

Predator foraging behaviour drives food-web topological structure

Xavier Lazzaro^{1*}, Gérard Lacroix², Benoît Gauzens², Jacques Gignoux² and Stéphane Legendre³

¹UMR 7208 Borea, CNRS, IRD, UPMC, MNHN, CP 53, 61 rue Buffon, F-75231 Paris cedex 5, France; ²UMR 7618 Bioemco, CNRS, UPMC, INRA, IRD, AgroParisTech, Université Paris-Est, ENS, 46 rue d'Ulm, 75230 Paris cedex 05, France; and ³UMR 7625 Ecologie et Evolution, CNRS, UPMC, ENS, 46, rue d'Ulm, 75230 Paris cedex 05, France

Summary

1. The structure and dynamics of prey populations are shaped by the foraging behaviours of their predators. Yet, there is still little documentation on how distinct predator foraging types control biodiversity, food-web architecture and ecosystem functioning.
2. We experimentally compared the effects of model fish species of two major foraging types of lake planktivores: a size-selective visual feeder (bluegill), and a filter feeder (gizzard shad). The visual feeder forages on individually captured consumer prey, whereas the filter feeder forages on various prey simultaneously, not only consumers but also primary producers. We ran a 1-month mesocosm experiment cross-classifying a biomass gradient of each predator type. We analysed the effect of each fish on food-web architecture by computing major topological descriptors over time (connectance, link density, omnivory index, etc.). These descriptors were computed from 80 predator–prey binary matrices, using taxa mostly identified at the species level.
3. We found that the visual feeder induced more trophic cul-de-sac (inedible) primary-producer species, lower link density and connectance, and lower levels of food-web omnivory and generalism than the filter feeder. Yet, predator biomass did not affect food-web topology.
4. Our results highlight that top-predator foraging behaviour is a key functional trait that can drive food-web topology and ultimately ecosystem functioning.

Key-words: connectance, generalism, omnivory, planktivorous fish, trophic cul-de-sac

Introduction

Food chains are simple ways to describe trophic cascade effects. The most successful models of food-web regulation in aquatic systems are based on aggregating real food webs into linear trophic chains of carnivores, herbivores and primary producers (Straile 2005). As such, the 'trophic cascade' hypothesis (Carpenter, Kitchell & Hodgson 1985; Strong 1992; Pace *et al.* 1999) is an efficient predictive tool for both ecologists and ecosystem managers. Food chains are however inappropriate to identify the direct and indirect mechanisms causing changes in the nature and strength of trophic cascades. Several studies (e.g. Hansson *et al.* 1998; Hulot *et al.* 2000) have confirmed that distinguishing organisms within a given trophic level can modify model predictions. Attributes such as prey-size refuges, edibility and omnivory play an important role in modifying not only the network structure, but potentially ecosystem responses. A current critical issue is thus how distinct predators, as individual species and/or

functional groups, may differentially modify the properties of food webs and ecosystems (e.g. Petchey & Gaston 2006).

Predator foraging mode, which interacts with prey anti-predator behaviour, is a key factor controlling food-web topology (Ings *et al.* 2009), and ecosystem functioning (Schmitz, Krivan & Ovadia 2004; Schmitz 2008). Consumers with contrasting foraging behaviours use distinct trophic pathways with feeding links characterized by different arrangements of interaction strengths (Schmitz 2008). The distinct foraging modes (e.g. sit-and-wait, sit-and-pursue, active hunting, particulate feeding on single prey one at a time, gulping or filtering to capture various prey simultaneously) may thus differentially affect food-web architecture and dynamics, and influence ecosystem functioning (Mittelbach & Osenberg 1994; Thébault & Loreau 2003). This arises by changing direct and indirect interactions among species (Schmitz & Suttle 2001), and favouring prey traits that reduce predation risk (Preisser, Orrock & Schmitz 2007). Besides, by using an optimal foraging behaviour model, Beckerman, Petchey & Warren (2006) demonstrated a strong relationship between predator foraging modes, expressed as diet breadths,

*Correspondence author. E-mail: xavier.lazzaro@ird.fr

and food-web connectance. Using an improved model linking foraging traits through the effects of body size, Petchey *et al.* (2008) showed that the arrangement of trophic links within food webs could emerge from optimally foraging individuals. Their results suggest that predators with distinct foraging strategies should determine different food-web structures.

These issues regarding predator foraging modes have been less studied (Williams & Moss 2003), major emphasis being dedicated to the role of basal species diversity (Duffy, Richardson & Canuel 2003). Foraging behaviour is usually not considered as a factor explaining the relationships between biodiversity, food-web architecture and ecosystem functioning. Cascading effects of predator diversity have rarely been theoretically considered (Duffy *et al.* 2007), with few exceptions such as Schmitz (2007) who classified the functional roles of the predator. Experimental studies have explored how reduction of predator diversity propagates through a web of species interactions to influence ecosystem functioning (e.g. Otto *et al.* 2008). Williams & Martinez (2000), Krivan & Schmitz (2003) and Duffy *et al.* (2007) have suggested exploring the possible roles of species functional traits on food-web architecture, comparing effects of specialist and generalist predators. Yet, no study has been designed for this purpose.

In aquatic ecosystems, fish–plankton interactions provide a suitable framework to analyse the relationships between predator type, food-web topology and ecosystem functioning. Within the last four decades, optimal foraging theory has been extensively used to predict the foraging patterns and selective consumption by planktivorous fish in relation to plankton composition and density (Werner *et al.* 1983), as well as shifts between foraging modes.

Herein, we selected the model fish species as representative of the two major planktivore foraging types that frequently coexist and can dominate the fish biomass of lakes in the central and southeastern United States of America: a size-selective visually feeding Centrarchid (bluegill, *Lepomis*

macrochirus, Rafinesque 1819), and a filter-feeding Clupeid (gizzard shad, *Dorosoma cepedianum*, Lesueur 1818). These species are archetypes of two contrasting foraging behaviours commonly found in lakes (Lazzaro 1987; Lacroix, Lescher-Moutoué & Pourriot 1996; Fig. 1). Visual feeders, such as Centrarchids and young Percids, are carnivorous size-selective planktivores. They consume zooplankton, individually or in groups (gulping), insects and occasionally small fish (Janssen 1976). They select the largest or most active prey (generalist cyclopoid copepods, large herbivorous cladocerans), but avoid small herbivores (rotifers, copepodites, nauplii, small cladocerans). Visual feeders may indirectly enhance phytoplankton and small zooplankters (Hambright *et al.* 1986). In contrast, filter feeders, such as Clupeids, Cyprinids in turbid lakes and Cichlids in the tropics, are pump-filter-feeding omnivorous planktivores (Drenner & McComas 1980). They select small herbivores, avoid fast-moving copepods and consume large phytoplankton species and detritus. By straining prey and particles using gillrakers or other entrapment structures (Drenner *et al.* 1987), filter feeders directly suppress poorly evasive cladocerans and large phytoplankton, and indirectly enhance evasive copepods and small algae (Drenner, Threlkeld & McCracken 1986; Drenner *et al.* 1987). Thus, for a given body size, filter feeders feed on smaller prey than visual feeders (Lazzaro 1987).

Herein, we analysed whether two predators with distinct foraging strategies determine different food-web topologies. We tested more specifically four hypotheses stated as follows.

First hypothesis: Visual feeders should more frequently lead to trophic cul-de-sac (inedible) basal species than filter feeders. Indeed, visual feeders have a stronger impact on large invertebrates, and a comparatively lower impact on small invertebrates, than filter feeders, which are less selective on their prey range. Thus, for a given fish biomass, visual feeders favour small prey, such as small invertebrate herbivores, which have narrower diet breadth than large invertebrate herbivores (e.g. Burns 1968; Humphries 2007).

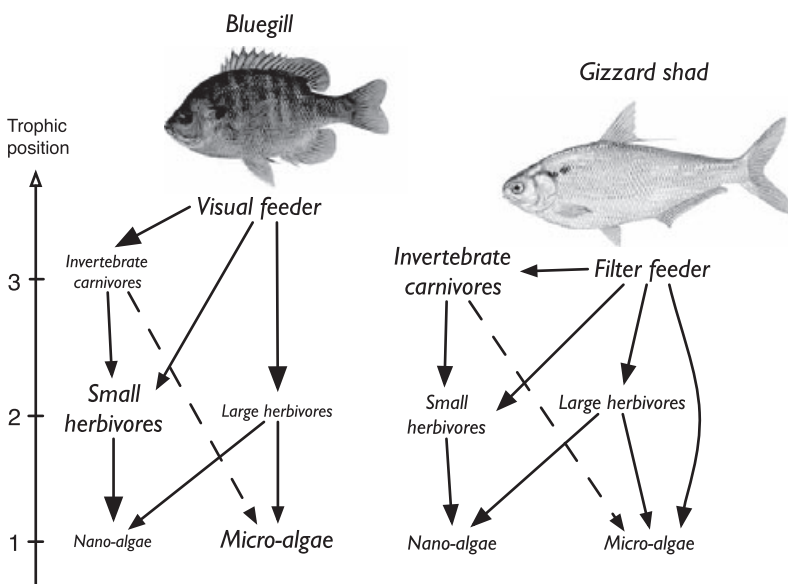


Fig. 1. Hypothesized food-web interactions between plankton functional groups in the presence of model fish species of planktivore foraging types: either a specialist visually feeding bluegill (left-hand side) or a generalist filter-feeding gizzard shad (right-hand side). Given the definition of omnivory (i.e. consuming prey belonging to more than one trophic level), both planktivores are omnivores. The strength of predation and grazing control are indicated by three line widths (thin, medium and thick). The resulting importance (biomass, richness) of the functional groups is indicated by three font sizes (small, medium and large). The trophic positions of the functional groups are indicated by their vertical positions along the y-axis.

Second hypothesis: Visual feeders should induce lower link density and connectance than filter feeders. This is supported by Beckerman *et al.*'s (2006) theoretical model, which predict that consumer diet breadth and connectance are positively linked.

Third hypothesis: Visual feeders should induce lower levels of food-web generalism (i.e. the mean number of taxa consumed by all consumer species) than filter feeders. Indeed, the number of prey species per consumer is linked to the size range of prey eaten. By selectively consuming the largest consumer prey with the widest diet breadth, visual feeders reduce the mean size of the remaining consumers, and consequently the mean number of species that they consume.

Fourth hypothesis: Visual feeders should induce lower food-web omnivory levels (i.e. variability in the prey trophic positions of all consumers) than filter feeders. Trophic position and body size being positively related in aquatic food webs, a reduction of the consumer size range should homogenize their trophic positions, and thus reduce food-web omnivory.

Using Lazzaro *et al.*'s (1992) data set, we analysed whether predator foraging type and predator biomass significantly and independently modify food-web topological characteristics. We discussed how the two topological alternate states generated by the two predator foraging types might distinctly control ecosystem functioning, particularly the omnivory level, and the importance of inedible primary producers.

Materials and methods

EXPERIMENTAL PROTOCOL

We re-analysed the results of a previous 4-week (13 April–17 May 1989) experiment conducted in 16 5.5-m³ above-ground fibreglass tanks at Texas Christian University (see Lazzaro *et al.* 1992 for details). Mesocosms were filled with water from a small, shallow, mesotrophic pond. The experimental design cross-classified four levels of fish biomass (10, 30, 50 and 75 g m⁻³, *c.* 200–1500 kg ha⁻¹) with two foraging types of planktivores: gizzard shad (13–16 cm standard length or SL), and bluegill (5–10 cm SL). Fish were weighted individually (nearest 0.1 g) in water-filled plastic bags, and stocked into tanks following this experimental design (1, 3, 5 and 7 gizzard shad, and 3, 9, 15 and 21 bluegill per tank). The highest biomass level was compatible with the maximum natural biomass of gizzard shad (1236 kg ha⁻¹), twice that of bluegill (750 kg ha⁻¹, *c.* 30 g m⁻³; Lazzaro *et al.* 1992). The resulting eight-treatment combinations were randomly assigned and replicated twice. Vertically integrated samples of zooplankton (triplicate tows of a 63-µm mesh net; 60-L samples, i.e. 1% of tank volume per sampling date) and phytoplankton (polyvinyl-chloride-tube sampler for cell counting and chlorophyll-*a*; 6-L samples, i.e. 0.1% of tank volume per sampling date) were collected on days -2 (before fish stocking), 5, 12, 19 and 26. After tank draining, chironomid tubes were sampled on the tank walls, and fish were recaptured. All stocked fishes were recovered, indicating the absence of mortality.

IDENTIFICATION OF TAXA AND TROPHIC LINKS

All taxa were identified at the species level, except copepod nauplii, benthic invertebrates (chironomids) and bacteria. The resulting

trophic species belong to either phytoplankton ($n = 45$; basal species with few taxa separated by morphs or colony size), detritus ($n = 1$; considered as a basal species), bacteria ($n = 1$; detritus consumers), zooplankton ($n = 8$; with cyclopoid nauplii as a trophic species, distinct from their copepodite and adult stages), chironomids ($n = 1$; detritivores) or fish ($n = 2$). Links were determined from either a detailed knowledge of the trophic species based on the literature (see Appendix S1), or the allometric relationships between predator and prey (e.g. Burns 1968) in the absence of specific information. Cannibalism was not observed in fish. Because of the high density of most available prey, cannibalism of copepodites, shad predation on adult cyclopoids and consumption of three poorly edible phytoplankton species were probably very weak links, and thus omitted. Although rarely acknowledged, the detection limits of sampling protocols may affect the assessment of not only species richness, but food-web topological structure. This may be an issue when using binary food webs (conversely to quantitative food webs), as the role of potentially weak links between rare species may become relevant. We were thus vigilant in omitting links that we assumed were most probably very weak. When using binary food webs, such *a priori* decisions have to be made, on a case-by-case basis, to minimize the relative role of rare species and weak links.

FOOD-WEB BINARY MATRICES

We represented trophic networks by binary matrices. Over time, by cumulating taxa from all tanks and all sampling dates, we observed 58 trophic species. We first constructed a predator–prey ‘cumulated’ matrix of size 58 × 58 (Appendix S1) with taxa listed as rows and columns. The intersection element values were either 0 (no consumption), or 1 (consumption). To analyse predator-type and biomass effects on food-web architecture, we then constructed an ‘instantaneous’ matrix for each tank and each sampling date, by including only the observed taxa. The size of the resulting 80 instantaneous matrices (two fishes × four biomasses × two replicates × five dates) varied between 18 × 18 and 35 × 35.

FOOD-WEB DESCRIPTORS

Food-web descriptors were computed for all instantaneous matrices, using a program developed in the Pascal language (Borland Delphi 6).

Species properties

We classified species as basal (B ; having no prey), and top-consumers (T ; having no predator). Basal species were either edible (Be ; initiating at least one food chain) or inedible (Bi ; having no consumer). Thus, basal species edibility was not defined *a priori*, but depended on the presence of at least one potential predator. We estimated the percentage of inedible basal species ($%Bi$) in relation to the basal species richness ($Be + Bi$), as a measure of the relative importance of trophic cul-de-sacs among primary producers.

Link and chain properties

The link density (L/S) was defined as the ratio between the number of trophic links (L) and the overall specific richness (S). Herbivore-specific richness was noted as H . Connectance ($C = L/S(S-1)$) represented the number of links over the number of possible links, excluding cannibalism. We defined a chain as a distinct path from a basal to a non-basal species, and chain length as the number of links

in the chain (our food webs did not contain cycles). The number of chains (NC) was the total number of paths linking basal species with non-basal species. Mean chain length ($MeanCL$) was computed as the total number of links in these paths divided by their number NC .

Trophic position of species

In a chain, a species trophic level was equal to one plus the number of trophic species (i.e. taxa) below it. Basal species had a trophic level of 1. The trophic position of a non-basal species was its average trophic level over all chains to which it belonged (Cohen, Jonsson & Carpenter 2002). We compared mean trophic positions of fish (Pf) and invertebrate carnivores (Pic ; cyclopoids plus *Asplanchna*).

Generalism and omnivory properties

We defined fish generalism index (Gf) as the number of taxa that it consumed [equivalent to Beckerman *et al.*'s (2006) diet breadth], and the food-web generalism index (Gw) as the mean value of the generalism indices of all constituent consumer species (Bersier, Banasek-Richter & Cattin 2002). A trophic species was omnivorous if it consumed prey from more than one trophic level. Fish omnivory index (Of) was the standard deviation of the trophic positions of its prey, while food-web omnivory index (Ow) was the mean omnivory index of all consumer species.

STATISTICAL ANALYSES

To verify that the food-web characteristics of tanks assigned to bluegill and gizzard shad treatments did not differ prior to fish stocking (day 0), we performed two-way ANOVA on data from day -2 (pre-treatment). Day -2 was excluded from subsequent analyses of fish effects. We analysed the main effects of planktivore foraging type and fish biomass, and their interaction effects (planktivore foraging type \times fish biomass) using repeated-measures ANOVA (RMA), with two grouping factors (two foraging types, and four fish biomass levels), and a time trial factor (four sampling dates: days 5, 12, 19 and 26). By performing multiple significance RMA, we may declare effects as significant whereas they are not. For 20 topological descriptors, we increase our chance of finding at least one significant test to $(1 - 0.95^{20}) = 0.64$. To avoid this, we adjusted the statistical significance of the effects using the sequential Bonferroni adjustment (Holm 1979), based on a significance level of $\alpha = 0.05$. For that, we ranked the 20 descriptor P -values from the lowest to the highest, and verified whether they remained smaller (significant) than $0.05/20$, $0.05/19$, ..., $0.05/1$, sequentially. To analyse whether food-web properties were correlated with S and C , as typically found, we performed correlation analyses between some food-web descriptors on the four time-averaged values (days 5–26). Then, we performed ANCOVA using planktivore foraging type and fish biomass as treatment factors and mean species richness (over days 5–26) as a covariate. All statistical tests were performed using SUPERANOVA v.1.11 (Abacus Concepts 1991; Berkeley, CA, USA) on non-transformed data.

Results

PRE-TREATMENT CONDITIONS

ANOVA performed on data collected 2 days prior to fish stocking, revealed that none of the studied food-web descriptors significantly differed between either fish or biomass treat-

ments attributed to tanks. Thus, data of days 5–26 were not biased by initial discrepancies between tanks.

EFFECTS OF PREDATOR FORAGING TYPE VS. BIOMASS

After sequential Bonferroni adjustments, predator foraging type significantly affected 19 out of the 20 food-web descriptors (Figs 2–5), having no effect only on the Pic . Most observed effects were highly significant ($P \leq 0.001$). Conversely, neither predator biomass nor predator type \times fish biomass interaction significantly affected the food-web descriptor. The Bonferroni adjustments suppressed the significance of the fish biomass effects on $\%Bi$ and Bi , NC , L/S , C and $MeanCL$, and the predator type \times fish biomass interaction effects on Ow and the invertebrate omnivory index (Oi).

SPECIES RICHNESS AND TROPHIC CATEGORIES

The S was significantly greater with the filter feeder (28.8 ± 0.7 , mean \pm SE) than with the visual feeder (24.7 ± 0.6 ; Fig. 2a). This enhancement reflected a significant increase in B (15.6 ± 0.4 vs. 9.0 ± 0.4 , respectively; Fig. 2d), H (6.0 ± 0.2 vs. 3.4 ± 0.2 ; Fig. 2c) and top consumers (Tc ; 2.8 vs. 0.1 vs. 1.2 vs. 0.1 ; Fig. 2b). In contrast, the richness of both Bi and $\%Bi$ was higher with the visual feeder than with the filter feeder (9.8 ± 0.4 vs. 5.4 ± 0.5 , and 52.4 ± 2.2 vs. 25.1 ± 1.9 ; Fig. 2f, g).

TROPHIC LINKS

Following the trend in species richness, the NC was significantly higher with the filter feeder (87.0 ± 6.6) than with the visual feeder (36.7 ± 5.1 ; Fig. 3a). The L was also significantly higher with the filter feeder (48.0 ± 2.1 vs. $25. \pm 2.1$; Fig. 3b). This was not an effect of increase in S *per se* (Fig. 2a), as L/S followed a similar pattern (1.7 ± 0.1 vs. 1.0 ± 0.1 , for filter and visual feeders, respectively; Fig. 3d). Consistently, C was also higher with the filter feeder (0.059 ± 0.003 vs. 0.039 ± 0.002 ; Fig. 3c). Moreover, the $MeanCL$ was higher in the presence of the visual feeder (2.88 ± 0.08 vs. 2.16 ± 0.04 ; Fig. 3e).

TROPHIC POSITIONS, GENERALISM AND OMNIVORY

The Pic of invertebrate carnivores (3.22 ± 0.02) was unaffected by fish (Fig. 4d). Because the visual feeder did not consume basal species, its Pf was always higher (3.89 ± 0.08) than that of the filter feeder (3.14 ± 0.04 ; Fig. 4h). As both gizzard shad and invertebrate carnivores mainly consumed small herbivores (Fig. 1), their trophic positions did not differ significantly (paired t -test, $P = 0.07$; Fig. 4d, h). S was higher in the presence of gizzard shad (see before). Therefore, the Gf of this filter feeder (9.59 ± 0.15) was much higher than that of the visual feeder (2.28 ± 0.18 ; Fig. 4f). In the presence of the filter feeder, both the invertebrate generalism index (Gi), and the Gw were higher (5.6 ± 0.2 vs. 4.4 ± 0.2 , and 6.10 ± 0.16 vs. 4.05 ± 0.23 , respectively; Fig. 4e, g). Because

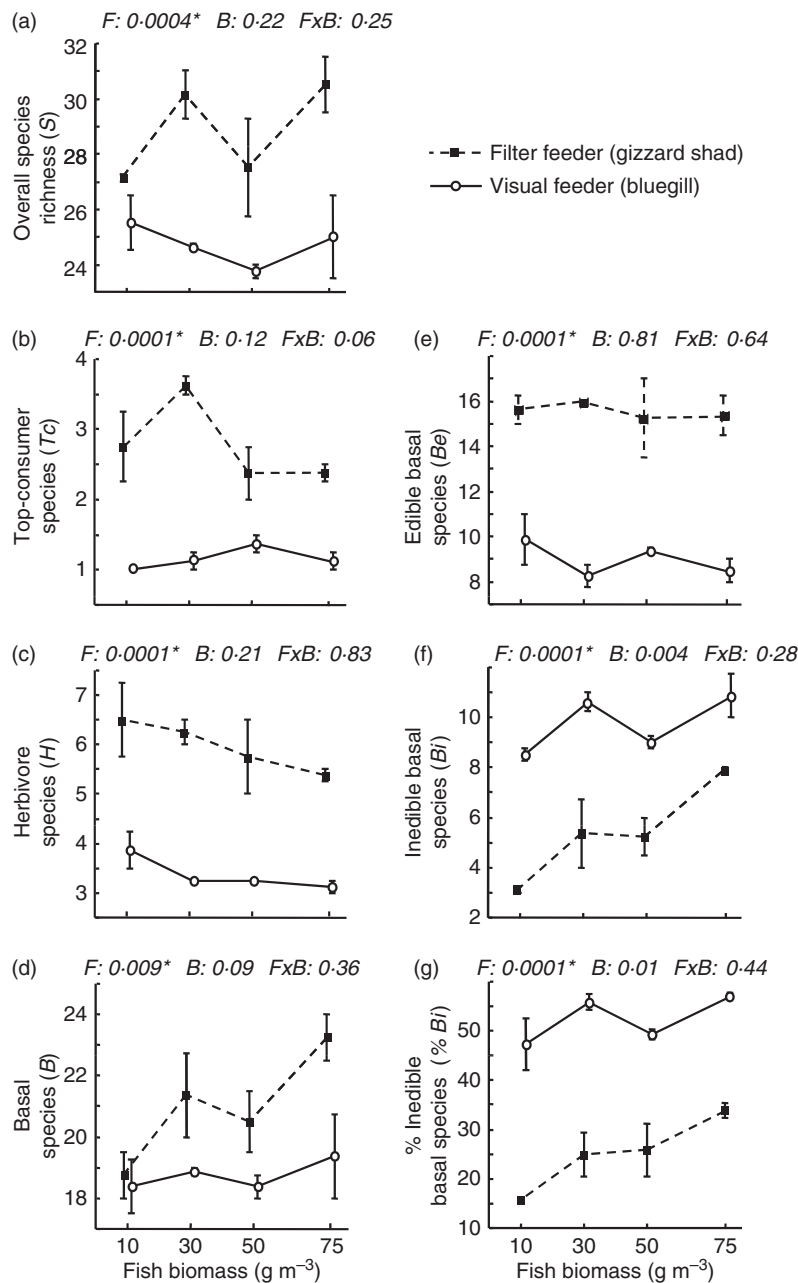


Fig. 2. Mean responses of: (a–d) trophic category descriptors of species richness and (e–g) edible and inedible phytoplankton descriptors over the four sampling dates (days 5, 12, 19 and 26). Data points and error bars are mean \pm SE of eight values (two replicate tanks \times four sampling dates). Probability values from repeated-measures ANOVA of planktivore foraging type (*F*) and fish biomass (*B*) main effects, and their interaction effects (*F* \times *B*) are indicated on the top of each. An asterisk indicates *P*-values of statistically significant effects after Bonferroni's sequential adjustments.

of its consumption at the three trophic levels (including basal species; Fig. 1 and Appendix S1), the *Of* of the filter feeder was significantly higher (0.63 ± 0.02) than that of the visual feeder (0.52 ± 0.04 ; Fig. 4b). In the presence of the filter feeder, the *O_i* and *O_w* were also higher (0.31 ± 0.01 vs. 0.27 ± 0.02 , and 0.35 ± 0.01 vs. 0.31 ± 0.02 , respectively; Fig. 4a, c).

LINKS BETWEEN SPECIES RICHNESS AND FOOD-WEB ARCHITECTURE

Correlation analyses between the time-averaged web descriptors in the 16 tanks revealed that the *S* was correlated with *L*

($r^2 = 0.64$, $P = 0.0002$) and link density L/S ($r^2 = 0.45$, $P = 0.005$). In contrast to the negative relationships widely found in the literature, herein *S* was not related to *C* ($r^2 = 0.19$, $P = 0.09$). From ANCOVA using planktivore foraging type and fish biomass as treatment factors, and *S* (over days 5–26) as covariate, the effects of planktivore foraging type were significant (after sequential Bonferroni adjustments) on the three major food-web descriptors corresponding to our hypotheses: number of *Bi* ($P = 0.003$), *C* ($P = 0.03$) and *G_w* ($P = 0.008$). A significant effect of species richness as covariate was only found for *G_w* ($P = 0.01$). Thus, the observed treatment effects did not reflect differences in *S* and *C*, but in underlying energy flow patterns.

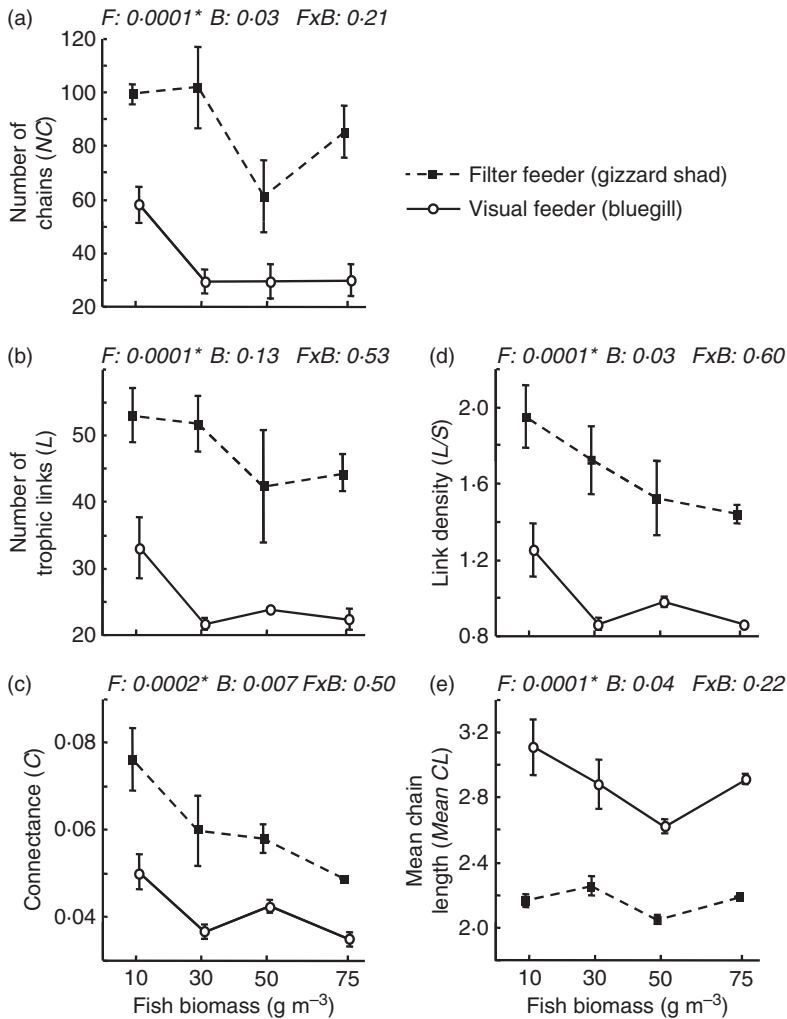


Fig. 3. Mean responses of: (a) number of chains, (b) number of trophic links, (c) connectance, (d) link density and (e) mean chain length descriptors over time. Sampling dates, probabilities, significance, means, error bars and Bonferroni sequential adjustments are as in Fig. 2.

TIME EFFECTS

With few exceptions, after fish stocking (days 5–26), most food-web descriptors increased over time in the presence of the visual feeder, while remaining rather constant in the presence of the filter feeder (Fig. 5a–e). These patterns mostly result from observed changes in S . Prior to fish stocking (pre-treatment values identified by triangles along the y -axis; Fig. 5a–e), S was $c.$ 30 (Fig. 5a). For the visual feeder, 5 days after fish introduction, S decreased to 22, then increased steadily up to the pre-treatment value. The strong selective predation of the visual feeder rapidly suppressed the most abundant consumers, subsequently favouring the growth of initially rare algal species. The more omnivorous filter feeder did not strongly affect S .

Differences between the two fish treatments decreased over time, suggesting that these differences might disappear if the experiment was run longer. This illustrates constraints inherent to closed systems (e.g. high fish biomass relative to natural systems, depletion of natural prey of predators) that typically limit the duration of mesocosm experiments to 4–5 weeks. We did not find a continuous chronological decrease for any descriptor. Thus, our results were not arte-

facts because of species erosion in tanks over time. Instead, these results reflected the progressive reconstruction of the food web in the presence of fish, particularly with the visual feeder.

Discussion

PREDATOR FORAGING TYPE, BIOMASS AND FOOD-WEB TOPOLOGY

Our results demonstrate that predator foraging type strongly affects food-web topology. More specifically our results supported the four working hypotheses. Compared with food webs with a visually feeding predator, food webs with a filter-feeding consumer displayed a higher S (B , H and T), and tended to share more Be species (Hypothesis 1). Food webs with a filter feeder were less pyramidal (higher percentage of T), more connected (Hypothesis 2) and characterized by higher NC that were shorter. In the presence of the filter feeder, consumers were also more generalist (Hypothesis 3) and omnivorous (Hypothesis 4). This increase in Of in the presence of the filter feeder might partly result from the increase in prey's S , and thus from the realized generalism level of

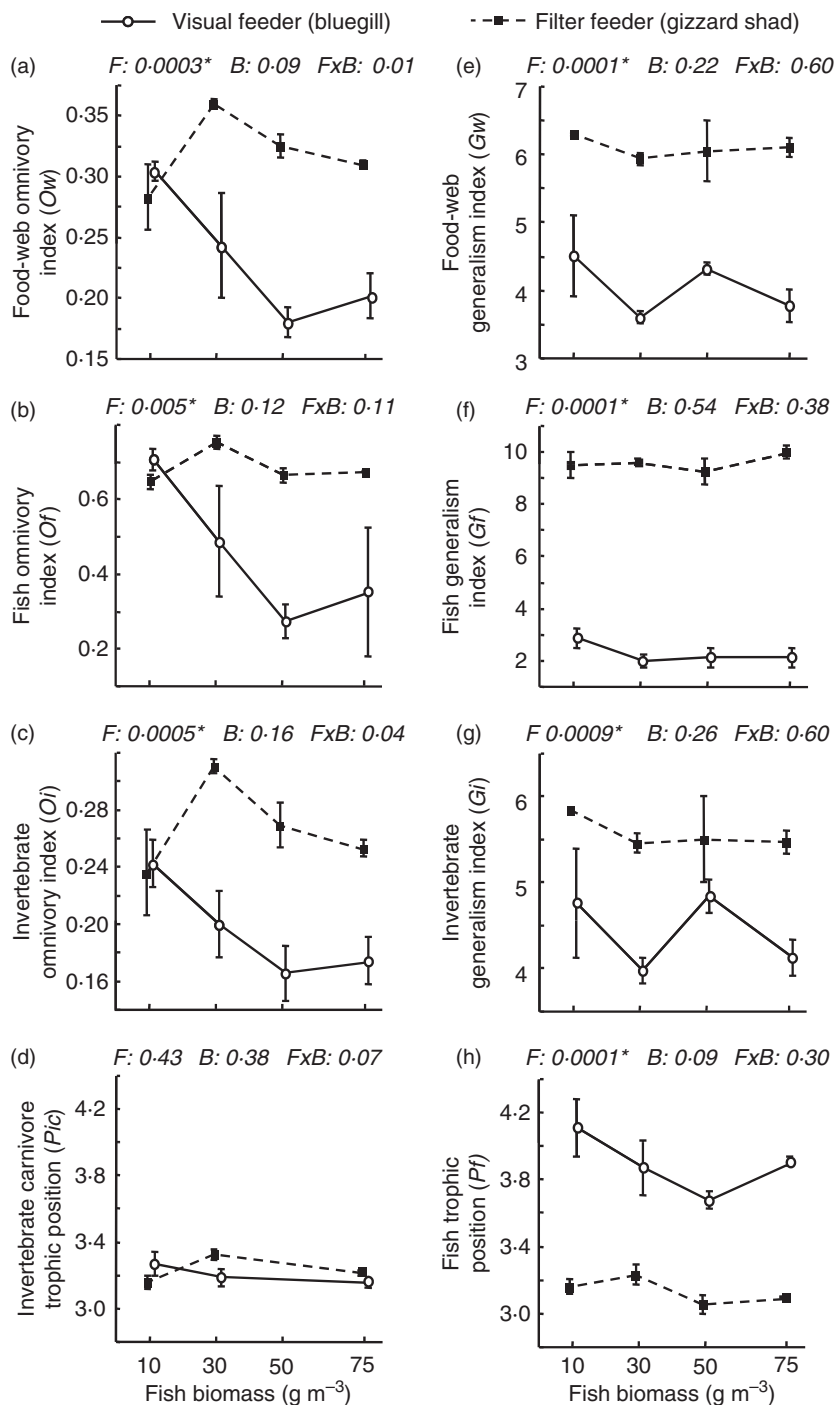


Fig. 4. Mean responses of: (a–c) omnivory and (e–g) generalism descriptors for the food web, fish and invertebrate carnivores, and trophic positions of (d) invertebrate carnivores and (h) fish over time. Sampling dates, probabilities, significance, means, error bars and Bonferroni's sequential adjustments are as in Fig. 2.

their consumers. Additionally, more omnivorous taxa, such as cyclopoids, were favoured (Lazzaro *et al.* 1992). Our findings are consistent with Petchey *et al.*'s (2008) theoretical predictions that predator foraging strategies drive the arrangement of trophic links. Ultimately, by changing chain lengths, trophic category weights and the occurrence of *Bi* species, predator foraging type should substantially influence the dominant energy pathways.

Herein, while all statistically significant biomass effects disappeared after correction for multiple testing, all fish-species effects remained significant. This supports our conclusion

that fish foraging behaviour is a major controlling factor of food-web topology.

Some descriptors may have been affected by the relative importance of feeding links. We thus performed complementary analyses on quantitative descriptors of trophic position, omnivory and generalism. Both unweighed indices and that weighed by the biomasses of prey species brought similar response patterns (unpublished data), confirming the robustness of our binary approach. As stressed by Berlow *et al.* (2004), it is worthy to further explore the functional importance of food-web quantification.

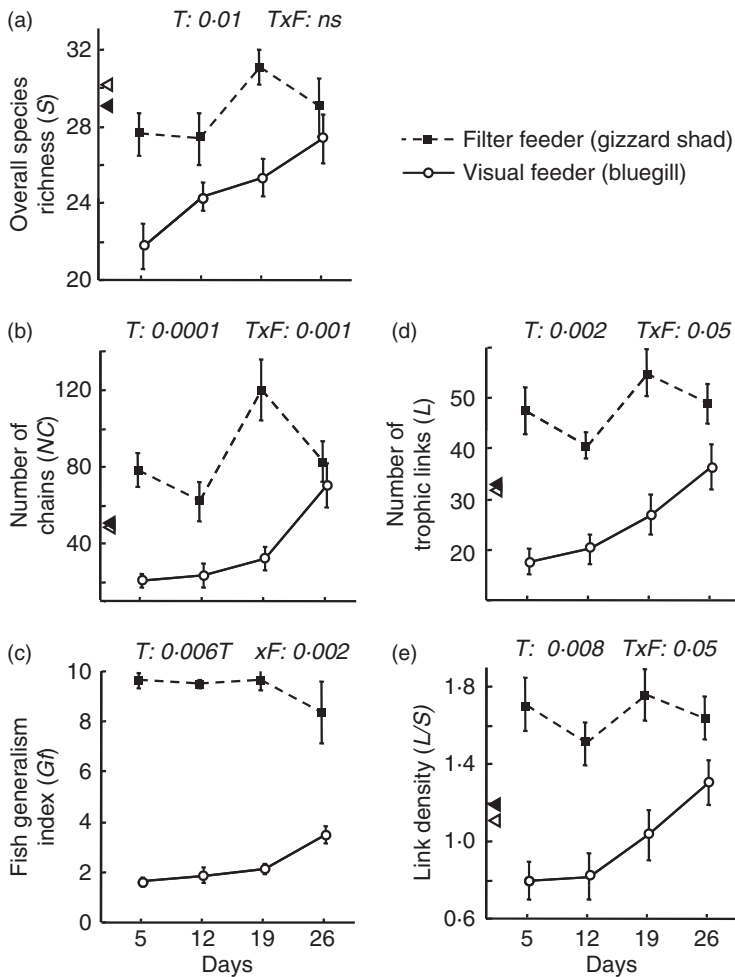


Fig. 5. Time responses of: (a) trophic species richness, (b) number of chains, (c) fish generalism, (d) number of trophic links and (e) link density descriptors to filter- and visual-feeder presence. Significant probability values from repeated-measures ANOVA of time main effects (T , as trial factor) and interaction effects of time \times planktivore foraging type ($T \times F$) are indicated at the top of each graph; ns indicates non-significant ($P \geq 0.05$). Data points and error bars are means \pm SE of eight values (two replicate tanks \times four biomass levels). Mean pre-treatment values (2 days prior to fish stocking) indicated by arrows – open arrows for visual feeders and black arrows for filter feeders – along the y-axis did not differ significantly between mesocosms that will receive either fish species.

BIMODALITY OF FORAGING BEHAVIOUR

The foraging behaviour of consumers is usually segregated into two contrasting modes, both in aquatic and terrestrial ecosystems: sit-and-wait vs. widely foraging predators (Perry & Pianka 1997), specialists vs. generalists (Thébault & Loreau 2003), passive suspension feeders vs. cruising raptorial feeders (Greene 1988) or visual vs. filter feeders (Lazzaro 1987). This dichotomy is valid among many organisms, within a large variety of ecosystems, and along the whole range of consumer sizes (Perry & Pianka 1997). While it is likely that additional or intermediate foraging modes exist and indeed some organisms may switch between modes (e.g. Drenner *et al.* 1982; Greene 1988; Lazzaro 1991; Butler 2005), this dichotomous view seems a reasonable and useful classification (Cooper 2007) for testing hypotheses regarding the effects of predator foraging modes on food-web topology. Interestingly, foraging mode not only influences consumer's diet, but also the nature of the typical predators. Empirical and simulation studies indicate that active foragers tend to eat rather sedentary prey and are preferentially eaten by sit-and-wait predators, and vice versa (see Perry & Pianka 1997; Rosenheim & Corbett 2003). Thus, top-predator type may partially control the foraging behaviour of intermediate

consumers, and ultimately the food-web architecture. Predator species with distinct functional roles can control the relationships between biodiversity and ecosystem functioning, as experimentally demonstrated by the review of Chalcraft & Reserits (2003). Hence, predator identity and diversity have been shown to drive the interaction strength of direct and indirect effects in food webs (Otto *et al.* 2008).

ECOLOGICAL VS. TOPOLOGICAL ALTERNATIVE STATES

Shifts in dominance between the two fish foraging guilds are frequent along nutrient gradients. In lakes, visually feeding zooplanktivores, typical of clear, oligo- to mesotrophic systems, are replaced by filter-feeding planktivores in more eutrophic systems, as demonstrated by Persson *et al.* (1988) in Europe (switch from Percids to Cyprinids), and Vanni *et al.* (2005) in the central and southeastern United States of America (switch from Centrarchids to Clupeids). From the observed differences in most descriptors between the visual and filter feeders, we can expect real differences in food-web architecture when either visual- or filter-feeding planktivores dominate lakes. However, few articles have considered the interaction between environmental conditions, foraging behaviour and food-web topology. Krivan & Schmitz (2003)

demonstrated theoretically that even a simple system, comprising an adaptive predator, a herbivore and two resources, can display either a linear or network topology according to productivity level and predator abundance.

BODY SIZE, NETWORK TOPOLOGY AND TROPHIC CASCADES

At the scale of our cumulated web, an organism's trophic position was significantly and positively related to the logarithm of its body length ($r^2 = 0.59$, $n = 57$, $P = 0.0001$). Yet, by construction our food-web cumulated matrix was partly based on body size as, in the absence of more pertinent information, we took into consideration morph shapes (colonial, filamentous, unicellular), and used size-dependent relationships for consumption of phytoplankton by zooplankton (e.g. Burns 1968). Body mass is widely recognized as a good predictor of trophic position and species-specific feeding ranges (Cózar *et al.* 2008; but see Woodward, Speirs & Hildrew 2005, for a review). However, different foraging strategies can alter this general relationship. For instance, Hambright, Zohary & Güde (2007) underlined that body size may not be a good predictor of phytoplankton ingestion by zooplankton. Our results suggest that, at the ecosystem level, communities should not be collapsed into a single 'niche-dimension' based on this attribute. They also indicate that foraging behaviour, in particular the dichotomy between specialists and opportunistic species, probably plays a key role in regulating ecosystem functioning. This dichotomy can be mathematically interpreted as a network shift from one basin of attraction to another. Whether such bimodality of food-web topology depending on the top-predator foraging behaviour could be a general property of ecosystems still remains to be demonstrated.

During the experiment, the %*Bi* (i.e. not consumed basal species) spanned a wide range of values (7–78%), although only three basal species (6.2%) were classified as inedible in the entire data set. In the presence of the highest biomass of the visual feeder, *Bi* became prevalent, and we observed the highest %*Bi*. Inedible species and biomass of phytoplankton displayed paired-response patterns. This suggests that changes in occurrence of potential predators directly modified phytoplankton control. This positive relationship between %*Bi* and the total phytoplankton biomass, plus the clear segregation between the filter- and visual-feeder treatments, confirm the importance of selective predation and food-web architecture on trophic cascades and ultimately, on the control of primary producers (e.g. Hulot *et al.* 2000).

BODY MASS DISTRIBUTION, OMNIVORY AND FOOD-WEB STABILITY

The topological structure of food webs influences their stability (Namba, Tanabe & Maeda 2008). Food-web stability mainly depends on the distribution of body mass (Emmerson & Raffaelli 2004; Loeuille & Loreau 2005; Brose, Williams &

Martinez 2006), although the mechanisms involved remain unclear. Because of physical constraints, body mass determines the diet breadth and foraging behaviour of individual species, and thus the topological food-web descriptors (Loeuille & Loreau 2005; Beckerman *et al.* 2006). In natural food webs, larger species typically feed on more prey and are consumed by fewer predators than small species. Using a simple three-species bioenergetic consumer–resource model, Otto, Rall & Brose (2007) demonstrated that this property is a major stabilizing mechanism, based on correlations between the body mass and degree of species (number of predator and prey links). Recent models suggest that omnivory is stabilizing, providing that interactions are prevalently weak (e.g. Fussmann & Heber 2002), and top-predator mortality is extremely low (Namba *et al.* 2008). Yet, they too are based on simple models with very few species and trophic levels. By controlling food-chain length, connectance, generalism and omnivory, the type of top-consumers may then ultimately affect food-web stability.

Conclusion

Our study demonstrated that by maintaining network comparability, experimental approaches provide an insightful contribution to theoretical advances regarding relationships between food-web topology and ecosystem functioning. We found that the contrasting foraging modes of the two predators differentially affected the architecture and omnivory level of the pelagic food web, with a probable influence on ecosystem functioning. We expect that differences between consumer foraging modes will influence the responses of ecosystems to perturbations. In addition, Duffy (2003) highlighted the greater vulnerability of large vertebrate consumers to anthropogenic threats. Thus, integrating consumer foraging behaviour into food-web analysis is critical in the understanding of ecosystem-level functional consequences of food-web modifications. The large body of experiments conducted on various food webs may provide data sets for studies that control environmental conditions (type and stock of top-predators, nutrient load, N : P balance, spatial heterogeneity, etc.), while maintaining network comparability. They could be analysed to identify the still poorly known relationships between predator foraging behaviour, food-web topology and ecosystem functioning.

Acknowledgements

The authors thank Élisabeth Thébault, David Hambright and Ian Davies who provided very helpful earlier discussion and comments, as well as Gary Mittelbach and an anonymous referee for their critical review of the submitted draft. This work was in part supported by the GIP ECOFOR/MEDDAAT programme (CyBiom Project) to X. Lazzaro and G. Lacroix, the IRD UR 167 CYROCO to X. Lazzaro, and the ANR programme (BioFun project) to J. Gignoux, and G. Lacroix. B. Gauzens was supported by a grant from the R2DS Ile-de-France programme (project no. 2007-14).

References

- Abacus Concepts (1991) SuperANOVA user's guide. Release 1.11. Abacus Concepts, Berkeley, CA.
- Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006) Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 13745–13749.
- Berlow, E.L., Neutel, A.-J., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. & Petchey, O. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, **73**, 585–598.
- Bersier, L.-F., Banasek-Richter, C. & Cattin, M.-F. (2002) Quantitative descriptors of food-web matrices. *Ecology*, **83**, 2394–2407.
- Brose, U., Williams, R.J. & Martinez, N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, **9**, 1228–1236.
- Burns, C.W. (1968) The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. *Limnology and Oceanography*, **23**, 675–678.
- Butler, M.A. (2005) Foraging mode of the chameleon, *Bradypodion pumilum*: a challenge to the sit-and-wait versus active forager paradigm? *Biological Journal of the Linnean Society*, **84**, 797–808.
- Carpenter, S.R., Kitchell, J.M. & Hodgson, J.R. (1985) Cascading trophic interactions and lake productivity. *BioScience*, **35**, 634–639.
- Chalcraft, D.R. & Reseratis, J.R. Jr (2003) Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology*, **84**, 2407–2418.
- Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2002) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 1781–1786.
- Cooper, W.E. (2007) Foraging modes as suites of coadapted movement traits. *Journal of Zoology*, **272**, 45–56.
- Cózar, A., García, C.M., Gálvez, J.A. & Echevarría, F. (2008) Structuring pelagic trophic networks from the biomass size spectra. *Ecological Modelling*, **215**, 314–324.
- Drenner, R.W. & McComas, S.R. (1980) The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. *Evolution and Ecology of Zooplankton Communities* (ed. W.C. Kerfoot), pp. 587–593. The University Press of New England, Hanover, New Hampshire, USA.
- Drenner, R.W., Vinyard, G.L., Gophen, M. & McComas, S.R. (1982) Feeding behavior of the cichlid, *Sarotherodon galilaeum*: selective predation on Lake Kinneret zooplankton. *Hydrobiologia*, **87**, 17–20.
- Drenner, R.W., Threlkeld, S.T. & McCracken, M.D. (1986) Experimental analysis of the direct and indirect effects of an omnivorous filter-feeding clupeid on plankton. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1935–1945.
- Drenner, R.W., Hambricht, K.D., Vinyard, G.L., Gophen, M. & Pollingher, U. (1987) Experimental study of size-selective phytoplankton grazing by a filter-feeding cichlid and the cichlid's effects on plankton community structure. *Limnology and Oceanography*, **32**, 1138–1144.
- Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, **6**, 680–687.
- Duffy, J.E., Richardson, J.P. & Canuel, E.A. (2003) Grazer diversity and ecosystem functioning in seagrass beds. *Ecology Letters*, **6**, 637–645.
- Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007) The functioning role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, **10**, 522–538.
- Emmerson, M.C. & Raffaelli, D. (2004) Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, **73**, 399–409.
- Fussmann, G.F. & Heber, G. (2002) Food web complexity and chaotic population dynamics. *Ecology Letters*, **5**, 394–401.
- Greene, C.H. (1988) Foraging tactics and prey-selection patterns of omnivorous and carnivorous calanoid copepods. *Hydrobiologia*, **167/168**, 295–302.
- Hambricht, K.D., Trebatoski, R.J., Drenner, R.W. & Kettle, D. (1986) Experimental study of the impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) on pond community structure. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1171–1176.
- Hambricht, K.D., Zohary, T. & Güde, H. (2007) Microzooplankton dominate carbon flow and nutrient cycling in a warm subtropical freshwater lake. *Limnology and Oceanography*, **52**, 1018–1025.
- Hansson, L.A., Brönmark, C., Nyström, P., Greenberg, L., Lundberg, P., Nilsson, A., Persson, A., Pettersson, L.B., Romare, P. & Tranvik, L.J. (1998) Consumption patterns, complexity and enrichment in aquatic food chains. *Proceedings of the Royal Society of London B*, **265**, 901–906.
- Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.
- Hulot, F.D., Lacroix, G., Lescher-Moutoué, F. & Loreau, M. (2000) Functional diversity governs response to nutrient enrichment. *Nature*, **405**, 340–344.
- Humphries, S. (2007) Body size and suspension feeding. *Body Size: The Structure and Function of Aquatic Ecosystems* (eds A. Hildrew, D. Raffaelli & R. Edmonds-Brown), pp. 98–117. Cambridge University Press, Cambridge.
- Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H. & Woodward, G. (2009) Ecological networks: beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.
- Janssen, J. (1976) Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). *Journal of Fisheries Research Board of Canada*, **33**, 1972–1975.
- Krivan, V. & Schmitz, O.J. (2003) Adaptive foraging and flexible food web topology. *Evolutionary Ecology Research*, **5**, 623–652.
- Lacroix, G., Lescher-Moutoué, F. & Pourriot, R. (1996) Trophic interactions, nutrient supply, and structure of freshwater pelagic food webs. *Aspects in the Genesis and Maintenance of Biological Diversity* (eds M. Hochberg, J. Clobert & R. Barbault), pp. 162–179. Oxford University Press, Oxford, UK.
- Lazzaro, X. (1987) A review of planktivorous fishes: their evolution, feeding behaviors, selectivities, and impacts. *Hydrobiologia*, **146**, 97–167.
- Lazzaro, X. (1991) Feeding convergence in South American and African zooplanktivorous cichlids *Geophagus brasiliensis* and *Tilapia rendalli*. *Environmental Biology of Fishes*, **31**, 283–293.
- Lazzaro, X., Drenner, R.W., Stein, R.A. & Smith, J.D. (1992) Planktivores and plankton dynamics: effects of fish biomass and planktivore type. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1466–1473.
- Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 5761–5766.
- Mittelbach, G.G. & Osenberg, C.W. (1994) Using foraging theory to study trophic interactions. *Theory and Application in Fish Feeding Ecology* (eds D.J. Stouder, K.L. Fresh & R.J. Feller), pp. 45–59. University of South Carolina Press, Columbia, USA.
- Namba, T., Tanabe, K. & Maeda, N. (2008) Omnivory and stability of food webs. *Ecological Complexity*, **5**, 73–85.
- Otto, S.B., Rall, B.C. & Brose, U. (2007) Allometric degree distributions facilitate food-web stability. *Nature*, **450**, 20–27.
- Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J. & Brose, U. (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology*, **89**, 134–144.
- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.
- Perry, G. & Pianka, E.R. (1997) Foraging behavior: past, present and future. *Trends in Ecology and Evolution*, **12**, 360–364.
- Persson, L., Andersson, G., Hamrin, S.F. & Johansson, L. (1988) Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. *Complex Interactions in Lake Communities* (ed. S.R. Carpenter), pp. 53–59. Springer-Verlag, New York, USA.
- Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.
- Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 4191–4196.
- Preisser, E.L., Orrock, J.L. & Schmitz, O.J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, **88**, 2744–2751.
- Rosenheim, J.A. & Corbett, A. (2003) Omnivory and the indeterminacy of predator function: can a knowledge of foraging behavior help? *Ecology*, **84**, 2538–2548.
- Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology*, **88**, 2415–2426.
- Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**, 952–954.
- Schmitz, O.J. & Suttle, K.B. (2001) Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, **82**, 2072–2081.
- Schmitz, O.J., Krivan, V. & Ovadia, O. (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153–163.
- Straile, D. (2005) Food webs in lakes – seasonal dynamics and the impact of climate variability. *Aquatic Food Webs: An Ecosystem Approach* (eds

- A. Belgrano, U. Scharler, J. Dunne & B. Ulanowicz), pp. 41–50. Oxford University Press, Oxford, UK.
- Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, **73**, 747–754.
- Thébault, E. & Loreau, M. (2003) Food-web constraints on biodiversity–ecosystem functioning relationships. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 14949–14954.
- Vanni, M.J., Arend, K.K., Bremigan, M.T., Bunnell, D.B., Garvey, J.E., González, M.J., Renwick, W.H., Soranno, P.A. & Stein, R.A. (2005) Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. *BioScience*, **55**, 155–167.
- Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
- Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180–183.
- Williams, A.E. & Moss, B. (2003) Effects of different fish species and biomass on plankton interactions in a shallow lake. *Hydrobiologia*, **491**, 331–346.
- Woodward, G., Speirs, D.C. & Hildrew, A.G. (2005) Quantification and temporal resolution of a complex size-structured food web. *Advances in Ecological Research*, **36**, 85–135.

Received 4 March 2009; accepted 8 June 2009

Handling Editor: Andrew Beckerman

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. A list of all trophic species/taxa identified in the binary predator–prey cumulated matrix and used for building the instantaneous matrices. Consumers (fish, zooplankton, benthic invertebrates, bacteria) and producers (phytoplankton, detritus) are identified by numbers (species #; $n = 58$). Prey (intermediate consumers and producers) consumed by predators (intermediate and top consumers) are indicated by their number in the right-hand column. Sizes of

organisms are indicated as the greatest axial linear dimension (GALD; standard length for fish). Phytoplankton shapes are indicated as unicells, colonies and filaments. Following the table is a list of major publications used to determine the list of potential prey species for each consumer (i.e. intersection element values = 1), thus building the trophic network.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.