2001

Effects of water color on food web structure in freshwater lakes

Bjoern Wissel

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EFFECTS OF WATER COLOR ON FOOD WEB STRUCTURE
IN FRESHWATER LAKES

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of the
Doctor of Philosophy

in

The Department of Biological Sciences

by

Bjoern Wissel
B.S., Justus Liebig University Giessen, 1993
M.S., University of Technology Dresden, 1996
December 2001
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ABSTRACT

Water color has multiple effects on freshwater lakes, changing the vertical profiles of light, temperature, and oxygen. Therefore, increased water color should reduce planktivory by visually guided fish, but invertebrate predators such as *Chaoborus* should become more important. Since fish prefer larger prey but *Chaoborus* can only ingest smaller zooplankton, increased water color should cause a shift from small to large zooplankton species. To test this hypothesis, I analyzed two lake data sets to examine how water color affects the relative importance of fish and *Chaoborus* as planktivores. Subsequently, I studied the vertical migration behavior of the zooplankton prey in response to gradients of light, temperature, and oxygen. Finally, I performed (1) an enclosure experiment to evaluate the effects of water color, fish, and *Chaoborus* on the food web structure under controlled conditions, and (2) analyzed the food webs of two lakes that were similar in morphology and fish assemblage, but strongly differed in water color.

Regression and canonical correspondence analysis confirmed my hypothesis that elevated water color negatively affected fish abundance and resulted in a change in species composition to brook trout, small native cyprinids, and bottom dwelling fish. While small chaoborids were unaffected by the presence of fish, larger species showed increased abundances in more colored lakes. Water color also influenced the vertical position of the zooplankton prey, especially the larger species. In clear lakes, large cladocerans and copepods stayed deeper in the water column than in colored lakes. The enclosure experiment showed the expected changes in predation regimes as well as zooplankton assemblage and migration behavior. In low color treatments, I observed a straight-line food web, where fish were able to eliminate *Chaoborus* and strongly suppress the large zooplankton species. In high color treatments the impact of fish was reduced and *Chaoborus* was able to compete with fish for prey (intra-guild predation). The resulting
zooplankton assemblage was dominated by large species such as *Daphnia* and *Holopedium*. The outcome of the whole-lake experiment and enclosure study were similar, which showed that the findings deriving from the enclosure study were applicable to natural lake communities.
CHAPTER 1

GENERAL INTRODUCTION
The biological community in freshwater lakes is affected by the physical habitat as well as direct and indirect interactions among individual members of the food web. The physical habitat of a lake mainly depends on external factors such as climatic region, lake morphometry, and water chemistry characteristics (e.g. nutrient load, pH, turbidity, and water color). To sort out the immense variability among lake types, Thienemann (1921) and Naumann (1929) developed lake classifications based on nutrients, turbidity, water color, pH, calcium, and iron concentrations (Wetzel 2001). Subsequently, additional variables such as fish, benthic invertebrate communities, phytoplankton, macrophytes, and microcrustaceans were used to further distinguish among lake types. Lake classification became so complex that Zafar (1959) actually developed a taxonomic key for lake type identification. Finally, lake classification became more generalized again and phosphorus concentration remained as the most important variable (Vollenweider and Kerekes 1980). Nevertheless, phosphorus proved to have only limited predictive power, especially for lakes with elevated water color (Chow-Fraser and Duthie 1983).

Recently, Williamson et al. (1999) proposed incorporating dissolved organic carbon (DOC) -- the major agent for water color -- into the traditional phosphorus-based lake classification scheme. Because water color not only influences light penetration, but also the vertical profiles of temperature and oxygen, water color should have an effect on the biological community as well. Over the last two decades, specific effects of water color and DOC on isolated abiotic and biotic factors in lakes have been studied. Yet, the overall effects of water color on food web structure have not been determined, even though a large proportion of temperate lakes are characterized by elevated water color (Thurman 1985).

DOC, which is primarily responsible for increased water color, is defined as the organic carbon fraction smaller than 0.5 µm (Thurman 1985, Wetzel & Likens 1991). It is mainly
composed of refractory humic substances, but also includes some readily available free amino acids, sugars, and peptides (Thomas 1997). The natural range of DOC, about 0.5 to 20 mg carbon L\(^{-1}\), is enough to span the range from crystal clear to darkly tea-colored waters. Increased concentrations of DOC in freshwater lakes are positively related to the ratio of watershed to lake area and wetland area in the watershed, but negatively associated with watershed slope (Rasmussen et al. 1989, Kortelainen 1993). Loss of DOC is caused by bacterial and photochemical breakdown (Hessen and Tranvik 1998).

The goal of this study was to complement existing research and evaluate the effects of water color on the food web structure of temperate freshwater lakes. Freshwater lakes are generally thought to have straight-line food webs, wherein piscivorous fish prey on planktivorous fish, which in turn prey upon zooplankton (Carpenter et al. 1985). Size-selective plaktivory by fish results in a zooplankton community dominated by small species (Brooks and Dodson 1965). To persist, large zooplankton species have to perform extended diurnal vertical migration (DVM), spending daytime in the deep and dark hypolimnion (Dodson 1990). DVM carries a cost because of low food concentration and low water temperature in deeper water. Some of the largest zooplankters that are most valuable to fish are invertebrate predators such as larvae of the phantom midge *Chaoborus*. Like fish, these invertebrate predators also consume zooplankton prey. Therefore, invertebrate predators suffer several disadvantages from fish predation: (1) they are directly vulnerable, (2) have to compete with fish for food, and (3) must undergo extensive DVM that reduces the time that they can forage in the upper waters.

In clear water lakes, light penetrates deeply, which should facilitate fish predation. Both zooplankton and invertebrate predators undergo more extensive DVM in clear lakes, and remain lower in the water column during the day (Dodson 1990). In contrast, in brown water lakes
reduced light penetration should impair prey perception by planktivorous fish thereby releasing large zooplankton species and invertebrate predators from predation pressure. Furthermore, altered light, temperature, and oxygen profiles should provide a valuable fish-free refuge, which would allow zooplankton and Chaoborus to lessen the degree of DVM. As a result, all fish prey would be exposed to warmer temperature and better food conditions favoring increased growth rates. With reduced fish predation, invertebrate predators should dominate and the preference of these predators for small-bodied prey should cause a shift in zooplankton composition towards larger species.

My central hypothesis is therefore that water clarity should determine whether fish predation or invertebrate predation shapes zooplankton community structure. The scientific approach I chose combined (1) analyses of multi-lake data sets in order to search for color-related patterns in predator assemblages, and (2) tests of my hypothesis about the role of water color in determining predatory effects in lakes using controlled field experiments.

First, I statistically analyzed the fish assemblages of a large number of lakes located in the northeastern U.S. (chapter 2). The data were provided by Thomas Whittier and were derived from the U.S. Environmental Protection Agency’s Environmental Monitoring and Assessment Program (EMAP) northeastern lake survey. The EMAP design applied a random stratified sampling technique and data were gathered on lake morphology, water chemistry, fish, and zooplankton for a total of 200 lakes (Baker et al. 1997). I used independent variables for lake morphometry (area, maximum depth, elevation) and water quality (total phosphorus, pH, turbidity, conductivity, and water color) to predict fish species assemblages. I applied stepwise multiple linear regressions to investigate species richness and total abundance, as well as canonical correspondence analysis (CANOCO) to analyze the resulting fish assemblages. My
analysis verified already known relationships between fish assemblage and measures such as lake area, depth, elevation, pH, turbidity, and nutrient load. Since the potential effects of water color on fish assemblage have thus far been neglected, I paid special attention to the relative importance of water color compared to lake morphometry and other water quality measures in affecting fish community composition. To remove confounding effects among lake characteristics, it was critical to use this comparative approach instead of just focusing on water color as the sole dependent variable. I tested the hypotheses that water color would significantly reduce overall abundance of fish and also affect species composition.

After establishing the effects of water color on the fish assemblage, the focus of the third chapter was a test for the potential effects of water color on abundance and species composition of *Chaoborus*, the invertebrate planktivore. As with fish, I chose to analyze a large, existing data set. Unfortunately, the different sampling techniques for fish and *Chaoborus* did not permit me to employ the previously used EMAP data set. Instead, I obtained access to the largest and most comprehensive lake survey for *Chaoborus*, including a total of 56 lakes located in central Ontario, Canada (Persaud and Yan 2001). The data were provided by Norman Yan from the Ontario Ministry of the Environment (OMOE). Beside species composition and abundance of Chaoboridae, this data set also incorporated information on lake morphometry and water quality. Water color data were not available for all lakes, but DOC concentration was. Because the relationship between color and DOC for the study lakes was strong ($r = 0.94$), I used DOC as a proxy variable for water color. Other independent variables were lake size and depth, total phosphorus, pH, and the presence or absence of fish.

To identify the factors that determine presence and abundance of different *Chaoborus* species, I performed logistic and multiple linear regressions, respectively, and then used
canonical correspondence analysis to assess the species composition of *Chaoborus*. I expected that the presence of fish would have an overall negative effect, especially on the large chaoborid species. I also expected that increased DOC concentrations should ameliorate fish impact by providing a refuge and reducing predation pressure on *Chaoborus*.

Following the analysis the effects of water color on fish and *Chaoborus*, the fourth chapter focused on the behavioral response of their zooplankton prey. To avoid visually guided predators such as fish, many zooplankton species perform diurnal vertical migration (DVM). Because low light intensities reduce the chance of being detected by a visual predator, the usual strategy is to spend daytime in the dark hypolimnion and to migrate upwards at night. The onset of DVM is triggered by the presence of fish, and the extent of DVM can be influenced by temperature (Davidson and Kelso 1997), oxygen (Field and Prepas 1997), water clarity (Dodson 1990), and intensity of fish predation (Bollens and Frost 1989, VanGool and Ringelberg 1998).

Furthermore, the intensity of DVM may differ among species as well as seasons. To analyze the relative importance of water color, temperature, and oxygen profiles for migration behavior, we examined the daytime vertical position of the three major crustacean zooplankton groups (large cladocerans, small cladocerans, and copepods) three times in May, June, and August 2000 in ten small, but stratified lakes located in Algonquin Park, central Ontario, Canada. The ten lakes strongly differed in their water color. For each sampling date and zooplankton group, I performed stepwise multiple regression, to discover which independent variables significantly influenced the migration behavior. Subsequently, I used analysis of covariance to determine whether migration behavior differed among zooplankton groups and sampling dates.

My final goal (chapter 5) was to integrate and test the results and conclusions derived from the preceding chapters. Chapters two through four established the effects of water color on the
two major predators and the behavioral response of their zooplankton prey. Nevertheless, these three studies were not performed using the same set of lakes. Instead, lakes from the different studies were up to several hundred kilometers apart. Furthermore, analysis of lake survey data can illuminate patterns but an experimental manipulation can provide a clearer test of hypotheses.

To test if water color could truly structure aquatic communities in the manner indicated in the previous chapters, I performed a controlled enclosure experiment and also analyzed data from a whole-lake experiment. Both studies were performed in Algonquin Park, Ontario, Canada. The enclosure experiment was designed to evaluate how water color affects predation regime thereby indirectly affecting zooplankton composition. The experiment was performed in two adjacent lakes that had comparable morphometry and water chemistry, but strongly differed in their water color. Presence and absence of fish and *Chaoborus* completed the 2x2x2 factorial design (Color x Fish x Chaoborus). The enclosures were made out of transparent polyethylene with a diameter of 1 m and a depth of 7 m. Every eight days for 40 days, we sampled the zooplankton composition, as well as water transparency (Secchi depth) and profiles of temperature and oxygen. Chlorophyll a (Chl. a), total phosphorus (TP), and day/night distribution of zooplankton was sampled twice during the 40 day experiment. For statistical analyses, I performed 3-way ANOVA with water transparency, temperature and oxygen profiles, Chl. a, and TP as different dependent variables and color, fish and *Chaoborus* as independent variables. To test the effects of color, fish, and *Chaoborus* on the zooplankton composition and individual zooplankton groups, I used 3-way MANOVA and 3-way ANOVA, respectively.

According to previous results, I expected fish to dominate in low color treatments, strongly suppressing large zooplankton species and *Chaoborus*. In high color treatments, I expected a
shift to larger zooplankton species due to limited visual acuity of fish and increased significance of planktivory by *Chaoborus*.

Even though enclosure experiments capture natural ambient conditions, they are restricted in space and time. This may limit the extent to which conclusions can be generalized and transferred to natural lake communities (Carpernter 1996). Therefore, I studied two additional lakes, Bena and Cecil, that were similar in morphometry but had very different water color (Algonquin Park, Ontario, Canada). Fortuiously for my purposes, in the spring of 1999, the Algonquin Fisheries and Assessment Unit (AFAU) removed all fish from both lakes and restocked them with equal densities of brook trout. This gave me the opportunity to assess the validity of the results from the enclosure study by testing my hypothesis under natural lake conditions. Twice, in July 1999 and in June 2000, I sampled the zooplankton composition as well as light, temperature, and oxygen gradients in both lakes. If the lake study confirmed the results of the enclosure experiments, I could make confident conclusions about how water color influences the relative importance of planktivory by fish and *Chaoborus* and the concomitant effects on the zooplankton.
CHAPTER 2

RELATIVE IMPORTANCE OF WATER COLOR FOR THE FISH ASSEMBLAGE IN FRESHWATER LAKES
Introduction

Fish represent the most diverse group of vertebrates with more than 24,000 species occurring in both marine and freshwater habitats (Nelson 1994). Characterizing certain fish assemblages and relating them to environmental variables has been a long ongoing effort. It is relatively easy to distinguish fish assemblages on a broad scale, e.g., between marine and freshwater fish or among zoogeographical regions (Berra 1981). On the other hand, the prediction of fish composition on a regional scale, and especially for individual lakes, has proven to be much more difficult. In addition to spatial factors, the abiotic and biotic environment becomes increasingly important at smaller scales (Jackson et al. 2001). Generally, larger as well as deeper lakes are characterized by increased species richness (Barbour and Brown 1974, Matuszek and Beggs 1988, Jackson and Harvey 1993, Whittier and Kincaid 1999), but elevation (Matuszek and Biggs 1988), post-glacial dispersal (Mandrak 1995, Wilson and Hebert 1998), and spatial isolation of lakes (Magnuson et al. 1998, Olden at al. 2001) can override this pattern. Within individual lakes, water temperature can limit the range of stenotherm species (Magnuson et al. 1979, Shuter et al. 1980, Grossman and Freeman 1987) and factors such as pH (Harvey 1975, Rahel 1986, Matuszek and Beggs 1988), oxygen (Zalewski and Naiman 1984), nutrients (Ryder 1982, Rempel and Colby 1991), and conductivity (Frenzel and Swanson 1996, Merigeaux at al. 1998, Brown 2000) are known to affect the fish community.

While both turbidity and water color reduce light intensity, only the effects of turbidity on prey perception have been studied (Nakamura 1989, Cuker 1993, Doergeloh 1995, Benfield and Minello 1996). Surprisingly, the potential effects of water color on the fish assemblage have thus far been neglected. Although Hessen and Travink (1998) have speculated about negative effects
of dissolved organic carbon -- the major source for increased water color – on feeding efficiency of fish, these speculations remain untested.

Because water color, as well as other chemical, physical, biological, and morphometric parameters act together to establish a lake habitat, none of these parameters should be considered separately. Only the analysis of combined morphometric and water quality characteristics can reveal the relative importance of individual factors for structuring the fish assemblage. Hence, I performed regression and canonical correspondence analysis to analyze the fish species composition of a large lake data set using lake area, depth, and elevation as lake morphometry parameters, and total phosphorus (TP), pH, turbidity, conductivity, and water color for characterizing water quality. This approach provided an opportunity to compare the results from this study to previous work performed on similar lake data sets and, more importantly, I could test if and how water color influenced the fish assemblage in freshwater lakes.

Methods

Survey Design and Field Methods

The data derived from a lake survey performed between 1991 and 1994 by the Environmental Monitoring and Assessment Program (EMAP) (Larsen et al. 1991, Baker et al. 1997). Three hundred and forty five lakes located in the northeastern U.S. (1 to 10,000 ha, deeper than 1 m) were randomly selected using a stratified design that properly represented different lake size classes (Larsen et al. 1994). Complete information on watershed and lake morphometry, water chemistry, and fish species composition and abundance were available for 202 of these lakes. Two lakes that were apparently fishless were excluded from the analysis. Most lakes were visited once, usually between early July through mid September. For lakes that were sampled repeatedly, I calculated averages for the appropriate variables. Samples for water
chemistry analyses were taken with a Van Dorn sampler at a depth of 1.5 m at the location of maximum depth. Fish were sampled with surface and submerged gillnets, minnow traps, trap nets, and seining, all deployed overnight (Whittier et al. 1997). For a more detailed description of the sampling methods see Baker et al. (1997).

Data Analysis

Initially, I tested if the data set would confirm previously described effects of environmental variables (e.g. lake area, elevation, TP, pH, and specific conductance) on species richness and total abundance of fish. Then, I narrowed the analysis to the relative importance of water color for fish abundance and species richness. Hence, I performed stepwise multiple linear regressions using species richness and total abundance and dependent variables, and lake area, mean lake depth, lake elevation, TP, conductivity, turbidity, pH, and water color as independent variables (SAS version 8). The significance level was set to 0.2 for variable entry and 0.05 for variable retention. To better resemble normal distributions, total fish abundance and all independent variables (except pH) were log-transformed.

Species richness and abundance are fundamental measures to describe fish communities but due to their univariate nature they conceal a tremendous amount of information. Consideration the whole fish assemblage can better reveal how occurrence and abundance of individual species may be affected by specific environmental variables. For this study, I used canonical correspondence analysis (CCA, CANOCO version 4) to investigate the relative importance of water color, compared to lake morphometry and other water chemistry parameters affecting the fish species assemblage. CCA is a direct gradient analysis that relates the pattern of community variation to the pattern of environmental variables (Ter Braak and Prentice 1988). Compared to other ordination techniques, CCA has several advantages. It is fairly robust and unaffected by
data transformations (Jackson 1993, 1997). CCA also performs well for nonlinear and unimodal relationships between species and environmental variables, which usually cause severe problems for linear ordination methods such as principal components analysis (Ter Braak 1986). Environmental variables were only included if a Monte Carlo test using 999 permutations was passed ($\alpha = 0.05/n$, $n =$ number of variables). The order in which variables were included was determined by stepwise selection (999 Monte Carlo simulations) using restricted models that only considered previously entered variables. Significance of the CCA axes of the final models were evaluated by running 999 unrestricted Monte Carlo simulations using the eigenvalues of the axes as test statistics.

Even though a total of 88 fish species were recorded during the study (Whitier et al. 2001), I only included those 36 species that occurred in at least 5% of the lakes. For morphometric variables, I included lake area, mean depth, and elevation, while water quality was characterized by water color, turbidity, total phosphorus (TP), pH, and specific conductance. Fish abundances as well as independent variables – except pH -- were log transformed to obtain normality.

In an initial CCA, I used the complete set of environmental variables to gain information on the overall relative importance of morphometric and water quality variables and their relationship to each other. Because morphometric characteristics such as lake area, depth, and elevation are already known to strongly influence the fish assemblage, I performed a second CCA using these parameters as covariables. This approach provides an opportunity to only focus on the relative importance of water quality characteristics for the fish species assemblage without losing information about lake morphometry.
Results

The number of fish species encountered in the study lakes varied from 1 to 30, with a range of 3 to 7718 individuals caught per lake (Table 2.1). Lake size and average depth ranged from 0.6 to 3300 ha and 0.5 to 22 m, respectively, with elevations between 2 and 627 m above sea level. Similar to morphological characteristics, water quality measures also covered a broad range, from oligo- to hyper-trophic and from clear to heavily stained lakes (Table 2.1).

Stepwise multiple regression showed that lake area was the overall most important predictor of species richness, with larger lakes harboring more species than small ones (Table 2.2). Positive relationships for species richness were also observed for TP and turbidity. Lake elevation was negatively related to species richness. These four variables combined resulted in an $R^2$ of 0.56.

Total fish abundance was significantly influenced by the four variables: lake area, turbidity, specific conductance, and water color. Lake area was the most important predictor (Table 2.2). Lake area and turbidity showed positive relationships with abundance, and specific conductance and water color had significant negative effects on total abundance. The $R^2$ value of the complete model was 0.26. According to the regression analyses, pH had a negligible effect on species richness and total fish abundance.

Regression analysis is only able to test the importance of environmental variables for univariate measures of the fish community such as abundance and richness. To investigate the effects on the fish assemblage in more detail, I performed canonical correspondence analysis (CCA). The first CCA, which included both morphological and water quality variables, confirmed that morphometric variables generally were more important than water quality variables (Figure 2.1).
Table 2.1: Morphometric and water quality parameters of the 200 study lakes located in the northeastern U.S.. Only lakes containing fish are included.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Range</th>
<th>Mean ± std. dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fish species</td>
<td>1 - 30</td>
<td>10 ± 5</td>
</tr>
<tr>
<td>Total fish abundance</td>
<td>3 - 7718</td>
<td>936 ± 1124</td>
</tr>
<tr>
<td>Lake area [ha]</td>
<td>0.6 - 3306</td>
<td>229 ± 456</td>
</tr>
<tr>
<td>Max. lake depth [m]</td>
<td>0.5 - 22.0</td>
<td>5.0 ± 4.8</td>
</tr>
<tr>
<td>Lake elevation [m]</td>
<td>2.0 - 627</td>
<td>239 ± 162</td>
</tr>
<tr>
<td>Water color [PTU]</td>
<td>0.0 - 200</td>
<td>23 ± 25</td>
</tr>
<tr>
<td>Turbidity [NTU]</td>
<td>0.2 - 14.0</td>
<td>1.3 ± 1.6</td>
</tr>
<tr>
<td>Total phosphorus [µg L⁻¹]</td>
<td>0.9 - 176</td>
<td>17 ± 21</td>
</tr>
<tr>
<td>Conductivity [µS cm⁻¹]</td>
<td>12.5 - 1073</td>
<td>103 ± 124</td>
</tr>
<tr>
<td>pH</td>
<td>4.5 - 8.7</td>
<td>7.5 ± 0.7</td>
</tr>
</tbody>
</table>

Table 2.2: Regression models for fish species richness and total fish abundance for 200 lakes located in the northeastern U.S..

<table>
<thead>
<tr>
<th>Regression model</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>abundance = 2.5 + 0.4 area − 0.3 color + 0.4 turbidity − 0.5 conductivity</td>
<td>0.56</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>richness = - 1.6 + 4.7 area − 0.2 elevation + 2.2 TP + 2.7 turbidity</td>
<td>0.26</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>
Figure 2.1: CCA axes one and two, showing the association of environmental lake variables and fish species composition of 200 lakes located in the northeastern U.S. Size of symbols for fish species represents frequency of occurrence (•, ••, •••, •••• found in > 50 %, 21 - 50 %, 11 – 20 %, 5 – 10 % of lakes, respectively) and font size represents fish abundance in lakes where species was present (N. pike = 1 – 20, SMB = 21 – 60, P. dace = 61 – 100, Y. perch = > 100). Common and scientific names of fish species are listed in table 2.3. For clarity, lakes are not shown in this graph.
Table 2.3: Common names, scientific names, and abbreviations of fish species that were encountered in the 200 study lakes. Only species that occurred in at least 5% of the lakes were included.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alewife</td>
<td><em>Alosa pseudoharengus</em></td>
<td>Alewife</td>
</tr>
<tr>
<td>American eel</td>
<td><em>Anguilla rostrata</em></td>
<td>Am. eel</td>
</tr>
<tr>
<td>Atlantic salmon</td>
<td><em>Salmo salar</em></td>
<td>Atl. salmon</td>
</tr>
<tr>
<td>Banded killifish</td>
<td><em>Fundulus diaphanus</em></td>
<td>Bd. killifish</td>
</tr>
<tr>
<td>Black crappie</td>
<td><em>Pomoxis nigromaculatus</em></td>
<td>Bl. crappie</td>
</tr>
<tr>
<td>Bluegill</td>
<td><em>Lepomis macrochirus</em></td>
<td>Bluegill</td>
</tr>
<tr>
<td>Blacknose dace</td>
<td><em>Rhinichthys atralutus</em></td>
<td>Bn. dace</td>
</tr>
<tr>
<td>Bluntnose minnow</td>
<td><em>Pimephales notatus</em></td>
<td>Bn. minnow</td>
</tr>
<tr>
<td>Brook trout</td>
<td><em>Salvelinus fontinalis</em></td>
<td>Brook trout</td>
</tr>
<tr>
<td>Brown bullhead</td>
<td><em>Ictalurus nebulosus</em></td>
<td>Br. bullhead</td>
</tr>
<tr>
<td>Brown trout</td>
<td><em>Salmo trutta</em></td>
<td>Br. trout</td>
</tr>
<tr>
<td>Burbot</td>
<td><em>Lota lota</em></td>
<td>Burbot</td>
</tr>
<tr>
<td>Chain pickerel</td>
<td><em>Esox niger</em></td>
<td>Pickerel</td>
</tr>
<tr>
<td>Common carp</td>
<td><em>Cyprinus carpio</em></td>
<td>C. carp</td>
</tr>
<tr>
<td>Common shiner</td>
<td><em>Notropis cornutus</em></td>
<td>C. shiner</td>
</tr>
<tr>
<td>Creek chub</td>
<td><em>Semothilus atromaculatus</em></td>
<td>Cr. chub</td>
</tr>
<tr>
<td>Fallfish</td>
<td><em>Semothilus corporalis</em></td>
<td>Fallfish</td>
</tr>
<tr>
<td>Finescale dace</td>
<td><em>Chrosomus neogaeus</em></td>
<td>Fs. dace</td>
</tr>
<tr>
<td>Golden shiner</td>
<td><em>Notemigonus crysoleucus</em></td>
<td>G. shiner</td>
</tr>
<tr>
<td>Lake chub</td>
<td><em>Couesius plumbeus</em></td>
<td>Lk. chub</td>
</tr>
<tr>
<td>Lake trout</td>
<td><em>Salvelius namaycush</em></td>
<td>Lk. trout</td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>* Micropterus salmoids*</td>
<td>LMB</td>
</tr>
<tr>
<td>Northern pike</td>
<td><em>Esox lucius</em></td>
<td>N. pike</td>
</tr>
<tr>
<td>Northern redbelly dace</td>
<td><em>Chrosomus eos</em></td>
<td>Rb. dace</td>
</tr>
<tr>
<td>Pearl dace</td>
<td><em>Semothilus margarita</em></td>
<td>P. dace</td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td><em>Lepomis gibbosus</em></td>
<td>PS</td>
</tr>
<tr>
<td>Rainbow smelt</td>
<td><em>Osmerus merdax</em></td>
<td>Rb. smelt</td>
</tr>
<tr>
<td>Rainbow trout</td>
<td><em>Oncorhynchus mykiss</em></td>
<td>Rb. trout</td>
</tr>
<tr>
<td>Redbreast sunfish</td>
<td><em>Lepomis auritus</em></td>
<td>Rb. sunfish</td>
</tr>
<tr>
<td>Slimy sculpin</td>
<td><em>Cottus cognatus</em></td>
<td>Sl. sculpin</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td><em>Micropterus dolomieu</em></td>
<td>SMB</td>
</tr>
<tr>
<td>Tessellated darter</td>
<td><em>Etheostoma olmstedi</em></td>
<td>Ts. darter</td>
</tr>
<tr>
<td>White perch</td>
<td><em>Morone americana</em></td>
<td>W. perch</td>
</tr>
<tr>
<td>White sucker</td>
<td><em>Catostomus commersoni</em></td>
<td>W. sucker</td>
</tr>
<tr>
<td>Yellow bullhead</td>
<td><em>Ictalurus natalis</em></td>
<td>Y. bullhead</td>
</tr>
<tr>
<td>Yellow perch</td>
<td><em>Perca flavescens</em></td>
<td>Y. perch</td>
</tr>
</tbody>
</table>
Lake area and depth were highly correlated, and both were unrelated to lake elevation. TP and turbidity, as well as pH and specific conductance, were strongly correlated, but no strong relationship between any of these water quality parameters and water color could be detected. While large, deep lakes were characterized by low turbidity and TP concentrations, lakes at high elevation had low pH and specific conductance. Overall, water color had a fairly distinct position, being separated from most morphometric and other water quality variables. Lake area entered the model as the first variable in forward selection, followed by elevation, and then water color; subsequently, TP, conductivity, lake depth, turbidity, and pH were included. CCA axis one and two explained roughly 40% and 22% of the species-environment variation, respectively.

More widespread fish species were located closer to the origin with yellow perch being most ubiquitous (Fig. 2.1). Salmonids were generally found more frequently in deep and large lakes with the exception of brook trout, which occurred in colored lakes. Six of the nine native cyprinids, brown bullhead, sucker, and burbot were more common in colored lakes as well. Overall, centrachids occurred in more eutrophic, turbid lakes with higher pH and specific conductance concentrations. Common carp, at the extreme, inhabited the most turbid lowland lakes with very high nutrient concentrations.

The second CCA, which focused on water quality variables, revealed that high water color coincided with low pH and low specific conductance, while turbidity and TP were fairly unrelated to this color – pH, specific conductance gradient (Fig. 2.2). Consequently, the fish species assemblage of the study lakes could be separated into four categories: (1) high color, low pH / specific conductance – high TP / turbidity, (2) high color, low pH / specific conductance – low TP / turbidity, (3) low color, high pH / specific conductance – low TP / turbidity, (4) low color, high pH / specific conductance – high TP / turbidity.
Figure 2.2: CCA axes one and two, showing the association of water quality characteristics and fish species composition of 200 lakes located in the northeastern U.S.. Size of symbols for fish species represents frequency of occurrence. Morphometric variables (lake area, depth, and elevation) are included as covariables. Symbols and abbreviations are as in figure 2.1.
The first two CCA axes were highly significant and explained 45% and 19% of the species-environment variation, respectively. All water chemistry variables were significant; specific conductance entered the model first, followed by water color, TP, turbidity, and pH.

Chub, burbot, salmonids, and shiners were more common in brown water lakes with high nutrient load (quadrant 1). Dace and redbreast sunfish occurred most frequently in colored lakes with low TP and turbidity (quadrant 2). Smallmouth and largemouth bass that were separated by lake size in the first CCA were more frequent in clear lakes with low TP and turbidity (Quadrant 3). Especially carp, but also pumpkinseed, bluegill, black crappie and yellow bullhead inhabited lakes of low color and high TP and turbidity (Quadrant 4).

**Discussion**

Since morphometric and water quality variables of the study lakes varied over a wide range, I felt confident that this data set was appropriate to analyze the effects of environmental variables on the fish species assemblage in temperate lakes. It was not surprising that the regression analysis identified factors already known to be important for species richness and abundance of fish. Previous work with this data set (Whittier and Kincaid 1999, Allen et al. 1999) as well as studies including hundreds of lakes in Ontario, Canada (Matuszek and Biggs 1988, Jackson and Harvey 1989, 1993), showed that lake area (positive relationship) and elevation (negative relationship) are the most important variables determining fish species richness. The importance of TP and turbidity suggests that more productive lakes generally support more species (Rader and Richardson 1994), at least as long as TP concentrations do not exceed 400 µg L⁻¹ (Jeppesen et al. 2000). The relative unimportance of pH in this data set was not surprising, given that only 7 out of 200 lakes had pH levels below 6. Analyzing almost 1000 lakes in Ontario, Matuszek and Beggs (1988) also did not find any effects of pH on fish species richness, but additional analysis
of a subset of 272 lakes with pH below 6 revealed that pH was the most important variable, significantly reducing species richness.

For total fish abundance, lake area again was the most important variable wherein larger lakes supported higher abundances. For this survey, sampling effort increased with lake size (Baker et al. 1997); therefore, the species-area relationship was not surprising. But interestingly, fish abundance was negatively related to water color, implying that brown water lakes could not support as many fish as clear water lakes, independent of their size and trophic state. Possible explanations are reduced prey perception due low light intensities (Link & Edsall 1996, O’Brien 1979, 1987, Vinyard & O’Brien 1976, Wright et al. 1980) and decreased habitat availability because brown water lakes frequently have low hypolimnetic oxygen concentrations (Arvola et al. 1996, Hessen et al. 1989, Kankaala et al. 1996, Salonen et al. 1983). More turbid lakes had higher fish abundance and these lakes also had higher TP concentrations. The relationship of abundance to nutrient levels has been described as the well-known morphoedaphic index (Rempel and Colby 1991, Ryder 1982).

On one hand, the regression analyses confirmed established patterns for species richness and abundance of fish, but it also elucidated that elevated water color can reduce overall abundance of fish. To further explore this novel result, canonical correspondence analysis (CCA) was able to determine if reduced fish abundance with elevated water color was a general trend affecting all species likewise, or if it was accompanied by a change in species composition.

Both CCAs showed that water color was one of the most important variables influencing the species composition of the study lakes. In the first CCA, which included morphometric and water quality variables, water color was the first non-morphometric variable entering the model, right after lake area and elevation. The second CCA, which focused only on water quality
variables by removing the effects of morphometric lake characteristics (included as covariables),
identified water color as the second most important variable. The primary gradient characterizing
water chemistry of the study lakes contrasted brown water lakes with reduced pH and clear lakes
with higher pH. A similar gradient was described by Driscoll at al. (1989) and Wetzel (2001).
The fact that nutrient concentration (TP) and water color were unrelated in this dataset supports
the more recent belief that brown water lakes cannot be considered somehow unsuitable for
aquatic life (Chow-Fraser and Duthie 1982, Jones 1992, Carpenter and Pace 1997, Williamson et
al. 1999), as previously stated by Hutchinson (1967).

The second CCA divided the fish assemblage in the study lakes into four groups. Species on
the left side occurred in more colored lakes with lower pH and specific conductance, and species
in the two bottom panels were found more frequently in lakes with increased TP and turbidity.
Fish species close to the origin, such as yellow perch and pumpkinseed, were ubiquitous and had
the least specific requirements related to water quality. Species further away from the origin
were more restricted to specific environmental conditions. Northern pike, for example, was only
found in clear lakes with low TP concentration while common carp occurred in clear lakes with
high TP concentration. Strongly colored lakes with low TP were most suitable for all species of
dace, while increasing TP concentration within colored lakes favored burbot, chub, common
shine, and salmonids. Interestingly, the first CCA only identified brook trout to be common in
brown water lakes, but the second CCA, after adjusting for lake morphometry, also found other
salmonids to occur in brown water lakes. An analogous mechanism could be observed for
smallmouth and largemouth bass. While the first CCA separated these two species according to
lake size, the second CCA identified similar water quality requirements for these two species.
Apparently, smallmouth bass as well as most salmonids inhabit large and deep lakes, which
distinguished these species from largemouth bass and brook trout, respectively. But, independent of lake size, in the second CCA smallmouth bass and largemouth bass on one hand and salmonids on the other hand occurred in similar environments relative to water quality.

In conclusion, my analysis showed that water color was one of the most important environmental variables significantly affecting the fish species composition in temperate lakes. My conclusions are valid beyond this particular lake data set, as this study confirmed established patterns of species richness, abundance, and fish assemblage related to lake morphometry and water quality found in other data sets. The lack of evidence from previous studies for the importance of water color in affecting fish assemblage is probably due to water color largely being neglected. Water color not only affects the fish assemblage, but also influences the species composition and abundance of invertebrate predators such as *Chaoborus* (Nilssen 1974, see chapter 3), the behavior of crustacean zooplankton (Dodson 1990, see chapter 4), and phytoplankton composition (Grandberg and Herjula 1982, Ferreyra et al. 1997, Carpenter at al. 1998). Perhaps brown water lakes will eventually be considered fairly distinct lake ecosystems with a specific food web structure.
CHAPTER 3

PREDATION AND REFUGIA: IMPLICATIONS FOR *CHAOBORUS* ABUNDANCE AND SPECIES COMPOSITION
Introduction

The larvae of the phantom midge *Chaoborus* (Chaoboridae, Diptera) occupy a central position in many lake ecosystems. Besides fish, these invertebrates are the most common planktivorous predators in freshwater lakes. Visually-guided fish prefer large prey items (Taylor 1980), leading to the dominance of small zooplankton species (Brooks and Dodson 1965, Wissel and Benndorf 1998, Yan et al. 2001). Due to mouth gape limitation, *Chaoborus* feeds on smaller prey (Pastorok 1981, Riessen et al. 1988, Vanni 1988, Auclair et al. 1993), thereby selecting for larger zooplankton species. Hence, the size distribution of the zooplankton community is strongly affected by the abundance and relative importance of fish and *Chaoborus*.

The relationship between fish and *Chaoborus* is not only restricted to competition for zooplankton prey, but chaoborids are also preyed upon by fish. The intensity of predation by fish increases with both body size and pigmentation of *Chaoborus* (Stenson 1980). In fishless lakes, populations of larger *Chaoborus* species can be enormous (von Ende 1979, Yan et al. 1991, Wissel and Benndorf 1998). However, in most lakes fish and *Chaoborus* co-exist and smaller *Chaoborus* species in particular can sustain relatively large populations (Pope et al. 1973, Nilsson 1974, von Ende 1979, Carter et al. 1980, Yan et al. 1985, Ramcharan et al. 2001). To reduce losses to fish in these lakes, *Chaoborus* undergoes a diurnal vertical migration (DVM) spending the day in the dark hypolimnion or lake sediments and migrating upwards at night to feed (Luecke 1986, Davidovicz 1990, Voss and Mumm 1999). If hypoxic or anoxic, the hypolimnion may be an even safer predation refuge because fish require higher oxygen concentrations than *Chaoborus*, which can withstand even prolonged hypoxia (Gade 1985, Hanazato 1992).
Of 12 described *Chaoborus* species in North America (Saether 1970), four chaoborids occur frequently in temperate freshwater lakes: *C. punctipennis, C. flavicans, C. trivittatus,* and *C. americanus.* These four species vary widely in morphology from the relatively small and transparent *C. punctipennis* to the large and strongly pigmented *C. americanus.*

Previous studies have shown that the largest species, *C. americanus,* is restricted to fishless lakes, as strong pigmentation (Stenson 1980) and lack of diurnal vertical migration (von Ende 1979) make this species especially vulnerable to fish (Stenson 1980). In fact, the presence of *C. americanus* remnants in sediment cores is used as evidence of the long-term absence of fish in lakes (Lamontagne and Schindler 1994, Uutula et al. 1994). Besides fish, factors such as pH (Yan et al. 1985), nutrients (Seminara and Bazzanti 1984), water color (Nilsson 1974), temperature (Lamontagne and Schindler 1994), elevation (Lamontagne and Schindler 1994), and intraspecific competition and predation (von Ende 1979, 1982, Sardella and Carter 1983) have been suggested to influence *Chaoborus* distribution.

Thus far, most studies have focused only on a few selected variables to explain *Chaoborus* presence and absence. Statistical evaluations have rarely been performed and especially surprising is that ordination techniques have never been used. Without these analytical techniques, the explanations of species’ distributions in past studies might be considered not as conclusions, but as hypotheses for testing. Only in a few cases, have experimental tests of ideas about fish predation and conspecific competition been conducted (von Ende 1979). Additionally, in some past studies, treatment effects were confounded. For example, Lamontagne and Schindler (1994) concluded that water temperature was the main factor limiting the distribution of different *Chaoborus* species. But elevation was strongly correlated with water temperature complicating a clear causation. Some of the explanations in the literature about factors that
influence species’ distributions are also contradictory. Rabette and Lair (1999) suggested that high oxygen levels were critical for the distribution of Chaoborus within a lake. However, other studies such as Rahel and Nutzman (1994) reported that Chaoborus frequented hypoxic zones. Similarly, Sardella and Carter (1983) concluded that resource competition among conspecifics controlled the Chaoborus species assemblage in lakes, while von Ende (1979) suggested that interspecific predation was the critical factor.

The sampling methods commonly employed in past studies further complicate their interpretation. There are two common methods to evaluate the presence, absence, and abundance of Chaoborus species. Sediment samples can reveal information about both current and historical populations (Chaoborus remnants). Alternatively, plankton hauls taken at night bear information about Chaoborus that are dispersed in the water column. Because most Chaoborus species not only perform a diurnal vertical migration (DVM) and avoid fish predation (Davidowicz 1990), but also a horizontal migration (Tsalkitzis et al. 1994, O’Bryan and Forrester 1997, Voss and Mumm 1999), a good sampling protocol is crucial for obtaining accurate information on Chaoborus presence, absence, and especially abundance. In earlier studies, the water column was either sampled only during the day (Bendall and McNicoll 1987, Carter et al. 1980, Pope at al. 1973) disregarding diurnal vertical migration, or samples were taken only at a single location (von Ende 1979, Campbell and Knoechel 1990). The latter approach is unlikely to result in reliable density estimates, since it does not account for patchiness in the horizontal distribution. Additionally, single-station sampling might not detect Chaoborus if their populations are small, hence the occurrence of rare species might be underestimated.

The goal of this study was to apply multivariable regression and ordination techniques to a large data set of 56 lakes in order to test which variables related to lake morphology, water
chemistry, and fish predation determine (1) the abundance of individual *Chaoborus* species and (2) species composition. A multi-station sampling protocol was used because I required precise estimates of abundance by species.

**Methods**

I obtained data for 56 Shield lakes located in central Ontario, Canada, which spanned a wide range of physical, chemical, ecological, and morphological lake characteristics. I assumed that this lake selection would also provide a wide range in *Chaoborus* densities and species compositions (Table 3.1).

Temperature and oxygen profiles, and volume-weighted water samples for pH, total phosphorus (TP), and dissolved organic carbon (DOC), were taken at the central station of each lake. These data provided information about potential stress from acidic precipitation, lake trophic state, and water transparency. Using the temperature profiles, I generated a new variable: Stratification (“present” when I encountered well-defined layers for epi-, meta-, and hypo-limnia and “absent” in the case of an isothermal water column). Additionally, I used the thickness of the oxygen-depleted layer, $Z_{O_2}$ (thickness (m) of less than 3 mg L$^{-1}$ O$_2$), to assess the suitability of a hypolimnetic low oxygen refuge for *Chaoborus* that would be inaccessible to fish. Because Chaoboridae are not evenly distributed over time and space (Davidovicz 1990, Tsalkitzis et al. 1994, Voss and Mumm 1999), it is difficult to acquire dependable information on their occurrence and abundance. To account for the variability in spatial distribution of *Chaoborus*, a stratified random sampling design was employed. All samples were collected in the fall from 1986 to 1988. After nightfall, vertical net hauls were taken at ten stations in each lake with a 46 cm conical net with a mesh size of 150 µm (Yan et al. 1985). Filtration efficiency was measured with a flow meter and the samples were preserved with 4% sugar formalin. Taxonomic
Table 3.1: Variables of the 56 study lakes used for the statistical analyses. Fish and stratification as categorical variables were not transformed. All other variables, besides pH, were log-transformed.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>SYMBOL</th>
<th>UNIT</th>
<th>RANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. punctipennis</td>
<td>ind. -m³</td>
<td>0.0 – 199</td>
<td></td>
</tr>
<tr>
<td>C. flav/triv</td>
<td>ind. -m³</td>
<td>0.0 – 156</td>
<td></td>
</tr>
<tr>
<td>C. americanus</td>
<td>ind. -m³</td>
<td>0.0 – 893</td>
<td></td>
</tr>
<tr>
<td>Lake area</td>
<td>Area</td>
<td>ha</td>
<td>2.3 – 679</td>
</tr>
<tr>
<td>Max. lake depth</td>
<td>Zmax</td>
<td>m</td>
<td>5.8 – 61</td>
</tr>
<tr>
<td>Mean lake depth</td>
<td>Zmean</td>
<td>m</td>
<td>1.82 – 20.5</td>
</tr>
<tr>
<td>Secchi depth</td>
<td>Secchi</td>
<td>m</td>
<td>0.9 – 9.5</td>
</tr>
<tr>
<td>Fish</td>
<td>Fish</td>
<td>absent / present</td>
<td></td>
</tr>
<tr>
<td>Dissolved organic carbon</td>
<td>DOC</td>
<td>mg L⁻¹</td>
<td>1.4 – 12.4</td>
</tr>
<tr>
<td>Total phosphorus</td>
<td>TP</td>
<td>µg L⁻¹</td>
<td>3.7 – 26</td>
</tr>
<tr>
<td>pH</td>
<td>pH</td>
<td></td>
<td>4.7 – 7.8</td>
</tr>
<tr>
<td>Stratification</td>
<td>Strat.</td>
<td>yes / no</td>
<td></td>
</tr>
<tr>
<td>Layer of &lt; 3 mg L⁻¹ O₂</td>
<td>ZO₂</td>
<td>m</td>
<td>0 - 16</td>
</tr>
</tbody>
</table>
identifications were made according to Saether (1972) and Borkert (1979). The final Chaoborus densities (ind. m$^{-3}$) represented a depth-weighted average for all ten stations. C. trivittatus only occurred at densities above 5 ind. m$^{-3}$ in five out of the 56 lakes. I pooled the data from this species with C. flavicans (C. flav/triv), as these two species are likely to fill similar ecological niches. Both species are larger than the smallest species, C. punctipennis, but are not restricted to fishless lakes as is C. americanus. It is likely that similar factors affect these two larger Chaoborus species. Not only was C. trivittatus found in high densities only when C. flavicans was abundant, but both species are also known to have similar vertical and horizontal distributions on the Shield, which differ from those of C. punctipennis (Tsalkitzis et al. 1994). The three Chaoborus groups in my analysis were thus: C. americanus, C. punctipennis, and C. flav/triv.

**Statistical Analysis**

Because the three Chaoborus taxa did not coexist in all the lakes, I initially performed multiple logistic regression (SAS version 8) to identify the most important factors influencing their probability of occurrence. As independent variables I used measures of lake morphometry, water chemistry, and presence of planktivorous fish in the 56 lakes (Table 3.1). Fish and Stratification as binary variables were not transformed. Except for pH, all other variables were log-transformed ($\log_{10}(x+1)$) to obtain approximately normally-distributed data. To determine the relative importance of the independent variables, I used stepwise logistic regression (significance level for variable entry = 0.2, and for variable retention = 0.1). I contrasted the three different logistic regression models; one for each of the dependent variables which were presence or absence of C. americanus, C. punctipennis, and C. flav/triv. Classification in each logistic regression model was based on the estimated probability (P) of a lake supporting a specific
Chaoborus group. P ranged from zero to one, with the mid-point of 0.5 as the threshold value between presence and absence.

The logistic regression provided presence/absence models. I used multiple linear regression (SAS version 8) for each Chaoborus group to determine the important variables influencing abundance in those lakes where each group was found. The same variables and transformations were used as for the logistic regressions. Additionally, the Chaoborus abundances were log-transformed. For the analysis of C. punctipennis, I included the abundance of C. flav/triv as a supplementary independent variable, because larger species might have either a predatory or competitive impact on C. punctipennis (Roth 1968, von Ende 1979, Tsalkitzis et al. 1994). Again, I used stepwise regression to only retain the stronger predictors in the models. To evaluate multicollinearity, I examined variance inflation factors and tolerance. Finally, I explored normality of the residuals using the Shapiro-Wilks test.

Regressions only focus on single response variables. I used canonical correspondence analysis (CCA, CANOCO version 4) to investigate the relative importance of the independent variables on the composition of the whole Chaoborus assemblage. CCA is a direct gradient analysis that relates the pattern of community variation to the pattern of environmental variables (Ter Braak and Prentice 1988). Compared to other ordination techniques, CCA has several advantages. CCA is fairly robust and unaffected by data transformations (Jackson 1993, 1997). It performs well for nonlinear and unimodal relationships between species and environmental variables, which usually cause severe problems for linear ordination methods such as principal components analysis (Ter Braak 1986). I included all environmental variables in the CCA that had been found to significantly influence at least one Chaoborus group in the linear regression models, namely Fish, DOC, TP, Zmean, and Area. Additionally, I used forward selection with
999 Monte Carlo simulations to decide if any further variables proved to be significant for CCA. As with the multiple linear regressions, *Chaoborus* abundances and all non-binary response variables (except pH) were log-transformed (Table 5.1). Significance of the CCA axes was evaluated by running 999 unrestricted Monte Carlo simulations using the eigenvalues of the axes as test statistics.

**Results**

*Chaoborus* occurred in 53 of the 56 sampled lakes with average abundances of 374 larvae m\(^{-3}\) for fishless lakes and 52 larvae m\(^{-3}\) for lakes that contained fish. Maximum abundances were 895 and 201.5 larvae m\(^{-3}\), respectively. The smallest species, *C. punctipennis*, was found in a total of 50 lakes; *C. flavicans*, *C. trivittatus*, and *C. americanus* occurred in 32, 15, and 7 lakes, respectively. Twenty-three lakes supported two species and one, three, and four species were encountered in 16, 12, and 2 lakes, respectively. Lakes with only one species were inhabited by either *C. punctipennis* (15) or *C. americanus* (1). Two-species assemblages mainly consisted of a combination of *C. punctipennis* and *C. flavicans* (21), and two lakes included *C. trivittatus* and *C. americanus*. The most frequent three-species combination was *C. punctipennis*, *C. flavicans*, and *C. trivittatus* (11) and in two lakes I found *C. americanus*, *C. punctipennis*, and either *C. flavicans* or *C. trivittatus*.

The data set included a wide range of lake size and depth, water transparency, pH and nutrient level (Table 3.2). Many of the environmental variables were highly correlated (Table 3.3). Two in particular, DOC and lake depth, were each correlated with several other variables. DOC was negatively correlated with mean (-0.44) and maximum lake depth (-0.43), and with Secchi depth (-0.91). DOC and total phosphorus were positively correlated (0.77). Mean lake depth (Zmean) was positively correlated with maximum lake depth (0.94), lake volume (0.72),
Table 3.2: Classification table for logistic regressions (P = 0.5)

<table>
<thead>
<tr>
<th>Chaoborus group</th>
<th>Correct</th>
<th>Incorrect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Presence</td>
<td>Absence</td>
</tr>
<tr>
<td>C. americanus</td>
<td>49</td>
<td>7</td>
</tr>
<tr>
<td>C. flav/triv</td>
<td>35</td>
<td>10</td>
</tr>
<tr>
<td>C. punctipennis</td>
<td>48</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 3.3: Pearson correlation coefficients (r) for the selected lake variables.

<table>
<thead>
<tr>
<th></th>
<th>C. punc</th>
<th>C. big</th>
<th>C. am</th>
<th>C. tot</th>
<th>DOC</th>
<th>Secchi</th>
<th>TP</th>
<th>pH</th>
<th>Zmean</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. punc</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. big</td>
<td>0.39</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. am</td>
<td>-0.30</td>
<td>0.17</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. tot</td>
<td>0.63</td>
<td>0.63</td>
<td>0.40</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>DOC</td>
<td>0.24</td>
<td>0.42</td>
<td>-0.01</td>
<td>0.26</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Secchi</td>
<td>-0.23</td>
<td>-0.39</td>
<td>-0.10</td>
<td>-0.33</td>
<td>-0.91</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TP</td>
<td>0.15</td>
<td>0.41</td>
<td>0.21</td>
<td>0.36</td>
<td>0.77</td>
<td>-0.81</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>-0.10</td>
<td>-0.09</td>
<td>-0.45</td>
<td>0.37</td>
<td>0.03</td>
<td>0.09</td>
<td>0.01</td>
<td>1.00</td>
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</tr>
<tr>
<td>Zmean</td>
<td>-0.41</td>
<td>-0.39</td>
<td>-0.30</td>
<td>-0.58</td>
<td>-0.44</td>
<td>0.53</td>
<td>-0.45</td>
<td>0.44</td>
<td>1.00</td>
</tr>
<tr>
<td>Area</td>
<td>-0.12</td>
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<td>-0.40</td>
<td>-0.48</td>
<td>-0.15</td>
<td>0.18</td>
<td>-0.47</td>
<td>0.20</td>
<td>0.44</td>
</tr>
<tr>
<td>Volume</td>
<td>-0.25</td>
<td>-0.52</td>
<td>-0.42</td>
<td>-0.59</td>
<td>-0.15</td>
<td>0.34</td>
<td>-0.53</td>
<td>0.32</td>
<td>0.71</td>
</tr>
<tr>
<td>ZO₂</td>
<td>-0.03</td>
<td>0.24</td>
<td>0.01</td>
<td>0.11</td>
<td>0.01</td>
<td>0.03</td>
<td>0.18</td>
<td>0.25</td>
<td>0.26</td>
</tr>
<tr>
<td>Fish</td>
<td>0.27</td>
<td>-0.22</td>
<td>-0.95</td>
<td>-0.38</td>
<td>0.05</td>
<td>0.04</td>
<td>-0.14</td>
<td>0.44</td>
<td>0.27</td>
</tr>
<tr>
<td>strata</td>
<td>-0.29</td>
<td>-0.01</td>
<td>0.03</td>
<td>-0.19</td>
<td>-0.28</td>
<td>0.33</td>
<td>-0.20</td>
<td>0.30</td>
<td>0.77</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th></th>
<th>Zmax</th>
<th>Area</th>
<th>Volume</th>
<th>ZO₂</th>
<th>Fish</th>
<th>Strata</th>
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<tbody>
<tr>
<td>Zmax</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>0.45</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Volume</td>
<td>-0.53</td>
<td>0.94</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ZO₂</td>
<td>0.28</td>
<td>-0.56</td>
<td>-0.18</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish</td>
<td>0.24</td>
<td>0.37</td>
<td>0.39</td>
<td>0.25</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>strata</td>
<td>0.68</td>
<td>0.05</td>
<td>0.29</td>
<td>0.40</td>
<td>-0.07</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Stratification (0.65), and Secchi depth (0.53). The correlation of depth and volume is spurious, given that lake volume is used in the calculation of mean depth. Zmean and TP (-0.45) were negatively correlated. According to the correlation coefficients, the most influential variables were presence of Fish for *C. americanus*, Zmean for *C. punctipennis*, and DOC, TP, ZO₂, and Area for *C. flav/triv*.

**Logistic Regression**

For *C. americanus*, I found a complete separation of data points using only presence and absence of Fish as the sole independent variable. All seven fishless lakes supported *C. americanus* but this species never occurred in any of the 49 lakes with fish. Accordingly, the classification was 100% correct (Table 3.2), as were sensitivity (correct prediction of true presence) and specificity (correct prediction of true absence).

The larger species, *C. flavicans* and *C. trivittatus* (*C.flav/triv*), occurred in 39 lakes and were absent in 17 lakes. The two most important variables found by the logistic regression were DOC (p = 0.06) and Area (p = 0.003) (Table 3.4). DOC had a positive regression coefficient and Area a negative coefficient, with 41% of the variance explained by the model (R² = 0.41). Eighty % of the lakes were classified correctly (Table 3.2 and 3.4); sensitivity and specificity were 90% and 59%, respectively.

Two significant variables were found to explain the presence and absence of *C. punctipennis*: Average depth (Zmean, negative coefficient) and Fish (positive coefficient) with p-values of 0.05 and 0.006, respectively (R² = 0.34). The classification was 87.5% correct (Table 3.2 and 3.4), with a sensitivity of 96% and a specificity of 17%. The low specificity showed that this model had little ability to accurately predict absence of *C. punctipennis* from these lakes. Low specificity is likely due to the small sample size (N = 6).
Table 3.4: Logistic regression models for the different *Chaoborus* groups including all 56 lakes. C. am. = C. americanus, C. punc. = C. punctipennis, C. fla/triv = C. flavicans + C. trivittatus (p-values for the individual variables are given in parenthesis following the variables)

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. am. = complete separation of data points</td>
<td></td>
</tr>
<tr>
<td>C. punc. = - 1.2 + 3.8 Fish [0.006] – 4.8 Zmean [0.05]</td>
<td>0.34</td>
</tr>
<tr>
<td>C. fla/triv = 5.3 + 2.7 DOC [0.06] – 5.3 Area [0.003]</td>
<td>0.41</td>
</tr>
</tbody>
</table>
Multiple Linear Regression

After selecting those variables that could be used to predict Chaoborus presence and absence, I were interested in determining if these variables could be used to predict Chaoborus abundance in those lakes where the species occurred. Hence, I performed multiple linear regressions for C. punctipennis, C. flav/triv, and C. americanus. Considering only the seven fishless lakes in which C. americanus was found, the most important variable for explaining abundance was total phosphorus (TP, positive coefficient) with a p-value of 0.07 (Table 3.5). The model accounted for 48% of the total variability. The analysis for the two larger species that can co-exist with fish (C. flav/triv) showed that both DOC (p-value = 0.003, positive coefficient) and Area (p-value = 0.0002, negative coefficient) had significant effects on abundance ($R^2 = 0.36$). Most important for the abundance of C. punctipennis were the abundance of large species (negative coefficient, Fig. 3.1), lake depth (negative coefficient), and fish (positive coefficient) with p-values of 0.005, 0.001, and 0.0002, respectively (Table 3.5). The proportion of total variance explained by the C. punctipennis model was 43%.

Canonical Correspondence Analysis

Forward selection of the environmental variables showed that only Fish, Area, and mean depth ($Z_{\text{mean}}$) were significant at a level of $\alpha = 0.05$. Additionally, pH, which was not selected by the regression approaches, was significant. Even though both DOC and TP were not significant in the forward selection, I still included them in the analysis since both variables were important in the regression analysis. The first two CCA axes of the ordination with the Chaoborus groups had eigenvalues of 0.479 and 0.054, respectively, explaining 68% of the total variance. Values for the species-environment correlation coefficients for axis 1 and 2 were 0.89
Table 3.5: Multiple linear regression models for the different *Chaoborus* groups. C. am. = *C. americanus*, C. punc. = *C. punctipennis*, C. flav/triv = *C. flavidans* + *C. trivittatus*. (n = number of lakes where species group occurred; p-values for the individual variables are given in parenthesis following the variables)

<table>
<thead>
<tr>
<th>Model</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. am. (n = 7) = -4.1 + 3.6 TP [0.07]</td>
<td>0.48</td>
</tr>
<tr>
<td>C. punc. (n = 50) = 3.2 +C.flav/triv [0.005] + 3.9 Fish [ 0.0002] – 1.2 Zmean [0.001]</td>
<td>0.43</td>
</tr>
<tr>
<td>C. fla/triv = (n = 39) 2.25 + 2.4 DOC [0.003] – 1.2 Area [0.0002]</td>
<td>0.36</td>
</tr>
</tbody>
</table>
Figure 3.1, top: *C. punctipennis* densities (ind. m$^{-3}$) as a function of *C. fla/triv* densities. Bottom: Lakes with less than 10 ind. m$^{-3}$ for *C. punctipennis* and less than 1 ind. m$^{-3}$ for *C. fla/triv* are omitted and the abundances for both species are presented on a logarithmic scale.
and 0.57, respectively, indicating strong correlations between the Chaoborus groups and the environmental variables. Species axis1 had the highest correlation with Fish followed by pH (Table 3.6). Because Fish and pH were correlated ($R^2 = 0.53$), axis 1 represented a gradient from low pH and absence of fish to higher pH values in combination with the presence of fish. Axis 2 had the highest correlations with pH, Area, and DOC, emphasizing lake chemistry and morphology (Table 3.6). Both axes were highly significant ($p = 0.004$, Monte Carlo test with 999 permutations). The resulting ordination diagram (Fig. 3.2) showed that axis 1 separated fishless lakes from lakes with fish. All seven fishless lakes were located on the right side of the diagram, mapping in close proximity to C. americanus. Axis 2 divided lakes that were either dominated by C. punctipennis or the two larger species C. flav/triv. C. punctipennis occurred more frequently in larger, but shallower lakes with lower values for pH and DOC. The larger species seemed to be favored in smaller and deeper lakes with elevated DOC concentrations.

**Discussion**

The multi-station sampling protocol greatly increased the precision ($P = SE/m$, where $SE = \text{Standard Error}$ and $m = \text{abundance}$) with which the mean abundance of Chaoborus could be accurately estimated. Persaud and Yan (2001) used a subset of the data presented here to calculate the number of samples required to obtain a specified precision for different ambient Chaoborus abundances. Precision ($P$), as a function of both abundance of Chaoborus sp. ($m$) and number of samples ($n$) is given as:

$$P = \left( \frac{n}{1.94 \times m^{-0.3}} \right)^{1/2}$$

(1)

Accordingly, the precision for a typical Chaoborus abundance of 50 larvae $m^{-3}$ is 0.25 for a 10-sample data set as opposed to 0.77 for a single sample. Even a very low abundance of 5
Table 3.6: Weighted correlation matrix for the canonical correspondence analysis of 56 Dorset lakes. SP 1 = species axis 1, SP 2 = species axis 2, EN 1 = environmental axis 1, EN 2 = environmental axis 2

<table>
<thead>
<tr>
<th></th>
<th>SP 1</th>
<th>SP 2</th>
<th>EN 1</th>
<th>EN 2</th>
<th>Fish</th>
<th>DOC</th>
<th>PH</th>
<th>TP</th>
<th>Zmean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>-0.87</td>
<td>0.06</td>
<td>-0.98</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DOC</td>
<td>-0.10</td>
<td>-0.22</td>
<td>-0.11</td>
<td>-0.39</td>
<td>0.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PH</td>
<td>-0.50</td>
<td>-0.27</td>
<td>-0.57</td>
<td>-0.47</td>
<td>0.53</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TP</td>
<td>0.20</td>
<td>-0.15</td>
<td>-0.22</td>
<td>-0.24</td>
<td>-0.13</td>
<td>0.78</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zmean</td>
<td>-0.30</td>
<td>-0.08</td>
<td>-0.34</td>
<td>-0.14</td>
<td>0.35</td>
<td>-0.33</td>
<td>0.47</td>
<td>-0.31</td>
<td></td>
</tr>
<tr>
<td>Area</td>
<td>-0.42</td>
<td>0.24</td>
<td>-0.47</td>
<td>0.43</td>
<td>0.44</td>
<td>-0.06</td>
<td>0.30</td>
<td>-0.41</td>
<td>0.37</td>
</tr>
</tbody>
</table>
Figure 3.2: Association of lakes based on CCA of *Chaoborus* groups and lake characteristics. Small open circles represent the individual lakes.
larvae m$^{-3}$ still yield reasonably good precision of 0.35 for 10 samples, but an individual sample at this density would lessen precision to a level of 1.09. At high Chaoborus abundances of 500 larvae m$^{-3}$ the multi-station and single-station approaches would result in precisions of 0.17 and 0.55, respectively. In this data set, 24 out of 53 lakes including Chaoborus had less than 50 larvae m$^{-3}$ and another 11 lakes contained between 50 and 100 larvae m$^{-3}$.

Because precision is reduced, especially at low abundances, only a multi-station sampling protocol provides a precise estimate of Chaoborus abundances for statistical analysis. Similar conclusions about the importance of multiple sampling stations per lake were also drawn by Visman et al. (1994), Tsalkitzis et al. (1994), and Veijola et al. (1996). In general, I think that the sampling protocol has two major advantages over previous studies of Chaoborus distribution: (1) better estimates of Chaoborus abundances and (2) the ability to detect multi-species occurrences. With the intensive sampling, I was able to detect three or more Chaoborus species in 14 out of 56 lakes (25%), whereas other studies recorded co-occurrence of three species in only zero to 15% the lakes. Moreover, four species have never been reported from an individual lake, but I found four-species assemblages in two lakes.

The regression and correspondence analyses indicate that both top-down (fish predation) and bottom-up (nutrient levels) factors can, at times, affect the distribution and abundance of the different species of Chaoborus. However, the different species of Chaoborus were not affected in the same manner by environmental gradients. The effects of fish predation in particular appear to vary with both Chaoborus body size and environmental factors that likely create fish-free refugia.

The first major division was presence and absence of fish, as C. americanus only occurred in fishless lakes, a pattern that is quite consistent with the literature (von Ende 1979, Yan et al.
Within fishless lakes, the abundance of *C. americanus* was positively correlated with total phosphorus (TP, Table 3.5). Hence, in the absence of predation, more productive systems appear to support higher *Chaoborus* densities (Yan et al. 1982).

Unlike *C. americanus*, *C. punctipennis* co-existed with fish, which is also a well-known pattern (Carter et al. 1980, Yan et al. 1985, Campbell and Knoechel 1990). Not only was *C. punctipennis* found in 46 of the 49 lakes with fish, but also there was a positive relationship between abundance and presence of fish (Table 3.5). This very transparent species is known to stay fairly high in the water column even during the day, without being eliminated by fish (Roth 1968, Tsalkitzis et al. 1994). Perhaps because of its already low visibility to fish, water clarity (DOC level) did not explain substantial variation in the abundance of *C. punctipennis*.

Aside from fish, *C. punctipennis* is vulnerable to the larger chaoborids, *C. flav/triv*, both through predation and competition for zooplankton prey (von Ende 1982, Roth 1968, Tsalkitzis et al. 1994). The deleterious effects of congeners is one possible explanation of the significant negative coefficient of *C. flav/triv* on abundance of *C. punctipennis*. Whenever the large species were abundant, *C. punctipennis* was rare (Fig. 3.1). Larger chaoborids can have substantial over-wintering populations of later instars, from which early instars of *C. punctipennis* can suffer heavy predation losses in the spring and early summer. In terms of competition, the larger chaoborids can consume larger zooplankton as well as smaller prey that are the only food source exploitable by *C. punctipennis*. Therefore, larger chaoborids not only compete directly with *C. punctipennis* but can also survive on larger zooplankton whenever small prey are rare. *Chaoborus punctipennis* has better chances to coexist with the larger chaoborids when habitat and food partitioning is possible (Roth 1968, Tsalkitzis et al. 1994).
Explaining the effects of lake depth on abundance of *C. punctipennis* is difficult. *C. punctipennis* tended to reach higher densities in shallower lakes. Perhaps the warmer waters of shallow lakes (Table 3.2) enhanced growth rates of *C. punctipennis* thereby supporting larger local populations. Another explanation may be that lake depth negatively affects the level of fish predation, as cold-water species such as salmonids tend to be excluded from shallow lakes (Jackson and Harvey 1989, 1993).

The two larger species (*C. flav/triv*) did not co-exist as well with fish as *C. punctipennis*. They were found in only 32 of the 49 lakes that had fish. Their abundances were higher in smaller lakes and lakes with elevated levels of DOC. As with *C. punctipennis*, smaller lakes may support higher densities of *C. flav/triv* because of reduced fish predation (Jackson and Harvey 1989, 1993) and perhaps also warmer water.

The positive effect of DOC on abundance of *C. flav/triv* is very interesting. DOC may create refugia for *Chaoborus* that are oxygenated yet free of fish predation. The humic components of DOC strongly reduce light penetration (Schindler 1971, Jones and Arvola 1984), which should impair the ability of fish to feed. Moreover, high DOC lakes are often characterized by low hypolimnetic oxygen concentrations that are restrictive to fish (Arvola et al. 1996, Kankaala et al. 1996), thereby providing an even safer fish-free refuge for *Chaoborus*. Elevated levels of DOC should also interfere with fish consumption of other zooplankton, especially small-bodied prey. In high DOC lakes, *Chaoborus* may thus enjoy the double advantages of reduced predation from fish and reduced competition with fish. Only Nilssen (1974) has previously considered the potential positive effect of DOC on larval *Chaoborus*.

Overall, I found that direct and indirect measures of predation pressure and refuge availability were most important for the presence and abundance of the different *Chaoborus*
groups. Furthermore, very different sets of environmental factors influenced occurrence and abundance of the three Chaoborus groups. The largest species, C. americanus, was excluded from lakes with fish. The smallest and most transparent species, C. punctipennis, seemed to be more affected by the presence of larger Chaoborus species than by fish. Larger chaoborids that were able to coexist with fish required higher DOC concentrations, probably to increase refuge availability. Generally, small lakes (for C. flav/triv) and shallow lakes (for C. punctipennis), which are inhabited by fewer fish species supported higher abundances of Chaoborus. Knowing the fish species composition and biomass of fish for the individual lakes would probably have improved the quality of the models; however, fish biomass estimates are largely unavailable for Shield lakes. The overall relatively low $r^2$ values for both types of regression analyses might have been -- at least partially -- caused by the lack of detailed fish information. Furthermore, even our intense sampling protocol still did not always result in high precision of Chaoborus abundances. Especially at low Chaoborus abundances, more samples would have been necessary to achieve adequate precision.
CHAPTER 4

PLASTICITY OF VERTICAL DISTRIBUTION OF CRUSTACEAN ZOOPLANKTON IN RESPONSE TO BIOTIC AND ABIOTIC FACTORS
Introduction

Many zooplankton organisms in both freshwater and marine systems perform diel vertical migration (DVM), spending daytime in deep water layers and migrating upwards at night. Potential explanations for this behavior have been manifold. Early on, the preferred light intensity hypothesis (Russell 1926, Clarke 1930) and the metabolic advantage hypothesis (McLaren 1963, Geller 1986) were favored, but today, there is general agreement that predator avoidance is the major cause of diel vertical migration (Zaret and Suffern 1976, Wright at al. 1980, Stich and Lampert 1981, Dodson 1988, Lampert 1993). Visually guided predators such as planktivorous fish can exert a very strong predation pressure on the zooplankton community (Brooks and Dodson 1965, Taylor 1980). To avoid predation, zooplankton migrate downwards to a depth where low light intensity prevents detection by planktivorous fish. The disadvantage of this behavior is exposure to cooler temperatures and lower food concentrations. Cool temperatures cause a significant reduction in growth rate since egg development time exponentially decreases with ambient water temperature (Bottrell at al. 1975). Sub-optimal food conditions might result in reduced growth rates as well (Lampert 1977), but luxury consumption during times of high food concentrations might mitigate this cost. Sterner and Schwalbach (2001) showed that Daphnia magna has to spend only 20 to 30% of total time at high food concentration to maintain near optimum growth rates. Furthermore, metalimnetic water often has higher Chl. a concentrations than epilimnetic water (Christensen et al. 1995) so that, depending on the extent of DVM, migration to deeper waters might actually be advantageous to zooplankton feeding.

The onset of DVM is largely related to changes in relative light intensity (Ringelberg 1993) but the patterns of DVM are strongly influenced by environmental factors. The presence of
visual predators initiates the downward migration (e.g., Bollens and Frost 1991, De Stasio 1993) and the intensity of predation pressure amplifies the degree of DVM (Bollens and Frost 1989, Loose 1993, VanGool and Ringelberg 1998). Abiotic factors can modify the basic DVM patterns. Dodson (1990) found a strong positive relationship between the intensity of DVM and water transparency, whereas others have found that low hypolimnnetic temperatures and oxygen concentrations might limit the extent of DVM (Davidson and Kelso 1997, Young and Watt 1993, Marcogliese and Esch 1992, Calaban and Makarewitz 1982, Field and Prepas 1997).

The relative importance of these environmental factors on DVM is still unknown. Han and Straškraba (1998) developed a model to predict DVM patterns of *Daphnia* in relation to food concentration, temperature, and predation pressure. But thus far many conclusions about DVM in response to environmental variables have been drawn from laboratory studies. Most studies focused on *Daphnia* in experimental water columns that were usually shorter than one or two meters. Therefore, it is uncertain how these laboratory results apply to natural lake conditions and zooplankton organisms other than *Daphnia*. With its large body size and poor ability to escape predator attacks, *Daphnia* might not be representative for other zooplankton groups, and the amplitude of DVM in lakes usually far exceeds the height of laboratory water columns. Furthermore, many important environmental variables not only differ among lakes but also change over time within an individual lake.

Appropriate systems to study DVM under natural conditions seem to be lakes with different concentrations of dissolved organic carbon (DOC). DOC not only determines water color (Rasmussen et al. 1989, Molot and Dillon 1997) -- an excellent predictor for water transparency, especially in oligo- and meso-trophic lakes (Koenings and Edmundson 1991, Lean 1998) -- but also alters temperature and oxygen gradients (Salonen at al. 1983, Arvola et al. 1996, Fee at al.
1996, Snucins and Gunn 2000). Hence, lakes that differ in water color should also vary in
temperature and oxygen profiles. While water color remains relatively stable throughout the
season, temperature and oxygen profiles, and Secchi depth might vary over time.

To test the effects of water transparency, temperature-, and oxygen-profiles on the daytime
vertical position of (1) small cladocerans, (2) large cladocerans, ands (3) copepods, I sampled the
crustacean zooplankton in ten lakes with different water color between May and August of 2000.
Because all lakes contained planktivorous fish, and vulnerability to fish predation increases with
zooplankton body size (Brooks and Dodson 1965, De Robertis et al. 2000), I expected small
species to stay higher in the water column than large ones. While clearer water should cause an
overall downward shift in vertical position, low temperatures and oxygen concentrations might
restrict this downward migration.

Methods

Field Sampling and Evaluation

Our study lakes were located in Algonquin Park, Ontario, Canada. Individual lakes were
selected on the basis of obtaining a set of small lakes with similar morphology and trophic state
that span a wide range in water color (Table 4.1).

All lakes were sampled three times in 2000. The first sampling took place between 21 May
and 24 May, except for Longairy Lake, which was not included into this study until 7 June. The
second sampling occurred between 24 June and 26 June, and the last sampling was performed
from the 3 to 5 of August.

At each sampling, I measured Secchi depth and obtained temperature and oxygen profiles in
1 m intervals at the site of maximum depth. I then defined the epilimnion (temperature decrease <
1 °C m⁻¹), metalimnion (temperature decrease > 1 °C m⁻¹), and hypolimnion (temperature
Table 4.1: Characteristics of the 10 study lakes, spring / summer 2000. Zmax = Max. depth, TP = total phosphorus, Chl. a = Chlorophyll a, \(Z_{8^\circ C}\) = depth at 8°C, \(Z_{O2}\) = Depth at < 3 mg O\(_2\) L\(^{-1}\)

<table>
<thead>
<tr>
<th>Lake</th>
<th>Area (ha)</th>
<th>Zmax (m)</th>
<th>Color (CoPt)</th>
<th>TP (µg L(^{-1}))</th>
<th>Chl. a (µg L(^{-1}))</th>
<th>Secchi (m)</th>
<th>(Z_{8^\circ C}) (m)</th>
<th>(Z_{O2}) (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Found</td>
<td>12.1</td>
<td>31.7</td>
<td>6</td>
<td>4.9</td>
<td>1.1</td>
<td>8.5 - 12.0</td>
<td>5.5 - 9.5</td>
<td>32 - 25</td>
</tr>
<tr>
<td>Scott</td>
<td>27.6</td>
<td>25.0</td>
<td>15</td>
<td>9.8</td>
<td>1.5</td>
<td>3.5 - 5.5</td>
<td>6.0 - 9.0</td>
<td>25 - 18</td>
</tr>
<tr>
<td>Longairy</td>
<td>28.3</td>
<td>17.4</td>
<td>20</td>
<td>13.2</td>
<td>2.0</td>
<td>4.5 - 5.2</td>
<td>5.5 - 7.5</td>
<td>17 - 10</td>
</tr>
<tr>
<td>Heron</td>
<td>24.3</td>
<td>10.7</td>
<td>21</td>
<td>11.3</td>
<td>3.0</td>
<td>3.5 - 4.5</td>
<td>5.5 - 10.0</td>
<td>10 - 7</td>
</tr>
<tr>
<td>Cecil</td>
<td>15.8</td>
<td>16.2</td>
<td>24</td>
<td>8.7</td>
<td>2.8</td>
<td>2.7 - 4.0</td>
<td>4.5 - 7.0</td>
<td>12 - 10</td>
</tr>
<tr>
<td>Peck</td>
<td>8.3</td>
<td>13.7</td>
<td>24</td>
<td>10.4</td>
<td>1.8</td>
<td>3.5 - 4.0</td>
<td>4.5 - 7.0</td>
<td>14 - 8</td>
</tr>
<tr>
<td>Brewer</td>
<td>39.7</td>
<td>14.3</td>
<td>39</td>
<td>9.1</td>
<td>1.0</td>
<td>3.0 - 4.5</td>
<td>4.5 - 6.0</td>
<td>13 - 11</td>
</tr>
<tr>
<td>Costello</td>
<td>33.5</td>
<td>18.9</td>
<td>45</td>
<td>11.1</td>
<td>1.3</td>
<td>2.3 - 3.5</td>
<td>5.0 - 6.0</td>
<td>19 - 17</td>
</tr>
<tr>
<td>Clarke</td>
<td>25.3</td>
<td>11.3</td>
<td>53</td>
<td>12.3</td>
<td>2.4</td>
<td>2.0 - 3.5</td>
<td>5.0 - 6.0</td>
<td>11 - 6</td>
</tr>
<tr>
<td>Kearney</td>
<td>32.0</td>
<td>18.3</td>
<td>58</td>
<td>9.7</td>
<td>1.4</td>
<td>2.0 - 2.8</td>
<td>4.0 - 5.5</td>
<td>18 - 14</td>
</tr>
</tbody>
</table>
decrease $< 1 \, ^{\circ}\text{C m}^{-1}$) as well as a low light layer (Secchi depth to $1.5 \times$ Secchi depth) and a low oxygen layer ($< 1 \, \text{mg L}^{-1} \text{O}_2$). To obtain zooplankton samples, I took vertical net hauls with a closing net (diameter 30 cm, 130 $\mu$m mesh size) for each of the five individual layers. Samples were preserved in 4% sugar formalin (Haney and Hall 1974) and enumerated under a dissecting microscope. Copepods were sorted into calanoids and cyclopoids. Cladocerans were identified to species and for *Daphnia* and *Holopedium* I also differentiated between small ($< 1 \, \text{mm body length}$) and large individuals ($> 1 \, \text{mm body length}$). If available, at least 100 individuals per species (cladocerans) or group (copepods) were counted. For further analyses, I combined the taxa *Daphnia* and *Holopedium* to “large cladocerans”, *Bosmina*, *Ceriodaphnia*, and *Diaphanosoma* to “small cladocerans”, and calanoids and cyclopoids to “copepods”. No other crustacean species occurred frequently enough to be included into the analysis.

For the analyses of water color, total phosphorus (TP), and Chl. *a*, I took integrated water samples for a combined epi- and metalimnion sample (June sampling). Water color was evaluated according to Cuthbert and Del Giorgio (1992) as the absorption at 440 nm. Chl. *a* was measured from algae samples (500 mL), filtered onto 1.2 $\mu$m GF/F filters, extracted over night with 100% acetone, and measured fluorometrically (Sterman 1988). TP samples were analyzed by the Ontario Ministry of the Environment using standard methods.

**Data Analysis**

To quantify the average depth of distribution for each zooplankton group, I calculated the density-weighted depths using the appropriate dimensions of epi-, meta-, and hypolimnia from each lake and sampling date. To evaluate the relative importance of abiotic factors in determining vertical position of the three zooplankton groups, I performed stepwise multiple linear regression (SAS version 8) for each sample date and for all dates combined. The
significance level was set to 0.1 for variable entry and to 0.05 for variable retention. As independent variables, I chose Secchi depth ($Z_{sec}$) as a measure for water transparency, depth at 8 °C ($Z_{8°C}$) to assess if cold hypolimnetic temperatures affect DVM, and the depth of hypoxic water ($< 1$ mg O$_2$ L$^{-1}$, $Z_{O2}$) to test the effects of low oxygen. Moderately low oxygen levels might offer a refuge for zooplankton since most species can withstand lower oxygen concentration than fish. However, very low oxygen concentrations can be restrictive for zooplankton as well.

I used analyses of covariance (SAS version 8) to test for differences in vertical position among zooplankton groups and sampling dates. Furthermore, I evaluated if the zooplankton depth differed within season and between seasons. To obtain normally distributed data (Shapiro-Wilk test; $p > 0.05$), the average depth of the zooplankton groups (dependent variable) and all independent variables were log-transformed. I included maximum lake depth in the stepwise regressions. Even though I did not expect this variable to affect the vertical position of zooplankton, I wanted to test if lake depth confounded any of the independent variables.

I did not have a direct measure of fish predation but I obtained recent information on fish presence and absence for all ten lakes from the Ontario Ministry of Natural Resources (MNR). In the early summer of 1999, the Algonquin Fisheries Assessment Unit (AFAU) tested fishing gear in one lake, Cecil Lake. The lake was cleared of fish and then was restocked only with large quantities of juvenile brook trout. The remaining nine lakes contained between seven and 21 fish species, with a tendency for clear lakes to have fewer species.

Results

The study lakes were fairly small (8.3 to 33.5 ha) but were deep enough (10.7 to 31.7 m) to stratify throughout the sampling period. All lakes were oligo- to meso-trophic (total phosphorus 4.9 to 13.2 µg L$^{-1}$) with Chl. $a$ concentrations between 1.0 and 3.0 µg L$^{-1}$. Although
morphometry and trophic state of the lakes were similar, water color varied over one order of magnitude (6 to 58 CPU). I did not detect a relationship between lake depth and area, but I found positive association between TP and Chl. al as well as between water color and lake area, and a negative association of water color and lake depth. Nevertheless, the slopes of the regression lines were not significantly different from zero in all cases. Consequently, I concluded that water transparency was the major factor distinguishing our study lakes while lake morphometry and nutrient levels were of minor importance.

Secchi depth ranged from 2 to 12 m and was highly correlated with water color ($R^2 = 0.92, 0.87, \text{and } 0.93 \text{ for May, June, and August, respectively}$). Throughout the season, I observed a decrease in Secchi depth, a trend that was consistent for all lakes (Figure 4.1). $Z_{8\degree C}$ was four to five meters in May and increased by August to about six meters in the more colored lakes, but reached up to 10 m in the clearest lakes (Figure 4.1). Concomitantly, the maximum hypolimnion temperature increased by 1 - 2 °C from May to August with overall cooler temperatures in more colored lakes. This trend of warmer hypolimnetic water in clear lakes has been previously described by Molot and Dillon (1997).

The hypoxic layer increased from May to August. In May, most lakes had oxygen concentrations of more than 3 mg L$^{-1}$ throughout the water column. By August, all lakes showed at least some degree of hypoxia, whereby the upward extension of $Z_{O2}$ was 1 - 4 meters in more colored lakes and 4 - 7 meters in the clearer lakes. Consequently, the depth at hypoxia ($Z_{O2}$) decreased from May to August and ranged from 6 to more than 30 m, depending on maximum lake depth. While water color was negatively correlated with $Z_{8\degree C}$ ($R^2 = 0.41, 0.62, 0.73 \text{ for May, June, and August, respectively}$), $Z_{O2}$ was neither related to water color nor to $Z_{8\degree C}$. 
Figure 4.1: Relationships between water color (CoPt Units) and Secchi depth (m, top panel), depth at 8°C ($Z_{8C}$ in m, middle panel), and depth at < 1mg O$_2$ L$^{-1}$ ($Z_{O2}$ in m, bottom panel). Open circles = May, Gray squares = June, Black triangles = August. Black bar = maximum lake depth (bottom panel).
The average zooplankton abundance in the study lakes ranged from less than 3 ind. L\(^{-1}\) to almost 20 ind. L\(^{-1}\) (Figure 4.2). Most abundant were copepods, representing 40 to 90% of total zooplankton abundance. Some lakes were dominated by calanoids and others by cyclopoids, but no clear patterns emerged in relation to either sampling date or other lake characteristics. The second most abundant group was large cladocerans, contributing up to 50% of the total abundance. *Holopedium* usually appeared during earlier sampling dates and *Daphnia* was more abundant later in the season, making co-occurrence rare. Small cladocerans were the least abundant zooplankton group and never contributed more than 25% of total abundance. Interestingly, small cladocerans were found in moderate to very clear lakes at all sampling dates, but became prevalent in more colored lakes only later in the season. While *Bosmina* was found consistently, *Diaphanosoma* occurred only in August, the last sampling date.

Vertical position significantly differed among zooplankton groups and sampling dates. Even though I observed a wide range in vertical position, small cladocerans usually stayed higher in the water column than large cladocerans. Copepods were usually deepest. This pattern was consistent independent of water color and season.

According to the stepwise logistic regressions, all three independent variables (Secchi depth, \(Z_{O2}\), and \(Z_{8\degree C}\)) significantly influenced the vertical position of zooplankton. Maximum lake depth never met the significance criteria to be included in a model (Table 4.2).

For all three sampling dates combined, large cladocerans and copepods followed similar trends: with increasing Secchi depth, \(Z_{O2}\), and \(Z_{8\degree C}\) the zooplankton stayed further down in the water column. For copepods, Secchi depth and \(Z_{8\degree C}\) were equally important, while large cladocerans were predominantly influenced by \(Z_{8\degree C}\) (Fig. 4.3 and 4.4). For small cladocerans, the only significant variable proved to be Secchi depth. Overall, the regression models explained 40,
Figure 4.2: Abundance (ind. L⁻¹) of the major zooplankton groups in the 10 study lakes in May, June, and August 2000. First letter: F = Found Lake, S = Scott Lake, H = Heron Lake, L = Longairy Lake, Ce = Cecil lake, P = Peck Lake, Br = Brewer Lake, Co = Costello lake, Cl = Clarke Lake, K = Kearney Lake; Second letter: M = May, J = June, A = August.
Figure 4.3: Mean depth (log_{10}, in m) of copepods (top panel), large cladocerans (middle panel), and small cladocerans (bottom panel) as a function of Secchi depth (log_{10}, in m). Open circles = May, Gray squares = June, Black triangles = August. R^2 values for regression lines are shown in upper right corner of each panel (top = May, Middle = June, Bottom = August). For large cladocerans, lakes with hypolimnetic *Daphnia* species are represented as open triangles. For small cladocerans, regression line is only shown for August.
Table 4.2: Multiple linear regressions using combined sampling dates for copepods, large cladocerans, and small cladocerans. Only variables are included where $\alpha < 0.05$. Actual p-values are shown in parenthesis.

<table>
<thead>
<tr>
<th>Zooplankton group</th>
<th>Model</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods</td>
<td>Avg. depth = -0.79 + 0.56 Secchi + 0.39 $Z_{O2}$ + 0.93 $Z_{8^\circ C}$</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large cladocerans</td>
<td>Avg. depth = -1.16 + 0.31 Secchi + 0.39 $Z_{O2}$ + 1.40 $Z_{8^\circ C}$</td>
<td>0.72</td>
</tr>
<tr>
<td>Small cladocerans</td>
<td>Avg. depth = -0.14 + 0.99 Secchi</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 4.4: Mean depth (log_{10}, in m) of large cladocerans as a function of depth at 8ºC (Z_{8C} log_{10}, in m). Open circles = May, Gray squares = June, Black triangles = August. R^2 values for regression lines are shown in upper right corner (top = may, Middle = June, Bottom = August).
74 and 72% of total variation (R^2) for small cladocerans, copepods, and large cladocerans, respectively (Table 4.2).

Multiple regressions for individual sampling dates revealed further differences among zooplankton groups (Table 4.3). For copepods, Secchi depth consistently proved to be the best predictor for vertical position. With R^2 values between 0.72 and 0.78, the fit of the individual models was very good. For large cladocerans, both Secchi depth and Z_{8°C} were important predictors with R^2 values ranging from about 0.5 to 0.9. While in August only Secchi depth turned out to be significant, the vertical position in May and June was significantly affected only by Z_{8°C}.

For small cladocerans, I did not find any significant relationships for May and June, possibly due to absence of these organisms from lakes with high water color. In August, a combination of Z_{O2} and Z_{8°C} best explained the vertical position of small cladocerans (R^2 = 0.86). Interestingly, Secchi depth could not further improve the model, even though Secchi depth significantly affected the vertical position of small cladocerans when used as solitary variable (R^2 = 0.41).

From our regression results, I inferred that Secchi depth was the variable with overall best predictive power. Even though Z_{O2} and Z_{8°C} yielded higher R^2 values for certain combinations of zooplankton group and sampling, only Secchi depth was significant for all zooplankton groups and sampling dates. Consequently, I performed an analysis of covariance (ANCOVA) using Secchi depth as sole covariable. This approach might have lowered our power to detect differences among groups and sampling dates, but I preferred a more purposeful selection of variables, rather than simply constructing models based on maximum R^2.

The ANCOVA with Secchi depth showed highly significant differences among sampling dates and zooplankton groups (p < 0.001) but no strong interaction (Table 4.4). Using pair-wise
Table 4.3: Multiple linear regressions for individual sampling dates for copepods, large cladocerans, and small cladocerans. Only variables are included where $\alpha < 0.05$. Actual p-values are shown in parenthesis. **Models with Secchi depth as independent variable used in subsequent analysis of covariance.

<table>
<thead>
<tr>
<th>Zooplankton group</th>
<th>Model</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Copepods</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>May</strong></td>
<td>Avg. depth = $0.01 + 0.94$ Secchi (0.0007)</td>
<td>0.78</td>
</tr>
<tr>
<td><strong>June</strong></td>
<td>Avg. depth = $0.21 + 0.94$ Secchi (0.0018)</td>
<td>0.73</td>
</tr>
<tr>
<td><strong>August</strong></td>
<td>Avg. depth = $0.07 + 1.19$ Secchi (0.0019)</td>
<td>0.72</td>
</tr>
<tr>
<td><strong>Large cladocerans</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>May</strong></td>
<td>Avg. depth = $-1.21 + 2.43$ $Z_{8^\circ C}$ (0.005)</td>
<td>0.64</td>
</tr>
<tr>
<td><strong>June</strong></td>
<td>Avg. depth = $0.03 + 0.69$ Secchi (0.025)</td>
<td>0.51</td>
</tr>
<tr>
<td><strong>August</strong></td>
<td>Avg. depth = $0.13 + 0.83$ Secchi (0.01)</td>
<td>0.67</td>
</tr>
<tr>
<td><strong>Small cladocerans</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>May</strong></td>
<td>Avg. depth = $-1.16 + 1.40$ $Z_{8^\circ C}$ $+ 0.39$ $Z_{O2}$ (0.001) (0.014)</td>
<td>0.86</td>
</tr>
<tr>
<td><strong>June</strong></td>
<td>Avg. depth = $-1.16 + 0.31$ Secchi (0.04)</td>
<td>0.41</td>
</tr>
</tbody>
</table>
Table 4.4: Results from analysis of covariance to test for effects of size and sampling date using Secchi depth as independent variable. Tukey test is used for pair wise comparisons. Due to absence from several lakes, small cladocerans are excluded from detailed within / between month comparisons.

<table>
<thead>
<tr>
<th>Effect</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size</td>
<td>0.0001</td>
</tr>
<tr>
<td>Sampling date</td>
<td>0.0001</td>
</tr>
<tr>
<td>Size * sampling date</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Pair wise comparisons

<table>
<thead>
<tr>
<th>Comparison</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods vs. lg. cladocerans</td>
<td>0.004</td>
</tr>
<tr>
<td>Copepods vs. sm. cladocerans</td>
<td>0.0001</td>
</tr>
<tr>
<td>Lg. cladocerans vs. lg. cladocerans</td>
<td>0.008</td>
</tr>
<tr>
<td>May vs. June</td>
<td>0.05</td>
</tr>
<tr>
<td>May vs. August</td>
<td>0.03</td>
</tr>
<tr>
<td>June vs. August</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Between month comparisons

<table>
<thead>
<tr>
<th>Comparison</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods</td>
<td>May vs. June</td>
</tr>
<tr>
<td>Copepods</td>
<td>May vs. August</td>
</tr>
<tr>
<td>Copepods</td>
<td>June vs. August</td>
</tr>
<tr>
<td>Lg. cladocerans</td>
<td>May vs. June</td>
</tr>
<tr>
<td>Lg. cladocerans</td>
<td>May vs. August</td>
</tr>
<tr>
<td>Lg. cladocerans</td>
<td>June vs. August</td>
</tr>
</tbody>
</table>

Within month comparisons

<table>
<thead>
<tr>
<th>Month</th>
<th>Comparison</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>copepods vs. lg. cladocerans</td>
<td>0.05</td>
</tr>
<tr>
<td>June</td>
<td>copepods vs. lg. cladocerans</td>
<td>0.04</td>
</tr>
<tr>
<td>Aug.</td>
<td>copepods vs. lg. cladocerans</td>
<td>n.s.</td>
</tr>
</tbody>
</table>
comparisons, I found that all three zooplankton groups were significantly different from each other, and for sampling dates, June and August formed a group that was different from May. For the comparison of zooplankton groups within and among sampling dates I only included large cladocerans and copepods. Small cladocerans occurred in all lakes only in August. The vertical position for both copepods and large cladocerans was significantly higher in May compared to the two subsequent sampling dates where these organisms stayed deeper in the water column. Contrasting the individual sampling dates showed that in May and June copepods were significantly deeper than large cladocerans while in August this difference was not significant.

**Discussion**

The selected study lakes were well suited for testing the relative importance of light, temperature, and oxygen gradients on patterns of zooplankton vertical distribution. I did not detect any significant confounding relationships between either lake area, depth, and water color and total phosphorus and Chl. *a*. Because all lakes were relatively small and deep, they were well stratified throughout the sampling period. Hence, I conclude that our study lakes were fairly homogenous in terms of morphology and trophic state, and the major source of variation among the lakes was water color with concomitant effects on light, temperature, and oxygen profiles. Furthermore, the prevailing zooplankton species assemblages were comparable to other Canadian Shield lakes (Yan et al. 1996) and canonical correspondence analyses did not reveal any significant patterns between species and environmental variables, neither for fish, nor for zooplankton (B. Wissel unpublished data).

Previous research suggests that light, temperature, and oxygen profiles could have a strong impact on the vertical position of zooplankton but conclusions about their relative importance have been controversial. For example low temperatures and oxygen concentrations might
actually be advantageous to copepods (Svetlichny et al. 2000), yet seem to be avoided by cladocerans (Haney 1993, Davidson and Kelso 1997, Field and Prepas 1997, Masson and Pinel-Alloul 1998). Unfortunately, studies on copepods were mainly performed in marine systems, while most cladocerans are restricted to freshwater. Thus, it is unclear if these divergent responses to environmental factors were taxon-specific or system-specific. Our analysis included all major zooplankton groups in several lakes that differed in light, temperature, and oxygen profiles. Therefore, I was able to not only relate specific vertical positions to environmental variables, but also to test if the observed patterns were consistent among lakes and over time.

In our study lakes, the average vertical position of the zooplankton ranged from less than one meter to more than 10 m, and relationships to environmental factors were quite variable, depending on zooplankton group and sampling date. Overall, Secchi depth was the most consistent variable for predicting vertical position. However, for individual zooplankton groups and sampling dates, temperature and oxygen profiles also significantly influenced zooplankton vertical position.

The vertical position of copepods was mainly dependent on Secchi depth, especially when individual sampling dates were analyzed individually. This result supports the contention that copepods are not strongly affected by low temperatures and oxygen concentrations. Nevertheless, $Z_{O2}$ and especially $Z_{S\text{C}}$ did significantly influence the vertical position, when all sampling dates were analyzed together. In this case, information on oxygen and temperature gradients improved the $R^2$ value from 0.55 for Secchi depth alone to 0.74 for the complete model. Together these results suggest that even though Secchi depth is the dominant factor affecting DVM patterns of copepods, temperature and oxygen are important as well. While the
literature suggests that low temperature and oxygen provide energetic advantages (Svetlichny et al. 2000) our data shows that the extent of DVM might still be limited by these factors.

Surprisingly, large cladocerans (*Holopedium* and *Daphnia*) were predominantly influenced in their migration behavior by temperature profile. For all sampling dates combined, as well as just in May and June, \(Z_{8\degree C}\) was by far the most important variable. These organisms were likely avoiding cold, hypolimnetic water that would have strongly reduced the population growth rate. While \(Z_{8\degree C}\) increased from May to August, Secchi depth decreased over the same time period. Consequently, in August, once a thick layer of warm water was established, large cladocerans were not restricted by cold temperatures anymore, Secchi depth became the most important factor influencing vertical position. The relatively low \(R^2\) value (0.49) for August can be explained by the occurrence of a hypolimnetic species, *Daphnia longiremis*, in two of the study lakes. In these two lakes, the average depth of large cladocerans was well below the regression line, and their omission improved the \(R^2\) value to 0.67. The discrepancy of results among sampling dates shows that Secchi depth cannot be used unambiguously as the sole variable to predict DVM, as suggested by Dodson (1990). The temperature profile is especially critical for both small lakes and for samples taken in early summer. The vertical position of large cladocerans in large lakes with an extensive epilimnion is probably less affected by the temperature profile.

The vertical position of small cladocerans was less affected by environmental factors. For the combined sampling dates, Secchi depth was the only significant variable, but the \(R^2\) value of only 0.39 shows that the majority of variation remained unexplained. For May and June, I could not find any significant variables, while in August \(Z_{O2}\) and \(Z_{8\degree C}\) proved to be significant. These inconclusive results made it difficult to relate the vertical position of small cladocerans to
environmental variables, partially because this zooplankton group did not occur in clear lakes until August. It is possible that the DVM patterns of small cladocerans might depend more on factors not considered in the analysis, such as abundance of larger, competitively superior zooplankton species. Moreover, the agency of invertebrate predators might be important as well, since small zooplankton species are their preferred prey (Pastorok 1981, Riessen at al. 1988, Vanni 1988).

Besides evaluating the response of the different zooplankton groups to environmental factors, it was fascinating to see how consistent vertical position of the different zooplankton groups were relative to each other. Independently of lake and sampling date, small cladocerans were always found higher in the water column than large cladocerans, followed by copepods. Small cladocerans suffer the least predation pressure from planktivorous fish (e.g., Sevrin-Reysac 1998), hence, extensive vertical migration and resulting exposure to lower temperatures is unnecessary. Unless small cladocerans prefer the hypolimnnion (Mueller 1984, Horppila 1997), these organisms are usually found in fairly shallow water (Wright et al. 1980, Makino at al. 1996).

Large cladocerans and copepods on the other hand, are well known to perform extensive vertical migrations, with adults tending to stay further down than juveniles of the same species (Vuorinen at al. 1983, Hays et al. 1994, Brancelj and Blejic 1994, Makino et al. 1996, Boronat and Miracle 1997). I observed this in our study lakes as well for both copepods and cladocerans. While in August, there was no significant difference among vertical positions, in May and June, and I found that copepods remained deeper than large cladocerans. In May and June, large cladocerans were restricted in their migration by low hypolimnetic temperatures, while in August, Secchi depth was the only variable affecting the vertical position of both copepods and
large cladocerans. Hence, these two zooplankton groups had a very similar response once the same environmental factor was responsible for their vertical migration.

According to the literature, the relative depth at which copepods and cladocerans are found is not consistent. In some cases, copepods were located at greater depth than large cladocerans (Buchanan and Haney 1980, Wright at al. 1980, Taleb et al. 1993), but in other studies large cladocerans migrated further down (Buchanan and Haney 1980, Angeli et al. 1995). These finding are not surprising since, in our study, these zooplankton groups often reacted to different environmental cues. Lake-specific gradients of environmental variables strongly affect migration behavior within individual lakes.

Finally, I observed that copepods and large cladocerans remained significantly deeper in June and August compared to May, a trend that was not apparent for small cladocerans. Neither Secchi depth, temperature, nor oxygen levels could explain this simultaneous downward-shift in vertical position. Since water clarity actually decreased from May to August, I would have expected the opposite trend, if Secchi depth had been influential. Hypolimnetic oxygen levels decreased from May to August, which should have acted to restrict the downward migration. The seasonal change in temperature profiles might have favored a downward migration, since hypolimnnion temperature increased from May to August. Yet, temperature further increased from June to August without an affect on migration behavior. Therefore, it is unlikely that temperature was a factor.

I suggest that predation from fish may have driven zooplankton deeper in the lakes. One common observation is that the predation from planktivorous fish increases during the summer months compared to spring (De Stasio 1991, Flik and Ringelberg 1993). In 2000, the spring was very cold, which kept water temperatures in May fairly low and hatching of fish eggs was
delayed (B. Wissel, personal observation). Since intensity of DVM is strongly dependent on predation pressure from fish, I concluded that increased predation, rather than abiotic factors caused the extended migration in June and August. This would also explain why only the more vulnerable copepods and large cladocerans were affected, while small cladocerans did not change migration behavior among sample dates.

Overall, due to our selection of study lakes and seasonal sampling dates, I was able to assign the migratory behavior of different zooplankton groups to specific combinations of biotic and abiotic variables. Even though the vertical position of individual zooplankton groups was quite variable, I still found consistent patterns among lakes, sampling dates, and zooplankton groups. Our results show that the relative importance of environmental factors is specific to different zooplankton groups and can also change seasonally in a taxon-specific manner.
CHAPTER 5

EFFECTS OF WATER COLOR ON PREDATION REGIMES AND ZOOPLANKTON ASSEMBLAGE IN FRESHWATER LAKES
Introduction

Typically, freshwater lakes are categorized according to their nutrient load on a scale ranging from oligo- to eutrophic, with total phosphorus explaining most of the variability (Vollenweider and Kerekes 1980). In general, this classification seems to work well for many lakes. However, lakes with strongly colored brown water are often classified incorrectly (Chow-Fraser and Duthie 1983). Early this century Thienemann (1925) described the concept of dystrophy (dy: Swedish for mud) to characterize brown water lakes, and Birge and Juday (1927) discovered that the organic matter in dystrophic lakes mainly derives from external (allochthonous) sources, as opposed to the internally (autochthonous) produced organic matter in clear lakes. Even though Rohde (1969) tried to incorporate the concept of dystrophy into the established nutrient-based classification, it was mainly thought of as a “pathological condition” of lakes (Hutchinson 1967). Recently, Carpenter and Pace (1997) suggested that eutrophy and dystrophy might be alternative stable states of lakes. Williamson et al. (1999a) have now argued that phosphorus and dissolved organic carbon (DOC) should both be considered for proper lake characterization, since phosphorus load accounts for the effects of eutrophication, whereas DOC interferes with light, oxygen, and temperature profiles, as well as toxin availability and acidification. The humic compounds of DOC are the major source for increased water color (Thurman 1985, Wetzel and Likens 1991), whereby DOC concentrations varying from 0.5 to 20 mg carbon L$^{-1}$ are enough to span the range from crystal clear to darkly tea-colored waters.

Over the last two decades, many studies have focused on the direct effects of DOC on isolated food web components, but the combined effects of DOC on food webs in brown water lakes remain unknown. Due to its pervasive effects, DOC influences several variables within aquatic systems, affecting all trophic levels. The humic components of DOC strongly attenuate
light (Schindler 1971, Jones and Arvola 1984), which may reduce foraging abilities of visually
guided predators such as fish. Reduced light intensity not only decreases the reactive distance of
Wright et al. 1980) but also their overall predation rate (Bergman 1987, Persson 1986). At
adequate light levels, planktivorous fish select larger prey (Brooks and Dodson 1965, Taylor
1980), but at reduced visibility they lose the ability for size-selective predation (Janssen 1980).
Accordingly, Wissel et al. (chapter 2) observed reduced fish abundances in strongly colored
lakes together with changes in the fish species composition.

Besides the attenuation of visible light, DOC also absorbs UV light (Williamson et al. 1996,
Yan et al. 1996). UV radiation can damage a broad range of biota, and particularly susceptible
are surface dwelling organisms that are highly exposed to UV radiation (Beardall et al. 1997,
1997), transparent organisms that lack protective pigmentation such as zooplankton (Williamson
et al. 1994, 1999b, Zaragese et al. 1994) and fish eggs and larvae (Williamson et al. 1997, 1999,
Hunter et al. 1981). Even adult fish might be affected, experiencing sunburn or damage to the
eyes (Blazer et al. 1997, Siebeck et al. 1994). In lakes with high DOC concentrations, UV
penetration is limited to only a few centimeters and organisms are well protected, but in lakes
with very low DOC concentrations, UV light can penetrate deep into the water body and may
cause serious damage to lake inhabitants.

Furthermore, increased DOC affects the vertical profile of temperature (Snucins and Gunn
2000). As more light energy is absorbed in the upper surface layer, epilimnion depth can be
reduced (Mazumder et al. 1990, Mazumder and Taylor 1994), most prominently in lakes smaller
than 500 ha (Fee at al. 1996). DOC also affects the vertical profile of oxygen. Less light is
available for photosynthesis, thereby reducing oxygen production. Bacteria directly metabolize
DOC leading to increased bacterial production and an even lower P/R ratio (oxygen-production /
These studies show that especially in the hypolimnion, reduced oxygen concentrations or even
anoxia is common in brown water lakes. On the other hand, increased bacterial production can
compensate for low primary production, since bacteria can be used as food source not only by
protozoans but also by filter feeders like *Daphnia* (Cladocera, Crustacea). Under these
conditions, carbon that cycles through bacteria can be the major energy source to daphnids

By attenuating light and oxygen, DOC may provide refugia against planktivorous fish for
many invertebrate predators and zooplankton prey. Unlike fish, zooplankters do not require light
for food gathering and can adapt to lower oxygen concentrations (Heisey and Porter 1977, Fox
lakes might be a warmer habitat temperature, especially for the many crustaceans that undergo a
diurnal vertical migration (DVM). To avoid visually guided predators, these species stay in the
dark and cold hypolimnion during the day and migrate upwards into the warm epilimnion at
The population growth rate (*r*) of cladocerans, copepods, and rotifers is critically dependent on
water temperature, and a prolonged time period spent in the cold hypolimnion reduces *r* (Bottrell
1975, Bottrell et al. 1976). Since the extent of DVM is inversely related to water transparency
(Dodson 1990, Wissel and Ramcharan submitted, chapter 4), increased water color enables
diurnally migrating species to spend daytime at moderately warm temperatures in the
metalimnion without being detected by visually guided predators. Hence, zooplankton in brown
water lakes enjoy warmer temperatures, lower fish predation, and also higher food in the metalimnion, compared to remaining in the hypolimnion of clear lakes.

Invertebrate predators such as larvae of the phantom midge *Chaoborus* (Chaoboridae, Diptera) particularly profit from increased DOC concentrations (Wissel et al. submitted, chapter 3). These gape-limited predators prey on small- to medium-sized zooplankton (Pastorok 1981, Riessen et al. 1988, Taylor 1980, Vanni 1988). Since *Chaoborus* is itself a preferred prey of planktivorous fish, it is usually forced to stay in the sediment during daytime in clear lakes (McEachern 1986, Rahel and Nutzmann 1994, Stenson 1980). But in brown water lakes, fish predation should be strongly reduced and *Chaoborus* might be able to stay higher in the water column and forage for longer time periods. Low visibility should not interfere with feeding by *Chaoborus*, because these tactile predators do not rely on light to detect prey (Giguere 1980, Spitze 1985). Furthermore, *Chaoborus* can withstand not only low oxygen concentrations but even prolonged anoxia (Wissel et al. 2000). Support for the importance of *Chaoborus* in structuring lake food webs comes from several whole-lake studies (Kitchell and Kitchell 1980, Carpenter and Kitchell 1985, Yan et al. 1991, Ramcharan et al. 2001a, b, c). Interestingly, all of these lakes were characterized by elevated DOC concentrations.

In general, planktivorous fish feed on the largest prey available, mainly invertebrate predators, large cladocerans, and large 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). However, in brown water lakes lakes, the dominance of planktivorous fish should diminish, because of their reduced foraging abilities. Simultaneously, invertebrate predators should gain more importance in structuring the zooplankton community, since they are released from fish predation, yet are otherwise unaffected by light and oxygen.
conditions typical for high DOC lakes. This shift in planktivory from fish to invertebrates should result in a zooplankton community dominated by large cladocerans and copepods.

To test this hypothesis, I performed an enclosure study and also analyzed results from a whole lake experiment. The goals of this study were to explore (1) if water color influences the relative importance of fish and *Chaoborus* as planktivores and (2) to investigate the concomitant effects on the zooplankton composition.

**Methods**

**Enclosure Study**

To evaluate the importance of water color in structuring the zooplankton community, I performed an enclosure study in the summer of 2000 in Algonquin Park (central Ontario, Canada). Two lakes with contrasting water color were chosen as study sites. Longairy Lake served as the clear water lake and Clarke Lake served as the brown water lake. The lakes were in close proximity (< 1 km) and had very similar morphology and water chemistry. Although lake morphometry, total phosphorus as well as pH were almost identical for these two lakes, water transparency characteristics such as Secchi depth and water color differed greatly (Table 5.1).

Presence and absence of fish (golden shiner, *Notemigonus crysoleucus*) and *Chaoborus trivittatus* allowed us to test the effects of these two most important planktivorous predators, whereby both predators were applied at natural lake densities (fish: 40 kg ha\(^{-1}\); *Chaoborus*: 0.3 ind. L\(^{-1}\)). Golden shiners were chosen over northern redbelly dace, pumpkinseed, and yellow perch because golden shiners had the highest survival rates in a preliminary enclosure experiment performed in the moderately stained Costello Lake (Böing and Wissel, unpublished data). With *Chaoborus trivittatus* I selected the largest Chaoboridae that co-occurs with fish.
Table 5.1: Lake characteristics of Longairy Lake (clear) and Clarke Lake (brown water), which were used for the enclosure study in summer 2000.

<table>
<thead>
<tr>
<th></th>
<th>Longairy Lake</th>
<th>Clarke Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (ha)</td>
<td>28.3</td>
<td>25.3</td>
</tr>
<tr>
<td>Max. depth (m)</td>
<td>17.4</td>
<td>11.3</td>
</tr>
<tr>
<td>Avg. depth (m)</td>
<td>6.0</td>
<td>5.3</td>
</tr>
<tr>
<td>pH</td>
<td>6.8</td>
<td>6.4</td>
</tr>
<tr>
<td>Total phosphorus (µg L⁻¹)</td>
<td>13.2</td>
<td>12.3</td>
</tr>
<tr>
<td>Color (CoPt units)</td>
<td>20</td>
<td>53</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>2.5</td>
<td>5.0</td>
</tr>
</tbody>
</table>
Because *C. trivittatus* is a voracious predator on a wide range of prey, I should have been able to detect potential *Chaoborus* effects on the zooplankton community within the short duration of this enclosure experiment. Furthermore, if this large species were found to survive well with fish under high water color conditions, smaller chaoborids should be affected even less by fish predation. Using *Chaoborus trivittatus* thus gave us a conservative estimate of the importance of *Chaoborus* in brown water lakes. Three replicates of this 2x2x2 factorial design (Color x Fish x *Chaoborus*) resulted in a total of 24 enclosures.

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

Ten days prior to the experiment, the enclosures were filled with a fire pump directed through a 200 µm mesh. After temperature stratification became established (3 days), equal aliquots of a mix of the natural zooplankton communities of both study lakes were added to each enclosure. The zooplankton was allowed to acclimate and grow for one week before predators were added. *Chaoborus* was added to the enclosures one day prior to fish to allow them to distribute vertically and avoid artificially high predation losses to fish.

Every eight days for about six weeks, I sampled the zooplankton with a closing net (Ø 30cm, 130µm mesh size) in three layers (0-3, 3-5, 5-7 m). Additionally, I took temperature and oxygen profiles as well as Secchi depth readings. Day/night distribution of the zooplankton (3rd and 6th sampling), Chlorophyll *a*, and total phosphorus (TP) were determined twice (2nd and 5th sampling).
Zooplankton samples were preserved in 4% sugar formalin (Haney and Hall 1973) and counted under a dissecting microscope. Taxonomic identifications of cladocerans were made according to Brooks (1957), Edmondson (1959), and Thorp and Corvich (1991). Saether (1970) was used for Chaoboridae. For large cladocerans, as well as copepods I distinguished between large (>1 mm length) and small individuals (<1 mm length), and estimates of biomass were conducted according to Bottrell et al. (1976).

Water color was measured as absorbance at 440 nm (Cuthbert and del Giorgio 1992). For Chl. a and TP determination I randomly selected two enclosures per treatment and used a pump sampler to collect 0.5 L of the upper (0–3 m) and lower part of each enclosure (3–7 m). After separating the edible (<30 µm) and inedible fractions (>30 µm) with a Nitex mesh, both fractions were filtered through a GF/C filter (1.2 µm pore size), extracted overnight in 100% acetone, and Chlorophyll a concentration was measured fluorometrically. Total phosphorus was analyzed according to standard methods by the Ontario Ministry for the Environment (OMOE). To ensure comparable fish biomass in all treatments throughout the experiment, every four days I verified fish survival with a submersible video camera and a large 1 m diameter net (5 mm mesh). Dead fish were removed and replaced immediately. After the second sampling date, I added small amounts of phosphorus and nitrogen (5 µg P L⁻¹, N:P ration 30:1) to each enclosure to counterbalance nutrient depletion due to sedimentation (P. Dillon, pers. communication).

Lake Study

Enclosure experiments are an extremely valuable tool in aquatic sciences to test hypotheses under fairly natural but controlled conditions without giving up replication. Nevertheless, time and space limitations of enclosure studies may limit extrapolation of results to natural lakes. Whole lake experiments on the other hand have been tremendously useful to help us understand
the structure of lake food webs (Carpenter 1989, 1996, Wissel at al. 2000, Ramcharan 2001a),
even if these experiments remained unreplicated. The Algonquin Fisheries Assessment Unit
(AFAU) chose two lakes of similar morphometry (Table 5.2) to compare various kinds of fishing
gear. Fortunately, these two lakes strongly differed in water color. In spring 1999, both lakes
were fished extensively until no more fish were caught. The lakes were then stocked with equal
amounts of brook trout (*Salvelinus fontinalis*) to test the efficiency of different kinds of fishing
gear (B. Monroe, pers. communication). Afterwards both lakes remained unaltered and their
location in the interior of Algonquin Park prevented recreational fishing and other human
disturbances.

In July 1999 and June 2000, I took separate zooplankton samples for epi-, meta-, and hypo-
limnia at the location of maximum depth of both lakes using a closing net (⌀ 30cm, 130µm
mesh size). Temperature and oxygen profiles, Secchi depth, as well as processing of samples
were carried out as described above for the enclosure experiments.

This approach gave us the opportunity to compare the effects of water color on the
zooplankton assemblage of both a controlled enclosure study and a whole-lake experiment. If
both approaches lead to similar conclusions, I would be able to make more confident predictions
about the relative importance of fish and *Chaoborus* as predators, and their impact on the
zooplankton assemblages in lakes with contrasting water color.

**Data Analysis**

For the enclosure experiment, to test for the effects of the main factors (Color, Fish,
*Chaoborus*) and their interactions on the zooplankton assemblage, I performed 3-way
MANOVAs for each sampling day. The zooplankton abundances were used as independent
Table 5.2: Basic lake characteristics of Cecil Lake (clear) and Bena Lake (brown water) which were cleared of fish and subsequently restocked with equal densities of brook trout in spring 1999. For water color and Secchi depth, values are given for July 1999 and June 2000, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Cecil Lake</th>
<th>Bena Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (ha)</td>
<td>15.8</td>
<td>12.6</td>
</tr>
<tr>
<td>Max. depth (m)</td>
<td>16.2</td>
<td>10.2</td>
</tr>
<tr>
<td>Color (CoPt units)</td>
<td>16/24</td>
<td>75/86</td>
</tr>
<tr>
<td>Secchi depth (m)</td>
<td>4.5/2.7</td>
<td>2.0/1.5</td>
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</table>
variables wherein the following groups were analyzed: *Daphnia*, *Holopedium*, *Bosmina*, small copepods, large copepods, and *Asplanchna*. Other taxa were found only at negligible abundances.

I used Wilk’s Lamda as a test statistic for the zooplankton assemblages (MANOVA) and an F-test for the individual groups (ANOVA). To analyze potential effect of Color, Fish, and *Chaoborus* on water temperature, oxygen concentration, Secchi depth, Chl. a, and total phosphorus, I performed 3-way ANOVAs for the appropriate sampling dates. For both temperature and oxygen I limited the analysis to the depths of 1 m and 5 m.

To test for differences in the zooplankton composition related to the whole lake experiment I used a paired T-test. Here, I limited the analysis to the abundances of large cladocerans (*Daphnia* and *Holopedium*), small cladocerans (*Bosmina* and *Diaphanosoma*), copepods, and *Chaoborus*, as the occurrence of other taxa was insignificant.

**Results**

**Enclosure Study**

Between sampling date five and six, I observed excessive growth of filamentous algae on the enclosure walls which started to interfere with the experiment, affecting sampling procedure and light regime of all enclosures. Concurrently, the crustacean zooplankton showed a strong decline, independent of the treatments. Therefore, I omitted the last sampling date and restricted all analyses to the first five sampling dates covering a total of 32 days.

**Light, Temperature, and Oxygen Gradients** The major difference in terms of water transparency was related to Color. Throughout the experiment, water transparency was significantly reduced in high Color treatments compared to low Color treatments (Table 5.3, Figure 5.1).
Table 5.3: P-values for main effects and interactions (3-way ANOVA, SAS version 8) for Secchi depth (m), temperature (°C) and oxygen (mg L⁻¹) at 1 and 5 m for sampling dates 1 through 5 of the enclosure study performed in summer 2000. Secchi depth values for the first sampling date were not available.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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<tbody>
<tr>
<td><strong>Secchi depth</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>COLOR (CO)</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
</tr>
<tr>
<td>FISH (FI)</td>
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<td>0.02</td>
<td>0.01</td>
<td>0.0001</td>
<td></td>
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<tr>
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<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>CO*FI</td>
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<td>0.01</td>
<td>0.006</td>
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<tr>
<td>CO*CH</td>
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<td>n.s.</td>
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<tr>
<td>FI*CH</td>
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<tr>
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<td>n.s.</td>
<td>n.s.</td>
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<tr>
<td><strong>Temperature (1m/5m)</strong></td>
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<tr>
<td>COLOR (CO)</td>
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<tr>
<td>FISH (FI)</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
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<tr>
<td>CHAOBORUS (CH)</td>
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<tr>
<td>CO*FI</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
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<tr>
<td>CO*CH</td>
<td>n.s./n.s.</td>
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<td>n.s./n.s.</td>
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<td>n.s./n.s.</td>
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<tr>
<td>FI*CH</td>
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<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
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<tr>
<td>CO<em>FI</em>CH</td>
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<td>n.s./n.s.</td>
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<tr>
<td><strong>Oxygen (1m/5m)</strong></td>
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<tr>
<td>FISH (FI)</td>
<td>n.s./n.s.</td>
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<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
</tr>
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<td>CHAOBORUS (CH)</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
</tr>
<tr>
<td>CO*FI</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
</tr>
<tr>
<td>CO*CH</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
</tr>
<tr>
<td>FI*CH</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
</tr>
<tr>
<td>CO<em>FI</em>CH</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
<td>n.s./n.s.</td>
</tr>
</tbody>
</table>
Fig. 5.1: Chl. a (µg L⁻¹) ± SD (bars, left Y-axis) and Secchi depth (m) ± SD (circles, right Y-axis) for sampling dates 2 (top panel) and 5 (bottom panel). CO = color, FI = fish, CH = Chaoborus; whereby capital letters represent presence in the case of predator treatments and high color for color treatments.
While Secchi depth was 3.5 to 5.8 m in low Color treatments, it ranged from 2.4 to 3.5 m in high Color treatments. Additionally, I detected a significant Fish effect, whereby the presence of fish resulted in reduced Secchi depth, but this effect was less pronounced in high Color enclosures (significant Fish x Color interaction).

The only significant differences in temperature profiles were associated with Color (Table 5.3, Fig. 5.2). Overall, the epilimnia in high Color treatments was warmer and shallower than in low Color treatments. While on three out of five sampling dates the water at 1 m was significantly warmer in high Color treatments compared to low Color treatments, at 5 m, the temperature in high Color treatments was consistently cooler by several °C than in low Color treatments.

Oxygen concentrations were generally lower in high Color enclosures (Table 5.3, Fig. 5.2). While this pattern was very pronounced at a depth of 5 m, at 1 m I found significantly lower oxygen concentration in high Color treatments only on two out of five sampling dates.

Total Phosphorus and Chl. a  For total phosphorus (TP) I did not detect significant differences related to any of the applied treatments (Table 5.4). Mean overall TP concentrations were 11.0 ± 1.1 µg L\(^{-1}\) and 14.2 ± 1.2 µg L\(^{-1}\) for sampling dates 2 and 5, respectively. The slight increase from sampling date 2 to sampling date 5 shows that the continual addition of 5 µg L\(^{-1}\) of P successfully prevented nutrient depletion and kept the enclosures at a mesotrophic state.

Chl. a concentrations increased approximately threefold from sampling date 2 to sampling date 5 (Fig. 5.1). The majority of Chl. a was contained in the edible fraction smaller 30 µm, supplying 80% and 90% of the total Chl. a on sampling date 2 and 5, respectively. The relative importance of the upper (0 – 3 m) and lower layer (3 – 7 m) did not differ significantly among either treatments or sampling dates. Yet, in low Color treatments the deeper layer supplied about
Fig. 5.2: Oxygen (mg L\(^{-1}\)) ± SD (left) and temperature (°C) ± SD (right) for sampling date 2 (top panel) and 5 (bottom panel). Solid bars represent depth at 1 m and striped bars depth at 5 m. Treatments are labeled as in figure 5.1. For the sake of efficiency, I present only data for sampling dates 2 and 5, but the results of the remaining sampling dates were very similar.
Table 5.4: P-values for main effects and interactions (3-way ANOVA, SAS version 8) for total phosphorus (µg L\(^{-1}\)) and edible fraction (< 30 µm) of Chl. a (µg L\(^{-1}\)), for sampling dates 2 and 5 of the enclosure study. No significant effects were found for the inedible fraction (> 30 µm).

<table>
<thead>
<tr>
<th>Total Phosphorus</th>
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<th>5</th>
<th>Chl. a</th>
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<th>5</th>
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</thead>
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<tr>
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<td>n.s.</td>
<td>COLOR (Co)</td>
<td>n.s.</td>
<td>n.s.</td>
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<tr>
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<td>n.s.</td>
<td>FISH (Fi)</td>
<td>n.s.</td>
<td>0.007</td>
</tr>
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<td>n.s.</td>
<td>CHAOBORUS (CH)</td>
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</tr>
<tr>
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<td>n.s.</td>
<td>Co*Fi</td>
<td>n.s.</td>
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</tr>
<tr>
<td>Co*Ch</td>
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<td>Co*Ch</td>
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</tr>
<tr>
<td>Fi*Ch</td>
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<td>Fi*Ch</td>
<td>n.s.</td>
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</tr>
<tr>
<td>Co<em>Fi</em>Ch</td>
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<td>n.s.</td>
<td>Co<em>Fi</em>Ch</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
</tbody>
</table>
60% of total Chl. a while in high Color treatments this portion was reduced to 40%, hinting at
light limitation in high Color treatments. Because I did not find significant differences between
the two layers, I used depth-weighted average Chl. a concentration of each enclosure for further
analyses. The large, inedible fraction slightly increased from sampling date 2 to 5, but no
significant treatment effects were found for any of the sampling dates (Table 5.4). The smaller,
edible fraction showed a much more pronounced increase from sampling date 2 to 5 and I did
detect significant effects due to Fish and Chaoborus for sampling date 5, wherein the presence of
predators resulted in higher Chl. a concentrations.

**Zooplankton Assemblage** Initial zooplankton densities were very similar for all treatments
and ranged from 1 to 2 ind. L\(^{-1}\). Final densities on the other hand varied tenfold, from 2 to almost
20 ind. L\(^{-1}\), depending on experimental treatment (Fig. 5.3). The overall most abundant organism
was *Bosmina*, but in individual cases *Asplanchna* and small copepods could be 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. 5.4). *Diaphanosoma brachyurum*, an intermediate sized
cladoceran, and large copepods were restricted to high Color x Fish treatments, but densities
never exceeded 0.15 and 0.5 ind. L\(^{-1}\), respectively.

Initially, densities of large and moderate sized zooplankton did not statistically differ among
treatments (Table 5.5). Nevertheless, small copepods were more common in high Color
treatments (1.5 ± 0.8 ind. L\(^{-1}\) vs. 0.4 ± 0.2 ind. L\(^{-1}\)) while *Bosmina* was more frequent in low
Color treatments (0.29 ± 0.15 ind. L\(^{-1}\) vs. 0.16 ± 0.07 ind. L\(^{-1}\)). There were no other initial trends
in zooplankton assemblage among the different treatments in the experiment.
Fig. 5.3: Zooplankton abundance (ind. L$^{-1}$) for sampling dates 1 through 5. Species with maximum abundances of less than 0.5 ind. L$^{-1}$ are not shown. Daphnia = Daphnia sp., Holop. = Holopedium gibberum, lg cope = large copepods, sm cope = small copepods, Bosmina = Bosmina longirostris, Aspl = Asplanchna priodonta. Treatments are labeled as in figure 5.1.
Fig. 5.4: Zooplankton biomass (mm$^3$ L$^{-1}$) for sampling dates 1 through 5. Daphnia = *Daphnia* sp., Holop. = *Holopedium gibberum*, Diaph = *Diaphanosoma brachyurum*, Ig cope = large copepods, sm cope = small copepods, Bosmina = *Bosmina longirostris*, Aspl = *Asplanchna priodonta*. Treatments are labeled as in figure 5.1.
As the experiment progressed, zooplankton assemblages deviated among treatments, with differenced most pronounced on sampling dates 3 and 4 (Fig. 5.3 and 5.4). Sampling date 5 showed an overall decrease in zooplankton biomass independent of treatment that was even more intense for the last (omitted) sampling date.

In the absence of either predator, large zooplankton species strongly increased. This effect was more pronounced in high Color treatments relative to low Color treatments, wherein *Daphnia* dominated high Color treatments but *Holopedium* was more important in low Color treatments (Fig. 5.4). In terms of biomass, small crustaceans were relatively unimportant in the absence of predators. The presence of fish heavily suppressed zooplankton abundances, especially in low Color treatments where only *Bosmina* and the rotifer *Asplanchna* occurred at relatively high densities. On the other hand, in high Color treatments with fish, small species were able to maintain densities comparable to no-predator treatments, and even large cladocerans could persist, but at reduced densities.

The effect of Chaoborus was ambiguous. As expected, *Bosmina* suffered the most serious predation losses in high Color treatments, but surprisingly, in low Color treatments large species – predominantly *Daphnia* – were reduced (Fig. 5.3 and 5.4).

The results of the combined predator treatments (Fish and Chaoborus) were similar to the Fish treatments, but the zooplankton was able to sustain overall higher densities. While 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 analysis, after the first sampling date all three main factors and most of their interactions significantly affected overall zooplankton composition as well as individual species (Table 5.5). A significant effect of Color meant that one or more zooplankton
Table 5.5: P-values for main effects and interactions for the zooplankton assemblage (MANOVA) and individual zooplankton groups (3-way ANOVA) for sampling dates 1 through 5 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 1 and 2). Significant differences are in bold numbers, n.s. = p-value > 0.05.

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<th>B</th>
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<th>sm cop</th>
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<td>n.s.</td>
<td>n.s.</td>
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<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
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<td>n.s.</td>
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<td>n.s.</td>
<td>n.s.</td>
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<td>0.01</td>
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<td>0.03</td>
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<td>n.s.</td>
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<td>0.02</td>
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<td>n.s.</td>
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<td>n.s.</td>
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<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
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groups would either benefit or suffer under conditions of high water color. The same conclusions could be drawn for effects of Fish and Chaoborus whereby the presence of a specific predator could be either advantageous or detrimental. While *Bosmina*, *Holopedium*, and *Asplanchna* remained unaffected by Color, *Daphnia* as well as small and large copepods had significantly increased abundances in 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*, while 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 impact of Fish varied between high and low Color treatments. Our results show 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, I did not detect either consistent Color*Chaoborus or Fish*Chaoborus interactions.

**Predation Regimes** In low Color treatments 11 of the 12 original fish survived until the termination of the experiment. In contrast, the high Color treatments had only seven of 12 fish surviving to the end. Starting at sampling date 3, individual fish had to be replaced with conspecifics. The presence of *Chaoborus* seemed to have enhanced fish survival, but this effect was not statistically 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, I could not assume that the initial densities of *Chaoborus* would remain unchanged in the presence of fish. Even though our sampling technique was inappropriate for *Chaoborus* (Persaud and Yan 2001),
our net hauls gave us a useful estimate about *Chaoborus* abundances in the different treatments. Here, I only present approximate densities for the night sampling (third sampling date), since during the day, *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 ind L$^{-1}$, which was slightly lower than initial densities. While 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 ind L$^{-1}$.

**Vertical Migration of Zooplankton** Due to omission of the last sampling date, I only present data on diurnal vertical migration (DVM) for the third sampling date. Because I did not detect species-specific differences in the vertical distribution of zooplankton, I 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), so it was excluded from the analysis. Two main patterns emerged from our results. First, in the absence of fish, neither large nor small crustaceans performed diurnal vertical migration. Independently of Color, the majority of organisms stayed high up in the water column during day and night (Fig. 5.5). Secondly, in high Color treatments both small and large crustaceans remained at shallow depth throughout day and night. The presence of fish triggered DVM only in low Color treatments. Nevertheless, this downward migration in low Color treatments was reduced in the presence of *Chaoborus* in the combined predator 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 PTU in July 1999 and June 2000, respectively. For the same dates the water color in Bena Lake was 75 and 86 PTU (Table 5.2). Nevertheless, this difference was not
Fig. 5.5: Day and night distribution of crustacean zooplankton on sampling date 3. Data are presented as relative frequency (0 to 1) found within the three sampling strata. Upper, middle, and lower bars represent the sampling strata 0 – 3 m, 3 – 5 m, and 5 – 7 m, respectively. The left and right sides of each graph show the vertical distribution during day and night, respectively. White portions are large species (*Daphnia*, *Holopedium*, *Diaphanosoma*) and dark portions are small species (*Bosmina* as well as small and large copepods).
Fig. 5.6: Zooplankton abundance (ind. L\(^{-1}\)) Bena Lake and Cecil Lake in July 1999 and June 2000. Daphnia = \textit{Daphnia sp.}, Holop. = \textit{Holopedium gibberum}, Diaph = \textit{Diaphanosoma brachyurum}, cyclo = cyclopoid copepods, cala = calanoid copepods, Bosmina = \textit{Bosmina longirostris}. Depth intervals (m) represent epi-, meta-, and hypo-limnia.
truly reflected in Secchi depth, probably due to an algae bloom in Cecil Lake in June 2000. The epilimnion in Bena Lake (1.0 and 2.0 m) was generally shallower than in Cecil Lake (3.0 m).

Even though these two lakes had a similar fish assemblage, the resulting zooplankton assemblages were very distinct (Fig. 5.6). Bena Lake had significantly more large 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 as well. In Bena Lake, maximum abundances were found in the epilimnion, even for the large species. Cecil Lake, on the other hand, was characterized by meta- and hypolimnetic maxima of zooplankton, independent of species. In Bena Lake I found a lot more *Chaoborus* larvae (0.3 and 0.1 ind.L\(^{-1}\) in 1999 and 2000, respectively) than in Cecil Lake (0.001 and 0.001 ind.L\(^{-1}\) in 1999 and 2000, respectively), but this difference was only marginally significant (p = 0.08).

**Discussion**

**Enclosure Study**

The experimental design I chose was very appropriate to study the effects of water color on the relative importance of fish and invertebrate predators in structuring the zooplankton community. Our high Color treatments closely re-created light, temperature, and oxygen gradients commonly described for brown water lakes. Secchi depth was significantly lower in high Color treatments, which is mainly a function of elevated DOC concentration (Jones 1992), especially in oligo- to meso-trophic lakes (Koenigs and Edmundson 1991, Lean 1998). I also found the typical shift in temperature profile, to a warmer but shallower epilimnion in high Color treatments, as described by Snucins and Gunn (2000). Finally, the oxygen concentrations in high Color treatments were significantly reduced compared to low Color treatments, predominantly in
deeper water. This is in good agreement with Arvola (1996) and Kankaala et al. (1996), who described very low oxygen concentrations for the hypolimnia of many brown water lakes in Scandinavia.

Our first concern was to evaluate if 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, I did not obtain accurate density estimates. Nevertheless, I could assume that Chaoborus densities in the absence of fish were between the initially added 0.3 ind. L$^{-1}$ and 0.2 ind. L$^{-1}$, our estimate originating from night sampling. While in high Color treatments, presence of fish only marginally affected Chaoborus densities, in low Color treatments Chaoborus were decreased by a factor of 10. Hence, I can conclude that high water color can protect even large species such as C. trivittatus from substantial losses due to fish predation. Reduced light intensities probably impeded fish perception of prey and size-selective feeding, thereby supplying a light refuge.

In a preliminary enclosure experiment, golden shiner had survival rates of about 90 %, exceeding the survival of other planktivorous fish species (Böing and Wissel, unpublished data). Although this study was performed in a colored lake (45 PTU, Secchi depth 2.3 to 3.0 m), 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 treatments during the experiment described here. Asphyxiation as a potential mortality factor could be ruled out, because oxygen concentrations never fell below 3.2 mg L$^{-1}$. Furthermore, I did not see any obvious signs of either fungus or other infections that could have weakened fish.
In conclusion, in low Color treatments fish were the dominant planktivore, independent of the presence or absence of Chaoborus. But in High Color treatments the impact of fish diminished and Chaoborus gained in significance. These experimental results confirm previous, empirical studies on the contrasting roles of fish and Chaoborus in food web of lakes with opposing water color (see chapter 1, chapter 2).

I hypothesized that these altered predation regimes should have effects on the zooplankton assemblages. The statistical analyses showed that all three main factors Color, Fish, and Chaoborus significantly affected zooplankton abundances. However, a credible interpretation of these effects is only valid if the initial prey densities were not significantly different. Even though I 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 µm mesh that I 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* this effect 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, I can assume that the initial zooplankton assemblages were comparable and subsequent changes could be accredited to treatment effects.

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, Ronneberger et al. 1993, Wissel et al. 2000).
Nevertheless, the fish effect was reduced in high Color treatments. Crustacean zooplankton, independently 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*, that were virtually absent in low Color treatments with Fish, persisted in high Color treatments. This significant Fish*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 for the vertical migration of crustacean zooplankton (Dodson 1990), wherein elevated water color resulted in a shallower daytime position of crustaceans (Wissel and Ramcharan chapter 3, submitted). In low Color enclosures containing fish, zooplankton was forced deep into the water column with maximum abundances in the hypolimnion. In high Color treatments, the zooplankton did not undergo DVM and stayed high up in the water column day and night. Hence, these organisms never exposed their eggs to low temperatures, which would have significantly increased egg development time (Bottrell et al. 1976) and decreased population growth rates (Orcutt and Porter 1983, Meyers 1984).

Due to mouth gape limitation, I expected *Chaoborus* to prey mainly on small species, which should release large species from competition and result in their dominance. This pattern has been widely described in the literature (von Ende and Dempsey 1981, Pastorok 1981, Elser et al. 1987, Hanazato and Yasumo 1989, Christofferson 1990, Arnott and Vanni 1993) and was clearly confirmed in our enclosures that had high water color. Carpenter et al. (1985) even suggested taking advantage 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 while for small species the presence of *Chaoborus* was beneficial. Even though unexpected, this result was not completely surprising. In the absence of fish, large Chaoboridae are capable of suppressing even large zooplankton species (Pope et al. 1973, von Ende and Dempsey 1981, Mac Kay et al. 1990, Stenson and Svensson 1994, Wissel and Benndorf 1998).

Interestingly, both potential effects of *Chaoborus* occurred during our enclosure experiment. Low water color caused a shift towards large zooplankton, and low water color caused a shift towards small species. Food limitation could be excluded as a possible confounding factor since Chl. a concentrations did not differ significantly among treatments, and the small, edible fraction was always dominating. Furthermore in the case of food limitation, one would rather expect *Bosmina* to decline and not *Daphnia*, since the latter is known to be the superior competitor (Gliwicz 1990). Instead, I suggest that differences in vertical migration behavior between high and low Color treatments were responsible for the opposite effects of *Chaoborus* on the zooplankton assemblage. 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 structures, which further supports the previously described ambiguity of *Chaoborus* effects on the zooplankton structure. The use of a smaller *Chaoborus* species such as *C. puntipennis* or *C. flavicans* might have concealed this result, since only large chaoboridae 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 variable effects of Chaoborus reminds us how critical the behavioral component is in determining the structure of a food web.

Lake Study

Finally, I wanted to test if the conclusions deriving from our enclosure study were applicable to natural lakes. Hence, I analyzed the zooplankton structure in two lakes with similar morphometry and fish composition that greatly differed in water color. The strongly colored Bena Lake had a consistently shallower epilimnion and a more pronounced anoxic zone than Cecil Lake. Since I found the anticipated color-related light, temperature, and oxygen profiles in these two lakes, I also expected Chaoborus to be more important in Bena Lake combined with a shift to large zooplankton species. Unfortunately, our sampling technique was inadequate for accurate estimates for Chaoborus densities. Nevertheless, in Bena Lake I did find 100 to 300 times more Chaoborus than in Cecil Lake. The fact that this difference was not significant was most likely due to the small sample size of two. The zooplankton compositions in Bena Lake and Cecil Lake strongly resembled the high and low Color treatments in our enclosure experiments, respectively. Bena Lake had significantly higher abundances of large species and reduced densities of copepods compared to Cecil Lake. Furthermore, the difference in water color was also reflected in 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 hypo-limnion. Since the abundances of fish in these two lakes were comparable, the differences in zooplankton assemblages and migration behavior could be attributed to poor
prey perception of planktivorous fish. Brook trout, the only prevailing fish species in these two lakes, is found more frequently in colored lakes (see chapter 2). Therefore, even this fairly well-adapted species was unable to impact the zooplankton in the way it should be in clear lakes.

Conclusions

In conclusion, the results from our enclosure and lake study showed that elevated water color resulted in reduced fish predation pressure on *Chaoborus* and zooplankton. The crustacean zooplankton was even 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* is usually strongly suppressed by fish in clear water lakes, as has been described in top-down food web models (Carpenter et al. 1985). In brown water lakes *Chaoborus* becomes a much more important part of the food web.

The fact that *Chaoborus* is preyed upon by fish but also competes with fish for prey results in a much more intriguing food web structure, called intraguild predation (IGP). To survive, the intra-guild 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).

*Chaoborus* as an ambush predator is known to be extremely energy-efficient (Giguere 1980). Recently, Ramcharan et al. (2001a) and McQueen et al. (2001) showed that in brown water lakes *Chaoborus* was a much more effective predator on zooplankton prey than fish. The effects were not only restricted to the zooplankton assemblage, but also changed the pattern of energy flow through the food web.

Thus, I agree with Rohde (1969) and Williamson et al. (1999) who suggested that brown water lakes represent a distinct lake type. First, water color affects light, temperature, and
oxygen profiles and thereby changes the physical habitat of a lake. Secondly, brown water lakes cannot considered to be unproductive (Hutchinson 1967) and cannot be classified just by their nutrient load (Chow-Fraser and Duthie 1983). Finally, the food web structure in brown water lakes switches from top-down to intra-guild predation affecting the zooplankton assemblage and energy flow through the food web.
CHAPTER 6

SUMMARY AND CONCLUSIONS
Brown water lakes have been described as a distinct lake type for more than 80 years. Nevertheless, our knowledge about the physical, chemical, and biological processes that are characteristic for these lakes is still limited. Over the last two decades, many studies focused on specific effects of water color and DOC on isolated biotic and abiotic components. From these studies, it emerged that not only light, but also temperature, and oxygen profiles in brown water lakes are distinct from those in clear water lakes. Hence, one would expect that the food web structure might be different as well. But surprisingly, the potential effects of water color on the aquatic food web structure have not been studied yet. Therefore, the focus of my dissertation was to explicitly compare the food web structures of brown water and clear water lakes.

I paid special attention to the planktivore-zooplankton link, since the two major planktivores, fish and *Chaoborus* not only compete for food but also have a predator-prey relationship. In brown water lakes, prey perception by visually guided fish should be strongly impaired. *Chaoborus* on the other hand, is a tactile predator that does not depend on light for prey detection and should benefit from elevated water color due to reduced predation pressure from fish. Therefore, water color has the potential to alter the relative importance of these two predators and change the food web structure from top-down to intraguild predation. Since fish prefer larger prey but *Chaoborus* feed on smaller zooplankton, an increased significance of *Chaoborus* in brown water lakes should further promote a shift in zooplankton composition to larger species.

I tested the above hypothesis by using a combination of analyses of large synoptic lake data sets and experimental manipulations. First, I examined the effects of lake morphometry and water quality on fish abundance and species composition of 200 lakes located in the northeastern U.S. Regression analysis confirmed established patterns for species richness and abundance of
fish that were already known from other studies. For example, species richness increased with lake size and depth, but decreased with lake elevation. Total phosphorus had a positive effect on overall abundance of fish. Water color, previously ignored in comparable analyses, proved to be very important. While water color did not affect fish species richness, it significantly reduced overall abundance, which supported my hypothesis that water color would be detrimental to fish. On one hand, reduced fish abundances could affect all species in the same manner, but could also be accompanied by a shift in species composition. According to the CANOCO, clearly the latter was true. Brook trout, most native cyprinids, brown bullhead, sucker, and burbot were more common in colored lakes. In contrast, centrachids, and especially common carp, were found more frequently in less colored but more eutrophic lakes. This pattern became even more obvious after separating the effects of lake morphology from water quality. For the first time, I could show the effects of water color on the fish assemblage. Elevated water color not only resulted in reduced fish abundances but also shifted the species composition to small native cyprinids and bottom-dwelling fish such as brown bullhead, sucker, and burbot.

In the next chapter, I analyzed the impact of lake morphology, water quality, and presence of fish on abundance and species composition of Chaoborus, the other important planktivore in freshwater lakes. Fortunately, I had access to the largest and most comprehensive lake survey for Chaoborus, which provided reliable abundances and species composition of Chaoborus for more than 50 lakes (Ontario, Canada). Overall, I found that direct and indirect measures of predation pressure and refuge availability were most important for the presence and abundance of the different Chaoborus groups. Furthermore, very different sets of environmental factors influenced occurrence and abundance of the three Chaoborus groups. The largest species, C. americanus, was excluded from lakes with fish. The smallest and most transparent species, C. punctipennis,
seemed to be more affected by the presence of larger Chaoborus species than by fish. Larger chaoborids required higher DOC concentrations to coexist with fish. DOC probably enhanced refuge availability. Generally, small lakes (for C. flavicans and C. trivittatus) and shallow lakes (for C. punctipennis), which are inhabited by fewer fish species supported higher abundances of Chaoborus.

Subsequently, I focused on the behavioral response of the zooplankton prey to vertical gradients of light, temperature, and oxygen. To examine the relative importance of light, temperature, and oxygen profiles in determining the extent of vertical migration, I sampled the zooplankton distribution in ten lakes that strongly differed in water color (Algonquin Park, Ontario, Canada). As dependent variables, I used mean depth for each of the three major crustacean zooplankton groups for all three sampling dates. Secchi depth, depth of hypoxic water, and depth at 8 °C were my independent variables. Regression analysis showed that small cladocerans did not respond to any of the independent variables. However, the vertical positions of large cladocerans and copepods were significantly affected by all three independent variables, Secchi depth was most important for copepods but large cladocerans were most strongly influenced by depth at 8 °C. Both groups migrated deeper into the water column in June and August rather than in May, coinciding with increased predation pressure due to the appearance of juvenile fish. Overall, due to my selection of study lakes and seasonal sampling dates, I was able to assign the migratory behavior of different zooplankton groups to specific combinations of biotic and abiotic variables. Even though the vertical position of individual zooplankton groups was quite variable, I still found consistent patterns among lakes, sampling dates, and zooplankton groups. This result shows that the relative importance of environmental factors is specific to different zooplankton groups and can also change seasonally in a taxon-specific manner.
Finally, to test if my results regarding the relative importance of fish and *Chaoborus* as predators were applicable to natural lake communities and could cause the changes in the zooplankton community outlined above, I carried out two controlled field studies. First, I conducted an enclosure experiment to specifically test the effects of water color, fish, and *Chaoborus* on light, temperature, and oxygen profiles as well as the zooplankton assemblage. As predicted, increased water color resulted in reduced light penetration, a shallower but warmer epilimnion, and reduced oxygen concentrations, especially in deeper water. Since fish rapidly eliminated *Chaoborus*, the predation regime in low color treatments was top-down controlled. On the other hand, in high color treatments the food web structure could be described as intraguild predation, since *Chaoborus* suffered only slight predation losses and was able to compete with fish for zooplankton prey.

Furthermore, water color also changed the vertical migration behavior of zooplankton prey. In low color treatments, the presence of fish forced the zooplankton to migrate into deeper water layers during the day. But in high color treatments, independently of presence or absence of fish, the zooplankton remained in shallow water during day and night. The altered predation regimes and migration patterns in high color treatments significantly changed the zooplankton composition. In low color treatments, fish were able to eradicate large species such as *Daphnia* and *Holopedium* and strongly reduced smaller cladocerans as well as copepods. Only the rotifer *Asplanchna* actually profited from the presence of fish, resulting in the typical zooplankton assemblage of high fish lakes dominated by small species. In high color treatments, fish were still able to significantly reduce zooplankton, but abundances of smaller and even large species were much higher than in low color treatments. Most likely, elevated water color provided a valuable refuge from fish, which on one hand reduced predation and, on the other hand,
increased growth rates since there was no necessity to perform DVM. *Chaoborus*, usually a
preferred prey for fish, was able to establish a significant role in the food web and its preference
for smaller zooplankton prey further shifted the zooplankton composition towards larger species.

Finally, the whole-lake study gave me the opportunity to test if my results from the short-
term enclosure experiment were relevant to natural lake conditions. The system I chose was
perfectly suited for this approach, because the two study lakes were similar in morphometry and
fish assemblage, but strongly differed in water color. Again, the vertical profiles of light,
temperature, and oxygen in Bena Lake and Cecil Lake were typical for brown and clear water
lakes, respectively. In good agreement with my hypothesis, Bena Lake had 100 to 300 times
higher *Chaoborus* densities than Cecil Lake. Furthermore, the vertical positions of the
zooplankton prey also confirmed my previous results. In Bena Lake, maximum zooplankton
densities were encountered in the epilimnion, while in Cecil Lake the zooplankton was primarily
located in the meta- and hypo-limnion. Therefore, it was not surprising that the zooplankton in
Cecil Lake was dominated by small species, typical for clear lakes. But in Bena Lake, large
species such as *Holopedium* and *Daphnia* developed very high abundances.

For the longest time, the potential differences between clear and brown water lakes have
been ignored. In my dissertation, I could show that the differences in physical habitat between
clear and brown water lakes also generated very distinct food web structures, expressed as (1)
changed predation regimes, (2) altered migration behavior of zooplankton, and (3) a shift in
zooplankton composition from small to large bodied species. Hence, water color -- or DOC --
should be included for proper lake classification, and results from studies performed in brown
water lakes should be re-evaluated in consideration of my findings.
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VITA

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