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Stability of oligotrophic and eutrophic planktonic communities after disturbance by fish

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The objective of our study was to investigate the relationship between resource availability and stability (resistance and resilience) in freshwater zooplankton communities and to assess their recovery after predation impact. We used 12 in-lake enclosures (3.8 m diameter × 3.5 m deep) treated with 6 combinations (replication n = 2) involving 2 nutrient concentrations and 3 fish densities. The experiment lasted 14 weeks and zooplankton and water chemistry were monitored throughout. The protocol involved 3 treatment-specific time periods: (a) the *before* fish treatment period comprising the first 2 weeks, (b) the *during* fish treatment period comprising the next 5 weeks, and (c) the *after* fish treatment period which lasted 6 weeks following fish removal. In terms of biomass and numbers, we found that the zooplankton in the fish treatments varied most and that the eutrophic biomasses were higher. In terms of stability, the zooplankton in the oligotrophic enclosures were more resistant to disturbance by fish and were more resilient after the fish were removed. Conversely, zooplankton communities in the eutrophic enclosures responded more strongly to fish predation and were less likely to return to the pre-disturbance community structure. Zooplankton at the top of the food web (top carnivores) were the most susceptible to planktivory, but recovered as quickly as the other zooplankton groups. Studies of trophic structure showed that the omnivorous, intermediate species group, had the highest species interaction levels and contributed most to community recovery in all of the treatments. Resource availability and disturbance magnitude are likely to determine post-disturbance biomass production. The stability of low productive systems seems to be maintained through strong food web links, while more productive systems are more loosely structured.

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Several publications (Pomeroy 1970, Jordan et al. 1972, McQueen et al. 1986, 1992, DeAngelis et al. 1989, Hastings and Powell 1991, Pimm 1991, DeAngelis 1992, Cottingham and Carpenter 1994) have advanced hypotheses to account for the stability patterns (defined in term of resilience, resistance and return time – Holling 1973, Pimm 1982, 1991) observed in aquatic ecosystems. The general consensus seems to be that there are fundamentally different suites of driving variables responsible for long-term as opposed to short-term stability patterns.

Long-term stability is seldom observed. DeAngelis (1992) credits this to the intervention of serendipitous physical events which shape community environments and tend to prevent biological communities from reaching stable equilibrium states that persist for long periods of time. Hastings and Powell (1991) used food web models, incorporating three or more species, to demonstrate that complex producer-consumer interactions (Pimm 1982) cause chaotic dynamics that make it difficult to predict stability in long-term system behavior.

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Such trends are exemplified by long-term aquatic community studies at Oneida Lake – New York, U.S.A., and Lake St. George – Ontario, Canada (McQueen et al. 1992) which showed that the longer the study period, the harder it was to detect strong and predictable top-down biological interactions between different trophic levels.

Local, short-term stability is often observed in aquatic ecosystems and is frequently credited to complex interactions between physical and biological factors (Carpenter 1988, Carpenter et al. 1992). However, different authors have attributed episodes of local stability to quite different relationships between controlling variables. For example, on one hand, DeAngelis et al. (1989) suggested that low nutrient environments are more stable because they have limited growth. Therefore, low phytoplankton growth rates prevent system instability by decreasing the chances of large oscillations in predator (zooplankton) – prey (algae) interactions. However, low nutrient systems would be affected by large biomass removals (DeAngelis et al. 1989, Pérez-Fuentetaja et al. 1995). This explanation is supported by observations made for coral reefs and rain forests (Pomeroy 1970, Jordan et al. 1972, Pimm 1991, DeAngelis 1992) which are characterized by low nutrient availability and high stability.

On the other hand, McQueen et al. (1986) suggested the opposite pattern and proposed that low nutrient availability might be associated with reduced community stability. The proposed mechanism is that in low nutrient communities, the species at the top of the food web depend on a tenuous resource base and are likely to succumb to modest external perturbations. This point of view is supported by data from Lake Mendota (Vanni et al. 1990) which suggested that top-down effects were stronger when nutrient availability was lower. However, this hypothesis has also been refuted by the theoretical analysis of Benndorf (1990) which suggested that increased resource bases might be expected to increase the scope for top-down biological effects.

In view of the substantial disagreements noted in the preceding paragraphs, we investigated planktonic community stability in 12 enclosures using six replicated (n = 2) treatments. The treatments involved two nutrient levels and three fish concentrations. The experiment comprised three time periods characterized as: *before*, *during* and *after* disturbance periods. The objective of the experiment was: (1) to monitor the zooplankton assemblages under low and high nutrient regimens in the absence of fish, (2) to "disturb" the zooplankton community through the addition of fish under both nutrient regimens and, (3) to remove fish and observe the patterns of recovery in the zooplankton communities under both high and low nutrient conditions.

The hypotheses that we intended to test were: (1) that the oligotrophic communities would be less resistant to fish additions and (2) that the eutrophic communities would be more resilient after fish removal. We also hypothesized that (3) zooplankton biomasses would be higher in the nutrient treatments and higher still in the nutrient + fish treatments (mostly comprised by small-size animals). So the general expectation was that resistance and resilience would be positively correlated with nutrient availability and plankton biomass.

Methods

Study site

Mesocosms were placed in Ranger Lake (45° 09' N, 78° 51' W) which is located on a granitic basin on the Canadian Precambrian Shield (Dorset, Ontario, Canada) at 342 m elevation. It is an 11.25-ha oligotrophic lake with a maximum depth of 13 m, brown coloration and high water residence time (Ramcharan et al. 1995). The lake has a soft muddy bottom with abundant woody debris around the shoreline.

Zooplankton species in the experimental enclosures included *Daphnia pulex* (Leidig), *Holopedium gibberum* (Zaddach), *Polyphemus pediculus* (L.), *Pleuroxus* sp., *Diaphanosoma brachyurum* (Liéven), *Bosmina longirostris* (O.F.M.), *Chydorus sphaericus* (O.F.M.), *Mesocyclops edax* (Forbes), *Cyclops* spp. (comprised by small cyclopoids), *Epischura lacustris* (Forbes), *Leptodiaptomus minutus* (Lillj.), and rotifers (dominated by *Asplanchna* sp., *Keratella* sp., and *Polyarthra* sp.).

Experimental design

Twelve waterproof, nylon woven polyethylene enclosures (mesocosms) were placed at the SW shore of the lake, along the 4-m isopleth in an area of sand-pebble bottom (low resuspension rates, Meijer et al. 1990). The diameter of the enclosures was 3.8 m, their depth was 3.5 m and their volume 27 m^3. The experimental design was a 2 × 3 factorial (n = 2). Six of the enclosures had the lake-ambient levels of nutrients (TP = 6 $\mu g\ l^{-1}$), and they were "closed" systems (sensu DeAngelis et al. 1989, DeAngelis 1992), where nutrients are conserved. We did not add any nutrients to these mesocosms and we called them oligotrophic systems. Beginning on 3 June, 1992, sodium nitrate and phosphoric acid were used to double the lake-ambient nutrient concentrations in the other 6 enclosures (TP = 12 $\mu g\ l^{-1}$), and we called them eutrophic systems. In the eutrophic systems, nutrients were monitored and added in order to maintain the ×2 lake nutrient concentrations. Nutrients were added once a week to free floating buckets with perforations on the bottoms. The eutrophic systems acted as "open" systems (sensu DeAngelis et al. 1989, DeAngelis 1992), or nutrient subsidized systems.

Fish treatments and controls (no fish) were assigned randomly to the oligotrophic and eutrophic mesocosms. The fish used for the treatments were age 1^+ yellow perch (*Perca flavescens* Mitchill), golden shiners

(*Notemigonus crysoleucas* Mitchill) and age 1+ pumpkinseeds (*Lepomis gibbosus* L.). 'High' and 'low' fish densities were used for the fish treatments. The 'low' fish treatment consisted of the addition of 54 ± 13 g (wet weight) of fish to each enclosure (47 kg ha^{-1}). The 'high' fish treatment consisted of the addition of 182 ± 9 g of fish to each enclosure (161 kg ha^{-1}). These fish densities were chosen to assure a strong impact of fish predation on the zooplankton populations.

Fish treatments started on 25 June, 1992 (week 4) and lasted for 34 d. At the end of the fish treatment period, 99% of the fish were recovered from the enclosures during the early part of week 9 (100% recovery by week 10) with minnow traps, and the experiment was run for another 34 d to September 6 (week 14). To ensure that all zooplankton species could invade the enclosures, 1000 l of lake water from about 1.5 m deep (3.7 % total enclosure volume) was pumped into each enclosure once a week during the fish addition period. The zooplankton biomass involved was 0.68% and 1.13% of the total zooplankton biomass in the eutrophic and oligotrophic treatments, respectively.

The enclosures were sampled weekly from 8 June to 6 Sept. (weeks 1 to 14). Samples for water chemistry were collected on each sampling date from the center of each mesocosm using a tube sampler (2 cm inside diameter, 3.5 m long). Special care was taken not to reach the bottom or disturb the walls. Zooplankton samples were collected weekly during daylight hours. Night zooplankton samples were also collected biweekly from 30 July (week 8) to the end of the experiment. A 25-l Schindler sampler (63 µm net) was used to collect zooplankton samples at the surface, 1.5-m and 3-m depths. Zooplankton samples were combined in the field.

Nutrient concentrations and chlorophyll *a* were analyzed by the Ontario Ministry of Environment and Energy (Dorset, Ontario, Canada) (Anonymous 1983). Zooplankton samples were counted using the computer programs ZCOUNT 2.2 (Sprules et al. 1981) and WSAM (Mills and Confer 1986).

To estimate periphyton growth on the mesocosms walls, glass slides (2.5 × 7.5 cm) were positioned in the center of each mesocosm at three depths (0, 1.5, 3 m).

Statistical analysis

The experiment ran for 14 weeks. On week 1 mesocosms were left to rest. Weeks 2 and 3 were termed the *before* fish treatment, when no manipulations were done in 6 of the mesocosms (oligotrophic treatment) and the other 6 mesocosms received nutrients (eutrophic treatment). Weeks 4 to 8 were termed the "disturbance period" or the *during* fish treatments. Fish were recaptured from the mesocosms during week 8 after sampling the zooplankton and water chemistry. Weeks 9 to 14 were zooplankton community recovery weeks, and were termed the *after* fish treatments.

Data were analyzed by orthogonal partitioning of treatment sum of squares. A 2 × 3 factorial experiment procedure was followed using the Statistical Analysis System (SAS Institute 1990). The data for each of the variables were divided into three periods: *before* fish additions, *during* fish presence and *after* removal of fish.

Data analysis to detect population responses to disturbance

To investigate the variability of species densities and community structure we used three different tests: coefficients of variation, contingency table and the Levene test.

To assess fluctuations in species densities we used *Coefficients of variation* (CV) based on the density of each species over time (Wolda 1978, Freeman et al. 1988, Grossman et al. 1990). We estimated individual CV's for each species and the average of these values across all species was used as a measure of variability. *Contingency table* analysis (Moyle and Vondracek 1985, Rahel 1990) was used to measure the variability of species densities. The columns were censuses and rows were species. The Chi-Square test (*G*-test) with $(r-1)(c-1)$ degrees of freedom was used to test the null hypothesis that species densities are independent across censuses at $\alpha = 0.05$. Failure to reject the null hypothesis indicates that species abundances are similar across time periods and that the community is stable. The *Levene test* (Manly 1986) was used to investigate community variability.

Zooplankton population responses to perturbation and the organization of the zooplankton communities were studied using species richness, trophic structure, species connectance, and community resistance and resilience.

Species *richness* was calculated by the rarefaction method (Simberloff 1972). Zooplankton *trophic structure* was assessed through categorization of community structure. Because many carnivorous zooplankters can feed on different kinds of prey and algae, the feeding categories were determined following Hall and Raffaelli (1991): top species were defined as those without zooplankton predators (in the enclosures), but which preyed on other species; intermediate species were preyed upon and were predators of other species, and basal species were defined as herbivores, and many of them were prey. Because copepod nauplii behave trophically as both predators and prey, they were treated as a separate, intermediate, feeding group.

Species *connectance* was measured as the number of predator-prey interactions present in the planktonic community (i.e., excluding fish), including cannibalism, over all possible interactions (Connectance = $n / S(S-1)$), where n is the number of effective interactions between two species (including phytoplankton), and S is the total number of species, excluding phytoplankton (Briand 1983, Sprules and Bowerman 1988). Zooplank-

ton feeding strategy for the connectance calculations followed Sprules and Bowerman (1988), Dodson and Frey (1991) and Williamson (1991).

Community *resistance* to disturbance was calculated as the relative change of zooplankton species (i) density (N) with respect to the densities before the addition of fish. For each species (i), the densities recorded during the disturbance by fish (weeks 4–8) ($N_{it(4-8)}$) were subtracted from the "before treatment" zooplankton densities recorded on week 3 (N_{i3}). The absolute values of the differences were then summed and averaged. Resistance was then calculated as the reciprocal of the average deviation. The algorithm used was:

$$\text{Resistance} = 1\ [\text{Avg.}\ (\sum |N_{i3} - N_{it(4-8)}|\ )]^{-1}$$

Resilience was calculated in two ways. First as the relative change of zooplankton population densities after the fish disturbance was removed (weeks 9–14) ($N_{it(9-14)}$) with respect to the densities during the same period for the controls. Resilience type one was calculated as the reciprocal of the average deviation. The algorithm used was:

$$\text{Resilience type one} = 1\ [\text{Avg.}\ (\sum |N_{it(9-14)control} - N_{it(9-14)treatment}|\ )]^{-1}$$

A second type of *resilience* was calculated as the relative change of zooplankton species (i) densities after the fish disturbance was removed (weeks 9–14) ($N_{it(9-14)}$) with respect to the densities recorded before the disturbance was applied (week 3 – N_{i3}). Resilience type two was calculated as the reciprocal of the average deviation. The algorithm used was:

$$\text{Resilience type two} = 1\ [\text{Avg.}\ (\sum |N_{i3} - N_{it(9-14)}|\ )]^{-1}$$

Results

Trends for standing stocks and concentrations

Temperature and dissolved oxygen were similar for all the enclosures during the experiment (weeks 1–14)(ANOVA, $P > 0.05$).

For total phosphorus (Fig. 1), oligotrophic and eutrophic treatments were significantly different during the experiment and the TP concentration was higher in the presence of fish compared to the control ($p < 0.05$) (Tables 1 and 2). 'High' fish treatments had the highest TP levels during fish presence (Table 3). Nitrate levels were different between the two nutrient levels throughout the whole experimental period (Table 2). For ammonia levels, differences between the control and fish treatments at the eutrophic level were statistically significant (Tables 1 and 3) with fish treatments having higher levels of ammonia than the controls. After fish removal, high levels of chlorophyll *a* were found in the eutrophic mesocosms, particularly in the EL (eutrophic – 'low' fish) treatments (Tables 2 and 3).

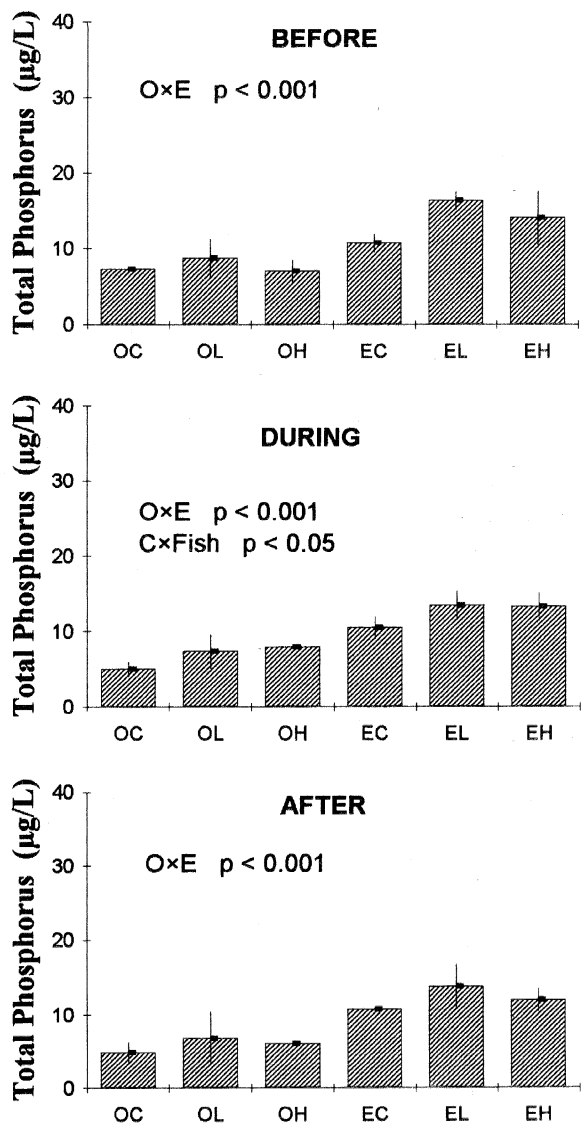

Fig. 1. Total phosphorus (µg l^{-1}) mean responses to treatments for each of the experimental periods (*before* fish additions, *during* fish presence and *after* fish removal). Bars are averages for each period for each treatment. Vertical lines are standard deviations for replicate mesocosms (n=2). Results from ANOVA analysis are shown in each panel. The treatments are: OH = oligotrophic – 'high' fish, OL = oligotrophic – 'low' fish, OC = oligotrophic control or oligotrophic – no fish, EH = eutrophic – 'high' fish, EL = eutrophic – 'low' fish, EC = eutrophic – no fish.

No statistical differences existed between day and night zooplankton density data (ANOVA, $P > 0.1$). For zooplankton biomass (Table 1) the eutrophic treatment means were significantly greater in the *before* and *during* periods (Table 1) suggesting strong bottom-up effects. Zooplankton biomasses were reduced *during* fish

Table 1. Means* and standard deviations for nutrient concentrations, chlorophyll *a*, zooplankton density, biomass and richness for oligotrophic and eutrophic mesocosms. Periods are: before fish, during fish and after fish. For all means, first date per period was eliminated except for species richness. Data are in µ/l for all the variables except for zooplankton density (l^{-1}) and richness.

	Oligotrophic				Eutrophic			
Treatment/period	TP	NO_3^--N	NH_4^+-N	Chl *a*	TP	NO_3^-–N	NH_4^+–N	Chl *a*
Control								
Before	7.30	44.00	22.50	0.25	10.75	153.50	18.50	0.34
During	4.83 (0.65)	10.38 (8.08)	10.63 (4.27)	0.98 (0.55)	10.84 (2.56)	94.25 (20.13)	10.25 (5.56)	0.20 (0.30)
After	4.95 (0.32)	7.00 (3.84)	15.30 (5.85)	1.29 (1.25)	10.29 (1.47)	79.10 (14.76)	15.70 (9.52)	0.65 (0.68)
Low fish								
Before	8.60	33.00	20.50	0.85	19.70	169.00	6.50	2.25
During	7.16 (0.66)	9.63 (7.82)	11.25 (6.33)	1.72 (1.08)	13.78 (3.43)	88.63 (27.36)	22.75 (4.48)	0.98 (0.86)
After	6.76 (1.28)	6.90 (4.42)	20.80 (9.66)	1.48 (0.95)	12.72 (2.38)	82.20 (46.00)	27.50 (11.57)	3.04 (1.96)
High fish								
Before	7.95	35.00	21.00	0.75	15.20	147.00	13.50	0.80
During	8.19 (1.14)	3.25 (1.94)	7.00 (4.76)	1.32 (1.56)	13.93 (3.41)	77.13 (17.47)	15.50 (6.96)	1.13 (0.95)
After	5.95 (0.71)	7.00 (4.34)	12.30 (4.92)	1.93 (1.76)	11.80(1.20)	78.80 (21.25)	30.30 (8.10)	1.15 (1.23)

	Density	Biomass	Richness	Density	Biomass	Richness
Control						
Before	54.29	75.01	5.95	159.92	304.96	6.20
During	54.04 (0.27)	66.57 (5.70)	5.50 (1.37)	90.19 (23.80)	163.73 (69.79)	4.18 (0.45)
After	97.19 (10.92)	179.47 (30.99)	5.54 (1.70)	82.18 (24.14)	146.44 (42.30)	5.13 (0.99)
Low fish						
Before	155.57	141.49	6.60	95.88	177.90	6.00
During	127.84 (41.31)	130.81 (58.50)	5.82 (0.98)	133.52 (101.32)	171.86 (142.79)	5.28 (1.09)
After	98.67 (9.78)	161.06 (29.49)	5.76 (1.69)	134.69 (30.47)	138.02 (76.77)	6.95 (1.09)
High fish						
Before	42.56	38.40	7.45	80.60	137.94	8.40
During	187.68 (191.96)	20.69 (2.43)	4.38 (0.42)	171.32 (152.03)	41.60 (3.04)	5.07 (0.46)
After	102.67 (23.94)	126.37 (36.37)	7.18 (0.65)	197.32 (72.45)	314.98 (116.34)	7.31 (0.78)

* For all variables, n = 1 for the period before fish. For TP, NO_3^- and $NH4^+$, n = 4 for the period during fish and n = 5 for the period after fish. For Chl *a* n = 3 for the period during fish and n = 5 for the period after fish. For zooplankton density and biomass, n = 2 for the period during fish and n = 3 for the period after fish. For zooplankton species richness, n = 3 for the period during fish and n = 4 for the period after fish.

presence in the 'high' fish treatments (P = 0.001). 'Low' fish treatments had the highest zooplankton biomasses (Tables 1, 2 and 3). After fish removal, the greatest increases in zooplankton biomass were observed in the 'high' fish treatments (Table 1) suggesting the importance of nutrient availability.

The mean dry weight of periphyton growing in the mesocosms for oligotrophic (10.17 ± 3.56 mg m^{-2}) and for eutrophic (13.36 ± 1.22 mg m^{-2}) treatments was not statistically different (two tail t-test, $P(T \leq t) = 0.31$)

Zooplankton species density and size

Many zooplankton species were present for only a portion of the experimental period (Appendix 1). Many were cropped by fish predation, which led to compensatory shifts towards smaller individuals or smaller species. Organisms like *Diaphanosoma brachyurum* and *Bosmina longirostris* were uncommon in the *before* fish period, but small individuals of these species were found in the presence of fish (Appendix 1) and at night. *Diaphanosoma brachyurum* were larger and more common after the fish were removed.

Other zooplankters were present throughout the summer. *Mesocyclops edax* did better in the OL (oligotrophic – 'low' fish) treatments than in the OH (oligotrophic – 'high' fish) treatments, and their highest density was found *after* fish removal in the eutrophic enclosures (Appendix 1). *Leptodiaptomus minutus* was the most abundant crustacean and, although their numbers declined slightly during fish presence, they recovered and increased in size *after* fish were removed (Appendix 1). Small *Cyclops spp.* had higher densities in the eutrophic enclosures (Appendix 1) and were frequently found in the night samples.

In general, the eutrophic enclosures had more nauplii than oligotrophic systems (Appendix 1). Nauplii were

Table 2. Mean Squares (ANOVA) results of nutrients, chlorophyll *a*, and zooplankton density, biomass and and species richness for each period and for their differences. Original data were transformed as ln(x+1). Treatment df = 5. Only contrasts that are significant for any of the variables are reported. TRMT = treatment, O = oligotrophic, E = eutrophic, C = control, LF = low fish, HF = high fish, INT = interaction, ns = no significant. Asteriks indicate level of significance for the p-values.

Period/Contrast	TP	NO_3^--N	NH_4^+-N	Chl *a*	Density	Biomass	richness
Before							
TRMT	0.153**	1.220***	0.241**	ns	ns	1.090**	ns
O × E	0.623***	5.998***	1.010**			3.090**	
During							
TRMT	0.262**	3.910***	ns	ns	ns	1.460**	ns
O × E	1.020***	18.562***				0.830**	
C × Fish	0.249**	0.645*				0.801**	
LF × HF	ns	ns				5.370***	
After							
TRMT	0.246**	3.220***	0.236*	0.193**	ns	ns	ns
O × E	1.140***	16.037***	0.295*	ns			
C × Fish	ns	ns	0.319*	0.350**			
LF × HF	ns	ns	ns	0.147**			
INT: C × Fish	ns	ns	0.338*	0.146**			
INT: LF × HF	ns	ns	ns	0.280**			

*P<0.10, **P<0.05, ***P<0.001.

common, but decreased in abundance and size in the presence of fish, and became larger and more abundant when fish were removed. *Asplanchna* sp., a large predatory rotifer, was common, particularly in the EH (eutrophic – 'high' fish) enclosures (Appendix 1). Rotifers were very abundant all summer, especially at night in the presence of fish (Appendix 1).

Trends in community descriptors

Zooplankton variability (coefficient of variation) (Fig. 2) was highest for *Mesocyclops edax* in the 'high' fish treatments, especially in the EH (eutrophic – 'high' fish) treatment. For *Leptodiaptomus minutus*, the CV was below 1 for all treatments, again, with maximum values for high predation levels. The *Cyclops spp.* population CV was higher at high nutrient levels and 'low' fish pressure. The *Bosmina longirostris* population was more variable in the eutrophic mesocosms with CV values above one. The *Asplanchna* population was very variable, especially in the EH (eutrophic – 'high' fish) treatments, with all treatments above one. Rotifer populations were more variable at 'high' fish densities. Nauplii densities did not vary greatly among treatments.

The overall average coefficients of variation (Table 4) were not different for paired oligotrophic and eutrophic treatments (OC vs EC, OL vs EL and OH vs EH).

Table 3. Estimates, standard errors, and p-values for main effects and simple effects when interaction was present. Symbols as in Table 1. Original data were logarithmically transformed (ln(x+1)).

Variable/Contrast	Estimate	S.E.	P-value	Variable/contrast	Estimate	S.E.	p-value
Total P				**Chlorophyll *a***			
Before				*After*			
O × E	0.455	0.071	0.0007***	C: O × E	0.429	0.162	0.038**
During				E: C × Fish	0.596	0.140	0.005**
O × E	0.583	0.093	0.0008***	E: LF × HF	0.646	0.162	0.007**
C × Fish	0.306	0.098	0.021**				
C × LF	0.265	0.114	0.058*	**Biomass**			
C × HF	0.346	0.114	0.023**	*Before*			
After				O × E	1.016	0.262	0.008**
O × E	0.616	0.111	0.001***	*During*			
				O × E	0.526	0.196	0.036**
NO_3^--N				C × Fish	0.548	0.208	0.039**
Before				C × HF	1.367	0.240	0.001***
O × E	1.414	0.121	0.0001***	LF × HF	1.634	0.240	0.0005***
During							
O × E	2.487	0.214	0.0001***	**NH_4^+-N**			
C × Fish	0.492	0.226	0.073*	*Before*			
C × HF	0.643	0.262	0.049**	O × E	0.580	0.124	0.003**
After				*After*			
O × E	2.312	0.172	0.0001***	E: C × Fish	0.702	0.257	0.03**

* P<0.10, **P<0.05, ***P<0.001.

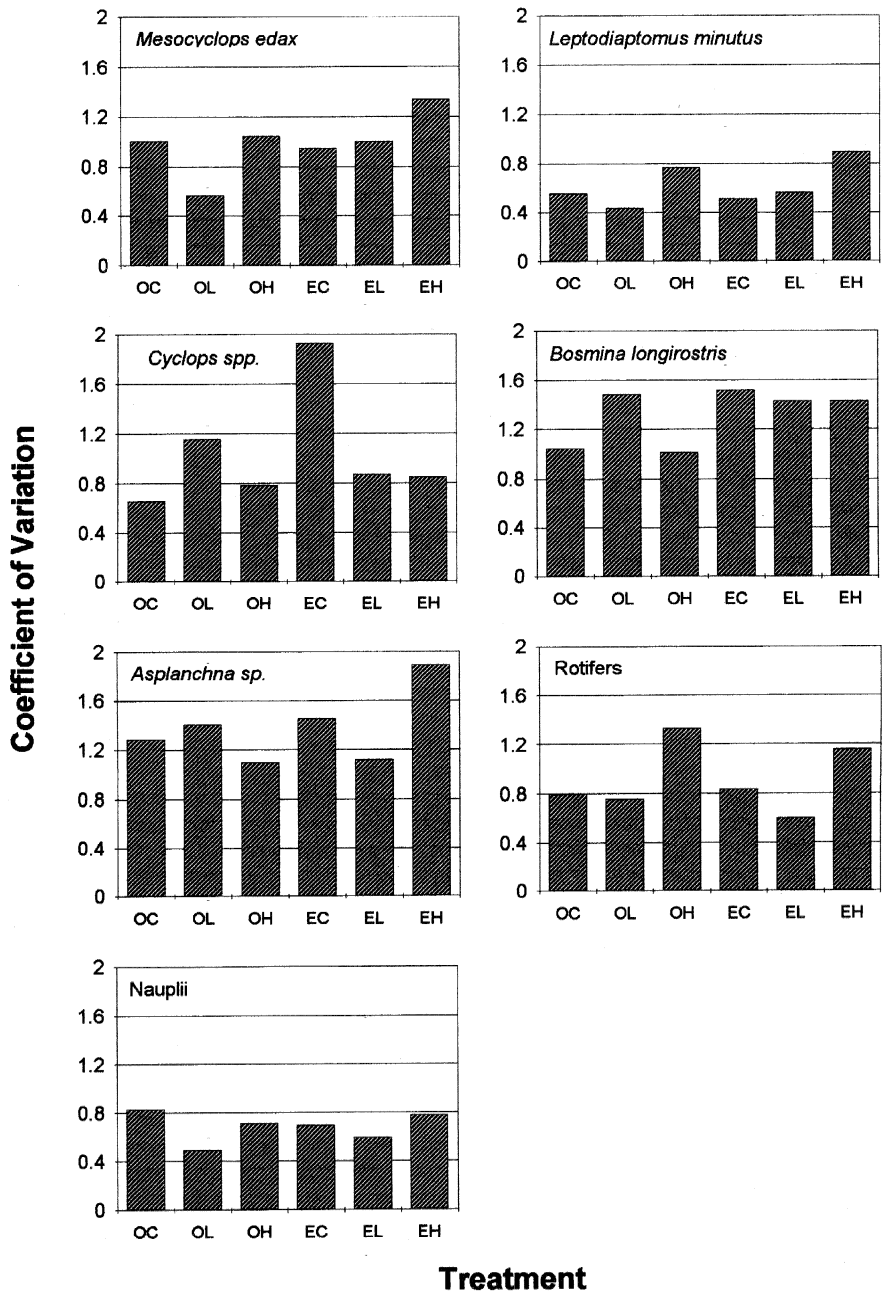

Fig. 2. Coefficient of variation for zooplankton species density per treatment during the whole experiment. The treatments are: OH = oligotrophic – 'high' fish, OL = oligotrophic – 'low' fish, OC = oligotrophic control or oligotrophic – no fish, EH = eutrophic – 'high' fish, EL = eutrophic – 'low' fish, EC = eutrophic – no fish.

Before the fish treatments were applied to the mesocosms, eutrophy was established in those with nutrient additions ($p < 0.001$) (Tables 1, 2, 3). Zooplankton had already responded to the increase in nutrient availability (biomass, ANOVA, $p < 0.05$). The coefficient of variation in the oligotrophic mesocosms in the second week of the *before* period for zooplankton density was CV = 80, compared with a CV = 40.6 for the eutrophic mesocosms, and for biomass, the oligotrophic mesocosms had a CV = 66.6 and the eutrophic mesocoms CV = 45.6. Therefore, the eutrophic mesocoms were less variable than their oligotrophic counterparts during the *before* period, suggesting that the zooplankters had already begun to adapt to a greater nutrient availability.

The only Levene's F statistic which suggested significant temporal trends was for the OH (oligotrophic – 'high' fish) treatment (Table 4). On the other hand, all of the contingency Chi-Square values were significant ($p << 0.01$) and suggested a strong pattern of increased deviation with increased disturbance by fish.

This pattern was also reflected in the estimations of resistance and resilience. In general, the 'high' fish treat-

Table 4. Statistical summary for analyses using the coefficient of variation (CV), Chi Square sums from contingency tables (G test) and F statistics from the Levene Test. Significant differences ($p < 0.05$) are noted with an asterisk. The treatments are: OH = oligotrophic – high fish, OL = oligotrophic – low fish, OC = oligotrophic control or oligotrophic – no fish, EH = eutrophic – high fish, EH = eutrophic – low fish, EC = eutrophic – no fish.

Treatment	CV	G test	Levene's Test
OC	145	174*	1.53
EC	141	212*	0.91
OL	129	230*	1.04
EL	126	320*	1.46
OH	148	447*	2.06*
EH	147	973*	1.42

ments showed the least resistance to change (Fig. 3 – top panel), and among pairs of the same treatments (OC vs EC, OL vs EL and OH vs EH), the oligotrophic communities showed more resistance to high fish disturbance, than did the eutrophic treatments. In terms of resilience (Fig. 3 – middle panel), the deviations from the controls during the recovery period showed the highest resilience in the oligotrophic fish treatments, and resilience decreased as eutrophy and fish impact increased. Finally, when resilience was measured in terms of the propensity of the communities to return to their pre-disturbance configurations, (Fig. 3 – bottom panel) the largest changes were observed for the enclosures receiving the strongest disturbances. However, as with resistance, the largest among-treatment resilience estimates were observed for the oligotrophic treatments.

Zooplankton species richness (rarefaction method, Simberloff 1972) was similar for all of the enclosures before any of the manipulations were done (Fig. 4). The addition of nutrients to the eutrophic mesocosms increased richness by week 3. All treatments showed a decrease in richness during the fish addition period, and an increase after fish were removed. In contrast to the other treatments, the 'high' fish treatments maintained high richness levels until the end of the experiment. None of the trends in species richness were significant (Table 2).

Zooplankton species connectance (Table 5) in the food web (predator-prey interactions) was not significantly different between oligotrophic and eutrophic treatments (ANOVA, $p > 0.05$). However, connectance increased during fish presence in the OH (oligotrophic – 'high' fish) treatments and decreased in the EH (eutrophic – 'high' fish) treatments compared to the con-

Table 5. Zooplankton connectance index. The dates are: before fish were introduced in the mesocosms, during fish predation and after fish were removed.

	Treatments					
Date	OC	OL	OH	EC	EL	EH
Before	0.43	0.51	0.48	0.45	0.41	0.38
During	0.74	0.57	0.76	0.78	0.65	0.56
After	0.66	0.61	0.45	0.60	0.50	0.46

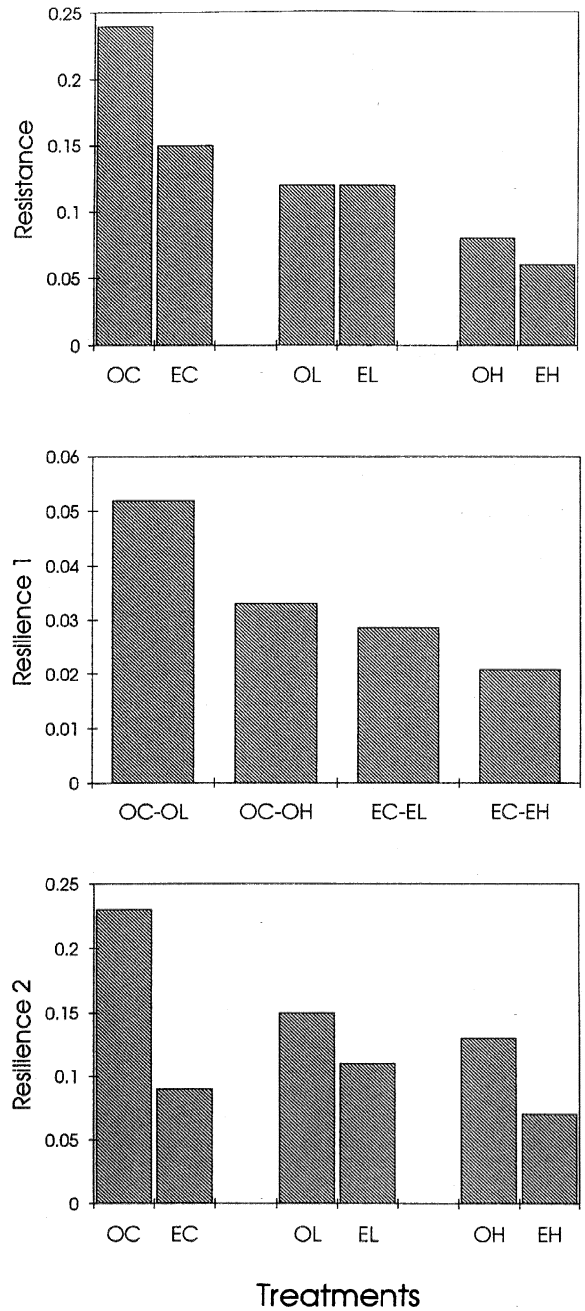

Fig. 3. Top panel: Zooplankton resistance as density (l^{-1}) deviations during the fish treatments. The treatments are: OH = oligotrophic – 'high' fish, OL = oligotrophic – 'low' fish, OC = oligotrophic control or oligotrophic – no fish, EH = eutrophic – 'high' fish, EL = eutrophic – 'low' fish, EC = eutrophic – no fish. Middle panel: Zooplankton resilience calculated as the relative change of zooplankton species densities during the post-disturbance period comparing the fish treatments with the controls for each nutrient concentration. Bottom panel: calculated as the relative change of zooplankton species densities after the fish disturbance was removed with respect to the densities recorded before the disturbance was applied.

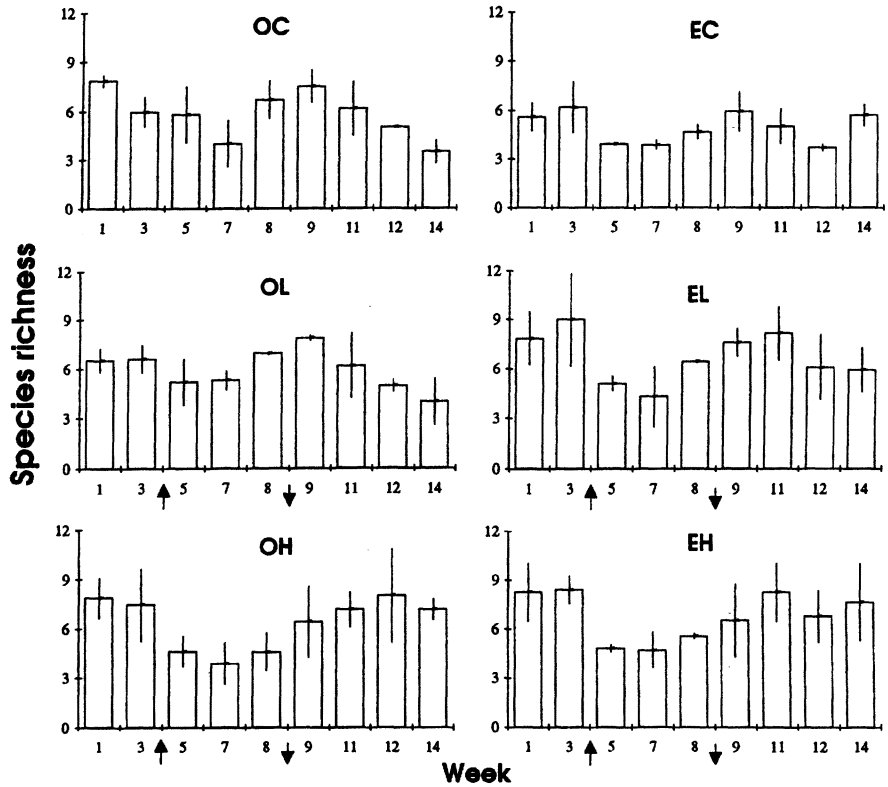

Fig. 4. Zooplankton species richness (rarefaction method) through time for the different treatments. Vertical lines are standard deviations for replicate mesocosms. Week 1 was no-treatment, week 3 was *before* fish, weeks 5–8 were *during* fish, and weeks 9–14 were *after* fish. Arrows indicate: up-arrow, fish introduction; down-arrow, fish removal from the mesocosms. The treatments are: OH = oligotrophic – 'high' fish, OL = oligotrophic – 'low' fish, OC = oligotrophic control or oligotrophic – no fish, EH = eutrophic – 'high' fish, EL = eutrophic – 'low' fish, EC = eutrophic – no fish.

trols. After fish removal, connectance values were lower in the OH (oligotrophic – 'high' fish) treatments and very similar in the EL (eutrophic – 'low' fish) and EH (eutrophic – 'high' fish) treatments.

Zooplankton interaction levels were higher in the eutrophic treatments *before* the fish were introduced (Fig. 5). The species at the top of the food web were the most sensitive group to predation. During fish predation, the number of interactions in the top species group decreased for the OH (oligotrophic – 'high' fish), EL (eutrophic – 'low' fish) and EH (eutrophic – 'high' fish) treatments. The basal species (herbivores) had similar levels of interaction in all treatments through time. Because of compensatory mechanisms induced by fish predation, larger species of herbivores were replaced by smaller ones. The intermediate species were the most heterogeneous group and the most resistant to change with similar levels of interaction throughout the experiment.

Discussion

Consistently higher nutrient concentrations were associated with periodically higher concentrations of chlorophyll *a* and zooplankton in the eutrophic enclosures. Temporal comparisons revealed that the fish treatments had consistently higher levels of total phosphorus, chlorophyll *a*, zooplankton biomass and zooplankton species richness, signifying the importance of bottom-up nutrient recycling and top-down reductions in competition mediated by the fish community. The highest chlorophyll *a* levels were observed in the EL (eutrophic – 'low' fish) treatments after fish removal and were associated with the combined effects of nutrient addition from the treatments and nutrient inputs by fish (Pérez-Fuentetaja et al. 1995). Chlorophyll *a* concentrations were also, on occasion, negatively associated with zooplankton biomasses which were highest in the eutrophic treatments (Pace 1986). Also, when fish were introduced at low densities, the biomass of small zooplankters reached high levels that were correlated with the algal biomass peaks.

The contingency analysis, revealed strong fish effects, but was unable to isolate different trends in the paired comparisons (OC vs EC, OL vs EL, and OH vs EH). This was also the case for the coefficients of variation and the Levene test (except for OH vs EH).

Estimators of resistance and resilience strongly suggested that the oligotrophic treatments were the most resistant to fish disturbance, and that the zooplankton communities in the fish treatments were the most variable through time. The post-disturbance oligotrophic zooplankton communities showed the greatest propensity to assume undisturbed (control) community compositions (Appendix 1).

DeAngelis et al. (1989) and DeAngelis (1992), suggested that in oligotrophic systems significant biomass removal would result in long return times due to low

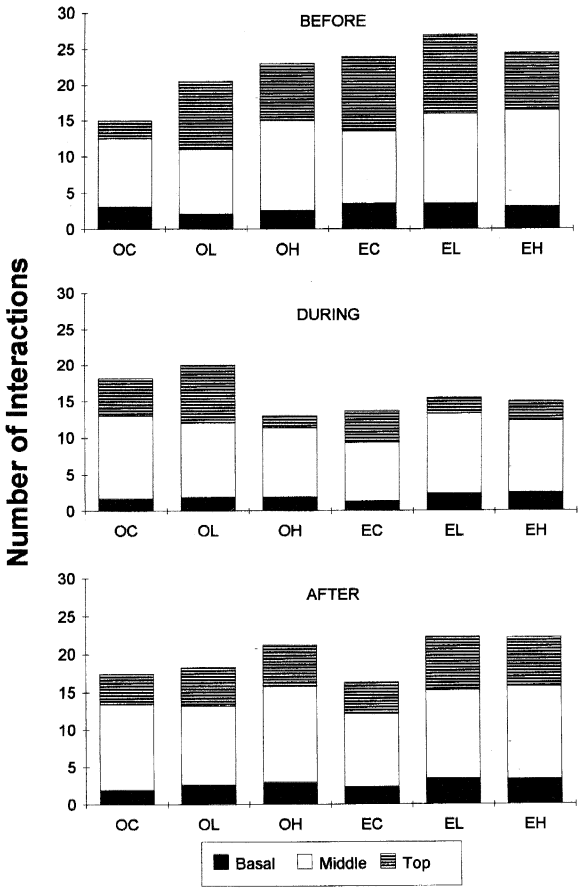

Fig. 5. Number of interactions in zooplanktonic feeding groups for the three experimental periods. Feeding groups follow the text descriptions. The treatments are: OH = oligotrophic – 'high' fish, OL = oligotrophic – 'low' fish, OC = oligotrophic control or oligotrophic – no fish, EH = eutrophic – 'high' fish, EL = eutrophic – 'low' fish, EC = eutrophic – no fish.

rates of production. However, in our oligotrophic systems the fish fed on zooplankton, but also they added nutrients through egestion and excretion. Fish were inducing bottom-up effects in the oligotrophic mesocosms, enhancing recycling rates and increasing the availability of nutrients that otherwise would have been lost (Pérez-Fuentetaja et al. 1995). Therefore, our choice of a natural perturbation, like fish feeding, may have increased the resilience of the oligotrophic systems, since nutrient removal through fish consumption was counteracted by accessible high-quality nutrient excretion into the water column. Had we removed zooplankton by some other method not involving nutrient recycling, the oligotrophic systems may have substantially deviated from the control conditions (DeAngelis 1992, Pérez-Fuentetaja et al. 1995).

Taxa specific differences based on size and strategy in avoiding fish predation shaped the zooplankton community in the treated mesocosms. The *Leptodiaptomus minutus* population was the most resistant to change because individuals maintained high reproductive rates (Pérez-Fuentetaja 1993) throughout the experiment. Small bodied *Cyclops* spp. were also resistant because their small sizes limited the effects of fish predation. Small *Bosmina longirostris*, on the other hand, showed a positive response to the presence of fish and took advantage of their size refugia, food availability, and low grazing competition. *Mesocyclops edax* were able to avoid planktivorous fish and had abundant small prey available.

Independent of their trophic status, the enclosures containing 'low' fish showed moderate recoveries of their zooplankton densities within a week of fish removal. This recovery resulted from the response of several grazer populations, such as *Holopedium, Diaphanosoma, Bosmina,* nauplii and rotifers in response to the availability of high algal biomass which was associated with fish excretion and low vertebrate predation. Increases in grazer prey densities also enhanced the recovery of predatory zooplankter populations, like *Mesocyclops, Cyclops* and *Asplanchna.* Stability in terms of biomass was provided by a very resistant species, *Leptodiaptomus minutus*, which responded to the release from fish predation by decreasing in density but increasing in size.

Periphyton usually acts as a nutrient sink. Because we controlled the nutrient inputs in the eutrophic mesocosms, we increased the likelihood that the pelagic algal community would not be nutrient depleted due to competition with periphytic algae. However, because we did not add nutrients to the oligotrophic mesocosms, we thought that nutrient competition might have occurred. To test this hypothesis, we measured periphyton colonization rates, but we found no statistical difference in terms of biomass. Despite the lack of different periphyton growth rates, we could not rule out the possibility that the walls may have been refugia for zooplankton, and that the periphyton community was a food web compartment that was weakly linked to the water column. Although this fact may have added "noise" to our resistance and resilience calculations, it seemed not to have important effects on the results, probably because similar periphytic communities were growing on the mesocosms in the *during* and *after* fish periods.

Zooplankton species connectance was not influenced by the level of nutrient addition used in these experiments (double ambient epilimnetic concentrations – ANOVA, $p > 0.05$), although the higher nutrient levels in the eutrophic systems may have buffered the impacts of predation on connectance.

Numbers of interactions between feeding groups (i.e., basal, intermediate and top species groups) decreased in response to fish predation and increased when fish were removed (Fig. 5). The intermediate group was more heterogeneous and opportunistic than the herbivores and top predators, and was more resistant to change. Conversely, herbivores and top predators were more dependent on the abundance of their food source and more

closely followed prey oscillations. The top predator group was most affected by fish disturbance, but recovered most quickly when the fish were removed.

In general our results support the predictions of DeAngelis (1992), who suggested that low nutrient availability limits growth and promotes nutrient recycling. It should be noted, however, that stability determined by our measures of resistance and resilience is a *relative* concept defined by deviations from community composition in the 'control' treatments and the pre-disturbance period. In fact, our results show (Table 1) that the greatest post-disturbance increases in zooplankton biomasses, perhaps in response to extensive nutrient pools, were found in the EH (eutrophic – 'high' fish) systems. Although these increases were chaotic, in the sense that they led to new community compositions which bore little relationship to the pre-disturbance or 'control' configuration, they could be viewed to confer biomass production advantages under extreme disturbance conditions.

In terms of local, short-term stability, our results are in accordance with the predictions and observations of Pomeroy (1970), Jordan et al. (1972), Pimm (1991) and DeAngelis (1992), who proposed an inverse relationship between stability and productivity. By implication, our results refute the opposing hypothesis proposed by McQueen et al. (1986) and reject two of the three hypotheses that we set out to test. On balance, our low nutrient and by implication, less productive enclosures, tended to have broader stability domains than the more productive systems which exhibited local instability and chaotic behavior (Beddington et al. 1976, Lawler and Morin 1993).

We conclude that the resistance and resilience components of community stability are likely to be enhanced by low productivity, but rates of post-disturbance biomass production are likely to be determined by the interaction of resource availability (nutrient concentrations) and disturbance magnitude (planktivore numbers). When disturbance magnitude is moderate, communities with low resource bases seem likely to be able to maintain stability through strongly linked food web interactions. However, when disturbance magnitude is high, communities that are more productive and more loosely structured, may be more capable of rapid biomass replacement leading to post-disturbance species abundances which deviate substantially from the pre-disturbance community composition.

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Appendix 1. Zooplankton species density (l^{-1}) and size (mm) in the three experimental periods: before fish were introduced in the mesocosms (n=1), during fish presence (n=3) and after fish were removed (n=4). Values are means and standard deviations (in parenthesis) for each period.

Period/Species	Treatments											
	OC		OL		OH		EC		EL		EH	
	density	size	density	size	density	size	density	size	density	size	density	size
Before												
D. pulex	0.86	1.6	2.94	0.80	1.10	1.41	2.61	1.12	2.93	1.30	1.34	1.50
H. gibberum			0.21	1.50			1.18	0.91	0.16	1.00	0.69	0.90
B. longirostris					0.11	0.30	0.15	0.40	0.16	0.40	0.91	0.23
E. lacustris			0.84	1.25	0.28	1.15	2.20	1.39	1.20	1.46	2.68	1.22
L. minutus	40.64	0.49	103.76	0.46	24.6	0.42	130.66	0.55	58.97	0.55	54.21	0.45
M. edax	0.16	0.60	1.9	0.78	0.23	0.50	0.82	0.96	0.45	0.75	0.26	0.85
Cyclops sp.	0.07	0.30	4.62	0.31	0.40	0.36	0.30	0.40	1.21	0.36	1.21	0.39
Nauplii	2.26	0.17	14.50	0.12	1.22	0.12	6.95	0.10	7.97	0.11	3.72	0.11
Asplanchna sp.	0.15	0.30	0.42	0.10	0.11	0.20	0.30	0.50	0.16	0.40	0.47	0.37
Rotifers	9.76	0.12	26.36	0.11	14.47	0.10	14.71	0.11	22.49	0.13	15.08	0.11
During												
D. pulex	0.07 (0.13)	0.97	0.14 (0.12)	1.03 (0.18)					0.22 (0.38)	1.21		
H. gibberum			0.10 (0.18)	0.70					0.44 (0.76)	0.86	0.22 (0.38)	0.65
D. brachyurum	0.03 (0.05)	0.82			0.34 (0.34)	0.54 (0.03)	0.84 (1.45)	0.71			0.18 (0.16)	0.56 (0.16)
B. longirostris	0.13 (0.12)	0.40 (0.16)	0.14 (0.12)	0.31 (0.12)	1.96 (3.40)	0.21			1.02 (1.45)	0.28	5.30 (6.19)	0.32 (0.06)
E. lacustris	0.15 (0.26)	1.38	0.07 (0.13)	1.37			0.60 (1.03)	1.58				
L. minutus	59.45 (48.75)	0.60 (0.06)	82.60 (51.70)	0.58 (0.07)	14.35 (15.76)	0.56	82.59 (33.60)	0.63 (0.04)	83.29 (42.31)	0.62 (0.06)	74.03 (105.6)	0.58 (0.04)
M. edax	0.76 (0.28)	0.80 (0.26)	1.98 (1.39)	0.85 (0.15)	0.07 (0.13)	0.74	0.31 (0.36)	0.96 (0.12)	0.68 (0.67)	0.87 (0.18)	1.79 (3.09)	0.82
Cyclops sp.	0.73 (0.23)	0.40 (0.02)	1.43 (1.84)	0.37 (0.05)	2.34 (0.91)	0.38 (0.08)	0.20 (0.35)	0.44	3.98 (2.41)	0.41 (0.02)	1.93 (2.60)	0.37 (0.05)
Nauplii	4.31 (1.13)	0.16 (0.02)	8.61 (8.18)	0.15 (0.02)	7.64	0.14	10.66 (6.01)	0.16 (0.02)	20.84 (10.36)	0.16 (0.01)	10.88 (5.94)	0.16 (0.02)
Asplanchna sp.	0.62 (1.07	0.47	0.66 (0.96)	0.43 (0.09)	0.21 (0.37)	0.50	0.08 (0.13)	0.40	0.22 (0.38)	0.50		
Rotifers	11.23 (11.67)	0.11 (0.01)	36.17 (31.32)	0.15 (0.04)	113.16 (155.0)	0.11 (0.02)	9.30 (10.61)	0.12 (0.02)	46.51 (39.33)	0.12 (0.02)	87.85 (111.0)	0.12
After												
D. pulex							0.11 (0.13)	1.25 (0.07)			0.18 (0.23)	0.75 (0.35)
H. gibberum	0.03 (0.05)	0.40	0.15 (0.24)	0.68 (0.18)	0.07 (0.14)	0.95	0.09 (0.11)	1.00	0.55 (0.42)	0.69 (0.27)		
D. brachyurum	0.24 (0.42)	0.33 (0.04)	0.39 (0.53)	0.47 (0.16)	0.68 (0.54)	0.57 (0.21)	0.73 (0.21)	0.69 (0.02)	0.40 (0.29)	0.84 (0.14)	1.36 (1.03)	0.56 (0.06)
B. longirostris	0.11 (0.16)	0.34 (0.09)			4.27 (2.51)	0.27 (0.06)	0.19 (0.22)	0.28 (0.11)	7.06 (6.74)	0.29	15.64 (18.75)	0.30 (0.04)
E. lacustris	0.03 (0.05)	1.30	0.09 (0.17)	1.80								
L. minutus	53.76 (20.99)	0.69	64.72 (17.82)	0.67 (0.04)	36.30 (23.0)	0.62 (0.11)	45.78 (7.96)	0.68 (0.05)	44.23 (25.33)	0.67 (0.04)	69.16 (37.34)	0.70 (0.04)
M. edax	0.76 (1.05)	0.80 (0.08)	2.25 (1.40)	0.83 (0.13)	1.10 (0.53)	0.78 (0.15)	0.62 (0.65)	0.68 (0.05)	5.61 (2.40)	0.70 (0.05)	8.74 (8.01)	0.75 (0.08)
Cyclops sp.	0.41 (0.29)	0.42 (0.09)	0.71 (0.58)	0.44 (0.03)	1.09 (1.12)	0.51 (0.09)	1.95 (2.86)	0.38 (0.10)	5.75 (5.13)	0.36 (0.04)	3.45 (2.21)	0.41 (0.04)
Nauplii	19.65 (7.08)	0.17 (0.01)	20.52 (2.44)	0.17 (0.02)	14.66 (5.81)	0.17 (0.03)	22.70 (12.45)	0.17 (0.02)	41.40 (15.19)	0.16 (0.02)	45.12 (11.89)	0.17 (0.01)
Asplanchna sp.	0.76 (0.81)	0.37 (0.02)	0.33 (0.55)	0.60	0.45 (0.38)	0.26 (0.09)	0.04 (0.08)	0.30	0.46 (0.43)	0.46 (0.14)	3.87 (4.88)	0.48 (0.12)
Rotifers	8.86 (6.81)	0.12 (0.01)	28.17 (24.10)	0.12(0.01)	57.87 (55.0)	0.13 (0.05)	9.74 (10.73)	0.12	46.39 (20.74)	0.12	58.05 (55.34)	0.13 (0.03)