

Complex shifts between food web states in response to whole-ecosystem manipulations

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Food webs can respond in surprising and complex ways to temporary alterations in their species composition. When such a perturbation is reversed, food webs have been shown to either return to the pre-perturbation community state or remain in the food web configuration that established during the perturbation. Here we report findings from a replicated whole-lake experiment investigating food web responses to a perturbation and its consecutive reversal. We could identify three distinct community states in the food web that corresponded to the periods before, during and after the perturbation. Most importantly, we demonstrate the establishment of a distinct post-perturbation food web configuration that differed from both the pre- and during-perturbation communities in phytoplankton biomass and micro- and mesozooplankton species composition. We suggest that the pre- and post-perturbation food web configurations may represent two alternative stable community states. We provide explanations for how each of the contrasting communities may be maintained through altered species interactions. These findings add to the discussion of how natural food webs react to environmental change and imply that the range of potential ecosystem dynamics in response to perturbations can be wider and more complex than is often recognized.

Natural food webs are highly complex dynamical systems that consist of large numbers of directly or indirectly interacting species. Under a given environment, food web dynamics and configurations, such as patterns in species presence/absence or relative abundances, are largely shaped by the trophic interactions within and between these species. For example, competition for a shared resource can exclude inferior species (Tilman 1982) and predation effects can cascade down through the food web influencing the density of species at lower trophic levels (Paine 1976, Carpenter and Kitchell 1993, Schmitz et al. 2000). Often it is the combination of competition and predation that determines patterns of species abundances because of non-linear interactions or indirect effects of species on each other (Hall et al. 1976, Chase et al. 2002). Environmental perturbations that alter species composition, for example by causing extinctions (Paine 1976, Elser et al. 1995) or invasions (Brooks and Dodson 1965, Carpenter and Kitchell 1993) can thus lead to a wide re-structuring of the whole food web as long as the perturbation lasts. Given that extinctions and invasions or major changes in densities of species in response to environmental change are frequently occurring in natural food webs (Houseman et al. 2008), this begs the question of what happens when such a perturbation is reversed. Will the whole food web recover to its previous state? If, will it do so rather instantaneously (Mittelbach et al. 2006) or more

gradual (Frost et al. 2006)? Or will the community that established during the perturbation period persist despite the return to the previous environmental conditions upon the relaxation of the perturbation (Schmitz et al. 2006, Persson et al. 2007)? This latter scenario occurs when the food web configurations that established in response to a perturbation are governed by new patterns in the strengths and/or types of trophic interactions between species that stabilize each state and counteract a recovery (Holling 1973, Suding et al. 2004). For example, Schmitz et al. (2006) showed in a meadow food web how temporary exclusion of predatory spiders led to a loss of plant species diversity. Freed from predation risk, a switch in herbivorous grasshoppers' foraging behavior away from the competitively superior plant species caused the plant to thrive and suppress other plant species leading to a decline in plant evenness. A re-introduction of predators did not cause the food web to return to the more diverse configuration as predators could not regain trophic control of herbivores and, indirectly, the superior plant. In contrast, Mittelbach et al. (2006) demonstrated in a lake ecosystem that a *Daphnia* sp. assemblage returned to the same species composition as was present before a temporary decrease in planktivorous fish density. Such apparent unpredictability and potential irreversibility of perturbation effects can be of considerable concern particularly when the new food web state is detrimental to human interests, e.g. when it

is characterized by low densities of a commercially important population or the absence of an endangered species (Carpenter 2003, Suding et al. 2004).

Perturbation-induced alteration of interaction patterns and the occurrence of alternative stable states are often promoted by intraspecific size-structure (Chase 2003, Persson et al. 2007). Since predation and competition are highly dependent on body size, individuals often change their resource use or trophic level. Thus, they change their status as prey or predator as they grow over their life cycle, thereby undergoing an ontogenetic niche shift (Werner and Gilliam 1984, Wilbur 1988, Rudolf and Lafferty 2011). This leads to a larger scope for flexible trophic interactions and indirect effects between species than in unstructured communities. For example, a predator that undergoes an ontogenetic resource niche shift (Olsson 1996) can be excluded from a food web by its later prey if the latter can outcompete the predators' offspring that need to grow through the size ranges of their later prey in order to become predators (Werner and Gilliam 1984, Wilbur 1988). This is an example of a direct juvenile recruitment bottleneck, but such bottlenecks can also be indirect. Neill (1985, 1988a, b) suggested that cladoceran mesozooplankton species in a size-structured pelagic food web depressed phytoplankton biomass and thereby outcompeted rotifers, indirectly limiting the survival of small phantom midge (*Chaoborus*) larvae that essentially depend on rotifers as a prey. This results in a food web configuration dominated by cladoceran mesozooplankton with absence of *Chaoborus* as well as low phytoplankton and rotifer densities. This community is stabilised by the competition between rotifers and cladocerans. Conversely, if *Chaoborus* larvae can grow to sizes where they switch to consume and thus suppress cladocerans, the larvae will indirectly release rotifers from competitive exclusion. *Chaoborus* thereby breaks its own bottleneck. This alternative community will be dominated by *Chaoborus* with high phytoplankton and rotifer but low cladoceran densities. *Chaoborus* consumption of cladocerans stabilises this state.

Neill based this hypothesis on a series of elegant enclosure experiments conducted within a *Chaoborus* generation. However, it is a debated and largely unresolved question to what extent extrapolation of conclusions from small-scale, short-termed studies with their inevitable spatio-temporally and trophically simplified food web to the scales of whole ecosystems is possible (Carpenter 1996, Benton et al. 2007). Whole-ecosystem manipulation experiments which looked at the effects of perturbation reversals and also ran long enough to assess the potential stability of perturbation-induced new food web states are still rare. In particular, the concept of alternative stable states has seldom been addressed experimentally on the ecosystem level and most of the evidence for it comes from micro- or mesocosm experiments (Schröder et al. 2005, but see Schmitz et al. 2006, Persson et al. 2007).

Here we tested whether the suggested indirect juvenile recruitment bottleneck in the *Chaoborus* system (Fig. 1) indeed operates on the scale of a whole ecosystem and over several life spans of the key species and whether it leads to the proposed alternative stable states. We temporarily suppressed the large phantom midge populations of two small lakes and assessed the type of food web configurations present

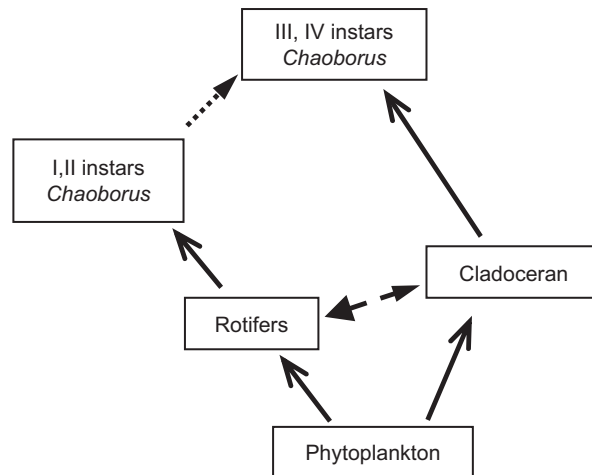


Figure 1. Schematic presentation of the simplified pelagic food web in the experimental lakes. Solid arrows indicate direct trophic interactions; the double-headed arrow indicates competition. The dotted arrow indicates individual growth of *Chaoborus* larvae.

before, during, and after the perturbation. We monitored *Chaoborus*, mesozooplankton, rotifer, and phytoplankton densities for several years for each treatment period. We hypothesised that while the perturbation lasts and *Chaoborus* is suppressed, cladoceran density would increase but phytoplankton and rotifer densities would decline. We further expected that upon removal of the perturbation factor the pre-perturbation state would not recover. High cladoceran density would prevent successful re-colonisation of *Chaoborus* and the perturbation-induced alternative food web configuration would thus be stable. With an additional, short-termed enclosure experiment in which we directly manipulated cladoceran mesozooplankton densities, we intended first to gain more mechanistic insight into the trophic interactions between the different zooplankton groups. We predicted that removal of cladocerans from enclosures would lead to high phytoplankton and rotifer densities and allow *Chaoborus* recruitment. Second, we wanted to assess the re-colonisation potential of *Chaoborus*. Absence of former dominant members of a community after a perturbation has removed them can also be due to dispersal limitation and not due to a change in the community attractor. Third, we wanted to contrast the dynamics of the zooplankton food web in whole lake ecosystems with those in spatio-temporally and trophically simplified enclosures.

Material and methods

Study system and natural history

The study was carried out from spring 1997 to autumn 2008 in two small fishless and unproductive lakes in northern Sweden (64°29'N, 19°26'E), Abborrtjärn 5 and Abborrtjärn 6 (hereafter AT5 and AT6). The lakes are separated by a 20 m wide stretch of dense *Sphagnum* bog. They are situated in a sandy area, surrounded by slow-growing pine *Pinus silvestris* forests with reindeer lichens *Cladonia rangiferina* and lingon berries *Vaccinium vitis-idaea* as the main ground

vegetation. Both lakes are similar in their basin morphology and abiotic conditions. AT5 had slightly higher total nitrogen concentration and lower conductivity and alkalinity (Table 1, Supplementary material Appendix A1). Prior to a rotenone treatment in autumn 1995, the lakes were inhabited by nine-spine stickleback *Pungitius pungitius*, but have been fishless thereafter. Instead, *Chaoborus flavicans* became the dominant predator species. A second species, *C. obscuripes*, was also present but always only in very low densities compared to *C. flavicans* (Supplementary material Appendix A2). *Chaoborus*, or phantom midge, is a dipteran insect and lives predominantly as planktonic larvae in ponds and lakes. In northern Scandinavia, *Chaoborus* has a univoltine life cycle with non-overlapping generations. The non-feeding, short-living adults emerge and lay eggs in late spring/early summer. The larvae grow to the fourth and final larval (IV-instar) stage during summer (Sæther 1997). Over their ontogeny they undergo a niche shift from feeding mainly on microzooplankton such as rotifers (instars I, II) to feeding mainly on crustacean mesozooplankton (instars III, IV), especially cladocerans (Neill 1985, Moore 1988, Persaud and Dillon 2010). Larvae overwinter as IV-instars before they pupate and emerge in late spring/early summer (Sæther 1997).

Lake manipulations

To perturb the food web by removing *Chaoborus*, the lakes were stocked with fish large enough to feed effectively only on pelagic macroinvertebrates such as *Chaoborus* but not on mesozooplankton. AT6 was stocked with Eurasian perch (*Perca fluviatilis*; 20 kg ha⁻¹, mean length 230 mm, range 135–290 mm) in May 2000. Only male perch were used to prevent the establishment of a long-term viable population. Since no effect of the perch stocking on *Chaoborus* densities could be detected in summer 2000, AT6 was additionally stocked with rainbow trout *Oncorhynchus mykiss* in May 2001. AT5 was stocked with only rainbow trout in May 2002. Each lake received 20 kg ha⁻¹ of rainbow trout with a mean length of 218 mm (range 190–240 mm). Rainbow trout was chosen because both lakes lack suitable spawning grounds thus preventing any recruitment. Stocking was staggered between lakes to create control years. From August to September 2003 and 2004, fish were removed from AT6 and AT5, respectively, using gill nets. Gill netting continued throughout the following seasons to ensure that all fish were removed. The last fish were caught in AT5 in September 2004 (four trout) and in AT6 in early May 2004 (four trout and one perch). Each lake was thus fish free after the removal season. This was confirmed by occasional angling. Furthermore, after the removal seasons, we did not see any fish feeding on the water surface anymore. The study period was consequently divided into three treatment periods for each lake: before, during and after the perturbation. For AT5, the pre-perturbation period was five years (1997–2001), the perturbation period lasted for three years (2002–2004), and the post-perturbation period for four years (2005–2008). For AT6, the corresponding periods spanned four years (1997–2000), three years (2001–2003), and five years (2004–2008), respectively.

Sampling and data acquisition

Chaoborus, mesozooplankton (cladocerans and copepods) and rotifers were sampled at two pelagic stations in each lake seven to eight times per year at regular intervals of ca. three weeks throughout the ice-free period between mid May and end of September. Because *Chaoborus* larvae can show diel vertical migration they were collected at day and at night (the latter apart from May and June when it is not getting dark at these latitudes) with vertical hauls of a 250 µm mesh net. Throughout the study *Chaoborus* densities at night were consistently higher than but were otherwise closely reflecting the day densities (bootstrapped Pearson's two-sided correlation coefficient and its bias-corrected and adjusted 95% confidence interval: 0.84 [0.57, 0.92], see also Supplementary material Appendix A3). Because *Chaoborus* day sampling was more complete, further analyses are based on day samples. Using night data did not change the conclusions. Mesozooplankton was sampled with vertical hauls of a 100 µm mesh net drawn at a speed of approximately 0.5 m s⁻¹. Rotifers were collected by sampling the water column from 0–3.5 m depth in intervals of 0.5 m with a Ruttner collector and filtering this water through a 25 µm mesh net. Rotifers were only regularly sampled from 1999 and onwards. All samples were preserved in Lugol's solution. In the laboratory, individuals were identified to genus or, if possible, species and counted with the help of a stereo microscope. For cladocerans and copepods, the body length of 15 randomly chosen individuals (or all if fewer were caught) of each species was measured and biomass was calculated from these lengths using length-weight regressions given by Botrell et al. (1976). Phytoplankton biomass was estimated as chlorophyll-a concentration. A mixed water sample from the epilimnion obtained at intervals of 1 m from the surface to the thermocline was filtered through a Whatman GF/C filter. The filter were then dried and frozen at -25°C before the algae were extracted in methanol. The extract was spectrometrically analysed and chlorophyll-a content was calculated based on the absorbance at 665 nm and 750 nm. To obtain only the size-fraction of algae < 35 µm that is efficiently edible by mesozooplankton, chlorophyll-a was also estimated for water filtrated through a 35 µm nylon cloth. However, since total and size-fractionated chlorophyll-a concentrations < 35 µm were always very similar (bootstrapped Pearson's two-sided correlation coefficient and its bias-corrected and adjusted 95% confidence interval = 0.95 [0.91, 0.98]), only the former was used in any analysis. Water transparency (estimated by Secchi depth) and total chlorophyll-a concentration were negatively correlated (Pearson's two-sided product-moment correlation coefficient and its bootstrap 95 % confidence interval: -0.59 [-0.75, -0.31]). Since light attenuation is a function of particle concentration, this relationship indicates that phytoplankton cell density decreased with decreasing chlorophyll-a concentration rather than that a lower chlorophyll-a concentration is the result of a major change in the phytoplankton community.

Enclosure experiment

We used lake enclosures to assess dispersal limitation of *Chaoborus* and the principal operation of the indirect

Table 1. Descriptive summary of basin morphology and mean and range (in brackets) of abiotic conditions of the experimental lakes through the different periods of the study.

	AT 5		AT 6	
	Before	After	Before	After
Area (ha)		0.42		0.38
Max. depth (m)		7		7
Mean depth (m)		4		4
Secchi depth (m) * (water transparency)	3.6 (3.0–4.4)	4.0 (3.7–4.1)	3.4 (2.4–4.3)	4.6 (4.2–5.0)
pH *	7.3 (7.0–7.5)	7.0 (6.5–7.6)	7.4 (7.2–7.5)	7.5 (7.3–7.7)
Conductivity (mS m ⁻¹)*•	10.7 (8.6–13.1)	8.8 (8.4–9.5)	15.7 (13.8–17.6)	11.6 (11.1–12.4)
Alcalinity (mekv l ⁻¹)*	0.05 (0.03–0.07)	0.04 (0.03–0.06)	0.09 (0.05–0.14)	0.07 (0.04–0.1)
Mean epilimnion temperature (°C)**	16.0 (15.4–16.8)	17.7 (16.1–20.3)	16.8 (15.8–17.7)	17.9 (16.7–19.4)
Total P (µg l ⁻¹)*	10.3 (9.5–11.6)	17.7 (12.6–24.4)	11.5 (9.3–13.4)	12.2 (10.7–13.7)
Total N (µg l ⁻¹)*	1019 (953–1135)	1035 (926–1150)	820 (730–923)	831 (794–868)

*based on 5–6 summer samples between late June and early September.

**based on the arithmetic mean across the depth profile from the surface to the thermocline.

•based on one spring and autumn sample in 1997 and 1998, autumn samples only after that. Data for 2000 and 2001 are not available.

*note that for the post-perturbation seasons, pH and conductivity were measured with a different method.

bottleneck mechanism. We filled six plastic bags with lake water filtrated through a 74 µm cloth to exclude mesozooplankton. Plastic bags (1.6 m ø, 4 m depth) were hanging in the water column supported by floating wooden frames. Three randomly chosen enclosures were then restocked with ambient mesozooplankton densities to serve as controls. The mesocosms were set out in late May 2005 in AT6. Flying adult *Chaoborus* were allowed to naturally deposit eggs into enclosures. Plankton community sampling in mesocosms was carried out as in the lakes throughout the ice free season of 2005 and by using the same sampling techniques. A similar experiment was conducted in AT6 in 2004, the first year after fish removal in this lake (Supplementary material Appendix A4).

Calculations and analyses

For the lakes we calculated the average density of each zooplankton group over each summer from late June to early September (5–6 samplings depending on year). We focused on this period because densities then were expected to be high and trophic interactions strongest in their influence on community dynamics (see Supplementary material Appendix 5 for the complete seasonal time series). As average density over the summer we used the geometric mean to account for the multiplicative character of seasonal population growth. We tested for differences in densities of plankton groups and species between pre-perturbation, perturbation, and post-perturbation periods in the lakes and between treatments over the course of the enclosure experiment by using bootstrapping (repeated re-sampling method with replacement; Davison and Hinkley 1997). Bootstrapping methods give reliable confidence intervals also with the low sample sizes that often are inevitable in large-scale studies. They are robust and assumption-free; in particular they do not require normality of residuals or equal variances across groups and are insensitive to serial autocorrelation of residuals. We used the geometric seasonal means as data (22 lake years). When bootstrapping lake time series, permutations were stratified by lake to account for potential random lake effects. Statistical significance was based on the bootstrapped bias-corrected and adjusted 95% confidence intervals resulting from 1000 re-sampling permutations. When these confidence intervals do not overlap, the means are statistically significant different at $\alpha = 0.05$. Bootstrapped Pearson's product-moment correlation coefficients were employed to investigate trophic relationships between several zooplankton groups. Correlation tests were one-sided according to our a priori hypotheses (Introduction, Fig. 1). We used non-metric multidimensional scaling (NMDS) to visualise the differences between pre-, perturbation and post-perturbation communities. NMDS was restricted to two dimensions because using more dimensions did not increase the explanatory power. Permutation ANOVA for distance matrices tests (Oksanen et al. 2008) were employed to assess the differences between communities of different treatment periods. Distance matrices were calculated with several similarity indices such as Bray-Curtis, Euclidean, Manhattan and Jaccard. When permutation ANOVAs produced p-values smaller than $\alpha = 0.05$, permutation dispersion tests (Oksanen et al. 2008) were used to investigate whether the significance is due to differences in

variance between communities or within communities. Calculations and analyses were performed in R 2.9.0 (R Development Core Team 2009) using the packages *boot* (Davison and Hinkley 1997) and *vegan* (Oksanen et al. 2008).

Results

Both lakes had similar zooplankton communities before the fish stocking and responded similarly to the perturbation

treatment (Fig. 2, 3, Table 2). During the pre-perturbation period *Chaoborus* larvae had overall high densities (arithmetic mean, $n = 2$, bootstrap 95% CI: 26.1 ind. m^{-3} , [8.8, 54.1], Fig. 3, Table 2A). Total cladoceran biomass was low ($6.2 \mu g l^{-1}$ [4.0, 10.0], Fig. 3) with the small-bodied *Bosmina* and *Ceriodaphnia* dominating the cladoceran mesozooplankton assemblage (Fig. 2C–D, Table 2A). Rotifer densities were also high before the perturbation (8291 ind. l^{-1} , [5424, 12421], Fig. 3) with a relative dominance of *Kellicottia longispina*, *Keratella spec.*, and *Conochilus* and comparably high

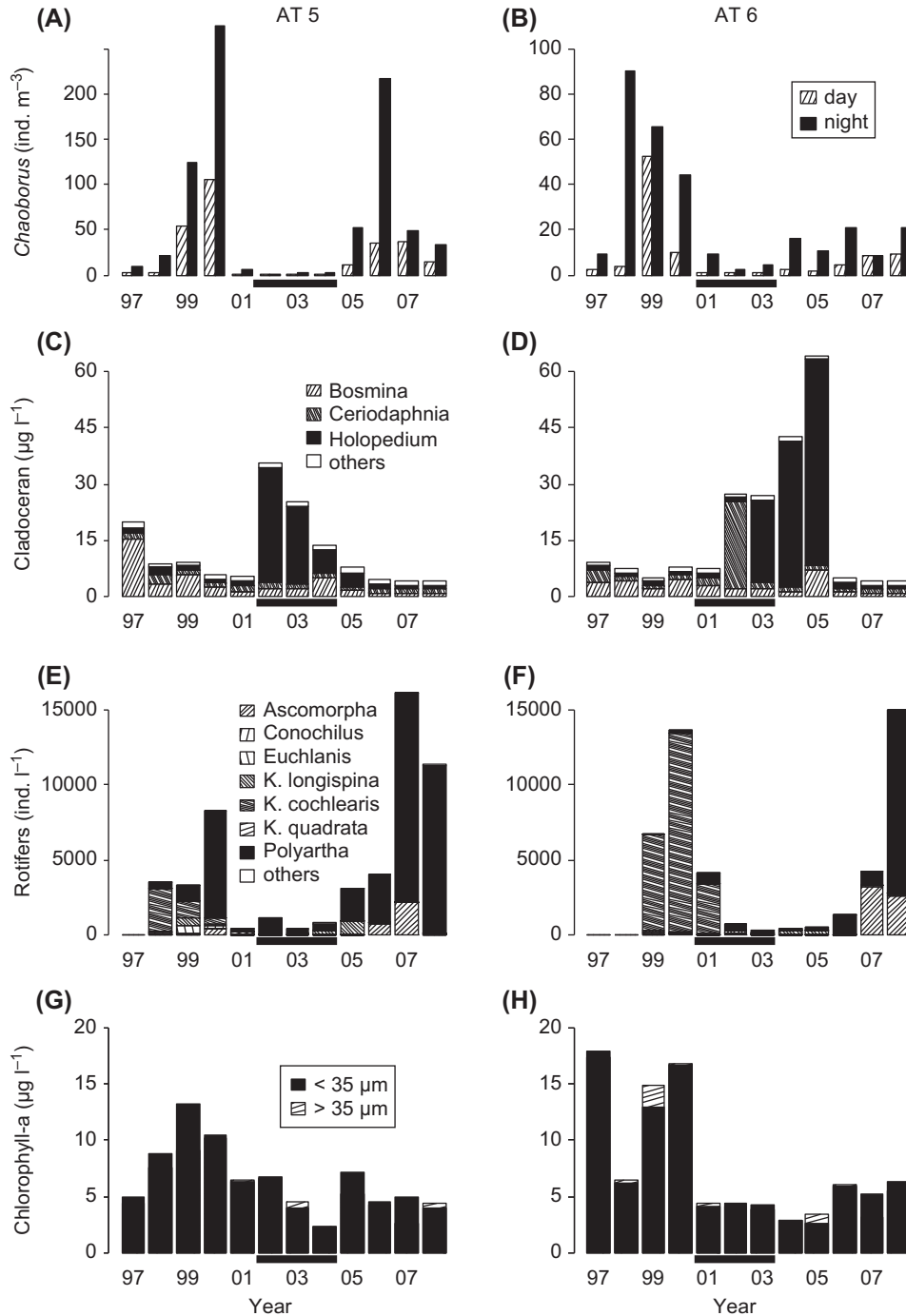


Figure 2. Density of *Chaoborus* larvae (A, B), cladocerans (C, D), rotifers (E, F) and phytoplankton (G, H) in lakes AT5 (left panels) and AT6 (right panels) over the course of the experiment. Bar heights show the geometric mean over the summer (end of June to early September) of each year. The lines below each x-axis depict the presence of fish. Note the different scale of the y-axis in panels (A) and (B).

Table 2. (A) Mean summer densities of main zooplankton species between treatment periods across lakes. (B) as A, but with the years 2004 and 2005 in AT6 classified as perturbation = 'Fish'.

	Before	Fish	After
(A)			
<i>Chaoborus</i> (day)*	26.1 [8.8, 54.1]	1.2 [1.1, 1.3]	14.0 [8.7, 19.1]
<i>Chaoborus</i> (night)*	72.0 [31.6, 146.2]	3.9 [2.6, 5.8]	47.6 [26.3, 104.8]
<i>Bosmina</i> †	4.9 [3.1, 9.2]	2.9 [2.2, 3.9]	1.9 [1.2, 3.8]
<i>Ceriodaphnia</i> ‡	1.6 [1.2, 2.4]	5.1 [1.4, 12.2]	1.02 [1.01, 1.04]
<i>Holopedium gibberum</i> †	1.2 [1.1, 1.4]	13.7 [6.2, 21.2]	11.6 [1.4, 24.2]
<i>Ascomorpha</i> ‡	94.5 [18.6, 233.5]	17.7 [4.8, 40.2]	994 [340, 1962]
<i>Asplanchna</i> ‡	10.2 [4.1, 21.5]	21.1 [3.3, 30.1]	1.2 [1.1, 1.4]
<i>Conochilus</i> ‡	55.4 [20.9, 94.1]	6.0 [2.2, 10.8]	12.9 [6.3, 19.7]
<i>Euchlanis</i> ‡	139.7 [39.8, 293.8]	2.6 [1.6, 3.2]	28.5 [6.6, 80.3]
<i>Kellikottia longispina</i> ‡	219 [97, 350]	145 [80, 219]	136 [11, 311]
<i>Keratella cochlearis</i> ‡	4028 [2449, 5754]	590 [28, 1686]	3.5 [2.1, 6.7]
<i>Keratella quadrata</i> ‡	14.6 [4.8, 23.6]	4.0 [2.4, 6.9]	4.0 [2.3, 6.9]
<i>Polyarthra</i> ‡	1490 [278, 3775]	537 [314, 789]	5014 [2397, 8890]
Phytoplankton†	10.8 [7.9, 13.2]	4.3 [3.6, 5.5]	4.9 [4.0, 5.8]
(B)			
<i>Chaoborus</i> (day)*	26.1 [8.8, 54.1]	1.4 [1.1, 1.9]	17.3 [10.2, 23.9]
<i>Chaoborus</i> (night)*	72.0 [31.6, 146.2]	6.2 [3.9, 8.8]	57.4 [30.6, 109.4]
<i>Bosmina</i> †	4.9 [3.1, 9.2]	3.3 [2.3, 5.1]	1.2 [1.1, 1.3]
<i>Ceriodaphnia</i> ‡	1.6 [1.2, 2.4]	4.1 [1.2, 12.3]	1.02 [1.00, 1.04]
<i>Holopedium gibberum</i> †	1.2 [1.1, 1.4]	22.0 [9.8, 35.7]	1.5 [1.1, 2.6]
<i>Ascomorpha</i> ‡	94.5 [18.6, 233.5]	14.4 [4.0, 40.3]	1277 [410, 2021]
<i>Asplanchna</i> ‡	10.2 [4.1, 21.5]	16.2 [1.9, 30.3]	1.2 [1.0, 1.3]
<i>Conochilus</i> ‡	55.4 [20.9, 94.1]	10.1 [5.0, 20.2]	10.2 [3.6, 16.7]
<i>Euchlanis</i> ‡	139.7 [39.8, 293.8]	3.7 [2.1, 6.9]	34.7 [5.7, 82.9]
<i>Kellikottia longispina</i> ‡	219 [97, 350]	111 [43, 204]	151 [45, 343]
<i>Keratella cochlearis</i> ‡	4028 [2449, 5754]	445 [21, 1669]	2.1 [1.7, 2.6]
<i>Keratella quadrata</i> ‡	14.6 [4.8, 23.6]	3.4 [2.1, 5.8]	4.8 [2.5, 8.3]
<i>Polyarthra</i> ‡	1490 [278, 3775]	447 [285, 713]	6396 [3162, 10693]
Phytoplankton†	10.8 [7.9, 13.2]	3.9 [3.1, 4.8]	5.4 [4.9, 6.4]

Entries are arithmetic bootstrap mean ($n = 2$, $R = 1000$, stratified by lake) and their bias-corrected and adjusted 95 % bootstrap confidence interval in square brackets.

*individuals m^{-3} .

† $\mu g l^{-1}$; phytoplankton measured as total chlorophyll-a concentration.

‡individuals l^{-1} .

densities of *Asplanchna* (Fig. 2E–F, Table 2A). Phytoplankton biomass was high ($10.8 \mu g l^{-1}$, [7.9, 13.2], Fig. 3).

Following the fish stocking, *Chaoborus* density decreased to very low levels in both lakes ($1.2 \text{ ind. } m^{-3}$, [1.1, 1.3], similar to densities in nearby fish lakes harbouring *Rutilus rutilus* and *Perca fluviatilis*, Fig. 3). Also rotifer abundance ($1603 \text{ ind. } l^{-1}$, [711, 3056]) and phytoplankton biomass ($4.3 \mu g l^{-1}$, [3.6, 5.5], Fig. 3) declined in comparison with the pre-perturbation period. In contrast, cladoceran biomass increased by a factor of ca three ($22.0 \mu g l^{-1}$, [12.6, 29.9], Fig. 3) and the cladoceran assemblage became dominated by the large-bodied species *Holopedium gibberum* except for 2002 in AT6, when *Ceriodaphnia* was the predominant species. Nevertheless, all cladoceran species densities increased in absolute values, too (Fig. 2, Table 2). Neither cyclopoid nor calanoid copepod biomass showed a consistent response to the fish stocking (Supplementary material Appendix A6).

After the fish were removed, the food web in both lakes returned to high *Chaoborus* densities ($14.0 \text{ ind. } m^{-3}$, [8.7, 19.1], Fig. 3), high rotifer abundances ($7037 \text{ ind. } l^{-1}$, [4104, 11798], Fig. 3), and low cladoceran biomass ($12.9 \mu g l^{-1}$ [1.9, 27.1], Fig. 3). However, a complete recovery did not occur as there were several differences in the food web states between the pre- and post treatment periods (Fig. 2, 3, Table 2). After the fish removal, phytoplankton biomass remained as

low as during the presence of fish ($4.9 \mu g l^{-1}$, [4.0, 5.8], Fig. 3) and did not reach the high pre-perturbation values again (Fig. 2G–H). Further, the rotifer assemblage became dominated by species of the genus *Ascomorpha* and *Polyarthra*, while *Asplanchna* density remained low (Fig. 2E–F, Table 2A). Also *Bosmina* and *Ceriodaphnia* biomass was lower after than before the fish presence (Fig. 2C–D, Table 2A).

There were also differences between the lakes after fish removal. The post-perturbation community was only established in AT6 following some delay. For the first two years after the fish removal, the community configuration in AT6 more resembled the state during the perturbation period with high cladoceran, especially *Holopedium gibberum*, biomass, low rotifer abundance, and somewhat lower, especially day, *Chaoborus* density (Fig. 3, Table 2B). When classifying these two seasons as belonging to the perturbation period, the variation in the community response to fish removal is substantially lower, in particular for cladoceran and phytoplankton biomass but also for some single species (Fig. 3, Table 2B). In the following summers *Chaoborus* in AT6 increased in density but did still not return to the high pre-perturbation densities (Fig. 2). Further, the *Chaoborus* population in AT5 showed rather pronounced fluctuations, mainly caused by very high densities in 2000 and 2006 and their consequential collapse in following seasons. However, autocorrelation

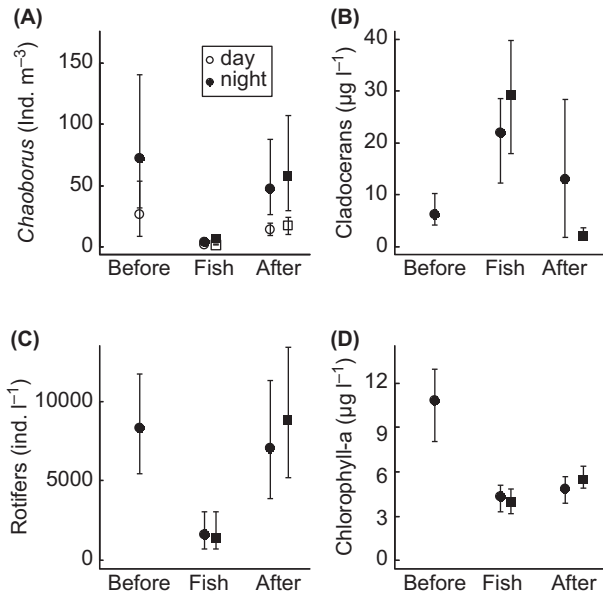


Figure 3. Arithmetic bootstrap treatment mean (dots; $n = 2$, $R = 1000$, stratified by lake) for *Chaoborus* larvae (A), cladoceran (B), rotifer (C) and phytoplankton (D) density. Error bars give the bias-corrected and adjusted 95% bootstrap confidence interval of the mean. Square symbols show the means when the first two years of the post-perturbation period in AT6 were classified as belonging to the perturbation period ('Fish').

coefficients were statistically insignificant ($p > 0.05$, standard time series analysis with fish years excluded, \log_e -transformed and detrended using splines). In AT6, the *Chaoborus* population appeared to be more stationary, especially after the perturbation (Fig. 2A–B). Also, only in AT6 calanoid copepods increased relatively and absolutely in comparison to cyclopoid copepods and the pre-perturbation period (Supplementary material Appendix A6). Finally, the large predacious cladocerans *Bythotrephes longimanus* and *Leptodora kindtii* who were previously absent, appeared in low densities in AT5 only (average across post-perturbation years: 1.4 ind. m⁻³ [1.1, 1.7] and 1.1 ind. m⁻³ [1.0, 1.2], respectively).

The community differences between pre-perturbation, perturbation and post-perturbation periods are also evident in the ordination plot. Samples within treatment periods are more similar to each other than across treatment periods (Fig. 4, Bray-Curtis index, permutation ANOVA: $F_{2,85} = 8.2$, $p < 0.001$). Treatment contrasts revealed significant differences between all communities. Since the various communities did not differ in their variability within treatments (permutation dispersion test: $F_{2,85} = 1.7$, $p = 0.208$), this result is most likely an effect of different community compositions between treatments and not due to different variability within different communities. These results were insensitive to the type of community similarity index used, whether we used geometric seasonal means or individual samplings over summer or whether the whole species set was analysed or whether the ordination was restricted to the most abundant zooplankton species (those in Table 2 plus copepods) or rotifers and mesozooplankton separately. The first two post-perturbation years after the fish removal in AT6 clustered closer to the perturbation than to the post-perturbation community. Permutation ANOVAs had

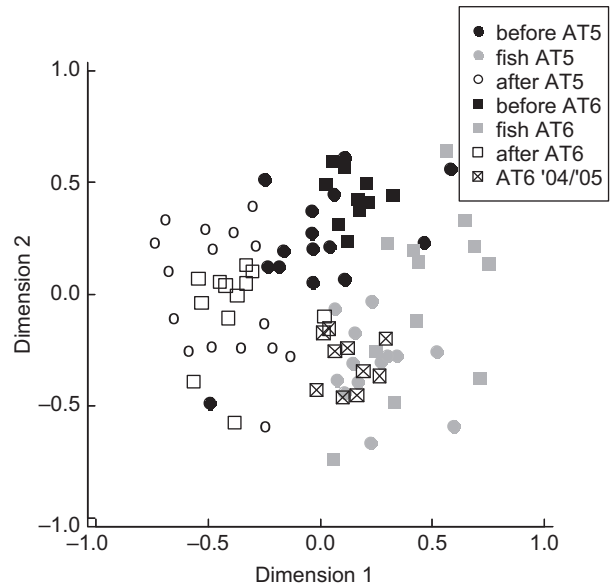


Figure 4. Ordination plot of non-metric multidimensional scaling (NMDS) based on the Bray-Curtis community similarity index. In contrast to other graphs and analyses, data are not geometric seasonal means but from individual samplings between June and September. Other indices (Euclidean, Manhattan, Jaccard) give similar results, as do ordinations based on geometric seasonal means or sub-groups of the species set. Each filling represents a different treatment period. Note how samplings of the first two post-perturbation years in AT6 (= AT6 '04/'05; crossed squares) cluster close to the perturbation years. See also Appendix 7.

consistently lower residual variance and higher R^2 -values when these years were classified as belonging to the perturbation period (Supplementary material Appendix A7).

Chaoborus density was negatively correlated with cladoceran biomass and was positively correlated with rotifer density and phytoplankton biomass (Table 3). Correspondingly, cladocerans showed a negative relationship with rotifers and phytoplankton, while rotifers and phytoplankton were positively correlated with each other. In the enclosure experiment (Fig. 5), initial reduction of mesozooplankton induced low cladoceran density, high phytoplankton and rotifer densities and led to high *Chaoborus* recruitment. In contrast, ambient cladoceran densities led to the reversed outcome, particularly to a complete *Chaoborus* recruitment failure. These results confirmed a similar pilot enclosure study in 2004 in AT6, the first fish-free season in this lake (Supplementary material Appendix A4).

Discussion

Overall patterns

In this study we have investigated the effects of a perturbation and its consecutive reversal on a pelagic size-structured zooplankton food web. We temporarily perturbed two small lakes by introducing non-reproducing fish populations and removing them again after three years. The food web in both lakes responded in a complex but consistent way to the fish introduction and to the fish removal. We could identify three distinct community states in the food web which corresponded well to the periods before, during and after the

Table 3. Correlations between zooplankton groups.

	Cladocerans	Rotifers	Phytoplankton
<i>Chaoborus</i> *	-0.65* (22) [-0.80, -0.42]	0.78* (19) [0.52, 0.89]	0.45* (22) [0.04, 0.72]
Cladocerans		-0.76* (19) [-0.92, -0.44]	-0.31 (22) [-0.60, 0.05]
Rotifers			0.57* (19) [0.24, 0.80]

Entries are the bootstrapped ($R = 1000$, stratified by lake) one-sided Pearson's product moment correlation coefficients.

Values in round brackets give the sample sizes; values in square brackets give the bias-corrected and adjusted bootstrap 95% confidence intervals of the estimated correlation coefficient. When these values do not include zero, the correlation coefficient is significantly different from zero at $* = \alpha = 0.05$.

All data were \log_e -transformed prior to analysis to linearise the relationship.

‡Data from day samplings. Night samplings give similar results.

Phytoplankton and cladocerans are in $\mu\text{g l}^{-1}$, *Chaoborus* in ind. m^{-3} and rotifers in ind. l^{-1} .

perturbation. These three food web configurations differed in the densities of *Chaoborus*, phytoplankton, rotifers, and mesozooplankton. Moreover, the three food web configurations also showed conspicuous differences in the species compositions of the latter two assemblages.

Overall, we conclude that the fish stocking as a perturbation treatment was successful. Fish consumption suppressed the *Chaoborus* population without causing a shift in *Chaoborus* species composition or a change in diel vertical migration pattern (Supplementary material Appendix A2, A3). Fish stocking led to high cladoceran density but to a reduction in phytoplankton and rotifer densities. These results are in line with the proposed trophical interactions between zooplankton groups (Neill 1988a, b) and the hypothesized simple food web in the experimental lakes (Fig. 1) as are the observed correlation patterns between zooplankton assemblages. Together these findings also imply

an indirect recruitment bottleneck in the size-structured *Chaoborus* population due to its ontogenetic niche shift from feeding on rotifers to feeding on cladocerans (Neill 1985, Moore 1988, Persaud and Dillon 2010). This view is further supported, independently and more directly, by the results of the enclosure experiment where only initial reduction of cladoceran mesozooplankton allowed high rotifer densities and successful recruitment of *Chaoborus*.

However, despite these findings and in contrast to our and Neill's (1988a, b) expectations, the food web configuration that established during the perturbation period did not last after the perturbation was relaxed by removing the fish. Neither did the food web completely recover to the pre-perturbation state despite the return to the pre-perturbation environment. Instead, a post-perturbation food web configuration developed (immediately in AT5, but delayed for two seasons in AT6) that differed from the pre-perturbation community in two aspects. First, phytoplankton did not recover to the pre-perturbation density but instead remained as low as during the fish presence and about half of the pre-perturbation biomass. Second, while the combined density of all rotifers reached pre-perturbation levels again, the assemblage was now dominated by another functional group of rotifers. From species with spines, hard shells or colonies such as *Kellikottia*, *Keratella*, and *Conochilus*, respectively, the rotifer assemblage shifted to dominance by soft-bodied, solitary species of the genera *Ascomorpha* and *Polyarthra*.

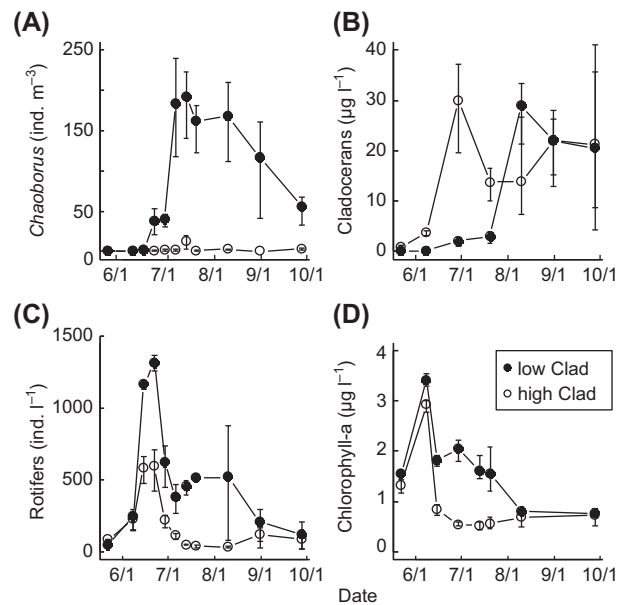


Figure 5. Density of *Chaoborus* larvae (A), cladocerans (B), rotifers (C) and phytoplankton (D) over the ice-free period of 2005 in enclosures placed in AT6 with (filled dots) and without (open dots) initial exclusion of mesozooplankton. Symbols show the arithmetic bootstrap mean ($n = 3$, $R = 1000$) for each date. Error bars give the bias-corrected and adjusted 95% bootstrap confidence interval of the mean.

Explanations for differences between pre- and post-perturbation communities

It may be argued that the observed shift in rotifer species assemblage is of limited relevance for the overall food web configuration as the total rotifer density was similar before and after the perturbation (but see below). However, the fact that phytoplankton biomass after the perturbation remained low in both lakes cannot be regarded as a minor effect. It rather indicates a major difference in community dynamics and its structuring trophic interactions between pre- and post-perturbation periods. This change in phytoplankton biomass in combination with the shift in overall, especially rotifer, community structure therefore leads us to conclude that the periods before and after the fish stocking represent contrasting communities. Below we explore three explanations for these differences in food web states.

First, the development of the post-perturbation state may be a successional phenomenon or a bottom-up effect related to temporal changes in abiotic environments (possibly carry-over effects arising from the fish stocking) as one may criticise our study for not having a real control. We attempted to create a control while keeping a sample size of two by staggering the fish introductions and removals between lakes. The absent impact of perch introduction on the *Chaoborus* population in AT6 in 2000 and the simultaneous collapse of the *Chaoborus* populations in 2001 in both lakes counteracted this. However, we argue that the collapse of *Chaoborus* in AT6 was caused by the rainbow trout introduction in May that year, while the collapse in AT5 was related to the previous year's high *Chaoborus* density.

Abiotic factors that may have induced the community shift through altered bottom-up effects are 1) slightly higher water temperatures during the post-perturbation period or 2) different nutrient regimes. For several reasons, we consider these unlikely explanations: the temperature difference was small (Table 1) and also in cool years during the post-perturbation period (e.g. 2008, Supplementary material Appendix A1A) did the rotifer assemblage not change despite high population growth rates of these fast reproducing animals. Total nitrogen was somewhat lower during the post-perturbation period (Table 1, Supplementary material Appendix A1F) but it is difficult to assess whether this is a cause or a consequence of the community shift since different nutrient recycling of different plankton communities can effect nutrient regimes (Elser et al. 2000). The fact that nitrogen only decreased after fish were removed and the new community had had established suggests the latter. While fish stocking seems to have slightly increased total P concentration, this effect did not last after fish removal (Table 1). Also, in later years both lakes were out of synchrony (e.g. delay in post-perturbation community establishment, *Chaoborus* population fluctuations). This further renders bottom-up explanations for the difference in communities unlikely which involve a biotic succession or changes in abiotic conditions as these would have been spatially auto-correlated. We thus conclude that the different food web configurations result from changes in local trophic interaction patterns and are not due to bottom-up effects.

Second, the post-perturbation food web state may be a transient phase in food web dynamics before the communities will return to the pre-perturbation state. However, the post-perturbation community in terms of rotifer densities and phytoplankton biomass has been sustained for many generations. In terms of *Chaoborus* life span it lasted for four generations in AT5 and for three generations in AT6. Note also that differences in relative abundances of species between years were conspicuously lower than between treatment periods. Connell and Sousa (1983, see also Scheffer and Carpenter 2003, Schröder et al. 2005) suggested that in order for a community to be judged as stable it should stay unchanged for more than the life spans of the species involved. Black and Hairston (1988) argued that communities are stable when there are few appearances or disappearances of species. Using these criteria, we regard the interpretation of the post-perturbation food web configuration as a transient phase as unlikely. We acknowledge that transitory dynamics can last for long times and ecosystems can hence still change quite a while after perturbations are reversed (van Geest et al.

2007). Nonetheless, in studies showing long transients after perturbations the slow recoveries to the pre-manipulation states were either due to a gradual return to the driving environmental abiotic (pH after artificial acidification; Frost et al. 2006) or biotic (planktivory after fish restocking; Carpenter and Kitchell 1993) conditions or due to the long life spans of the organisms involved (fish in Meijer et al 1999, shrubs in Valone et al. 2002).

Third, the observed dynamics can be explained by that the post-perturbation community with its low phytoplankton and its distinct microzooplankton assemblage represents an alternative stable food web configuration to the pre-perturbation community. Similar, Houseman et al. (2008) report the formation of three distinct grassland communities in response to one-time vegetation removal. But contrary to our findings, this occurred only when the environment had permanently been altered by constant high fertiliser input. Note also that the perturbation community in the presence of fish is not alternative (even if it may or may not be stable) because the temporary introduction of non-reproducing fish constitutes a fundamental change in the lake environment.

If one follows this last interpretation, the question arises which mechanisms may maintain each state. We propose the following scenario. The pre-perturbation state is, in line with our original hypotheses, regulated by *Chaoborus* predation on cladoceran zooplankton. Low cladoceran density freed *Kellicottia longispina*, *Keratella* sp. and *Conochilus* from competition for phytoplankton. These species have morphological anti-predator defence mechanisms in form of spines, hard shells or colonies whose costly defences may need high food levels (Harvell 1990). The dominance of these well-defended rotifers was maybe related to the high density of the predatory rotifer *Asplanchna* which feeds on other rotifers. *Chaoborus* consumption of rotifers seems not to be affected by these defence mechanisms. High rotifer densities fed back to high recruitment of *Chaoborus* larvae. During the presence of fish whose consumption led to the exclusion of *Chaoborus* and thus low predation pressure on mesozooplankton, cladocerans and especially *Holopedium gibberum* increased in density. The small-bodied cladocerans *Bosmina* and *Ceriodaphnia* did not respond as strongly to the absence of *Chaoborus* because the larger *Holopedium* suppressed phytoplankton densities below the smaller species' minimum resource requirements. Filtration rates and thus competitiveness among cladocerans are often positively correlated with body size (Chow-Fraser and Knoechel 1985, Gliwicz and Lampert 1990). The low phytoplankton and high cladoceran biomass also limited rotifers to low densities. The low phytoplankton biomass during the fish presence could have supported *Ascomorpha* and *Polyarthra* as it did after fish removal. But note that cladocerans can limit rotifers not only by exploitative competition but also through physical interference (Gilbert 1988). The mechanism maintaining the post-perturbation community, characterised by low cladoceran but also low phytoplankton biomass is more difficult to explain. In full apprehension that it is based more on first principles than it is substantiated by independent data we find the following mechanism conceivable: the low phytoplankton biomass that resulted from the high grazing pressure during the perturbation period kept the well defended but high food levels requiring rotifers out. Simultaneously, it allowed more competitive but less defended rotifers like the

soft-bodied species of *Ascomorpha* and *Polyarthra* to increase once *Chaoborus* returned and cladoceran densities collapsed. High rotifer densities in turn benefitted further *Chaoborus* recruitment and detrimentally affected cladocerans further. It is unclear why *Asplanchna* (if it indeed played a role) did not come back and shifted the rotifer assemblage back to dominance by the defended functional group.

Effects of spatial scale and lake differences in response

The enclosure experiment supported the mechanisms proposed by Neill (1988a, b) for the presence of two alternative stable states in the *Chaoborus* system. Specifically, it demonstrated on a within-generation time scale that the indirect juvenile recruitment bottleneck can operate in principle. The lake experiment however implies that on a long-term, between-generation time scale and on a whole-ecosystem level, including the emergence of *Chaoborus* out of and their re-dispersal into the lakes this may not be the case. After fish removal, *Chaoborus* returned to high densities again. Micro- and mesocosm experiments with their simplified spatio-temporal scale are often well-mixed systems. In contrast, whole ecosystems are usually much more heterogeneous in space and over time. Such spatio-temporal heterogeneity can influence trophic interactions by violating the mass balance assumption. Sarnelle (1997), for example, demonstrated ecosystem size dependent trophic interactions and food web responses between enclosures of different sizes and lake studies. We therefore argue, as others did before us (Carpenter 1996, Sarnelle 1997), for caution when extrapolating ecosystem responses based on results from short-term, small-scale studies. Note also how difficult it can be to unravel the full dynamical potential of ecosystems with such experiments (Schröder 2008).

As mentioned above the two lakes differed in that the new post-perturbation community established directly following the perturbation relaxation in AT5 whereas this happened with a delay in AT6. The enclosure experiment showed that communities in the control enclosures with a *Chaoborus* recruitment failure corresponded well to what was observed in the whole lake AT6 for the first two years after fish removal, i.e. during the delay in the establishment of the new post-perturbation community in this lake. In AT6 cladoceran mesozooplankton remained high for two years after the fish were removed with correspondingly low phytoplankton and rotifer densities and with somewhat lower *Chaoborus* densities than in later years. Since in both years, *Chaoborus* readily recruited to enclosures in this lake when cladocerans were excluded, dispersal limitation can be ruled out as a cause for this pattern. Because of its short duration (two generations of *Chaoborus*; the absolute minimum of Connell and Souza's (1983) criterion) we regard this delay period as a transient phase before the shift to the new community state occurred. However, given that this 'delay' community resembled the control enclosure communities with their operating bottleneck and so strikingly matched our hypothesis, it may actually represent the alternative stable state proposed by Neill (1988 a, b). This state may have a low resilience, i.e. low capacity to withstand environmental change (Holling 1973), explaining its short duration and restriction to one lake only.

Concerning the observed population fluctuations in *Chaoborus*, time series analysis did not support any cyclic dynamics. Also, since no connection between community state and *Chaoborus* population dynamics was found (the post-perturbation food web established in both lakes despite potentially contrasting *Chaoborus* population dynamics) we argue that for the questions raised in this study population oscillations are of low interest and we therefore focused instead on the overall community dynamics.

General conclusions and remarks

Manipulation experiments employing temporary perturbations as means to assess food web dynamics have still only been rarely applied on the scale of whole ecosystems and have led to different, contrasting outcomes. This is especially true for studies running long enough to assess the stability of community states. While some whole ecosystem experiments have reported direct recovery of pre-perturbation states (Ives et al. 1999, Mittelbach et al. 2006), others have reported delayed returns to it (Meijer et al. 1999, Frost et al. 2006). Others again have demonstrated the persistence of the state that established during the perturbation period upon the reversal of a perturbation (Schmitz et al. 2006, Persson et al. 2007). So far, ecologists have mainly focused on this dichotomy between recovery and non-recovery (Scheffer et al. 2001, Suding et al. 2004, Schröder et al. 2005). We have here proposed a third alternative: The post-perturbation food web in our lakes developed to a state distinct from the one before the perturbation, something that has rarely been considered so far. It thus becomes more and more evident that the responses of food webs and ecosystems to environmental disturbances can be much more complex than is often recognized. These responses can involve many different dynamics, such as instantaneous (Mittelbach et al. 2006) or delayed recovery (Frost et al. 2006), complete state recovery failure (Schmitz et al. 2006, Persson et al. 2007), intermittent state shifts (Blindow et al. 1993), regular state fluctuations (Ives et al. 2008) and, as we argue here, establishment of distinct alternative stable post-perturbation states.

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