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The Dynamics of Location: Influence of Predation by Chaoborus Larvae on Rotifer Diel Vertical Migration Patterns

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By Kristina Riemer

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"*Nothing in evolution or ecology makes sense except in the light of the other.*"
Pelletier et al. 2009

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Abstract

The locations of freshwater organisms in lakes are determined by the convergence of many competing factors. While predation pressure is one of these, also important are areas of food concentration and the physical and chemical constraints of a system. Diel vertical migration is a behavior exhibited by freshwater organisms in many taxa that is the result of balancing these factors. Diel vertical migration consists of movement by these organisms throughout the water column in accordance with a 24 hour cycle. This oscillation is generally driven by the competing factors of predation pressure and food acquisition, and is modified by physical and chemical requirements.

In the Low Lake system during the summer of 2012, two groups of organisms were engaged in diel vertical migration: rotifers and *Chaoborus.* While some instars of *Chaoborus* were exhibiting a typical diel vertical migration pattern, the migration pattern of the rotifers was the opposite. While the migration pattern of the *Chaoborus* was likely driven by fish predation, that of the rotifers was driven by *Chaoborus* predation pressure resulting from their diel vertical migration. The migration patterns in both of these groups of organisms were also driven by differential locations of food resources. The migration patterns of rotifers and *Chaoborus* in Low Lake are an excellent example of how the changing locations of organisms in a lake are the result of balancing many factors that influence the fitness of these organisms.

Introduction

Every freshwater organism chooses a location based on a balance between the chemical and physical characteristics of the body of water they inhabit with its food concentrations and areas of predation risk. All of these components of a body of water can be dynamic, and may fluctuate over time. The process by which freshwater organisms choose locations therefore must be flexible enough to deal with changing conditions. Different morphological, behavioral, and life history adaptations are used to address the varied conditions of the freshwater habitat and play a role in this process.

One such behavioral adaptation that has been observed in many freshwater zooplankton is diel vertical migration. This behavior entails that an organism moves vertically throughout the water column of a lake, and this movement corresponds to a daily cycle. The most common diel vertical migration pattern exhibited by zooplankton consists of downward movement in the water column during the day and upward movement at night, followed by a return to deeper depths of the water column the next day, and these movements occur repeatedly.

It has been determined that this diel vertical migration of freshwater zooplankton is the result of these organisms balancing predation pressure with the physical characteristics of a lake and the ability to acquire sufficient food by choosing different locations in the water column at different times. One type of predator that preys on zooplankton is visual feeders, which require sufficient light to see and consequently capture zooplankton. Such light is only present in lakes during daylight hours, and therefore visually feeding predators are only able to actively feed during these hours. One behavior that zooplankton can use to avoid being consumed by visually feeding predators is to move deep in the water column during the day, and consequently away from the areas of the lake which are light enough for these predators to feed. It is disadvantageous for zooplankton to be located deep in the water column, though, because food resources tend to be more plentiful closer to the surface in the areas where light is present during the day. Also, the warmer temperatures near the surface contribute to

higher reproductive and growth rates of zooplankton. Therefore, at night, when the light is not sufficient for visually feeding predators to locate prey anywhere in the lake, zooplankton can move upward in the water column to take advantage of the resource- and temperature-related benefits of the areas near the surface. This results in the upward movement of many zooplankton at night and downward movement during the day, which is the most common diel vertical migration pattern.

Lake Formation and Morphometry

Freshwater lakes consist of a basin, or depression in the ground, that is filled with water. According to Hutchinson, there are 76 different types of lakes based on their basin formation (1967). Wetzel groups these lake types into nine categories: tectonic, volcanic, landslide, glacier, solution, river, wind, shoreline, and organic (2001). Tectonic lakes are created by shifting of tectonic plates, which can cause uplifting, warping or faulting in the earth's crust, which results in a depression. Most volcanic lakes are formed from craters in the cone of a volcano. Landslides form lakes, which are usually temporary, by creating dams that block streams. Many types of lakes result from activity of glaciers; they can either form on or next to the glacier itself, or result from depressions formed by glacier-induced changes in the ground. Solution lakes occur when water dissolves rock to create a depression. Rivers can form lakes in the following ways: waterfalls creating plunge pools, sediment movement leading to lateral levees, and flooding filling nearby depressions with water. Wind can cause the erosion or movement of ground material that results in a depression. Water action on a shoreline can produce coastal lakes by closing off bays with barriers such as sand bars. Lastly, organic lakes are those created by plant growth, beavers, or humans. Extensive plant growth can cause damming action, while beavers use various materials to dam streams and produce a lake, and humans create lakes by making holes, such as when digging quarries.

Size, shape, and composition material of lake basins vary and these characteristics change over time. In different regions, the definition of a lake varies. One is that lakes are usually deeper than three

meters and have a surface area greater than 1-10 hectares, while anything smaller than this is considered a pond (Dodson 2005). Lake basins have different geometries; cross-sections range from semicircular to rectangular, while surfaces can vary from circular to extremely irregular and lobed. Generally, the maximum width of a lake greatly exceeds its depth. Basins are composed of a variety of materials, including rock, dirt, or sand. Lake basins are very dynamic; their size, geometry, and composition change due to the influence of those forces that also cause basin formation. This often happens on a greater time scale than that of a human lifespan.

Lake basins contain freshwater that is lentic, or does not have a consistent flow due to gravity (Wetzel 2001). There are also saline lakes, which are alkaline and have high salt concentrations, that are usually created due to low water inputs and high outputs (Goldman & Horne 1983). Water enters lake basins via surface flow from streams or rivers, ground flow, including springs, and precipitation. Water also leaves a lake due to surface flow and ground flow, and additionally through evaporation (Dodson 2005). Usually surface flow affects water inputs and outputs to a much greater extent than ground flow (Wetzel 2001). The amount of water in a lake changes as rates of inputs and outputs change.

Water movement occurs on both small and large scales. Individual water molecules are constantly moving due to energy exchanges. Causes of large scale movement include wind, gravity, and water inputs. Wind causes the periodic motions of waves, which are limited to depths near the surface of a lake, and seiches, in which all the water in a lake moves. Gravity causes periodic motions to continue, and also causes lunar tides, though these have little impact on large-scale water movement in lakes, even in very large ones (Dodson 2005).

Physical and Chemical Characteristics of Lakes

The ultimate source of light that reaches a lake is the sun. Light consists of electromagnetic waves that are produced by the sun, and is characterized by intensity, or amount of energy from light

that passes through a given area, and wavelength, which quantifies the distance of a wave's oscillation. Light from the sun that reaches the surface of the earth consists of visible light, which has wavelengths of 400-700 nm, ultraviolet light, with shorter wavelengths than visible light, and infrared light, with longer wavelengths than visible light. Not all light produced by the sun reaches the surface of a lake because the absorption of some wavelengths through the atmosphere is limited and because the intensity and wavelength of light is affected by particles in the air, including those from clouds and dust. Half of the energy from light that reaches a lake is in the visible spectrum. Some of this light is reflected off the lake surface, and more is reflected when the incident angle is greater. The incident angle at which light hits the surface of a lake depends on time of day, time of year, and latitude, with the angle being greater at dawn and dusk and at higher latitudes. Incident angle is also affected by the path of indirect light, which is scattered off of other objects, such as trees and mountains, before it hits the lake surface. Lastly, the incident angle is influenced by irregularities of the lake surface (Goldman & Horne 1983).

Light in a lake decreases exponentially with increasing depth (Fig. 1). Once light enters a lake, it is refracted, which changes the angle of the light and causes the light to be separated into different wavelengths. It is then scattered or absorbed. Scattered light bounces off objects in the lake, including dissolved substances and particles, and either reflects back out of the lake or remains in the lake and continues to be scattered until absorbed. Light of shorter wavelengths is scattered more than that of longer wavelengths. Clear lakes look blue because much of the short-wavelength blue light is scattered back out of the lake, but this does not occur in unclear lakes because they contain many dissolved substances and suspended particles that prevent back-scattering. The color of unclear lakes depends on the types of particles present in the water. Scattered light that does not leave the lake is eventually all absorbed by water molecules, dissolved substances, or particles. This absorption produces heat that warms the water of the lake. Absorption occurs exponentially with increasing lake depth, and is

expressed by the extinction coefficient, which is the amount of light held back per meter of depth. The extinction coefficient is low for transparent water, through which light travels further before being absorbed, and higher for unclear water that contains more particles or dissolved substances. Absorption of light also depends on its wavelength. Generally, ultraviolet and infrared light is absorbed first, followed by red, green, and then blue light, though red light moves relatively further in unclear lakes (Goldman & Horne 1983).

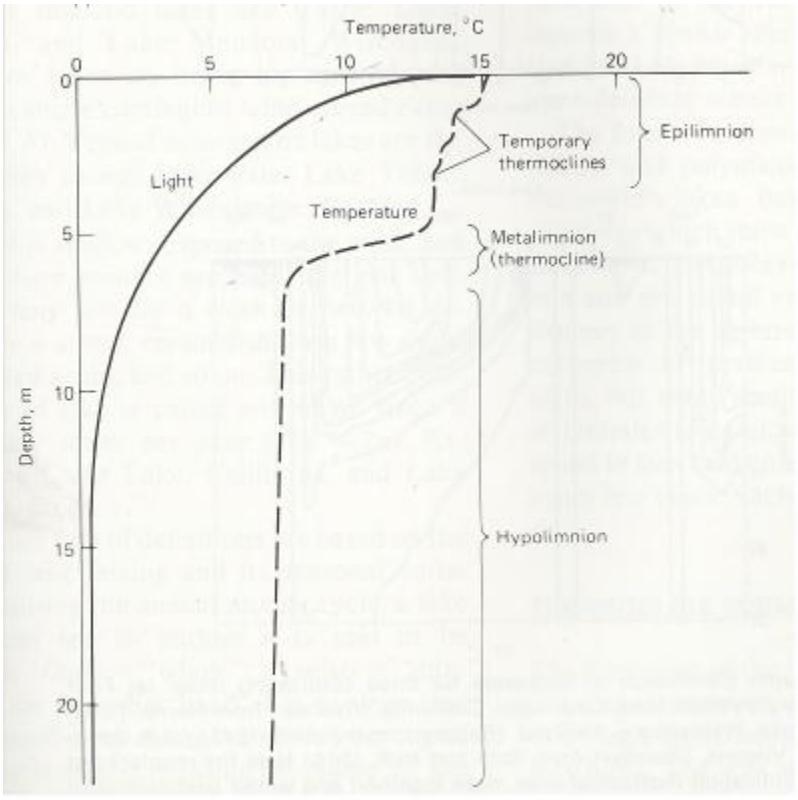
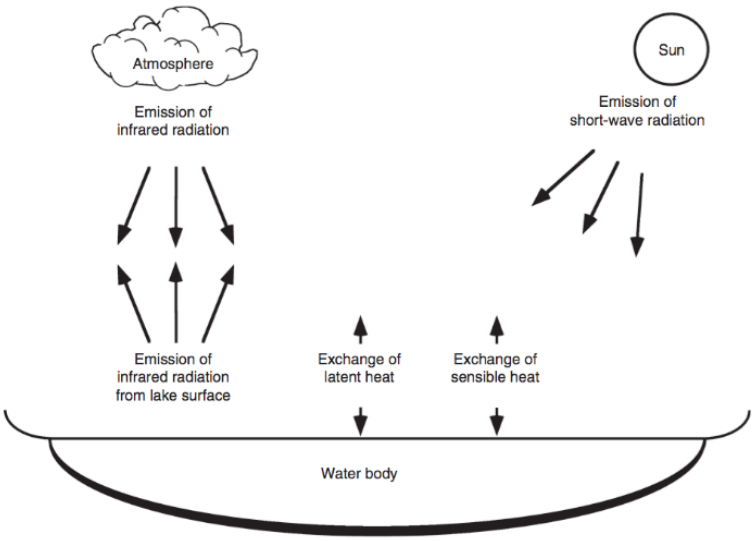


Figure 1. Example of light and temperature profiles of a typical temperate lake. Light is shown as percent of incident light at surface. Epilimnion, metalimnion, and hypolimnion are indicated. Adapted from Goldman & Horne (1983).

The temperature of a lake is based on energy transfer between the lake's water with both light and the adjacent air. De Stasio et al. (2009) describes the ways in which these transfers occur. Two types of radiation, which consists of electromagnetic waves, cause energy transfer. Solar radiation, or light from the sun, is absorbed as previously discussed. Also, infrared radiation is absorbed by or emitted from a lake depending on the temperature difference between the air and water. Evaporation

and condensation between the lake and atmosphere result in latent heat transfers, with the former decreasing energy in the lake and the latter increasing energy. Lastly, convection between a lake and the adjacent atmosphere results in sensible heat exchange (Fig. 2).

Figure 2. Diagram showing the methods of energy transfer into and out of a lake. Solar radiation,



infrared radiation, latent heat exchange, and sensible heat exchange are shown. Adapted from De Stasio et al. (2009).

The temperature profile of a typical temperate lake is characterized by stratification in the summer. A lake is stratified when it contains at least two distinct temperature layers, which are formed as a result of energy input from the sun and the characteristics of water. The upper layer, or epilimnion, is warmer and less dense, while the lower, more dense, cooler layer is the hypolimnion. They are separated by the metalimnion, in which temperature is changing. The thermocline, or depth at which temperature change is greatest, is within the metalimnion and has at least 1°C change per meter of depth (Fig. 1). In the summer, solar radiation heats the water at the surface, which becomes much less dense and forms the epilimnion. The water closer to the bottom is much colder and more dense than that in the epilimnion. Because small temperature changes in water cause great differences in density, the epilimnion and hypolimnion resist mixing with each other due to their density differences. If the

water in a lake is initially fairly warm and the water in the epilimnion becomes even warmer, the density difference between the layers is much greater than if the initial temperature of the water was cooler. Water also has a very high specific heat, requiring great energy input to change its temperature, and there is not enough energy available in the hypolimnion for its density to be similar to that of the epilimnion.

A typical temperate lake has two periods of mixing, in the spring and fall, and ice cover in the winter. Mixing occurs when stratification is broken down and the lake becomes isothermal, or has the same temperature at all depths. This requires that the density difference between epilimnion and hypolimnion decreases, which is caused by a decreased temperature difference between the two layers due to less energy input from solar radiation in the epilimnion, and also sometimes due to strong winds moving the water. Mixing occurs in the spring and fall because there is less energy input into the lake from direct light; as the earth tilts on its axis away from the sun, the incident angle of light increases. Cooling also happens due to evaporation, which is assisted by wind, and conduction. In the winter, water at the surface becomes ice, while below the surface it is still in the liquid phase. This is because the maximum density of water occurs when it is at 3.98°C, so ice is less dense than water at this temperature and will only occur at the surface of a lake. Ice cover prevents wind from reaching the water and therefore mixing, so lakes often become inversely stratified during the winter, with the coldest temperature occurring near the surface and water becoming increasingly warm near the bottom (Goldman & Horne 1983).

While the mixing pattern described above is referred to as dimictic, there are other possible patterns. Dimictic indicates that there are two periods of mixing in a single year in a lake; this is the most common pattern for temperate lakes. Monomictic lakes only have a single mixing period in a year. Some monomictic lakes mix throughout the winter instead of becoming inversely stratified because they are not ice covered, while other lakes that are covered with ice most of the year will have a single

mixing period during the short summer. Conversely, polymictic lakes are often shallow and so easily mixed, and may mix every few days to every day. Meromictic lakes are always stratified, usually because they are extremely deep lakes, while amictic lakes never mix due to being ice-covered throughout the entire year.

Oxygen that is dissolved in lake water comes from the adjacent air and from photosynthesis, and is removed by various additional processes. Air is composed of about 20% oxygen, some of which dissolves in water. Because oxygen is not very soluble in water, though, lakes often have low oxygen concentrations that can be easily depleted. Additionally, there is an inverse relationship between oxygen and temperature, with oxygen levels decreasing as temperature increases. Strong wind may increase oxygen content in lakes because it helps mix gases with the water. Biological processes also influence oxygen concentrations; photosynthesis produces oxygen, though this is restricted to the euphotic zone, while respiration consumes oxygen. The peak in photosynthetic rates tends to occur in the morning, with a decrease in the afternoon. Because oxygen is only produced by photosynthesis while there is light but respiration is not a light-dependent process, oxygen depletion can occur at night. Also, when organic materials decompose, they remove oxygen from the water and can further contribute to oxygen depletion. Therefore, oxygen concentrations usually fluctuate throughout the day, with some extremely productive lakes varying from no oxygen to supersaturation throughout the course of a day. Oxygen levels also vary throughout the year and across depths. Orthograde lakes, which show little decrease in oxygen levels with increasing depth (Fig. 3), are usually characterized by low productivity, while more productive lakes tend to have a clinograde profile that shows a significant decrease in oxygen concentrations in the hypolimnion. Some lakes have irregular increases or decreases in oxygen concentrations at certain restricted depths, usually in the metalimnion, that result from high photosynthetic or respiration rates due to a concentration of animals. These patterns are referred to as positive heterograde and negative heterograde, respectively (Goldman & Horne 1983).

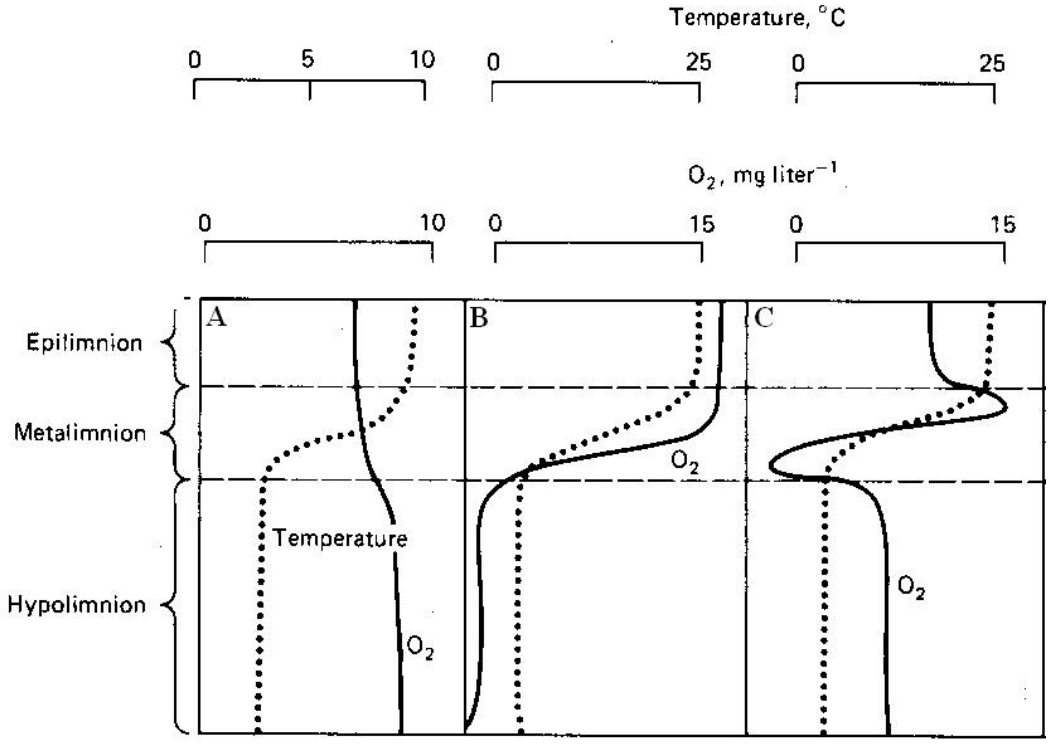


Figure 3. A comparison of lakes with (A) orthograde, (B) clinograde, and (C) positive and negative heterograde oxygen profiles. Temperature profiles and stratification layers are also shown. Adapted from Goldman & Horne (1983).

Carbon dioxide concentrations are often inversely related to oxygen levels because of the processes that affect carbon dioxide in lakes. Carbon dioxide comes from the adjacent air but, even though only a fraction of a percent of air is carbon dioxide, carbon dioxide is many times more soluble in water than oxygen is. Carbon dioxide is produced by respiration and consumed in the photosynthetic process, accounting for the inverse relationship between oxygen and carbon dioxide. Decomposition of organic matter also produces carbon dioxide. Because neither respiration or decomposition of organic matter are light-dependent processes, carbon dioxide is often produced throughout the day and carbon dioxide concentrations may not fluctuate as greatly as oxygen does. Carbon dioxide levels greatly depend on temperature, especially because low temperatures decrease respiration (Goldman & Horne 1983).

pH is a measurement of the hydrogen ion concentration in water. Water molecules in the liquid

phase normally dissociate into hydrogen and hydroxyl ions. These ions are dissolved in liquid water. When the amount of one of these three groups changes, the others change correspondingly because they must remain in equilibrium, so changes in other chemicals in a lake can alter its pH. The pH of a lake also varies with temperature. pH is calculated by taking the negative logarithm of the hydrogen ion concentration. When this value is less than seven, water is considered acidic, while alkaline water has a pH that is greater than seven. Though the pH of lakes vary from zero to more than ten, they commonly have a pH of 7-9 (Dodson 2005).

Locations of Organisms in Lakes

There are three conventional systems used to classify parts of lakes; each is based on abiotic and biotic characteristics of the lake's different parts (Fig. 4). The first and most common method is based on physical locations in the lake. The entire lake bottom is referred to as the benthic zone, and this zone is further distinguished using two categories. The littoral zone is the nearshore section of the benthic zone that contains rooted macrophytes. In shallow lakes, the entire benthic zone is littoral because there are rooted macrophytes at every location. In deeper lakes, the section of the benthic zone that does not contain rooted macrophytes is referred to as the profundal zone. The open water area of a lake is variously called either the limnetic, pelagic, or planktonic zone. All of these lake parts are distinguished as different zones because they generally have unique abiotic and biotic factors.

The different parts of lakes can also be classified based on light. The euphotic zone extends from the surface to the depth at which light is 1% of the surface light intensity. The aphotic zone, where light intensity is less than 1% of surface light, is below this (Thorp & Covich 2001). Stratified lakes have a third type of classification that results from the two distinct regions formed by the epilimnion and hypolimnion, which have different abiotic and biotic characteristics. There is a high concentration of nutrients in the hypolimnion and a low concentration in the epilimnion; because the regions do not mix, nutrients are not transferred from the hypolimnion to epilimnion until stratification breaks down.

As a result, the nutrient contents of the two regions are very different, as are the temperatures.

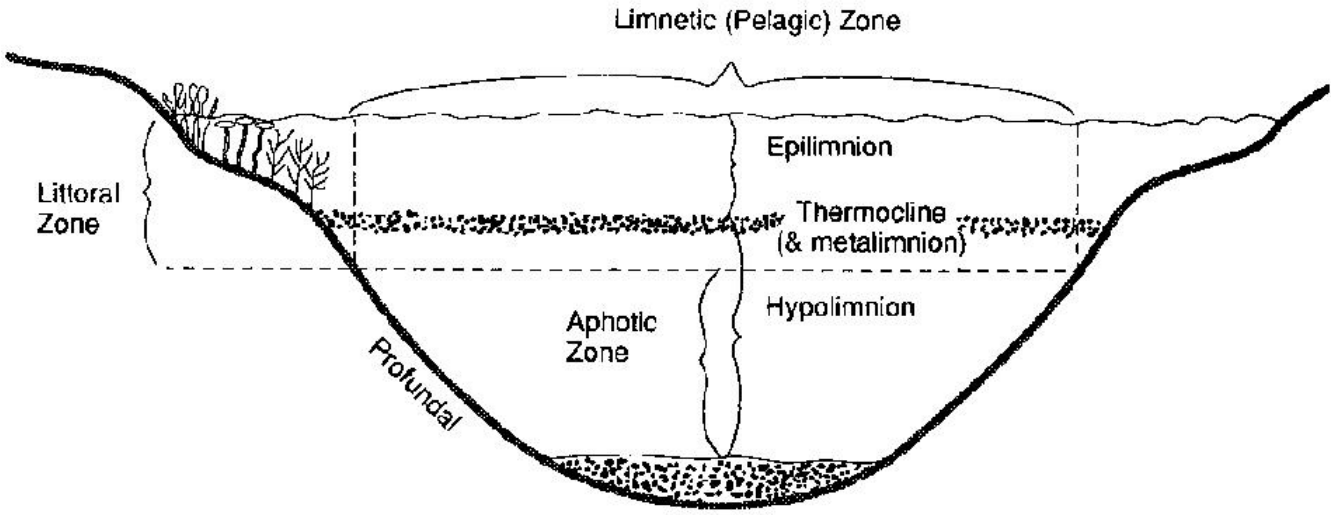


Figure 4. A cross-section of a lake with zones from the different classification systems shown. Adapted from Thorp & Covich (2001).

Organisms are classified based on their occurrence in the different locations of a lake. Planktonic organisms are free-floating in the pelagic zone; their motions are primarily due to movement of water, though they often can swim weakly. Nekton inhabit the same zone as plankton but their movement is mostly due to their own locomotive abilities. The benthos are in the benthic zone, and are split into three types based on arbitrarily chosen sizes. They are, from largest to smallest, macroinvertebrates, meiofauna, and microbenthos. Lastly, the neuston are organisms occurring at the air-water interface near the surface of a lake (Thorp & Covich 2001).

The food-web in the pelagic zone of freshwater lakes consists of two major groups of organisms: fish and plankton. Fish are nekton, and are generally either piscivorous or planktivorous. Piscivorous fish are top predators and consume both planktivorous and other piscivorous fish. Piscivorous fish larvae often eat plankton, though. Planktivorous fish consume plankton and are either visual feeders or filter feeders. Plankton are classified into several groups. Zooplankton contain the largest plankton; they are solely secondary producers and include microcrustaceans, such as copepods and cladocerans,

and rotifers. Zooplankton eat phytoplankton or other zooplankton. Phytoplankton are autotrophic algae and are smaller than zooplankton. Some of these phytoplankton are photosynthetic, while others are chemosynthetic and derive energy from a chemical source (Goldman & Horne 1983). The bacterioplankton group also consists of small organisms, primarily heterotrophic microbes including bacteria and protozoans. Primary producers in lakes include cyanobacteria, green algae, euglenoids, diatoms, dinoflagellates, and sulfur bacteria (Dodson 2005).

Abiotic constraints affect where organisms in the pelagic zone can be located. Visual feeding fish require light to find prey, so they will feed in the euphotic zone during the day using light. Conversely, most of the heterotrophic plankton and filter-feeding fish use chemoreception or mechanoreception to find food and do not necessarily need light for this process. Photosynthetic plankton must be in the euphotic zone, but very high light levels can cause photoinhibition that decreases the rate of photosynthesis, so these plankton may not be near the surface where light levels are highest. Temperature influences all organisms' metabolic rate; some organisms function better in the cool water of the hypolimnion while others need to be in the warm epilimnion. All organisms also require oxygen for respiration. While some organisms can tolerate the anoxic conditions in the hypolimnion, most need more oxygen than is available there and tend to occur at oxygen-rich depths closer to the surface. Like high light levels, high oxygen levels can also decrease photosynthetic rates (Dodson 2005). Nutrient concentrations are different in different parts of a lake, especially between the epilimnion and hypolimnion in stratified lakes, and therefore affect where organisms are located. The limiting nutrient varies amongst primary producers; for most algae, phosphorous is the most limiting nutrient in lakes, while nitrogen is secondarily limiting, but diatoms are limited by silica levels.

Biotic factors that influence organisms' locations in lakes include location of food sources, intra- and interspecific competition, and predation. Heterotrophic organisms consume other organisms; one prerequisite for this behavior is that both groups occupy the same temporal and spatial location.

Consumers therefore evolve to maximize this co-occurrence while the consumed evolve to move away from their consumers in space and time, though such adaptations must be balanced with adaptations that address other factors. One such factor is intra- and interspecific competition. Not only do heterotrophic organisms need to consume other organisms as food, they are competing for these food sources with individuals of both the same species and other species. Organisms that eat similar food sources can deal with this by, for example, preferring slightly different types of these similar foods or consuming similar foods at different times. While organisms must be able to obtain enough food, they also have to avoid predation to continue living, which sometimes requires temporal or spatial separation from predators.

Anti-Predation Adaptations

Morphological, life history, and behavioral adaptations are the three types of adaptations that have evolved in organisms to reduce predation risk. Morphological adaptations are changes to an organism's physical structure which decrease or eliminate the risk of predation. For example, gape-limited predators prefer prey that are the largest size possible, but these predators are physically incapable of consuming prey that are greater than a certain size. When planktivorous fish, which are gape-limited predators, are exposed to zooplankton such as copepods or cladocerans, they preferentially consume the larger adult zooplankton but are unable to consume zooplankton that are greater than a certain size (Zaret 1980). Therefore, a morphological adaptation of zooplankton would be attaining a size at which fish are incapable of consuming them. Life history adaptations are those aspects of organisms' reproductive and growth methods that reduce predation risk. One way that zooplankton can maximize the morphological adaptation previously described is through a life history adaptation. Zooplankton that use energy for growth more efficiently can grow to the adult size more quickly, which limits the amount of time spent as a juvenile that is small enough to be eaten by gape-limited planktivorous fish. Organisms also have evolved behavioral adaptations that reduce their

predation risk. Planktivorous fish produce suction streams that are used to capture zooplankton. When zooplankton perceive these suction streams, they may exhibit a behavioral escape response in which they swim quickly away from these streams, thereby avoiding predators.

Diel Vertical Migration

Diel vertical migration is a common behavioral adaptation in which organisms in lakes change their location to reduce predation risk. This behavior entails organisms moving vertically through the water column in a repeating 24-hour pattern. The "normal" diel vertical migration pattern (Fig. 5) occurs when organisms are deep in the water column during the day and migrate upward towards the surface at night, then repeat this pattern by moving down again during the day (Forward 1993). A "reverse" pattern has also been observed, though more rarely, in which organisms are closer to the surface during the day and deeper in the water column or randomly distributed at night (Lampert 1989). Diel vertical migration in lakes has been observed most commonly for cladocerans, especially *Daphnia*. Organisms from many other groups, including calanoid and cyclopoid copepods, mysids and other shrimp, insect larvae including *Chaoborus*, and rotifers, have been shown to migrate.

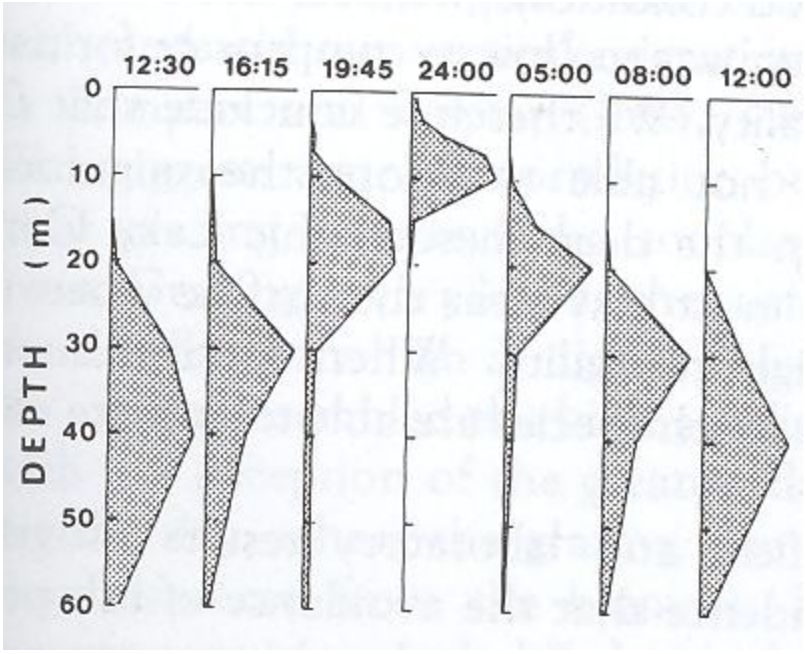


Figure 5. The vertical distribution of the cladoceran *Daphnia hyalina* in a lake at six time intervals throughout the course of a day. A normal diel vertical migration pattern is apparent. Adapted from Lampert (1989).

Initial hypotheses about the ultimate cause of diel vertical migration were based on metabolic or demographic advantages afforded to organisms which migrated. These hypotheses resulted from the perspective that descent during the day is advantageous for organisms (Lampert 1993). McLaren, for example, argued that organisms gain energetically by migrating to colder waters during the day because it is metabolically advantageous (1963). This was referred to as the "McLaren effect". He later revised this to a demographic hypothesis based on a study showing that the female copepod *Pseudocalanus minutus* benefited reproductively from migration to colder waters because it resulted in more fecund females of a larger size (McLaren 1974). This only applied to certain populations and the benefits only occurred if organisms began migrating in later stages of their life cycle. Other benefits that were proposed as advantages of being deep in the water column included increased genetic exchange, better use of food sources, regulation of population, and competition avoidance (Zaret 1980; Zaret & Suffern 1976).

These hypotheses, and similar ones from that time period, have been shown experimentally to

be incorrect (Lampert 1993). In one study of a tropical lake, the adult copepod *Diaptomus gatunesis* was shown to have a strong vertical migration pattern, with an amplitude of at least 12 m, in a lake that was isothermal within a range of 0.2°C year-round (Zaret & Suffern 1976). *Diaptomus gatunesis* could not, therefore, be migrating to reap the benefits of colder waters, as McLaren had suggested (1963; 1974), because there was no temperature difference from which to benefit. Swift also examined McLaren's hypothesis using a population of normally migrating insect larvae *Chaoborus trivittatus* and determined that the energetic predictions made by McLaren were not fulfilled (1976). Most diel vertical migration hypotheses based on metabolic and demographic advantages have similarly been shown to be incorrect (Lampert et al. 1988).

The hypothesis that diel vertical migration is an adaptation to avoid exposure to ultraviolet radiation has not been fully examined. Ringelberg & Gool hypothesized that the initial ultimate cause of the normal migration pattern was avoidance of ultraviolet radiation near the surface of the lake during the day (2003). Such radiation can cause damage to organisms. Because ultraviolet light does not penetrate far into lakes, this factor alone would only initiate a very small-scale migration; the presence of fish kairomones and high food concentrations would amplify this migration. Kessler et al. determined that ultraviolet light was more strongly correlated with zooplankton vertical distributions in lakes with few fish, which was termed the transparency-gradient hypothesis, while fish predation was the more important driver of migration when fish were abundant in lakes (2008). This hypothesis accounts for the occurrence of diel vertical migration in fish-less lakes. They separated out the influences of the two factors, ultraviolet light and fish predation, by examining both ultraviolet light and visible light, on the assumption that zooplankton that were migrating due to fish predation would be deeper than visible light penetrated. Copepods and *Chaoborus* do not respond to ultraviolet light, while the remaining zooplankton have been shown to, and the impact of ultraviolet light is species-specific.

The current perspective on diel vertical migration has shifted; while descent during the day is seen as necessary for some organisms, the emphasis has been placed on the advantage of being able to ascend at night (Lampert 1993). Being deep in the water column entails costs which decrease the fitness of an organism. Growth and reproductive rates are depressed at colder temperatures in the deeper depths of lakes. One aspect of this is slow egg development (Ringelberg & Gool 2003; Hutchinson 1967). Food sources are also generally limited at deeper depths in lakes. Algae tend to be in the upper strata of lakes, especially the photosynthetic algae which must be located in the euphotic zone, and many vertically migrating organisms consume algae. The driving influence that results in daytime descent must therefore be strong enough that the benefits of the behavior compensate for the costs associated with descent. One way to minimize these costs is to ascend to the more favorable conditions at shallower depths when it is possible, which most migrating organisms do at night.

The currently accepted hypothesis for the ultimate cause of diel vertical migration is predation pressure; the necessity of daytime descent is explained by strong pressure from visual predators. Visual predators must remain near the surface, in the euphotic zone, to search for prey during the day. Their prey can therefore avoid them spatially by migrating to deeper depths, where light intensity is weak or absent. At night, the lack of light in the entire lake prevents visual predators from being able to seek prey, allowing prey to return to the surface and benefit from the advantages there.

Zaret and Suffern presented a study in which predation pressure appeared to be a strong driver of diel vertical migration patterns (1976). They examined two lakes, one tropical and the other temperate, both of which contained a visual-feeding fish species and the zooplanktonic prey of this species. In both lakes, the zooplanktonic prey had strong normal diel vertical migration patterns. They completed both field and feeding studies on organisms from the two lakes that confirmed that predation pressure was the ultimate cause of migration. One very intriguing addendum to this study was that fish primarily consumed adult zooplankton, while they consumed juveniles to a lesser extent and rarely

consumed early juveniles. This was correlated to migration patterns; the adult zooplankton migration patterns had the greatest amplitude, while the pattern of the juveniles was less pronounced, and early juveniles exhibited nearly no vertical migration. It has been observed that, while adult zooplankton migrate, juveniles of the same species often do not do so, though they are capable of it (Haney 1993), which may be explained by the lack of predation pressure on juveniles by visual predators.

Additional evidence for the predation pressure hypothesis of diel vertical migration results from a whole-lake experimental study. A small pond in which all fish had been killed due to harsh winter conditions was divided into quarters. One quarter was restocked with the species of sunfish that had previously been in the pond, while another quarter was left fishless. The diel vertical migration pattern of the copepod *Diaptomus sanguineus*, which was present in the entire pond, was much less pronounced in the fishless quarter than the quarter that had been restocked. It was assumed that there was no difference in the two quarters beyond the presence of fish, indicating that sunfish were responsible for differences in vertical migration patterns of the two populations of *D. sanguineus* (De Stasio 1993).

There is much variation in the migration patterns of different species and amongst individuals of the same species. Different species may have very different vertical distributions, and how these distributions change over time also varies (Fig. 6). These changes in distribution do not always present a clear pattern, and sudden changes in environmental factors may result in unexpected distributions. Also, distributions show the patterns of an entire population, not necessarily those of individuals. For example, the amplitude of migration for a particular species is a summary of the movement of an entire population; therefore, many individuals of that population may move further or less far than the amplitude distance. This was shown in a study on *Chaoborus flavicans* by Dawidowicz (1993). Individual *C. flavicans* were placed in separate enclosures and their vertical locations in these enclosures were measured. It was determined that the average depth of the group of *C. flavicans* did not

necessarily reflect the movements of individuals. Even when the average depth of the group did not change over time, some individuals had migration amplitudes that were over half of the available vertical space.

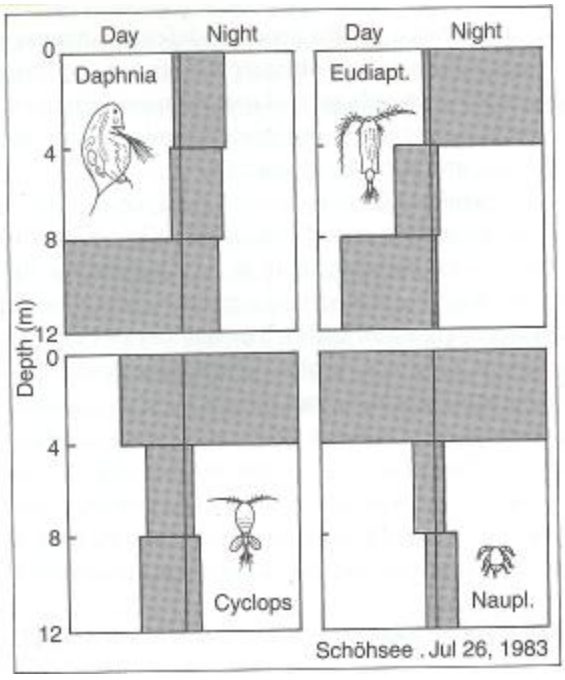


Figure 6. Vertical distributions of four different species of zooplankton in the same lake during the day and night. Normal diel vertical migration patterns exhibited by three of the species are unique from one another, while the nauplii appear to have little change in vertical distribution. Adapted from Lampert & Sommer (1997).

The initiation and amplitude of the migration patterns of different species depends on when the predator that drives the pattern is introduced. Diel vertical migration can be initiated very rapidly for some species following predator introduction. In a study completed by Neill, the copepod *Diaptomus kenai* began a reverse migration pattern less than four hours after being re-introduced to *Chaoborus*, which exhibits normal diel vertical migration, in enclosures (1990). Similarly, Forward showed that a migration pattern was induced in brine shrimp after being exposed to fish larvae for a single day (1993). The extent of diel vertical migration is also influenced by the length of time the migrating species has co-occurred with the predator that drives the migration. Gliwicz examined migrations of the copepod *Cyclops abyssorum* in different lakes; some lakes that were studied had contained fish for more than

100 years, while others had only recently acquired fish populations. It was shown that the longer a fish population had been established, the greater the amplitude of migration by *C. abyssorum* was (1986). It is therefore possible that, for systems in which visual predators have only been recently introduced, migrating patterns by their prey are not detectable except on a very fine scale.

Factors Affecting Diel Vertical Migration

Light is considered the most important proximate factor that influences diel vertical migration (Forward 1993). All organisms that have been shown to engage in diel vertical migration can perceive light. There are four ways in which light influences diel vertical migration (Haney 1993). First, light determines the relevant location of visual predators; the prey of visual predators need to avoid locations where light is strong enough for predators to detect them in order to minimize predation risk. Light also represents the circadian cycle and accounts for the regular daily pattern of diel vertical migration. Additionally, if ultraviolet light influences diel vertical migration, the interaction between light and the water of a lake determines the extent of this radiation and therefore the occurrence and extent of the migrations of organisms. Lastly, light limits photosynthetic organisms to the euphotic zone. Because photosynthetic organisms are often food sources for migrating organisms, ascent towards the surface is beneficial.

Organisms specifically use the intensity of light to guide their vertical migrations. When the rate of change of light intensity passes a certain threshold, negatively phototactic behavior, or movement away from light, is initiated in organisms that migrate normally. This response becomes positively phototactic when light intensity decreases (De Meester et al. 1999). The study completed by Forward on the combined influences of light and predation on brine shrimp exemplifies this. He exposed one group of brine shrimp to predatory fish larvae for a single day, and did not expose a second control group of brine shrimp. After that day, he increased the light intensity in a step-wise fashion and noted the vertical locations of the shrimp. After a certain light threshold was exceeded, the fish-exposed

shrimp descended proportionately to the increase in light intensity while the vertical location of the control group did not change (1993).

While it is currently believed that light is the most important proximate cue that drives diel vertical migration, other factors that influence the specific migration pattern of a given organism include food concentration, chemicals, and temperature. Zooplankton have been observed to not migrate deep during the day when food concentration is low. This is presumably because organisms are more willing to risk predation in order to avoid starvation (Haney 1993). It has also been shown that the presence of chemicals produced by fish or other visual predators can lead to an increase in the amplitude of migration, and this occurs very rapidly after chemical introduction, but such chemicals do not cause diel vertical migration (Haney 1993). While it has been hypothesized that fish kairomones are the proximate cue for migration, these chemicals do not provide the directional, circadian cue which is essential for the proximate cue for migration (Ringelberg & Gool 2003). Temperature preferences can also limit the extent of vertical migration. *Daphnia*, for example, avoid cold waters (Haney 1993).

Kairomones can be the initiating cue for diel vertical migration. Kairomones are chemicals that are produced by predators and are advantageous for prey, and can result in the induction of morphological, behavioral, or life history adaptations in prey (Tollrian & Dodson 1999). They are useful for initiation of vertical migration patterns because they indicate presence, density, and species of predators; kairomones are predator-specific and their concentrations are proportional to predator density. Kairomones produced by visual predators have been shown to induce a negatively phototactic response in prey during the day, corresponding to a normal diel vertical migration, while those produced by invertebrate predators induce the positively phototactic response associated with reverse vertical migration (De Meester et al. 1999).

Other factors that affect the extent of diel vertical migration are the visibility of the migrating prey and the clarity of the water. Studies have shown, for the most part, that organisms which are

smaller or more translucent have a decreased migration amplitude, presumably because they cannot be seen as easily by visual predators. Differing sizes not only account for the different migration amplitudes of different species, but also those of different-sized individuals of the same species; smaller individuals do not migrate as far as large individuals (De Meester et al. 1999). Similarly, in lakes with low water clarity, the amplitude of migrating organisms may be decreased because light does not penetrate as far and visual predators have decreased visual capabilities (Lampert 1993).

Reverse diel vertical migration patterns, which are unusual, may be explained by trophic cascades. While most vertically migrating organisms exhibit the normal migration pattern, some instances of a pattern that is reversed from this, which consists of daytime ascent and nighttime descent, have been observed. These patterns may occur because visual predators induce a normal migration pattern in their prey, and the normal pattern of these prey induces a reverse migration pattern in their prey. An example of this cascade was shown in a study by Gilbert and Hampton. In a small lake, visual-feeding insects called notonectids induced a normal migration pattern in the copepod *Tropocyclops extensus*. This copepod was a predator of the rotifer *Polyarthra remata*, also present in the pond, and presumably induced the reverse migration pattern that *P. remata* exhibited (2001). A similar cascade may have been recorded in a fishless lake that contained normally migrating *Chaoborus*. The notonectids in this lake may have induced the *Chaoborus* migration pattern, which consequently induced what appeared to be a reverse migration pattern in *Diaptomus kenai*, the primary prey of these *Chaoborous* (Swift 1976).

Rotifers: General Biology

Rotifers are invertebrate animals that are often extremely abundant in lake systems and can constitute the majority of the biomass (Williamson 1983). Herzig estimated that rotifers are 10-44% of zooplankton biomass in many lakes (1987). They live an average of 11 days, but lifespans of different species range from a few days to over a month. They are microscopic or nearly so, with lengths from

100 to more than 2,000 μm (Thorp & Covich 2001). All are eutelic, or have a fixed number of cells as adults, with most species consisting of around 1000 cells, and they exhibit bilateral organization. Rotifers also have several organs which are synctial, or a single cell with a fixed number of multiple nuclei.

Although rotifers are unsegmented, their body organization generally implies distinct head, trunk, and foot regions. The entire body of a rotifer is covered in an integument that is thin and flexible at some points but may be developed into a thicker lorica at others. Some species are almost entirely loricate, while others lack this development. The corona aids in locomotion and feeding; it is located in the head region and consists of a ring of cilia which surrounds the mouth. The cilia create a buccal field around the mouth which leads to the buccal cavity. Inside this cavity is the mastax, or muscular pharynx, which controls the trophi, or jaws, that are used to capture and process food. The trophi are specialized for the type of food that is consumed and the method by which it is captured. Because trophi are species-specific, they can be used for identification. The rotifer digestive system is simple and consists of, in order from the trophi, esophagus, stomach, intestine, and cloaca, through which waste exits. The excretory system is protonephridial, with flame bulbs occurring regularly throughout the body. Rotifers have a simple nervous system consisting of ganglia, concentrated in the head region, and connective nerve fibers throughout the body (Pennak 1989). The foot region often contains an actual foot in sessile species, which is used for attachment or crawling, though some species lack a distinct foot region. The foot may have up to four toes and, in sessile species, produces a cement for attachment to surfaces (Thorp & Covich 2001). Projections from the trunk, including spines and paddles, are not uncommon in rotifers species.

All rotifers are capable of swimming, but only planktonic rotifers swim exclusively. While most use the coronal cilia to swim, some species have paddle appendages that aid in locomotion. Many of the sessile or benthic species crawl or creep, or are attached to substrates (Clement et al. 1983).

Swimming is influenced by age of the organism and presence of calcium in water (Clement 1987).

While most species of rotifers are solitary, coloniality occurs in the Flosculariidae and Conochilidae families, with colonies recorded for 25 species. These colonies consist of two to more than 1000 individuals, and are usually intraspecific and sessile. Although coloniality is rare, this adaptation may result in significant sexual advantages and predation deterrence for those species that engage in it (Wallace 1987).

Rotifers are predominately parthenogenetic, with natural populations consisting almost entirely of amictic females producing unfertilized eggs. The sexual cycle only occurs when eggs that result in mictic females are produced, which is likely in response to environmental cues such as high population densities, increased day lengths, or the chemical alpha-tocopherol (vitamin E) (Gilbert 2007). Mictic females are morphologically similar to amictic females but produce eggs that become males if not fertilized. Males are greatly reduced in size, receptor function (Wurdak et al. 1983), and structure compared to females, and they fertilize mictic female eggs to produce resting eggs. These resting eggs enter obligatory diapause, which allows populations to persist through unfavorable environmental conditions, and eventually develop into amictic females (Gilbert 2007).

Rotifers have abiotic preferences, which are generally species-specific. As a group, rotifers can tolerate a wide range of temperatures; individual species can often be categorized based on more restricted temperature preferences though. Cold-stenothermal species prefer cooler temperatures, and therefore tend to have population maximums in the winter and occur in the hypolimnion during the summer. Though the distinction is less clear, warm-stenothermal species generally have population maximums in the summer and prefer warmer temperatures (Berzins & Pejler 1989b). Using another set of distinctions, perennial species tolerate a wide range of temperatures, from 1°-20°C, while winter and spring species prefer less than 10°C and summer species greater than 10°C (Herzig 1987). Similarly, while rotifers as a whole can inhabit bodies of water with a wide range of pH, most species live in

water that has a pH close to neutral. A few species seem to be adapted to very acidic environments and are rarely found in alkaline waters. There are no correlations between temperature and pH preferences for any species (Berzins & Pejler 1987). Decreased pH (or increased acidity) in lake systems is correlated with increased overall rotifer biomass (Frost et al. 1998). Rotifers also can tolerate a wide range of oxygen concentrations. While it is expected that cold-stenothermal species have low oxygen preferences because there tends to be low oxygen concentrations in cooler water, this does not seem to be so (Berzins & Pejler 1989a). Some species can tolerate low oxygen levels, especially if preferred food items such as bacteria are present in areas with low oxygen (Herzig 1987), while a few species thrive at lower oxygen concentrations (Berzins & Pejler, 1989a). Rotifers require high levels of phosphorous and are probably limited by this nutrient (Walz 1995).

Rotifers: Reception and Locomotion

Rotifers respond to external stimuli via their nervous system and do not exhibit any ability to learn. Receptors on the rotifer body receive external stimuli, which then send signals to the ganglia through the nervous system. The ganglia consequently send out signals to effectors in the body, resulting in behavior (Clement et al. 1983). Rotifers have three known types of receptors: light, mechano-, and chemoreceptors. Most of these are concentrated in the head region. Signals to the receptors cause behaviors, especially those specific to movement and feeding.

Although rotifers have light receptors, they do not have vision. All light receptors are located in the eye, which consists of four cells, and ocelli. These receptors may be affected by direction, duration, intensity, quantity, quality, or wavelength of light, depending on the species (Clement et al. 1983). Rotifers exhibit both photokinesis, or light-induced activity (Clement 1987), and phototaxis, or movement with respect to light orientation (Clement et al. 1983). For example, light can directly affect the amplitude of ciliary beat, causing changes in swimming behavior.

Mechanoreceptors in rotifers are highly concentrated in the cilia and the coronal region, and are

present in and on the mastax. These receptors are affected by signals both through contact and at a distance. Mechanoreceptors are affected by touch, and may be sensitive to form and texture of objects (Clement et al. 1983). For example, female *Asplanchna brightwelli* only consume food items that are big enough to touch mechanoreceptors on both sides of the buccal cavity (Wurdak et al. 1983). Some mechanoreceptors respond to more distant stimuli, including vibration of nearby objects and changes in water pressure.

Rotifer chemoreceptors usually co-occur with mechanoreceptors and also respond to chemicals that contact them or are at a distance. For example, males must contact a certain glycoprotein on females with their coronal receptors in order to initiate mating (Wallace & Snell 2001). Rotifers also may reject certain food items after they are evaluated by chemoreceptors in their buccal cavity (Clement et al. 1983).

Swimming is an energetically expensive behavior for rotifers. Although the theoretically calculated energy expense of swimming is low, the inefficiency of rotifer cilia causes actual energy expenditure to be high (Epp & Lewis 1984). Half of the energy produced by *Brachionus*, for example, is used for swimming. Cilia limit swimming speed because they are only present on the head region of rotifers, and would not be useful for organisms much bigger than the largest rotifer species (Epp & Lewis 1984).

Both certain abiotic conditions and characteristics of individuals affect the maximum swimming speeds of rotifers. Swimming speeds are greatest when the temperature is 20°-32°C, calcium is present, and the intensity and wavelength of light increases (Salt 1987). Female rotifers generally swim more slowly than males of the same species (Clement et al. 1983), and very young or old rotifers swim slower than when mature (Salt 1987). It is also advantageous for rotifers to be smaller. Small rotifers move relatively more body lengths than larger ones (Epp & Lewis 1984). When relativized to mass, rotifers of greater mass move more slowly (Stemberger & Gilbert 1987a). Swimming speed is also

species-specific and there is great variation in maximum possible speeds. Individual *Asplanchna sieboldi* have been reported to swim at a maximum speed of 1.3 mm/s, while *Brachionous plicatilis* has a maximum swimming speed of 0.8 mm/s and *Ptygura beauchamps* has a maximum speed of ~3 mm/s (Salt 1987).

Rotifers: Feeding and Resource Competition

Rotifers are generally either predatory or suspension feeders. The specific feeding method of any individual can be determined by characteristics of their trophi because the trophi structure has evolved to match preferred food. Predatory rotifers have either incudate or forcipate trophi (Fig. 7), which are optimal for grasping food items. Microphagous or filter feeding rotifers are characterized by trophi used for crushing food, which are either malleate and ramate. Rotifers with virgate trophi either suck or pump food items, and an uncinate trophi indicates a rotifer which traps food (Clement et al. 1983).

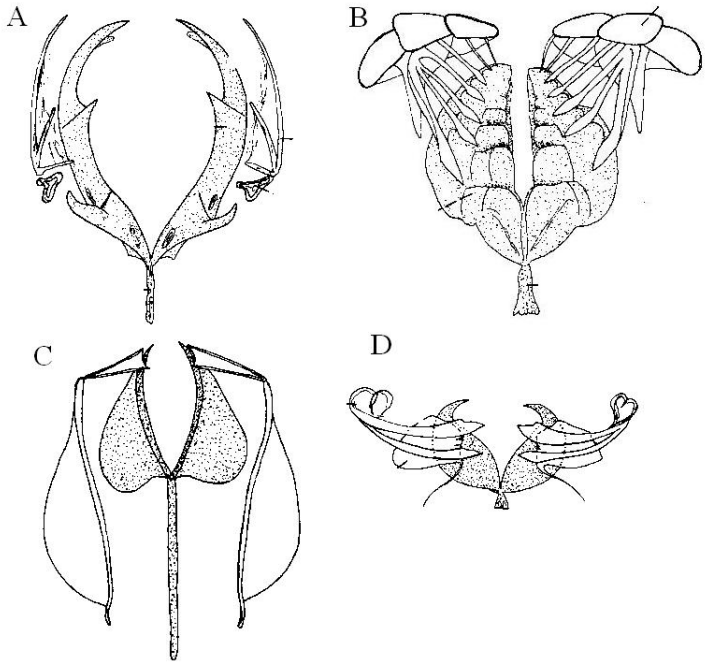


Figure 7. Examples of trophi structures: (A) Incudate trophi of *Asplanchna*, (B) malleate trophi of

Ephiphanes senta, (C) virgate trophi of *Synchaeta*, and (D) uncinate trophi of *Stephanceros*. Adapted from Pennak (1989).

Preferred food items for most suspension-feeding rotifers include phytoplankton, flagellates, and yeast (Clement et al. 1983), and they also consume protozoans (Walz 1995). While bacteria can be consumed by rotifers, they avoid this food source unless necessary (Walz 1995; Starkweather et al. 1979). Predatory rotifers such as *Aplanchna* may consume other rotifers. Rotifers are often unaffected by toxic phytoplankton such as cyanobacteria (Walz 1995), and it has been shown that the toxic algae *Rhodomonas* do not negatively affect the growth of *Keratella cochlearis* (Stemberger & Gilbert 1985).

Different factors affect the ability of rotifers to sense and retrieve food. Encounter rates between rotifers and food items increase with bigger food items and greater food concentrations. When food concentration is low, ingestion rates are correspondingly low, but high food concentrations also limit ingestion rates, resulting in intermediate food concentrations being optimal (Starkweather 1980; Salt 1987). Temperature also influences feeding rates (Herzig 1987).

The ability of rotifers to sense and retrieve food is also affected by their morphology. Because locomotion is related to size, size is consequently related to feeding rates. Smaller rotifers are exposed to relatively more food items than larger rotifers. For example, a rotifer that is twice as long as another has only half of its food-finding volume per unit body volume (Salt 1987). Because larger rotifers cover relatively less area, and require more food, they cannot subsist in environments with lower food concentrations like smaller rotifers can (Stemberger & Gilbert 1985). Size of corona is another important factor in feeding rates. Rotifers only sense food items when there is contact with the corona, so a corona with a larger surface area will increase the encounter rate between rotifer and food items (Salt 1987). While larger coronas are more advantageous for feeding, their size is limited because of mechanical constraints, the cost of having more cilia, and because larger coronas increase invertebrate predation risk (Stemberger & Gilbert 1987a).

Rotifers are selective with food items. This is apparent because their clearance rate and ingestion rate often differ (Starkweather 1980). Cells may be selected based on ease of consumption, and rotifers "taste" food items with the chemoreceptors in the cilia and mastax. They have been shown to prefer intermediate cell sizes, usually from 4-17 μm (Gilbert 1985). There are several ways rotifers can control ingestion of food items. They have been shown to reject food items, possibly due to mechanical difficulties associated with handling such items (Salt 1987). While they cannot make their corona larger, rotifers can make their corona smaller by withdrawing it. Some species also have a pseudotrochal screen that can be moved over the corona to filter out certain particles. *Brachionus* have been shown to use the screen to prevent ingestion of large items (Starkweather et al. 1979). While hunger leads to feeding, we know very little about the influence of rotifer hunger on selectivity (Salt 1987).

Feeding selectivity in rotifers is species-specific. While rotifers may not be able to be selective when food concentration is low, it has been shown, based on gut analyses, that when food concentration is high and cell types are varied, rotifers are especially selective (Starkweather 1980). Rothhaupt showed that three different species of *Brachionus* selected different sizes of food items, and that larger species selected larger food items (1990). Some species, such as *Keratella* and *Brachionus*, are considered generalists in comparison to those that are more specialized, including *Polyarthra* and *Synchaeta*. Nevertheless, because all species have different specific preferences, interspecific competition for resources is reduced (Herzig 1987).

Rotifers compete amongst one another for resources. Competition is either intraspecific, between organisms of the same species, or interspecific, between organisms of differing species, and rotifers compete for food. In an intraspecific example, Snell combined two clones of *Asplanchna* in a laboratory setting. One clone always very clearly outcompeted the other, shown by loss of fitness and eventual depletion of that clone population (1979). Though the clones were very similar, they were

different enough that one clone always had a higher feeding rate than the other and would drive it to starvation. This differential use of resources led Snell (1979) to hypothesize that different clones must occupy different temporal or spatial locations in order to exist in the same lake because all but one will be outcompeted if they occupy the same locations. Rotifers, both intra- and inter-specifically, have different food preferences and different temperature preferences. Population maxima of different species occur at different times of the year, indicating preferences for slightly different conditions (Herzig 1987). George and Fernando observed spatial segregation of rotifer populations of varying species and they hypothesized that the vertical distribution of *Polyarthra* may have been due to avoidance of *Filinia* and *Keratella* (1970). Another example, from a different lake, was the spatial segregation of *Kellicottia* and *Polyarthra* (Gonzalez 1998).

Rotifers: Predation

Predation pressure on rotifers can be strong because they have many types of predators. Rotifers are small enough that few of their predators are visual feeders; most of their predators use either mechano- or chemoreceptors to locate prey (Stemberger & Gilbert 1987a). Adult fish generally do not prey on rotifers because they cannot see them, though some filter feeders may occasionally consume rotifers (Stemberger & Gilbert 1987a). Fish larvae can also consume rotifers, but they are often littoral and cannot due to this spatial segregation (Herzig 1987; Walz 1995). Both cyclopoid and calanoid copepods, the former being raptorial and the latter both raptorial and filter-feeding, are predators of rotifers (Herzig 1987). Early instars of *Chaoborus* often feed on rotifers, while later instars tend not to (Stemberger & Gilbert 1987a). Mysids, which are filter feeders or raptorial, may feed on rotifers (Herzig 1987), as can some cnidarians and protozoans (Williamson 1983). Some raptorial rotifers prey on other rotifers; *Asplanchna* is the best known of the raptorial rotifers and feeds using suction. It is also possible that the rotifer *Ploesoma* feeds on other rotifer species because rotifer trophi have been found in gut analyses of this species (Stemberger & Gilbert 1987a).

Cladocerans also, unintentionally, fulfill the role of rotifer predator. Cladocerans such as *Daphnia* are filter feeders and sometimes mistakenly capture and ingest rotifer species, usually damaging or killing them in the process (Gilbert & Kirk 1988). This is interference or mechanical competition. *Daphnia* have also been shown to reduce rotifer populations via exploitative competition. Rotifers and cladocerans such as *Daphnia* have similar diets that consist primarily of algae, but *Daphnia* are larger, have higher clearance rates, and can consume larger algae. Rotifers often cannot compete with *Daphnia* and starve because they have no food refuges from them. This was shown experimentally; *Daphnia* eliminated populations of *Brachionus* and *Keratella* in two to three weeks and one week, respectively, due to starvation (Gilbert 1985). While cladocerans have not been shown to directly and selectively prey on rotifers, they can indirectly decrease rotifer abundance.

Rotifers: Anti-Predation Adaptations

The model of predation by cyclopoid copepods on rotifers highlights the different factors, of both predator and prey, which affect this predation (Williamson 1983). The rate of predation by cyclopoid copepods depends on the sex, age, and species of a specific individual. Increased hunger level or density of the predator will increase predation rates on rotifers. Whether a certain rotifer species is successfully preyed upon depends on density and individual size. The specific morphological and behavioral adaptations of rotifers also can decrease predation by cyclopoid copepods.

Some morphological adaptations of rotifers that affect the ability of their predators to find them are only applicable to visual feeding predators. Because rotifers are small, they cannot be found or seen easily by visual predators such as fish. Similarly, the translucent integuments of rotifers make it difficult for predators to see them.

Other rotifer morphological adaptations which have evolved limit the ability of predators to consume them. Coloniality greatly increases the size of rotifers compared to the size of an individual,

which decreases predation risk (Wallace 1987). Similarly, rotifers like *Asplanchna* are large enough to avoid predation by some of the smaller predators such as copepods (Stemberger & Gilbert 1987a). Some *Asplanchna* species additionally have body wall outgrowths that make them more difficult to consume (Williamson 1983). A well-developed lorica decreases predation risk and may be even more effective at this than spines (Williamson 1983), which will be discussed shortly. *Keratella*, for example, is almost entirely covered with a hard lorica except for a small opening for the buccal cavity, making it difficult for some predators to manipulate and digest this species (Gilbert & Williamson 1987). *Asplanchna*, on the other hand, is a soft-bodied species and does not benefit from a lorica, but when a predator makes contact with them, they withdraw their corona and become turgid and more difficult to handle (Gilbert & Williamson 1987).

Rotifers exhibit some morphological adaptations that decrease predation risk but may not have evolved for this reason. Some rotifers, including species of *Brachionus, Keratella, Kellicottia,* and *Notholca*, have developed spines; this makes them difficult to catch and consume, especially by copepods and predatory rotifers (Stemberger & Gilbert 1987a). After an experimental increase in acidity in one lake, biomass of *Keratella taurocephala* increased while spine length decreased, both likely in response to decreased predation pressure (Frost et al. 1998). *Keratella* have been shown to avoid predation by *Mesocyclops* due to presence of spines (Gilbert & Williamson 1978). It is interesting to note that spines can be induced in *Brachionus* in a single generation after exposure to chemicals produced by the predatory rotifer *Asplanchna* (Gilbert 1966). Nevertheless, spines may not have evolved for this purpose. Spines decrease the sinking rate of *Brachionus* that have them, which is advantageous because they then utilize less energy to prevent sinking and can instead use it for higher reproductive rates or for survival in low food concentrations (Stemberger 1990). Some species of *Ascomorpha* and *Conochilus* have developed mucus sheaths that reduce predation risk, especially against copepods. These rotifers do not have any other morphological or behavioral defenses against

predation, so the mucus sheaths are useful for this. These sheaths also decrease their respiration rate, though, and therefore may not have initially evolved for predation protection (Stemberger & Gilbert 1985).

Rotifers also exhibit life history adaptations that reduce predation risk. Rotifers have many predators, which often results in high mortality rates. Some species have evolved to have high population growth rates, preventing populations from being entirely decimated due to predation (Walz 1995). This adaptation is less important for those rotifer species that have morphological and behavioral adaptations that deal more effectively with predation risk (Stemberger & Gilbert 1987a). While rotifers are predominantly parthenogentic, they also may reproduce sexually, increasing genetic variation in a population and potentially resulting in adaptations that are more effective against predation. Sexual reproduction occurs infrequently because it requires high abundances to ensure high encounter rates between male and female rotifers (Snell & Garman 1986). The sexual cycle produces resting eggs that undergo diapause in order to resist unfavorable environments, including those with high predation risk (Gilbert 2007). The method of egg production in different rotifer species is varied to deal with different predation risk and depends on characteristics of the specific rotifer, including size and presence or absence of lorica. The eggs of some species remain attached to the mother, with some attached directly to the body, and others by a mucus thread or in a mucus sheath. Other species release their eggs into the water, while a few give live birth to their offspring (Stemberger & Gilbert 1987a).

Some rotifer species have developed highly effective behavioral adaptations. Some rotifers retract their corona when it is contacted, which causes them to sink, possibly out of the vicinity of predators (Clement 1987; Wallace 1987). *Brachionus* combine this behavioral adaptation with a morphological adaptation; when their corona retracts, their spines stick out further and more effectively impede predation attempts (Gilbert 1966) (Fig. 8). These adaptations are a form of passive escape from predators. An active escape from predators is exhibited by three rotifer species: *Keratella, Polyarthra,*

and *Filina*. When individuals of these species are contacted, they increase their swimming speed rapidly and move away from the source of contact. *Polyarthra* moves quickly away to a distance that is about ten times its body length after it is contacted (Gilbert & Williamson 1978), while *Keratella* move 12-18 body lengths away (Gilbert & Kirk 1988). Though the contact does not necessarily have to be from a predator to induce this escape response, it has been shown that *Keratella* can actually distinguish between predators, specifically *Daphnia* and *Asplanchna*, and modify their response accordingly (Gilbert & Kirk 1988). This active escape response is a very effective behavioral adaptation against predation.

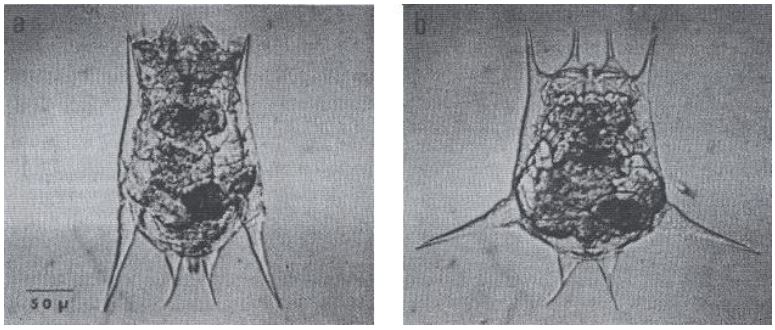


Figure 8. An individual *Brachionus* with (A) its corona expanded and spines retracted and (B) its corona retracted and its spines extended, exhibiting a behavioral adaptation that results in reduced predation risk. Adapted from Gilbert (1966).

Rotifers: Diel Vertical Migration

Some rotifers have also developed diel vertical migration, another behavioral adaptation. In most studies, if rotifers have exhibited a migration pattern, it is a normal pattern and not a reverse pattern (Gilbert & Hampton 2001). Normal rotifer migration patterns have been recorded for *Conochilus hippocrepis, Conochilus unicornis, Keratella cochlearis, Notholca longispina* (Pennak 1944), *Kellicottia longispina* (Plew & Pennak 1949), *Conochilus unicornis* (Grover & Coker 1940), two species of *Synchaeta* (Burris 1980), *Keratella crassa* (Magnien & Gilbert 1983), and *Hexarthra bulgarica* (Carrillo et al. 1989). Reverse diel vertical migration patterns have been observed in

Keratella quadrata (Pennak 1944, Burris 1980), *Keratella cochlearis* (Pennak 1944), and *Polyarthra remata* (Gilbert & Hampton 2001). Some of the reverse migration patterns can be attributed to predators that have normal patterns (Gilbert & Hampton 2001), while one species had a normal migration pattern in a lake which contained no visual predators (Carrillo et al. 1989). The migration amplitudes of these rotifer species varied wildly, from 0.9m in *Kellicottia longispina* (Plew & Pennak 1949) to 8m in *Keratella cochlearis* (Pennak 1944).

Not enough studies have been completed that are designed specifically to detect rotifer diel vertical migration. Because rotifers are small organisms and their mode of locomotion requires high energy expenditures, the amplitudes of their migration would be much smaller than that of other zooplankton such as *Daphnia*. Therefore, while no migration pattern has been observed for several rotifer species in some studies (Pennak 1944; Grover & Coker 1940; Burris 1980), most of them were conducted primarily with the intention of determining migration patterns of larger zooplankton and the sampling was not necessarily appropriate to determine rotifer migration patterns. Migration in rotifers is not only species-specific, but also may vary amongst different sexes and different types of females. For example, Magnien & Gilbert noted that egg-carrying females of *Keratella crassa* had different migration amplitudes than non-egg-carrying females (1983).

Chaoborus: General Biology

Larvae of the family Chaoboridae are one of the most important invertebrate predators in aquatic systems. They are often the only insect present in the limnetic zone of lakes (Hilsenhoff 2001), and especially influence the structure of zooplankton communities (Swift 1992). Referred to collectively as phantom midges, there are 14 known species of *Chaoborus*. The larvae are transparent, have great length relative to their width, and are characterized by laterally-moving mandibles and a lack of segmented legs (Hilsenhoff 2001). They respire through their integument, and their respiration rates are low enough that most energy can be used for growth (Wetzel 2001). Reproduction occurs once

or several times a year (Hilsenhoff 2001). Multiple species of *Chaoborus* can simultaneously survive in the same lake if extensive resources are available or if certain morphological, behavioral, or life history adaptations differ between species (Wetzel 2001). Federenko and Swift (1972), for example, determined that *C. americanus* and *C. trivittatus* could coexist in Eunice Lake because of their differential vertical distributions, feeding habits, and breeding periods.

The *Chaoborus* life cycle consists of an aquatic larval stage and a subsequent short aerial adult stage. Individuals can remain in the complete larval stage for six weeks to a year. In that time, they progress through four instar developments, all of which are present in the limnetic zone. Both first and second instar stages are short, usually lasting several weeks. The third and fourth instar stages are longer, lasting up to several months, or more if instars overwinter in the benthic zone. Between the fourth instar and adult stages is the pupal stage; it is the shortest and has a maximum duration of two weeks. Adult *Chaoborus* live for less than a week, and reproduce but do not feed (Hilsenhoff 2001; Wetzel 2001; Tollrian & Dodson 1999).

Chaoborous larval instars often exhibit a normal diel vertical migration pattern. All four larval instars and pupae have been shown to migrate, and can move an average of 4-6 m hr^{-1}, or 1-2 mm/s, through the water column (Wetzel 2001). The primary predator of *Chaoborus* larvae is fish. Because predation pressure from fish on first and second instars is limited, their migration amplitude is often restricted to the limnetic zone. Migration is more pronounced in the later third and fourth instars because they are larger and less transparent; they often move between the benthic zone during the day to the limnetic zone at night (Hilsenhoff 2001). For example, the migration amplitude of fourth instars of *C. trivittatus* was shown to be 9m, between the epilimnion and hypolimnion of the 20m deep Eunice Lake (Swift 1976), while in another study third instars of *C. trivittatus* had a migration amplitude of 5m but the fourth instar of this species had an amplitude of 12m (Federenko & Swift 1972). The migration cue for *Chaoborus* is known to be a change in light intensity (Wetzel 2001). The ultimate cause of

Chaoborus diel vertical migration is fish predation, and species in fish-less lakes do not exhibit migration behavior (Tollrian & Dodson 1999). Fish kairomones can induce vertical migration behavior in *Chaoborus* (Tjossem 1990). Additionally, both *C. flavicans* and *C. punctipennis* were shown to be negatively phototactic in response to fish kairomones (De Meester et al. 1999). Migration is also influenced by oxygen levels, as later larval instars may not move out of the benthic sediments when oxygen concentrations are sufficiently high in the benthic zone (Wetzel 2001).

Chaoborus: Role As Predators

Chaoborus are ambush predators that remain stationary in the water column until prey enters their vicinity. They detect vibration from prey using mechanoreceptors located along the entire length of their body (Riessen et al. 1984), resulting in predation success that is influenced by the amount and type of vibration produced by prey, which differs according to prey morphology. An enlarged antenna is used for prey capture (Hilsenhoff 2001). Intensity of *Chaoborus* predation is also influenced by prey density and swimming patterns of prey (Swift & Federenko 1975). Effective defenses by prey against *Chaoborus* include gelatinous sheaths, deadman's response, faster swimming speeds (Swift 1992), large size, and unusual morphology.

Chaoborus are selective and prey on a variety of planktonic organisms. They generally consume prey that is 0.5-2.5 mm (Tollrian & Dodson 1999); most of the prey consumed is in the middle of this range because, as prey size increases, encounter rate with prey increases but successful capture rate simultaneously decreases. For example, using *Daphnia* of many sizes, those that were in the middle of the size range, around 1.51 mm, were most susceptible to predation by fourth instars of *Chaoborus* (Pastorak 1981). All instars prey on rotifers and larger phytoplankton, and can also consume protozoans and insect larvae (Swift 1992). Third and fourth instars additionally consume copepods and cladocerans, and later instars of *Chaoborus* may cannibalistically consume early instars of the same species (Federenko 1975). *Chaoborus* tend to be more selective when satiated (Riessen et

al. 1984) and prey is abundant. Therefore, in different lake systems, *Chaoborus* can greatly influence rotifer, copepod, or *Daphnia* populations depending on specific factors including prey density, prey abundance, and predator selectivity (Moore 1988; Tollrian & Dodson 1999).

Diet composition differs between the earlier first and second instars and the later third and fourth instars. The primary reason for this ontogenetic diet shift is an increase in gape width as instars mature; later instars have bigger gapes and consequently can consume larger prey (Persaud & Dillon 2010). Although later instars preferentially consume larger prey, they are also still able to consume smaller prey such as rotifers and phytoplankton (Swift 1992; Gilbert & Moore 1987). The different diet compositions of different larval instars is also due to their differing spatial overlap with prey (Federenko 1975), which is to some extent affected by vertical migration patterns.

First and second instars are more significant predators of rotifers and phytoplankton than later instars are (Moore & Gilbert 1987), and rotifers often account for most of the biomass consumed by first and second instars (Moore 1988) (Fig. 9). Nevertheless, Moore & Gilbert showed that third and fourth instars have the highest recorded predation rate on rotifers compared to all other invertebrate predators, though they still may not significantly impact rotifer populations (1987). Third and fourth instars prefer copepods to cladocerans; while they capture both types of crustaceans equally, they ingest copepods more frequently (Swift & Federenko 1975). For example, when a variety of prey species were available, one species of *Chaoborus* chose to consume primarily the copepod *Diaptomus kenai* (Swift 1976).

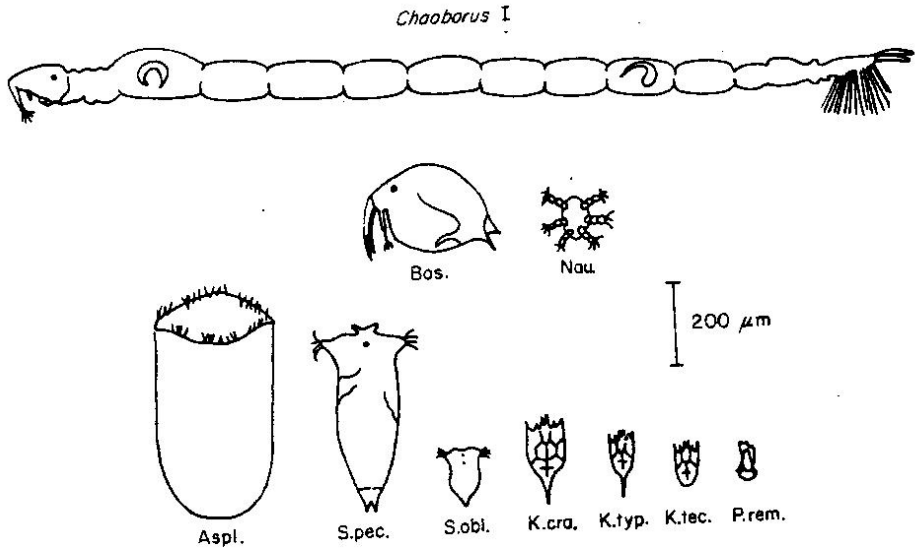


Figure 9. A diagram showing size differences of a first instar of *Chaoborus* with various species of prey, including rotifers from the genera *Asplanchna, Synchaeta, Keratella,* and *Polyarthra*. Adapted from Moore & Gilbert (1987).

Kairomones produced by *Chaoborous* have been shown to induce morphological or behavioral changes in prey. This kairomone is a nonprotein that is water-soluble and contains hydroxyl and carboxyl groups. It is a byproduct of feeding and is therefore produced by fed *Chaoborus*, but not starved individuals (Tollrian & Dodson 1999). Some well-studied morphological changes that are elicited by the presence of *Chaoborus* kairomones include increased helmet size and lengthened spines in *Daphnia* (Wetzel 2001; Tollrian & Dodson 1999). *Chaoborus* kairomones have also been shown to induce a reverse diel vertical migration pattern in the following zooplankton: *Daphnia galeata mendotae, Daphnia pulex, Daphnia pulicaria,* and *Diaptomus kenai* (De Meester et al. 1999). Both types of kairomone-induced adaptations have the potential to decrease predation risk due to *Chaoborus*; the morphological adaptations in *Daphnia* would make it more difficult for individuals to be consumed, while the reverse migration pattern of prey would limit spatial overlap with *Chaoborus* engaged in a normal migration pattern.

Study Site: Low Lake

Low Lake is an oligotrophic lake located in St. Louis county, Minnesota, United States. The

lake is in Superior National Forest, about ten miles north of the town of Ely, MN. The lake is formed of two long, narrow lobes joined at the ends in an L-shape (Fig. 10), and has a total surface area of 1.3 km^2 (Minnesota Department of Resources 2012). The Coe College Wilderness Field Station is located on the eastern shore of the northernmost lobe about halfway down the length of the lobe. The southernmost lobe, which is oriented in a northeast-southwest direction, has a maximum width of 500m and maximum length of 2,500m. The maximum depth of the lake is 10m.

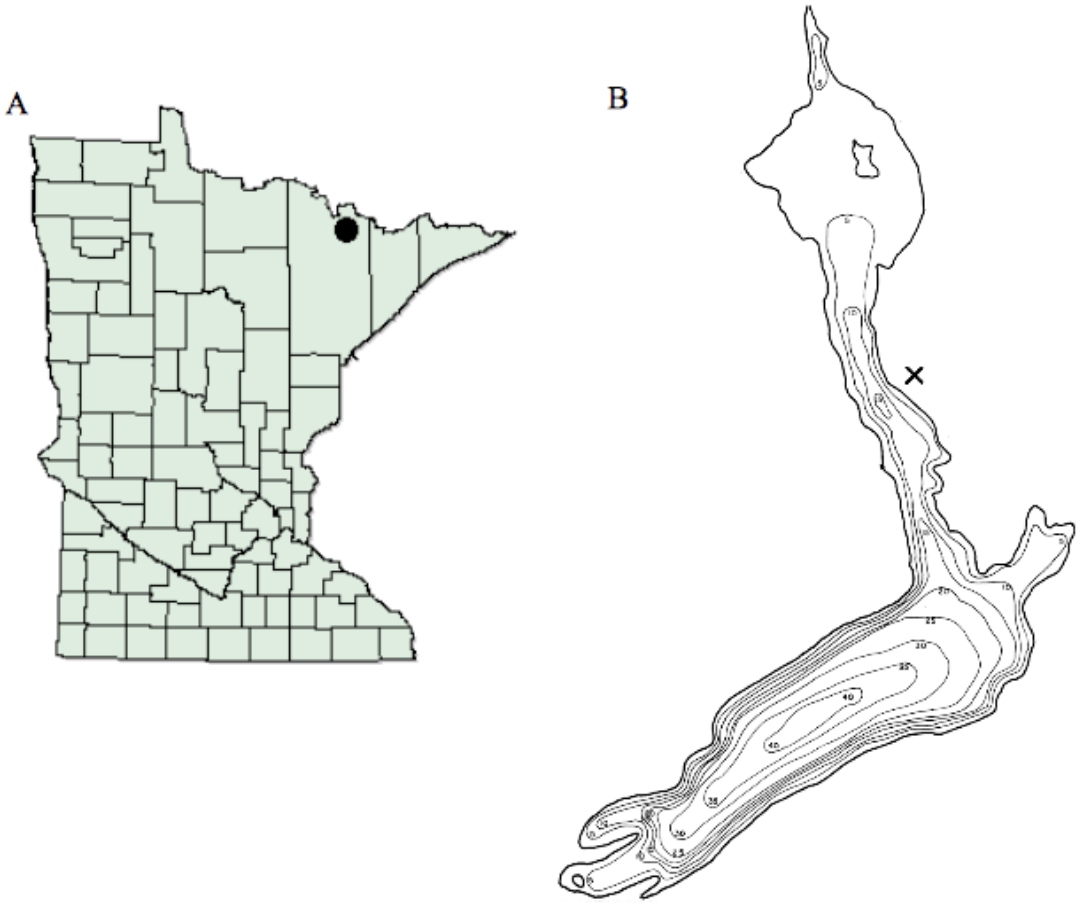


Figure 10. (A) Map of Minnesota with the approximate location of Low Lake designated with a black circle; (B) map of Low Lake with the approximate location of the Coe College Wilderness Field Station designated with an X. Adapted from the Minnesota Department of Resources (2012).

Low Lake is dimictic, with stratification being established in late spring and breaking down in the fall. The metalimnion is generally the middle third of the lake, and the thermocline is around 4m

(Fig. 11A). During June, the epilimnion is 20-25°C while the hypolimnion is 7-10°C. Low Lake is a clear oligotrophic lake with a euphotic zone that extends from the surface down through 4m (Fig. 11B). The dissolved oxygen in the lake exhibits a positive heterograde pattern (Fig. 11C). There is a constant oxygen concentration of ~8 mg/L in the epilimnion, a sharp increase in oxygen at 4.5m, and continually decreasing oxygen concentration in the hypolimnion. The increase in oxygen concentration at 4.5m is likely due to a high abundance of photosynthetic organisms immediately below the thermocline, which is referred to as an algal plate. The lake contains fish, which included black crappie, bluegill, largemouth bass, northern pike, rock bass, smallmouth bass, walleye, white sucker, and yellow perch in 2010. It was stocked with walleye fry every other year beginning in 2003 (Minnesota Department of Resources 2012).

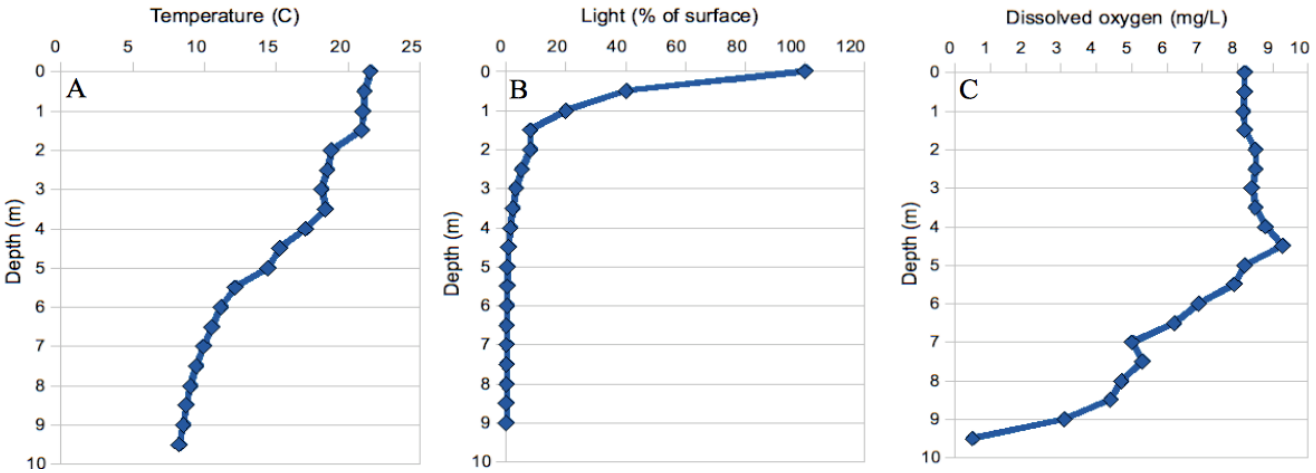


Figure 11. (A) Temperature, (B) light, and (C) dissolved oxygen profiles of Low Lake. Data were taken at half meter intervals from 0m to 9.5m on June 13, 2011.

Purpose of the Study

The intent of this study was to determine if some of the organisms in Low Lake exhibited vertical migration patterns and, if so, how the vertical migration patterns of these organisms were related. Specifically, the diel vertical migration patterns of both rotifer and *Chaoborus* larval instar populations were ascertained, which required that appropriate samples of these populations were taken from the lake. Samples were taken every other meter, which was a fine enough scale that would allow

the determination of rotifer vertical migration patterns. The samples were then used to determine the vertical distributions of the two groups of organisms and shifts in these distributions over time.

In addition to determining the vertical migration patterns of both the instars and rotifers and comparing their patterns to understand whether they influenced one another, feeding studies were completed to confirm that the *Chaoborus* of Low Lake were capable of successfully preying upon select rotifer species. These studies were completed using only first and second instars of *Chaoborus* because it has been shown that rotifers account for a greater proportion of the diet composition of these earlier instars. If *Chaoborus* instars were able and willing to feed on rotifers, it would further strengthen the possibility that the vertical migration patterns of rotifers were induced by those of the instars due to predation pressure.

The null hypothesis of the study was that neither the *Chaoborus* instars or rotifer species would have diel vertical migration patterns; that is, these organisms would have equal distributions across all depths of the lake that did not change regularly over time. Additionally, that the early instars would not successfully feed on the selected rotifer species.

It was hypothesized that these *Chaoborus* instars would exhibit the normal diel vertical migration pattern that has commonly been observed in *Chaoborus* that inhabit lakes, like Low Lake, which contain fish. Consequently, it was predicted that the normal diel vertical migration pattern of the *Chaoborus* instars would induce a reverse vertical migration pattern in the rotifer species that would limit the predation risk imposed by the instars. It was also predicted that the *Chaoborus* instars would be capable of feeding on rotifers.

Materials and Methods

Sample Collection

All samples were collected from the deepest location in Low Lake. The lake was approximately 10m deep at this location. The GPS coordinates for this location were measured with a Garmin GPS 72 unit. The initial GPS coordinates, which were taken immediately prior to the first sampling time in the first sampling period, were N 47° 58.361' W 091° 49.635' (Fig. 12). The GPS location was measured at multiple times throughout sampling to ensure that the samples were taken from the same location, and these measurements were generally within 15 feet of one another. The location was marked with a buoy that consisted of a cinderblock on the bottom of the lake tied to a rope of the appropriate length, to which were attached several closed milk jugs that floated on the surface of the lake.

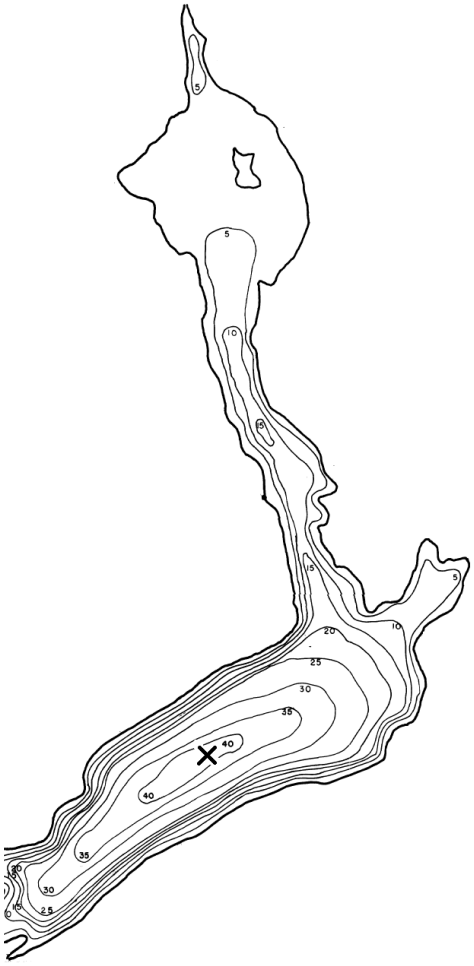


Figure 12. Map of Low Lake with the GPS coordinates for the sample collection location shown with an X. Adapted from the Minnesota Department of Natural Resources (2012).

A Grumman canoe was used for sample collection. Samples were taken with a 26 L plexiglass Schindler-Patalas trap, which was attached to a rope with meter increments marked on it and had a net made of 63 μm mesh. Samples were taken so that the lid of the trap coincided with the desired depth, e.g., the lid of the trap was at the surface of the lake for 0m samples, was at 1m for 1m samples, etc. The densities of both rotifers and *Chaoborus* were determined using the same samples.

A total of 540 samples were collected throughout three sampling periods for the vertical migration analysis. Each sampling period was 48 hours long. These sampling periods began at noon on the first day and extended continuously until noon two days following. Three sampling periods were

completed during the summer of 2011; the first was June 18-June 20, the second was June 23-June 25, and the third was July 10-12. During each sampling period, samples were taken every six hours throughout the following 48 hours, for a total of nine sampling times. During each sampling time, 20 samples were taken, with two replicate samples taken at meter intervals from 0m to 9m. For each sampling time, the date, starting time, sampling period, approximate cloud cover, and weather were recorded (Table 1).

Table 1. Date, sampling time, start time, cloud cover, and weather conditions for each of the nine sampling times in the three sampling periods.

Sampling period	Date	Sampling time	Start time	Cloud cover (%)	Weather
1	6/18/11	noon	11:55	100	light to no rain
	6/18/11	6 PM	17:53	95	light to no rain
	6/18/11	midnight	00:01	100	light to no rain
	6/19/11	6 AM	05:55	100	clear
	6/19/11	noon	11:46	100	light rain
	6/19/11	6 PM	17:51	100	light rain, windy
	6/19/11	midnight	23:45	100	calm, no rain
	6/20/11	6 AM	06:04	100	light to no rain
	6/20/11	noon	11:59	100	no rain, slightly wind
2	6/23/11	noon	12:01	100	light to moderate rain
	6/23/11	6 PM	17:58	100	light to no rain
	6/23/11	midnight	23:55	70	clear and calm
	6/24/11	6 AM	06:30	0	clear and calm
	6/24/11	noon	12:01	0	clear and calm
	6/24/11	6 PM	17:45	20	clear and calm
	6/24/11	midnight	23:56	0	clear and calm
	6/25/11	6 AM	05:59	95	clear and calm
	6/25/11	noon	12:04	80	clear and calm
3	7/10/11	noon	11:58	0	calm and clear
	7/10/11	6 PM	17:52	10	calm and clear
	7/10/11	midnight	23:49	50	calm and clear
	7/11/11	6 AM	06:08	0	calm and clear
	7/11/11	noon	12:03	20	windy

7/11/11	6 PM	17:56	40	windy
7/11/11	midnight	23:53	0	calm and clear
7/12/11	6 AM	06:24	60-80	calm
7/12/11	noon	11:51	100	windy

Samples were concentrated and preserved in the field, and then again in the laboratory. Each sample was initially concentrated at the sample collection location from 26 L to ~100 mL using the Schindler-Patalas trap. The sample was transferred from the trap cup to a 250 mL opaque plastic bottle using water from a plastic squirt bottle. Lugol's solution was added to the 250 mL bottle immediately to kill and preserve all of the organisms (Lund et al. 1958); for the initial samples, 0.3-0.5 mL of Lugol's solution was added to each 250 mL bottle, but the amount was later decreased to 0.3-0.4 mL. Each bottle was capped and shaken, then taken to the laboratory. In the laboratory, samples were concentrated further using a 63 μm mesh plankton filtering cup and then transferred to ~15 mL glass shell vials with a funnel and squirt bottle. Either 0.1 or 0.15 mL of Lugol's solution was added to each shell vial, depending on how much water the sample contained, and each vial was then capped and shaken; in some initial samples only 0.05 mL Lugol's solution was added erroneously, and an additional amount of that same volume was added later. The Lugol's solution also stained the organisms, to make later identification easier. These samples were kept in closed cardboard boxes to prevent photobleaching of the Lugol's solution due to light exposure.

Sample Counts

The seven most prevalent rotifer species in the samples from Low Lake were *Keratella, Polyarthra, Kellicottia, Synchaeta, Conochilus, Asplanchna,* and *Trichocerca*. *Keratella* was the species with the most extensive, well-developed lorica, and individuals of this species also had two longer posterior spines and two shorter anterior spines that flanked the buccal cavity. Semi-loricate species included *Polyarthra, Kellicottia,* and *Trichocerca*. *Polyarthra* was a relatively small species with a rectangular body shape and paddle-like appendages used for an active escape response. The

species of *Kellicottia* and *Trichocerca* in Low Lake had long cylindrical bodies and were spined. *Kellicottia* had a single long posterior spine and three anterior spines, one of which was as long as the posterior spine while the others were much shorter, and *Trichocerca* had a single short posterior spine. The soft-bodied rotifers were *Synchaeta* and *Asplanchna*. They both had sack-shaped bodies, and *Synchaeta* was usually half the size of *Asplanchna*. Only one species of *Chaoborus* was present in Low Lake, and this species was tentatively identified as *Chaoborus flavicans* (Mike Swift, pers. comm.).

Subsamples were taken from the samples in each shell vial to determine the number of rotifers per liter of water in that sample, and these were returned to the shell vials afterward. Later, the numbers of *Chaoborus* per liter of water in each selected sample were determined by counting the *Chaoborus* individuals in the entire sample. While rotifers were identified to the genus level, it was probable that only one species per genus was present in the samples. *Chaoborus* individuals were differentiated based on instar. Due to time constraints, numbers of organisms were only determined in samples from the first and second sampling periods, and both replicates at 0m, 2m, 4m, 6m, and 8m from these two sampling periods were counted. This resulted in a total of 180 samples from which the densities of both the rotifer species and *Chaoborus* instars were determined.

Rotifer samples were counted by retrieving subsamples that were either 1% or 2% of the entire sample contained in each shell vial. The size of the subsample was chosen by comparing the density of animals in each selected shell vial, by eye, to a shell vial that was used as a standard, which contained a density of animals that was optimally subsampled at 1.5% of the original sample. Both standard and selected shell vials were shaken well initially. Each selected sample was diluted to either 50 mL, for 2% subsamples, or 100 mL, for 1% subsamples, using a 50 mL graduated cylinder. The contents of the shell vial were emptied into the graduated cylinder, and the shell vial was rinsed with water from a plastic squeeze bottle into the graduated cylinder. For 50 mL dilutions, water was added to the graduated cylinder up to the 50 mL mark, then the contents of the cylinder were mixed well and

transferred to a 100 mL glass beaker. This was also carried out for the 100 mL dilutions, but the graduated cylinder was filled with water to the 50 mL mark a second time and that water was also added to the 100 mL glass beaker, resulting in a total of 100 mL of water. A 1 mL Stenson-Hempel subsampler was used to remove a 1 mL subsample from the well-mixed dilution in the glass beaker. This subsample was transferred to a round counting chamber. A small amount of water was added to this subsample in the counting chamber, and the subsample was mixed to ensure an even distribution of animals in the counting chamber. The counting chamber was moved to the microscope stand for counting.

After each subsample was counted, it was returned to the beaker that contained the remainder of the sample and the counting chamber was rinsed well with water into the beaker. The entire sample was re-concentrated using a 63 μm mesh plankton filtering cup, and was transferred back into the original shell vial with a funnel and water from the plastic squeeze bottle. Depending on how much water the shell vial contained, 0.1 or 0.15 mL of Lugol's solution was added to the shell vial to maintain sample preservation.

The number of rotifers in each subsample was counted using a Nikon Wild Heerbrugg dissecting microscope at 25x magnification. Animals were counted continually from one end of the counting chamber to the other to ensure that all rotifers in the subsample were counted. The numbers of the most common seven rotifer genera were recorded in detail, while occasional animals of rare genera were noted separately. These rotifer counts were transferred to an Excel spreadsheet. Each count was multiplied by the appropriate dilution volume, either 50 mL or 100 mL, and then divided by the subsample volume, either 1 mL or 2 mL. This determined the number of animals in the entire sample. This number was then divided by 26.1375, the volume of the trap sampler in liters, to determine the original number of animals per liter of water.

The number per liter of water of each of the seven rotifer species was determined for both

replicates for each of the five depths at each sampling time. This was repeated for all nine sampling times in the first two sampling periods. All of the chosen samples from the first sampling period were counted first, and then those from the second sampling period were counted. The order in which samples were counted within sampling period was determined randomly. Each sample was numbered in order from 1 to 90, and then the order in which to count samples was chosen randomly with the random number generator from http://www.random.org, which used atmospheric noise to generate numbers. This was repeated for the samples from the second sampling period.

Several aspects of the counting procedure for *Chaoborus* were different than that for the rotifers. The same samples were counted for *Chaoborus* as had been counted for rotifers, but all of the samples from the second sampling period were counted first and then the samples from the first sampling period were counted. The order in which samples within each sampling period were counted was determined randomly following the same manner which the rotifer samples had been. Instead of using subsamples, all *Chaoborus* individuals in each full sample were counted. For each sample, the entire contents of the shell vial was transferred to a plastic petri dish marked into four quadrants with a marker, and the vial was rinsed out with water from a plastic squeeze bottle into the dish. The petri dish was placed on the microscope stand and all of the *Chaoborus* individuals were counted.

After the *Chaoborus* were counted, the sample from the petri dish was re-concentrated using the 63 μm mesh plankton filtering cup and transferred back into the original shell vial with a small plastic funnel and the squeeze bottle. To ensure that the sample was still preserved, 0.1 or 0.15 mL of Lugol's solution were added to the sample, depending on how much water the sample contained. The shell vial was capped and shaken.

When the petri dish, which contained a single full sample, was placed on the microscope stand, it was examined by eye for individuals of *Chaoborus*. If any were present and visible in the upper left quadrant of the petri dish, a probe was used to move these individuals to one of the other quadrants.

The microscope, set at 6x magnification, was then used to confirm that no *Chaoborus* individuals were present in the upper left quadrant. Each of the remaining quadrants were then examined for *Chaoborus* at 50x magnification. When an individual was found, the probe was used to manipulate its head so that it was flat, and the head gape width was measured. A 25 mm ocular micrometer was placed in the left eyepiece of the microscope for this purpose. Head gape widths of *Chaoborus* are proportional to their mouth gapes, and instar stage can be determined from this measurement (Mike Swift, pers. comm.). Head gape widths of the different instars were estimated using the average of five published values for various species of *Chaoborus* (Swift 1992; Federenko 1975; Swift & Federenko 1975). Individuals with a head gape width of 0.16 mm or less were considered first instars, second instars had head gape widths around 0.32 mm, third instars had head gape widths around 0.48 mm, and fourth instars had head gape widths around 0.64 mm. Because size differences between the four instars were relatively discrete, it was possible to determine the difference between these instars.

While each sample was being examined under the microscope, the instar stage of each *Chaoborus* individual was recorded by hand. After an individual had been examined, it was moved to the upper left quadrant of the petri dish. Each of the remaining quadrants were checked thoroughly at 6x magnification to ensure that all of the *Chaoborus* individuals had been observed. The numbers of each *Chaoborus* instar for each sample were transferred to an Excel spreadsheet. These numbers were divided by 26.1375, the volume of the trap sampler in liters, to determine the number of each instar in each sample per liter of water.

Calculations and Statistical Analysis

Both depth-specific abundances and integrated water column abundances were calculated for each sampling time. The number of animals per liter at each sampling time for two replicates at each depth had been determined for both the seven species of rotifers and the four instars of *Chaoborus*. The average of these numbers for the two replicates at each depth for each species and instar was found,

and this average was considered the abundance of each type of animal at that depth and time. The integrated water column abundance of a given animal was the sum of the abundances at the five depths for each sampling time for that animal.

The coefficient of variation was calculated to determine how much variation there was in the integrated water column abundance at each time of each type of animal throughout each sampling period. A high coefficient of variation indicated that the integrated water column abundance of a given animal changed greatly between the nine sampling times in a sampling period. A high coefficient of variation could be due to rapid population growth from reproduction, high predation rates at different times of the day, or movement into or out of the water column by animals, either from horizontal movement or movement to the benthic zone.

To calculate the coefficient of variation, the total abundance of animals in the entire water column had to be estimated. This was determined by converting the number of animals per liter at each depth to number of animals per cubic meter by multiplying by 1000. This value was assumed to be the number of animals in a single cubic meter at that depth. Because only every other meter was sampled, this number was multiplied by two to estimate the number of animals in both that meter and the meter below it, e.g., the value for 0m was multiplied by two to account for the number of animals in the water column between 0m and 2m. These values for all five of the sampled depths were summed to produce an estimate of the total number of animals in the entire water column, so that there was one value for each type of animal at each sampling time. Both the average and standard deviation of the nine values for each sampling period for each type of animal were determined. The coefficient of variation was found by dividing the standard deviation by the average, resulting in one coefficient of variation value for each type of animal for each sampling period.

The coefficients of variation for each of the seven rotifer species were compared to each other, and were compared to those of each of the instars of *Chaoborus*. To determine the difference in

coefficients of variation between the two sampling periods for each type of animal, the percent difference of the coefficients of variation for the two sampling periods was found using the following equation:

$$\% \text{ difference} = 100 \times \frac{|A - B|}{\text{smaller of A \& B}}$$

where A was the coefficient of variation from the first sampling period, and B was the coefficient of variation from the second sampling period.

The weighted mean depths were calculated for each type of animal at each sampling time in both sampling periods. The weighted mean depth was used to summarize the vertical distribution of an animal throughout the water column at a specific time, and it used the abundances at discrete depths while taking into account the values of those depths. The equation for the weighted mean depth was as follows:

$$WMD = \frac{\sum (N_i \cdot i)}{\sum N_i}$$

where N_i was the abundance of animals at each depth and i was the depth. This method was described by De Stasio (1993). By examining the weighted mean depths at each of the nine sampling times for a single type of animal, it could be determined if the vertical distribution of that animal was changing over time or not, and the pattern of that change. The relative vertical distributions of two or more types of animals were also compared by examining the changes in their weighted mean depths.

The Schoener overlap index, as described by Schoener (1970), was intended to compare the extent of overlap in the distributions of a pair of animals. The index was used in this study to compare the overlap between the vertical distributions amongst all of the rotifer species, and between the rotifer

species and the first and second instars of *Chaoborus*. The Schoener overlap index was calculated as a percentage for each sampling time using the abundances at the five depths for each pair of animals. A greater percentage indicated more overlap between the distributions of the pair of animals at that time. To determine the Schoener overlap index, the following equation was used:

$$\text{Schoener overlap index percentage} = 100 \left(1 - 0.5 \cdot \sum \left[\left| P_{x,i} - P_{y,i} \right| \right] \right)$$

where $P_{x,i}$ was the relative abundance of the first type of animal at each depth and $P_{y,i}$ was the relative abundance of the second type of animal at the same depth. Out of the many indexes that have been used in ecology for comparisons such as these, Bloom determined that the Schoener overlap index and its derivatives were the most accurate (1981).

Feeding Studies

Feeding studies were completed to determine if *Chaoborus* could successfully feed on select rotifer species. In each trial of the feeding study, a single *Chaoborus* individual was placed in a dish that contained filtered water and rotifers of the selected species at a density that was great enough for encounters between predator and prey to occur. The behavior of the instar was observed. The following rotifer species were used: *Polyarthra, Asplanchna*, and *Conochilus*. These species were chosen to be representative of the variety of behavioral and morphological characteristics of rotifers. *Polyarthra* individuals were small and had a partially developed lorica, and also exhibited an active escape response from sources of contact, including predators. Individuals of the genus *Asplanchna* were large and completely lacked a lorica. *Conochilus* were colonial, with only colonies that contained ten to twenty individuals used, and were of a size intermediate between that of *Polyarthra* and *Asplanchna*. Only first and second instars of *Chaoborus* were used in the feeding studies because it was assumed that predation by these earlier instars on rotifers was greater than that by the later third and

fourth instars, which are capable of consuming larger prey than rotifers and therefore tend to prefer them.

Samples for the feeding study were taken separately from those used for the vertical migration analysis. These samples were collected from the same sampling site as that used for the vertical migration data collection, and the same 26 L Schindler-Patalas trap was used for collection. Rotifer samples were taken from shallow depths, usually within several meters of the surface, while *Chaoborus* samples were taken from deeper in the lake (Table 2). The depths from which these samples were taken were approximated using the rope attached to the trap. Each sample for each type of organism consisted of 2-6 full trap samples, which were all concentrated to about 100 mL using the trap. These trap samples for the rotifers were combined in a 4.25 L plastic bucket for transportation back to the laboratory, while the *Chaoborus* trap samples were placed in a separate similar bucket.

Table 2. Date, time, cloud cover, and weather conditions for all feeding sampling collections. Also listed are the approximate depths from which the samples were taken and number of trap samples for both rotifer and *Chaoborus* samples.

				Rotifer		*Chaoborus*	
Date	Time	Cloud cover (%)	Weather	Sample depth (m)	Trap samples	Sample depth (m)	Trap samples
07/07/11	09:00	80	Light wind, clear	1 – 2	3	5 – 6	4
07/08/11	14:15	20	Calm and clear	1 – 2	3	5 – 6	6
07/10/11	13:00	0	Calm and clear	1 – 2	3	6 – 7	4
07/11/11	12:45	20	Windy	1 – 2	2	--	--
07/12/11	12:45	100	Windy	1 – 2	2	5 – 6	4

The removal process of *Chaoborus* from the samples was different than that used for the rotifers, but both were always completed within several hours of sample collection. Smaller portions of the *Chaoborus* samples were taken from the plastic bucket and placed into a 1 inch deep white pan, and then examined under strong light. Large-bore glass pipettes were used to remove *Chaoborus*, which was completed by eye. Only first and second instars of *Chaoborus* were removed; this distinction

between earlier first and second instars of *Chaoborus* and later third and fourth instars was based on size. The organisms were individually transferred to ~200 mL water, which came from the same sample and had been filtered with a 63 μm mesh plankton filtering cup. Filtered water contained only algae and occasional copepod nauplii, which ensured that there was no food source available for *Chaoborus*. The filtered water and *Chaoborus* were held in a 250 mL white plastic bottle, which was capped and allowed to sit for at least 24 hours in order to starve the *Chaoborus*.

To obtain rotifers, 1-2 mL subsamples of the rotifer samples were examined at a time. These subsamples were placed in a 6 cm wide glass Pyrex dish and examined with a dissecting microscope. Rotifers were removed one at time from this dish with a pipette and transferred to a second slightly smaller dish, which contained water from the original rotifer samples that had been filtered with a 63 μm mesh plankton filtering cup. Rotifers remained in this second dish until they were used for the studies. Rotifers were used as soon as possible, either the same day they were collected or the following day.

Selected *Chaoborus* were placed individually into a separate 5.7 cm wide plastic dish that contained filtered water and were examined using the dissecting microscope prior to the beginning of the feeding study. Three things were determined: the instar of the organism, whether the crop of the organism was empty, and if the organism exhibited typical movement behavior. Instars were differentiated based on eye formation; individuals that had compound eyes were classified as second instars and those with simple eyes were classified as first instars (Mike Swift, pers. comm.). *Chaoborus* individuals that had full crops or abnormal movement behavior were not used because it was assumed that they would not exhibit typical feeding behaviors. Rotifers were sorted by species when transferred to the 3.5 cm glass dish that was used for the feeding studies. The entirety of this glass dish could be seen through the scope of the dissecting microscope that was used; this dish also held a small amount of water, resulting in a sufficiently high density of rotifers.

After a *Chaoborus* individual had been examined separately, it was transferred with a pipette to the glass dish that contained the rotifers and observed using the dissecting microscope. Individuals were examined for a maximum of 15 minutes because it had been determined that individuals that did not feed within 15 minutes would not feed. Individuals that were observed feeding on a rotifer were considered successful; they were removed immediately after and preserved in several ~15 mL shell vials that contained distilled water and ~0.2 mL Lugol's solution. *Chaoborus* individuals that did not feed or were otherwise unsuccessful were removed and discarded. All data recorded were qualitative. Some of the rotifers used were kept separated by species and preserved in the same manner as the *Chaoborus* individuals. A total of 31 trials were completed using both first and second instars of *Chaoborus*, with ten trials each using *Polyarthra* and *Conochilus*, and eleven trials using *Asplachna*.

Results

Feeding Studies

Chaoborus individuals in the feeding studies were able to consume rotifers. First and second instars of *Chaoborus* were observed successfully feeding on *Polyarthra* and *Asplanchna* but not on *Conochilus* (Tables 3-5). Six *Chaoborus* were observed feeding on *Polyarthra* while eight *Chaoborus* successfully fed on *Asplanchna*. This did not occur for any of the ten instars in the trials that had *Conochilus* as the prey items. Most of the *Chaoborus* used in these trials were second instars; only seven first instars were examined.

Both first and second instars of *Chaoborus* were capable of feeding on *Polyarthra*. In ten trials, one first instar and five second instars successfully fed on a *Polyarthra* individual (Table 3). These instars remained motionless in the water, for the most part, and were able to strike at prey items once they were detected. Prey were properly captured when the instar grasped them with its antennae, and *Polyarthra* were swallowed whole almost immediately. The one unsuccessful *Chaoborus* individual exhibited strikes but failed to capture a prey item, while two second instars made no attempt at feeding and a third individual had erratic behavior that was not consistent with successful feeding. Most of the *Chaoborus* individuals that were observed were able to successfully feed on *Polyarthra*.

Table 3. Outcomes of ten feeding study trials on first and second instars of *Chaoborus* using *Polyarthra*. Sampling dates of *Chaoborus* and rotifer species are listed, as are the date and starting time of each trial. Outcome values were successful capture and ingestion (S), unsuccessful due to failed attempts (U), no feeding attempts (N), or other (O).

Date	Start time	Rotifer sample date	*Chaoborus* sample date	*Chaoborus* instar	Outcome
7/7/11	19:00	7/7/11	7/5/11	1	S
7/7/11	19:00	7/7/11	7/6/11	2	S
7/8/11	15:00	7/7/11 + 7/8/11	7/7/11	2	S
7/8/11	15:00	7/7/11 + 7/8/11	7/7/11	2	S
7/8/11	15:00	7/7/11 + 7/8/11	7/7/11	2	S
7/8/11	15:00	7/7/11 + 7/8/11	7/7/11	2	S
7/7/11	19:00	7/7/11	7/6/11	2	U
7/7/11	19:00	7/7/11	7/5/11	2	N
7/8/11	15:00	7/7/11 + 7/8/11	7/7/11	2	N
7/7/11	19:00	7/7/11	7/5/11	2	O

Similar to the trials with *Polyarthra*, both first and second instars fed on *Asplanchna*. Eight instars of *Chaoborus* successfully captured and ingested *Asplanchna* individuals, including one first instar and seven second instars (Table 4). Unlike in the process of feeding on *Polyarthra*, once *Chaoborus* instars had detected and captured these *Asplanchna*, they had to use their mandibles and antennae to manipulate the prey before successful ingestion. *Asplanchna* individuals were generally wider and longer than the gape width of the *Chaoborus* instars, but because these individuals lacked a lorica, the instars were able to compress the prey to a consumable size. This resulted in slightly longer time elapsing between capture and ingestion of *Asplanchna* compared to that of *Polyarthra.* Nevertheless, the *Chaoborus* instars were overwhelmingly successful in consuming *Asplanchna*. *Chaoborus* instars did not successfully ingest *Asplanchna* in three of the eleven trials; in two unsuccessful trials, instars made no attempt at feeding, and in the third trial the instar was observed ingesting an organism but this prey item was not properly identified. Because there may have been other prey items present in the dish used for the feeding studies, we can not conclusively state that this

latter instar successfully consumed an *Asplanchna* individual, though this was likely what occurred. The *Chaoborus* instars were successful in most of the trials, indicating that these instars were capable of consuming *Asplanchna*.

Table 4. Outcomes of eleven feeding study trials on first and second instars of *Chaoborus* using *Asplanchna*. Sampling dates of *Chaoborus* and rotifer species are listed, as are the date and starting time of each trial. Outcome values were successful capture and ingestion (S), unsuccessful due to failed attempts (U), no feeding attempts (N), or other (O).

Date	Start time	Rotifer sample date	*Chaoborus* sample date	*Chaoborus* instar	Outcome
7/8/11	09:00	7/7/11	7/5/11	1	S
7/7/11	19:00	7/7/11	7/6/11	2	S
7/7/11	19:00	7/7/11	7/6/11	2	S
7/8/11	09:00	7/7/11	7/6/11	2	S
7/8/11	09:00	7/7/11	7/6/11	2	S
7/8/11	09:00	7/7/11	7/6/11	2	S
7/8/11	09:00	7/7/11	7/6/11	2	S
7/8/11	09:00	7/7/11	7/6/11	2	S
7/8/11	09:00	7/7/11	7/5/11	1	U
7/7/11	19:00	7/7/11	7/6/11	2	U
7/7/11	19:00	7/7/11	7/6/11	1	O

Chaoborus may not be capable of consuming *Conochilus*. Out of ten trials, no instars successfully consumed *Conochilus* (Table 5). In the four unsuccessful trials, three of the instars made clear strikes at *Conochilus* individuals but never captured any of them. In the fourth unsuccessful trial, the first instar of *Chaoborus* did capture a *Conochilus* individual and spent approximately ten seconds manipulating the prey item with its mandibles in an attempt to fit the too-large prey in its mouth, but dropped the *Conochilus* individual shortly thereafter. Two of the second instars of *Chaoborus* made no attempt to feed during their respective trials. In the four remaining trials, one instar exhibited erratic behavior, a second had an abnormal twisted crop, and the last two were killed by heat from the microscope lamp.

Table 5. Outcomes of ten feeding study trials on first and second instars of *Chaoborus* using *Conochilus*. Sampling dates of *Chaoborus* and rotifer species are listed, as are the date and starting time of each trial. Outcome values were successful capture and ingestion (S), unsuccessful due to failed attempts (U), no feeding attempts (N), or other (O).

Date	Start time	Rotifer sample date	*Chaoborus* sample date	*Chaoborus* instar	Outcome
7/11/11	15:30	7/11/11	7/10/11	1	U
7/12/11	10:00	7/11/11	7/10/11	1	U
7/13/11	13:30	7/12/11	7/10/11	1	U
7/12/11	10:00	7/11/11	7/10/11	2	U
7/13/11	13:30	7/12/11	7/10/11	2	N
7/13/11	18:30	7/12/11	7/10/11	2	N
7/10/11	20:30	7/10/11	7/6/11	2	O
7/10/11	20:30	7/10/11	7/7/11	2	O
7/10/11	20:30	7/10/11	7/7/11	2	O
7/11/11	15:30	7/11/11	7/10/11	2	O

Vertical Migration Patterns of Chaoborus Instars

Second instars were the only instar stage of *Chaoborus* that conclusively exhibited a strong diel vertical migration pattern. In both sampling periods, these instars were generally only present below 4m at all times except midnight (Fig. 13). Of the five sampled depths at each of these times, the greatest abundance was always 6m and this abundance was nearly always much greater than that at 8m. Abundances at the shallower depths above 6m were either zero or extremely small in comparison to those at 6m and 8m. Therefore, these instars were highly concentrated at the deepest depths at all times except midnight. Conversely, in the midnight samples, second instars were present in fairly equal numbers at both the shallow and deep depths. This even distribution of instars amongst all depths at midnight clearly differed from all other times when instars were highly concentrated at the deepest depths. Second instars were deep in the water column most of the time but the population shifted upwards towards the surface at midnight, and this occurred consistently throughout the two sampling periods. The trends of the weighted mean depths showed this shift in distribution; weighted mean

depths at midnight were always shallower than those at the other times. Because the second instars of *Chaoborus* were undergoing regular vertical shifts in distribution in relation to time, they were clearly exhibiting diel vertical migration.

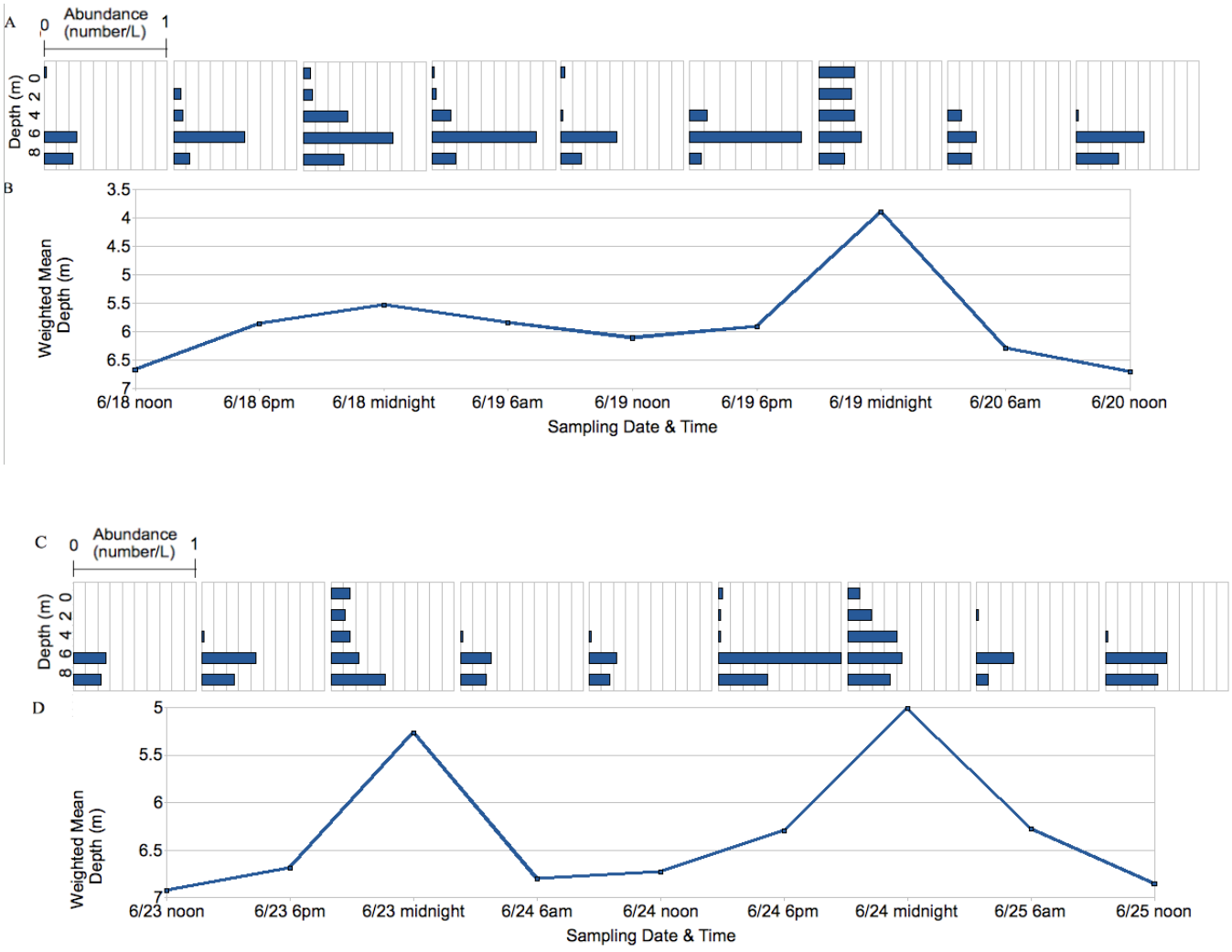


Figure 13. Abundances of second instars of *Chaoborus* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

Low coefficients of variation further support the observation of a vertical migration pattern in second instars. The coefficients of variation for the second instars were low during the first and second sampling periods (Fig. 14). This indicated that the integrated water column abundance of the second

instars was not changing much over time. Therefore, these instars were likely not migrating into and out of the water column or exhibiting great changes in life history over time, and it is reasonable to conclude that the changes in their vertical distribution over time were due to vertical migration behavior.

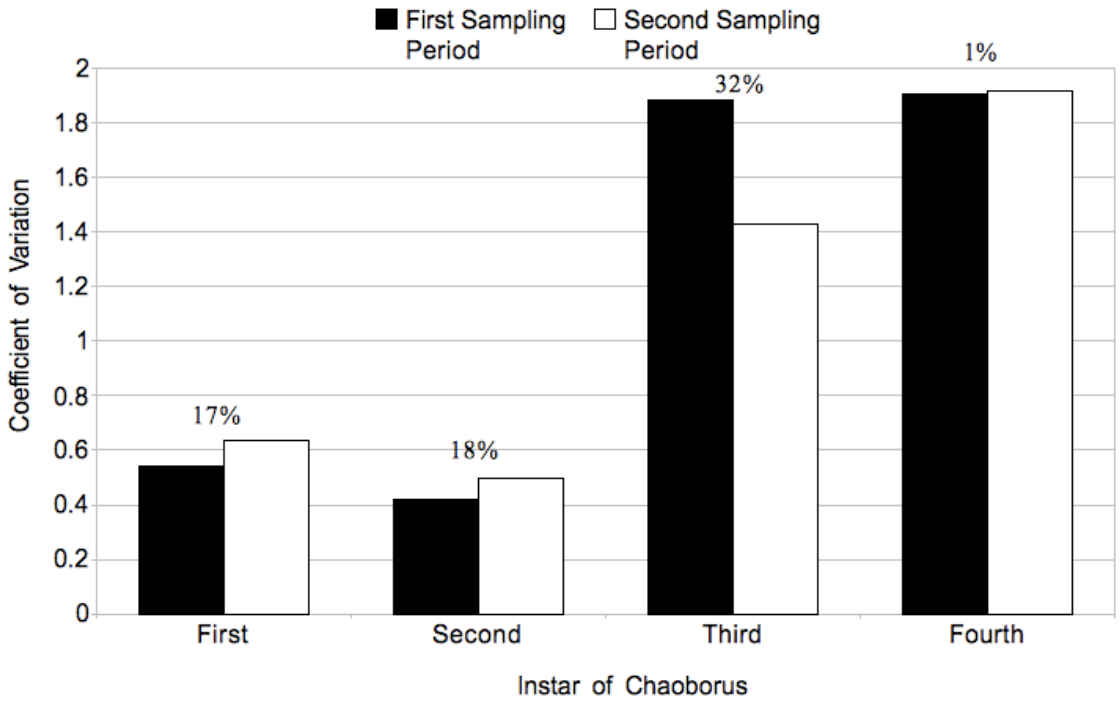


Figure 14. The coefficients of variation of each of the four instars of *Chaoborus* for the first and second sampling periods. Percent differences in coefficients of variation between sampling periods are shown above sets of bars for each species.

Third and fourth instars of *Chaoborus* were only present in the water column at this location in the lake at midnight (Fig. 15). There were no fourth instars of *Chaoborus* present at any depth in either sampling period except at midnight. Similarly, in the first sampling period, third instars were absent entirely from the water column at times except midnight; they were occasionally present at times other than midnight in the second sampling period, but at these times they were present at 6m or 8m and their abundances were very low relative to that at midnight. At midnight in both sampling periods, third and fourth instars were present at nearly all depths. Their distributions at night were mostly equal amongst

all depths, except abundances at 0m were often low. The drastic change in integrated water column abundances of the third and fourth instars accounted for their extremely high coefficients of variation (Fig. 14), which were at least three times as large as those of the first and second instars.

Figure 15. Abundances of third and fourth instars of *Chaoborus* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

The pattern in the changes in abundance of third and fourth instars was clear and likely due to vertical migration. Third and fourth instars moved into the water column at this location before midnight and out of it after midnight, as shown by their unique presence at night (Fig. 15A, 15C). The

locations of third and fourth instars at times other than midnight is unknown and beyond the scope of this study. It was likely that these instars were migrating vertically into the benthic zone below the 8m sample depth, though another possibility was that they were migrating horizontally away from this location during the day.

First instars of *Chaoborus* exhibited no consistent vertical migration patterns. These instars had low abundances that never exceeded 0.2 animals per liter at any depth at any time (Fig. 16). While first instars were consistently present at every time in both sampling periods, the depths at which they occurred varied. These instars were never concentrated at any depth; when they occurred, first instars were often distributed equally across several depths. No location in the water column appeared to be preferred by first instars at any time. Therefore, the population of the first instars of *Chaoborus* was not moving vertically throughout the water column on a regular basis.

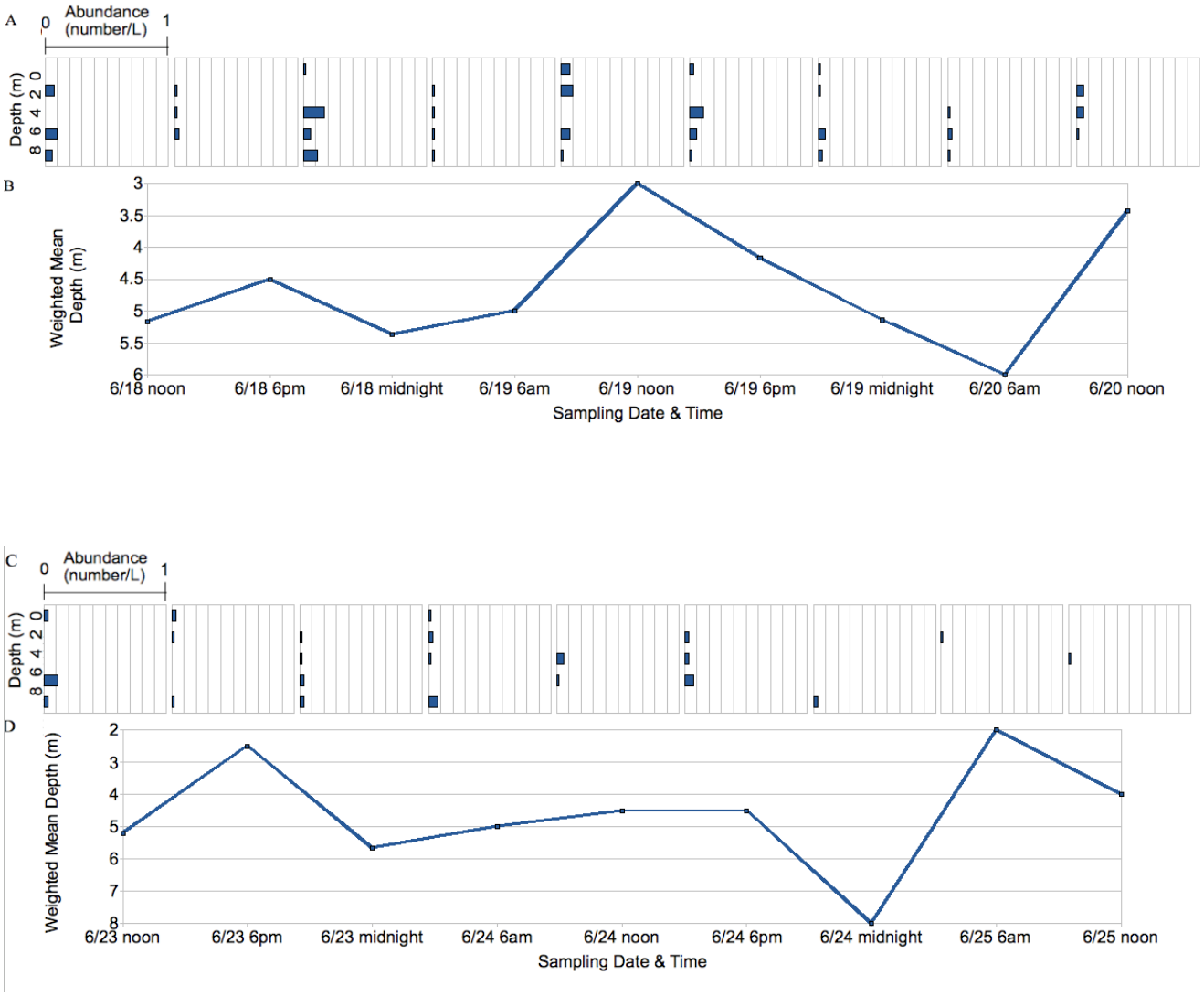


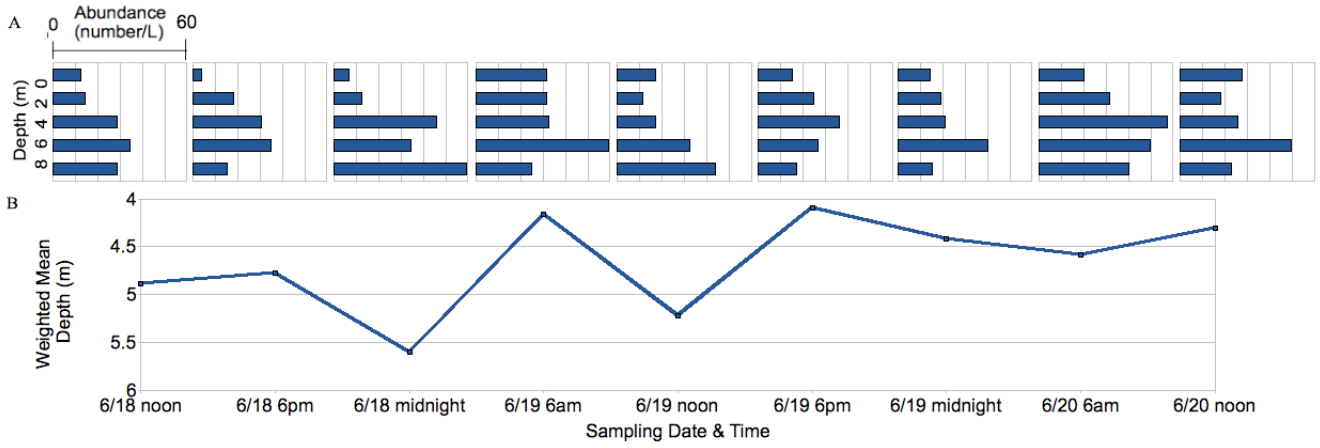
Figure 16. Abundances of first instars of *Chaoborus* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

The populations of all the *Chaoborus* instars except that of the first instars moved vertically closer to the surface at midnight, but because second instars were relatively more prevalent than the other instars of *Chaoborus,* they likely had a greater influence on the migration patterns of prey species in this lake system. Of the first and fourth instars, there was never more than 0.2 animals per liter of water at any depth during any sampling time. The abundance of third instars was also generally below 0.2 animals per liter of water, though a few of the depths from the midnight samples had abundances

that exceeded this value. Conversely, the abundances of second instars were much higher than this at many depths for most times. Because *Chaoborus* second instars were the most abundant, they would have exerted a stronger predation pressure on prey than the other instars, though the similar vertical migration patterns of the second, third, and fourth instars all had the potential to induce vertical migration behavior in prey species.

Distributions of Rotifer Species and Their Interspecific Spatial Overlap

Most of the *Keratella* population was concentrated at or just below 4m. The depth with the greatest abundance of *Keratella* was 4m or 6m at most of the sampling times (Fig. 17). The abundance of this species at the shallowest depths was usually low, and the lowest abundance of the five depths was 0m at most of the sampling times. Correspondingly, all of the weighted mean depths of this species were deeper than 4m, with the weighted mean depths from the first sampling period between 4m and 6m and those of the second sampling period restricted even more to between 4m and 5m. Therefore, *Keratella* was not common near the surface of the lake and tended to be most prevalent just below the middle of the water column.



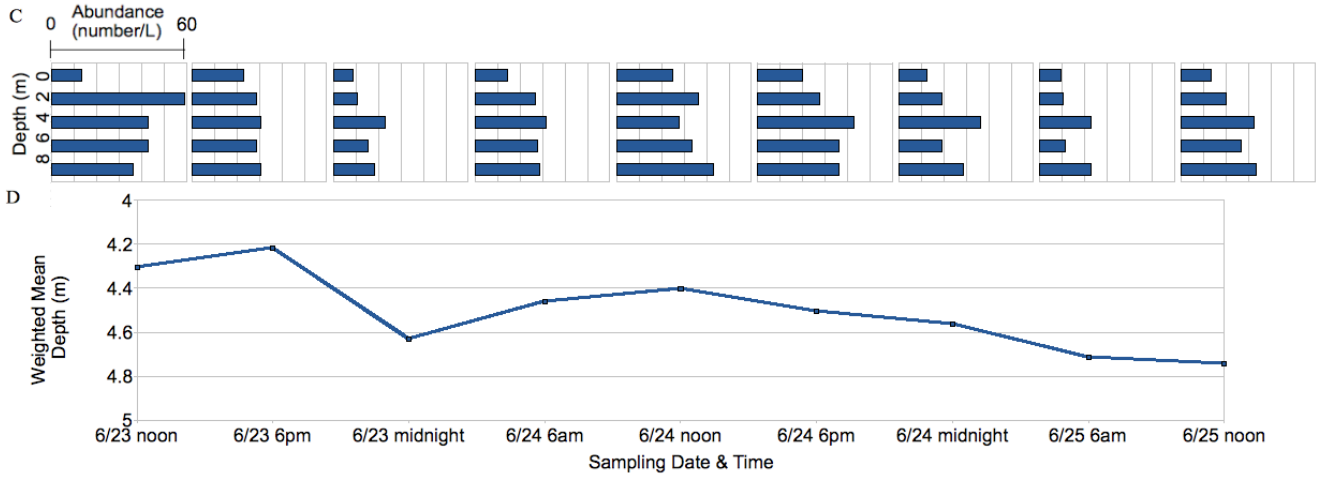


Figure 17. Abundances of *Keratella* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

Some vertical migration by *Keratella* was apparent. In the first sampling period, there was a regular vertical oscillation in the population. This was shown by the weighted mean depth, which increased and then decreased between each of the sampling times in the first sampling period. This was corroborated by the abundances of *Keratella* at each sampling time. The population shifted up and down between 4m and 8m between the sampling times, with the depth of greatest abundance at 6m during noon and 6pm on June 18, then to 8m at midnight, back to 6m at 6 am on June 19, and to a shallower 4m at noon (Fig. 17A). These shifts in population distributions were mostly limited to 4m and deeper, and no shifts to the depths closer to the surface occurred. Such population shifts did not occur in the second sampling period. Abundances were equal across depths at most of the times, such as 6am on June 24. At times when abundances were not equal, there was a consistent pattern; the greatest abundance was at 4m and most of the remainder of the population was at 6m and 8m.

The differences in the distributions of *Polyarthra* and *Keratella* at the same times indicated spatial segregation of the two species. The distribution of *Polyarthra* was always closer to the surface than that of *Keratella.* The greatest abundance of *Polyarthra* was at 2m for many of the sampling times

in both sampling periods, with abundances decreasing with increasing depth (Fig. 18). There were low abundances at 8m, and also very low abundances at 0m. Therefore, most of the population was concentrated between 2m and 4m. This was shallower than the *Keratella* population, which was concentrated at 4m or deeper (Fig. 17). Correspondingly, almost all of the weighted mean depths of *Polyarthra* were shallower than those of *Keratella* at the same times. These differences in population distributions indicated spatial segregation of the two species, with the *Polyarthra* population generally shallower in the water column and that of *Keratella* deeper.

Figure 18. Abundances of *Polyarthra* at each depth and sampling time in (A) the first sampling period

and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

The spatial segregation between *Polyarthra* and *Keratella* was subtle enough that it was not reflected in the Schoener overlap index values between the two species. The overlap values between these species were relatively high, around 80% in the first sampling period and 90% in the second sampling period (Fig. 19). These values were high because there was still a lot of overlap in the distributions of *Keratella* and *Polyarthra*, as both species were present at all depths. Nevertheless, it was apparent from the abundances of these two species that the *Keratella* population was concentrated at deeper depths than *Polyarthra*.

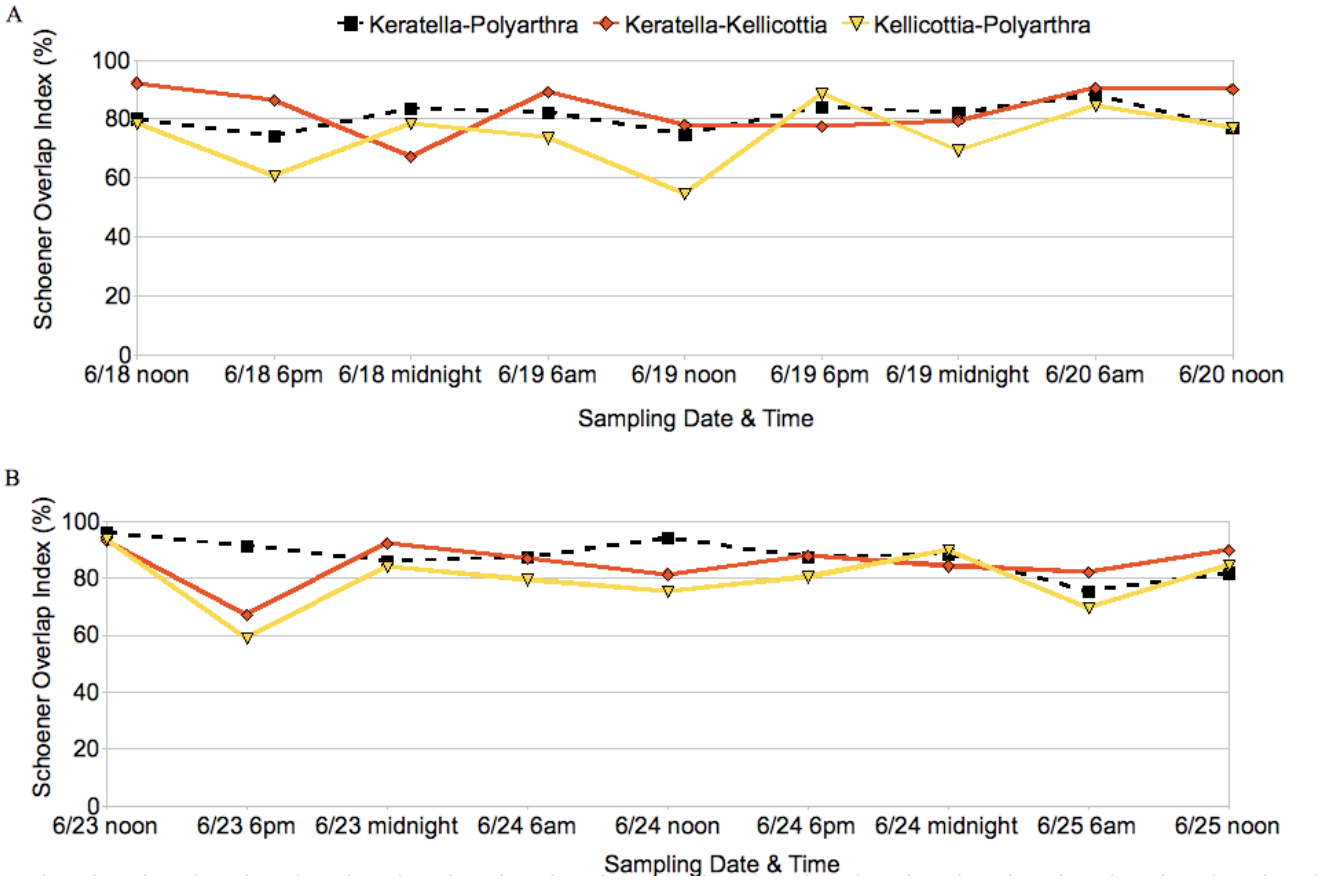


Figure 19. Schoener overlap index percentages between *Keratella* and *Polyarthra*, *Keratella* and *Kellicottia*, and *Kellicottia* and *Polyarthra* at each sampling time in (A) the first sampling period and (B) the second sampling period.

Keratella and *Polyarthra* had similar vertical migration patterns, primarily movements of these populations deeper in the water column at midnight, indicating that whatever influences were driving these changes in vertical distribution may have affected both species. The vertical migration patterns of *Keratella* and *Polyarthra* were similar in the first sampling period. As shown by a comparison of the weighted mean depths, population shifts towards the surface occurred at the same time for both species, as did shifts away from the surface (Fig. 17B, 18B). At midnight, the populations of both species exhibited shifts to deeper depths. This was apparent in the abundances of *Keratella* and *Polyarthra*; distributions from 6pm, the time before the midnight sample, were closer to surface than the midnight distributions, and the 6am distributions immediately after midnight were shifted back towards the surface (Fig. 17A, 17C, 18A, 18C). These shifts were also reflected in the weighted mean depths of the two species because the midnight weighted mean depths were nearly always deeper than those of the other times. This vertical migration pattern was more pronounced in *Polyarthra*, as shown by greater differences in weighted mean depths between midnight and other times.

Keratella and *Polyarthra* had low coefficients of variation in both sampling periods (Fig. 20). The coefficients of variation of these two rotifer species were similar to the low values of the second instars of *Chaoborus* (Fig. 14). These values showed that there was very little change in the integrated water column abundances over time for *Keratella* and *Polyarthra*, so animals of these species were not leaving or entering the water column unusually or exhibiting great fluctuations in population size due to birth or death rates. This contributes to the assertion that *Keratella* and *Polyarthra* had different population concentrations in the water column but similar vertical migration patterns because we can be certain that changes in these two populations were not due to animals moving into and out of the water column.

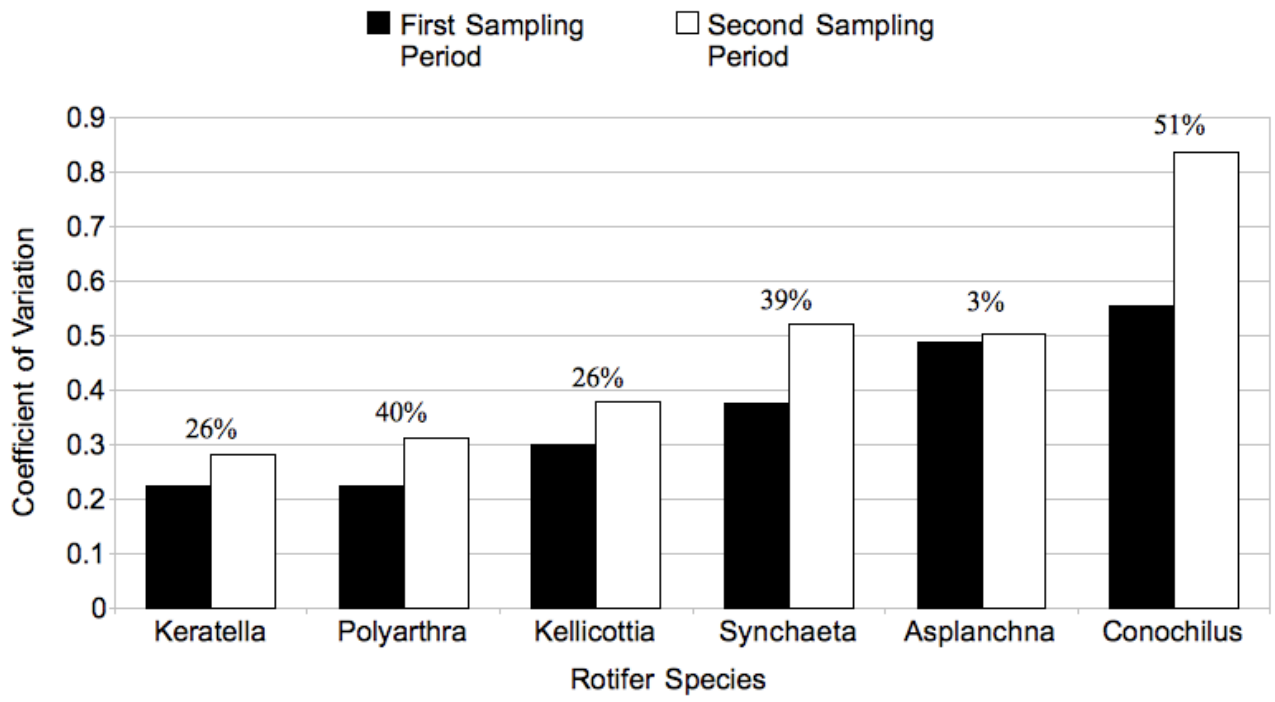


Figure 20. The coefficients of variation of all rotifer species except *Conochilus* for the first and second sampling periods. Percent differences in coefficients of variation between sampling periods are shown above sets of bars for each species.

The vertical migration patterns of the *Asplanchna* population were similar to those of *Keratella* and especially *Polyarthra*. At times other than midnight, the *Asplanchna* population tended to be at shallower depths. This was shown by the absence of *Asplanchna* individuals at deeper depths, which occurred often during the first sampling period, or the greater abundances at shallower depths (Fig. 21). At midnight, the *Asplanchna* population was shifted to deeper depths relative to the other times; this was most apparent at midnight on both June 18 and June 23. This vertical migration pattern was most similar to that of *Polyarthra*, because both populations tended to be concentrated above 4m at times other than midnight and were shifted deeper at midnight. *Asplanchna* was even more limited to shallow depths than *Polyarthra*. *Keratella* also exhibited downward shifts in distribution at midnight, but at times other than midnight tended to be deeper in the water column than the *Polyarthra* and *Asplancha* populations.

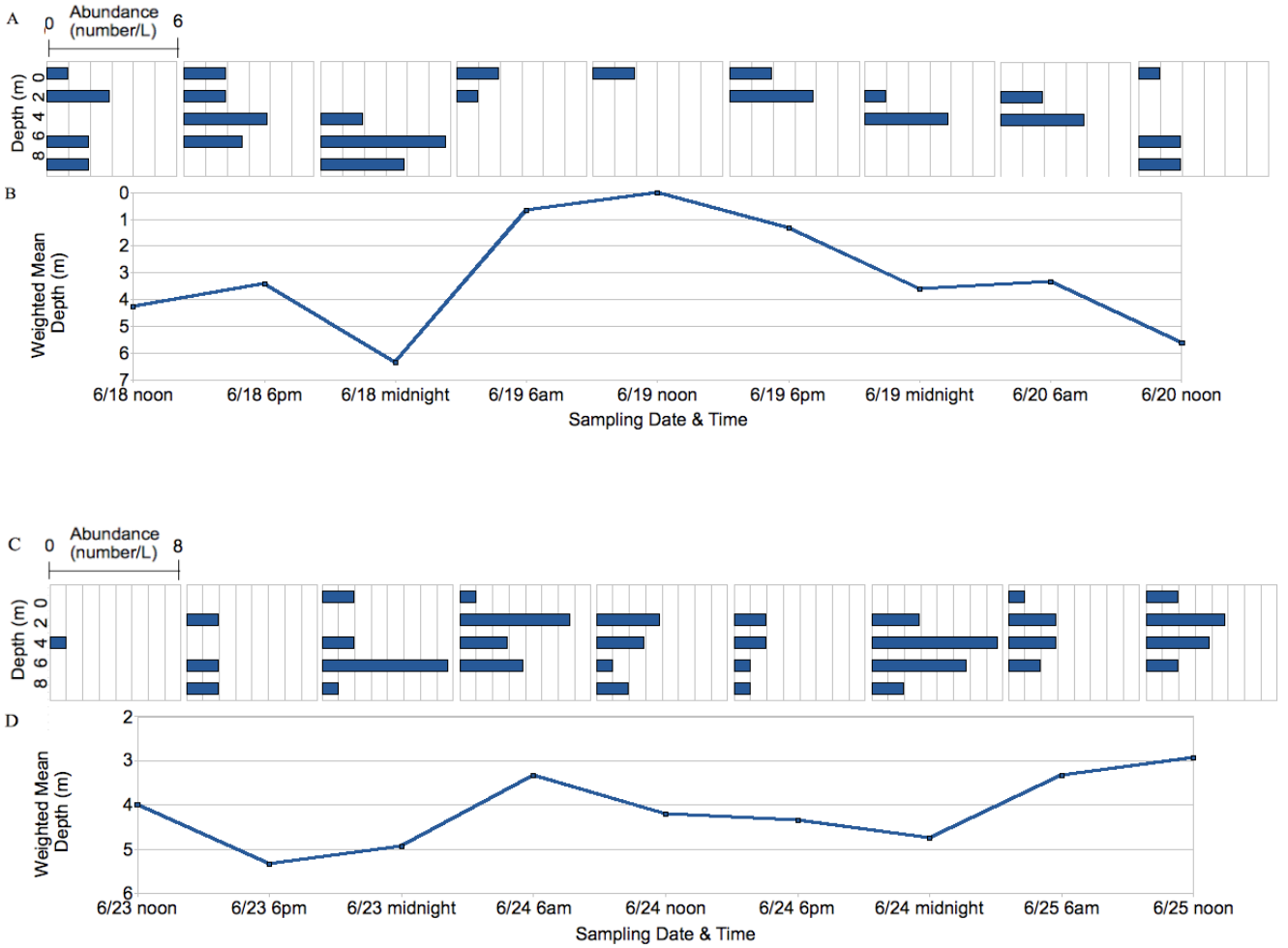


Figure 21. Abundances of *Asplanchna* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

The Schoener overlap index values of *Asplanchna* with *Polyarthra* and *Keratella* were lower than expected because of the patchy presence of *Asplanchna*. Because *Asplanchna* and *Polyarthra* had similar distributions and vertical migration patterns, it was expected that this would be reflected in high overlap values. The same was also expected of the values for *Asplanchna* and *Keratella*, though these two rotifer species had distributions that were less similar than those of *Asplanchna* and *Polyarthra* and therefore the values between *Asplanchna* and *Keratella* would have been relatively lower. This did not occur because of the highly variable presence of *Asplanchna* (Fig. 21), which was shown by the higher coefficients of variation of this species (Fig. 20). All overlap values with *Asplanchna* were somewhat

low but extremely variable (Fig. 22). Also, the values between *Asplanchna* and *Polyarthra* were similar to those between *Asplanchna* and *Keratella*.

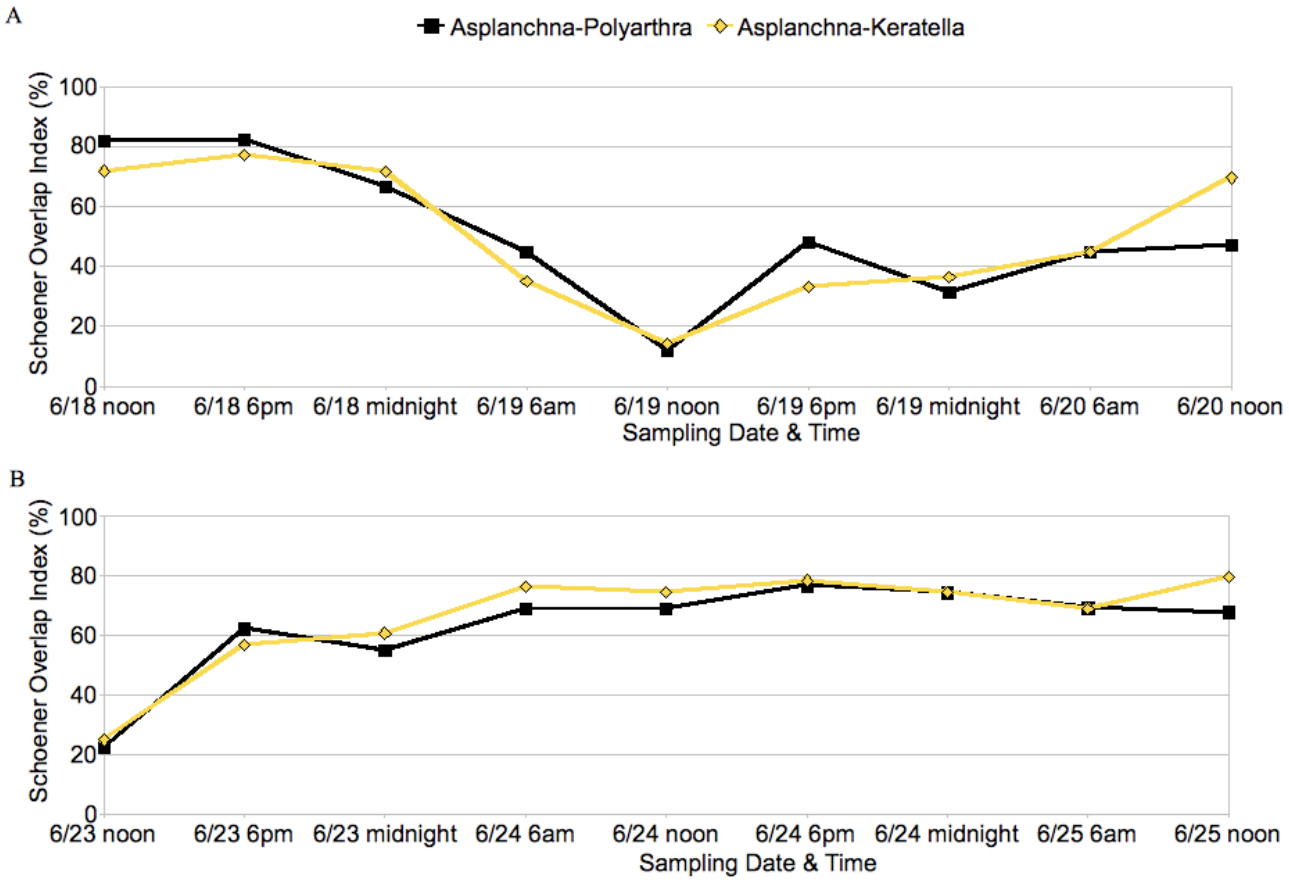


Figure 22. Schoener overlap index percentages between *Asplanchna* with *Polyarthra* and *Keratella* at each sampling time in (A) the first sampling period and (B) the second sampling period.

The *Kellicottia* population tended to be concentrated in the lower half of the water column and did not exhibit consistent vertical migration. At most sampling times, the greatest abundances of *Kellicottia* were at 4m, 6m, or 8m (Fig. 23). Abundances at 2m, and especially at 0m, were relatively low at all times. This concentration at deeper depths was reflected in the weighted mean depths of this species, which were generally around 5m. The distribution of the *Kellicottia* population was shifted deeper in the water column at nearly all times. At some of the times, the distribution across depths was somewhat more even, but there was always greater abundance below the 0m surface sample. Because

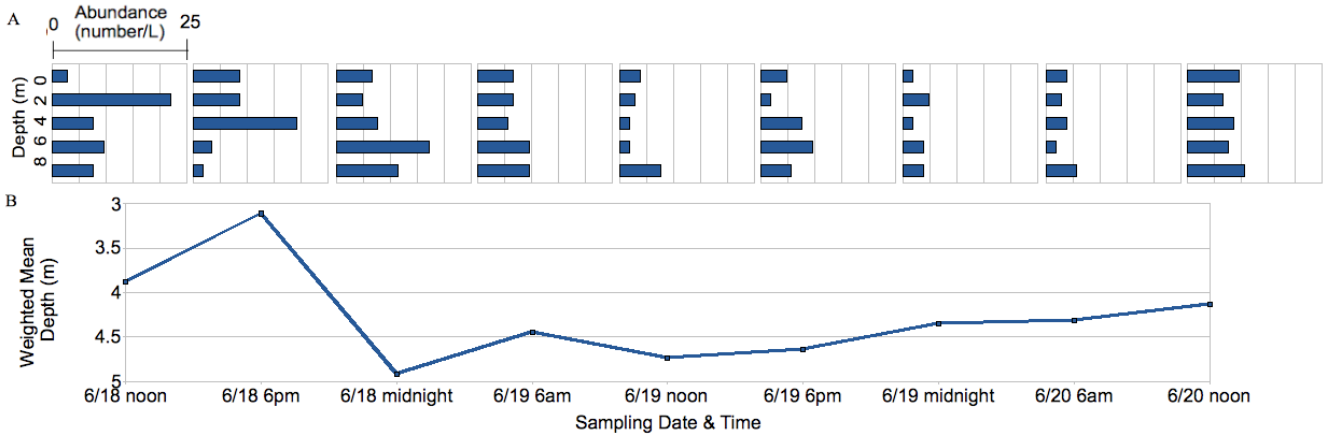
there were no noticeable population shifts, *Kellicottia* was not vertically migrating.

Figure 23. Abundances of *Kellicottia* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

There was very little spatial segregation between the populations of *Keratella* and *Kellicottia*, and therefore *Kellicottia* had similar spatial segregation with *Polyarthra* as *Keratella* did. As noted, both *Keratella* and *Kellicottia* tended to be concentrated in the lower half of the water column. Their distributions were very similar, and at many times the greatest abundances of these species were at the same depths. For example, on June 18 at 6pm and June 19 at 6am, the greatest abundances of both species were at 6m and their abundances near the surface were much lower (Fig. 17A, 23A). *Keratella*

and *Kellicottia* therefore had very high spatial overlap, as shown by the Schoener overlap index between the two species, which was often higher than those of all other rotifer species pairs (Fig. 19). Because the *Polyarthra* population was generally concentrated at shallower depths in the lake, while *Kellicottia* was present deeper in the water column, there was less spatial overlap between these two species, as shown by their Schoener overlap index values (Fig. 19), just as there was between *Polyarthra* and *Keratella*.

Unlike the other rotifer species, *Synchaeta* was evenly distributed across depths at all times and did not exhibit any vertical migration. At over half of the sampling times, the *Synchaeta* population had equal abundances at all depths (Fig. G). At some of the other times, one depth had a relatively much greater abundance than the four other depths, such as the relatively very high concentration of *Synchaeta* at 2m on June 18 at noon. Because there was no apparent pattern in the occurrences of these high relative abundances and they were infrequent, they did not indicate true population shifts in this species. The fairly even distribution of *Synchaeta* across all depths resulted in a variable but often high spatial overlap between this species and the other rotifer species, as shown by the average Schoener overlap index values between *Synchaeta* and *Kellicottia*, *Keratella*, and *Polyarthra* (Fig. 25).



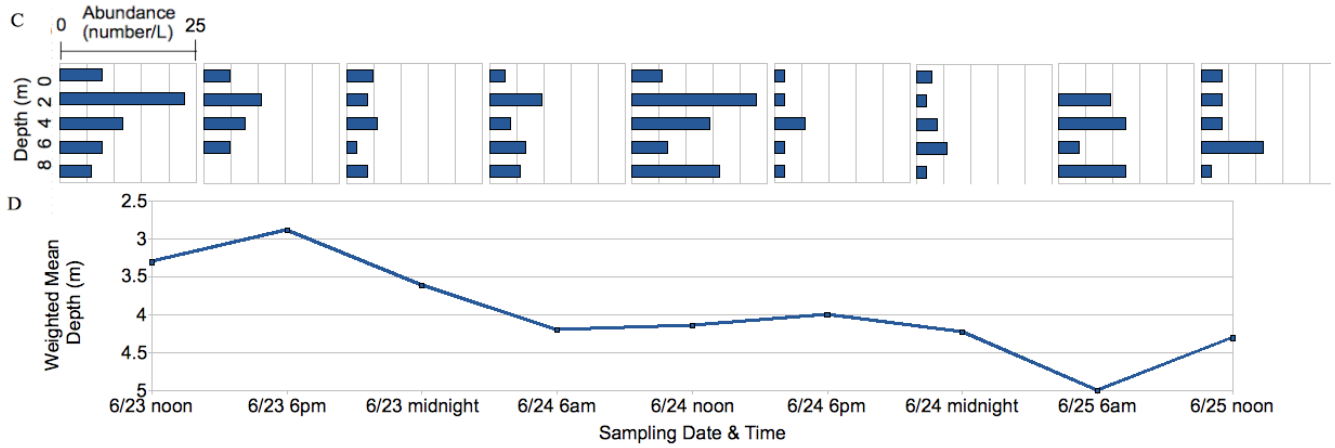


Figure 24. Abundances of *Synchaeta* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

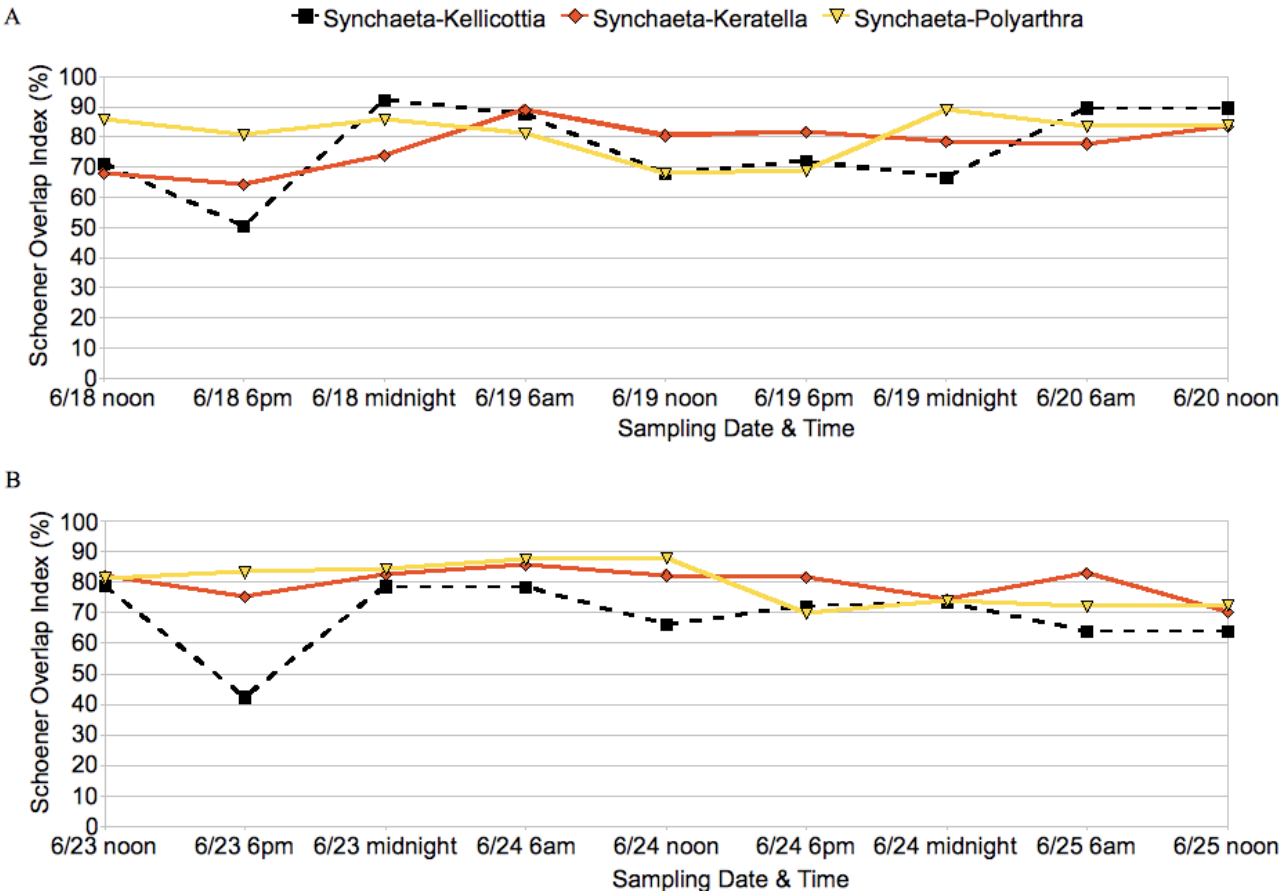


Figure 25. Schoener overlap index percentages between *Synchaeta* with *Kellicottia, Keratella,* and *Polyarthra* at each sampling time in (A) the first sampling period and (B) the second sampling period.

While the *Conochilus* population was distributed deep in the water column and may have exhibited some vertical shifts, we cannot conclude that this population was vertically migrating. *Conochilus* was generally not abundant near the surface at 0m, and the greatest abundances at most times were at 6m and 8m (Fig. 26). There were some vertical shifts in distribution at these deeper depths, with the depth of greatest abundance changing between 4m, 6m, and 8m throughout the two sampling periods. This was reflected by the weighted mean depths of this species, which changed regularly over time. Nevertheless, it cannot be concluded that this population of *Conochilus* was vertically migrating because its integrated water column abundance changed greatly over time. This was especially notable in the second sampling period, when the integrated water column abundance was much greater at noon and 6pm on June 23 compared to times later in the sampling period, such as 6pm on June 24 (Fig. 26C). These changes in integrated water column abundances were apparent in the very high coefficients of variation for *Conochilus*, which indicated that *Conochilus* individuals were entering and leaving the water column. While the reason for this is beyond the scope of this study, it may have been due to population density changes or movement out of the water column. Because of this, apparent shifts in vertical distributions may actually be due to horizontal migration into and out of the water column, resulting in the possible vertical migration of *Conochilus* being undetectable.

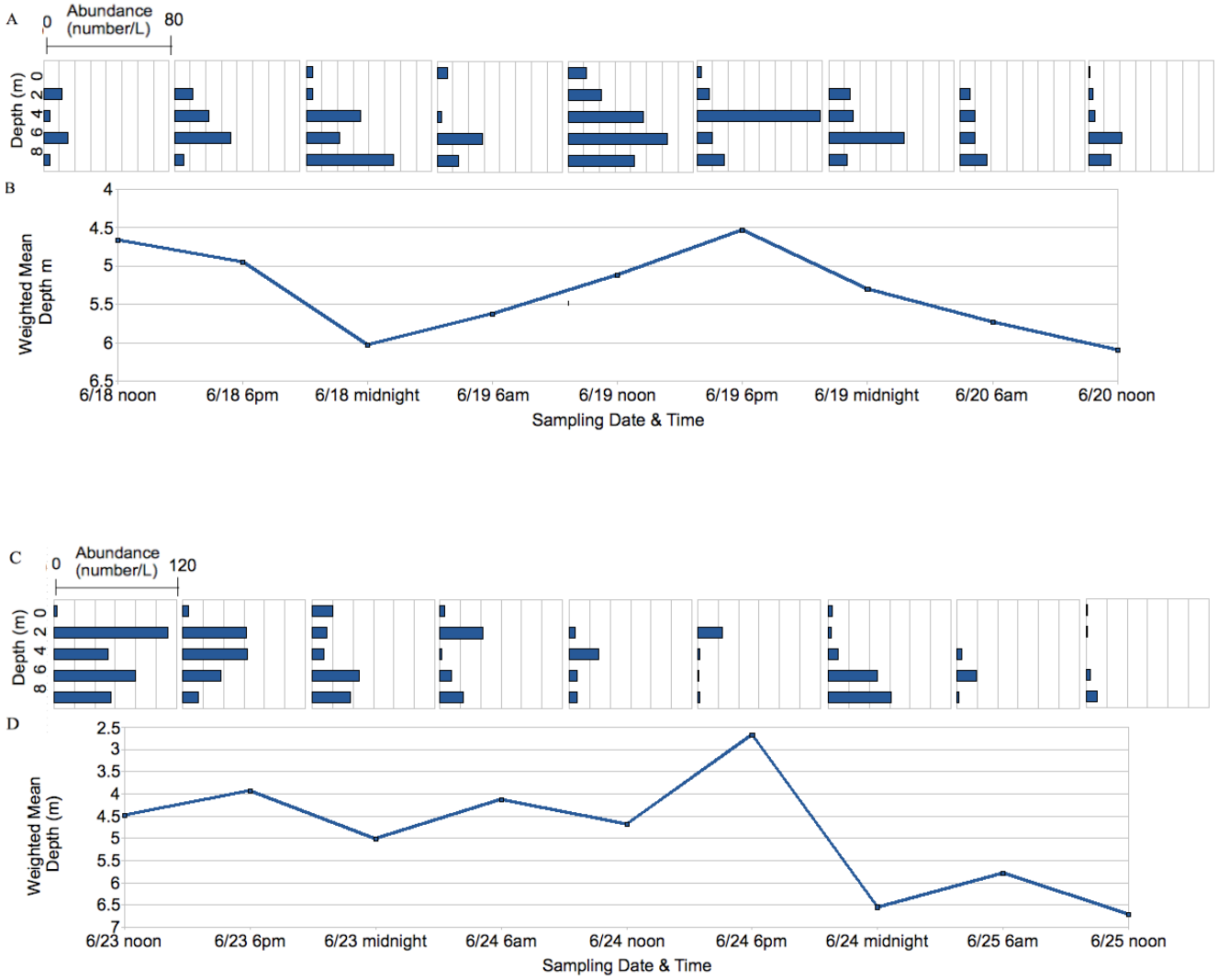


Figure 26. Abundances of *Conochilus* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

Abundances of *Trichocerca* were too low for any conclusions to be drawn about their vertical migration patterns or distributions. When animals were present, abundances were very low, and the distributions of these abundances were random (Fig. 27). This was reflected in the weighted mean depths of *Trichocerca*, which were extremely varied and presented no pattern. There were also two times, one in each sampling period, at which *Trichocerca* were not found at any depth. The random, patchy distributions of this species resulted in high coefficients of variation and low overlap values

with the other rotifer species and with first and second instars of *Chaoborus*. These will not be discussed further because the depths at which *Trichocerca* were found to be present were arbitrary due to low abundances and therefore not indicative of either the distributions or spatial relationships of *Trichocerca* with other species.

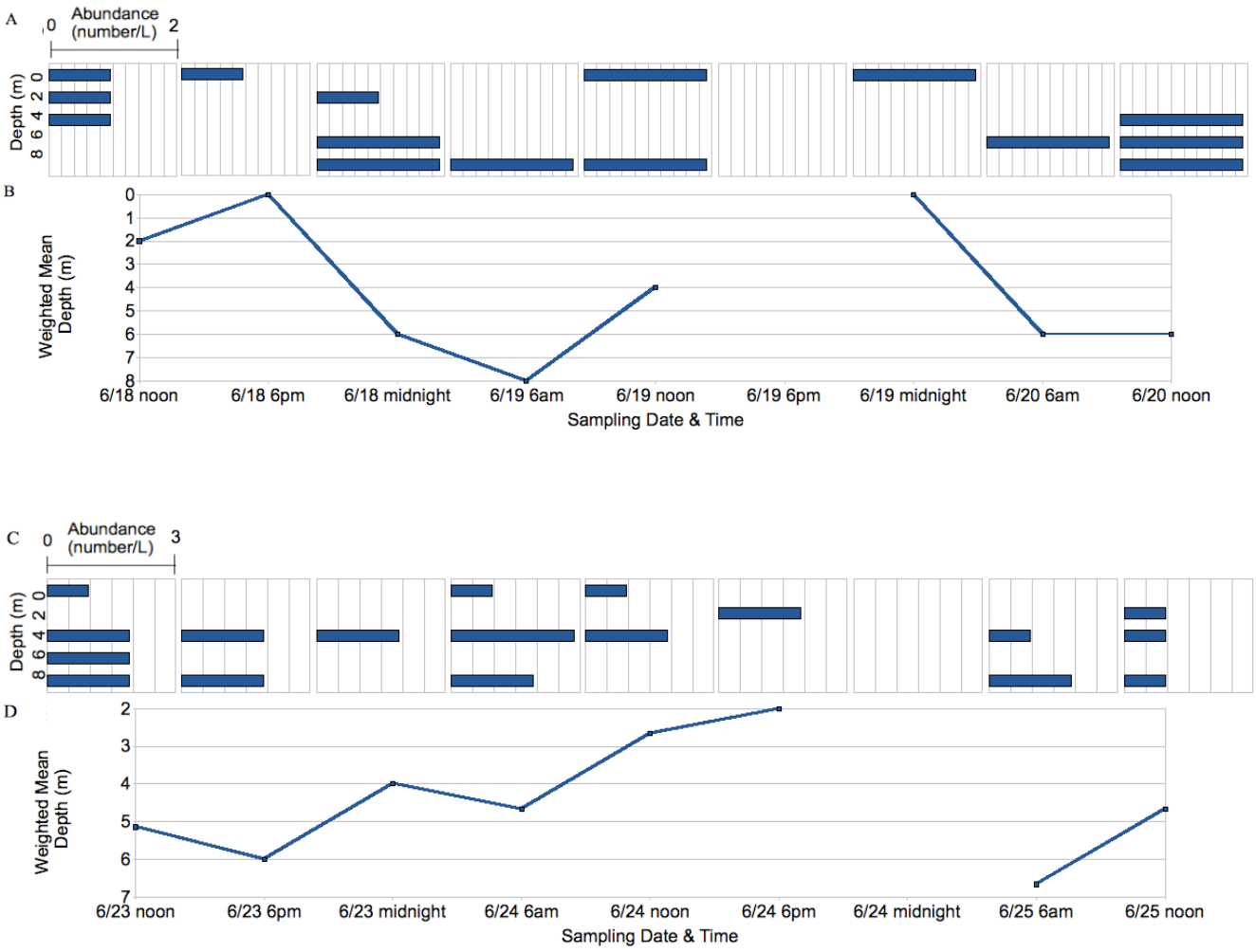


Figure 27. Abundances of *Trichocerca* at each depth and sampling time in (A) the first sampling period and (C) the second sampling period. The weighted mean depths for each time are shown below their respective abundance graphs for (B) the first sampling period and (D) the second sampling period.

Spatial Overlap Between Chaoborus Instars and Rotifer Species

Even though there was some fine spatial separation between *Polyarthra* with *Keratella* and *Kellicottia*, these three species of rotifers had similar distributions in terms of the entire water column.

The populations of these species tended to be concentrated about halfway down the water column, between 2m and 6m, at most times. This was summarized clearly by the weighted mean depths of these three rotifer species, which were all within a narrow range between 3m and 6m (Fig. 28). Therefore, *Polyarthra, Keratella,* and *Kellicottia* were highly concentrated around 4m, or halfway between the surface and benthic zone of the lake.

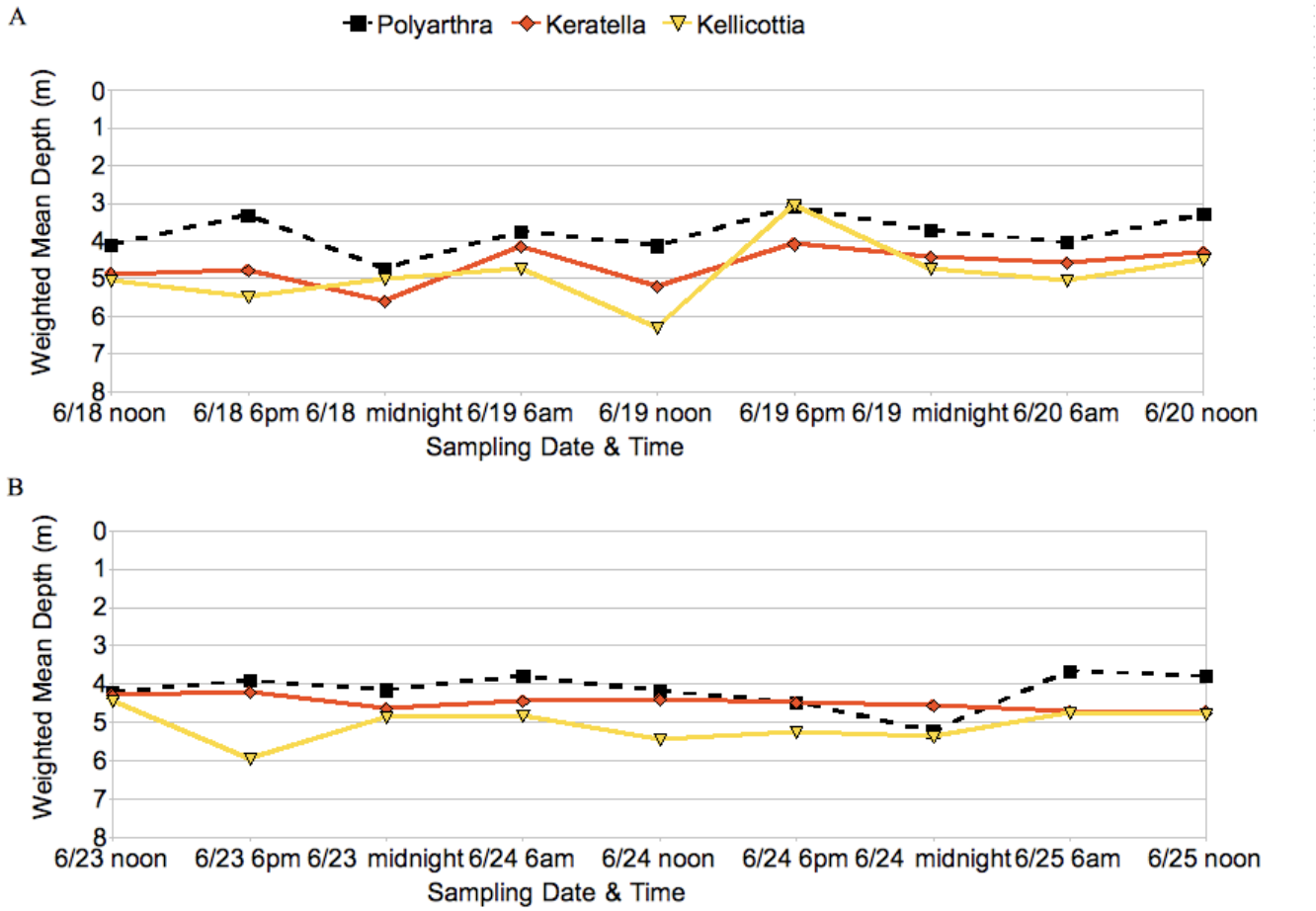


Figure 28. Weighted mean depths of *Polyarthra, Keratella,* and *Kellicottia* at every sampling time in (A) the first sampling period and (B) the second sampling period.

The distribution of these three species resulted in some spatial separation between the rotifers and the second instars of *Chaoborus* at all times except midnight. This could be seen clearly when the abundances of *Polyarthra* were compared with those of the second instars. Second instars were primarily only present at 6m and 8m in both sampling periods. While there were *Polyarthra* present

throughout the depths of the water column, most of this population was concentrated at 4m or above, with lower abundances at 6m and 8m. This resulted in a spatial separation between the second instars of *Chaoborus* and most of the *Polyarthra* population at times other than midnight (Fig. 29A). This spatial separation also occurred between *Keratella* and the second instars at times other than midnight, especially during the second sampling period when most of the greatest abundances of *Keratella* were at 4m. The spatial separation between *Keratella* and second instars occurred to a lesser extent during the first sampling period because more of the rotifer population was present at 6m. There was much less spatial separation between the *Kellicottia* population and the second instars, compared to that with the other two rotifer species; much of the population of *Kellicottia* was concentrated at 6m and 8m, just like that of the second instars, though some of the *Kellicottia* population was present at the shallow depths at which no second instars were found.

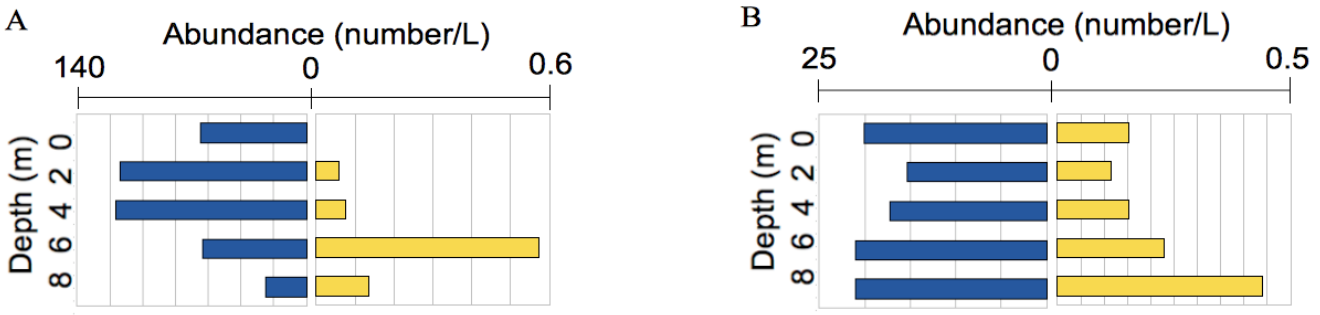


Figure 29. Comparison of abundances of *Polyarthra* (on left) and second instars of *Chaoborus* (on right) at (A) 6pm on June 18 and (B) midnight on June 23.

The *Asplanchna* population was concentrated at very shallow depths and had even less spatial overlap with second instars of *Chaoborus* during times other than midnight. In comparison to *Polyarthra*, *Asplanchna* was generally even closer to the surface of the lake at these times. Because the *Asplanchna* population was much closer to the surface, especially in the first sampling period when this species was only present at 0m and 2m, there was very little spatial overlap with second instars, which were only present at the deepest depths of 6m and 8m (Fig. 30A).

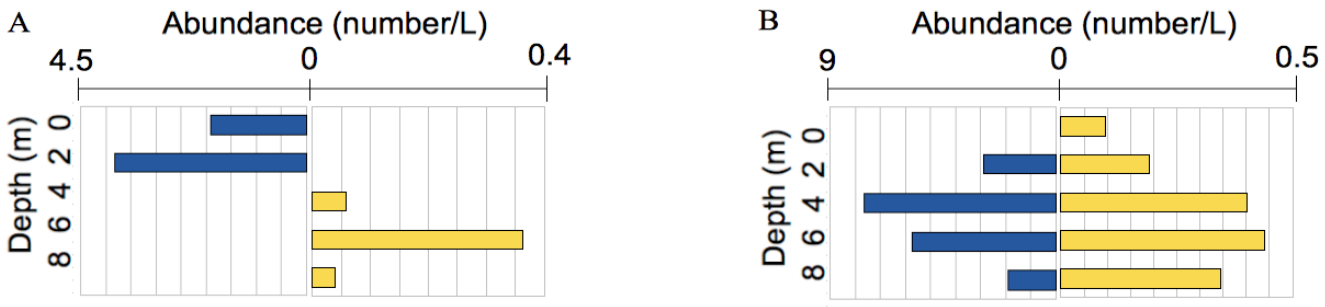
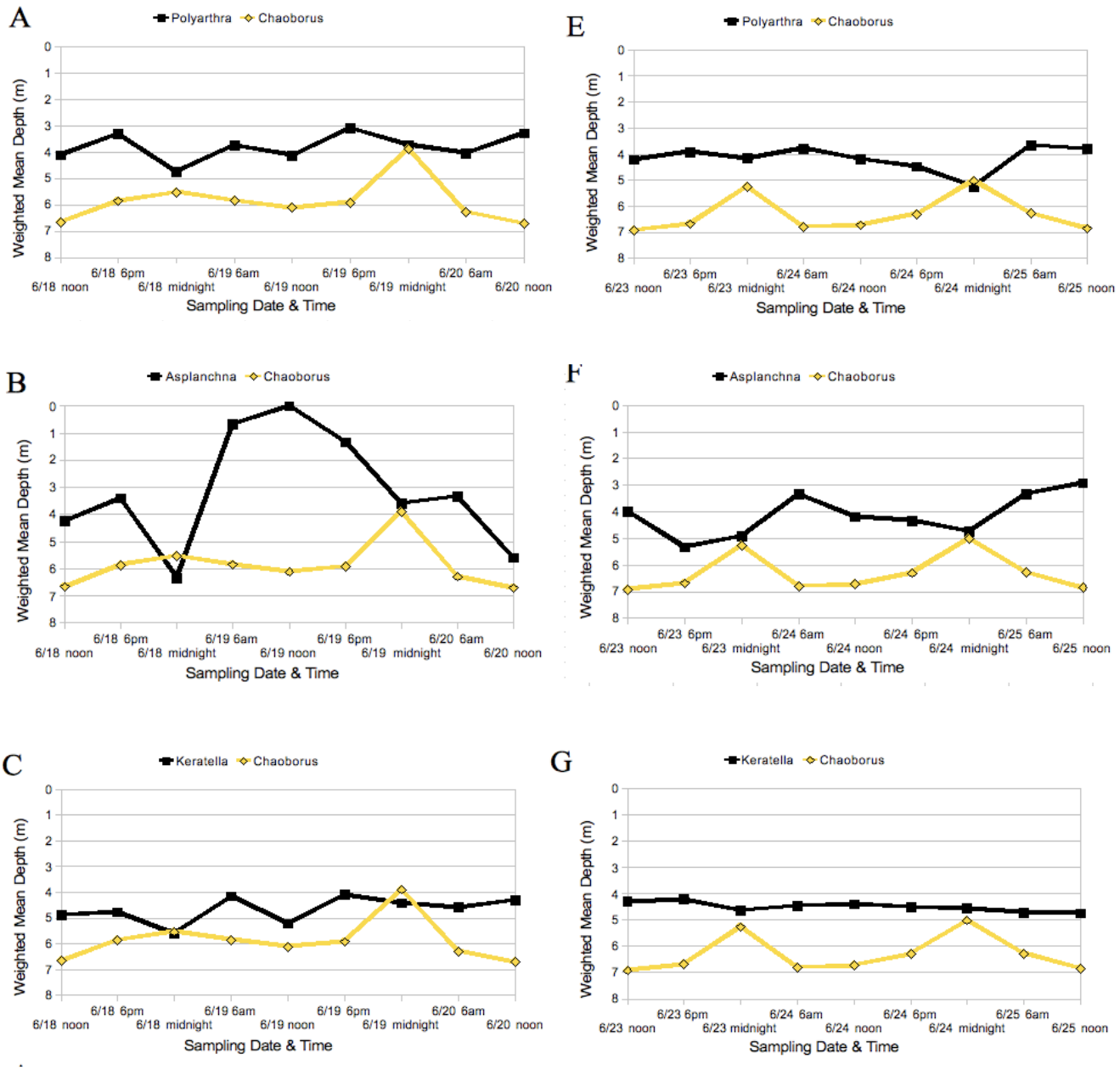


Figure 30. Comparison of abundances of *Asplanchna* (on left) and second instars of *Chaoborus* (on right) at (A) 6pm on June 19 and (B) midnight on June 24.

Conversely, there was a lot of spatial overlap between these four rotifer species and second instars of *Chaoborus* at midnight. At midnight, the second instar population shifted upwards towards the surface and, instead of being concentrated at 6m and 8m, second instars were present almost equally at all depths. Simultaneously, the populations of *Keratella, Polyarthra*, and *Asplanchna* shifted to deeper in the water column while the *Kellicottia* distribution remained the same. This resulted in greater spatial overlap between the second instars and the four rotifer species at midnight than at other times (Fig. 29B). This was especially pronounced for *Asplanchna*, which had nearly no overlap with second instars at all other times because *Asplanchna* was located close to the surface and the second instars were deep in the water column, while at midnight *Asplanchna* moved away from the surface as the population of second instars moved up in the water column (Fig. 30B). This was especially apparent in the first sampling period. At midnight, all four of the rotifer species moved downward in the water column as the second instars moved upward, resulting in much greater spatial overlap between the two groups at this time.

The differences in spatial overlap of second instars with *Polyarthra*, *Keratella*, *Kellicottia* and *Asplanchna* during midnight and during all other times were apparent due to both a comparison of their weighted mean depths and from the Schoener overlap index. At midnight, the weighted mean depths of

Polyarthra and *Asplanchna* were similar to those of the second instars, while the weighted mean depths of the rotifers were shallower than the second instars' weighted mean depths at all other times (Fig. 31). This also occurred with the weighted mean depths of both *Keratella* and *Kellicottia*, though the differences were less extensive. The Schoener overlap index values between the four rotifer species and second instars of *Chaoborus* were always higher at midnight than the other times (Fig. 32).



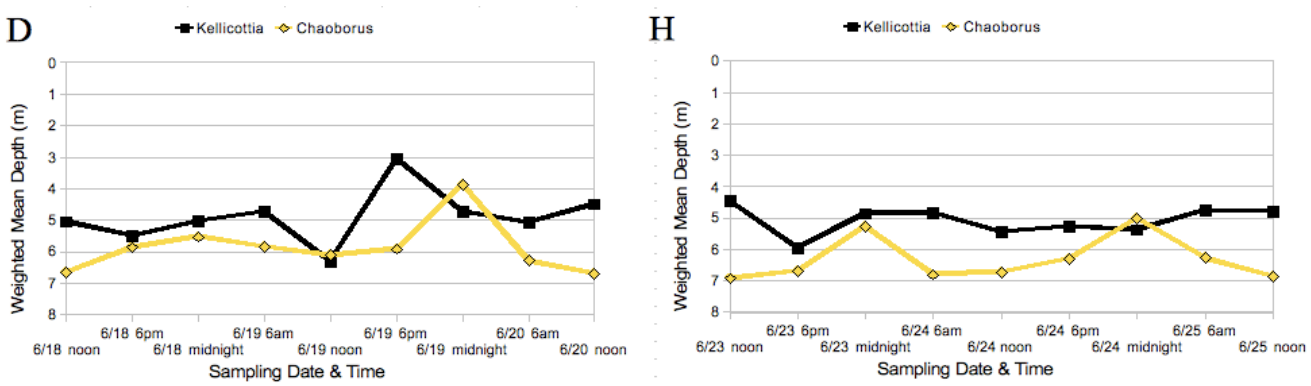


Figure 31. Comparison of weighted mean depths of second instars of *Chaoborus* with the rotifers *Polyarthra*, *Asplanchna, Keratella,* and *Kellicottia* in (A-D) the first sampling period and (E-H) the second sampling period.

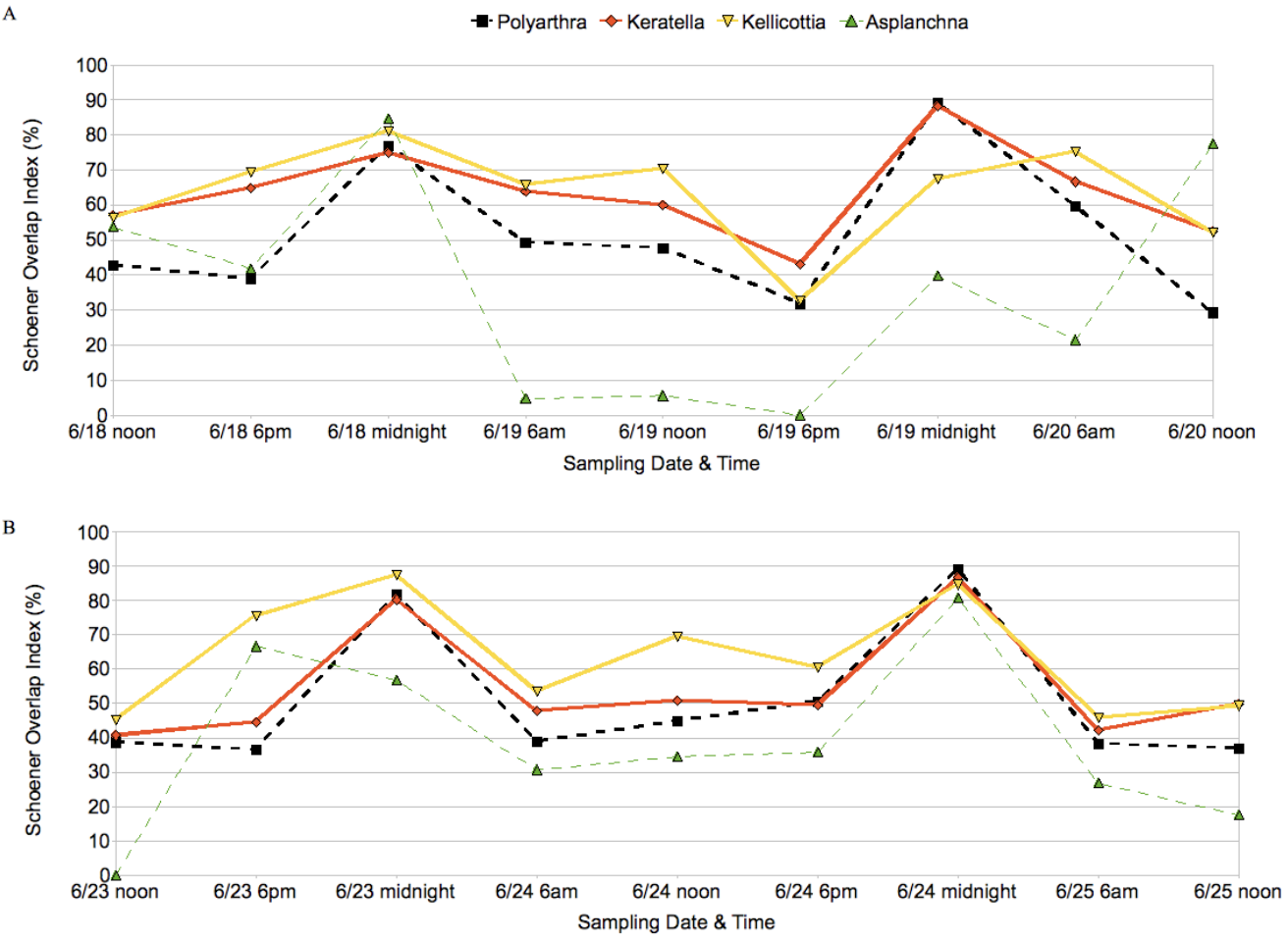


Figure 32. Schoener overlap index percentages between second instars of *Chaoborus* and the rotifers *Polyarthra, Keratella, Kellicottia,* and *Asplanchna* at each sampling time in (A) the first sampling period and (B) the second sampling period.

Discussion

Three of the four *Chaoborus* instars exhibited strong diel vertical migation patterns, and the patterns of the different instars were similar. Second instars were deep in the water column at 6m and 8m during the day, while third and fourth instars were in the benthic zone of the lake at these times. All three instars migrated upward in the water column at midnight, resulting in even distributions of these instars across all depths of the lake. Conversely, there were no patterns in the vertical distributions of the first instars of *Chaoborus* and these instars did not appear to be vertically migrating.

Except for *Trichocerca*, all of the rotifer species had clear distribution patterns in the water column, and some of these species exhibited vertical migration. The distributions of *Keratella, Kellicottia,* and *Conochilus* indicated that these populations tended to be deeper in the water column, while the populations of *Polyarthra* and *Asplanchna* were shallower and closer to the surface. *Synchaeta* was equally distributed throughout the water column. Both *Kellicottia* and *Synchaeta* exhibited no vertical migration patterns, while that of *Conochilus* was not able to be determined. The populations of *Polyarthra, Keratella*, and *Asplanchna* exhibited vertical migration patterns that were similar; all of these populations shifted deeper in the water column at midnight compared to all other times.

Chaoborus Diel Vertical Migration Patterns

The fish in Low Lake are potential predators of the *Chaoborus* instars. Of the nine known species of fish in Low Lake, the following seven are known to be piscivorous as adults: black crappie, largemouth bass, northern pike, rock bass, smallmouth bass, walleye, and yellow perch (Mittelbach & Persson 1998). These fish species may consume instars of *Chaoborus*.

It is likely that the induction of a normal diel vertical migration pattern in *Chaoborus* is due to predation by these fish. Second, third, and fourth instars of *Chaoborus* in Low Lake exhibited a vertical

migration pattern in the water column, in which these instars were deep in the water column, and potentially in the benthic zone, during all times except midnight. At midnight, the instars moved towards the surface, resulting in more even distributions throughout the water column. This pattern is consistent with normal diel vertical migration. Therefore, during times when there is light penetrating the lake, which included all of the sampling times chosen except midnight, the fish in the lake were able to locate and consume *Chaoborus* instars. This resulted in these instars adapting a behavioral pattern in which they were preferentially located deep in the water column during daylight hours to avoid predation by fish. When it was dark at midnight, risk of fish predation was minimal because the predators were unable to see the *Chaoborus* instars. This allowed the instars to move towards the surface, which was beneficial because prey species, such as rotifers, tended to be located much closer to the surface than *Chaoborus* were able to be during the daylight hours.

The induction of normal diel vertical migration behavior in *Chaoborus* instars has been shown to be caused by fish. It has been conclusively determined in multiple studies that kairomones produced by fish induce vertical migration in *Chaoborus* (De Meester et al. 1999). For example, Tjossem exposed *Chaoborus* larvae to clean water or fish-treated water in vertical columns and determined their vertical locations (1990). Those larvae in the fish-treated water had much greater vertical migration amplitudes than those that were in clean water.

The clarity of the water in Low Lake accounts for the extensive migration amplitudes of the second, third, and fourth instars of *Chaoborus*. The population of second instars moved between the deepest depths of the lake during the day to the surface at midnight. The amplitude of the migration pattern of third and fourth instars was even greater because some of these individuals moved between the benthic zone during the day to the surface at midnight. Low Lake is a clear lake, as shown by its euphotic zone, which extends between the surface to a depth below 4m. Therefore, visual feeding fish can locate prey in large areas of the lake because much of the lake contains enough light for them to see

and capture prey items. Because the predation range of these visual feeding fish is extensive, it requires that the instars of *Chaoborus* which they prey upon move very deep in the water during the day to avoid this predation. If Low Lake were a much less clear lake with a limited euphotic zone, it is likely that the diel vertical migration amplitudes of these instars of *Chaoborus* would be much more limited and the instars would not be as deep in the water column during the day.

The migration patterns of third and fourth instars were more pronounced than those of second instars, and first instars exhibited no vertical migration, due to size and visibility differences. Second instars were concentrated at the deeper depths in the lake during daylight hours. The third and fourth instars were even lower than the second instars, and were presumably in the sediment of the benthic zone, which often occurs in later instars of *Chaoborus* (Wetzel 2001). This is because third and fourth instars are much larger than the second instars and are more visible to fish, so they must migrate even further than second instars during the day to avoid the areas in the lake in which fish are capable of seeing the instars. Second instars are not as visible and can be slightly shallower in the water column. Conversely, first instars had no vertical migration pattern and were distributed throughout the water column at different depths at all times. First instars are much smaller and more translucent than the other instars, resulting in their low visibility and consequently low fish predation risk. Therefore, first instars did not need to vertically migrate to avoid fish.

Influence of Biotic Factors on the Rotifer Species' Distributions

The *Asplanchna* population was located close to the surface, which may have been due to its susceptibility to predation by *Chaoborous*. Of all the rotifer species, *Asplanchna* had a distribution that was shifted to the shallowest depths. This resulted in the low spatial overlap between *Asplanchna* and second instars of *Chaoborus* at all times except midnight, and this was lower than that of the other rotifer species. The distribution of *Asplanchna* may have been due to it being a preferred prey species of *Chaoborus*. In the feeding studies, first and second instars were easily able to consume *Asplanchna*

individuals. This is because of the soft non-loricate body of *Asplanchna*, and also because this rotifer species has no effective mechanism of escape from *Chaoborus*, like that of *Polyarthra*. Because *Asplanchna* is a preferred food item for *Chaoborus*, it would be beneficial for this rotifer to have significant spatial segregation from the predatory *Chaoborus*, as was seen in this study.

Three of the rotifer species, *Polyarthra, Keratella,* and *Kellicottia*, were likely deeper in the water column than *Asplanchna* because of food resources. Low Lake has a positive heterograde dissolved oxygen profile, with an increase in dissolved oxygen in the metalimnion at 4.5m. The metalimnetic peak in oxygen levels likely indicates an accumulation of photosynthetic phytoplankton at that depth. This concentration of algae, which results because there is both abundant light at this depth, due to the clarity of the water of the low productivity lake, and higher nutrient concentrations from the adjacent hypolimnion, is often referred to as an algal plate (Dodson 2005). The rotifer diet is typically composed of mostly algae, and it would therefore be advantageous for the rotifer species in Low Lake to be present near the algal plate where their preferred food resources are abundant.

Polyarthra, Keratella, and *Kellicottia* were also able to be located deeper in the water column near the algal plate, unlike *Asplanchna,* because they have some morphological or behavioral defenses useful in preventing predation by *Chaoborus*. Although *Polyarthra* were readily captured and consumed by first and second instars in the feeding studies, they were nevertheless capable of exhibiting an active escape response using their paddles that would likely be effective against *Chaoborus* predation some of the time. *Keratella* also are capable of an active escape response from predators. Additionally, *Keratella* are almost completely loricate, with only the area around the buccal cavity being soft. It has been shown that the copepod *Mesocyclops edax* has extreme difficulty in successfully consuming *Keratella* individuals because of this (Gilbert & Williamson 1978). Lastly, *Kellicottia* have a well developed lorica and two long spines, one anterior and one posterior, which would make consumption by predators difficult. Conversely, *Asplanchna* are capable of avoiding

predation by small predators such as copepods because of their size (Stemberger & Gilbert 1987a), but they have no effective morphological or behavioral defenses against relatively large predators such as *Chaoborus* instars. Therefore, *Polyarthra, Keratella,* and *Kellicottia* were likely located deeper in the water column near the abundant food resources of the algal plate because they had potentially effective defenses against predation by the second instars of *Chaoborus* which were occasionally located higher in the water column at times other than midnight.

Keratella and *Kellicottia* likely were able to have similar spatial occurrences due to differential use of food resources. These two rotifer species were both located somewhat deeper in the water column than *Asplanchna* and *Polyarthra*, near or just below 4m. Such high spatial overlap between the two species may result in interspecific competition. Nevertheless, the two species were able to spatially coexist and one possible explanation for this was differential use of resources. Different rotifer species sometimes prefer and select for different types of food, which is especially true when food is abundant or many types are available (Herzig 1987). *Keratella* and *Kellicottia* were mostly concentrated at the same depth near the algal plate, where more phytoplankton was available, which may have limited their interspecific resource competition.

There was some fine scale spatial segregation between *Polyarthra* with *Keratella* and *Kellicottia*, though the reason for this was unknown. The *Polyarthra* population was shifted closer to the surface than those of *Keratella* and *Kellicottia*, though this species was still close enough to the algal plate to make use of its resources. Spatial segregation amongst these species has been observed before in other systems. In Sunfish Lake, the *Polyarthra* population was located at shallower depths than the *Keratella* population at all times of the year (George & Fernando 1970), similar to the patterns in this study. In a separate study, spatial segregation was seen between *Polyarthra* and *Kellicottia*; the *Polyarthra* population was present at deeper depths at night while *Kellicottia* was deeper during the day (Gonzalez 1998). No explanations for the spatial segregations of these rotifer species were

suggested. It it possible that these species pairs were not able to use available food resources differently, like *Keratella* and *Kellicottia* may have been able to, and therefore spatial segregation was necessary to maintain all populations.

It is also possible that the abundances of food items influenced the differences in vertical distributions of *Asplanchna* and *Polyarthra* as compared to those of *Keratella* and *Kellicottia*. Both the *Asplanchna* and *Polyarthra* populations were shifted closer to the surface than those of *Keratella* and *Kellicottia*. Rotifers prefer intermediate food concentrations because high concentrations can limit their ingestion rates (Salt 1987). While the abundances of algae in the algal plate are unknown, it is possible that these abundances exceed the food concentrations preferred by *Asplanchna* and *Polyarthra*. If so, these rotifer species may choose to be located higher in the water column above the algal plate, where it is likely that algal abundances are lower, because these food concentrations are more optimal for these two species.

Similarly, the size of *Polyarthra* may account for the shift in this population towards the surface where food resources were more scarce. It is known that rotifers that have a smaller size have relatively greater search volumes than larger rotifers because they move further relative to body size (Salt 1987). *Polyarthra* were the smallest rotifer species present in Low Lake. Therefore, because *Polyarthra* has a greater search volume than the other species of rotifers and a consequently higher encounter rate with food items, it is more feasible for this rotifer species to be present higher than the algal plate in the water column where algae abundances are lower. *Keratella* and *Kellicottia* are larger rotifer species and may have vertical distributions limited to the algal plate because they would not encounter enough food items for their population to subsist if it were shifted closer to the surface. Therefore, *Polyarthra* can be closer to the surface because they are capable of surviving under conditions with lower food abundances.

The relatively low integrated water column abundances of *Asplanchna* may be explained by the

size of individuals of this species and its concentration near the surface. The integrated water column abundances of *Asplanchna* were generally lower than those of the other species of rotifers besides *Trichocerca,* and the distribution of this species was shifted closer to the surface than the other rotifer species. The algal abundance was likely low near the surface of the lake, which is typical for clear oligotrophic lakes such as Low Lake, resulting in *Asplanchna* being located in an area with limited food resources. Furthermore, the ability of *Asplanchna* to procure food items was limited due to its size. Unlike *Polyarthra*, *Asplanchna* was the largest rotifer species in Low Lake and therefore had the lowest search volume and a low encounter rate with food items. The combination of limited food resources near the surface, where *Asplanchna* were located, and the limited search volume of this species account for the low abundances of *Asplanchna*. Such constraints limit the possible size of the *Asplanchna* population.

The vertical distribution of *Asplanchna* may have influenced the distributions of *Polyarthra* and *Keratella* due to its predation. There was substantial spatial segregation between *Asplanchna* and *Keratella* because the former was closer to the surface while the latter was near 4m, while there was much less spatial segregation between *Asplanchna* and *Polyarthra*. This may have been because of the predatory capabilities of *Asplanchna*. *Asplanchna* has been shown to be an effective predator of *Keratella*, but is not capable of preying upon *Polyarthra. Asplanchna* cannot capture *Polyarthra* because of the active escape response exhibited by the latter rotifer species (Gilbert & Williamson 1978). Therefore, it is possible for *Polyarthra* to be shallower in the water column than *Keratella*, and consequently have greater spatial overlap with *Asplanchna*, because the risk of predation to *Keratella* by *Asplanchna* is much greater.

Interestingly, *Asplanchna* also can not prey upon *Kellicottia*. Because the predation risk by *Asplanchna* on *Kellicottia* is low, like that of *Polyarthra*, the *Kellicottia* population could potentially be distributed closer to the surface of the lake and have greater spatial overlap with *Asplanchna*. This may

not occur because it is more beneficial for the rotifer species to be located further down in the water column, closer to the food resources of the algal plate. It is possible that the only reason that *Polyarthra* is not located deeper in the water column is because the interspecific competition between this species and *Keratella* or *Kellicottia* is too strong and decreases the fitness of *Polyarthra*. But, because the risk of predation by *Asplanchna* on *Polyarthra* is not great, the *Polyarthra* population can be shifted somewhat closer to the surface, resulting in some spatial segregation between *Polyarthra* with *Keratella* and *Kellicottia*, but still deep enough to access the resources of the algal plate. Like *Kellicottia, Asplanchna* additionally does not consume *Conochilus*, though there was very low spatial overlap between these two species because *Conochilus* tended to be deep in the water column while *Asplanchna* was much closer to the surface.

The high spatial overlap between *Conochilus* and the second instars of *Chaoborus* may have been due to a lack of predation pressure. Both *Conochilus* and these instars were located deep in the water column at times other than midnight, usually at the deepest depths. The high spatial overlap between the second instars and a potential prey species may have occurred because these instars were unable to feed effectively on *Conochilus*. It was shown by the feeding studies that early instars have difficulty feeding on *Conochilus*, likely because they are colonial and therefore large and bulky. It has been shown that coloniality in rotifers decreases predation pressure (Wallace 1987). Therefore, *Conochilus* was able to have high spatial overlap with second instars at some times because they were not at risk of predation by these insects.

Rotifer Diel Vertical Migration Patterns

Some of the diel vertical migration patterns by rotifer species noted in this study are corroborated in the literature. In this study, it was determined that *Keratella* and *Polyarthra* were vertically migrating. Their migration pattern is considered reverse diel vertical migration because they were higher in the water column during the day and moved deeper in the water at night. Reverse diel

vertical migration patterns have been observed in these two genera before. Two species of *Keratella* have been determined to exhibit a reverse vertical migration, and this has been observed in one of these species, *Keratella quadrata*, in two studies on separate lakes (Pennak 1944; Burris 1980). The authors of these studies did not speculate about why these species of *Keratella* were doing reverse diel vertical migration. Also, there has been a recorded case of *Polyarthra remata* exhibiting reverse diel vertical migration (Gilbert & Hampton 2001). It was determined in this study that this rotifer species was migrating in response to the normal diel vertical migration pattern of a copepod which preyed on *Polyarthra remata,* which is similar to the hypothesis explaining the reverse vertical migrations of the rotifer species in this study.

Of the rotifer species whose vertical migration patterns were unable to be determined or which did not exhibit vertical migration, species from the same genera have been observed engaging in diel vertical migration in the past. The vertical migration pattern of *Conochilus* in Low Lake was unable to be determined. Species of *Conochilus* have previously been observed exhibiting normal diel vertical migration patterns in several previous studies, and some of these patterns included dramatically large amplitudes (Pennak 1944; Grover & Coker 1940). In this study, neither *Kellicottia* or *Synchaeta* were vertically migrating through the water column and had fairly even distributions at most times. Both of these species have been observed doing normal diel vertical migration in different lake systems (Plew & Pennak 1949; Burris 1980). The relevant differences between the lake systems in which *Conochilus, Kellicottia,* and *Synchaeta* were vertically migrating and that of Low Lake are unknown.

Explanations for the Induction of Diel Vertical Migration in Rotifer Species

It is possible that the induction of vertical migration behavior in prey species of *Chaoborus* is due to the migration patterns of these predators. *Chaoborus* instars often exhibit a normal diel vertical migration pattern; they are therefore deep in the water column during the day and closer to the surface at night. Consequently, prey species of *Chaoborus* may avoid predation by being spatially separate

from these predators. They may therefore be shallower in the water column during the day, while the *Chaoborus* instars are deeper, and then vertically migrate downward at night as the instars are migrating upward. That is, these prey species often develop a reverse vertical migration pattern.

This induction of reverse vertical migration in prey species of *Chaoborus* has been documented previously. For example, the copepod *Diaptomus kenai* from Lake Gwendoline was re-exposed to *Chaoborus* in enclosures two years after *Chaoborus* had been eliminated from the lake by fish predation. The *Chaoborus* instars had a well-established normal vertical migration pattern, and *D. kenai* very shortly thereafter exhibited a reverse migration pattern. Initially the instars were near the surface of the water in the enclosures, resulting in the population of *D. kenai* moving deep in the water column. *Diaptomus kenai* in control enclosures that contained no *Chaoborus* did not exhibit vertical migration (Neill 1990). Similarly, vertical migration was induced in *Daphnia pulex*, a cladoceran that is preyed upon by *Chaoborus*, in response to the vertical migration of *Chaoborous* when both of these species were contained in enclosures (Nesbitt & Riessen 1996).

It appears that the *Chaoborus* instars induced a vertical migration pattern in three rotifer species in Low Lake. The second, third, and fourth instars were located deep in the water column during the day while the rotifers were concentrated between the surface and 4m. Therefore, during the day there was significant spatial separation between the predatory *Chaoborus* and the rotifers, their prey. At midnight the *Chaoborus* instars moved up in the water column and were evenly distributed throughout the depths; simultaneously, the distributions of *Keratella, Polyarthra*, and *Asplanchna* were shifted deeper in the water column. That is, the normal vertical migration pattern of the *Chaoborus* instars induced a reverse diel vertical migration in these three rotifer species.

It seems that the equal distributions across depths of most of the instars of *Chaoborus* would not result in the vertical migration of any of the rotifer species. When a non-visual predator such as *Chaoborus* is distributed equally across all depths, no depth is more advantageous for its prey because

predation pressure is the same at all depths. The second, third, and fourth instars of *Chaoborus* were equally distributed throughout the water column at midnight. It therefore seems that *Keratella, Polyarthra*, and *Asplanchna* should not be vertically migrating as they are because equal numbers of instars are present at both their day and midnight depths, and this behavior would not result in a decrease in predation pressure. This would especially apply to rotifers because swimming is an energetically expensive behavior for them (Epp & Lewis 1984), indicating that any vertical migration behavior would be energetically expensive and would not be undertaken without a corresponding increase in fitness.

It is possible that the reverse diel vertical migration pattern of these three rotifer species did result in reduced predation pressure by *Chaoborus* instars. The temperature of the water in Low Lake decreases with increasing depth. This change is especially drastic in the metalimnion, where these three rotifer species were mostly concentrated. For example, the temperature was 17°C at 4m and decreased by 2°C only half a meter deeper than that. Therefore, small changes in vertical location resulted in great changes in temperature. It has been shown that the swimming speed of rotifers decreases with decreasing temperature. In one study, the mean swimming speeds of *Brachionus plicatilis* at various temperature between 16°C and 32°C were determined. While the speeds of this rotifer species were similar enough to not be statistically distinguishable at temperatures between 20°C and 32°C, mean swimming speeds decreased steadily at temperatures below 20°C (Epp & Lewis 1984). The swimming speeds of rotifers decrease at lower temperatures because of the resulting lower metabolic rates and therefore lower energy availability. Swimming is an energetically expensive behavior for rotifers, so with less energy for swimming, their swimming speeds decrease. Also, lower temperatures decrease the rate of enzyme reactions in all living organisms, which would consequently decrease the muscle movements of rotifers that are required for swimming.

This decrease in rotifer swimming speed results in a decrease in predation pressure. The

swimming speed of rotifers is proportional to their encounter rate with *Chaoborus*. That is, the encounter rate between rotifers and instars of *Chaoborus* depends only on the swimming speed of the rotifers because *Chaoborus* are stationary predators. When rotifers swim more slowly, their encounter rate with *Chaoborus* decreases because the probability that rotifers will enter the vicinity of the stationary instars decreases (Pastorak 1981). When encounter rates are lower, there is a corresponding decrease in predation pressure because a predator cannot consume as many prey items if they are not encountered as often.

Therefore, the vertical migration behavior of the three rotifer species can result in decreased predation pressure by *Chaoborus* instars. At midnight, *Keratella, Polyarthra*, and *Asplanchna* move deeper in the water column to cooler temperatures. These temperatures decrease their swimming speed, which consequently decreases their encounter rates with the *Chaoborus* instars, which results in decreased predation pressure. While it seems counterintuitive that predation pressure by *Chaoborus* on rotifers can be decreased by the rotifers moving deeper in the water column even though the *Chaoborus* are evenly distributed across all depths, it is possible that moving to a location with cooler temperatures can produce this effect.

Although the downward shift of rotifer populations at midnight is not great, the change in temperature this provides is substantial. The decrease in swimming speed of rotifers as temperature decreases is very pronounced because rotifer locomotion is extremely inefficient. Even a small decrease in temperature decreases the amount of energy available to the rotifers, much of which must be used for locomotion because of their inefficient cilia, resulting in decreased swimming speeds.

Although *Asplanchna* did not migrate between as great of a temperature difference as the other rotifer species, it was still sufficient to reduce predation pressure. The larger the size of a rotifer, the less it swims per body length. Therefore, *Asplanchna*, the largest of the seven rotifer species in Low Lake, has the slowest swimming speed. This population was generally concentrated closer to the

surface of the lake where temperatures were more isothermal, so vertical movements by this rotifer species would not result in great changes in temperature. Because *Asplanchna* moves relatively slowly, a much smaller decrease in temperature would be needed to decrease predation pressure on this species by *Chaoborus*.

Future Studies

While the presence of an algal plate has been assumed, confirming its presence and determining the species of algae and their abundances would confirm some of the patterns seen in the vertical distributions of the rotifer species. Algal plates in oligotrophic lakes such as Low Lake are common, and would account for both the positive heterograde pattern in dissolved oxygen in the lake and the concentration of several of the rotifer species in the metalimnion. Knowing the actual abundances of the algae of the algal plate would determine whether these abundances are high enough that they are limiting for *Asplanchna* and *Polyarthra*, which had distributions shifted towards the surface and therefore somewhat away from the algal plate. Knowing the species of algae that were present, and which were preferred or consumed by the different rotifer species, may explain the spatial overlap of *Keratella* and *Kellicottia* and the spatial segregation between these species and *Polyarthra*. These relative spatial locations may be due to differential diet preferences, and knowing the locations of the different algal species would shed light on this.

Because there are many possible predators that prey upon rotifers, it would be interesting to determine which of these are present in Low Lake and compare their vertical distribution patterns to those of the rotifer species. Many groups of organisms, including filter feeding fish, copepods, and mysids consume rotifers (Stemberger & Gilbert 1987a; Herzig 1987). Additionally, while cladocerans such as *Daphnia* are not intentional predators of rotifers, interference and exploitative competition happen often amongst them (Gilbert & Kirk 1988). It is very likely that some of these species were present in Low Lake. At least one species of copepod was noted in the vertical distribution samples, as

were several potential species of *Daphnia*. Whether these potential predators had high abundances and could exert substantial predation pressure on rotifers is unknown. Some of these predators also have been shown to exhibit diel vertical migration patterns; it is well established that copepods and cladocerans are able to migrate and many of them are susceptible to fish predation because they are of a large enough size (Wetzel 2001), and consequently may engage in a normal diel vertical migration pattern to avoid the planktivorous fish of Low Lake. Therefore, determining the distributions and vertical migration patterns of the rotifer predators besides the *Chaoborus* instars would be illuminating.

To determine if the hypothesis that the rotifer diel vertical migration in Low Lake is due to the influence of temperature, the swimming speeds of the pertinent rotifer species should be measured. While it is known that rotifers swim more slowly at lower temperatures (Epp & Lewis 1984), the extent of this effect on the rotifer species in Low Lake could be determined using controlled laboratory studies. The three rotifer species that are known to migrate vertically, *Keratella, Polyarthra*, and *Asplanchna*, could be exposed to a range of temperatures and their resulting swimming speeds measured. Their swimming speeds at the temperature of the depth at which the populations are concentrated during the day should be compared to their swimming speeds at the cooler temperature of the depths at which the populations are concentrated at midnight. This would show that the cooler temperatures that the rotifer species inhabit at night result in lower swimming speeds, and would also show the extent of the differences in swimming speeds in the day and at night.

These data could be used to determine the influence of the changing swimming speeds on the encounter rates between the vertically migrating rotifer species and the *Chaoborus* instars. There have been equations developed that accurately determine the encounter rate between a stationary predator, like *Chaoborus* instars, and a mobile prey, like rotifers, that take into account the densities of the predator and prey and the swimming speed of the prey (Pastorak 1981). The densities of the *Chaoborus* instars and rotifer species have been determined in this study. If the swimming speeds of rotifers at the

higher temperatures they inhabit during the day and the lower temperature they inhabit at midnight were determined, the two encounter rates with *Chaoborus* instars that result from these two swimming speeds could be determined and compared. This would confirm that the encounter rate between predator and prey decreases when the rotifers are at cooler temperatures.

Lastly, it would be useful to determine if the differences in the distributions of the rotifer species at midnight and at all other times are statistically significantly different. While the differences in distributions of *Keratella, Polyarthra*, and *Asplanchna* at midnight and at all other times constitute a repeating and apparent trend, if these differences were determined to be statistically significantly different, it would further strengthen this conclusion.

Conclusion

Both rotifer species and instars of *Chaoborus* in Low Lake exhibit diel vertical migration patterns. While not all seven of the rotifer species exhibited vertical migration, *Polyarthra, Keratella,* and *Asplanchna* had definite reverse diel vertical migration patterns. These three rotifer species were present about halfway down the water column of the lake, near the greatest concentration of food resources, throughout the day and migrated deeper in the water column at night. Similarly, the second, third, and fourth instars of *Chaoborus* had shifts in vertical distribution at midnight. During the day, these instars were located deep in the water column near or in the benthic zone, and then migrated upward towards the surface at night.

The migration patterns of the rotifers were induced by those of the *Chaoborus* instars, with the consequence of a reduction in predation pressure. As the instars spread out through the water column at midnight, the rotifers migrated deeper into cooler water. The cooler temperatures reduced the swimming speeds of the rotifers, and therefore their encounter rates with the *Chaoborus*. Although the shifts in rotifer distributions at midnight were not great, they were sufficient to reduce predation pressure on the rotifers by the instars of *Chaoborus*. There is clear adaptive significance in the diel

vertical migration in the rotifer species of Low Lake due to reduced predation pressure from *Chaoborus*.

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I hereby reaffirm the Lawrence University Honor Code