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Food-chain length and adaptive foraging

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Food-chain length, the number of feeding links from the basal species to the top predator, is a key characteristic of biological communities. However, the determinants of food-chain length still remain controversial. While classical theory predicts that food-chain length should increase with increasing resource availability, empirical supports of this prediction are limited to those from simple, artificial microcosms. A positive resource availability–chain length relationship has seldom been observed in natural ecosystems. Here, using a theoretical model, we show that those correlations, or no relationships, may be explained by considering the dynamic food-web reconstruction induced by predator's adaptive foraging. More specifically, with foraging adaptation, the food-chain length becomes relatively invariant, or even decreases with increasing resource availability, in contrast to a non-adaptive counterpart where chain length increases with increasing resource availability; and that maximum chain length more sharply decreases with resource availability either when species richness is higher or potential link number is larger. The interactive effects of resource availability, adaptability and community complexity may explain the contradictory effects of resource availability in simple microcosms and larger ecosystems. The model also explains the recently reported positive effect of habitat size on food-chain length as a result of increased species richness and/or decreased connectance owing to interspecific spatial segregation.

Keywords: food web; food-chain length; energy limitation hypothesis; adaptive foraging

1. INTRODUCTION

Food-chain length, the number of feeding links from a basal species to a top predator, has been considered a key characteristic of food webs because it regulates a wide range of ecological processes (Hairston *et al.* 1960), including trophic cascades (Carpenter & Kitchell 1993) and toxin biomagnification (Cabana & Rasmussen 1994). Given the central role played by chain length in those processes, understanding food-chain length determinants is of particular importance for ecosystem management and biodiversity conservation.

Studies are accumulating on the determinants of food-chain length (Pimm 1982; Post 2002). Pimm (1982) summarized four hypotheses of food-chain length: (i) food-chain length is limited by available energy and should increase with increasing resource availability (the energy limitation hypothesis; Elton 1927; Lindemann 1942; Hutchinson 1959); (ii) a longer food chain is less persistent under disturbed environments (the dynamic stability hypothesis; Pimm & Lawton 1977; but see Sterner *et al.* 1997); (iii) optimal diet choices of individual species determine the food-chain length (the optimal foraging hypothesis; Hastings & Conrad 1979); and (iv) food-chain length is limited by the constraint that a predator should be larger than its prey (the design constraint hypothesis). In addition, empirical evidence from both aquatic (Spencer & Warren 1996; Vander Zanden *et al.* 1999; Post *et al.* 2000a; Doi *et al.* 2009) and terrestrial ecosystems (Schoener 1989; Takimoto *et al.* 2008) suggests that food-chain length is positively correlated

with habitat area (Cohen & Newman 1988), raising another possible determinant of food-chain length.

The energy limitation hypothesis (Elton 1927; Lindemann 1942; Hutchinson 1959) is the most widely discussed hypothesis to explain the variation in food-chain length. However, despite formal theory often assuming that increasing resource availability allows addition of trophic levels (Oksanen *et al.* 1981; Pimm 1982; Abrams 1993), empirical studies provide limited support of the positive resource availability effect (Post 2002). While the hypothesis has been supported by experiments using simple, artificial microcosms (Jenkins *et al.* 1992; Kaunzinger & Morin 1998), no clear positive correlation was observed between resource availability and food-chain length in natural ecosystems (Spencer & Warren 1996; Post *et al.* 2000a; but see Doi *et al.* 2009). Those conflicts may suggest possible interactive effects of resource availability and community complexity (Post 2002); however, the causal mechanism is not understood.

Recent reports suggest that consumers may temporally change diet through learning and phenotypic plasticity (Kause *et al.* 1999; Dukas & Bernays 2000; Egas & Sabelis 2001), which may provide a potential driving force for the introduction of temporal variability in food-web structure (Warren 1989; Winemiller 1990; Eveleigh *et al.* 2007). Given this inherent flexibility in trophic interactions (MacArthur & Pianka 1966; Murdock 1969; Stephens & Krebs 1986), an environmental change that may alter a predator's diet selection behaviour (e.g. changes in prey abundance, prey species composition and predator's energetic requirement) would potentially alter food-web structure. This leads to a hypothesis that food-web structure and its response to environmental

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variables may arise from adaptive diet choices. Attempts to explain food-web structure as a consequence of foraging adaptation have been reported (Hastings & Conrad 1979; Matsuda & Namba 1991; Křivan 2000; Post *et al.* 2000b; Loeuille & Loreau 2005; Beckerman *et al.* 2006; Petchey *et al.* 2008). However, those studies do not explicitly discuss why food-chain length shows correlation or no relationship with specific environmental factors such as resource availability. Some studies that have explicit or implicit prediction on resource availability effects only analyse the dynamics of a simple module that consists of a few species (Hastings & Conrad 1979; Holt & Polis 1997; Křivan 2000) and have left unclear their applicability to more complex food webs (e.g. Pimm 1982, arguing on limitation of the adaptation-based theory of Hastings & Conrad 1979, which assumes a simple linear food chain).

Here, using a model community composed of interacting adaptive foragers, we studied how food-chain length responds to changes in resource availability (i.e. growth rate of basal species) and community complexity (species richness and number of trophic links). We suggest that interacting adaptive foragers can give rise to the following food-chain length patterns: (i) chain length is relatively static or may decrease with increasing resource availability; (ii) resource availability effect on chain length varies with food-web complexity; and (iii) chain length increases with increasing species richness or decreasing species connectance. These patterns provide possible explanations of the aforementioned contradictory responses of chain length to resource availability in simple microcosm communities and complex natural systems. Furthermore, the positive relationship between habitat size and chain length may be a consequence of increased species richness and/or interspecific segregation.

2. MODEL

(a) *Network of potential prey–predator interactions*

Consider an ‘animal portion’ (Beckerman *et al.* 2006) of a food web, consisting of N animal species, of which B are ‘basal’ species (species 1 to B , which do not eat within the focal food web) and the remainder ($N - B$) are non-basal species (species $(B + 1)$ to N). A minimal ecological constraint on diet choice was assumed; that is, trophic interaction occurs according to a unique interspecific hierarchy, which may be related to body size (Warren & Lawton 1987; Cohen *et al.* 1990; Williams & Martinez 2000; Cattin *et al.* 2004). All basal species were at the lowest position, above which non-basal species were arranged in a hierarchy. Hierarchically higher species can prey on lower-positioned species; however, the opposite does not occur. This constraint sets the maximum possible number of potential links at $L_{\max} = (\text{all the possible pairs among } N \text{ species}) - (\text{the pairs among } B \text{ basal species}) = (N(N - 1) - B(B - 1))/2$.

A predator species may not be able to prey on all species in hierarchically lower positions. This would happen, for example, when a predator does not encounter a prey owing to spatial segregation. Thus, the number of potential links, L , in the network could be smaller than L_{\max} . To examine how this restriction affects food-chain length and its response to changing resource availability, we constructed food-web models with $L (< L_{\max})$ links

as follows. First, a prey species at a lower position was randomly chosen for each predator species to ensure that every non-basal species had at least one resource species. Then, $(L - (N - B))$ pairs randomly chosen from the rest are connected by trophic links. Although other topological constraints have been reported to affect structural patterns observed in natural food webs (Williams & Martinez 2000; Cattin *et al.* 2004), we did not consider such constraints in our model. Our approach was taken to clarify the extent to which food-web patterns are explained by adaptive foraging alone.

(b) *Population dynamics and adaptive diet choice*

The dynamics of biomass, X_i , of species i ($1, 2, \dots, N$) is described by:

$$\frac{dX_i}{dt} = X_i \left\{ r_i - s_i X_i + \sum_{k \in \text{species } i\text{'s prey}} e_{ik} f_{ik} a_{ik} X_k - \sum_{k \in \text{species } i\text{'s predator}} f_{ki} a_{ki} X_k \right\} + I_i, \quad (2.1)$$

where r_i is an intrinsic growth rate of species i ; s_i a self-regulation intensity set to 1.0 and 0.0 for basal and non-basal species, respectively; f_{ik} the foraging efficiency of i on resource species k , set to a random value between 0 and 1; a_{ik} the foraging effort of i allocated to k ($0 \leq a_{ik} \leq 1$, $\sum_{k \in \text{species } i\text{'s prey}} a_{ik} = 1$); e_{ik} the conversion rate of consumer species i set to a constant ($e = 0.15$); and I_i represents the immigration to the community. In some model runs, I_i was set to a small positive value ($I = 10^{-13}$) to make the community more persistent and reduce computational time. Thus, predators that have the same potential diet only differ in the foraging efficiency, f_{ik} , in this model. The intrinsic growth rate r_i was set as negative for non-basal species to represent a loss owing to mortality, but set to a positive constant, R , for basal species and was used as a proxy of resource availability.

The dynamics of the foraging effort of an adaptive consumer species i on a resource species j (a_{ij}) is then given by:

$$\frac{da_{ij}}{dt} = G_i a_{ij} \left(e_{ij} f_{ij} X_j - \sum_{k \in \text{species } i\text{'s prey}} a_{ik} e_{ik} f_{ik} X_k \right), \quad (2.2)$$

where G_i is the adaptation rate of consumer i , set to a constant value ($G = 0.25$). Equation (2.2) represents a simple diet-choice rule that maximizes energy gain (Kondoh 2003), in which a consumer species prefers a resource species that provides higher than average energy gain per unit effort ($e_{ij} f_{ij} X_j$). A true specialist with only one potential resource species stays specialist in this model. Equation (2.2) can be viewed as representing a process in which a strategy (diet choice, in this study) with a greater fitness is ‘copied’ more by other individuals, the key feature shared by evolution via natural selection and adaptation via social learning (Hofbauer & Sigmund 1998). Note that it always holds that $d \sum_{j \in \text{species } i\text{'s prey}} a_{ij} / dt = 0$, representing a constraint in the total foraging effort ($\sum_{j \in \text{species } i\text{'s prey}} a_{ij} = \text{const.}$) and thus a trade-off between the number of used prey species (i.e. diet breadth) and resource use performance

(Cody 1974). An important consequence of using this model is that multiple predator species switch to more abundant species (switching behaviour; Murdock 1969), as supported by recent empirical reports (Eveleigh *et al.* 2007; Carnicer *et al.* 2008). The initial a_{ij} was $1/(\text{number of potential prey species})$ ($\sum_{j \in \text{species } i\text{'s prey}} a_{ij} = 1$). Throughout the paper, no trade-offs are assumed between foraging efficiency and escape from predation. Thus the adaptive change in a_{ij} does not affect the attacks that species i receives from higher-ranked foragers. If a_{ij} becomes smaller than 10^{-13} in the numerical calculation, we set the a_{ij} to 10^{-13} .

(c) Model analysis

The effects of three ecological factors—species richness (N), number of potential trophic links (L) and resource availability (R) on chain length of an adaptive food web—were evaluated. The potential trophic link between predator i and prey j may be dynamically connected or disconnected, depending on diet choice by predator i . Foraging effort a_{ij} can take very low values, but does not become 0 if its initial value is positive ($a_{ij}(0) > 0$). Thus a trophic link between i and j was regarded as ‘connected’ when i allocates more than 1 per cent of its total foraging effort to j ($a_{ij} > 0.01$) in the simulation. Food-chain length was measured using three indices: the largest link number from the base to the top along the maximum number of steps (maximum chain length), the minimum number of steps (minimum chain length; Pimm 1982) and the maximum trophic position calculated based on material flow pattern (Post & Takimoto 2007). Trophic position of species i (τ_i) is defined by

$$\tau_i = \sum_{j \in \text{species } i\text{'s prey}} w_{ij} \tau_j + 1, \quad (2.3)$$

where w_{ij} is the proportion of species j in the diet of species i (Post & Takimoto 2007), calculated as $[e_{ij} f_{ij} a_{ij} X_i / \sum_{k \in \text{species } i\text{'s prey}} e_{ik} f_{ik} a_{ik} X_k]$ in our model. This value can be estimated in natural ecosystems by using the stable isotope technique (Vander Zanden *et al.* 1999; Post *et al.* 2000a; Takimoto *et al.* 2008; Doi *et al.* 2009). For runs with multiple top predators and/or basal species, we used the maximum value among all combinations of top predator and basal species.

The structural analysis was performed for snapshot food webs at $T = 10\,000$. Food webs where any species became extinct ($X_i < 10^{-13}$) at $T = 10\,000$ were not used for the analysis because a non-persistent food web is unlikely to exist and thus would not be observed in nature. Further, this approach allowed us to avoid the confounding effects of decreasing species richness on food-chain length; if probability of species extinction changes with changing resource availability or presence/absence of adaptation, we cannot distinguish the focal effect of resource availability or adaptation. In the present study, a shorter chain length indicated a ‘fatter’ food web. Prediction obtained through this approach can be tested by the assessment of food-chain length variation between ecosystems with similar species richness. Our approach differs from that in other studies (Pimm & Lawton 1977; Oksanen *et al.* 1981), in which model analysis was conducted for a linear food chain and chain length was correlated with the number of coexisting

species. Our approach cannot detect resource availability effects on food-chain length through alteration of species richness.

We collected 1000 persistent food webs using most of the parameter combinations. However, for some parameter combinations that did not consistently produce persistent food webs, we used less than 1000 persistent food webs for the analysis. Robustness of the model analyses was checked by varying parameter values. Parameter values used were $N = 3$ to 50, $B = 1$ to $0.2N$, $L = (N - B)$ to L_{\max} and $R = 0.04$ to 125.

To evaluate how adaptive diet choice affects food-chain length and its response to changing resource availability, we compared the outcome of the earlier-mentioned adaptive food-web model with those of two other models: a non-adaptive model governed by population dynamics alone (equation (2.1) with $I_i = 0$; equation (2.2) with $G_i = 0$) and a static model without population or adaptive dynamics, identical to a cascade model (Cohen *et al.* 1990). The former predicts the chain-length patterns emerging from dynamic or energetic constraints alone, while the latter evaluates patterns expected from random connections between species.

The comparison of the models required the collection of persistent communities for all models. However, without adaptation, community persistence tends to decrease with increasing species richness (Kondoh 2006), making the computation of persistent, non-adaptive food-web predictions time-consuming. Thus, we started with a relatively simple community comprising 10 species. At that complexity level, a sufficient number of persistent communities were obtained for all three models within an acceptable computational time. Subsequently, we expanded the adaptive model to include more complex communities to test the robustness of the patterns obtained and to examine the effects of food-web complexity (N, L).

3. RESULTS

(a) Resource availability and food-chain length

We started with a relatively simple case in which one basal and nine non-basal species coexist and an adaptive predator is potentially able to use any species at hierarchically lower positions (i.e. $L = L_{\max}$). An adaptive predator uses only a small fraction of the available resources. Thus, as the community develops, the realized link number (L^*) eventually fell within the range $9 \leq L^* \leq 17$ in more than 99 per cent of the model runs. As food-chain length is sensitive to link number, the link numbers modelled were set to similar levels when comparing predicted food-chain lengths in the different models. Thus, L -values in the non-adaptive and static models were set to 9, 13 and 17. In these model runs, immigration ($I = 0$ or 10^{-13}) did not strongly affect the food-chain length in the presence of adaptation (figure 1).

The chain lengths in adaptive food webs were, in general, shorter than those in the non-adaptive or static food webs (figure 1). Furthermore, the presence of adaptation altered the effect of resource availability (R) on chain length. In the absence of adaptation, the chain lengths (minimum and maximum chain lengths and maximum trophic position) increased with increasing R (figure 1d–f). However, in the presence of adaptation, the responses to increased R differed depending on

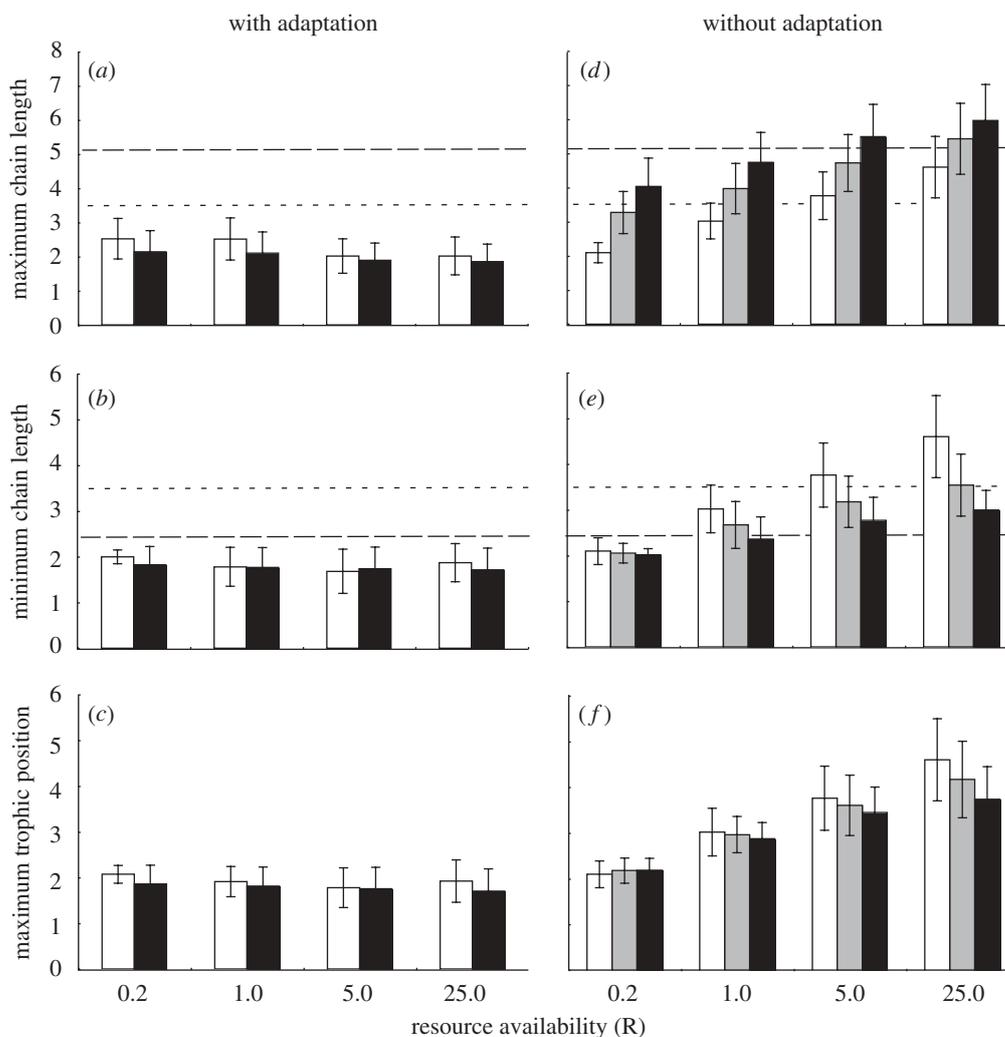


Figure 1. The maximum (*a,d*) and minimum (*b,e*) food-chain lengths and maximum trophic position (*c,f*) of adaptive (*a–c*) and non-adaptive (*d–f*) webs at varying resource availability ($R = 0.2, 1.0, 5.0, 25.0$). Model settings examined are (*a–c*) adaptive food webs without immigration ($I = 0$; white); (*a–c*) adaptive food webs with immigration ($I = 10^{-13}$; black); and (*d–f*) non-adaptive food webs with links $L = 9$ (white), $L = 13$ (grey), $L = 17$ (black). Vertical lines represent standard deviations. Dotted and broken lines represent the food-chain length expected from the static cascade model with $L = 9$ and 17 , respectively. Species richness parameters (N, B) = (10, 1). Values for $(L, R) = (17, 0.2)$ without adaptation are based on 594 simulation runs because of difficulty in obtaining persistent communities.

which chain-length index was used. Maximum chain length tended to decrease slightly with increasing R (figure 1*a*), whereas the minimum chain length and maximum trophic position were relatively invariant under changing R (figure 1*b,c*). A qualitatively similar pattern was observed in the adaptive model under a wider range of species richness (5–50 species; figure 2).

Figure 3 shows changes in food-web linkage patterns with increasing R in a 20-species community ($N = 20, B = 4$). At higher values of R , hierarchically lower species were consumed by more predator species, whereas hierarchically higher species tended to have fewer predator species (figure 3*a*). Those changes were accompanied by a decrease in the number of prey species for most predators (figure 3*a,b*). The combined patterns indicate that predators drop hierarchically higher species from their diet at higher resource availability.

(b) Network complexity and food-chain length

Food-chain length and its response to changing resource availability (R) are influenced by species richness (N).

Figure 2 shows the response of food-chain length to changing R , in the presence of adaptation, under varying species richness levels ($N = 5, 10, 20, 50$) and with a constant proportion of basal species ($B/N = 0.2$). Two patterns were identified: first, both maximum and minimum food-chain lengths and maximum trophic position increased with increasing N , as observed in a static cascade model (Newman & Cohen 1986); second, while the maximum chain length markedly decreased with increasing R at relatively low resource availability under higher N , the minimum chain length and maximum trophic position tended to be relatively invariant to changing R within the tested range of species richness.

The number of potential links (L) influences chain length and its response to changing R . Both the maximum and the minimum chain lengths and maximum trophic position tended to decrease with increasing L (figure 4). This is in contrast to the patterns expected in a static cascade model that an increasing L increases the maximum chain length, but decreases the minimum chain length (as is easily understood by

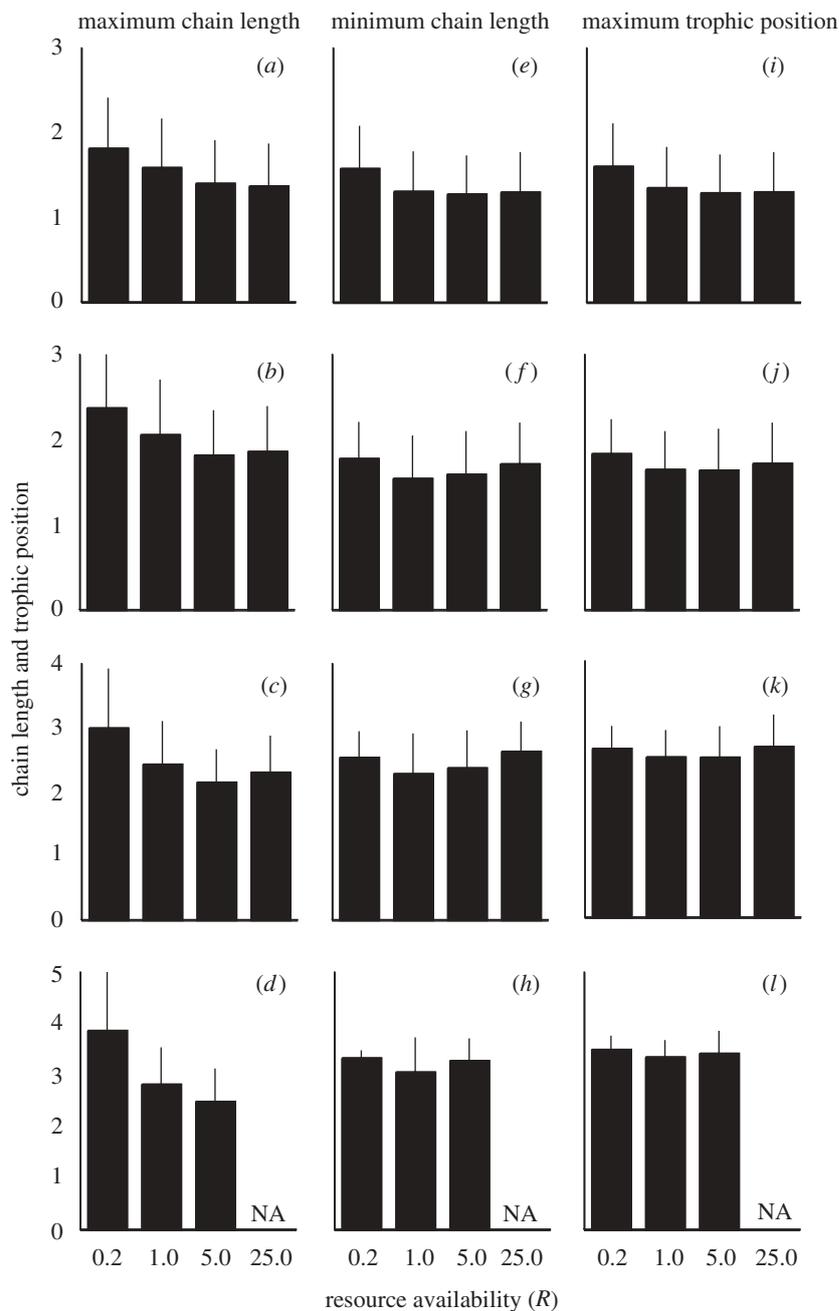


Figure 2. The effect of species richness (N) on food-chain length and its response to changing resource availability (R). Species richness (N, B) combinations are (a, e, i) (5, 1), (b, f, j) (10, 2), (c, g, k) (20, 4) and (d, h, l) (50, 10). The potential link numbers were set at the maximum ($\{N(N-1) - B(B-1)\}/2$). The left ($a-d$), middle ($e-h$) and right ($i-l$) panels are for the maximum and minimum chain lengths and maximum trophic position, respectively. Vertical lines represent standard deviations. Chain length for (N, R) = (50, 25.0) was not available as the community was not persistent.

noting that an addition of a link to a web never shortens the maximum chain length or lengthens the minimum chain length). In addition, changes in the relationship between R and food-chain length, with changing L , are more complex (figure 4). With increasing L , the relationship between R and the maximum chain length changed from unimodal ($L = 61-143$) to negative ($L = 184$; figure 4a), whereas the relationship between R and minimum chain length or maximum trophic position changed from positive ($L = 20-102$) to invariant ($L = 143, 184$; figure 4b). In all of those responses, the variability observed in food-chain length under changing resource availability was less than those in the non-adaptive case (figure 1).

4. DISCUSSION

Our study suggests that adaptive diet choice can result in shorter food-chain lengths than those expected from a random static model with the same levels of complexity (species richness and realized link number; figure 1). This implies that adaptive foragers prefer prey species at lower trophic levels than expected from random prey selection in agreement with Hastings & Conrad (1979). Furthermore, the decrease in the maximum chain length observed during increasing resource availability indicates that the adaptive predator's tendency to feed on lower trophic levels is enhanced by increased resource availability. This is supported by the model prediction that predators may switch from hierarchically higher to

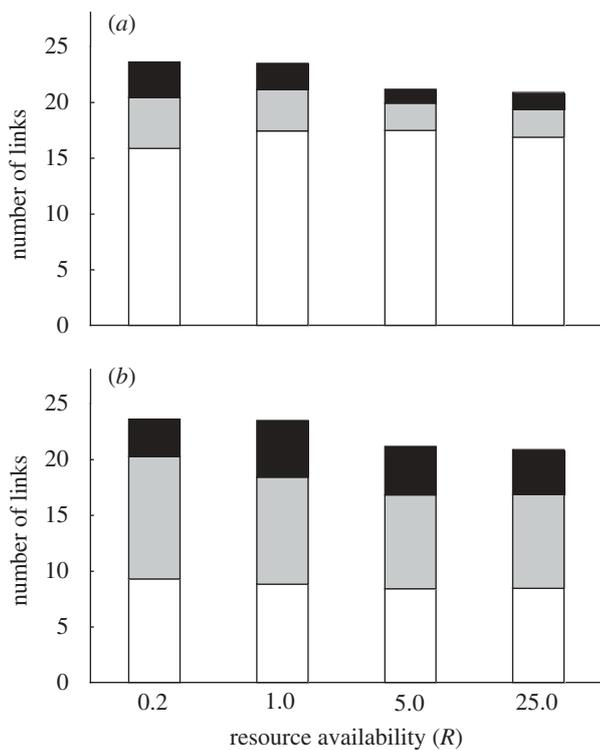


Figure 3. Food-web linkage patterns in the presence of adaptation. The number of links to (a) predator and (b) prey species is shown for the hierarchically lowest to the highest species for varying resource availability ($R = 0.2, 1.0, 5.0, 25.0$). White, grey and black bars are for (a) basal species 1–4, species 5–12 and species 13–19, and for (b) species 5–12, species 13–19 and top predator 20, respectively. Species richness and immigration parameters used were $N = 20$, $B = 4$ and $I = 10^{-13}$.

lower preys at higher resource availability (figure 3). This pattern agrees with that of Holt & Polis (1997), who considered a simple trophic module consisting of an intraguild prey and its intraguild predator competing for the same resource. They argued that, if the intraguild predator follows the optimal foraging theory, an increase in resource availability should shorten the maximum chain length when the intraguild predator drops the intraguild prey from its diet (see Křivan 2000 for a formal model). Our model is the first to demonstrate this pattern in a complex food web.

The present model predicts that adaptive foraging can turn the positive relationship between resource availability and food-chain length into a less dependent or even a negative one. This suggests that adaptive diet choice can mask the positive effect of resource availability on food-chain length and thus may explain observations that food-chain length is not positively correlated with a measure of per-unit-area productivity in natural ecosystems (Spencer & Warren 1996; Post *et al.* 2000a). Food-web reconstruction induced by adaptive diet choice provides a possible resolution of the apparent contradiction between energy-based theory and empirical observations. A study of predator diets at different trophic and resource availability levels may be a useful approach to identify the mechanisms behind the observed invariance in food-chain length under changing resource availability.

Given that foraging adaptation can mask the positive effect of resource availability on food-chain length, we developed two theories to explain the positive effects of productivity on food-chain lengths observed in simple microcosms (Jenkins *et al.* 1992; Kaunzinger & Morin 1998). One possible explanation is that the observed positive effect is a reflection of adaptive incapability in microcosms. A lack of, or a limit on, foraging adaptation owing to predators' physiological or genetic limitations could reduce food-web flexibility and thus enhance the positive resource availability effect (figure 1). This is likely to occur in small microcosms where a population bottleneck can result in low genetic diversity—that is, the founder effect (Leberg 1992)—or where predators are often filter feeders and thus likely to be less capable of shifting their diets in a refined fashion. The other explanation is based on the low complexity of microcosm communities. As predicted by our model, low species richness lessens the negative effect of resource availability on the maximum chain length (figure 2). This alone would not create a positive relationship, but may permit the development of a positive relationship when combined with other forces that can potentially increase chain length, such as increased species richness. Those theoretical possibilities should be tested in future studies.

Recent empirical studies have shown that food-chain length is positively correlated with habitat size (Spencer & Warren 1996; Post *et al.* 2000a; Takimoto *et al.* 2008; Doi *et al.* 2009). Our model provides two possible explanations for these observations: one is related to changes in species richness and the other to interspecific spatial segregation. In a static cascade model, food-chain length increased with increasing species richness. Cohen & Newman (1991) used that relationship to explain their positive correlation between food-chain length and habitat size. The positive relationship between species richness and chain length was preserved in the present adaptive model (figure 2); therefore, the same argument should give rise to a positive habitat size–chain length correlation in the presence of foraging adaptation. Second, a larger habitat size is often accompanied by an increase in habitat types. As species distributions may be restricted by habitat type, some species combinations would not occur in the same habitat type and those species would not interact. Thus, potential connectance would be lower in larger, more complex habitats and food-chain length could increase in the presence of adaptation (figure 4). This would result when interspecific segregation prevents predators from switching to lower trophic levels. Note that this does not happen in non-adaptive food webs, where the maximum chain length decreases with decreasing link number.

As presented in the foregoing hypothesis, food-chain length can increase with increasing habitat size because of increased interspecific segregation. However, it should be noted that increased interspecific segregation also has a potential to shorten (not lengthen) food chains. If resource species are more spatially segregated than their predators in a larger habitat, it would be easier for predators to allocate time among different habitat types, automatically leading to predator's allocation of foraging effort among potential prey species. This would result in a shorter food chain. Thus, whether spatial heterogeneity increases or decreases food-chain length would

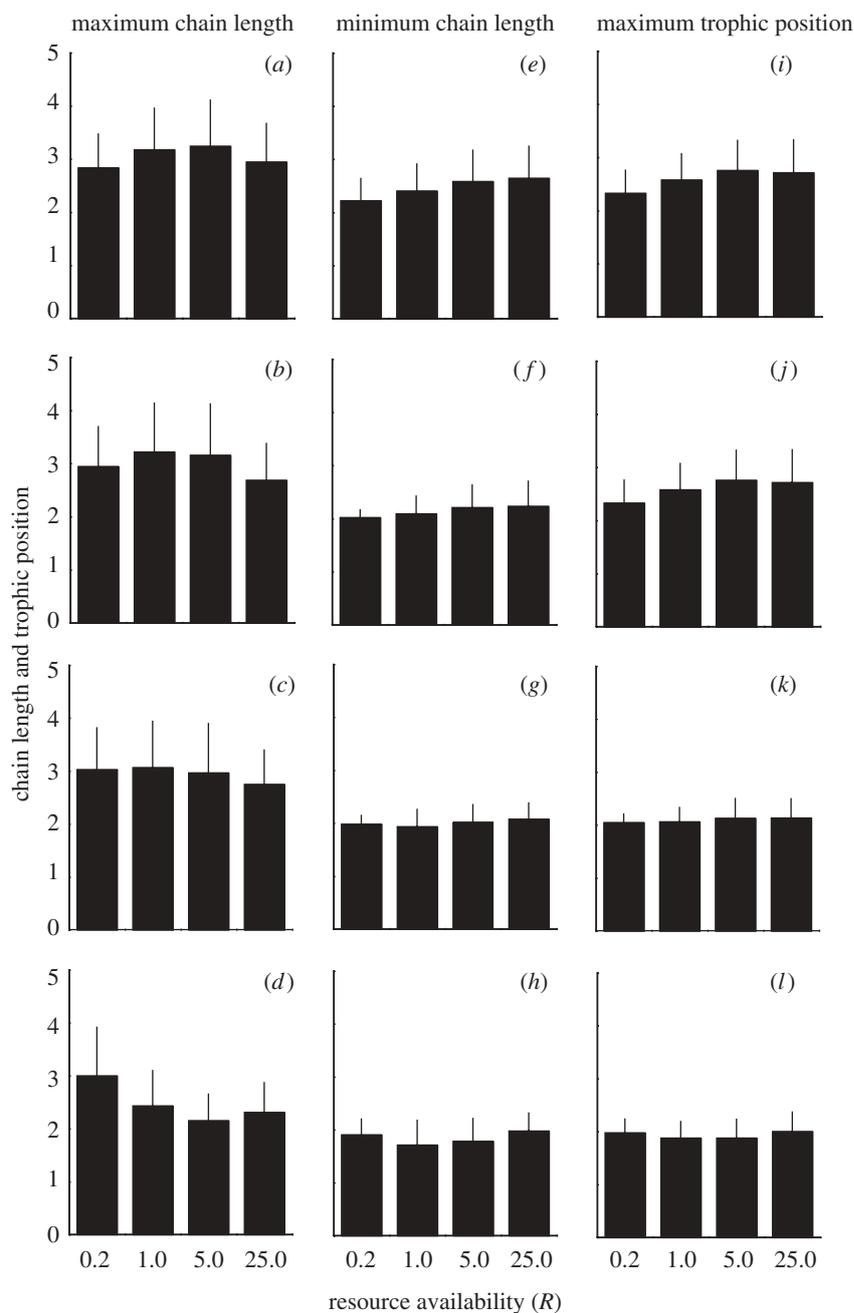


Figure 4. The effect of link number (L) on food-chain length and its response to changing resource availability (R). Species richness set at $(N, B) = (20, 4)$. The potential link numbers (L) were (a,e,i) 61, (b,f,j) 102, (c,g,k) 143 and (d,h,l) 184. The left (a–d), middle (e–h) and right (i–l) panels are for the maximum and minimum chain length and maximum trophic position, respectively. Vertical lines represent standard deviations.

depend on which species are actually segregated as a result of increased habitat size.

Although several explanatory hypotheses have been presented for determinants of food-chain length (Pimm & Lawton 1977; Hastings & Conrad 1979; Pimm 1982; Cohen & Newman 1988), few are supported by empirical studies (Post 2002), resulting in a gap between theoretical and observed patterns. The present study suggests that food-web reconstruction induced by adaptive foraging may narrow this gap. A significant feature of our model is that adaptation, a distinguishing feature of organisms, is used as a primary principle. This is in contrast to the classical theory in which the response of food-web structure to environmental variables has been regarded as a

consequence of a ‘selection’ of energetically or dynamically stable food-web structures (Pimm & Lawton 1977; Pimm 1982; Cohen & Newman 1988). The present theoretical framework constitutes one end of the continuum between a population-oriented view (dynamic constraints on a static food-web structure) and an adaptation-oriented view (flexible food-web structure shaped by adaptation).

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