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## Effects of Enrichment on Simple Aquatic Food Webs

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**ABSTRACT:** Simple models, based on Lotka-Volterra types of interactions between predator and prey, predict that enrichment will have a destabilizing effect on populations and that equilibrium population densities will change at the top trophic level and every second level below. We experimentally tested these predictions in three aquatic food web configurations subjected to either high or low nutrient additions. The results were structured by viewing the systems as either food chains or webs and showed that trophic level biomass increased with enrichment, which contradicts food chain theory. However, within each trophic level, food web configuration affected the extent to which different functional groups responded to enrichment. By dividing trophic levels into functional groups, based on vulnerability to consumption, we were able to identify significant effects that were obscured when systems were viewed as food chains. The results support the prediction that invulnerable prey may stabilize trophic-level dynamics by replacing other, more vulnerable prey. Furthermore, the vulnerable prey, such as *Daphnia* and edible algae, responded as predicted by the paradox of enrichment hypothesis; that is, variability in population density increased with enrichment. Hence, by describing ecosystems as a matrix of food web interactions, and by recognizing the interplay between interspecific competition and predation, a more complete description of the ecosystem function was obtained compared to when species were placed into distinct trophic levels.

Simple models, often based on Lotka-Volterra-like interactions between predator and prey populations, have a long tradition in ecology due to the relatively simple mathematics involved. Such models have been extended to ecosystems to describe trophic-level biomass in food chains of systems at equilibrium, assuming that trophic levels act as populations (Fretwell 1977; Oksanen et al. 1981; Oksanen 1988). Most attention has been directed toward stable equilibrium conditions, with a locally stable point, whereas dynamic behaviors, that is, limit cycles or chaos, have received less attention (Hastings et al. 1993; Hastings 1996) because such states have been considered unlikely to persist in nature.

A fundamental prediction from Lotka-Volterra-type predator-prey models (i.e., with prey-dependent functional response), termed the “paradox of enrichment,” states that increasing the carrying capacity of the prey will force the equilibrium density of the prey and the predator to move from a stable focus to limit cycles (Rosenzweig 1971). Data from natural systems suggest that both prey and predator densities are less sensitive to the destabilizing effect of enrichment than such simple theoretical models predict (McCauley and Murdoch 1987; McCauley et al. 1988). This has sometimes been explained by the fact that there is more to enrichment than just energy availability. For example, both environmental condition and food web structure may be functions of productivity. In plant-herbivore systems, an increase in carrying capacity of the plant may be associated with a decrease in the attack rate of the herbivore due to a succession toward inedible prey (Leibold 1989; McCauley and Murdoch 1990). Similarly, an increase in carrying capacity may be associated with an increase in the mortality rate of the herbivore due to a shift in the community composition of top predators (Persson et al. 1988, 1991; Sarnelle 1992). Such modified performance of interacting participants may affect equilibrium densities of both predator and prey, as well as counteract the destabilizing effects of enrichment predicted from simple models. The discrepancy between

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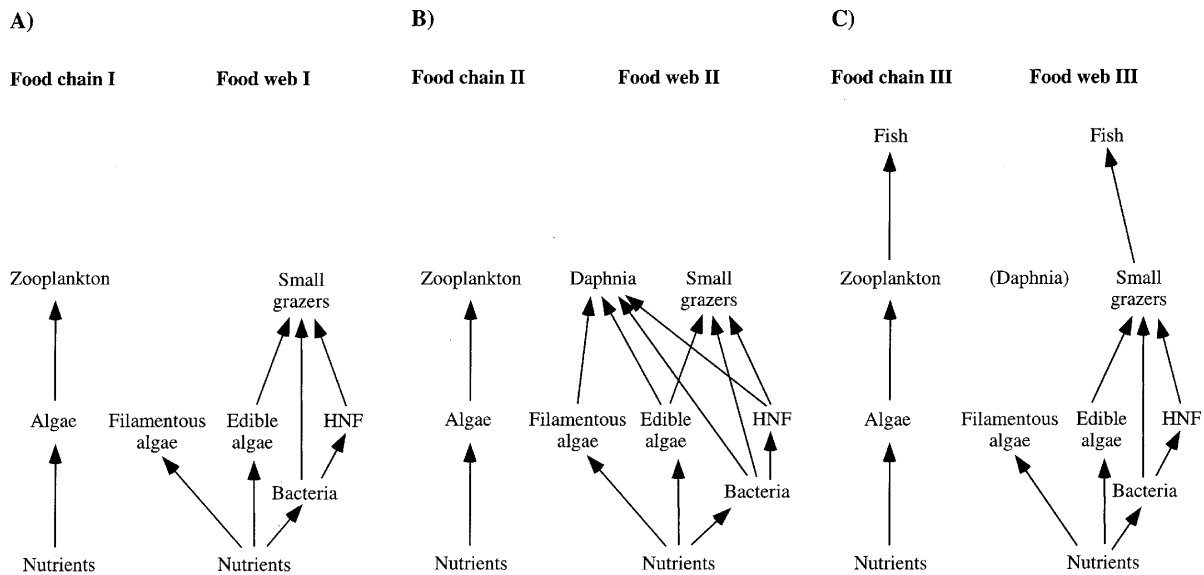
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**Figure 1:** Feeding links in food web treatment I (A), II (B), and III (C), viewed as either food chains or food webs. Arrows denote direction of nutrient flow. In chain/web II, no fish were present, and in chain/web I, no fish or *Daphnia* were present. When viewing the systems as food chains, *Daphnia* and small grazers together were pooled as total zooplankton, and edible and filamentous algae were pooled as total algae. Heterotrophic nanoflagellates (HNF) and bacteria are not included in the classical food chains. Note that when fish are present, *Daphnia* are suppressed, and when *Daphnia* are present, the number of links is higher due to generalized feeding by *Daphnia*.

model predictions and field data has resulted in a number of proposed model modifications, introducing stabilizing factors, such as predator interference (Arditi and Ginzburg 1989), omnivory (McCann and Hastings 1997), spatial heterogeneity (Jansen 1995; Scheffer and de Boer 1995; Abrams and Walter 1996), and heterogeneity within trophic levels (Yodzis and Innes 1992; Abrams 1993). While the development of theoretical explanations has received much attention, empirical tests of the hypothesis are still quite rare (but see McCauley et al. 1988; McCauley and Murdoch 1990).

In this study, we tested the prediction that enrichment destabilizes population dynamics. Here, we restrict our definition of destabilization to an increase in variability in population density. We hypothesize that whether a population is destabilized by enrichment is dependent on two factors: prey vulnerability and predator-exploitation efficiency. First, a decrease in prey vulnerability as a response to increased predation intensity stabilizes predator-prey dynamics (e.g., Leibold 1989; Scheffer and de Boer 1995; Abrams and Walters 1996; Bohannan and Lenski 1997; Fryxell and Lundberg 1997). This may take place either because prey use refuge habitats and become unavailable to predators (Turner and Mittelbach 1990; Scheffer and de Boer 1995; Abrams and Walters 1996) or because of progressive replacement by species (or individuals) that

are less susceptible to predation (from the predator's point of view, the attack rate decreases; Kerfoot et al. 1988; Leibold 1989; Sarnelle 1992; Brönmark and Weisner 1996; Bohannan and Lenski 1997). Second, the consumer itself may experience predation from a top predator (i.e., the death rate of the intermediate consumer is increased), thereby preventing overexploitation of the resource population (May 1973; Kretzschmar et al. 1993). Hence, introduction of a top predator (fish) is hypothesized to stabilize the populations of lower organization (zooplankton and algae) because death rate of intermediate predators increase and because selection toward less efficient intermediate predators should occur, causing exploitation efficiency to decrease (May 1973; Kretzschmar et al. 1993). This indirect form of density dependence (Abrams and Walters 1996) was early proposed as a plausible cause for the absence of paradox of enrichment behavior (May 1973; Rosenzweig 1973). More recent analyses of model behavior of three-species food chains suggest that enrichment may cause both population cycles and chaos (Hastings and Powell 1991; Abrams and Roth 1994a, 1994b; Lundberg and Fryxell 1995). Thus, model predictions of the effects of enrichment on the stability properties in three-species food chains are contradictory.

Analyses of links and connectedness between species in natural ecosystems have shown that idealized food chains

often do not adequately capture the complexity found in nature (Pimm 1982; Polis 1991). This discrepancy, between the simplicity of theoretical models and the complexity of natural food webs, may obstruct elucidation of the dynamics of natural systems. Indeed, determination of causes and effects are difficult in natural food webs due to the high number of possible links between the various participants and their habitats, causing patterns to be obscured by complex indirect effects (Pimm et al. 1991; Polis and Strong 1996). One way of approaching this problem is to conduct experiments in simplified systems to reduce the number of links as well as the influence of external interference due to migration between habitats or systems. To reduce complexity, we employed indoor tank experiments with inocula from the field (fig. 1). Our analysis was structured by splitting trophic levels into functional groups, differing in vulnerability to predation (fig. 1). Thus, the resulting systems were webs rather than chains. The density variability of each compartment, measured as coefficient of variation (CV), was then used as a measure of sensitivity to destabilization by enrichment.

## Material and Methods

### *Experimental Design*

The experiment was carried out in 36 tanks in a greenhouse from November 21, 1995, to April 2, 1996 (133 d). A  $2 \times 3$  factorial design was used with low and high nutrient conditions crossed with three different food webs. The basic food web included bacteria, heterotrophic flagellates, algae, and small grazers (small cladocerans and rotifers). This food web was either unaltered (web I), received an addition of large grazers (web II), or an addition of both large grazers and fish (web III; fig. 1). For webs II and III, we used 400-L cylindrical tanks (height: 1.0 m, diameter: 0.74 m). Web I was stocked in 80-L cylindrical tanks (height: 0.70 m, diameter: 0.46 m). Each of the six treatments was replicated six times.

We used different-sized containers due to logistical reasons. The largest organism (fish) was not added to any of the small containers. Our experience is that smaller organisms (zooplankton and algae) are not affected by container size as long as the volume is reasonably large, which was the case here. Moreover, the walls of the containers were scrubbed twice a week to keep epiphytic algae biomass low throughout the experiment, thereby reducing any biases caused by different area to volume ratio.

In webs II and III, habitat complexity was increased by adding two net cylinders (mesh size: 2 mm; total volume of 36 L) and four artificial macrophytes (untwined polypropylene ropes reaching from the bottom to the surface of each tank). In web I, one artificial macrophyte and a

net with an area 25% of that used for nets in webs II and III were added. The water in each tank was continuously aerated, and to protect cladoceran zooplankton from air bubbles, a cylindrical net (mesh size: 200  $\mu\text{m}$ ) surrounded each air outlet. Temperature in the experimental tanks was  $23^\circ \pm 3^\circ\text{C}$  throughout the experiment. Artificial light (13,000 lux) was used between 0600 and 2200 hours during periods when sunlight decreased below 17,000 lux.

Before the start of the experiment, tanks were filled with aerated water, and a phytoplankton inoculum from the eutrophic Lake Ringsjön was added. In addition to algae, this inoculum also contained small grazers, such as rotifers and small cladocerans (*Chydorus*). A week later, large zooplankton were added to webs II and III. The zooplankton suspension consisted of a mixture of natural zooplankton communities from a fishless pond and laboratory cultures of *Daphnia magna* and *Daphnia obtusa*. To compensate for nutrients, algae, and microbes added with zooplankton, tanks assigned to web I were supplied with the same relative amount of water as webs II and III, after filtering out the zooplankton with a 10- $\mu\text{m}$  net. At the start of the experiment, two adult female and two adult male guppies (*Poecilia reticulata*) were added to each web III tank. Extra nutrients (proportion phosphorus 1%, ammonium 2%, nitrate 3.1%) were added initially to all tanks, corresponding to an increase in phosphorus concentration of 125  $\mu\text{g L}^{-1}$  in the treatments with high nutrient concentration and 12.5  $\mu\text{g L}^{-1}$  in the low nutrient treatments. This addition was repeated after the first sampling occasion. Thereafter, the high nutrient tanks received the same nutrient addition after each sampling occasion, whereas nutrients were no longer added to the low nutrient tanks.

To ensure fish reproduction, a minimum of one individual of each sex was maintained in each tank by replacing dead fish. To prevent any stochastic species extinction within tanks, an inoculum of 1.2% of the tank volume (5 L from large tanks and 1 L from small tanks) was taken weekly from each web II and III tank, combined and mixed, and then returned to the tanks in equal parts. Web I was treated in the same way but separated from webs II and III to avoid introduction of larger zooplankters. Consequently, by running the experiment for a long time, introducing inocula from different systems, and enhancing the dispersal between mesocosms by mixing, the experimental setup allowed for compositional change (sensu Leibold et al. 1997). However, it should be kept in mind that the possible responses in the experiment were within the scope of the species pool originally introduced.

### *Sampling*

All tanks were sampled every 4 wk, making a total of six sampling occasions. Before each sampling, refuges were

**Table 1:** Summary of repeated-measures ANOVA on the effects of food web structure (web) and nutrient level (nutrient) on zooplankton groups over time

Source of variation	df	SS	F	P
<b>Total zooplankton:</b>				
Between subjects:				
Web	2	23.79	63.17	<.001
Nutrient	1	14.47	76.83	<.001
Web × nutrient	2	.67	1.77	.187
Error	30	5.65		
Within subjects:				
Time	5	123.87	217.23	<.001
Time × web	10	24.25	21.21	<.001
Time × nutrient	5	7.53	13.16	<.001
Time × web × nutrient	10	1.11	.97	.470
Error	150	17.15		
<b>Daphnia (only web II and III):</b>				
Between subjects:				
Web	1	196.19	438.65	<.001
Nutrient	1	41.20	92.11	<.001
Web × nutrient	1	39.80	88.98	<.001
Error	20	8.95		
Within subjects:				
Time	5	49.54	10.90	<.001
Time × web	5	37.97	8.35	<.001
Time × nutrient	5	23.79	5.23	<.001
Time × web × nutrient	5	30.94	6.81	<.001
Error	100	90.92		
<b>Small grazers:</b>				
Between subjects:				
Web	2	88.67	43.33	<.001
Nutrient	1	64.43	62.72	<.001
Web × nutrient	2	1.17	.57	.572
Error	30	30.82		
Within subjects:				
Time	5	639.51	200.61	<.001
Time × web	10	127.83	20.05	<.001
Time × nutrient	5	36.07	11.31	<.001
Time × web × nutrient	10	8.15	1.28	.25
Error	150	95.64		

Note: Data were  $\ln(x + 1)$  (*Daphnia*) or  $\log(x)$  (others) transformed before analysis.

cleaned and removed, tank walls were scrubbed, and the water in each tank was mixed. From each tank, water was sampled from surface to bottom with a Plexiglas tube. Ten liters from each tank were filtered through a 55- $\mu\text{m}$  mesh for zooplankton analysis. The zooplankton samples were preserved in Lugol's solution and the filtered water returned to the tanks. One liter from each tank was brought into the laboratory for analysis of phytoplankton biomass.

Algal samples were preserved with Lugol's solution, and permanent slides were made using HPMA (2-hydroxypropyl-metacrylate with the catalyst azo-bis-iso-butyrone-tri-; Crumpton 1987). Algae were counted at  $\times 200$  mag-

nification, and in each sample, a minimum of 200 cells were counted. Twenty individuals of each algal species were measured with an ocular micrometer, and the biovolumes were calculated using formulae for a double cone (*Monoraphidium*), ellipsoid with circular cross section (*Scenedesmus*), and cylinder (all filamentous species). Algae were separated into two functional groups that were expected to differ in vulnerability to grazing due to differences in size. Consequently, small genera were assigned to edible algae (*Scenedesmus* and *Monoraphidium* constituted more than 95% by numbers), and colonial genera were assigned to filamentous algae (*Oscillatoria*, *Tribonema*, *Anabaena*, and *Pseudoanabaena* constituted more than 95% by numbers).

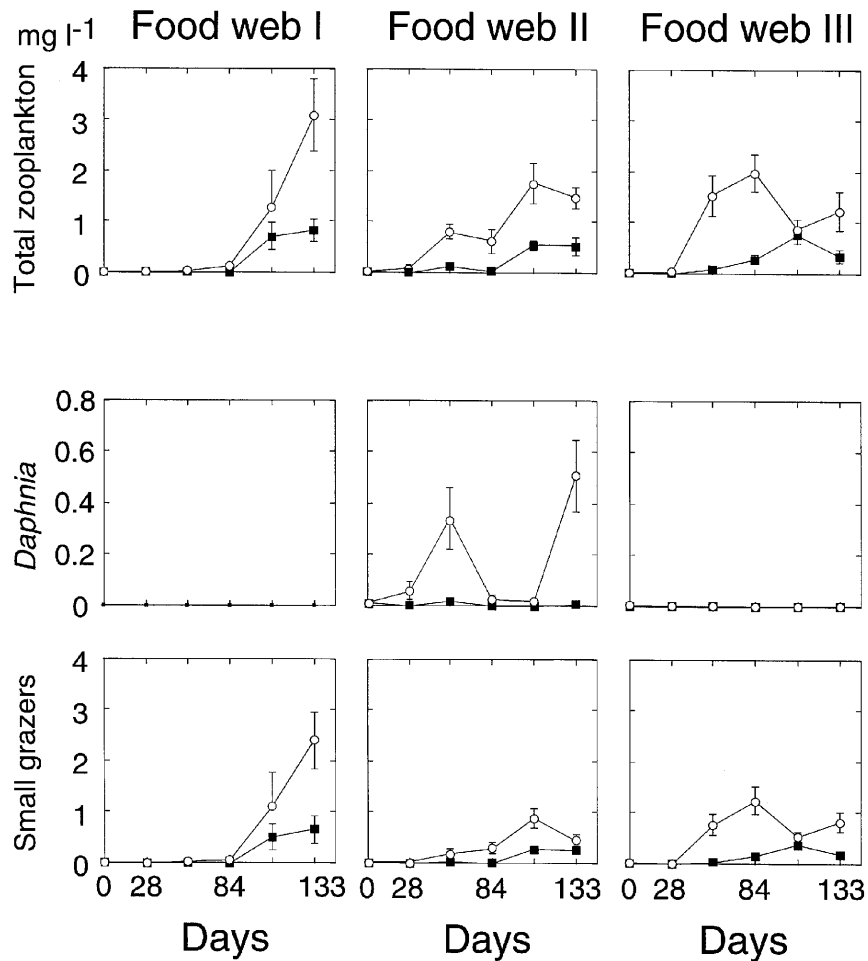
The biomass of zooplankton was estimated by using the length-weight regressions presented by Bottrell et al. (1976). The rotifer community was dominated by *Lecane* spp., for which a constant body weight of 0.2  $\mu\text{g}$  dry weight was used (Bottrell et al. 1976). Zooplankton grazers were divided into two functional groups based on diet breadth: *Daphnia* spp., which have a broad diet that covers prey sizes from bacteria to filamentous algae, and a second group termed "small grazers," consisting of rotifers (*Lecane* spp.) and small cladocerans (mainly *Chydorus* spp.), which have a more specialized diet based on edible algae and heterotrophic flagellates (fig. 1).

Bacteria and heterotrophic flagellates were preserved according to the Lugol/-formaldehyd/thiosulfate method (Sherr and Sherr 1993) and counted by epifluorescence microscopy after staining with DAPI (Porter and Feig 1980). At least 250 bacteria, or 10 fields of view, were counted. Heterotrophic flagellates (lacking autofluorescence) were counted in 25–50 fields of view, generally resulting in total counts of at least 50 cells.

#### Statistical Analysis

The effects of nutrient enrichment and food web composition on each response variable (i.e., the functional groups *Daphnia*, small grazers, edible algae, filamentous algae, heterotrophic flagellates, and bacteria) over time were tested using repeated-measure ANOVA (rmANOVA). For filamentous algae, only the last five samples were used because their estimated biomass was zero in all treatments in the first sample. Corresponding statistics were also computed for the response variables when these were pooled as total algae and total zooplankton. Data were transformed before analyses to homogenize variances. Specific transformations used are given in figures and tables.

The effects of nutrient enrichment and food web composition on the ratio of edible algae : total algae were analyzed using a univariate ANOVA on the values from the last sampling only. This was because there was no variance



**Figure 2:** Zooplankton biomass ( $\pm 1$  SE) over time in experimental tanks containing different food web configurations (webs I, II, and III). Each food web treatment received either high (*open circles*) or low (*filled squares*) nutrient additions. Note that zooplankton biomass increased with enrichment in all food webs but that the difference between high and low nutrient treatments differed depending on food web configuration. *Daphnia* persisted only in web II, whereas small grazers were present in all treatments, although suppressed in web II.

for the first two sampling dates (i.e., the ratio was 1 in all treatments).

As a measure of variability in density (heterotrophic flagellates and bacteria) or biomass (others), the CV among all sampling dates was calculated for each replicate. The advantage of this approach is that it enables us to investigate the variability during the experiment despite rather few samples. However, it should be kept in mind that all food web components might not have passed through initial transient dynamics, even though the experimental time covered two generations of fish and more than 10 generations of other components. To test whether transient dynamics were present, we performed a series of calculations within each replicate, starting with the CV from the last two dates, then the last three dates, the last four, five, and finally all dates. Thus, we obtained five

values of CV for each replicate. As dependent variable, we assigned each of the CV estimates a value between  $-1$  and  $-5$ , where  $-1$  corresponds to the CV estimate of the last two dates and  $-5$  the CV estimate including all dates. We then performed a linear regression of these values using the inverted rank in time as a dependent variable. The regression tested whether a trend in the CV over time was present and, if so, the direction of such a trend. Moreover, the intercept served as a measure of the CV at the end of the experiment. A linear regression was selected because the data generally fitted well to a linear model and because a polynomial fit would be biased by the few data points.

Two-way ANOVA was used to test for the effect of nutrient level and food web composition on the CV of all sampling dates. If the ANOVA showed a significant effect, the test proceeded by performing Tukey mean compari-

**Table 2:** Summary of repeated-measures ANOVA on the effects of food web structure (web) and nutrient level (nutrient) on biomass of algal groups over time

Source of variation	df	SS	F	P
<b>Total algae:</b>				
Between subjects:				
Web	2	9.13	15.15	<.001
Nutrient	1	29.12	96.64	<.001
Web × nutrient	2	8.92	14.81	<.001
Error	29	8.74		
Within subjects:				
Time	5	18.04	13.14	<.001
Time × web	10	18.22	6.64	<.001
Time × nutrient	5	3.55	2.59	.028
Time × web × nutrient	10	24.27	8.84	<.001
Error	145	39.82		
<b>Edible algae:</b>				
Between subjects:				
Web	2	37.25	22.19	<.001
Nutrient	1	4.90	5.83	.022
Web × nutrient	2	21.36	12.72	<.001
Error	29	24.34		
Within subjects:				
Time	5	100.64	62.57	<.001
Time × web	10	38.81	12.07	<.001
Time × nutrient	5	6.16	3.83	.003
Time × web × nutrient	10	29.03	9.02	<.001
Error	145	46.64		
<b>Filamentous algae:</b>				
Between subjects:				
Web	2	7.96	5.27	.011
Nutrient	1	20.67	27.37	<.001
Web × nutrient	2	5.86	3.88	.032
Error	29	21.90		
Within subjects:				
Time	4	66.94	51.95	<.001
Time × web	8	35.83	13.90	<.001
Time × nutrient	4	6.03	4.68	.002
Time × web × nutrient	8	35.39	13.73	<.001
Error	116	37.37		

Note: Data were  $\ln(x + 1)$  (filamentous algae) or  $\log(x)$  (others) transformed before analysis.

sons between pairs of treatments using the following criteria. First, if the main test showed a significant effect of nutrient level only, no further statistic was performed. Second, if the effect of food web composition was significant, each web was tested against the other regardless of nutrient level. Third, if the interaction between nutrient level and food web composition was significant, the effect of nutrient level within each treatment was tested, resulting in three different comparisons. We examined the residuals of the CV data and tested the assumption of normal distribution using Kolmogorov-Smirnov one-sample test. Data were log transformed before performing the ANOVA

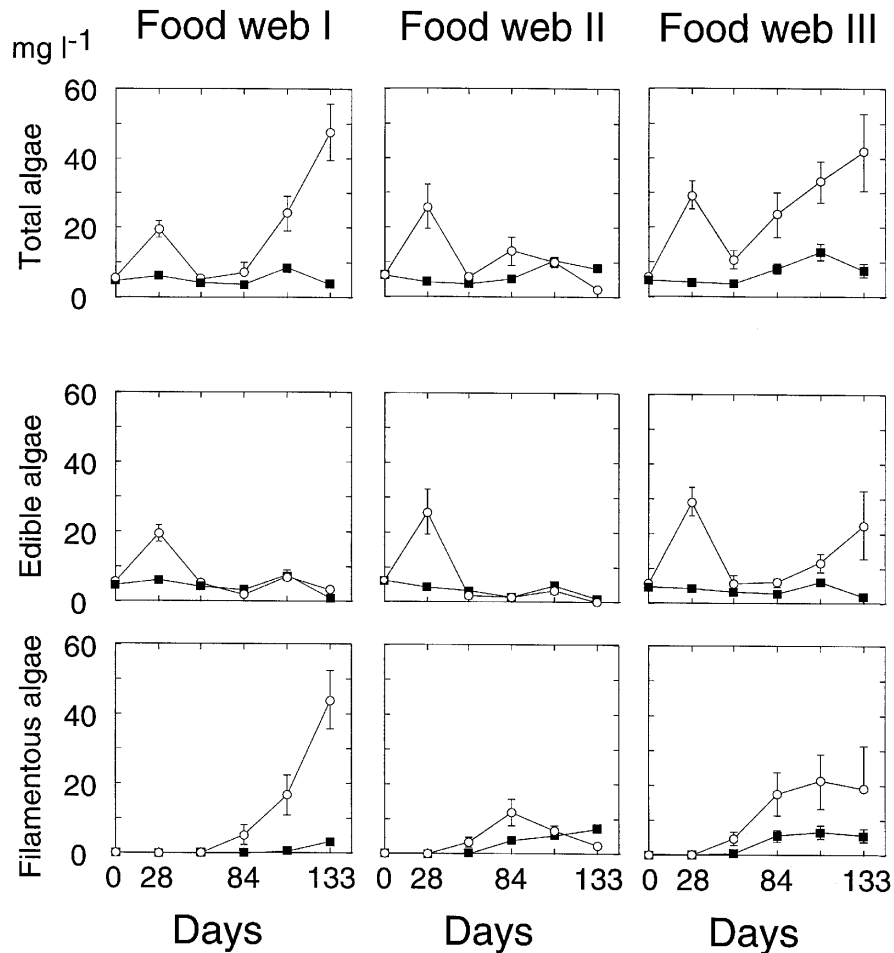
when necessary to ensure normality and homogeneity of variances.

## Results

Fish biomass at the end of the experiment was significantly greater in enriched webs compared to unenriched ( $t$ -test,  $P < .001$ ). When viewing the systems as chains, that is, pooling planktonic herbivores as total zooplankton and producers as total algae, total zooplankton biomass development was significantly different in the different web treatments (rmANOVA, time × nutrient × web,  $P < .001$ ; table 1). Grazers appeared earlier in webs II and III than in web I, where zooplankton was almost absent the first half of the experimental period (fig. 2). Despite this, total zooplankton biomass was higher at the end of the experiment in web I. Food web structure affected the biomass development of total algae over time in enriched systems (rmANOVA, time × nutrient × web,  $P < .001$ ; table 2), resulting in a lower biomass during the second half of the experiment in web II compared to webs I and III (fig. 3). The three unenriched web treatments had fairly similar developments of both zooplankton and algal biomass over time (figs. 2, 3).

Over time, biomass and density of all functional groups (i.e., *Daphnia*, small grazers, edible algae, filamentous algae, heterotrophic flagellates, and bacteria) was significantly greater in high nutrient treatments than in low (figs. 2, 3). This trend was observed irrespective of web treatment. Separating the algae and zooplankton compartments into functional groups revealed a different pattern compared to their treatment as single units. Enrichment increased biomass of all functional groups, whereas food web structure influenced both abundance and presence of the functional groups. *Daphnia* were only persistent in enriched web II but largely absent from web III and unenriched web II (fig. 2). Food web structure also had impacts on other functional groups by causing a tendency toward divergence from the equivalent unenriched web treatment. The biomass of filamentous algae was only moderately increased by enrichment in web II, where *Daphnia* were present, compared to the other web treatments, in which there was a greater increase. Edible algae in enriched treatments showed a single peak in biomass during the first half of the experimental period in webs I and II but showed a second peak in web III (fig. 3). The density of heterotrophic flagellates showed only a minor response to enrichment in web II compared to webs I and III (fig. 4). Bacteria had a pattern different from all other groups by attaining a much higher final density in the enriched web III than in the other webs (table 3; fig. 4).

Succession toward less vulnerable algal species was sig-



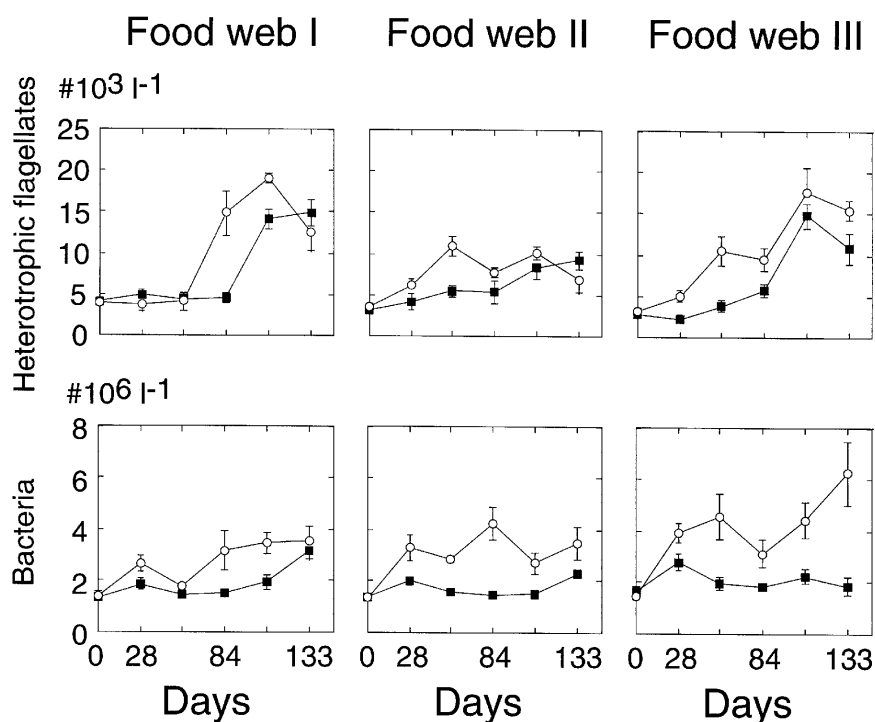
**Figure 3:** Algal biomass ( $\pm 1$  SE) over time for different food web configurations and nutrient treatments. Open circles denote high and filled squares denote low nutrient additions. In web II, algae biomass was suppressed, especially due to low filamentous algal biomass. At the end of the experiment, edible algae were only abundant in web III.

nificantly affected by food web composition. Hence, at the end of the experiment, filamentous algae dominated the algal community in webs I and II, where grazers were not affected by predation from fish (fig. 5). In web III at the end of the experiment, the proportion of edible algae of total algae biomass was significantly higher than in other web treatments (ANOVA, Tukey's post hoc test,  $P \leq .001$ ), being 34% at low and 59% at high nutrient conditions. Edible algae dominated the algal community in web I until small grazers became abundant at the end of the experiment, when the proportion of filamentous algae increased rapidly (fig. 3). In web II, this shift in dominance took place earlier in the experiment. For both webs I and II, the shift tended to occur at a faster rate in the enriched treatments (fig. 5).

The temporal variability, expressed as CV, of biomass

and density differed between treatments and functional groups. Enrichment significantly increased the CV for *Daphnia* (fig. 6), total algae, and edible algae (fig. 7), as well as for bacteria (ANOVA,  $P \leq .001$ ; fig. 8; table 4). Although all the above groups responded in a similar way to enrichment, they differed with respect to responses to web treatment. In the case of total algae, enrichment affected all webs in a similar way, namely by increasing the CV. For edible algae, the CV was significantly higher in web II compared to webs I and III (Tukey's post hoc test,  $P < .01$ ; fig. 7). The CV of bacteria density was affected by the interaction between nutrient level and web treatment, illustrating that food web structure influenced the magnitude by which enrichment affected population variability. Accordingly, the CV in web I was similar in high and low nutrient treatments, whereas the CV in webs II and





**Figure 4:** Abundance ( $\pm 1$  SE) of bacteria and heterotrophic flagellates in experimental tanks for three different food web treatments and two different nutrient treatments. Both bacteria and heterotrophic flagellate abundance was higher in enriched (*open circles*) than in unenriched (*filled squares*) treatments.

III were greater in high than in low nutrient treatments (fig. 8).

The CV of heterotrophic flagellate density and edible algal biomass were both affected by food web structure (fig. 8). However, the CV of edible algae was significantly higher in web II than in webs I and III, whereas the CV for heterotrophic flagellates showed the opposite response, being lower in web II than in the other webs. Note that these two groups rely on totally different resources (fig. 1) and, therefore, might not respond to enrichment similarly. Indeed, the CV of edible algae was higher in enriched treatments, whereas the CV of heterotrophic flagellates was slightly lower in enriched treatments (ANOVA,  $P = .01$ ; table 2).

The CV of total zooplankton, filamentous algae, and small grazers were unaffected by enrichment (ANOVA,  $P > .8$ ; table 2). However, the CVs of these groups were significantly affected by food web structure (ANOVA,  $P < .001$ ; table 2), being significantly higher in web I than in webs II and III (Tukey's post hoc test,  $P < .001$ ; fig. 6). However, this was mostly due to transient dynamics when moving from low biomass at the start of the experiments to high biomass at the end of the experiments (figs. 2, 3). Both small grazers and filamentous algae started up with

extremely low biomass. Filamentous algae were not even detected in any replicates the first sampling occasion. Thus, the higher CV for small grazers and filamentous algae in web I was simply a result of higher densities in that treatment at the end of the experiment and not a result of any cyclicity in population density. The higher CV for total zooplankton biomass in web I was largely a reflection of the dynamics of small grazers.

There was a significant time trend in the CV for all response variables, except for *Daphnia* (table 5). Generally, the trend was a decrease in CV (positive slope) as fewer sampling occasions were included in the calculations, that is, toward the end of the experiment. However, notable exceptions were edible algae in all low nutrient treatments and bacteria in web II treatments (table 5), for which the CV increased over time (negative slope).

## Discussion

Ecosystem enrichment may have three principal effects on food webs: one or more of the equilibrium population densities change (Rosenzweig 1971; Abrams and Roth 1994a, 1994b), the stability properties of the web change (Rosenzweig 1971; Abrams and Roth 1994a, 1994b), or

**Table 3:** Summary of repeated-measures ANOVA on the effects of food web structure (web) and nutrient level (nutrient) on abundance of heterotrophic flagellates and bacteria over time

Source of variation	df	SS	F	P
Heterotrophic flagellates:				
Between subjects:				
Web	2	.88	2.55	.095
Nutrient	1	5.12	29.77	<.001
Web × nutrient	2	1.53	4.45	.020
Error	30	5.15		
Within subjects:				
Time	5	53.54	67.85	<.001
Time × web	10	9.41	5.96	<.001
Time × nutrient	5	3.75	4.76	<.001
Time × web × nutrient	10	5.29	3.35	<.001
Error	150	23.67		
Bacteria:				
Between subjects:				
Web	2	2.55	8.76	.001
Nutrient	1	11.35	78.01	<.001
Web × nutrient	2	.49	1.67	.205
Error	30	4.36		
Within subjects:				
Time	5	12.56	22.99	<.001
Time × web	10	2.57	2.35	.013
Time × nutrient	5	2.96	5.43	<.001
Time × web × nutrient	10	2.56	2.35	.013
Error	150	16.39		

Note: Data were  $\log(x)$  transformed before analysis.

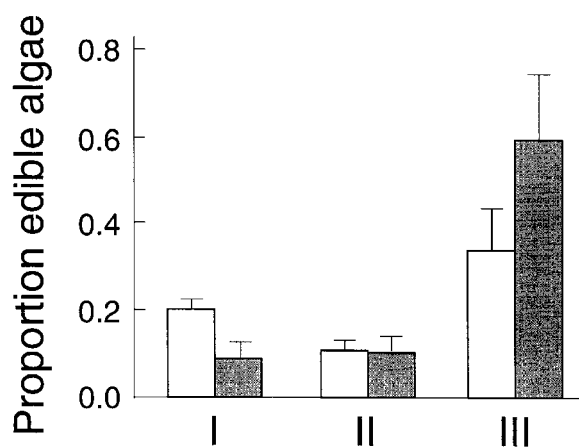
the entire web structure changes (Arditi and Michalski 1996). Below, we will relate our results to each of the effects separately. Our approach is a further development of the trophic-level concept. By viewing the experimental systems as either food chains or food webs, we compared the information lost by lumping species into trophic levels versus the information gained by splitting trophic levels into functional groups. We acknowledge that the food webs are still simplified, but they nevertheless represent one step toward a web rather than a chainlike analog of natural ecosystems.

#### *Effects on Biomass Distribution*

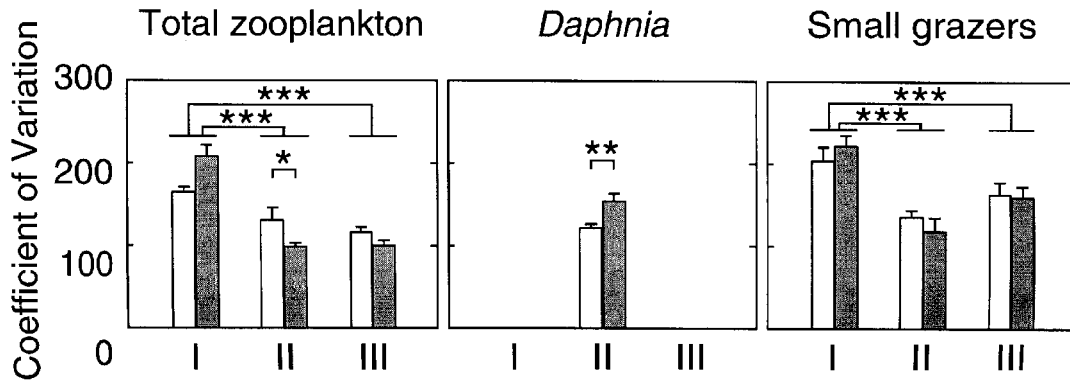
Prey-dependent models of linear food chains (Rosenzweig 1971; Oksanen et al. 1981; Oksanen 1991) predict that enrichment will increase the population size of the top predator and every second link below in the food chain. In general, we found total biomass to increase with enrichment independent of trophic position (see Hansson et al. 1998). This contradicts traditional food chain theory (Fretwell 1977, 1987; Oksanen et al. 1981) but is consistent with previous field studies (Hansson 1992; Leibold and Wilbur 1992; Persson et al. 1992; Schmitz 1993; Mazumder

1994; Brett and Goldman 1997) and with predator-prey models that either are based on ratio-dependent functional responses (Arditi and Ginzburg 1989; Akçakaya et al. 1995) or include a negative feedback between exploitation intensity and resource vulnerability. More specifically, zooplankton biomass was independent of food web structure when the systems were analyzed as food chains, for example, when the biomass of functional groups within a trophic level were clumped. Introduction of a third trophic level (fish) did not decrease the zooplankton biomass response to enrichment, in contrast to theoretical predictions (Oksanen et al. 1981). However, fish predation had qualitative effects on the zooplankton species composition (see below) that in turn indirectly affected algal biomass. Hence, algal biomass was higher in enriched systems but lower in enriched food web II than in the enriched webs I and III. Similar patterns have been obtained in the field, where grazers have been shown to modify the algal response to enrichment, resulting in different slopes between system productivity and algal biomass in odd- and even-link lake ecosystems (Hansson 1992; Mazumder 1994). Although algal biomass may be positively related to system productivity, trophic interactions may partly explain the variation in the relationship between algal biomass and productivity (Carpenter et al. 1985; Carpenter and Kitchell 1988).

Predation from uncontrolled predators promoted succession toward inedible resources irrespective of whether fish or zooplankton were top consumers. In the presence of fish, *Daphnia* was replaced by less vulnerable forms, such as rotifers and the small cladoceran *Chydorus*. Similarly, presence of *Daphnia* promoted a succession toward



**Figure 5:** Fraction of edible algae relative to total algal biomass (+1 SE) at the end of the experiment in food web treatments receiving low (filled bars) and high (open bars) nutrient additions.

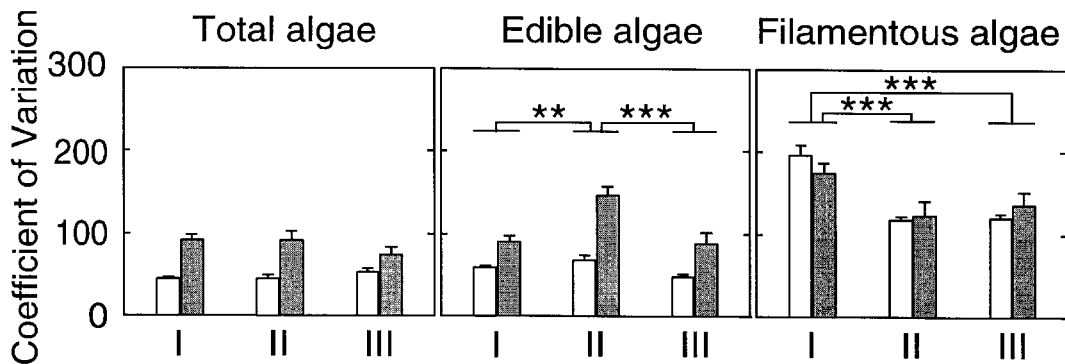


**Figure 6:** Coefficient of variation (CV; +1 SE), based on all six sampling dates, of *Daphnia*, small grazers, and total zooplankton biomass in food web treatments receiving either low (open bars) or high (filled bars) nutrient additions. The CV of *Daphnia* was significantly higher at high nutrient conditions. Both small grazers and total zooplankton biomass were significantly higher in web I than in webs II and III. The effects of nutrient condition and food web composition were tested using ANOVA followed by Tukey's post hoc test. Asterisks denote significantly different treatments: one asterisk indicates  $P < .05$ ; two asterisks,  $P < .01$ ; and three asterisks,  $P < .001$ .

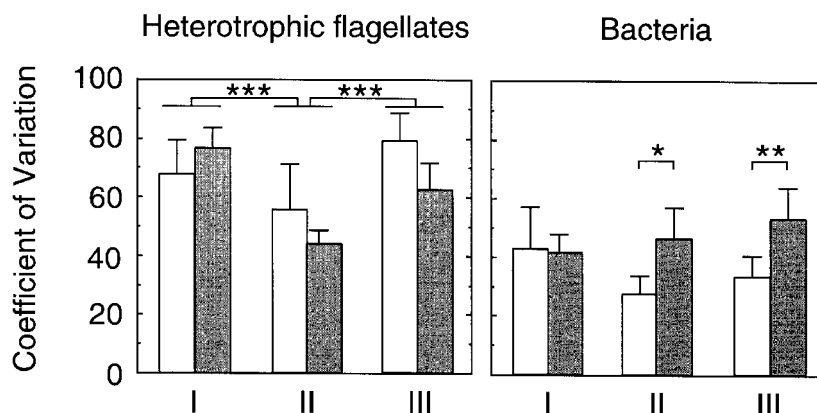
the less vulnerable filamentous algae. Although zooplankton biomass did not differ between food web treatments, grazer community composition did, which in turn influenced algal succession. When efficient grazers, such as *Daphnia*, dominated the grazer community, filamentous algae were favored. Enrichment also had structural effects on the food web because it was crucial for the persistence of the *Daphnia* populations. Thus, enrichment of web II initially facilitated *Daphnia* growth, causing a high grazing pressure on edible algae and a subsequent increase of less vulnerable, filamentous algae. Also in field studies, *Daphnia* density has been shown to determine the resource

quality of the algal community composition (Kerfoot et al. 1988; Vanni and Temte 1990; Leibold et al. 1997). However, Sarnelle (1993) showed that *Daphnia* promoted a transition from edible spring-bloom species to the similarly edible cryptophytic flagellates but, in contrast, retarded any further succession toward grazing resistant species.

Small grazers also responded to food web structure. When filamentous algae dominated the autotrophic community and *Daphnia* abundance decreased, small grazers became abundant, not because they fed on filamentous algae but more likely because heterotrophic flagellates and



**Figure 7:** Coefficient of variation (CV; +1 SE), based on all six sampling dates, of edible, filamentous, and total algae. Nutrient level is denoted as in figure 6. The CV of total and edible algae was significantly higher in nutrient enriched treatments, whereas the CV of filamentous algae was not affected by enrichment. Edible algae were sensitive to both nutrient and food web treatment, the CV being largest when web II was enriched. Filamentous algae were sensitive to web treatment. The effects of nutrient condition and food web composition were tested using ANOVA followed by Tukey's post hoc test. Asterisks denote significantly different treatments: one asterisk indicates  $P < .05$ ; two asterisks,  $P < .01$ ; and three asterisks,  $P < .001$ .



**Figure 8:** Coefficient of variation (CV; +1 SE), based on all six sampling dates, of heterotrophic flagellate and bacteria abundances. Nutrient level is denoted as in figure 6. The CVs of bacteria abundance in webs II and III were significantly higher in enriched than in unenriched treatments. The CV of heterotrophic flagellate abundance, however, was only affected by web treatment. The effects of nutrient condition and food web composition were tested using ANOVA followed by Tukey's post hoc test. Asterisks denote significantly different treatments: one asterisk indicates  $P < .05$ ; two asterisks,  $P < .01$ ; and three asterisks,  $P < .001$ .

edible algae became available as food resources in the absence of the competitor *Daphnia* (Gilbert 1988a, 1988b).

#### *Effects on Variability*

The paradox of enrichment (Rosenzweig 1971) predicts that enrichment destabilizes population dynamics, leading to an unstable equilibrium and population cycles. We tested this prediction by measuring the effects of enrichment on density variability, the variability being an index of stability. It should be kept in mind that the model prediction refers to the long-term state of a system, whereas the trend analysis in CV suggests transient dynamics during the experiments for all functional groups except *Daphnia*. This was particularly evident in web I, and consequently, the discussion relating to the paradox of enrichment hypothesis is restricted to the *Daphnia*-edible algae interaction in food webs II and III.

Large-amplitude predator-prey cycles in a *Daphnia*-edible algae system have been generated when the environment matched theory assumptions (McCauley et al. 1999). However, stability is induced when *Daphnia* divert energy by producing ephippia instead of immediate young (i.e., considerably delaying the numerical response) or when inedible algae act as a nutrient sponge and reduce the carrying capacity of edible algae (Murdoch et al. 1998; McCauley et al. 1999). We could not distinguish between destabilization due to a paradox of enrichment behavior or any other mechanism due to the low sampling frequency in comparison to the generation time of the organisms. However, we conclude that enrichment did increase the variability in the dynamics of *Daphnia* and

edible algae. For multispecies trophic levels, population-level dynamics is not necessarily reflected in trophic-level dynamics. Notably, a decreasing trend over time in CV was observed for the zooplankton and algae levels. We interpret this as a reflection of transient dynamics due to replacement of edible algae by filamentous algae. The increase in filamentous algae during the experiment decreased resource availability (McCauley et al. 1999). Thereby, the potential for population increase in edible algae following release from herbivory also decreased. This, in combination with the variability in filamentous algae being unaffected by enrichment, stabilized both population-level (edible algae) and trophic-level (total zooplankton and algae) dynamics.

It is notable that functional groups showing a significant effect of enrichment also were strongly connected and defined as vulnerable to predation. The observed response in biomass variability of *Daphnia* and edible algae is exactly what classical predator-prey theory predicts (Rosenzweig 1971). *Daphnia* and edible algae share one common characteristic despite being vulnerable to predation, namely, high exploitation efficiencies of their respective resource. In our experiment, edible algae consisted of small cells, mainly *Scenedesmus* sp. and *Monoraphidium* spp., with a capacity for rapid nutrient uptake and high growth rate (Reynolds 1984). This makes edible algae competitively superior to filamentous algae in the absence of grazers. In a similar vein, *Daphnia* is able to ingest prey of a broader size range than the other grazers present in this study (Burns 1969).

We also predicted that if an intermediate consumer suffered from predation by a top predator, density variability

**Table 4:** ANOVAs of the effects of nutrients and food web composition (web) on the coefficient of variation of the abundance (bacteria and heterotrophic flagellates) or the biomass (other groups) of each response variable

Response variable/ source of variation	df	SS	F	P
<b>Total zooplankton:</b>				
Web	2	.321	30.85	<.001
Nutrient	1	.015	2.79	.105
Web × nutrient	2	.084	8.08	.002
Error	30	.156		
<b>Small grazers:</b>				
Web	2	.339	27.18	<.001
Nutrient	1	.006	.25	.623
Web × nutrient	2	.058	4.62	.018
Error	30	.187		
<b>Daphnia (web II):</b>				
Nutrient	1	.037	10.83	.008
Error	10	.034		
<b>Total algae:</b>				
Web	2	.003	.12	.890
Nutrient	1	.554	47.19	<.001
Web × nutrient	2	.053	2.27	.121
Error	30	.352		
<b>Filamentous algae:</b>				
Web	2	.248	17.63	<.001
Nutrient	1	.00003	.004	.952
Web × nutrient	2	.013	.96	.395
Error	30	.211		
<b>Edible algae:</b>				
Web	2	.223	12.24	<.001
Nutrient	1	.586	64.39	<.001
Web × nutrient	2	.038	2.11	.139
Error	30	.273		
<b>Heterotrophic flagellates:</b>				
Web	2	.210	22.92	<.001
Nutrient	1	.020	4.33	.046
Web × nutrient	2	.049	5.29	.011
Error	30	.138		
<b>Bacteria:</b>				
Web	2	.041	2.26	.122
Nutrient	1	.188	20.47	<.001
Web × nutrient	2	.089	4.84	.015
Error	30	.275		

Note: Tukey's pairwise mean comparisons of the effect of nutrients (within each web) and food web structure (between each web) are given in figures 6 (zooplankton), 7 (algae), and 8 (bacteria and heterotrophic flagellates).

would decrease. Indeed, presence of fish caused reduced variability in edible algal biomass, especially when the enriched treatments were compared. Fish had an overall stabilizing effect on food web dynamics, reducing variability of both grazer and producer biomass. Even though planktivorous fish are poor predators on small grazers, such as rotifers and small cladocerans, fish predation reduced den-

sity variability of small grazers and eliminated *Daphnia*, thereby preventing overexploitation and destabilization of the algal community. Similarly, when *Daphnia* was the top predator, heterotrophic flagellate density was less variable than in treatments without *Daphnia*.

A predator-prey cycle is the result of the interactions between predation and resource availability, such that the stabilizing effect of density-dependent growth in the prey counteracts the destabilizing effect of predation (Lundberg and Fryxell 1995). Here, edible algae and heterotrophic flagellates illustrate this. Due to their size, edible algae and heterotrophic flagellates constitute an appropriate resource for a variety of grazers and would be expected to respond similarly to herbivory. However, variability of heterotrophic flagellate abundance was lower in the presence of *Daphnia*, whereas edible algae showed higher variability. This does not indicate that heterotrophic flagellates were more sensitive to predation from small grazers than to *Daphnia*. On the contrary, both heterotrophic flagellates and edible algae were more suppressed by *Daphnia* than by small grazers. The resource base for edible algae is nutrients, whereas heterotrophic flagellates are considered the most important predators, alongside large cladocerans, of bacteria (Tranvik 1989; Pace et al. 1990; Riemann and Christoffersen 1993; Pace and Cole 1996). Consequently, a high abundance of *Daphnia* may reduce the abundance of edible algae, heterotrophic flagellates, and bacteria and simultaneously increase resource availability for edible algae (i.e., nutrients) but decrease resource abundance for heterotrophic flagellates (i.e., bacteria; Pace and Funke 1991; Vaque and Pace 1992; Pace and Vaque 1994). In our experiment, this hypothesized two-directional impact of *Daphnia* might have resulted in the observed response in variability of the heterotrophic flagellate population.

The significant effect of enrichment and food web interaction on the CV of bacteria is somewhat surprising. Previous studies illustrate the difficulties in showing any grazing effects on bacteria. Pace and Cole (1996) reported only minor effects of fertilization and food web structure on bacterial abundances, although bacterial production increased significantly by both enrichment and predation on large grazers. Bacteria comprise many species that probably differ morphologically and in vulnerability to predation (Güde 1988; Jürgens 1994). It is therefore likely that replacements within the bacterial compartment would compensate for grazing effects from zooplankton, leading to a stabilization of the zooplankton-bacteria interaction. Despite the fact that we lumped all bacteria in one functional group, enrichment significantly increased the CV in both webs II and III. However, it should be emphasized that the variability in bacteria density, although significantly affected by enrichment, was low in comparison to

**Table 5:** Results of trend analysis in coefficient of variation (CV) of response variables

Treatment	Total zooplankton	<i>Daphnia</i>	Small grazers	Total algae	Edible algae	Filamentous algae	Heterotrophic flagellates	Bacteria
Slope ( <i>a</i> ):								
IL	-29.5 ± 1.3		-29.3 ± 1.3	4.6 ± 1.9	13.4 ± 2.2	-24.6 ± .7	-11.7 ± 1.5	-1.6 ± 1.4
IH	-25.2 ± 1.6		-25.7 ± 1.4	-9.2 ± 2.0	-10.5 ± 5.3	-24.6 ± .5	-11.7 ± 2.1	-5.3 ± .8
III	-18.8 ± 4.5	9.1 ± 1.7	-19.7 ± 4.4	-5.1 ± 2.0	8.6 ± 3.5	-25.3 ± .9	-6.9 ± 1.9	1.2 ± 1.3
IIH	-16.5 ± 1.8	-4.1 ± 1.2	-16.0 ± 2.5	-3.2 ± 2.3	-9.1 ± 4.5	-14.2 ± 2.5	-1.4 ± 2.5	1.0 ± 2.3
IIIL	-15.2 ± 2.6		-14.6 ± 2.5	-4.0 ± 2.4	6.8 ± 2.7	-22.9 ± 3.0	-13.2 ± 2.8	-1.2 ± .7
IIIH	-15.7 ± 1.7		-14.1 ± 1.9	-6.3 ± 3.7	-11.5 ± 3.0	-20.8 ± 2.2	-9.2 ± 1.4	-3.5 ± 2.3
Intercept ( <i>b</i> ):								
IL	24.2 ± 8.7		27.9 ± 11.0	67.4 ± 7.6	119.5 ± 8.8	76.7 ± 10.5	18.0 ± 3.8	35.7 ± 7.6
IH	82.0 ± 16.8		85.9 ± 17.3	51.4 ± 6.4	44.7 ± 17.2	55.4 ± 11.9	21.4 ± 9.4	16.0 ± 2.5
III	53.2 ± 20.8	165.7 ± 13.5	50.9 ± 19.8	25.4 ± 5.9	105.2 ± 11.9	4.1 ± 3.5	24.3 ± 7.2	32.1 ± 5.3
IIH	18.7 ± 8.5	129.3 ± 7.2	41.6 ± 13.2	73.4 ± 11.8	96.3 ± 9.2	46.9 ± 8.7	33.7 ± 12.1	46.6 ± 6.5
IIIL	44.0 ± 15.4		45.6 ± 14.5	34.9 ± 10.3	78.5 ± 12.2	23.3 ± 10.8	18.4 ± 9.8	27.2 ± 3.6
IIIH	20.1 ± 10.4		25.2 ± 12.6	41.5 ± 23.4	33.9 ± 11.8	34.8 ± 11.8	16.6 ± 6.4	34.5 ± 10.1

Note: All variables, except *Daphnia*, showed significant effects of time on CV (linear regression,  $P < .05$ ). Data (mean  $\pm$  1 SE) on CV of different sampling intervals was fitted to a linear model ( $y = ax + b$ ). The slope (*a*) represents the trend over time, where a negative value denotes a decreasing trend and a positive value denotes an increasing trend over time. The intercept (*b*) represents an estimation of the CV at the end of the experiment based on the linear trend. L = low nutrient treatment; H = high nutrient treatment. See "Material and Methods" for details.

the variability in the density of other functional groups, such as edible algae and *Daphnia*.

#### *Effects of Food Web Resolution*

Aggregating species into trophic levels is one way to overcome much of the complexity observed in nature (Hairston and Hairston 1993; but see Cousins 1987), and general conclusions have been drawn on the basis of the trophic-level concept (Persson et al. 1988; Hansson 1992; Hairston and Hairston 1993, 1997; Mazumder 1994; Hansson et al. 1998). However, by aggregating species, there is a risk of excluding important trophic links that may seem unimportant. Polis and Strong (1996) argued that the complexity, when properly taken into account, will reveal interactions and processes that otherwise would remain unknown. It is beyond doubt that community ecology in the future must embrace the complexity of natural systems, but at present, there is no appropriate conceptual framework that generates testable predictions (Paine 1988; Diehl 1994).

We expanded the food chain perspective by splitting each trophic level into functional groups dominated by a few species. The resulting food webs were of low complexity, and yet they embraced some of the complexity by acknowledging processes at the population level. Hence, the food web perspective not only gave us information about the response of different functional groups but also indicated which functional groups were responsible for the observed general patterns. Total algal biomass responded to enrichment with increased variability, and this response

was independent of food web configuration. In contrast, when the systems were viewed as webs, it was evident that only edible algae were destabilized and, moreover, that the variability of edible algae increased more in the presence of *Daphnia*. Filamentous algae, on the other hand, did not respond to enrichment in terms of variability. Thus, the destabilization of algae in general was due to a response in edible algae in particular.

In conclusion, predator-prey dynamics were destabilized by enrichment but were stabilized by changes in both resource edibility and consumer mortality. Thus, vulnerable prey responded in accordance with the paradox of enrichment hypothesis, whereas invulnerable prey were not destabilized to the same extent by enrichment. Moreover, enrichment changed the entire web structure, as illustrated by the occurrence of a persistent *Daphnia* population upon enrichment in our experiment. By breaking up the food chain concept into a matrix of food web interactions, and by recognizing the interplay between interspecific competition and predation, a more thorough picture of the function of ecosystems is obtained compared to when species are simply grouped into distinct trophic levels.

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### Literature Cited

- Abrams, P. A. 1993. Effects of increased productivity on the abundances of trophic levels. *American Naturalist* 141:351–371.
- Abrams, P. A., and J. D. Roth. 1994a. The effects of enrichment of three-species food chains with nonlinear functional responses. *Ecology* 75:1118–1130.
- . 1994b. The responses of unstable food chains to enrichment. *Evolutionary Ecology* 8:150–171.
- Abrams, P. A., and C. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. *Ecology* 77:1125–1133.
- Akçakaya, H. R., R. Arditi, and L. R. Ginzburg. 1995. Ratio-dependent predation: an abstraction that works. *Ecology* 76:995–1004.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio dependence. *Journal of Theoretical Biology* 139:311–326.
- Arditi, R., and J. Michalski. 1996. Food web models and their responses to increased basal productivity. Pages 122–133 in G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Bohannon, B. J. M., and R. E. Lenski. 1997. Effects of resource enrichment on a chemostat community of bacteria and bacteriophage. *Ecology* 78:2303–2315.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24:419–456.
- Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science (Washington, D.C.)* 275:384–386.
- Brönmark, C., and S. E. B. Weisner. 1996. Decoupling of cascading trophic interactions in a freshwater, benthic food chain. *Oecologia (Berlin)* 108:534–541.
- Burns, C. W. 1969. Relation between filtering rate, temperature and body size in four species of *Daphnia*. *Limnology and Oceanography* 15:693–700.
- Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. *BioScience* 38:764–769.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Cousins, S. 1987. The decline of the trophic level concept. *Trends in Ecology & Evolution* 2:312–316.
- Crumpton, W. 1987. A simple and reliable method for making permanent mounts of phytoplankton for light and fluorescence microscopy. *Limnology and Oceanography* 32:1154–1159.
- Diehl, S. 1994. Implications of omnivory and habitat complexity for aquatic community structure. Ph.D. thesis. University of Umeå, Sweden.
- Fretwell, S. D. 1977. The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine* 20:169–185.
- . 1987. Food chain theory: the central theory of ecology? *Oikos* 50:291–301.
- Fryxell, J. M., and P. Lundberg. 1997. Individual behavior and community dynamics. Chapman & Hall, New York.
- Gilbert, J. J. 1988a. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnology and Oceanography* 33:1286–1303.
- . 1988b. Susceptibilities of ten rotifer species to interference from *Daphnia pulex*. *Ecology* 69:1826–1838.
- Güde, H. 1988. Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. *Hydrobiologia* 159:63–73.
- Hairston, N. G., Jr., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* 142:379–411.
- . 1997. Does food web complexity eliminate trophic-level dynamics? *American Naturalist* 149:1001–1007.
- Hansson, L.-A. 1992. The role of food chain composition and nutrient availability in shaping algal biomass development. *Ecology* 73:241–247.
- Hansson, L.-A., C. Brönmark, P. Nyström, L. Greenberg, P. Lundberg, P. A. Nilsson, A. Persson, L. B. Pettersson, P. Romae, and L. J. Tranvik. 1998. Consumption patterns, complexity and enrichment in aquatic food chains. *Proceedings of the Royal Society of London B, Biological Sciences* 265:901–906.
- Hastings, A. 1996. What equilibrium behaviour of Lotka-Volterra models does not tell us about food webs. Pages 211–217 in G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Hastings, A., and T. Powell. 1991. Chaos in a three species food chain. *Ecology* 72:896–903.
- Hastings, A., C. L. Hom, S. Ellner, P. Turchin, and H. C. J. Godfray. 1993. Chaos in ecology: is mother nature a strange attractor? *Annual Review of Ecology and Systematics* 24:1–33.
- Jansen, V. A. A. 1995. Regulation of predator-prey systems through spatial interactions: a possible solution to the paradox of enrichment. *Oikos* 74:384–390.
- Jürgens, K. 1994. Impact of *Daphnia* on planktonic microbial food webs: a review. *Marine Microbial Food Webs* 8:295–324.

- Kerfoot, W. C., C. Levitan, and W. R. DeMott. 1988. *Daphnia*-phytoplankton interactions: density-dependent shifts in resource quality. *Ecology* 69:1806–1825.
- Kretzschmar, M., R. M. Nisbet, and E. McCauley. 1993. A predator-prey model for zooplankton grazing on competing algal populations. *Theoretical Population Biology* 44:32–66.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922–949.
- Leibold, M. A., and H. M. Wilbur. 1992. Interactions between food-web structure and nutrients on pond organisms. *Nature (London)* 360:341–343.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28:467–494.
- Lundberg, P., and J. M. Fryxell. 1995. Expected population density vs. productivity in ratio-dependent and prey-dependent models. *American Naturalist* 146:153–161.
- May, R. M. 1973. Time-delay versus stability in population models with two and three trophic levels. *Ecology* 54:315–325.
- Mazumder, A. 1994. Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. *Ecology* 75:1141–1149.
- McCann, K., and A. Hastings. 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London B, Biological Sciences* 264:1249–1254.
- McCauley, E., and W. W. Murdoch. 1987. Cyclic and stable populations: plankton as a paradigm. *American Naturalist* 129:97–121.
- . 1990. Predator-prey dynamics in environments rich and poor in nutrients. *Nature (London)* 343:455–457.
- McCauley, E., W. W. Murdoch, and S. Watson. 1988. Simple models and the variation in plankton densities among lakes. *American Naturalist* 132:383–403.
- McCauley, E., R. M. Nisbet, W. W. Murdoch, A. M. deRoos, and W. S. C. Gurney. 1999. Large-amplitude cycles of *Daphnia* and its algal prey in enriched environment. *Nature (London)* 402:653–656.
- Murdoch, W. W., R. M. Nisbet, E. McCauley, A. M. deRoos, and W. S. C. Gurney. 1998. Plankton abundance and dynamics across nutrient levels: test of hypotheses. *Ecology* 79:1339–1356.
- Oksanen, L. 1988. Ecosystem organisation: mutualism and cybernetics or plain Darwinian struggle for existence? *American Naturalist* 131:424–444.
- . 1991. Trophic levels and trophic dynamics: a consensus emerging. *Trends in Ecology & Evolution* 6:58–60.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary production. *American Naturalist* 118:240–261.
- Pace, M. L., and J. J. Cole. 1996. Regulation of bacteria by resources and predation tested in whole-lake experiments. *Limnology and Oceanography* 41:1448–1460.
- Pace, M. L., and E. Funke. 1991. Regulation of planktonic communities by nutrients and herbivores. *Ecology* 72:904–914.
- Pace, M. L., and D. Vaque. 1994. The importance of *Daphnia* in determining mortality rates of protozoans and rotifers in lakes. *Limnology and Oceanography* 39:985–996.
- Pace, M. L., G. B. McManus, and S. E. G. Findlay. 1990. Plankton community structure determines the fate of bacterial production in a temperate lake. *Limnology and Oceanography* 35:795–808.
- Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69:1648–1654.
- Persson, L., G. Andersson, S. F. Hamrin, and L. Johansson. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. Pages 45–56 in S. R. Carpenter, ed. *Complex interactions in lake communities*. Springer, Berlin.
- Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1991. Shift in fish communities along the productivity gradient of temperate lakes: patterns and the importance of size-structured interactions. *Journal of Fish Biology* 38:281–293.
- . 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *American Naturalist* 140:59–84.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, London.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature (London)* 350:669–674.
- Polis, G. A. 1991. Complex interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138:123–155.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Porter, K. G., and Y. S. Feig. 1980. The use of DAPI for identifying and counting bacteria and blue-green algae. *Limnology and Oceanography* 25:943–948.
- Reynolds, C. S. 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.
- Riemann, B., and K. Christoffersen. 1993. Microbial trophodynamics in temperate lakes. *Marine Microbial Food Webs* 7:69–100.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science (Washington, D.C.)* 171:385–387.



- . 1973. Exploitation in three trophic levels. *American Naturalist* 107:275–294.
- Sarnelle, O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* 73:551–560.
- . 1993. Herbivore effects on phytoplankton succession in a eutrophic lake. *Ecological Monographs* 63:129–149.
- Scheffer, M., and R. J. de Boer. 1995. Implications of spatial heterogeneity for the paradox of enrichment. *Ecology* 76:2270–2277.
- Schmitz, O. J. 1993. Trophic exploitation in grassland food chains: simple models and a field experiment. *Oecologia* (Berlin) 93:327–335.
- Sherr, E. B., and B. F. Sherr. 1993. Preservation and storage of samples for enumeration of heterotrophic protists. Pages 207–212 *in* P. F. Kemp, B. F. Sherr, E. B. Sherr, and J. J. Cole, eds. *Handbook for methods in aquatic microbial ecology*. Lewis, Boca Raton, Fla.
- Tranvik, L. J. 1989. Bacterioplankton growth, grazing mortality and quantitative relationship to primary production in a humic and a clearwater lake. *Journal of Plankton Research* 11:985–1000.
- Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71:2241–2254.
- Vanni, M. J., and J. Temte. 1990. Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. *Limnology and Oceanography* 35:697–709.
- Vaque, D., and M. L. Pace. 1992. Grazing on bacteria by flagellates and cladocerans in lakes with contrasting food-web structure. *Journal of Plankton Research* 14:307–321.
- Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. *American Naturalist* 139:1151–1175.

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