Factors influencing zooplankton community structure in lakes along a
gradient of residential lakeshore development

Abstract. — I investigated the factors influencing zooplankton community composition and size structure in lakes spanning a gradient of residential lakeshore development. Twenty southern Michigan lakes were sampled once in late summer for physical and chemical parameters and for zooplankton community and size structure. Water clarity appeared to be the most important abiotic factor related to community composition and indirectly related to size structure in the study lakes. Zooplankton communities in lakes with greater water clarity were dominated by large-bodied cladocerans such as *Daphnia*. Percentage of the community comprised of calanoid copepods was inversely related to percent cladocerans, *Daphnia* and cyclopoid copepods, which suggests that biotic interactions may also play a role in shaping community structure in these lakes. *Daphnia* mean length was negatively correlated with dwelling density.

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INTRODUCTION

Zooplankton are an integral part of freshwater lake ecosystems. As primary consumers, zooplankton can control the abundance and composition of phytoplankton and can affect water quality, trophic state, nutrient cycling, and food web resilience to perturbations (Dini et. al., 1987, Carpenter et. al., 1992, Cottingham et. al., 1997, Taylor & Carter, 1997, Stephen et. al., 1998). Zooplankton are also an important food source for planktivorous fishes and larval fish of many species (Wetzel, 1975), and can affect growth rates and survival and recruitment of planktivores (Cryer et. al., 1986, Bremigan & Stein, 1997, Dettmers et. al., 2003). The relative influence of zooplankton on lower and higher trophic levels varies as a function of community composition and size structure (Brooks & Dodson, 1965, Galbraith, 1975, Dini et. al., 1987, Bremigan & Stein, 1997, Dettmers et. al., 2003). Therefore, understanding the factors that regulate community composition and size structure is of great interest.

Biotic interactions such as predation and competition are important in shaping zooplankton community composition and size structure (Brooks & Dodson, 1965, Gliwicz & Lampert, 1993). These processes do not act independently and Brooks and Dodson's (1965) "size-efficiency hypothesis" describes how zooplankton community composition, and thus size structure, change via different competitive scenarios under varying predation pressure. Fish tend to be size-selective in their feeding and prefer larger-bodied individuals (Brooks & Dodson, 1965), especially large cladocerans such as *Daphnia* (Brooks, 1968, Vinyard, 1980, Turner & Mittelbach, 1990). This size-

selectiveness means that fish predation serves to shape zooplankton community composition and size structure (Mills and Schiavone, 1982, Hobæk et. al., 2002).

The stability of predator-prey dynamics often depends upon the presence of a prey refuge from predation (Sih, 1987). In a broad sense, a refuge is a strategy that decreases the risk of predation. One common strategy is the use of a spatial refuge (Sih, 1987). Seven possible refuges from predation have been identified for lacustrine zooplankton: gradients of light, temperature, and dissolved oxygen (DO), macrophytes or other physical refuges, open water interference refuges, behavioral refuges, and predator inefficiency refuges (Shapiro, 1990). Perhaps the most important physical-chemical refuge for *Daphnia* is a region with DO concentrations too low for fish survival (Shapiro, 1990). Avoidance of predation has been accepted as the ultimate reason for diel vertical migration (DVM) by many zooplankton species between these oxygen-poor deeper waters and feeding areas (Zaret & Suffern, 1976, Stich & Lampert, 1981, Gliwicz, 1986, Dodson, 1990, DeStasio, 1993). Tessier and Welser (1991) found that the presence of a refuge from predation was important in determining zooplankton species abundance and diversity. Refuge availability also plays a significant role in *Daphnia* population dynamics (Wright & Shapiro, 1990).

There are many possible ways to define the extent of hypolimnetic refuges available to zooplankton. Tessier & Welser (1991) defined a refuge as the thickness of the water column between the bottom of the epilimnion and the depth at which DO is less than 0.5 ppm (hereafter referred to as critical depth) . The controls on these two parameters will thus affect the presence and size of refuges for zooplankton in lakes. Thermocline depth is a function of lake morphometry (particularly fetch), wind strength,

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and turbidity (Patalas, 1984, Mazumder & Taylor, 1994, Kalff, 2002). Hypoxia is a natural occurrence in the hypolimnion of stratified lakes (Charlton, 1980) because respiration rates are higher than photosynthesis rates in deep, unmixed waters. Oxygen depletion can be greater in eutrophic lakes due to large amounts of organic matter sinking to the lake bottom and being decomposed, and although eutrophication can be a natural process, it is often accelerated by human activities (Wetzel, 1975). Deforestation increases runoff and results in more minerals being leached from soil, providing ample nutrients for algal blooms (Hargrave, 1991). The dumping of wastewater into aquatic systems and runoff from agricultural fields can also contribute to nutrient enrichment (Kalff, 2002).

It is clear that anthropogenic forces can cause or exacerbate eutrophication that results in hypolimnetic anoxia – one of the parameters determining refuge size. Human perturbations that increase the turbidity of water also can affect thermocline depth (Mazumder & Taylor, 1994), the second control on refuge thickness. Therefore, humans could have a significant impact on the size of the refuge available to crustacean zooplankton. Since refuge size has been shown to influence zooplankton community structure (Tessier & Welser, 1991, Bertolo et. al., 1999), human activities could potentially affect community structure as well. My goal in this study was to determine what factors influence zooplankton community and size structure in lakes in southern Michigan. In particular, I was interested in whether or not residential lakeshore development has an affect on zooplankton community metrics such as taxa richness and mean size.

METHODS

Study Lake Selection

All lakes used in this study were warmwater and located in southern Michigan. Study lakes were selected by first identifying all southern Michigan lakes that had a surface area between 4.0 and 81.0 ha and a maximum depth of at least 6.1 m. These selection criteria were used to reduce the influence of lake size (Dodson et. al., 2000, Kalff, 2002) and stratification pattern on zooplankton community composition and size structure. To ensure that the study lakes spanned a gradient of residential lakeshore development, lakes on the initial list were plotted on a map of public land ownership using a Geographic Information System (GIS). Lakes were grouped into three categories based on the amount of state- or federally-owned land surrounding their shores: Group 1 lakes were surrounded by two-thirds or more state land and were defined as low impact, Group 2 lakes were surrounded by between one-third and two-thirds state land and were defined as medium impact, and Group 3 lakes were surrounded by less than one-third state land and were defined as high impact. Three lakes from each impact group were selected for sampling. Data from an additional 11 lakes fitting the selection criteria and representing a range of human development were obtained from the Michigan Department of Natural Resources (MDNR). All data were collected using similar methods and were pooled for analysis.

Limnological Sampling

All lakes were sampled between early August and early September from 2003 to 2006. Temperature and dissolved oxygen profiles were measured in the deepest basin of

each lake using a YSI 600 QS-650 MDS water quality monitor. Readings were taken every 0.91 m until the thermocline was reached or the lake bottom was approached, in which case readings were taken every 0.30 m. Water clarity was assessed by measuring Secchi depth. In lakes with more than one distinct basin, profiles and Secchi depths were measured for each basin. A plankton net with a mesh size of 153 μm and a diameter of 0.13 m was used to make vertical hauls from each of four quadrants (approximately aligned with the cardinal directions) in each basin (Galbraith & Schneider, 2000). The mouth of the net was lowered to the critical depth. In lakes having no critical depth, the mouth of the net was lowered to approximately 0.91 m above the lake bottom in order to avoid stirring up sediments and sampling benthic organisms. Zooplankton were anesthetized in carbonated water and immediately preserved in a 70% ethanol solution.

Temperature and oxygen profiles were used to estimate a hypolimnetic refuge following the methods of Tessier and Welser (1991). They defined a refuge as the thickness of the water column between the thermocline and the critical depth. This definition was appropriate for this study because southern Michigan lakes are dominated by Centrarchids (particularly bluegill sunfish) that are unable to feed below the thermocline (Werner & Hall, 1977, Tessier & Welser, 1991) and because zooplankton typically are not found in water with a DO concentration of less than 0.5 ppm (Tessier & Welser, 1991). In lakes with more than one basin, thermocline depths and critical depths were averaged across all basins to obtain an average refuge thickness.

Human development was quantified by counting the number of houses located directly on the shoreline of each lake. Houses on artificial channels or across roads were

not included in these counts. House counts were divided by shore perimeter to obtain a dwelling density for each lake.

Zooplankton Enumeration

Each zooplankton sample from each lake was subsampled and placed in a counting wheel to estimate taxa richness, relative abundance, and size structure. The first 50 zooplankton encountered in each subsample were identified and their lengths were measured using Image-Pro Plus imaging software. The remaining individuals in the counting wheel were counted. Most zooplankton were identified to genus using keys in Edmondson et. al. (1959), Balcer et. al. (1984), and Aliberti et. al. (2007). A few genera that were difficult to identify were grouped together. *Skistodiaptomus* and *Leptodiaptomus* were considered *Diaptomus* and *Acanthocyclops, Diacyclops*, and *Tropocyclops* were all considered *Cyclops*. Zooplankton lengths were measured from the top of the head to the end of the caudal rami for copepods and to the base of the tail spine for cladocerans.

Data Analysis

Taxa richness for each lake was defined as the total number of taxa present among the subsamples for that lake. Relative abundance of each taxa was determined by summing the estimated number of individuals for each taxa across all samples from a lake and dividing by the sum of the estimated total number of individuals across all samples from that lake. To determine differences in community composition across lakes, the relative abundances of cladocerans, calanoid copepods, and cyclopoid copepods were

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calculated for each lake. Mean lengths were calculated for all zooplankton individuals, for cladocerans, and for *Daphnia* for each lake by averaging the measured lengths across all subsamples for that lake. Cladoceran and *Daphnia* size characteristics and their relationship to other lake parameters were investigated separately because these taxonomic groups are highly sought after by planktivorous fishes (Brooks & Dodson, 1965, Brooks, 1968, Vinyard, 1980, Turner & Mittelbach, 1990). The effects of residential lakeshore development on refuge size and zooplankton composition and size structure were determined using Pearson correlations and regression analysis. Variables were log transformed to meet assumptions of normality. All analyses were conducted using SPSS and significance was set at $P<0.05$.

RESULTS

Limnological characteristics for the study lakes are summarized in Table 1. The 20 study lakes ranged in surface area from 11.9 to 260.6 ha with a mean size of 78.8 ha. Maximum depth ranged from 6.1 to 31.1 m with an average maximum depth of 14 m. Most of the study lakes were classified according to the Michigan Department of Environmental Quality as mesotrophic, but several were oligotrophic. Water clarity varied among the lakes; Secchi depths ranged from 1.5 to 5.0 m with a mean of 3.6 m. Three of the lakes did not stratify and thermocline depth varied from 3.1 to 7.0 m among those that did. Size of available refuge from predation ranged from zero (in lakes with no stratification) to 16.8 m, with a mean thickness of 5.3 m. Refuge thickness tended to increase with maximum depth ($r=0.497$, $P<0.05$) and thermocline depth ($r=0.560$, $P<0.05$) across the study lakes. Dwelling density ranged from zero to 33 houses per km

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of shoreline, with an average dwelling density of 10.2. In general, larger lakes tended

have higher dwelling densities (r=0.512, P<0.05).

Twelve different crustacean zooplankton taxonomic groups were identified across

the study lakes (Table 2). Cladocerans, and calanoid and cyclopoid copepods were found

in all lakes. Among cladocerans, *Daphnia* were most ubiquitous followed by

Diaphanosoma, *Bosmina*, and *Ceriodaphnia*. *Eubosmina*, *Chydorus*, and the predacious

Leptodora were relatively less common, occurring in only 3 of the study lakes. Among

calanoid copepods, *Diaptomus* were most ubiquitous, being found in every lake, while

Epischura were less common, occurring in only six of the study lakes. Among cyclopoid

copepods, taxa in the groups *Cyclops* and *Mesocyclops* were very common, occurring in

all lakes. *Ergasilus* were found in only five of the study lakes. A higher number of

cladoceran genera appear in Table 2 because members of this group were more easily

identified and were not lumped together as was done for copepods.

Zooplankton community metrics are summarized in Table 3. Taxa richness varied

from five to ten across the study lakes with a mean of 7.5. Taxa richness was not

influenced by dwelling density or by any of the lake morphology metrics measured. Taxa

richness tended to be lower in lakes having a larger mean length of cladocerans (R=-

0.514, P<0.05).

Lakes varied in the percentage of the zooplankton population composed of

cladocerans (range from 11.5 to 63.7%), calanoid copepods (2.8 to 77.5%) and cyclopoid

copepods (9.5 to 63.7%) (Figure 1). Percent cladocerans was higher in lakes having a

deeper Secchi depth (Figure 2) and was strongly influenced by the percentage of *Daphnia*

(r=0.769, P<0.01). Calanoid copepods comprised a large proportion of the zooplankton

community in lakes where cladocerans ($r=-0.576$, $P<0.01$) and cyclopoid copepods ($r=-0.653$, $P<0.01$) were less abundant, and to a lesser extent where *Daphnia* ($r=-0.494$, $P<0.05$) were less abundant. Proportion of the zooplankton community comprised of cyclopoid copepods tended to decrease with increasing lake surface area ($r=-0.450$, $P<0.05$). Proportion of the community compriseed of *Daphnia* ranged from 0.9 to 62.8% across the study lakes. The relationship between percent *Daphnia* and Secchi depth (Figure 3) was somewhat stronger than that observed for percent cladoceran.

Measures of size structure appeared to be influenced by zooplankton community composition. Proportion of the community comprised of *Daphnia* had the strongest influence of any variable on mean length of all zooplankton (Figure 4) and mean length of cladocerans (Figure 5). Zooplankton mean length and cladoceran mean length tended to increase with refuge thickness, although these trends were not significant. Mean length of *Daphnia* was the only measure of size structure that was correlated with dwelling density (Figure 6).

DISCUSSION

Secchi depth appeared to be the most important abiotic factor controlling community composition and indirectly controlling size structure in the study lakes. This finding contrasts with Tessier and Welser's (1991) finding that seasonal zooplankton community change within a similar set of southern Michigan lakes was best predicted by the decrease in refuge size over the summer. The difference between these studies may be due to the time scale over which response variables were measured. Since the present study focused on refuge and zooplankton community characteristics for a single point in

time, a hypolimnetic refuge may still be important in the study lakes if viewed across the growing season.

Across the study lakes, as Secchi depth increased the zooplankton community shifted to a cladoceran-dominated, and more specifically, a *Daphnia*-dominated assemblage. Since *Daphnia*-dominated zooplankton communities tend to have larger mean lengths (Taylor & Carter, 1997), this result is consistent with Stemberger and Miller's (2003) finding that mean cladoceran body length was positively correlated with Secchi depth. A possible explanation for this result is *Daphnia*'s superior ability to reduce phytoplankton biomass through grazing (Dini et. al., 1987, Carpenter et. al. 1992, Cottingham et. al., 1997). Another possible explanation for the increase in percentage cladoceran with increasing water clarity involves the differences in feeding strategies between cladocerans such as *Daphnia* and copepods. The foraging efficiency of *Daphnia* decreases at very high food densities due to their complicated filtering mechanism (Wetzel, 1975, Starkweather, 1978, Rigler, 1961). In the study lakes with shallower Secchi depths, phytoplankton concentrations may have been too high for *Daphnia* to forage efficiently, allowing copepods to exploit the food base in lakes where *Daphnia* handling costs are high.

The results of this study also suggested that biotic interactions may be important in structuring zooplankton community composition. Percent of the community that was comprised of calanoid copepods was inversely related to percent cladocerans, *Daphnia* and cyclopoid copepods. These relationships could be a result of competitive effects between superiorly competitive cladocerans such as *Daphnia* and copepods (Brooks and Dodson, 1965, Gliwicz and Lampert, 1993). It could also be due to the complicated

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interactions described in Brooks and Dodson's (1965) size-efficiency hypothesis. Indirect effects of predation and trophic cascades could also be shaping the community composition in these lakes. For example, in the presence of bass, cladocerans tend to be more abundant, while copepods are more abundant when bass are absent (Turner and Mittelbach, 1990). Additional information on fish assemblages in the study lakes would be valuable in understanding the factors influencing zooplankton community structure.

Variation in zooplankton size structure across the study lakes was strongly influenced by community composition, in particular, the relative abundance of *Daphnia*. This finding supports previous conclusions that zooplankton assemblages dominated by *Daphnia* tend to have larger mean lengths due to the large body size of members of this genus (Taylor & Carter, 1997).

Dwelling density, the variable being tested for its effect on zooplankton community structure, was not significantly related to many parameters in this study. It was, however, negatively correlated with mean *Daphnia* length (i.e. lakes with a larger number of houses per km shoreline had smaller *Daphnia*). The reasons underlying this relationship are not clear. It is possible that people prefer to live on lakes with good recreational fishing quality and thus lakes with smaller *Daphnia* were lakes with high numbers of fish whose preferred food is large cladocerans like *Daphnia* (Brooks & Dodson, 1965, Brooks, 1968, Vinyard, 1980, Turner & Mittelbach, 1990). The observed decline in *Daphnia* mean length with increasing residential shoreline development also could be due to a refuge effect. If it is hypothesized that residential shoreline development changes limnological conditions in a way that would decrease the size or availability of a refuge from predation, since large-bodied *Daphnia* are preferred by fish

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(Brooks & Dodson, 1965, Brooks, 1968, Vinyard, 1980, Turner & Mittelbach, 1990) they should disappear first in zooplankton communities in lakes with more development. A positive trend was seen between refuge thickness and cladoceran mean length, but this relationship was not significant.

For the purposes of this study, it was assumed that the relative effectiveness of a refuge was positively related to its thickness (Wright & Shapiro, 1990). However, it should not be assumed that the presence of these refuges is an indication that DVM is taking place or that the refuges represent an area of decreased predation pressure (Wright & Shapiro, 1990); if this were the case, refuge availability and size would have no impact on zooplankton community structure. There are at least four plausible explanations for why refuges may not actually be regions of decreased predation: firstly, zooplankton may not have been present in the refuges at all. Horppila et. al. (2000) found that most cladocerans in a stratified lake inhabited the epiliminion due to several factors, including a metalimnetic oxygen minimum and predation by the midge larva *Chaoborus* in the hypolimnion. While no metalimnetic oxygen minima were observed on the sampling days, *Chaoborus* was found in several lakes. Deep water refuges are less important in lakes with effective deep water predators (DeMott & Edington, 2004), so DVM may not have occurred in lakes where *Chaoborus* exerted predation pressure in the hypolimnion. Secondly, even if zooplankton were distributed throughout the water column, including in the refuge, this does not necessarily imply predator avoidance behavior – they could simply be distributed such that the most vulnerable individuals occupy the deepest layers. This phenomenon is related to food distribution; with homogenously distributed food it is not necessary for zooplankton to pay the energetic costs associated with DVM

(Pijanowska & Dawidowicz, 1987). Thirdly, in conditions of extremely scarce food, zooplankton will expose themselves to greater predation risk by remaining near the lake surface to feed during the day and night (Johnsen & Jakobsen, 1987). Lastly, fish may feed below the bottom of the epilimnion and the refuge definition used in this study, therefore, may be inappropriate. In order to be confident in the definition used, planktivore distribution in the water column would need to be determined. Information on the abundance and vertical distribution of zooplankton, their food, and their predators within the entire water column would need to be collected in order to be certain that refuges are affecting zooplankton community structure.

The temporal component of refuges also must be considered. Thermocline depth and hypolimnetic anoxia change both seasonally and from year to year (Shapiro, 1990, Tessier & Welser, 1991). In lakes in southwestern Michigan, refuge size was reduced by 50% between June and August (Tessier & Welser, 1991). Zooplankton community composition and size structure may change as a result of changes in refuge thickness (Wright & Shapiro, 1990). Since my study lakes were sampled once during the entire season, only a snapshot of refuge availability and thickness was obtained.

The results of this study indicate that zooplankton community structure is affected by numerous, interrelated factors. Information on the distribution and community structure of both fish and phytoplankton populations would lend much more insight into the factors shaping the zooplankton populations in these lakes. It is possible that human shoreline development could have an important influence on any number of things that would in turn affect zooplankton, and future research should take a holistic ecosystem approach in investigating these connections.

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Table 1. Summary statistics for physical parameters of 20 study lakes sampled for zooplankton species composition in southeast Michigan, summer 2003-summer 2006.

Variable (units)	Mean (± 1 SE)	Minimum	Maximum
Surface area of lake (hectares)	78.8 (15.15)	11.9	260.6
Maximum depth (m)	14.0 (1.45)	6.1	31.1
Secchi depth (m)	3.6 (0.21)	1.5	5.0
Refuge thickness (m)	5.3 (1.10)	0.0	16.8
Thermocline depth (m)	4.6 (0.37)	3.1	7.0
Shoreline dwelling density (houses/km)	10.2 (2.19)	0.0	33.0