviews Molecular Cell Biology*, **2**, 48–54.
- Hansen, B., Björnsten, P. K. & Hansen, P. J. (1994). The size ratio between planktonic predators and their prey. *Limnology and Oceanography*, **39**, 395–403.
- Horning, M. & Trillmich F. (1997). Development of hemoglobin, hematocrit and erythrocyte values in Galápagos fur seals. *Marine Mammal Science*, **13**, 100–113.
- Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.
- Jonsson, T. & Ebenman, B. (1998a). Trophic links and the relationship between predator and prey body sizes in food webs. Chapter 2 in T. Jonsson, *Food Webs and the Distribution of Body Sizes*. Linköping Studies in Science and Technology, Dissertation 535, Linköping, Sweden, pp. 63–81.
- Jonsson, T. & Ebenman, B. (1998b). Effects of predator-prey body size ratios on the stability of food chains. *Journal of Theoretical Biology*, **193**, 407–417.
- Jonsson, T., Cohen, J. E. & Carpenter, S. R. (2005). Food webs, body size and species abundance in ecological community description. In *Food Webs: From Connectivity to Energetics, Advances in Ecological Research* Vol. 36, ed. H. Caswell. San Diego: Elsevier, pp. 1–84.
- Kleiber, M. (1961). *The Fire of Life: An Introduction to Animal Energetics*. New York: John Wiley.
- Leaper, R. & Huxham, M. (2002). Size constraints in a real food web: predator, parasite and prey body-size relationships. *Oikos*, **99**, 443–456.
- Memmott, J., Martinez, N. D. & Cohen, J. E. (2000). Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*, **69**, 1–15.

- Menge, B. A., Lubchenco, J., Gaines, S. D. & Ashkenas, L. R. (1986). A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. *Oecologia* (Berlin), **71**, 75–89.
- Pauly, D. & Christensen, V. (1995). Primary production required to sustain global fisheries. *Nature*, **374**, 255–257.
- Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Reuman, D. C. & Cohen, J. E. (2004). Trophic links' length and slope in the Tuesday Lake food web with species' body mass and numerical abundance. *Journal of Animal Ecology*, **73**, 852–866.
- Reuman, D. C. & Cohen, J. E. (2005). Estimating relative energy fluxes using the food web, species abundance, and body size. In *Food Webs: From Connectivity to Energetics, Advances in Ecological Research* Vol. 36, ed. H. Caswell. San Diego: Elsevier, pp. 137–182.
- Rott, A. S. & Godfray, H. C. J. (2000). The structure of a leafminer-parasitoid community. *Journal of Animal Ecology*, **69**, 274–289.
- Schoener, T. W. (1968). Size of feeding territories among birds. *Ecology*, **49**, 123–141.
- Sheldon, R. W., Prakash, A. & Sutcliffe, W. H., Jr. (1972). The size distribution of particles in the ocean. *Limnology and Oceanography*, **17**, 327–340.
- Vézina, A. F. (1985). Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia* (Berlin), **67**, 555–565.
- Wallace, A. R. (1858). On the tendency of varieties to depart indefinitely from the original type. In C. R. Darwin & A. R. Wallace, On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *Journal of the Proceedings of the Linnean Society, Zoology*, 20 Aug. 1858, **3**, 45–62. Online: <http://pages.britishlibrary.net/charles.darwin3/jpls.html#natsel>
- Warren, P. H. & Lawton, J. H. (1987). Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* (Berlin), **74**, 231–235.
- Yoshimura, J. & Shields, W. M. (1995). Probabilistic optimization of body size: a discrepancy between genetic and phenotypic optima. *Evolution*, **49**, 375–378.