34 Stenseth, N.C. (1999) Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87, 427–461

35 Dennis, B. *et al.* (2001) Estimating chaos and complex dynamics in an insect population. *Ecol. Monogr.* 71, 277–303

36 Bjornstad, O.N. *et al.* (2001) The impact of specialized enemies on the dimensionality of host dynamics. *Nature* 409, 1001–1006

37 Leslie, P.H. (1959) The properties of a certain lag type of population growth and the influence of an external random factor on a number of such populations. *Physiol. Zool.* 32, 151–159

38 Berryman, A.A. (1996) What causes population cycles of forest Lepidoptera? *Trends Ecol. Evol.* 11, 28–32

39 Ginzburg, L.R. and Taneyhill, D.E. (1994) Population cycles of forest Lepidoptera – a maternal effect hypothesis. *J. Anim. Ecol.* 63, 79–92

40 Inchausti, P. and Ginzburg, L.R. (1998) Small mammals cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. *J. Anim. Ecol.* 67, 180–194

41 Erelli, M.C. and Elkinton, J.S. (2000) Maternal effects on gypsy moth (Lepidoptera: Lymantriidae) population dynamics: a field experiment. *Environ. Entomol.* 29, 476–488

42 Diss, A.L. *et al.* (1996) Effects of maternal nutrition and egg provisioning on parameters of larval hatch, survival and dispersal in the gypsy moth, *Lymantria dispar* L. *Oecologia* 106, 470–477

43 Turchin, P. and Hanski, I. (2001) Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol. Lett.* 4, 267–276

44 Crone, E.E. (1997) Delayed density dependence and the stability of interacting populations and subpopulations. *Theor. Popul. Biol.* 51, 67–76

45 Benton, T.G. *et al.* (2001) Maternal effects and the stability of population dynamics in noisy environments. *J. Anim. Ecol.* 70, 590–599

46 Fox, C.W. and Savalli, U.M. (1998) Inheritance of environmental variation in body size: superparasitism of seeds affects progeny and grandprogeny body size via a nongenetic maternal effect. *Evolution* 52, 172–182

47 Agrawal, A.A. (2001) Transgenerational consequences of plant responses to herbivory: an adaptive maternal effect? *Am. Nat.* 157, 555–569

48 Benton, T.G. *et al.* The population response to environmental noise: population size, variance and correlation in an experimental system. *J. Anim. Ecol.* (in press)

49 Clark, C.W. and Mangel, M. (2000) *Dynamic State Variable Models: Methods and Applications*, Oxford University Press

50 Coulson, T. *et al.* (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292, 1528–1531

51 Nisbet, R.M. *et al.* (2000) From molecules to ecosystems through dynamic energy budget models. *J. Anim. Ecol.* 69, 913–926

52 Muller, E.B. and Nisbet, R.M. (2000) Survival and production in variable resource environments. *Bull. Math. Biol.* 62, 1163–1189

53 Stenseth, N.C. *et al.* (1998) Frontiers in population ecology of microtine rodents: a pluralistic approach to the study of population biology. *Res. Popul. Ecol.* 40, 5–20

54 Krebs, C.J. *et al.* (2001) *Ecosystem Dynamics in the Boreal Forest: The Kluane Project*, Oxford University Press

55 Hilborn, R. and Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*, Princeton University Press

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The long and short of food-chain length

David M. Post

Food-chain length is a central characteristic of ecological communities that has attracted considerable attention for over 75 years because it strongly affects community structure, ecosystem processes and contaminant concentrations. Conventional wisdom holds that either resource availability or dynamical stability limit food-chain length; however, new studies and new techniques challenge the conventional wisdom and broaden the discourse on food-chain length. Recent results suggest that resource availability limits food-chain length only in systems with very low resource availability, and call into question the theoretical basis for dynamical stability as a determinant of food-chain length. Evidence currently points towards a complex and contingent framework of interacting constraints that includes the history of community organization, resource availability, the type of predator–prey interactions, disturbance and ecosystem size. Within this framework, the debate has shifted from a search for singular explanations to a search for when and where different constraints operate to determine food-chain length.

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Food webs depict the complex trophic interactions inherent among organisms within ecosystems. The number of transfers of energy or nutrients from the base to the top of a food web is often called FOOD-CHAIN LENGTH (see Glossary). Food-chain length is a central characteristic of ecological communities that influences community structure by altering the organization of trophic interactions [1–3]; modifying key ecosystem functions, such as nutrient cycling, primary productivity and atmospheric carbon (C) exchange [1]; and influencing the concentration of contaminants in top predators, including many of the fish that humans eat [4]. Although considerable progress has been made in understanding the effects of food-chain length on ecological processes and food web dynamics [1–3,5], only limited progress has been made in understanding what determines food-chain length in natural ecological systems.

Conventional wisdom holds that food-chain length is determined either by the dynamical stability of food webs or by the availability of limiting food resources (often represented as energy). Some recent studies strongly challenge this conventional wisdom [6–8], whereas others reframe the question to accommodate functional definitions of food-chain length [3,9,10]. These and other studies suggest a complex relationship between food-chain length and ecological processes, such as the history of community organization, RESOURCE AVAILABILITY, habitat stability and ecosystem size. No single determinant of food-chain length emerges from these studies; indeed, some of the determinants are intimately related [5,10,11] and the importance of each determinant depends, in part, on which definition of food-chain length is being used [9].

Here, I briefly discuss the various ways in which food-chain length is defined and measured, highlighting the crucial difference between estimates

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Box 1. Unit of assessment for food-chain length

Food-chain length can describe both the number of links leading to a single species in a food web and the height of an entire food web or food-web compartment. These different definitions have led to some confusion over the unit of assessment being referenced. An alternative is to define trophic position as the location of an individual organism or species within a food web, and food-chain length or maximum trophic position as the height of the food web (where maximum trophic position = food-chain length + 1). Trophic position and maximum trophic position imply less about food-web structure than food-chain length (e.g. linear chains and discrete number of links [a]), and therefore provide more semantically flexible expressions for understanding this aspect of food-web structure.

Reference

a Yodzis, P. (1984) Energy flow and the vertical structure of real ecosystems. *Oecologia* 65, 86–88

of realized food-chain length derived from energy webs or connectance webs, and estimates of functional food-chain length derived from interaction webs. I outline the emerging mosaic of constraints on food-chain length and the interplay between these constraints. Within this framework, I find little evidence for resource availability or dynamical stability as singular determinants of food-chain length. They are, however, important components of the mosaic of constraints in which the history of community organization and resource availability are ultimate constraints on food-chain length, but disturbance, the type of predator–prey interactions and ecosystem size explain much of the proximate variation in food-chain length.

Box 2. Interaction strength and energy flow as metrics for describing food web structure

Food webs can be assembled using the patterns of feeding links or energy flow as the metric of measurement (connectance webs and energy webs *sensu* [a,b]) or using interaction strength as the metric of measurement (functional or interaction webs *sensu* [a,b]). Food webs based on energy flow provide estimates of realized trophic position and realized food-chain length, which represent the number of times energy or material is transferred as it is moved up through a food web to an organism. Realized trophic position and realized food-chain length are necessarily based on all trophic pathways that lead from the base of a food web to a consumer; thus it is imperative to include pathways derived from primary producer and detrital energy sources. By contrast, food webs based on interaction strength can provide estimates of functional trophic position based on the effect of an organism or group of organisms on some community attribute (e.g. food web structure or species diversity) or ecosystem functions (e.g. primary production) [b–e]. Typically, only food-web pathways that have substantial impacts upon key community or ecosystem properties are considered when defining functional trophic position. To minimize confusion derived from the metric of measurement used to quantify food-web structure, I suggest using trophic position, maximum trophic position and food-chain length either without a modifier or prefaced by realized (e.g. realized food-chain length) when the metric of measurement is energy flow, and using the preface functional (e.g. functional food-chain length) when the metric of measurement is influence on community structure or ecosystem function.

References

a Paine, R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49, 667–685
b Persson, L. *et al.* (1996) Productivity and consumer regulation – concepts, patterns, and mechanisms. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 396–434, Chapman & Hall
c Oksanen, L. *et al.* (1996) Structure and dynamics of arctic–subarctic grazing webs in relation to primary production. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 231–244, Chapman & Hall
d Oksanen, L. and Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.* 155, 703–723
e Power, M.E. *et al.* (1996) Disturbance and food chain length in rivers. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 286–297, Chapman & Hall

What is food-chain length?

Considerable confusion surrounds the phrase 'food-chain length', both because of what it implies about food-web structure (i.e. linear food chains; even though it is widely recognized that there are few if any true linear food chains) and because it has been defined and measured in different ways. Disparate definitions of food-chain length arise from using different units of assessment (Box 1), using different metrics to measure food-web structure (Box 2) and using different methods to estimate food-chain length from food webs (Box 3). Differences in the metric of measurement are particularly important, because they produce functional and realized measures of food-chain length that derive from fundamentally different ways of looking at food-web structure (e.g. interaction strength versus energy flow) (Box 2). Many theoretical and empirical predictions do not explicitly differentiate between functional and realized estimates of food-chain length, and this has inhibited integration of food-web theories and has limited progress in understanding what determines food-chain length.

Functional and realized measures of food-web structure could be the same in some systems (particularly in small, simple food webs [12]); however, they will produce different pictures of food-web structure in most systems [5,9,12]. There is a great need to explicitly evaluate functional and realized food-chain length simultaneously in natural and experimental systems to explore the relationship between these two important, but different measures of food-web structure. Here, I focus primarily on the determinants of realized food-chain length because there is little quantitative information on variation in functional food-chain length in natural communities.

Broadening the dialectic for realized food-chain length

Recent studies suggest that simple energetic and dynamical stability arguments independently fail to explain adequately extant patterns of food-chain length [6–8,13,14], in part because they might interact [10,11] and because they are embedded within the complex and contingent framework of community assembly [5,14–16]. Rather than searching for singular explanations for variation in food-chain length across all systems, it might be more productive to contemplate the multiple constraints that could determine food-chain length in any given food web [14,16] (Fig. 1).

Community organization

The history of community organization (which includes colonization and *in situ* evolution) is an important, but difficult to quantify, constraint on food-chain length [16]. Colonization history influences food-web structure and food-chain length most strongly in ecologically isolated or evolutionarily young systems. If a top or key intermediate predator is unable to invade a system or evolve *in situ*, food-chain length might remain short, regardless of the intrinsic potential of the system for longer food-chain length [5,16]. This argument is reminiscent of Pimm's design constraint hypothesis [17] (and suffers similarly in its *post hoc* nature): the history of community organization can induce design constraints, because it limits which types of species can join the local community and food web. Constraints on local community membership might, in turn, modify available predatory–prey interactions and the resulting patterns of food-chain length. The impact of community organization will operate at both short and long temporal scales in ways that relate to other important ecosystem characteristics, such as ecosystem size and disturbance [14,16,18–20].

Box 3. Methods for measuring food-chain length

There are many methods for estimating food-chain length, reflecting both different metrics for measuring food-web structure (Box 2) and different techniques for calculating food-chain length. The same food web can be drawn as a connectance web (Fig. Ia), energy web (Fig. Ib) or interaction web (Fig. Ic) [a], where thicker arrows represents greater energy flow or interaction strength. Connectance and energy webs provide estimates of realized food-chain length, whereas interaction webs provide an estimate of the functional food-chain length. For all three webs, food-chain length can be estimated either by collapsing food web complexity into linear or nearly linear chains where each species or species group occupies a trophic level (typical for functional food-chain length) or by estimating food-chain length directly from the full, complex food web (typical for realized food-chain length).

Most estimates of realized food-chain length derive from the direct analysis of connectance webs because of their relative ease of construction. Food-chain length has been estimated from connectance webs as maximum, mean and minimum food-chain length, each of which reflects different assumptions about the realized pattern of energy flow through a food web. Estimates of food-chain length derived from connectance webs have been criticized because connectance webs are often incomplete (which is not a problem unique to connectance webs), suffer from inconsistent taxonomic resolution and do not explicitly account for energy flow through different pathways [b–e]. In Fig. Ia, maximum and mean food-chain lengths are four and minimum food-chain length is two. By contrast, the energy web suggests a realized food-chain length of around three (Fig. Ib).

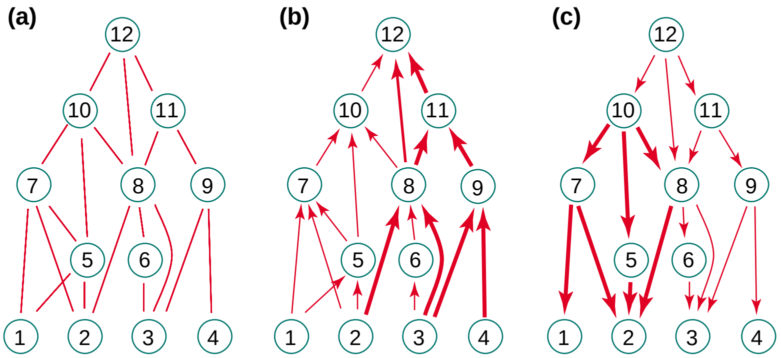

Fig. I

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The best measures of realized food-chain length derive from fully delineated energy webs; however, energy webs are extremely time consuming to construct and are therefore seldom available. An alternative is to employ stable isotope techniques to provide a measure of realized food-chain length that integrates the assimilation of energy or mass flow through all the trophic pathways leading to top predators [f]. Stable isotopes offer improved estimates of food-chain length because they avoid both the methodological artifacts and poor data problems that afflict estimates derived from connectance webs, and they simultaneously summarize information about energy flow and complex food web interactions [f].

Functional food-chain length is typically estimated by converting interaction webs to trophic levels. Functional food-chain length is the uppermost trophic level that affects the community or ecosystem measure of interest, and is likely to be an integer (e.g. three trophic levels in Fig. Ic). Even though interactions can flow up, down and horizontally across food webs, functional food-chain length is characteristically estimated only from top-down interactions. Functional food-chain length could also be estimated directly from interaction webs, in which case functional food-chain length depends on the metric of interaction strength used [g] and how investigators integrate interactions that move up and across food webs.

References

a Paine, R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49, 667–685
b Hall, S.J. and Raffaelli, D.G. (1993) Food webs – theory and reality. *Adv. Ecol. Res.* 24, 187–239
c Martinez, N.D. (1991) Artifacts or attributes – effects of resolution on the Little-Rock Lake food web. *Ecol. Monogr.* 61, 367–392
d Paine, R.T. (1988) Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69, 1648–1654
e Lawton, J.H. (1989) Food webs. In *Ecological Concepts* (Cherrett, J.M., ed.), pp. 43–78, Blackwell Scientific
f Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718
g Berlow, E.L. *et al.* (1999) Quantifying variation in the strengths of species interactions. *Ecology* 80, 2206–2224

Resource availability

Energy or resource availability might limit food-chain length when colonization does not. The importance of energy or resource availability in explaining variation in food-chain length has been discussed, debated and integrated into ecological theory for over 40 years [8,17,21–24]. Energetic arguments suggest that food-chain length should increase as the amount of energy or limiting resources available to top predators increases because energetic efficiencies are typically low (on average ~10%, but ranging between 2% and 50% [17,22,25]) and there is, therefore, a diminishing amount of energy available to support each subsequent trophic level. This argument predicts that food-chain length should increase both as the energetic efficiency of organisms within a food web increases [26] and as the amount of resources available at the base of the food web increases.

Productive space hypothesis

The most widely discussed and tested energetic prediction is that food-chain length should increase

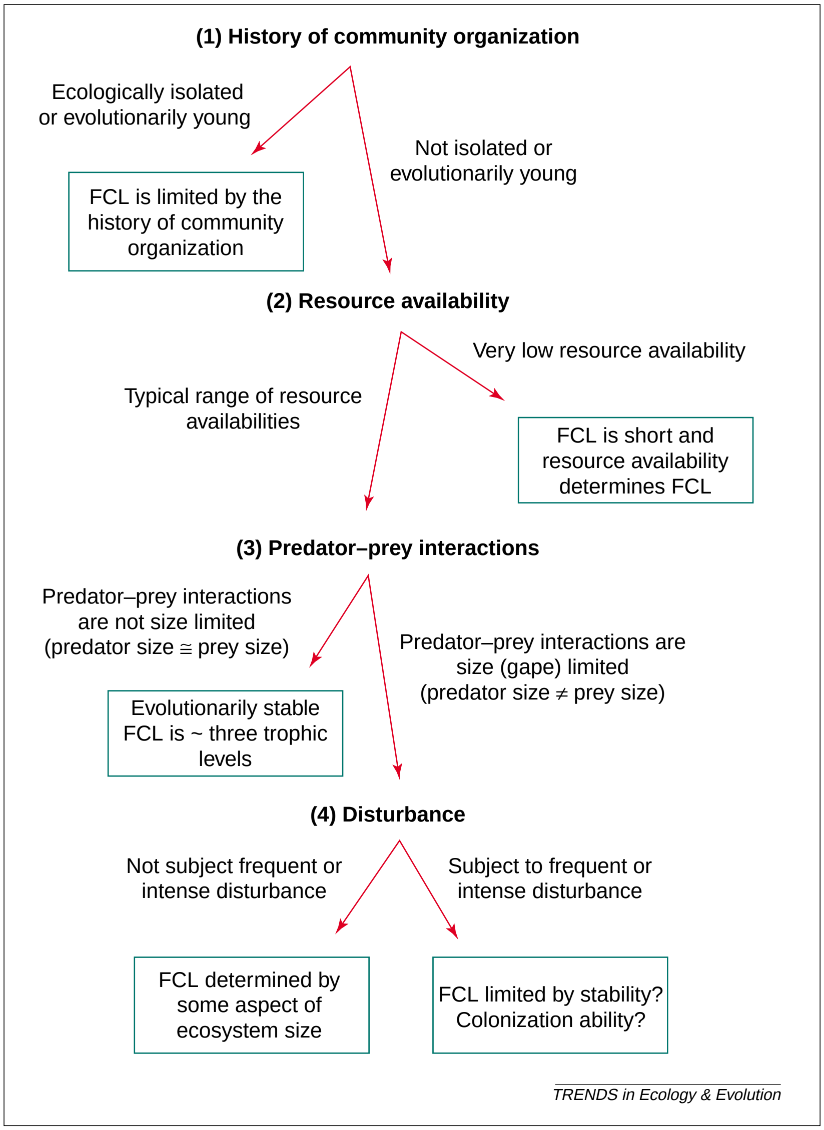

Fig. 1. Flow chart outlining the contingent nature of potential constraints on realized food-chain length (FCL). The characteristics of a food web and the ecosystem in which it is located (as outlined by the text labels next to the arrows) establish the proximate constraint on realized food-chain length and, in some cases, suggest the realized food-chain length (as outlined by the text in the boxes). For example, in food webs that are: (1) not ecologically isolated; (2) have moderate resource availability; (3) dominated by size-structured predator–prey interactions; and (4) are not subject to frequent or intense disturbance, realized food-chain length should be determined by some aspect of ecosystem size.

as resource availability increases; for example, as primary production or detrital input increases [6,8,17,24,27,28]. This prediction was formalized most recently as the productive space hypothesis [13], which predicts that food-chain length should increase as a function of total ecosystem productivity – the product of ecosystem size (area or volume) and some measure of per-unit-size productivity or resource availability (e.g. $\mathrm{g\ C\ m^{-2}\ y^{-1}}$). Unlike previous energetic hypotheses based on estimates of only per-unit-size resource availability (e.g. productivity hypothesis [17,27]), the productive-space hypothesis explicitly includes a spatial component to estimate more accurately the total availability of resources for upper trophic levels. In this framework, ecosystem size should reflect the area or volume supporting a population of top predators (e.g. island area for lizards [13] or lake volume for fish [8]) or relate to the spatial scale over which top predators range in systems with more permeable boundaries (e.g. home range) [29].

The productive-space hypothesis can be tested by simply looking for a relationship between productive space and food-chain length [13,28]. However, this is not a particularly informative test, because a positive relationship between food-chain length and productive space could be caused by the influence of per-unit-size resource availability alone, ecosystem size alone or the combination of both as specified by the productive-space hypothesis (David M. Post, PhD thesis, Cornell University, 2000). A more informative test of the productive-space hypothesis is to evaluate variation in food-chain length across independent gradients of ecosystem size and per-unit-size resource availability [6,8]. Separating the effects of ecosystem size from those of per-unit-size resource availability provides more information about the underlying mechanisms determining food-chain length by removing the potential spatial effects of ecosystem size from the direct effect of ecosystem size on total resource availability.

There have been three explicit quantitative tests of the productive-space hypothesis to date [6,8,28], all of which document a strong influence of ecosystem size, but little effect of per-unit-size resource availability on food-chain length. Spencer and Warren [6] found strong evidence for an effect of microcosm size on food-chain length (measured from connectance webs), but no evidence for an effect of resource availability. Post *et al.* [8], using stable isotope techniques [30], found that food-chain length was positively related to ecosystem size, but not to per-unit-size resource availability in 25 north temperate lakes. Vander Zanden *et al.* [28], also using stable isotope techniques, found that food-chain length was positively related to both ecosystem size and water clarity (their measure of resource availability); however, because ecosystem size and water clarity were correlated in their study, they were unable to clearly separate the effects of ecosystem size from those of total resource availability [28]. The results of Vander Zanden *et al.* probably represent an effect of only ecosystem size on food-chain length. Taken together, these three studies [6,8,28], along with previous studies [17,27,31,32], suggest that resource availability has little direct role in determining food-chain length in most natural systems.

Contradictory results

The conclusion that resource availability does not directly determine food-chain length in many natural systems is in stark contrast to the results of microcosm experiments that have shown an effect of resource availability on food-chain length [24,33]. The contrary results might derive from some combination of differences in the complexity of food webs studied (e.g. complex natural food webs versus simple, artificially constructed food webs), differences in the range of resource availability employed, or differences in the location of the resource availability range employed along a resource gradient.

Theoretical studies demonstrate clearly that the complex, reticulate food webs found in natural systems often operate differently from the simple linear food chains typically found in artificially constructed microcosms [34–36]. The presence of omnivory, intraguild predation, or inedible prey could obscure or complicate direct effects of resource availability on food-chain length [12,36,37]. As demonstrated for intraguild predation [36], the longest food chains are often found at intermediate, rather than at high resource availability. At high resource availability, top predators can reach higher densities and can extirpate or nearly extirpate intermediate predators, thereby shortening realized food-chain length [12,36]. The relationship among food-web complexity, food-web architecture, resource edibility and food-chain length deserves more attention.

A limited range of per-unit-area resource availabilities could also provide very little power to detect an effect of resource availability on food-chain length [38]. Some of the studies indicating a negative effect of resource availability on food-chain length examined only a limited range of resource availabilities [31,33]. However, at least for the Post *et al.* results [8], the range of resource availabilities employed provided sufficient power to detect an effect of per-unit-size resource availability on food-chain length, if there was indeed an effect (David M. Post, PhD thesis, Cornell University, 2000).

The location of the range of resource availabilities employed along a resource gradient, particularly the extent of the lower end of the range, might play an important role in explaining these contradictory results [17]. Modeling studies [11,39] suggest that effects of resource availability on food-chain length should be greatest when per-unit-size resource availability is <~1–10 g C m^{-2} y^{-1}. Studies that have found a strong influence of resource availability on food-chain length [24,33] all employed minimum per-unit-size resource availability treatments <10 g C m^{-2} y^{-1}, whereas studies that found little or no influence [6,8,28] all employed minimum per-unit-area resource availabilities >10 g C m^{-2} y^{-1}.

These results suggest a threshold below which resource availability constrains food-chain length, but above which food-chain length is determined by other factors [17,31,33]. Rather than asking ‘does resource availability limit food-chain length?’, we should ask ‘where along the gradient of total resource availability does resource availability limit food-chain length?’ The answer is probably between 1 and 100 g C m^{-2} y^{-1}, and probably depends on both the energetic efficiency of key organisms in the food webs being studied [26,39] and the area over which they range. It is not clear how this threshold in per-unit-area resource availability translates into total resource availability (a crucial next step), but it suggests that resources limit food-chain length only in small systems with very low total resource availability [8,16]. Ecosystems with resource availability <1–10 g C m^{-2} y^{-1} are found only in the most unproductive deserts, deep reaches of caves, at extreme altitude and latitude or in the most unproductive regions of the central ocean [39,40]. Conclusively documenting the location of the resource availability threshold might be difficult because low total resource availability is typically found only in small or environmentally harsh systems in which top predators might be absent for other reasons, such as ecosystem size, disturbance and the history of community organization [8,16,18–20,41].

Predator–prey interactions

Where resource availability and colonization are not limiting, the size structure of predator–prey interactions might influence food-chain length. Hastings and Conrad [42] argued that, in the absence of nutritional or physical size constraints (e.g. predators are similar in size to their prey), the evolutionary stable food-chain length is around three trophic levels. They point out that there is little evolutionary advantage to feeding on other carnivores when herbivores are generally more abundant, offer similar energetic and nutritional value and are less well defended. This hypothesis provides a parsimonious answer for food-chain length in mammal-dominated terrestrial food webs where there is often little size difference between primary producers, herbivores and carnivores [43]. This argument predicts that food-chain length in food webs that are not size structured should be near three, with little variation (except when limited by other constraints, such as resource availability [3]).

Most food webs, however, are dominated by size-structured predator–prey interactions where body size increases with TROPHIC POSITION [44]. In these food webs, food-chain length is a function of both the predator body size:prey body size ratio, and the range in body size between organisms at the top and bottom of the food web [45]. These two factors might be influenced by some combination of productivity, disturbance, ecosystem size and the history of community organization, but no study has yet addressed these issues. Future work should link variation in food-chain length to both variation in predator–prey body size ratios and the size of organisms at the top and bottom of food webs, and use these size relationships to link food-chain length to the mosaic of constraints discussed here (e.g. community organization or ecosystem size).

Dynamical constraints and disturbance

The other widely discussed explanation for variation in food-chain length is the dynamical constraints hypothesis [46], developed by Pimm and Lawton [46] by studying the resilience stability of randomly assembled Lotka–Voltera models. They assembled

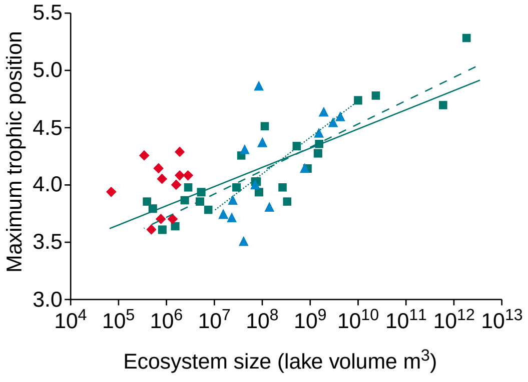

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Fig. 2. The relationship between maximum trophic position and ecosystem size (lake volume) based on data from studies [8,28,59,60] that all used similar stable isotope methods to estimate maximum trophic position in north temperate lakes ([8], squares; [60], diamonds; [28,59], triangles). Maximum trophic position = food-chain length + 1. The relationship for data drawn from all studies (solid line) is: maximum trophic position = 2.83 + 0.17 × log (ecosystem size); for the Post *et al.* data [8] (dashed line): maximum trophic position = 2.51 + 0.2 × log (ecosystem size); and for the Vander Zanden *et al.* data [28,59] (dotted line): maximum trophic position = 1.52 + 0.32 × log (ecosystem size). The Vander Zanden *et al.* data presented here differ from those presented in [28] because I have included additional isotopic evidence that showed lake trout were not the top predator in some of the smallest lakes [59].

four-species communities arranged in two, three and four trophic levels, where all the basal species exhibited self-damping (i.e. negative feedbacks on their own densities). Pimm and Lawton found that longer food chains had longer return times, suggesting that they were less stable than shorter food chains. This implies that food webs with short food-chain lengths should dominate natural systems, particularly in those that are subject to frequent and extreme disturbance. These results [46] provide the theoretical foundation for the hypothesis that dynamical stability constrains food-chain length; however, the theoretical generality of the results has been challenged because of the way that self-damping was incorporated into the model communities [7,47]. Stability of linear models is strongly influenced by the fraction of species with self-damping [47]; thus, by including self-damping terms for only basal species, the Pimm and Lawton models confounded food-chain length and self-damping [7]. When the effect of self damping is controlled for in model communities, longer food chains can be more stable than are shorter food chains [7]. By contrast, more structurally complex ecosystem models, mostly based on food webs in lakes, tend to support the idea that longer food-chains are less stable [48,49], although the results are drawn from only one ecosystem type and are not always consistent [49]. Therefore, there is, at best, very limited theoretical support for the idea that dynamical stability limits food-chain length.

There is also only tentative empirical support for dynamical stability limiting realized food-chain length in small experimental systems [31,33,50,51]. Some evidence exists that population fluctuations increase with longer food-chain length [50], and that food webs with longer food-chain lengths might be more susceptible to shortening by disturbance [33] and might re-assemble more slowly after disturbance than would food webs with shorter food chains [31]. However, all these responses represent spatially and temporally localized effects that depend strongly on the magnitude and spatial extent of the disturbance relative to the spatial distribution and colonization ability of key species in the food web [10,15]. No study has yet shown that food-chain length is shorter in more highly disturbed extant food webs [27,51], although several studies have shown an effect of disturbance on the presence and absence of top predators in smaller ecosystems [18,20,41,52]. Thus, in spite of the considerable intuitive appeal of the idea that disturbance could limit food-chain length through dynamical constraints [10,15], there is no strong theoretical or empirical evidence to directly support this idea. Streams could be an ideal place to look for such an effect. All things being equal, streams subject to frequent and strong disturbance events, such as floods and desiccation, should have shorter food-chain lengths than do streams with a more stable hydrograph. This trend might be manifest as a threshold effect that is influenced by resource availability [10,11], ecosystem size [18,20,53] and colonization ability [10,15,18].

Ecosystem size

There is mounting evidence for the role of ecosystem size in determining food-chain length in aquatic [6,8,28] and terrestrial systems [13], where larger ecosystems support food webs with longer food-chain lengths (Fig. 2) and the influence of ecosystem size on food-chain length is independent of any effect it might have on total resource availability [6,8]. The increase in food-chain length observed for lakes (~1.5 trophic levels; Fig. 2) probably underestimates the potential increase in food-chain length of two to three trophic levels as aquatic ecosystem size increases from small aquatic pothole ecosystems (10^{-2}–10^{1} m^3) to the great lakes and oceans of the world (10^{12}–10^{14} m^3 for lakes, 10^{17} m^3 for oceans). Observations from lakes and islands suggest that some combination of the addition of new top predators in larger ecosystems, changes in the structure of the middle of the food web and changes in the degree of trophic omnivory must contribute to longer food chains in larger ecosystems [8,13]. It is not yet clear, however, which attributes of ecosystem size best explain these changes in food web structure and the observed variation in food-chain length [8].

A growing body of theory, arising from island biogeographical and metapopulation perspectives, and some very limited empirical evidence [28] suggests that the observed relationship between food-chain length and ecosystem size could derive from the positive relationship between ecosystem size and species richness [54,55]. When the relationship between ecosystem size and species richness is linked mechanistically by theory to the dynamics of colonization and extinction [54], the theory does not necessarily imply that longer food chains are dynamically less stable; the predicted effects of ecosystem size can arise from constraints on colonization alone. This theory and other studies suggest that the effect of ecosystem size on food-chain length could be tied tightly to the history of community organization and disturbance through colonization and extinction [18–20,53,54]. This theoretical framework does not yet predict the magnitude of the ecosystem size effect, nor does it fully portray the complex changes in food-web structure contributing to the observed changes in food-chain length [8]. A fuller appraisal of these potential causal factors will require both further theoretical development and careful implementation of experimental and observational studies at appropriate spatial and temporal scales.

The evidence for an effect of ecosystem size on food-chain length currently derives from relatively isolated ecosystems (e.g. lakes and oceanic islands) [8,13,28]. This bias in study systems reflects the relative ease of estimating ecosystem size in discrete systems, but also raises the question of how best to test the generality of the observations in open systems where ecosystem size is more difficult to define. One possibility is to link the scale of analysis in some way to the spatial scale over which the top predator ranges (e.g. home range) [29].

Broadening the dialectic for functional food-chain length

As with realized food-chain length, the determinants of functional food-chain length are embedded within the complex and contingent framework of community assembly such that no single process is sufficient to explain variation in functional food-chain length. The history of community organization and resource availability are again important ultimate constraints. Disturbance, ecosystem size and the form of predator–prey interactions are probably also important, although there are currently little available data to evaluate their importance. The effect of all these factors on functional food-chain length might be quite different from their effect on realized food-chain length, such as in the cases of resource availability and disturbance.

Resource availability

The assumption that resource availability determines functional food-chain length is central to the HYPOTHESIS OF EXPLOITATION ECOSYSTEMS [3,5]. Although there have been many efforts to test portions of this hypothesis [1–3,5], there are little data available to test the central assumption that functional food-chain length increases with resource availability. Because realized and functional food-chain length will be the same or very similar in some systems, particularly small, simple systems [24], functional food-chain length is likely to be limited by resource availability in the same systems where this factor limits realized food-chain length; that is, small ecosystems with extremely low resource availability [3,24,39]. Little evidence exists for a positive relationship between functional food-chain length and resource availability in ecosystems within the typical range of resource availabilities ([10,32,56], but see [3]), with the extent and quality of this evidence being very limited. There is even some evidence that increased resource availability can reduce functional food-chain length in systems where high resource availability facilitates dominance by well-defended, often slow-growing, species that can truncate functional food-chain length because of their limited vulnerability to predation [10,37]. This process, however, interacts with and strongly depends on the magnitude and frequency of disturbance events that reset community succession and resource sequestration, which favor fast-growing, less well-defended species [10].

Disturbance

Although theory predicts that functional food-chain length should decline with increased disturbance [15], empirical observations suggest that disturbance can facilitate elongation of functional food-chain length [10,56,57]. These observations suggest that functional food-chain length can be longest at an intermediate level of disturbance [10]. Like increased resource availability, limited disturbance facilitates dominance by well-defended, but often slow-growing and less mobile, species that effectively shorten functional food-chain length because of their limited vulnerability to predation [10,37]. By contrast, extreme and frequent disturbance events maintain short functional food-chain length by eliminating all but those species that are most resistant to disturbance – often those near the base of the food web [10,15]. As with realized food-chain length, the response of functional food-chain length to disturbance depends strongly on the magnitude and spatial extent of the disturbance relative to the spatial distribution and colonization ability of species that form the strongest interactions within the food web [10,15].

Other constraints

As for the other constraints, predator–prey interactions will set an upper limit on functional food-chain length of three in food webs that are not size structured, but other processes, such as disturbance, could reduce functional food-chain length to below three in those systems [3,10]. It is not immediately clear that ecosystem size should have a simple effect on functional food-chain length, but ecosystem size influences habitat complexity, habitat stability, species richness and disturbance, all of which can be important to functional food-chain length.

Glossary

Connectance web: a food web depicting trophic (feeding) links among species, where links are typically assigned without consideration of the magnitude of energy flow through each link [a].

Energy web: a food web depicting the flow of energy through trophic links among species or species groups [a].

Exploitation ecosystems (hypothesis): a hypothesis that proposes: (1) that functional food-chain length should increase with increasing primary productivity; and (2) that changes in functional food-chain length along a productivity gradient result in alternating patterns of population regulation by predation or resource productivity [b,c].

Food-chain length: (also food-web height) typically the number of transfers of energy or nutrients from the base to the top of a food web, but see Boxes 1–3 for further clarification.

Functional (food-chain length, trophic position, maximum trophic position): measures of food web structure based on interaction webs.

Interaction strength: the magnitude of the effect of one species on another species [d,e].

Interaction web: a food web depicting the strength of interactions among species or species groups [a]. Typically derived from manipulative studies.

Productive space hypothesis: hypothesis that food-chain length should increase as the product of ecosystem size and per-unit-size productivity [f].

Productivity hypothesis: hypothesis that food-chain length should increase with increasing per-unit-size productivity or resource availability [g,h].

Realized (food-chain length, trophic position, maximum trophic position): measures of food web structure based on energy or connectance webs.

Resource (availability): all things consumed by an organism that, as a result, become unavailable to other organisms (e.g. nutrients, food or nest sites). In the context of food-chain length, resource availability typically refers to the availability of food resources.

Trophic position: location of an individual organism or species within a food web. Maximum trophic position is a measure of food-chain length defined as the trophic position of the species with the highest trophic position in a food web [i], where maximum trophic position = food-chain length +1. Typically based on stable isotope analyses [i].

References

a Paine, R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49, 667–685
b Oksanen, L. *et al.* (1981) Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118, 240–261
c Oksanen, L. and Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.* 155, 703–723
d Berlow, E.L. *et al.* (1999) Quantifying variation in the strengths of species interactions. *Ecology* 80, 2206–2224
e Laska, M.S. and Wootton, J.T. (1998) Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79, 461–476
f Schoener, T.W. (1989) Food webs from the small to the large. *Ecology* 70, 1559–1589
g Briand, F. and Cohen, J.E. (1987) Environmental correlates of food chain length. *Science* 238, 956–960
h Pimm, S.L. (1982) *Food Webs*, Chapman & Hall
i Post, D.M. *et al.* (2000) Ecosystem size determines food-chain length in lakes. *Nature* 405, 1047–1049

Because the explicit distinction between functional and realized food-chain length is relatively new [5,10,56], there is a need to develop theory that specifically addresses the determinants of functional food-chain length rather than realized food-chain length, and to quantify functional food-chain length to test the theory. This will not be easy because functional food-chain length derives from interaction webs that require experimentation, and empirical results will probably point to constraints different from those for realized food-chain length [5,10]. Constraints on functional food-chain length probably operate at more localized spatial and temporal scales than do constraints for realized food-chain length (partially because functional food-chain length is typically measured at the local scale), possibly making the determinants of functional food-chain length less amenable to generalization.

Human influences on food-chain length

Human activities strongly influence food-chain length both directly, through the over-exploitation of top predators [58], and indirectly, through their impact on constraints of food-chain length. Humans modify disturbance regimes, change ecosystem size through habitat fragmentation, and change resource availability by translocating large quantities of nutrients, water and CO_2. Humans also move species around the landscape in ways that homogenize fauna and reduce colonization constraints, and fragment the landscape in ways that increase colonization constraints by reducing colonization rates. Because food-chain length (in particular, functional food-chain length) strongly influences community structure and ecosystem processes [1,2], human activities that affect food-chain length might cause a cascade of unintended ecological changes.

Conclusions

Recent studies have considerably advanced our understanding of the ecological determinants of food-chain length [6,24,28,34], whilst clarification of the metric used to measure food-chain length (Box 2) and development and application of new techniques to measure food-chain length [30] provide the foundation for rapid future advances. The two most commonly cited explanations for variation in food-chain length, resource availability and dynamical constraints, have limited explanatory power. Recent results suggest that resource availability does not directly determine food-chain length in most natural systems [6,8,28], and that it might be important only in ecosystems with very low total resource availability [24,39]. Likewise, the idea that dynamical stability (and disturbance) might determine food-chain length currently has little theoretical or empirical support [7].

Although disturbance and resource availability explain little of the variation in food-chain length, they are important to the complex and contingent framework of community assembly that is crucial to understanding food-chain length in any given food web (Fig. 1). Within this framework, ecosystem size has emerged as a crucial determinant of food-chain length in aquatic systems [6,8,28], but it is not yet clear which aspects of ecosystem size are most important [8]. The debate now shifts away from a search for a single explanation for variation in food-chain length to a search for when and where a suite of interacting constraints operates to determine variation in food-chain length.

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References

1 Pace, M.L. *et al.* (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* 14, 483–488
2 Persson, L. (1999) Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85, 385–397
3 Oksanen, L. and Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.* 155, 703–723
4 Kidd, K.A. *et al.* (1998) Effects of trophic position and lipid on organochlorine concentrations in fishes from subarctic lakes in Yukon Territory. *Can. J. Fish. Aquat. Sci.* 55, 869–881
5 Persson, L. *et al.* (1996) Productivity and consumer regulation – concepts, patterns, and mechanisms. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 396–434, Chapman & Hall
6 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
7 Sterner, R.W. *et al.* (1997) The enigma of food chain length: absence of theoretical evidence for dynamic constraints. *Ecology* 78, 2258–2262
8 Post, D.M. *et al.* (2000) Ecosystem size determines food-chain length in lakes. *Nature* 405, 1047–1049
9 Oksanen, L. *et al.* (1996) Structure and dynamics of arctic–subarctic grazing webs in relation to primary production. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 231–244, Chapman & Hall
10 Power, M.E. *et al.* (1996) Disturbance and food chain length in rivers. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 286–297, Chapman & Hall
11 Moore, J.C. *et al.* (1993) Influence of productivity on the stability of real and model ecosystems. *Science* 261, 906–908
12 Diehl, S. and Feissel, M. (2001) Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology* 82, 2977–2983
13 Schoener, T.W. (1989) Food webs from the small to the large. *Ecology* 70, 1559–1589
14 Kitching, R.L. (2000) *Food Webs and Container Habitats*, Cambridge University Press
15 Menge, B.A. and Sutherland, J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130, 730–757
16 Kitching, R.L. (2001) Food webs in phytotelmata: ‘bottom-up’ and ‘top-down’ explanations for community structure. *Annu. Rev. Entomol.* 46, 729–760
17 Pimm, S.L. (1982) *Food Webs*, Chapman & Hall
18 Tonn, W.M. and Magnuson, J.J. (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63, 1149–1166
19 Losos, J.B. and Schluter, D. (2000) Analysis of an evolutionary species-area relationship. *Nature* 408, 847–850
20 Spiller, D.A. *et al.* (1998) Impact of a catastrophic hurricane on island populations. *Science* 281, 695–697
21 Hutchinson, G.E. (1959) Homage to Santa Rosalia; or, why are there so many kinds of animals? *Am. Nat.* 93, 145–159
22 Slobodkin, L.B. (1961) *Growth and Regulation of Animal Populations*, Holt, Rinehart and Wilson
23 Oksanen, L. *et al.* (1981) Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118, 240–261
24 Kaunzinger, C.M.K. and Morin, P.J. (1998) Productivity controls food-chain properties in microbial communities. *Nature* 395, 495–497
25 Pauly, D. and Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature* 374, 255–257
26 Yodzis, P. (1984) Energy flow and the vertical structure of real ecosystems. *Oecologia* 65, 86–88
27 Briand, F. and Cohen, J.E. (1987) Environmental correlates of food chain length. *Science* 238, 956–960
28 Vander Zanden, M.J. *et al.* (1999) Patterns of food chain length in lakes: a stable isotope study. *Am. Nat.* 154, 406–416
29 Cousins, S.H. (1990) Countable ecosystems deriving from a new food web entity. *Oikos* 57, 270–275
30 Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718
31 Pimm, S.L. and Kitching, R.L. (1987) The determinants of food chain lengths. *Oikos* 50, 302–307
32 Persson, L. *et al.* (1992) Trophic interactions in temperate lake ecosystems: a test of food chain theory. *Am. Nat.* 140, 59–84
33 Jenkins, B. *et al.* (1992) Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. *Oikos* 65, 249–255
34 Post, D.M. *et al.* (2000) Prey preference by a top predator and the stability of linked food chains. *Ecology* 81, 8–14
35 McCann, K. *et al.* (1998) Weak trophic interactions and the balance of nature. *Nature* 395, 794–798
36 Holt, R.D. and Polis, G.A. (1997) A theoretical framework for intraguild predation. *Am. Nat.* 149, 745–764
37 Leibold, M.A. (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* 134, 922–949
38 Lawton, J.H. (1989) Food webs. In *Ecological Concepts* (Cherrett, J.M., ed.), pp. 43–78, Blackwell Scientific
39 Moore, J.C. and de Ruiter, P.C. (2000) Invertebrates in detrital food webs along gradients of productivity. In *Invertebrates as Webmasters in Ecosystems* (Colman, D.C. and Hendrix, P.F., eds), pp. 161–184, CABI Publishing
40 Whittaker, R.H. (1975) *Communities and Ecosystems*, Macmillan
41 Schneider, D.W. (1997) Predation and food web structure along a habitat duration gradient. *Oecologia* 110, 567–575
42 Hastings, H.M. and Conrad, M. (1979) Length and evolutionary stability of food chains. *Nature* 282, 838–839
43 Hairston, N.G., Jr and Hairston, N.G., Sr (1993) Cause-effect relationships in energy flow trophic structure and interspecific interactions. *Am. Nat.* 142, 379–411
44 Cohen, J.E. *et al.* (1993) Body size of animal predators and animal prey in food webs. *J. Anim. Ecol.* 62, 67–78
45 Cousins, S. (1987) The decline of the trophic level concept. *Trends Ecol. Evol.* 2, 312–316
46 Pimm, S.L. and Lawton, J.H. (1977) The number of trophic levels in ecological communities. *Nature* 275, 542–544
47 Saunders, P.T. (1978) Population dynamics and the length of food chains. *Nature* 272, 189–190
48 Carpenter, S.R. *et al.* (1992) Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. *Am. Nat.* 140, 781–798
49 DeAngelis, D.L. *et al.* (1989) Effects of nutrient recycling and food-chain length on resilience. *Am. Nat.* 134, 778–805
50 Lawler, S.P. and Morin, P.J. (1993) Food web architecture and population dynamics in laboratory microcosms of protists. *Am. Nat.* 141, 675–686
51 Townsend, C.R. *et al.* (1998) Disturbance, resource supply, and food-web architecture in streams. *Ecol. Lett.* 1, 200–209
52 Werner, E.E. and McPeek, M.A. (1994) Direct and indirect effects of predators on 2 anuran species along an environmental gradient. *Ecology* 75, 1368–1382
53 Holt, R.D. *et al.* (1999) Trophic rank and the species-area relationship. *Ecology* 80, 1495–1504
54 Holt, R.D. (1996) Food webs in space: an island biogeographic perspective. In *Food Webs: Integration of Pattern and Process* (Polis, G.A. and Winemiller, K.O., eds), pp. 313–323, Chapman & Hall
55 Cohen, J.E. and Newman, C.M. (1992) Community area and food-chain length: theoretical predictions. *Am. Nat.* 138, 1542–1554
56 Marks, J.C. *et al.* (2000) Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos* 90, 20–27
57 Power, M.E. (1995) Floods, food chains, and ecosystem processes in rivers. In *Linking Species and Ecosystems* (Jones, C.G. and Lawton, J.H., eds), pp. 52–60, Chapman & Hall
58 Pauly, D. *et al.* (1998) Fishing down marine food webs. *Science* 279, 860
59 Vander Zanden, M.J. *et al.* (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401, 464–467
60 Lake, J.L. *et al.* (2001) Stable nitrogen isotopes as indicators of anthropogenic activities in small freshwater systems. *Can. J. Fish. Aquat. Sci.* 58, 870–878