Feeding Rates of Chaoborus on Daphnia and Copepods and the Effect of Fish Presence

BIOS 35502: Practicum in Field Biology

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2014

Abstract

Chaoborus can influence zooplankton populations through predation, although specific feeding rates and effects on prey populations are unknown. Planktivorous fish similarly influence *Chaoborus* populations, which affects zooplankton populations in a trophic cascade. In lakes without planktivorous fish, *Chaoborus* are the primary drivers of top-down influences on zooplankton populations; therefore, it is important to understand *Chaoborus* feeding rates in both the presence and absence of fish. This study investigated Chaoborus feeding rates on *Daphnia* and copepods and compared feeding rates in the presence and absence of fish. Based on established literature, it was hypothesized that *Chaoborus* would prefer copepods over *Daphnia* and that *Chaoborus* feeding rates would be higher in the absence of fish. Zooplankton and *Chaoborus* were collected from Long Lake at the University of Notre Dame Environmental Research Center (UNDERC) in Wisconsin, placed in five-gallon buckets, and counted after six hours. Trials were run with water from Long Lake (fish present) and tap water (fish absent). *Chaoborus* ate a higher proportion of *Daphnia* and *Holopedium* than calanoids and copepods, and feeding rates decreased significantly as *Chaoborus* density increased. *Chaoborus* ate a higher proportion of *Daphnia*, cyclopoids, and *Holopedium* in tap water than in Long water. Although there was no significant difference between feeding rates in Long water and tap water, several factors such as density of Chaoborus, density of fish, and interactions among trophic levels influence Chaoborus behavior and its role in lake trophic cascades.

Introduction

Chaoborus, a group of dipteran insects, have aquatic larvae that are found in the pelagic area of freshwater environments such as lakes or ponds (Berendonk 1999). *Chaoborus* prey on zooplankton, such as *Daphnia* and copepods (Yan et al. 1991). Research suggests selectivity for specific taxa may be species specific: *C. flavicans* is more selective for copepods (Kajak and Rybak 1979), *C. trivittatus* larvae prey mainly on *Daphnia pulicaria*, although copepods are their secondary prey (Pastorok 1981), and *C. flavicans* selected for cyclopoids and *D. longispina* but avoided *D. cucullata* (Kajak and Rybak 1979). *C. puncipennis* and other small *Chaoborus* species eat large algae as well (Yan et al. 1991). Due to differences of zooplankton composition and density and presence of predators in experiments, there are varying opinions on whether *Chaoborus* are more selective for copepods or cladocerans (Kajak and Rybak 1979).

Chaoborus larvae feeding rates increase with temperature, prey density, and larval size (Fedorenko 1975). At low prey densities, *Chaoborus* moves around a lot when searching for prey, but when a lot of prey is available, *Chaoborus* stays still before lunging at prey. Therefore, the movement patterns of either the predator *Chaoborus* or the zooplankton prey determine encounter frequencies (Moore 1988). Seasonal factors can also affect *Chaoborus* selectivity; *Chaoborus* selected for copepodites in July, August, and September and negatively selected for big Cladocera in August. Motivation for prey selection is unknown, but results indicate that prey movement patterns and ability to get away is an important contributing factor to *Chaoborus* prey selectivity (Kajak and Rybak 1979). Prey size also influences selectivity; for example, it is easier for *Chaoborus* to handle soft bodied rotifers than *Daphnia*. When there are a lot of prey available, *Chaoborus* is less selective when feeding (Moore 1988).

Large densities of *Chaoborus* larvae can regulate the density of their prey (Yan et al. 1991). Changing *Chaoborus* density impacts prey populations, especially calanoid copepods in spring, when there is a low density of prey (Neill 1981). Neill found that there were no long term effects on zooplankton populations from *Chaoborus* predation, but there were some temporary effects in the spring due to low densities of other *Chaoborus* prey. However, populations recovered quickly because they have high reproductive potential, although they did not recover well in colder temperatures. Acid lake water allows for larger *Chaoborus* populations, and *Chaoborus* population size decreases due to fish predation. When lakes can no longer support fish because they have been acidified, *Chaoborus* populations increase (Yan et al. 1991). Many species, including *Chaoborus,* alter their behavior in response to kairomones released by their predators (Berendonk 1999). When there are no fish in a nutrient-rich lake, *Chaoborus* can drastically impact zooplankton populations because of their large populations due to more food and no fish (Yan et al. 1991). However, some organisms, such as *Keratella taurocephala*, were not regulated by *Chaoborus* and reproduced more quickly than it was consumed by *Chaoborus* (Yan et al. 1991). The evidence that shows that *Chaoborus* can dictate zooplankton populations in acidified lakes is not strong (Yan et al. 1991). However, *Chaoborus* affect vertical migration of *Daphnia pulex*, which avoid deep water where *Chaoborus americanus* are found (Burks et al. 2002).

Although *Chaoborus* prey on zooplankton and influence their populations, specific feeding rates are not known. Specific information about *Chaoborus* feeding rates can be valuable for zooplankton models. This study examines predation rates of *Chaoborus* when both *Daphnia* and copepods are available and investigates the effect of the presence of fish on *Chaoborus* predation rates. It is expected that *Chaoborus* will prey more on copepods in water with mixed populations, and *Chaoborus* will be more active in low fish density water than high fish density water and therefore will have a higher predation rate.

Methods

Initial Calibration Experiments

To determine the zooplankton density and time for each trial, initial trials with varying zooplankton densities were run for different amounts of time. *Chaoborus* and zooplankton were collected with a zooplankton net (Aquatic Research Instruments, Hope, ID) from Bay Lake and Long Lake at the University of Notre Dame Environmental Research Center. Trials were run for three hours with 3 Bay tows:1 Long tow, 2 Bay tows:1 Long tow, and 1 Bay tow:1 Long tow and for three, six, 12, and 24 hours with 2 Bay tows:1 Long tow. From these trials, it was determined that trials should be run for six hours, and samples from Bay were omitted because the ratio of zooplankton to *Chaoborus* was too high.

Zooplankton Collection and Trials

Chaoborus and zooplankton were collected with a zooplankton net at a depth of 3 meters from Long Lake. Each tow was divided in half, and the number of *Daphnia*, calanoids, cyclopoids, *Holopedium*, and *Chaoborus* in each half tow was counted under a microscope at 1.0x magnification. Each half tow was placed in a five gallon bucket filled with water from Long Lake in the laboratory. Several trials were not counted initially and were run with one tow. The initial density for these trials was measured by counting the zooplankton in a tow immediately after sampling. After six hours, the zooplankton from each bucket were collected and counted under a microscope at 4.0x magnification.

Chaoborus Predation in the Presence of Fish

Chaoborus and zooplankton were collected from Long Lake and counted as above but each half tow was placed in a bucket filled with water from Long Lake or a bucket filled with tap water in the laboratory. Each bucket also had rocks on the bottom to provide a place for

Chaoborus to hide from possible fish predation. The zooplankton were collected after six hours and counted.

Data Analysis

A chi square test in SYSTAT determined if *Chaoborus* had a significant preference for *Daphnia* or copepods. Regressions comparing zooplankton eaten to zooplankton present, zooplankton eaten to *Chaoborus* present, and *Chaoborus* feeding rate ($\frac{number\ of\ zooplankton\ eaten}{number\ of\ Chaoborus}$) to *Chaoborus* present were run for zooplankton in water from Long. A t test compared *Chaoborus* feeding rates on zooplankton in water with kairomones from fish and tap water without kairomones to determine if *Chaoborus* were significantly more active predators in the absence of fish. Descriptive statistics (mean, standard error, and standard deviation) for proportions eaten were also obtained in SYSTAT.

Results

Chaoborus Feeding Rates

On average, *Chaoborus* ate a higher proportion of *Daphnia* (mean=0.44 zooplankton eaten/zooplankton initially present, standard error=0.04, standard deviation=0.21) and *Holopedium* (mean=0.41, standard error=0.05, standard deviation=0.24) than calanoids (mean=0.36, standard error=0.05, standard deviation=0.23) and cyclopoids (Figure 1; mean=0.35, standard error=0.04, standard deviation=0.19). A chi square test (Figure 2) showed a significant difference between observed percentages of *Daphnia*, calanoids, cyclopoids, and *Holopedium* after *Chaoborus* feeding and initial sample densities from Long Lake (p value<0.01, $\chi^2=7.20$, degrees of freedom=1).

Regression analysis showed a significant positive relationship between zooplankton present and zooplankton eaten (Figure 3; p value<0.01, R^2=0.36, degrees of freedom=1). There was a significant negative relationship between *Chaoborus* present and zooplankton eaten (Figure 4; p value=0.03, R^2=0.19, degrees of freedom=1) and between *Chaoborus* present and *Chaoborus* feeding rate (Figure 5; p value<0.01, R^2=0.54, degrees of freedom=1).

Feeding Rates in Long Water vs. Tap Water

Chaoborus ate a similar proportion of calanoids (mean=0.47, standard error=0.11, standard deviation=0.32), cyclopoids (mean=0.45, standard error=0.05, standard deviation=0.14), and *Holopedium* (mean=0.40, standard error=0.11, standard deviation=0.30) but ate a much smaller proportion of *Daphnia* (mean=0.21, standard error=0.07, standard deviation=0.21) in water from Long. In tap water, *Chaoborus* ate a similar proportion of cyclopoids (mean=0.57, standard error=0.02, standard deviation=0.07) and *Holopedium* (mean=0.59, standard error=0.10, standard deviation=0.31) but ate a smaller proportion of *Daphnia* (mean=0.39, standard error=0.08, standard deviation=0.23) and calanoids (mean=0.21, standard error=0.09, standard deviation-0.26). The proportion of *Daphnia*, cyclopoids, and *Holopedium* eaten increased in tap water, but the proportion of calanoids eaten decreased (Figure 6). *Chaoborus* feeding rates were higher in tap water than in lake water (Figure 7), but a t test showed no significant difference between *Chaoborus* feeding rates and water type (p value=0.14, t=2.44, degrees of freedom=15).

Discussion

This research contrasts previously reported studies on Chaoborus feeding preferences, as *Chaoborus* prefered cladocerans to copepods in this experiment. The relative abundances of

Daphnia and *Holopedium* in the trials decreased while the relative abundances of calanoids and cyclopoids in the trials increased. Although this does not support the original hypothesis that *Chaoborus* prefer copepods, it could be the result of the zooplankton composition and density used in this experiment (Kajak and Rybak 1979). These factors could greatly affect *Chaoborus* feeding because *Chaoborus* do not pursue prey and only eat what comes in their strike zone. *Chaoborus* strike equally at cladocerans and copepods, but Swift and Fedorenko1975 found that copepods are more likely to be eaten than same sized cladocerans. This is due to body shape; copepods are thinner and therefore easier to handle and swallow than cladocerans (Swift and Fedorenko 1975).

The more zooplankton present initially in the buckets, the more zooplankton *Chaoborus* ate. However, as more *Chaoborus* were placed in the buckets, the number of zooplankton eaten and the number of zooplankton eaten per *Chaoborus* decreased, probably due to competition among *Chaoborus*. Increased competition decreases *Chaoborus* feeding rates, but it is unclear whether this is caused by less successful feeding or if there is some interaction among *Chaoborus* that causes them to eat less.

Chaoborus ate a higher proportion of *Daphnia*, cyclopoids, and *Holopedium* in tap water than in lake water, but the proportion of calanoids eaten decreased in tap water. This fits the hypothesis that *Chaoborus* would be more active and therefore eat more in water without kairomones from fish. The proportion of *Daphnia* and *Holopedium* eaten increased in tap water; this could be because *Chaoborus* do not have to avoid fish and can afford more handling time for bigger prey (Swift and Fedorenko 1975). In this case, *Chaoborus* can influence zooplankton populations more in the absence of planktivorous fish, which follows the trophic cascade model

(Carpenter et al. 1987) that reducing the planktivore population increases *Chaoborus* populations, which decreases other zooplankton populations.

The t test did not find a significant difference in feeding rates in lake water and tap water, which does not support the hypothesis that *Chaoborus* would have higher feeding rates in tap water. This could be explained by small sample size or low *Chaoborus* density in the trials. Trophic cascades vary in strength (Borer et al. 2005); it could be that the interaction between the planktivorous trophic level and zooplankton trophic level is not strong enough to cause a significant difference in *Chaoborus* feeding rates. Additionally, the *Chaoborus* may not have been exposed to the tap water long enough or there may not have been enough kairomones in the lake water to cause a behavioral response. Diel vertical migration by *Chaoborus* may not actually occur without fish in system. Further research could be done with varying *Chaoborus*, zooplankton, and fish densities and trial times.

Many lake systems involve a trophic cascade with piscivores, planktivores, herbivores, and phytoplankton. As the biomass of piscivores increases, the planktivore biomass decreases, the herbivore biomass increases, and the phytoplankton biomass decreases. In Tuesday Lake, another lake on the UNDERC property, increasing piscivores and decreasing planktivores led to more zooplankton and less phytoplankton, which follows the trophic cascade model (Carpenter et al. 1987). In these trophic cascades, zooplankton are preyed on by fish and *Chaoborus*. However, many lake systems (Long being an example) have little or no planktivorous fish but high *Chaoborus* densities (Kelly et al. 2014), so zooplankton are primarily predated on by *Chaoborus*. Therefore, it is important to understand *Chaoborus* feeding rates in lakes with and without plantivores and how *Chaoborus* affect zooplankton communities and the rest of the trophic cascade.

Acknowledgements

I would like to thank Patrick Kelly for his guidance in designing and implementing this experiment, for assisting with statistical analysis, and reviewing this paper. Many thanks to Sarah Clark and Abby Shepherd for their assistance in the field and to Hannah Madson, Christy Lowney, Lauren Eckert, and Will West for advising me with statistical analysis. I would also like to thank Gary Belovsky and Michael Cramer for their support and the Bernard J. Hank Family Endowment, without which this project would not have been possible.

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Figures

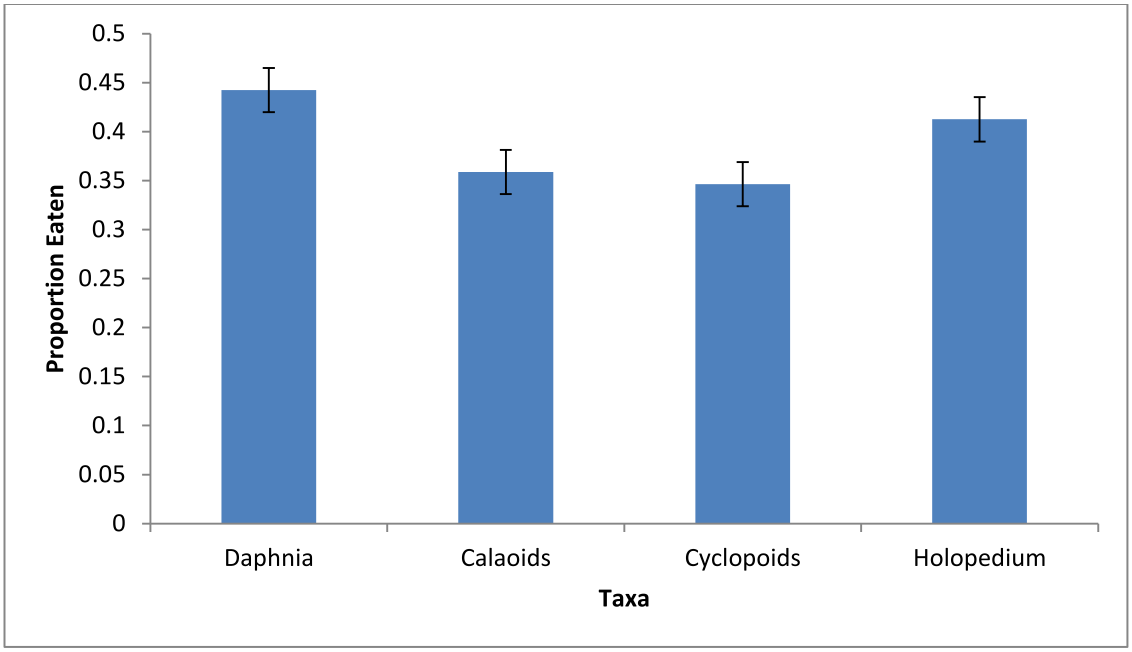

Figure 1. Average proportion of zooplankton eaten by *Chaoborus* during a six hour trial. A higher proportion of *Daphnia* (mean=0.44, standard error=0.04, standard deviation=0.21) and *Holopedium* (mean=0.41, standard error=0.05, standard deviation=0.24) were eaten than calanoids (mean=0.36, standard error=0.05, standard deviation=0.23) and cyclopoids (mean=0.35, standard error=0.04, standard deviation=0.19).

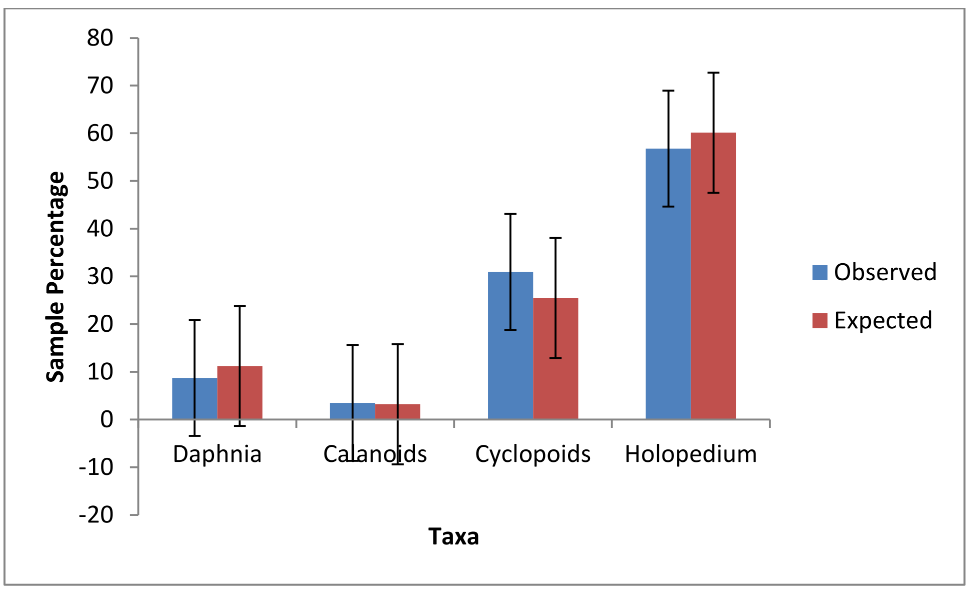

Figure 2. Average percentage of zooplankton in samples after six hour trials (observed) and samples not run in trials (expected). A chi square test showed a significant difference between the observed and expected percentages ($p<0.01$); this difference was caused by *Chaoborus* feeding lowering the percentages of *Daphnia* and *Holopedium* while increasing the percentages of calanoids and cyclopoids.

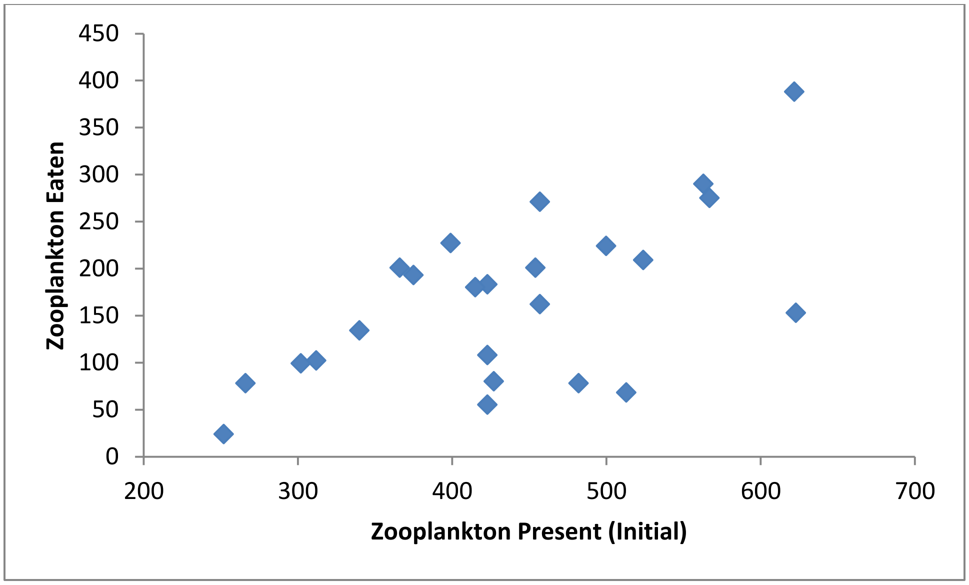

Figure 3. Zooplankton eaten vs. zooplankton present in buckets with water from Long Lake. Regression analysis showed a significant positive relationship between zooplankton present and zooplankton eaten (p value<0.01, R^2=0.36, degrees of freedom=1). As initial zooplankton density increased, the number of zooplankton eaten by *Chaoborus* increased.

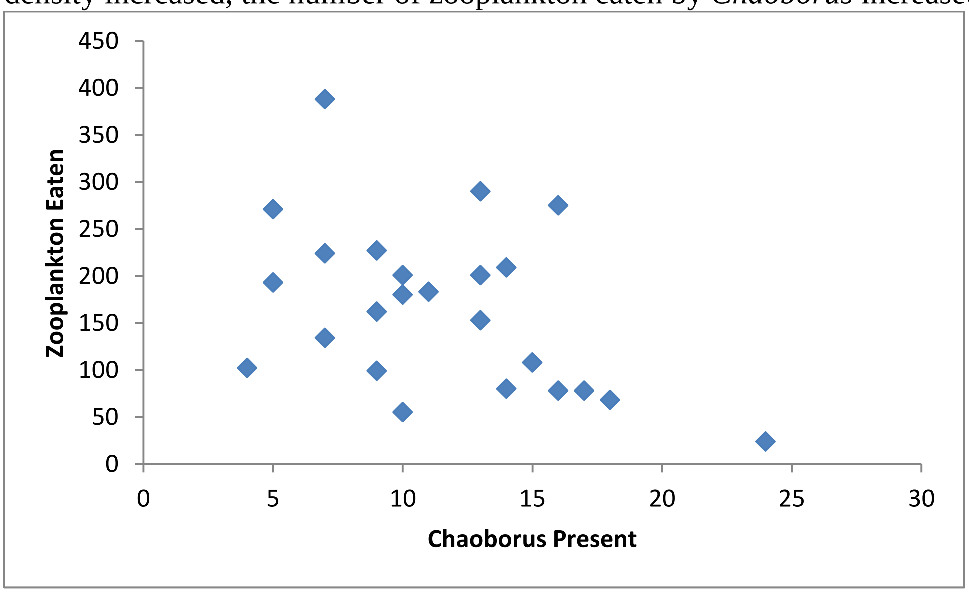

Figure 4. Zooplankton eaten vs. *Chaoborus* present in buckets with water from Long Lake. There was a significant negative relationship between *Chaoborus* present and zooplankton eaten (p value=0.03, R^2=0.19, degrees of freedom=1). Increasing the *Chaoborus* density decreases the total number of zooplankton eaten.

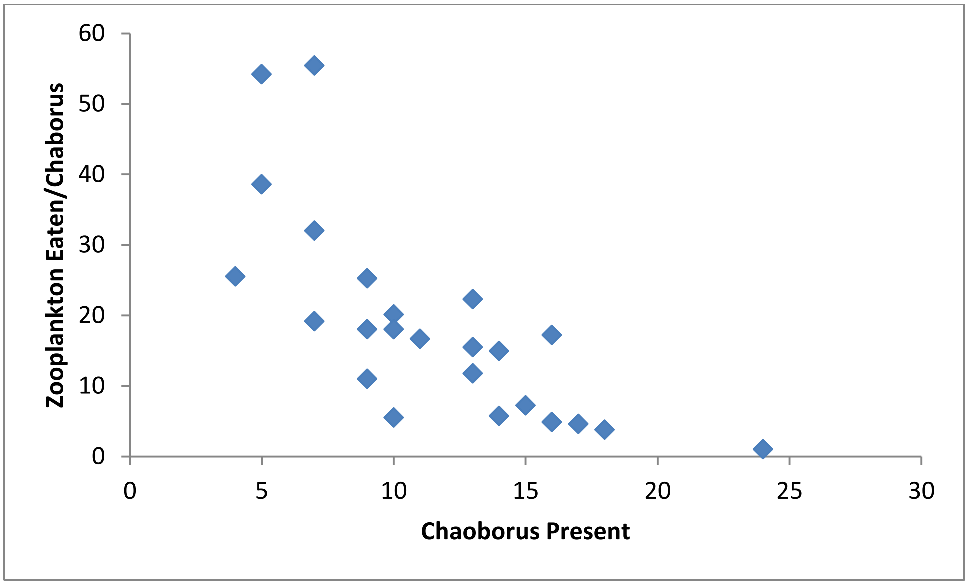

Figure 5. Zooplankton eaten per *Chaoborus* vs. *Chaoborus* present in buckets with water from Long Lake. Regression analysis showed a significant negative relationship between *Chaoborus* present and *Chaoborus* feeding rates (p value<0.01, R^2=0.54, degrees of freedom=1). As the number of *Chaoborus* increased, the *Chaoborus* feeding rate decreased.

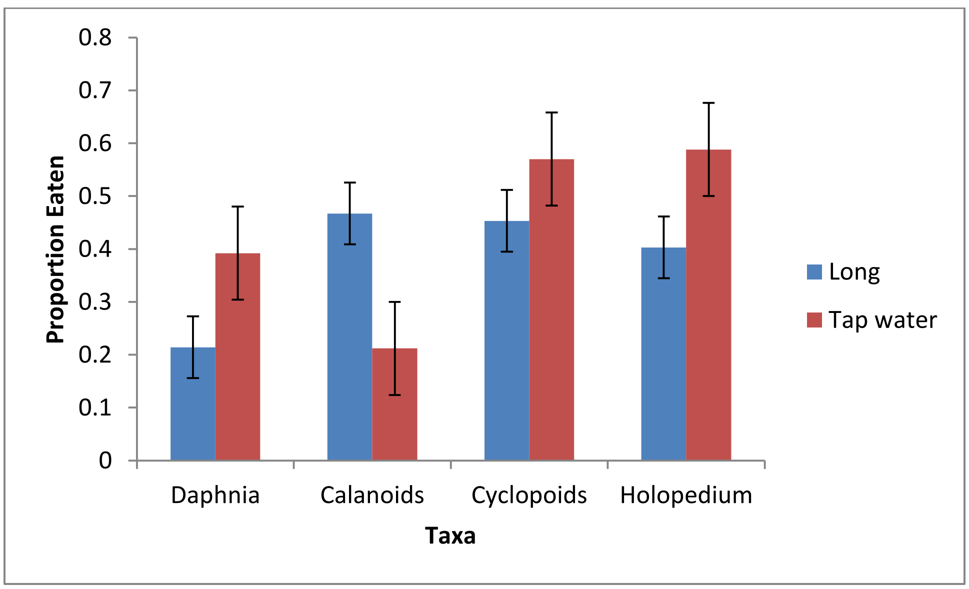

Figure 6. Average proportion of zooplankton eaten by *Chaoborus* during a six hour trial in buckets with Long water and tap water. The proportion of *Daphnia*, cyclopoids, and *Holopedium* eaten increased in tap water, but the proportion of calanoids eaten decreased. *Chaoborus* ate more *Daphnia*, cyclopoids, and *Holopedium* in tap water than in lake water.

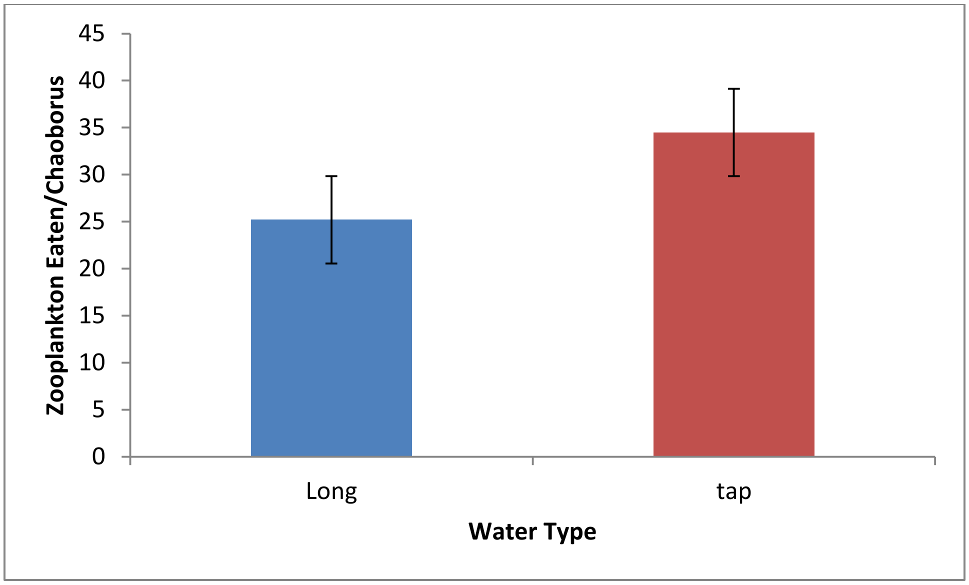

Figure 7. Average zooplankton eaten per *Chaoborus* by water type. Feeding rates were higher in tap water than in lake water, but a t test showed that there is a no significant difference between *Chaoborus* feeding rates in water from Long and tap water (p value=0.14, t=2.44, degrees of freedom=15).