

Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes

B. Wissel¹ and W. J. Boeing²

Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803

C. W. Ramcharan³

School of the Coast and Environment, Louisiana State University, Baton Rouge, Louisiana 70803

Abstract

Northern temperate lakes often have high water color because of high concentrations of dissolved organic carbon (DOC). Altered light, temperature, and oxygen profiles in these brown-water lakes should reduce the foraging abilities of planktivorous fish and reduce predation on zooplankton and invertebrate predators such as *Chaoborus*. Additionally, reduced diurnal vertical migration should limit exposure to cold temperatures and increase zooplankton growth rates. We hypothesized that, with increasing water color, *Chaoborus* would become more important, and this change would be followed by a shift in the zooplankton assemblage toward larger species. To test this hypothesis, we carried out a $2 \times 2 \times 2$ factorial enclosure study to examine the effects of high and low color and the presence and absence of both fish and *Chaoborus* on zooplankton assemblages. We also analyzed the zooplankton community structure of two lakes with similar morphometry and fish composition but very different water color. Both studies showed that, in highly colored water, *Chaoborus* was more abundant and the zooplankton community shifted from small species, such as *Bosmina* and small copepods, to large species, such as *Daphnia* and *Holopedium*. Concurrently, the food web structure changed from top-down control to intraguild predation. Because not only the physical habitat differs between clear- and brown-water lakes, but also the predation regimes and food web structure, we conclude that brown-water lakes are a distinct lake type.

The humic compounds of DOC are the major factor controlling water color in lakes (Thurman 1985; Pace and Cole 2002). DOC concentrations vary from 0.5 to 20 mg C L⁻¹, enough to span the range from crystal clear to darkly tea-colored waters. Elevated levels of DOC (>5 mg L⁻¹) are typical for many northern temperate lakes. A study including more than 1,000 Finnish lakes revealed that >80% had DOC concentrations >5 mg L⁻¹ (Kortelainen 1993). The proportion of lakes with elevated DOC in the northeastern United States and Ontario, Canada, is about 40% (Carter et al. 1980; EMAP 1996).

Attenuation of light by DOC could be detrimental to fish planktivory in two ways: low light could directly interfere with visual foraging by planktivorous fishes, and DOC could

also enhance a refuge within which zooplankton can avoid fish. Reduced light intensities are well known to decrease both the reactive distance of planktivorous fish (Vinyard and O'Brien 1976; Wright et al. 1980) and their overall predation rate (Persson 1986; Bergman 1987). At adequate light levels, planktivorous fish select larger, more visibly conspicuous prey (Brooks and Dodson 1965; Taylor 1980), but in dim light, they lose their ability for size-selective predation (Janssen 1980).

By absorbing light, DOC could also enhance a refuge for zooplankton from fish. In many lakes, zooplankton undergo diurnal vertical migration (DVM). During the day, they hide from visual predators by remaining in deeper, darker waters but rise at night to feed in more alga-rich surface waters (Zaret and Suffern 1976; Gliwicz 1986; Ringelberg 1991). The cost of this defense against fish is that deeper waters are colder. Zooplankton egg development, and therefore population growth rate (r), is critically dependent on water temperature, and a prolonged time period spent in the cold hypolimnion reduces r (Bottrell et al. 1976). With the high rate of light absorption found in high-DOC lakes, the metalimnion and even the epilimnion might have areas of dark but warm water. Zooplankton might be able to remain in warmer water with more abundant algal food, while still protected from fish. Perhaps for these reasons, the extent of DVM is reduced in water that is less clear (Dodson 1990).

DOC absorbs infrared light, which can lead to a shallower and warmer epilimnion and a colder hypolimnion (Fee et al. 1996; Snucins and Gunn 2000). Moreover, the hypolimnia of high-DOC lakes tend to have lower oxygen levels than clear lakes, making them less accessible to fish. Oxygen levels are reduced in colored lakes partly because bacterial pro-

¹ To whom correspondence should be addressed. Björn Wissel, Coastal Ecology Institute, Louisiana State University, 1243 ECE Building, Baton Rouge, Louisiana 70803 (bwissel@lsu.edu).

² Present address: University of Washington, Joint Institute for the Study of Atmosphere and Oceans, Seattle, Washington 98195.

³ Present address: Department of Biology, Laurentian University, Sudbury, Ontario P3E 2C6, Canada.

Acknowledgments

We thank Joelle Young, Emily Hyfield, Amanda Logue, Shannon Allen, Zoraida Quiñones, Kenyatta Esters, and Michelle Menard for assistance in the field and laboratory. Howard Riessen, Norm Yan, Peter Dillon, and Mark Ridgway were helpful with the experimental design and in locating field sites. We are grateful to the Ontario Ministry of Natural Resources, the Algonquin Provincial Park, and the Algonquin Fisheries Assessment Unit, who gave us the opportunity to perform the experiments and let us generously use their resources. Finally, we thank Barry Moser for helping with the statistical analysis and two anonymous reviewers for their comments.

duction is enhanced by DOC (Hessen and Andersen 1990; Arvola et al. 1996) and also because rapid warming in the spring causes these lakes to stratify early, before water mixing can replenish oxygen levels in the hypolimnia. Hypoxia is restrictive to fish but not most zooplankton. Therefore, the hypolimnia of high-DOC lakes could provide refugia for zooplankton against fish predation because they are both too dark for fish feeding and too low in oxygen for fish survival.

Unfortunately for the zooplankton, the same conditions that make high-DOC lakes favorable for avoiding fish predation also make them better environments for supporting large invertebrate predators. Planktonic macroinvertebrates such as larvae of the phantom midge *Chaoborus* (Chaoboridae, Diptera) are voracious predators of zooplankton, often playing as important a role as fish in zooplankton population dynamics (Kajak and Rybak 1979; Johannsson et al. 1994; Ramcharan et al. 2001a,b). Because chaoboridae are large and conspicuous, these predators are themselves favored prey of planktivorous fishes, and they typically employ DVM to avoid fish just as smaller zooplankton do (Stenson 1980; Rahel and Nutzmam 1994). In high-DOC lakes, invertebrate predators would have the same benefits as their zooplankton prey: faster development time and a low-oxygen hypolimnetic refuge from fish.

If elevated levels of DOC do interfere with fish planktivory, then large invertebrate predators should enjoy a double advantage. In high-DOC lakes, not only should predation from fish be relaxed, but also competition from fish for zooplankton prey. Most invertebrate predators are tactile, not visual, hunters, and unlike fish, they do not rely on light to detect prey (Giguere 1980).

With their different feeding modalities, the two types of planktivores—fish and invertebrates—exert divergent selective pressures on zooplankton communities. In general, planktivorous fish feed on the largest, most visibly conspicuous prey, mainly invertebrate predators and large cladocerans and copepods, resulting in a zooplankton community dominated by small zooplankters such as *Bosmina* and rotifers (Brooks and Dodson 1965; Taylor 1980; Wissel and Benndorf 1998). Invertebrate predators are gape limited and, in some cases, handling limited. Although some large species of invertebrate predators can consume the same sizes of zooplankton prey that fish eat, these prey are not preferred (Pastorok 1981). In contrast to fish, invertebrate predators mostly consume small- to medium-sized prey (Taylor 1980; Riessen et al. 1988), and zooplankton communities subjected to heavy invertebrate predation are commonly dominated by large-bodied species (Riessen et al. 1988).

Because of the effects of DOC on vertical gradients of light, temperature, and oxygen, we hypothesize that the effect of planktivorous fishes on zooplankton communities should be strongest in clear lakes. As a result, invertebrate predators should be relatively unimportant, and the zooplankton of clear-water systems might be mostly rotifers, small-bodied cladocerans, and copepods. In colored lakes with high levels of DOC, feeding by planktivorous fish should be impaired. Invertebrate predation should then be the dominant force structuring the zooplankton community. Large-bodied zooplankton such as daphnids and large copepods should be prevalent. Thus far, some of the strongest

effects of invertebrate predation have been found in brown-water lakes (Carpenter et al. 1985; Ramcharan et al. 2001c).

To test the hypothesis that DOC has important effects on fish planktivory, we performed an enclosure study and also made use of data from a whole-lake fish manipulation experiment. The goals of this study were (1) to determine whether water color influences the relative importance of fish and *Chaoborus* as planktivorous predators and (2) to investigate the effects of DOC-mediated changes in predation regimes on zooplankton community composition. We chose two lakes for the enclosure study that were similar in morphology and water chemistry, but contrasted in water color. Longairy Lake had clear water, whereas Clarke Lake was colored. In each lake, enclosure treatments were set up with and without planktivorous fish and with and without *Chaoborus*. We also took advantage of a previous whole-lake experiment, wherein all fish had been removed and just a single species restocked in two lakes that were otherwise similar but contrasted greatly in their water color. Analysis of species composition of zooplankton and *Chaoborus* in these two lakes allowed us to study the influence of DOC on planktivory regime in natural systems.

Methods

Enclosure study—The enclosure study was conducted in the summer of 2000 in two lakes (45°32'N, 78°32'W) with contrasting water color located in Algonquin Park, Ontario, Canada. Longairy Lake had clear water, whereas Clarke Lake had brown water. The lakes were <1 km apart and had similar morphology and water chemistry (Table 1). In particular, values for total phosphorus and pH, two parameters that often differ between clear and colored lakes, were nearly identical in our study lakes. As would be expected from its high levels of DOC, Clarke Lake had lower Secchi depths and higher water color than Longairy Lake.

Each enclosure was made of transparent non-UV-coated polyethylene with a diameter of 1 m and a length of 8 m. They were suspended in the water column from a floating wooden frame anchored at the 10-m isopleth in each of the lakes. The top of each enclosure was 0.5 m above the water level, and the bottom was sealed and anchored to the lake bottom. The enclosed water column was approximately 7 m deep with a volume of 5,500 liters.

The predators chosen for our experiments were golden shiner (*Notemigonus crysoleucas*) and *Chaoborus trivittatus*, and the enclosures were initialized within the upper range of natural predator levels (fish, 40 kg ha⁻¹; *Chaoborus*, 0.3 individual L⁻¹). Golden shiner was chosen over northern redbelly dace, pumpkinseed, and yellow perch because this species had the highest survival rates in a preliminary experiment that we conducted using enclosures suspended in a moderately stained lake (Boeing and Wissel unpubl. data). *C. trivittatus* is the largest chaoborid that co-occurs with fish. Chaoborids this large typically have strong effects on the species composition and biomass of a wide range of prey (e.g., Arnott and Vanni 1993; Ramcharan et al. 2001b), which we thought would enhance our ability to detect the signal of invertebrate predation in a short duration experi-

Table 1. Characteristics of study lakes. Longairy Lake (clear water) and Clarke Lake (brown water) were the site of enclosure experiments carried out during the summer of 2000. Cecil Lake (clear water) and Bena Lake (brown water) were voided of fish in spring 1999 and subsequently restocked with equal amounts of brook trout. For these latter two lakes, water color and Secchi depth values are given for both July 1999 and June 2000.

	Longairy Lake	Clarke Lake	Cecil Lake	Bena Lake
Area (ha)	28.3	25.3	15.8	12.6
Maximum depth (m)	17.4	11.3	16.2	10.2
Mean depth (m)	6.0	5.3	—	—
pH	6.8	6.4	—	—
Total phosphorus ($\mu\text{g L}^{-1}$)	13.2	12.3	—	—
Color (PTU)	20	53	16/24	75/86
Secchi depth (m)	2.5	5.0	4.5/2.7	2.0/1.5

ment. Furthermore, if a species this large were found to survive well with fish in water conditions of high color, smaller chaoborids should be affected even less by fish predation. Three replicates of this $2 \times 2 \times 2$ factorial design (Color \times Fish \times Chaoborus) resulted in a total of 24 enclosures.

Ten days prior to the experiment, the enclosures were filled using a fire pump directed through a 200- μm mesh. After temperature stratification was established (3 d), we collected a mix of the natural zooplankton communities from both study lakes by taking an equal number of vertical net hauls (7 m to surface) in each lake with a plankton net (130- μm mesh size). The sampled volume of water represented the combined volume of all 24 enclosures. Subsequently, equal aliquots of the zooplankton mix were added to each enclosure. The zooplankton was allowed to acclimate and grow for 1 week before predators were added. *Chaoborus* was added to the enclosures 1 d prior to fish to allow chaoborids to distribute vertically and avoid artificially high predation losses to fish.

Every 8 d for about 6 weeks, we sampled the zooplankton with a closing net (inside diameter (\emptyset) 30 cm, 130- μm mesh size) deployed at three depth intervals (0–3, 3–5, 5–7 m). Prior to zooplankton sampling, we took temperature and oxygen profiles as well as Secchi depth readings. Day/night distribution of the zooplankton (on days 16 and 40 since the start of the experiment) and chlorophyll *a* (Chl *a*) and total phosphorus (TP) were determined twice (days 8 and 32). The sampling order for the two lakes was random; Clarke Lake (high DOC) was sampled first on days 0 and 24.

Zooplankton and *Chaoborus* samples were preserved in 4% sugar-saturated formalin (Haney and Hall 1973), identified to species (Brooks 1957; Saether 1970), and enumerated under a dissecting microscope. For cladocerans and copepods, we distinguished between large (>1 mm length) and small individuals (<1 mm length). Within each size class, we measured approximately 10 individuals/species and used published estimates of species-specific weights provided by Bottrell et al. (1976) in order to calculate biomass. Because the biomass estimate was based on a low number of individuals, we performed all statistical analyses solely on abundances.

Water color was measured as absorbance at 440 nm (Cuthbert and del Giorgio 1992) and expressed in cobalt platinum units (PTU). For Chl *a* and TP determination, we randomly selected two of the three replicates per treatment (time con-

straints due to sample filtering immediately after collection did not allow us to use all three replicates). We used a pump sampler to collect 0.5 liters of the upper (0–3 m) and lower (3–7 m) part of each enclosure. After separating the edible (<30 μm) and inedible fractions (>30 μm) with a Nitex mesh, both fractions were filtered through GF/C filters and extracted overnight in 100% acetone, and Chl *a* concentration was measured fluorometrically. Total phosphorus was analyzed according to standard methods by the Ontario Ministry for the Environment (OME 1984). To ensure comparable fish biomass in all fish treatments throughout the experiment, every 4 d, we verified fish survival using a submersible video camera and a large 1-m-diameter net (0.5-cm square mesh). Whenever dead fish were discovered, they were removed and replaced immediately. After the second sampling date (day 8), we added small amounts of phosphorus and nitrogen (5 $\mu\text{g P L}^{-1}$, N:P ratio 30:1) to each enclosure to counterbalance nutrient depletion from sedimentation.

Lake study—Enclosure experiments are a valuable tool in aquatic sciences to test hypotheses under fairly natural but controlled conditions without sacrificing replication. Nevertheless, any mesocosm is an abstraction of nature with compromises in terms of species diversity, time, and habitat characteristics. For these reasons, patterns found in mesocosm studies are more convincing when verified with whole-lake experiments (Carpenter 1989). The Algonquin Fisheries Assessment Unit (AFAU) had selected two lakes of similar morphometry (Cecil and Bena Lakes; Table 1) in order to study different methods of sampling fish. Fortunately, these two lakes strongly differed in water color. In spring 1999, both lakes were fished to depletion with several types of gear and then restocked with brook trout (*Salvenius fontinalis*), an opportunistic feeder on benthos, zooplankton, and small prey fish (Scott and Crossman 1973). After the experiments involving fishing gear, both lakes remained undisturbed and their remote location in the interior of Algonquin Park prevented recreational fishing and other human influences.

In July 1999 and June 2000, we used a closing net (\emptyset 30 cm, 130- μm mesh size) to collect zooplankton from the epi-, meta-, and hypolimnia at the location of maximum depth of both lakes. Measurements of temperature, oxygen, and Secchi depth, as well as processing of samples, were carried out as described above for the enclosure experiments.

Table 2. Main effects and interaction p -values (three-way ANOVA, SAS version 8) for Secchi depth (m), temperature ($^{\circ}\text{C}$), and oxygen (mg L^{-1}) at 1 and 5 m for the first five sampling dates of the enclosure study performed in summer 2000. Secchi depth values for the first sampling date were not available. Results for main factors and interactions with $p > 0.05$ are omitted.

	1	2	3	4	5
Secchi depth					
Color		0.0001	0.0001	0.0001	0.0001
Fish		0.004	0.02	0.01	0.0001
Color \times Fish		0.04	0.01	0.006	n.s.
Temperature					
Color (1 m depth)	0.0001	n.s.	n.s.	0.0001	0.0002
Color (5 m depth)	0.0001	0.0001	0.0001	0.0001	0.0001
Oxygen					
Color (1 m depth)	0.0001	n.s.	n.s.	n.s.	0.0002
Color (5 m depth)	0.0001	0.0001	0.0001	0.0001	0.0001

Data analysis—To test for both main and interaction effects in the enclosure experiments of the factors Color (clear-water Longairy Lake or dark-water Clarke Lake), Fish, and Chaoborus on the zooplankton assemblage, we performed three-way multivariate analyses of variance separately for each sampling day. The abundances of zooplankton were first grouped into different taxa (*Daphnia*, *Holopedium*, *Bosmina*, small copepods, large copepods, and *Asplanchna*) before being used as independent variables. Other taxa were only found at negligible abundances. We used the Wilk's lambda test for the zooplankton assemblages and an F -test for the individual groups. To analyze the effects of the experimental treatments on water temperature, oxygen concentration, Secchi depth, Chl a , and total phosphorus, we performed three-way analyses of variance for the appropriate sampling dates. For both temperature and oxygen, we limited the analysis to the depths of 1 and 5 m. In the whole-lake experiment, we tested for differences in zooplankton composition between the lakes using a paired t -test (1999 vs. 2000). We limited our analysis to the abundance of large cladocerans (*Daphnia* and *Holopedium*), small to medium cladocerans (*Bosmina* and *Diaphanosoma*), copepods, and *Chaoborus*, since other taxa were uncommon to rare.

Results

Enclosure study—Between days 32 and 40, we observed filamentous algae on the enclosure walls, which affected sample collection and light regime of the enclosures. At the same time, crustacean zooplankton showed a strong decline independently of treatments. Therefore, we omitted the last sampling date and restricted all analyses to the first five sampling dates, covering a total of 32 d.

The physical environments within the enclosures closely matched the conditions found in the respective lakes, which also means that the conditions within the clear and high-DOC enclosures contrasted strongly. Throughout the experiment, water transparency was significantly reduced in the treatments with high color (high color treatments) compared

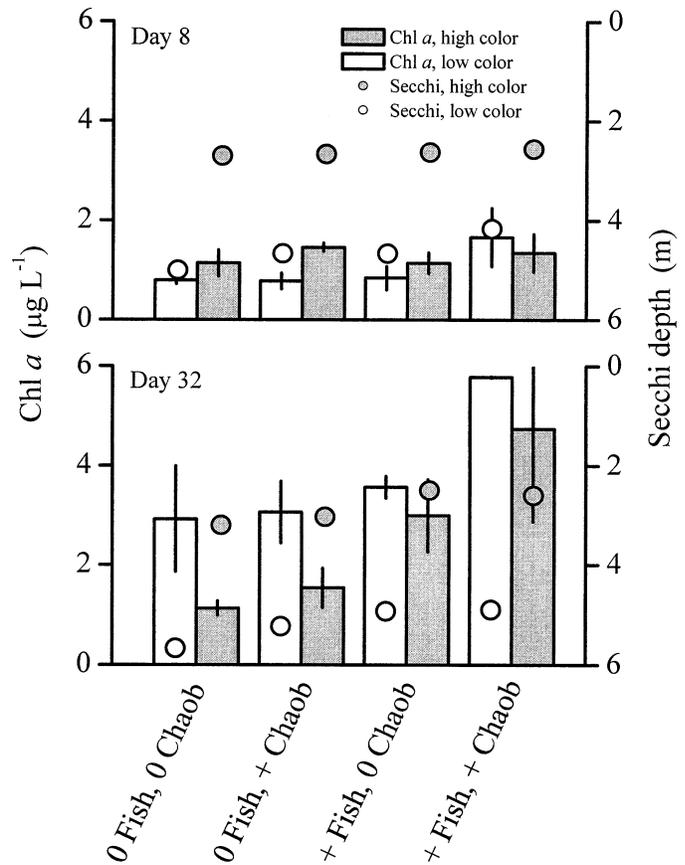


Fig. 1. Values for Chl a (mg L^{-1} , vertical bars) and Secchi depth (m, circles) in the different enclosure treatments. The upper and lower panels show 27 June and 21 July, respectively. Symbols for enclosures from the high color lake are shaded, whereas those from the clear lake are open. Each value is the mean for three replicate enclosures. Error bars for Chl a indicate one standard deviation. Error bars for Secchi depth do not appear because they are smaller than the diameter of the plot symbol.

to the low color treatments (Table 2; Fig. 1). Although Secchi depth varied between 3.5 and 5.8 m in low color treatments, it ranged from 2.4 to 3.5 m in high color treatments. Most of this variation in water transparency was explained by Color. Additionally, we detected a significant Fish effect, where the presence of fish resulted in reduced Secchi depth; this effect was less pronounced in high color enclosures (significant Fish \times Color interaction). The only significant differences in vertical gradients of temperature were associated with Color (Table 2, Fig. 2). At 5 m, the temperature in high color treatments was consistently cooler by several degrees C than in low color treatments. This effect could be observed at depths < 2 m throughout the experiment (Fig. 2). The differences at 1 m depth were probably related to the order in which the two lakes were sampled, with higher temperatures for the lake that was visited last. Oxygen concentrations were generally lower in high color enclosures (Table 2; Fig. 2). Although this pattern was pronounced at a depth of 5 m, at 1 m, we found significantly lower oxygen concentration in high color treatments only on two out of five sampling dates.

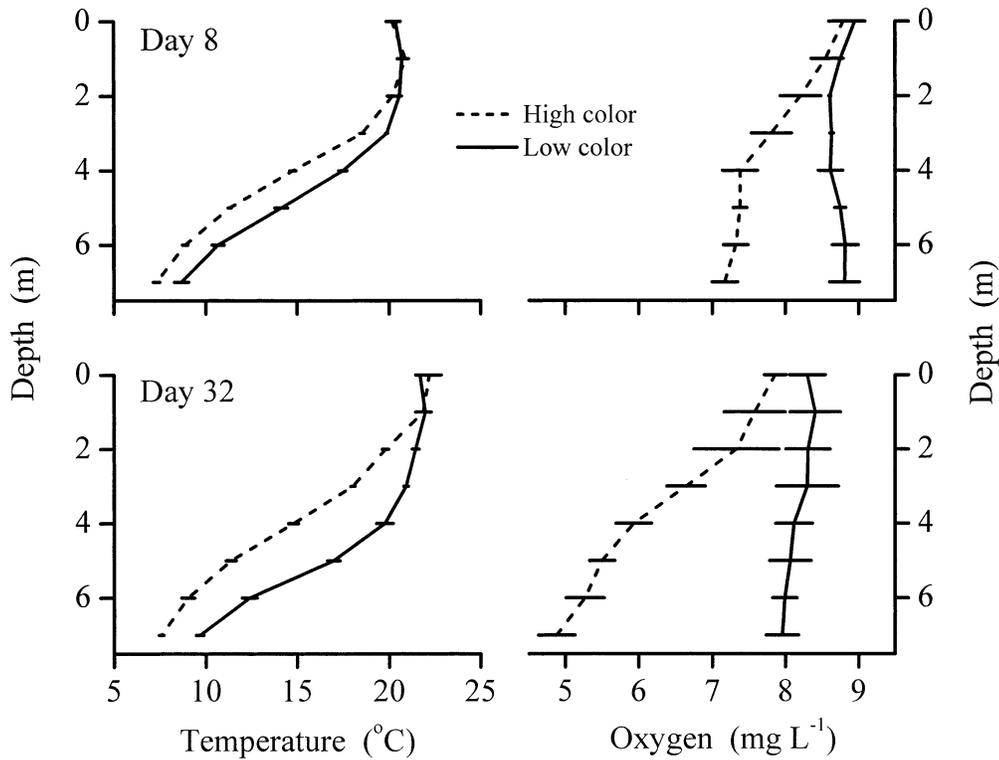


Fig. 2. Vertical distribution of temperature ($^{\circ}\text{C}$, left panels) and oxygen (mg L^{-1} , right panels) in enclosures from the low and high color lakes. Profiles for the different predator treatments were so similar that the values for each depth were averaged (all three replicates); the horizontal error bars represent one standard deviation. The upper and lower panels show 27 June and 21 July, respectively.

There were no significant differences in total phosphorus (TP) among treatments (Table 3). TP concentrations were $11.0 \pm 1.1 \mu\text{g L}^{-1}$ and $14.2 \pm 1.2 \mu\text{g L}^{-1}$ for days 8 and 32, respectively. The slight increase between sampling dates shows that our addition of $5 \mu\text{g L}^{-1}$ successfully prevented nutrient depletion and kept the enclosures at a mesotrophic state.

Chl *a* concentrations increased approximately threefold from day 8 to day 32 (Fig. 1). The majority of Chl *a* was

contained in the edible fraction ($<30 \mu\text{m}$), supplying 80 and 90% of the total Chl *a* on days 8 and 32, respectively. The relative importance of the upper layer (0–3 m) and lower layer (3–7 m) did not differ enough among either treatments or sampling dates to be statistically significant. Yet, in low color treatments, the deeper layer supplied about 60% of the total Chl *a*, whereas in high color treatments, this portion was reduced to 40%, likely because of light limitation. Because we did not find significant differences between the two layers, we used depth-weighted average Chl *a* concentration of each enclosure for further analyses. The large, inedible fraction slightly increased from day 8 to 32, but no significant treatment effects were found for any of the sampling dates (Table 3). The smaller, edible fraction showed a much more pronounced increase from days 8 to 32, and we detected significant increases in Chl *a* concentrations due to Fish and Chaoborus for day 32.

Table 3. Main effects and interaction *p*-values (three-way ANOVA, SAS version 8) for total phosphorus ($\mu\text{g L}^{-1}$) and edible fraction ($<30 \mu\text{m}$) Chl *a* ($\mu\text{g L}^{-1}$) for sampling dates two and five of the enclosure study performed in summer 2000. No significant effects were found for the inedible fraction ($>30 \mu\text{m}$). Results for main factors and interactions with $p > 0.05$ are omitted.

	2	5
Total phosphorus		
Color	n.s.	n.s.
Fish	n.s.	n.s.
Chaoborus	n.s.	n.s.
Chl <i>a</i>		
Color	n.s.	n.s.
Fish	n.s.	0.007
Chaoborus	n.s.	0.04

Initial zooplankton densities were very similar for all treatments and ranged from 1.0 to 2.0 individuals L^{-1} . Final densities, however, varied tenfold, from 2.0 to almost 20 individuals L^{-1} , depending on treatment (Fig. 3). The overall most abundant organism was *Bosmina*, but occasionally *Asplanchna* and small copepods were plentiful as well. In terms of biomass, enclosures were either dominated by large cladocerans (*Daphnia galeata mendota*, *D. dubia*, *Holopedium gibberum*) or smaller zooplankton (*Bosmina longirostris*, small copepods, *Asplanchna priodonta*) (Fig. 4). *Dia-*

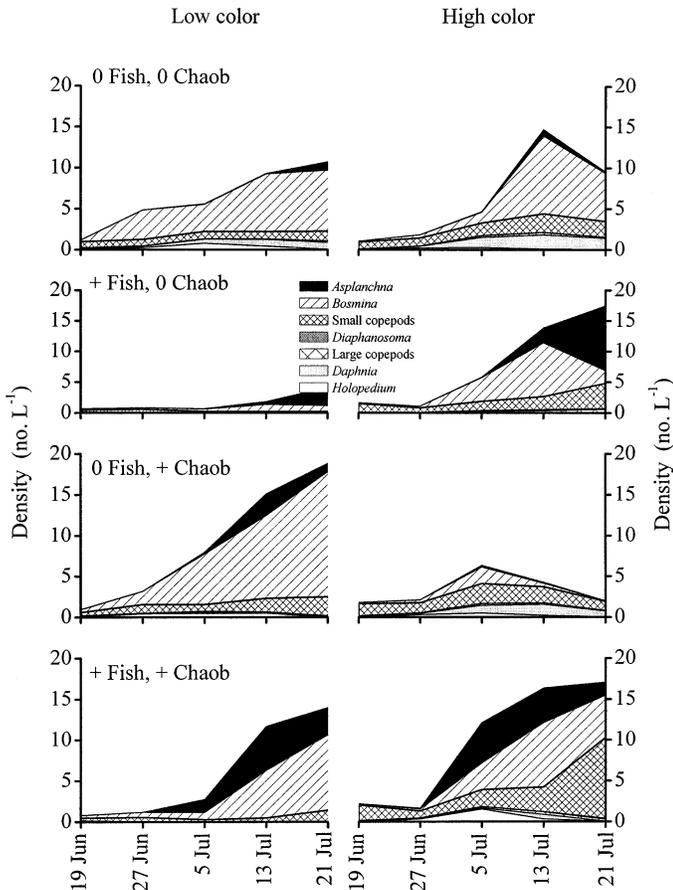


Fig. 3. Density (individuals L^{-1}) of the most common zooplankton groups found in the enclosures. Data for the low and high color lakes are on the left and right columns, respectively, whereas the rows show different predator treatments.

phanosoma brachyurum, an intermediate-sized cladoceran, and large copepods were restricted to high water Color \times Fish treatments, but densities never exceeded 0.15 and 0.5 individual L^{-1} , respectively.

Initially, densities of large- and moderate-sized zooplankton did not statistically differ among treatments (Table 4). Nevertheless, small copepods were more common in high color treatments (1.5 ± 0.8 vs. 0.4 ± 0.2 individuals L^{-1}), whereas *Bosmina* was more frequent in low color treatments (0.29 ± 0.15 vs. 0.16 ± 0.07 individual L^{-1}). There were no other initial trends in zooplankton assemblages among the different treatments.

As the experiment progressed, zooplankton assemblages deviated among treatments, with differences most pronounced for days 16 and 32 (Figs. 3, 4). In the absence of either type of predator, large zooplankton species strongly increased. This effect was more pronounced in high, relative to low, color treatments. *Daphnia* was the dominant organism in high color treatments, and *Holopedium* was more important in low color treatments (Figs. 3, 4). In terms of biomass, small crustaceans were relatively insignificant in the absence of predators. The presence of fish heavily suppressed zooplankton abundance, especially in low color treatments where only *Bosmina* and the rotifer *Asplanchna*

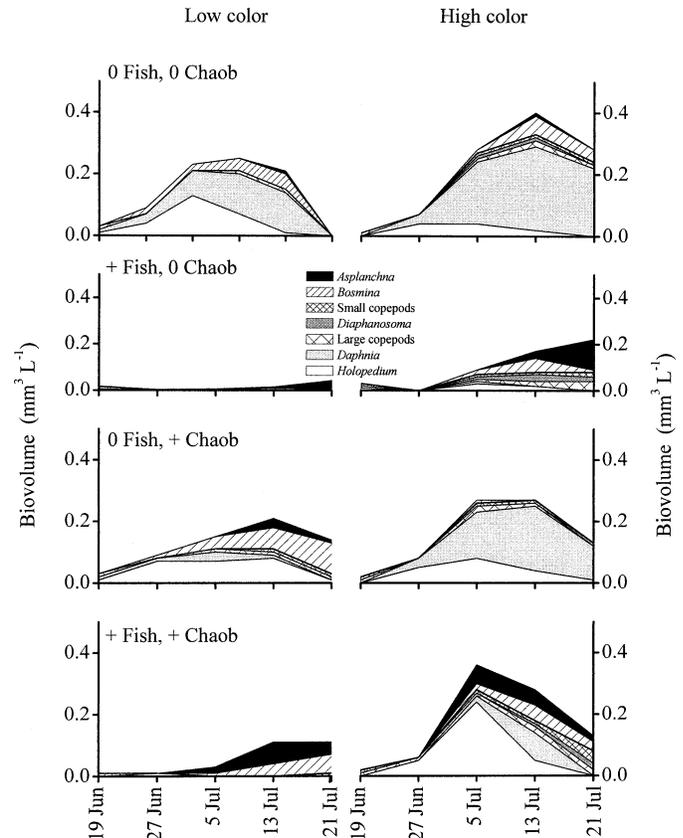


Fig. 4. Biovolume ($mm^3 L^{-1}$) of the most common zooplankton groups found in the enclosures. Data for the low and high color lakes are in the left and right columns, respectively, whereas the rows show different predator treatments.

persisted at fairly high densities. On the other hand, in high color treatments, despite the presence of planktivorous fish, small species were able to maintain densities comparable to the predator-free treatments, and even large cladocerans were present, although at reduced densities.

The effect of *Chaoborus* was ambiguous. As expected, *Bosmina* suffered the most serious predation loss in high color treatments, but surprisingly, in low color treatments, large species—predominantly *Daphnia*—were reduced (Figs. 3, 4).

The results of the combined predator treatments (Fish and *Chaoborus*) were similar to Fish treatments, but the zooplankton was able to sustain overall higher densities. Whereas in low color treatments this effect was limited to *Bosmina* and *Asplanchna*, in high color treatments, mainly *Daphnia* and *Holopedium* reached higher densities relative to Fish predation alone.

According to the statistical analyses, following the first sampling date, all three main factors and several of their interactions significantly affected zooplankton community composition as well as the abundance of individual species (Table 4). A significant effect of Color meant that one or more zooplankton groups would either benefit or suffer under conditions of high water color. The same conclusions could be drawn for effects of Fish and *Chaoborus*, where

Table 4. Values for main effects and interactions for the zooplankton assemblage (MANOVA) and individual zooplankton groups (three-way ANOVA) for the first five sampling dates of the enclosure study performed in summer 2000. ZA, zooplankton assemblage; D, *Daphnia*; H, *Holopedium*; B, *Bosmina*; Lg cop, large copepods; Sm cop, small copepods; Asp, *Asplanchna* (not encountered in sampling one and two). Significant differences are bold. n.s., $p > 0.05$.

	ZA	D	H	B	Lg cop	Sm cop	Asp
Sampling 1							
Color (CO)	0.001	n.s.	n.s.	0.01	n.s.	0.0003	
Fish (FI)	n.s.	n.s.	n.s.	n.s.	n.s.	hn.s.	
Chaoborus (CH)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
CO × FI	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
CO × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
FI × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
CO × FI × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
Sampling 2							
CO	0.003	0.01	n.s.	0.02	0.0001	0.005	
FI	0.001	0.0001	0.02	0.02	n.s.	0.001	
CH	0.03	n.s.	n.s.	n.s.	0.0001	n.s.	
CO × FI	0.0006	n.s.	n.s.	0.03	0.0001	n.s.	
CO × CH	0.001	n.s.	n.s.	n.s.	0.0001	n.s.	
FI × CH	0.02	n.s.	n.s.	n.s.	0.02	n.s.	
CO × FI × CH	n.s.	n.s.	n.s.	n.s.	0.001	n.s.	
Sampling 3							
CO	0.0001	0.002	0.02	n.s.	0.0001	0.001	0.04
FI	0.0001	0.0001	n.s.	0.007	0.002	0.01	0.001
CH	0.0001	n.s.	0.02	0.03	n.s.	0.01	0.0003
CO × FI	0.0001	0.01	0.001	0.001	n.s.	n.s.	0.04
CO × CH	0.0001	n.s.	0.001	0.04	n.s.	0.02	0.04
FI × CH	0.0001	n.s.	0.001	0.02	n.s.	n.s.	0.001
CO × FI × CH	0.001	n.s.	n.s.	n.s.	n.s.	n.s.	0.04
Sampling 4							
CO	0.002	0.03	n.s.	n.s.	0.0001	0.0001	n.s.
FI	0.006	0.0002	0.009	n.s.	n.s.	n.s.	0.005
CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.007
CO × FI	0.0004	0.03	0.003	0.01	n.s.	0.04	n.s.
CO × CH	n.s.	n.s.	n.s.	0.01	n.s.	n.s.	0.04
FI × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
CO × FI × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sampling 5							
CO	n.s.	n.s.	n.s.	n.s.	0.03	0.02	n.s.
FI	0.02	0.01	0.008	0.01	n.s.	n.s.	0.007
CH	n.s.	n.s.	n.s.	0.02	n.s.	n.s.	n.s.
CO × FI	n.s.	0.03	n.s.	n.s.	0.005	0.01	n.s.
CO × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
FI × CH	n.s.	0.006	n.s.	n.s.	n.s.	n.s.	n.s.
CO × FI × CH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

the presence of a specific predator could be either advantageous or detrimental. Whereas *Bosmina*, *Holopedium*, and *Asplanchna* remained unaffected by Color, the abundances of *Daphnia* and small and large copepods were significantly increased by high color treatments. Fish on the other hand, significantly suppressed *Daphnia* and *Holopedium* but resulted in increased *Asplanchna* densities. Copepods and *Bosmina* did not show clear responses to Fish. Chaoborus treatments had significantly higher densities of copepods, and especially *Asplanchna*, whereas cladocerans did not show a uniform response to these invertebrate predators.

Even more intriguing than the main effects was the interaction of Color × Fish, where the effect of Fish varied be-

tween high and low color treatments. Our results showed that the presence of fish led to higher abundances of all zooplankton groups in high color treatments compared to low color treatments. Because Chaoborus effects on the zooplankton assemblage were not uniform, we did not detect consistent Color × Chaoborus or Fish × Chaoborus interactions.

In low color treatments, 11 of the 12 original fish survived until the end of the experiment. In contrast, the high color treatments had only 7 of 12 fish surviving to the end. Starting at day 16, individual fish had to be replaced with conspecifics. The presence of *Chaoborus* seemed to have enhanced fish survival, but this effect was not significant.

Chaoborus not only compete with fish for zooplankton prey but are also preyed upon by fish (intraguild predation, Polis and Strong 1996; Holt and Polis 1997). Hence, we could not assume that the initial densities of *Chaoborus* would remain unchanged in the presence of fish. Even though our sampling technique was not optimized for *Chaoborus* (Persaud and Yan 2001), our net hauls did give us a useful rough estimate of *Chaoborus* abundances in the different treatments. Here, we only present approximate nighttime densities (day 16), because during daytime, *Chaoborus* was heavily aggregated at the bottom of the enclosures and avoided being caught. Overall, *Chaoborus* densities in enclosures without fish were about 0.2 individual L^{-1} , which was slightly lower than the densities we had initially added. Whereas in high color treatments, *Chaoborus* densities were about 30% lower in the presence of fish, in low color treatments, *Chaoborus* densities were reduced tenfold, to about 0.02 individual L^{-1} .

Because the last sampling date is omitted, we only present data on diurnal vertical migration (DVM) for day 16. Because we did not detect species-specific differences in the vertical distribution of zooplankton (above), we combined *Daphnia* and *Holopedium* into "large species" and the remaining crustaceans into "small species." The rotifer *Asplanchna* is known to not perform DVM (Wetzel 2001) and was excluded from this analysis. Two main patterns emerged from our results. First, in the absence of Fish, neither large nor small crustaceans performed diurnal vertical migration. Regardless of Color, the majority of organisms stayed high up in the water column during day and night (Fig. 5). Second, the presence of fish triggered DVM only in low color treatments. In high color treatments with fish both small and large, crustaceans remained at a shallow depth throughout the day and night. Although *Chaoborus* alone had no effect on vertical migration, the extent of downward migration was reduced in the *Chaoborus* + Fish treatment relative to Fish predation alone.

Lake study—The two study lakes significantly differed in water transparency ($p = 0.008$). Cecil Lake had a water color of 16 and 24 CoPt units (PTU) in July 1999 and June 2000, respectively. For the same two dates, the water color in Bena Lake was 75 and 86 PTU, respectively (Table 1). Nevertheless, this difference was not fully reflected in Secchi depth, probably because of an obvious algal bloom in Cecil Lake in June 2000. The epilimnion in Bena Lake (1.0 and 2.0 m in the 2 yr) was generally shallower than in Cecil Lake (3.0 m in both years).

Even though these two lakes had a similar fish assemblage, the resulting zooplankton compositions were very different (Fig. 6). Bena Lake (high color) had significantly more large- to medium-sized cladocerans (*Daphnia* and *Holopedium*, $p = 0.03$) but fewer copepods ($p = 0.01$) than Cecil Lake. Small cladocerans did not differ significantly between the lakes. Furthermore, the vertical distributions of zooplankton were contrasting. In Bena Lake, maximum zooplankton abundance was found in the epilimnion, even in the case of large species. Cecil Lake, on the other hand, was characterized by meta- and hypolimnetic maxima in zooplankton abundance independent of species. Furthermore, in

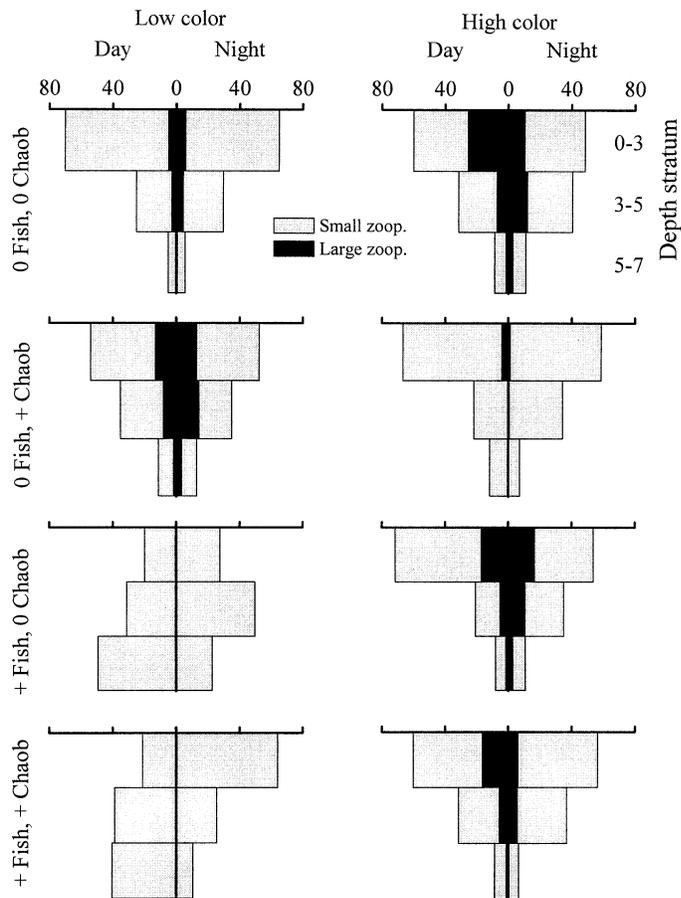


Fig. 5. Vertical distribution (individuals L^{-1}) of small-bodied (shaded bars) and large-bodied (filled bars) zooplankton in the enclosures during day and night. Data for the low and high color lakes are in the left and right columns, respectively, whereas the rows show different predator treatments.

Bena Lake, we found a lot more *Chaoborus* larvae (0.3 and 0.1 individual L^{-1} in 1999 and 2000, respectively) than in Cecil Lake (0.001 individual L^{-1} in 1999 and 2000), but this difference was only marginally significant ($p = 0.08$).

Discussion

Enclosure study—The experimental design we chose was appropriate to study the effects of water color on the relative importance of fish and invertebrate predators in the structure of the zooplankton community. Our high color treatments closely approximated light, temperature, and oxygen gradients commonly described for brown-water lakes. Secchi depth was significantly lower in high color treatments, which was mainly a function of elevated DOC concentration (Jones 1992), especially in oligo- to mesotrophic lakes (Lean 1998). We also found the typical shift in temperature profiles, to a shallower epilimnion and colder hypolimnion, in high color treatments, as described by Snucins and Gunn (2000). Finally, the oxygen concentrations in high color treatments were significantly reduced compared with low color treatments, predominantly in deeper water. This is in good agree-

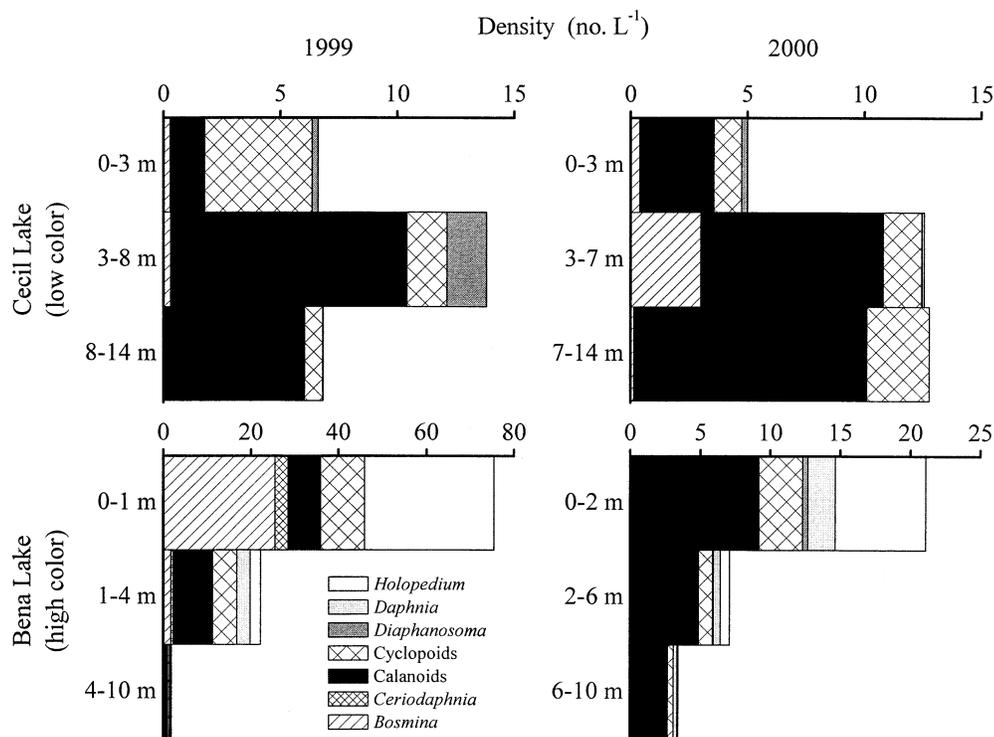


Fig. 6. Density (individuals L^{-1}) of the most common groups of zooplankton in a low color (Cecil) and a high color (Bena) lake in July 1999 and June 2000. Depth strata indicate the epi-, meta-, and hypolimnia. Note that both the depth strata (y-axis) and the range of the density values (x-axis) vary among lakes and years.

ment with findings of Arvola et al. (1996) and Kankaala et al. (1996), who described very low oxygen concentrations in the hypolimnia of many brown-water lakes in Scandinavia.

Our first goal was to evaluate whether *Chaoborus* would be more successful in enduring the presence of fish in high color treatments compared to low color treatments. Because our sampling technique was not optimized for *Chaoborus*, we did not obtain accurate density estimates (Persaud and Yan 2001). Nevertheless, we could assume that *Chaoborus* densities in the absence of fish were between the initially added $0.3 \text{ individual } L^{-1}$ and the $0.2 \text{ individual } L^{-1}$ estimate originating from night sampling. Whereas in high color treatments, *Chaoborus* densities were only marginally affected by the presence of fish, in low color treatments, the densities were reduced by a factor of 10. Hence, we can conclude that high water color can protect even large species such as *C. trivittatus* from substantial losses by fish predation. Reduced light intensities probably impeded prey perception and size-selective feeding of fish, thereby providing a refuge from predation.

Our preliminary enclosure experiment showed that golden shiner had survival rates of about 90% (Boeing and Wissel unpubl. data). This study was performed in a colored lake as well (45 PTU units, Secchi depth 2.3–3.0 m), but fish were fed large amounts of zooplankton on a daily basis. Because food supply was the major difference between the preliminary and final experiment, starvation was the most likely cause for reduced fish survival in high color treat-

ments during the experiment described here. Asphyxiation as a potential mortality factor could be ruled out because oxygen concentrations never fell below $3.2 \text{ mg } L^{-1}$ in either of the experiments. Furthermore, we did not see any obvious signs of fungus or other infections that could have affected fish survival. In low color treatments, fish were the dominant planktivore, independent of the presence or absence of *Chaoborus*, but in high color treatments, the effect of fish diminished while *Chaoborus* gained in significance.

We hypothesized that these altered predation regimes should have profound effects on the zooplankton assemblages. The statistical analysis showed that all three main factors—Color, Fish, and *Chaoborus*—significantly affected the zooplankton abundances. However, a credible interpretation of these effects is only valid if the initial densities were not significantly different. Even though we added equal amounts of a zooplankton mix of both study lakes to each enclosure, densities of *Bosmina* and small copepods for the first sampling date showed significant differences according to Color. The $200\text{-}\mu\text{m}$ mesh that we used during the filling process of the enclosures successfully kept out large species, but obviously juvenile *Bosmina*, as well as copepodites and nauplii, could not be completely excluded. Nevertheless, for *Bosmina*, the differences between color treatments disappeared after the second sampling date. Small copepods were consistently more abundant in high color treatments, but their overall biomass remained low throughout the experiment in all treatments. Consequently, we can assume that

among-treatment variation in initial zooplankton assemblages were not a substantial confounding factor.

The presence of fish significantly decreased crustacean zooplankton, which was more pronounced for larger species. On the other hand, *Asplanchna* had higher abundances in treatments with fish. This shift in species composition and size distribution was originally described as the size efficiency hypothesis (Brooks and Dodson 1965) and has been found in many other studies (e.g., Lynch 1979; Wissel et al. 2000).

Nevertheless, this fish effect differed between color treatments. Crustacean zooplankton, independent of size, was less affected by fish in high color treatments. In low color treatments, the only crustaceans that could somewhat resist fish predation were small species—*Bosmina* and small copepods. Large species, such as *Daphnia* and especially *Holopedium*, virtually absent in low color treatments with fish, persisted in high color treatments. This significant Fish \times Color effect was likely caused by a combination of reduced prey perception of fish in high color treatments and altered vertical migration behavior of the zooplankton prey. Water transparency is one of the most important predictors of the vertical distribution of crustacean zooplankton (Dodson 1990), wherein elevated water color results in a shallower daytime position of crustaceans. In low color enclosures containing fish, zooplankton was forced deeper into the water column, with maximum abundances in the hypolimnion. In high color treatments, the zooplankton did not undergo diurnal vertical migration and stayed high up in the water column day and night. Hence, the eggs of these organisms were never exposed to low temperatures, which would have significantly decreased their development time (Bottrell et al. 1976) and population growth rates (Orcutt and Porter 1983). Because at equal depths, temperatures were lower in high color treatments, the preference of zooplankton for the uppermost water layer could have been further reinforced in these treatments—without increasing predation risk.

Because of mouth gape limitation, we expected *Chaoborus* to prey mainly on small species, which would release large species from competition and result in their dominance. This pattern has been widely described in the literature (Pastorok 1981; von Ende and Dempsey 1981; Christofferson 1990) and was confirmed in our enclosures that had high water color. Carpenter et al. (1985) even suggested that an advantage should be taken of this “*Chaoborus* effect” to further support large filter-feeding cladocerans for lake management purposes (biomanipulation). Nevertheless, in low color treatments, the effect of *Chaoborus* was reversed, and large species, especially *Daphnia*, were suppressed, whereas for small species, the presence of *Chaoborus* was beneficial. Even though unexpected, this result was not completely surprising. In the absence of fish, large chaoborids are capable of suppressing even large zooplankton species (Pope et al. 1973; von Ende and Dempsey 1981; MacKay et al. 1990; Stenson and Svensson 1994; Wissel and Benndorf 1998). Interestingly, both scenarios occurred during our enclosure experiment. High water color caused a shift toward large zooplankton, and low water color resulted in a shift toward small species. Food limitation could be excluded as a possible confounding factor because Chl *a* concentrations did

not differ significantly between treatments, and the small, edible fraction was always dominating. Furthermore, in case of food limitation, one would expect *Bosmina* to decline and not *Daphnia*, since the latter species is known to be a superior competitor for food (Gliwicz 1990).

We think, instead, that differences in vertical migration behavior between high and low color treatments were responsible for the contrasting effects of *Chaoborus* on the zooplankton assemblages. In low color treatments, small species were found higher up in the water column than in high color treatments, and large species showed the opposite trend. Furthermore, *Chaoborus* tended to be more evenly distributed throughout the water column in low color treatments. Consequently, predator–prey overlap was increased for large species but decreased for small species in low color treatments compared to high color treatments. The relatively small change in migration behavior resulted in completely different zooplankton compositions, which further supports the previously described ambiguity of *Chaoborus* effects on the structure of zooplankton communities. The use of a smaller *Chaoborus* species such as *C. puntipennis* or *C. flavicans* might have concealed this result, because only large chaoborids are known to successfully prey on large zooplankton species.

Generally, the enclosure study strongly supported our hypothesis that increased water color could shift the balance between fish and *Chaoborus* as planktivorous predators, leading to the dominance of large zooplankton species in brown-water lakes. Furthermore, the ambiguous effects of *Chaoborus* reminded us how critical the behavioral component is in determining the structure of a food web.

Lake study—Finally, we wanted to test whether the conclusions deriving from our enclosure study were applicable to natural lakes. Hence, we analyzed the zooplankton compositions of two lakes that greatly differed in water color but had similar morphometries and fish compositions. The strongly colored Bena Lake had a consistently shallower epilimnion and a more pronounced anoxic zone than Cecil Lake. Because we found the common color-related light, temperature, and oxygen profiles in these two lakes, we also expected that *Chaoborus* would be more important in Bena Lake, associated with a shift to large zooplankton species. Unfortunately, our sampling technique did not guarantee accurate estimates for *Chaoborus* densities. Nevertheless, in Bena Lake, we found 100 to 300 times more *Chaoborus* than in Cecil Lake. This difference was only marginally significant and most likely was due to our small sample size of two. The resulting zooplankton compositions in Bena Lake and Cecil Lake strongly resembled high and low color treatments in our enclosure experiments. Bena Lake had significantly higher abundances of large species and reduced densities of copepods compared to Cecil Lake. Furthermore, the difference in water color also influenced the vertical position of zooplankton. In Bena Lake, zooplankton was predominantly found in the epilimnion, but in Cecil Lake, maximum abundances always occurred in the meta- and hypolimnion. Because the abundances of fish in these two lakes were comparable, the differences in zooplankton assemblages and mi-

gration behavior could be attributed to poor prey perception of planktivorous fish.

The results of our enclosure and lake studies showed that the elevated water color resulted in reduced fish predation pressure on *Chaoborus* and zooplankton. The crustacean zooplankton was able to abandon the strategy of avoiding fish predation by diurnal vertical migration. The resulting increased growth rates, combined with reduced predation pressure, enabled even large zooplankton species to persist in strongly colored water in spite of the presence of fish. *Chaoborus* usually is strongly suppressed by fish in clear-water lakes, which can be described as top-down food webs. In brown-water lakes, *Chaoborus* becomes a much more significant part of the food web.

Chaoborus is preyed upon by fish but also competes with fish for prey, which leads to a much more intriguing food web structure, called intraguild predation. To survive, the intraguild prey (*Chaoborus*) has to be a more efficient predator for the shared prey (zooplankton) than the top predator (fish) (Polis and Strong 1996; Holt and Polis 1997). As an ambush predator, *Chaoborus* is known to be extremely energy efficient (Giguere 1980). Moreover, Ramcharan et al. (2001a) and McQueen et al. (2001) recently showed that, in brown-water lakes, *Chaoborus* was a much more effective predator on zooplankton prey than fish. This not only influenced the zooplankton composition, but also changed the energy flow through the food web. Both of our experimental studies excluded piscivorous fish. One could argue that, in brown-water lakes, impeded visual feeding of piscivores would relieve planktivorous fish from predation and enhance predation pressure on zooplankton. Nevertheless, the relatively high predator density in our experiments should have accounted for this effect. Furthermore, whole-lake experiments performed in brown-water lakes (Ramcharan et al. 2001a–c) did not detect any significance of such an effect.

Thus, we agree with Rohde (1969) and Williamson et al. (1999), who suggested that brown-water lakes represent a distinct lake type. Water color affects light, temperature, and oxygen profiles and thereby changes the physical habitat of a lake. Brown-water lakes also cannot be considered unproductive (Hutchinson 1967) or classified according to their nutrient load (Chow-Fraser and Duthie 1983). Finally, the food web structure in brown-water lakes switches from top-down to intraguild predation, affecting the zooplankton assemblages and energy flow through the food web.

References

- ARNOTT, S. E., AND M. J. VANNI. 1993. Zooplankton assemblages in fishless bog lakes—influence of biotic and abiotic factors. *Ecology* **74**: 2361–2380.
- ARVOLA, L., P. KANKAALA, T. TOLONEN, AND A. OJALA. 1996. Effects of phosphorus and allochthonous humic matter enrichment on the metabolic processes and community structure of plankton in a boreal lake (Lake Pääjärvi). *Can. J. Fish. Aquat. Sci.* **53**: 1646–1662.
- BERGMAN, E. 1987. Temperature-dependent differences in foraging abilities of two percid, *Perca fluviatilis* and *Gymnocephalus corneus*. *Environ. Biol. Fish.* **19**: 45–53.
- BOTTRELL, H. H., AND OTHERS. 1976. A review of some problems in zooplankton production studies. *Nor. J. Zool.* **24**: 419–456.
- BROOKS, J. L. 1957. The systematics of North American *Daphnia*. *Mem. Conn. Acad. Arts. Sci.* **13**: 1–180.
- , AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 26–35.
- CARPENTER, S. R. 1989. Replication and treatment strength in whole-lake experiments. *Ecology* **70**: 453–463.
- , J. F. KITCHELL, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. *Bioscience* **35**: 634–639.
- CARTER, J. C. H., M. J. DADSWELL, J. C. ROFF, AND W. G. SPRULES. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North-America. *Can. J. Zool.* **58**: 1355–1387.
- CHOW-FRAZER P., AND H. C. DUTHIE. 1983. An interpretation of phosphorus loadings in dystrophic lakes. *Arch. Hydrobiol.* **97**: 109–121.
- CHRISTOFFERSON, K. 1990. Evaluation of *Chaoborus* predation on natural populations of herbivorous zooplankton in a eutrophic lake. *Hydrobiologia* **200–201**: 459–466.
- CUTBERT, I. D., AND P. DEL GIORGIO. 1992. Toward a standard method of measuring color in freshwater. *Limnol. Oceanogr.* **37**: 1319–1326.
- DODSON, S. I. 1990. Predicting diel vertical migration of zooplankton. *Limnol. Oceanogr.* **35**: 1195–1200.
- EMAP (Environmental Monitoring and Assessment Program). 1996. 1991–1994 northeast lakes, water chemistry data. <http://www.epa.gov/emap/html/data1/surfwatr/data/nelakes>.
- FEE, E. J., R. E. HECKY, S. E. M. KASIAN, AND D. R. CRUIKSHANK. 1996. Effects of lake size, water clarity, and climatic variability on mixing depth in Canadian Shield lakes. *Limnol. Oceanogr.* **41**: 912–920.
- GIGUERE, L. A. 1980. Metabolic expenditures in *Chaoborus* larvae. *Limnol. Oceanogr.* **25**: 922–928.
- GLIWICZ, Z. M. 1986. Predation and the evolution in vertical migration zooplankton. *Nature* **320**: 746–748.
- . 1990. Food thresholds and body size in cladocerans. *Nature* **343**: 691–702.
- HANEY, J. F., AND D. J. HALL. 1973. Sugar coated *Daphnia*: A preservation technique for cladocerans. *Limnol. Oceanogr.* **18**: 331–333.
- HESSEN, D. O., AND T. ANDERSEN. 1990. Bacteria as a source of phosphorus for zooplankton. *Hydrobiologia* **206**: 217–223.
- HOLT, R. D., AND G. A. POLIS. 1997. A theoretical framework for intraguild predation. *Am. Nat.* **149**: 745–764.
- HUTCHINSON, G. E. 1967. A treatise on limnology. II. Introduction to lake biology and the limnoplankton. Wiley.
- JANSSEN, J. 1980. Alewives (*Alosa pseudoharengus*) and ciscoes (*Coregonus artedii*) as selective and non-selective planktivores, p. 580–586. *In* W. C. Kerfoot [ed.], Evolution and ecology of zooplankton communities. American Society of Limnology and Oceanography Special Symposium 3, Univ. Press of New England, Hanover.
- JOHANSSON, O. E., L. G. RUDSTAM, AND D. C. LASENBY. 1994. *Mysis relicta*: Assessment of metalimnetic feeding and implications for competition with fish in lakes Ontario and Michigan. *Can. J. Fish. Aquat. Sci.* **51**: 2591–2602.
- JONES, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia* **229**: 73–91.
- KAJAK, Z., AND T. RYBAK. 1979. The feeding of *Chaoborus flavicans* Meigen (Diptera, Chaoboridae) and its predation on lake zooplankton. *Int. Rev. Gesamten Hydrobiol.* **64**: 361–378.
- KANKAALA, P., L. ARVOLA, T. TOLONEN, AND A. OJALA. 1996. Carbon budget for the pelagic food web of the euphotic zone in a boreal lake (Lake Pääjärvi). *Can. J. Fish. Aquat. Sci.* **53**: 1663–1674.
- KORTELAINEN, P. 1993. Content of total organic carbon in Finnish

- lakes and its relationship to catchment characteristics. *Can. J. Fish. Aquat. Sci.* **50**: 1477–1483.
- LEAN, D. 1998. Attenuation of solar radiation in humic waters, p. 107–124. *In* D. O. Hessen and L. J. Tranvik [eds.], *Aquatic humic substances, ecology and biogeochemistry*. Springer-Verlag.
- LYNCH, M. 1979. Predation, competition, and zooplankton community structure: An experimental study. *Limnol. Oceanogr.* **24**: 253–272.
- MACKEY, N. A., S. R. CARPENTER, P. A. SORRANO, AND M. J. VANNI. 1990. The impact of two *Chaoborus* species on a zooplankton community. *Can. J. Zool.* **68**: 981–985.
- MCQUEEN, D. J., C. W. RAMCHARAN, AND N. D. YAN. 2001. Summary and emergent properties. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **56**: 257–288.
- [OME] ONTARIO MINISTRY OF THE ENVIRONMENT. 1984. Ontario Ministry of the Environment handbook of analytical methods. Laboratory Services Branch, OME.
- ORCUTT, J. D., AND K. G. PORTER. 1983. Diel vertical migration by zooplankton: Constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnol. Oceanogr.* **28**: 720–730.
- PACE, M. L., AND J. J. COLE. 2002. Synchronous variation of dissolved organic carbon and color in lakes. *Limnol. Oceanogr.* **47**: 333–342.
- PASTOROK, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* **62**: 1311–1324.
- PERSAUD, A. D., AND N. D. YAN. 2001. Accounting for spatial variability in the design of sampling programmes for *Chaoborus* larvae. *J. Plankton Res.* **23**: 279–285.
- PERSSON, L. 1986. Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): Implications for coexistence between poikilotherms. *J. Anim. Ecol.* **55**: 829–839.
- POLIS, G. A., AND D. R. STRONG. 1996. Food web complexity and community dynamics. *Am. Nat.* **147**: 813–846.
- POPE, G. F., J. C. H. CARTER, AND G. POWER. 1973. The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River system, Quebec. *Trans. Am. Fish. Soc.* **102**: 707–714.
- RAHEL, F. J., AND J. W. NUTZMAN. 1994. Foraging in lethal environment: Fish predation in hypoxic waters of a stratified lake. *Ecology* **75**: 1246–1253.
- RAMCHARAN, C. W., N. D. YAN, D. J. MCQUEEN, A. PEREZ-FUENTETAJA, E. DEMERS, AND J. A. RUSAK. 2001a. Complex responses of *Chaoborus* to changes in fish populations. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **56**: 81–100.
- _____, _____, _____, _____, AND _____. 2001b. Analysis of food webs using individual-based models to estimate *Chaoborus* production and consumption. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **56**: 101–126.
- _____, _____, _____, _____, AND _____. 2001c. Dynamics of zooplankton productivity under two different predatory regimes. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **56**: 151–169.
- RIESSEN, H. P., J. W. SOMMERVILLE, C. CHIAPPARI, AND D. GUSTAFSON. 1988. *Chaoborus* predation, prey vulnerability, and their effect in zooplankton communities. *Can. J. Fish. Aquat. Sci.* **45**: 1912–1920.
- RINGELBERG, J. 1991. A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyalina*. *J. Plankton Res.* **13**: 83–89.
- ROHDE, W. 1969. Crystallization of eutrophication concepts in northern Europe, p. 50–64. *In* *Eutrophication: Causes, consequences, correctives*. Natl. Acad. Sci. Washington D.C.
- SAETHER, O. A. 1970. Nearctic and palaeartic *Chaoborus* (Diptera: Chaoboridae). *Fish. Res. Board Can. Bull.* **174**: 1–57.
- SCOTT, W. B., AND E. J. CROSSMAN. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada.
- SNUCINS, E., AND J. GUNN. 2000. Interannual variation in the thermal structure of clear and colored lakes. *Limnol. Oceanogr.* **45**: 1639–1646.
- STENSON, J. A. E. 1980. Predation pressure from fish and two *Chaoborus* species as related to their visibility, p. 618–622. *In* W. C. Kerfoot [ed.], *Evolution and ecology of zooplankton communities*. American Society of Limnology and Oceanography Special Symposium 3, Univ. Press of New England, Hanover.
- _____, AND J. E. SVENSSON. 1994. Manipulation of planktivore fauna and development of crustacean zooplankton after restoration of acidified Lake Gaardsjoen. *Arch. Hydrobiol.* **131**: 1–23.
- TAYLOR, B. E. 1980. Size-selective predation on zooplankton, p. 377–387. *In* W. C. Kerfoot [ed.], *Evolution and ecology of zooplankton communities*. American Society of Limnology and Oceanography Special Symposium 3, Univ. Press New England, Hanover.
- THURMAN, E. M. 1985. *Organic geochemistry of natural waters*. Dordrecht.
- VINYARD, G. L., AND W. J. O'BRIEN. 1976. Effects of light and turbidity on the reactive distance of Bluegill (*Lepomis macrochirus*). *J. Fish. Res. Board Can.* **33**: 2845–2849.
- VON ENDE, C. N., AND D. O. DEMPSEY. 1981. Apparent exclusion of the cladoceran *B. logirostris* by the invertebrate predator *Chaoborus americanus*. *Ecology* **60**: 119–128.
- WETZEL, R. G. 2001. *Limnology—lake and river ecosystems*. Academic Press.
- WILLIAMSON, C. E., D. E. MORRIS, M. L. PACE, AND O. G. OLSON. 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. *Limnol. Oceanogr.* **44**: 795–803.
- WISSEL, B., AND J. BENNDORF. 1998. Contrasting effects of the invertebrate predator *Chaoborus obscuripes* and planktivorous fish on plankton communities of a long-term biomanipulation experiment. *Arch. Hydrobiol.* **143**: 129–146.
- _____, K. FREIER, B. MÜLLER, J. KOOP, AND J. BENNDORF. 2000. Optimum planktivorous fish biomass stabilizes biomanipulation by suppressing large invertebrate predators and supporting *Daphnia*. *Arch. Hydrobiol.* **149**: 177–192.
- WRIGHT, D., W. J. O'BRIEN, AND G. L. VINYARD. 1980. Adaptive value of vertical migration: A simulation model argument of the predation hypothesis, p. 138–147. *In* W. C. Kerfoot [ed.], *Evolution and ecology of zooplankton communities*. American Society of Limnology and Oceanography Special Symposium 3, Univ. Press New England, Hanover.
- ZARET, T. M., AND J. F. SUFFERN. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**: 804–813.

Received: 19 December 2002

Accepted: 4 April 2003

Amended: 14 May 2003