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# Effects of the Invasive Zooplankter Bythotrephes longimanus on the Aquatic Food Web in Green Bay, Lake Michigan

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Effects of the Invasive Zooplankter *Bythotrephes longimanus* on the Aquatic-Food Web in Green Bay,  
Lake Michigan

By: Arianna Neumeyer

A Thesis Submitted in Candidacy for Honors at Graduation  
from Lawrence University

May 2019

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## **Introduction**

### *Aquatic Invasive Species*

Aquatic Invasive Species (AIS) have had a devastating impact on the Laurentian Great Lakes region over the past few decades. Over 180 invasive species have been introduced causing many biotic and abiotic changes for northeastern Wisconsin. Zebra mussels cost the United States over \$60 million dollars each year because they attach themselves to any hard surface such as water pipes, boats, rocks, etc., costing us millions of dollars to remove. An individual female zebra mussel releases up to a million eggs in a single year and a male zebra mussel releases up to two hundred million sperm into the water resulting in a very high reproductive rate (Borcherding, 1991). Zebra mussels are filter feeders and express particle selectivity when feeding on phytoplankton and may be responsible for the shifts in the phytoplankton community structure that some systems have previously experienced (Heath, Fahnenstiel, Gardner, Cavaletto, & Hwang, 1995). The rapid ingestion of green algae and rejection of cyanobacteria increases the population density of cyanobacteria in the water, causing harmful algal blooms.

The sea lamprey is another invasive species that has been established in the Great Lakes. They also cost the U.S. millions of dollars annually and require annual application of lampricides to keep the population levels under control. Lampricides have been known to decrease the fast-reproductive rates by 72%-88%, which is the recommended amount to ensure long-term suppression of the populations (Velez-Espino, McLaughlin, & Pratt, 2008). If the control efforts



of sea lamprey are stopped, the population will quickly rebound resulting in a decline of native fish populations.

In the 1980's an invasive zooplankter, known as *Bythotrephes longimanus*, began to alter the ecosystem of the Great Lakes, decreasing the species richness and species diversity of native species (Yan, et al., 2001). Changes in the zooplankton populations can lead to a decrease in most people's bigger interest, fish populations. Fish are affected negatively when zooplankton populations decline because zooplankton are the primary food source for all juvenile fish. *Bythotrephes* also negatively affects the native predatory water flea *Leptodora kindtii*. Since *Leptodora* not only compete directly with them for their food source, they also have to avoid the predation pressures from *Bythotrephes*. The population of *Leptodora* have been declining in abundances since the introduction of this invasive. It is theorized that it's the result of a decrease in food availability and direct predation on the juvenile *Leptodora* by *Bythotrephes* (Lehman & Caceres, 1993).

Not only are there negative impacts on the habitats and ecosystems due to AIS, they can also impact the economy through real estate. Certain invasive species reduce the water quality resulting in the decrease of property values in surrounding waters. When Eurasian watermilfoil began to spread to inland lakes, there was an average of a 13% decrease in land values in the invaded lakes (Horsch & Lewis, 2009). Eurasian watermilfoil forms thick layers of plants on the surface of the water limiting recreational uses of the lake.

Previous examples have given evidence to the causes of enhancement and prevalence of algal blooms (Knoll, et al., 2008). A combination of nutrient loading and invasive species, such as zebra mussels and *Bythotrephes*, which feed on algae-grazing zooplankton, lead to an increased amount of algal blooms (De Stasio, Beranek, & Schrimpf, 2018; Vanderploeg H. A., et

al., 2011; Walsh, Lathrop, & Zanden, 2017). Declining populations of native zooplankton that graze on algae allows for the algae populations to skyrocket. For example, the Great Lakes have had multiple outbreaks of the blue-green algae *Microcystis*, which is a cyanobacterium that produces neurotoxins, affect the nervous system, and hepatotoxins, affect the liver. *Microcystis* thrives because it is a light-tolerant algae that in turn outcompetes other algae by monopolizing the light in the photic zone. *Microcystis* produces a toxin called microcystin which gets released into the water when the cell wall breaks down during decomposition. It is difficult to monitor this toxin because it is odorless and clear. Microcystin is harmful to humans and has demonstrated involvement in developing primary liver tumors (Zegura, Sedmak, & Filipic, 2003). Ingestion or dermal contact with this toxin can cause skin rashes, asthma, pneumonia, vomiting and other gastrointestinal symptoms, hay fever, ear and eye irritation, severe headaches, vertigo, blistering in the mouth, among other symptoms (Drobac, et al., 2013).

Severe cyanobacterial blooms can also lead to closure of large water treatment plants due to high levels of toxins in the water that may still be present even after it has been treated. The acceptable level of these toxins in drinking water is one part per billion. Toledo, Ohio has experienced numbers between 10-20 parts per billion in their pipes. Toledo has experienced multiple cases where the water treatment facility was forced to be shut down due to this issue. The most recent and severe case happened in August 2014. Over 400,000 people lost their water supply for three days. Toledo is just one of many cities experiencing the shut-down of their water supply because of algal blooms. There are also indirect ways of ingesting these harmful toxins like microcystin. Bioaccumulation of the toxin is present in the fish making the fish dangerous to consume (Freitas de Magalhaes, Soares, & Azevedo, 2001). A high level of toxins in the fish results in lower food quality and less consumption by humans. Algal blooms also are harmful to

many fish not only because of bioaccumulation of toxins but because during the death of the algae cells, bacterial decomposition of the cells require oxygen to function, depleting the water of its oxygen supply, depriving the fish of their available oxygen. This suffocates the fish and limits them to areas with sufficient oxygen levels. A decrease in fish populations negatively affects the economic benefits of the Great Lakes.

Some transportation capabilities in the United States have been lost because of invasive species. For example, in the Fox River boaters have lost the ability to travel from Green Bay to Lake Winnebago using the river as their route. There is a total of seventeen locks between the two bodies of water containing a central lock that acts as an invasive barrier preventing secondary dispersal to smaller inland lakes throughout Wisconsin and their neighboring states. Passing through all seventeen of these locks at once has been prohibited for the last few decades because of invasive species.

These invasive species got here by what was thought to be one of the greatest engineering projects: the St. Lawrence Seaway. This series of locks, canals and channels has turned out to be more detrimental to the Great Lakes than anything else. It was created to allow for easier transportation to the Midwestern cities of the United States (Egan, 2017). Introductions of invasive species through international shipping ballast water has resulted in 24 species taking home to the Great Lakes since 1959 (Christopher Costello & Lodge, 2007). Cargo ships require large amounts of water to be stored in their ballast tanks to allow for safer travels when cargo is not being carried on the ship. When these large cargo ships return, they must release the water from the ballast tank to allow for the cargo to be loaded without sinking the ship. However, they aren't just releasing the water but also the organisms inhabiting the water. These organisms are either alive or in their dormant stages which can withstand extreme conditions. It is important to

keep these lakes free from invasive species to prevent the loss of habitat, species diversity and money. Multiple solutions are possible to avoid invasive species. The first step is closing the St. Lawrence Seaway. Building a barrier prevents shipping vessels from releasing their ballast water into the lakes. Vessels would then unload their cargo onto the land, bringing it around the barrier to a Laker. This is a ship that stays only on the Great Lakes and does not travel anywhere else. Having Lakers eliminates the transfer of invasive species through ballast water.

### *Ecological Questions*

Invasive species often alter the ecosystems by changing the abundances and types of species that flourish in the water. By 1988, the spiny water flea *Bythotrephes longimanus* was introduced to Lake Michigan and has been changing the ecosystem ever since. In the near shore habitat of southern Green Bay, there is a negative correlation between the invasive zooplankter *Bythotrephes longimanus* and the native zooplankter *Leptodora kindtii*. However, *Bythotrephes* population abundances in Green Bay alternate from high to low densities among years. In years when *Bythotrephes* is abundant, *Leptodora* exhibits low densities. I will be studying whether *Bythotrephes* are directly affecting the population dynamics of *Leptodora* and if *Bythotrephes* are physically capable of feeding on *Leptodora*. I will also be looking at how *Bythotrephes* are affecting the population dynamics of herbivorous zooplankton in Green Bay, Lake Michigan. In addition to investigating the relationship between *Bythotrephes* and *Leptodora*, my results will shed a light on the role of food limitation as a possible driving factor of this pattern of *Bythotrephes* population dynamics across years.

### *Importance of the Great Lakes*

The Great Lakes is a series of five interconnected lakes that are located within the upper mid-east region of North America and the southern region of Canada. These lakes are known as Lake Superior, Michigan, Huron, Erie and Ontario. They formed approximately 10,000 years ago at the end of the last glacial period. They are the largest group of freshwater lakes and contain 20 percent of all accessible freshwater in the world. Ice sheets carved basins, allowing for the melted water to fill the basins as the ice sheets retreated. Water flows from Lake Superior into Lake Huron and Lake Michigan, which are technically one lake because the straits keep their water levels in near-equilibrium and water can flow either direction depending on current conditions. The water then exits through the south end of Lake Huron into Lake Erie, down Niagara Falls, into Lake Ontario and out the St. Lawrence Seaway to the Atlantic Ocean.

The Great Lakes provide food for many Americans and Canadians. According to the National Oceanic Atmospheric Administration (NOAA), the total number of fish harvested from the Great Lakes in 2016 was approximately 8 million pounds of fish, resulting in over \$16.5 million in revenue. This number has fluctuated over the years because of invasive species and overfishing altering the population abundances of native fish. The Great Lakes are home to an estimated 150 native fish species. The commercial, recreational and tribal fisheries of the Great Lakes are collectively valued at \$7 billion annually. Water from the Great Lakes is used for agricultural production giving the United States 7% of our agricultural water and Canada with 25% of their agricultural water.

Transportation is a major factor when thinking about the importance of the Great Lakes. The St. Lawrence Seaway connects the Great Lakes to the Atlantic Ocean. This man-made seaway is comprised of locks, canals and channels that allow oceangoing vessels to travel from the Atlantic Ocean to the Great Lakes region. Creating this seaway for easier access to Midwestern cities allowed for increased trade from European countries. Increasing trade meant more cargo ships releasing invasive organisms into the water. It opened in 1959 and contributed to the industrial and agricultural boom of Chicago, Milwaukee, Toronto, Toledo, Cleveland, and Detroit (Saint Lawrence Seaway, 2019).

Clean drinking water is arguably the most important aspect the Great Lakes contributes to society. Water is essential for life. There are many controversies when it comes to who has access to water. Ethically, everyone should have access to clean water but more than 800 million people worldwide do not. However, no one wants to give up their own source of water resulting in millions of people not getting a clean source of drinking water. This is important because the Great Lakes supply one-fifth of the world's water supply. Depletion and pollution have substantial impacts on the areas around the Great Lakes. Access to a vast amount of fresh water is a privilege and should be managed carefully.

### *Green Bay, Lake Michigan*

Lake Michigan is the only Great Lake that is entirely located within the United States. It is joined with Lake Huron through the Straits of Mackinac. Green Bay is the largest embayment in Lake Michigan and results in easy access for secondary dispersal of invasive species inland

because of the Fox River. The Fox River flows north into Green Bay at the southernmost point of the bay. Secondary dispersal of multiple invasive species is being stopped at a lock located in Wrightstown, Wisconsin. If the invasive species can get past this lock, the population dynamics in many lakes, streams and rivers will be changed. Lake Winnebago is a large, shallow freshwater lake in Wisconsin and is a key dispersal point for invasive species. Changing this lake's ecosystem will largely impact the ecosystem and the communities that depend on it for ecosystem services.

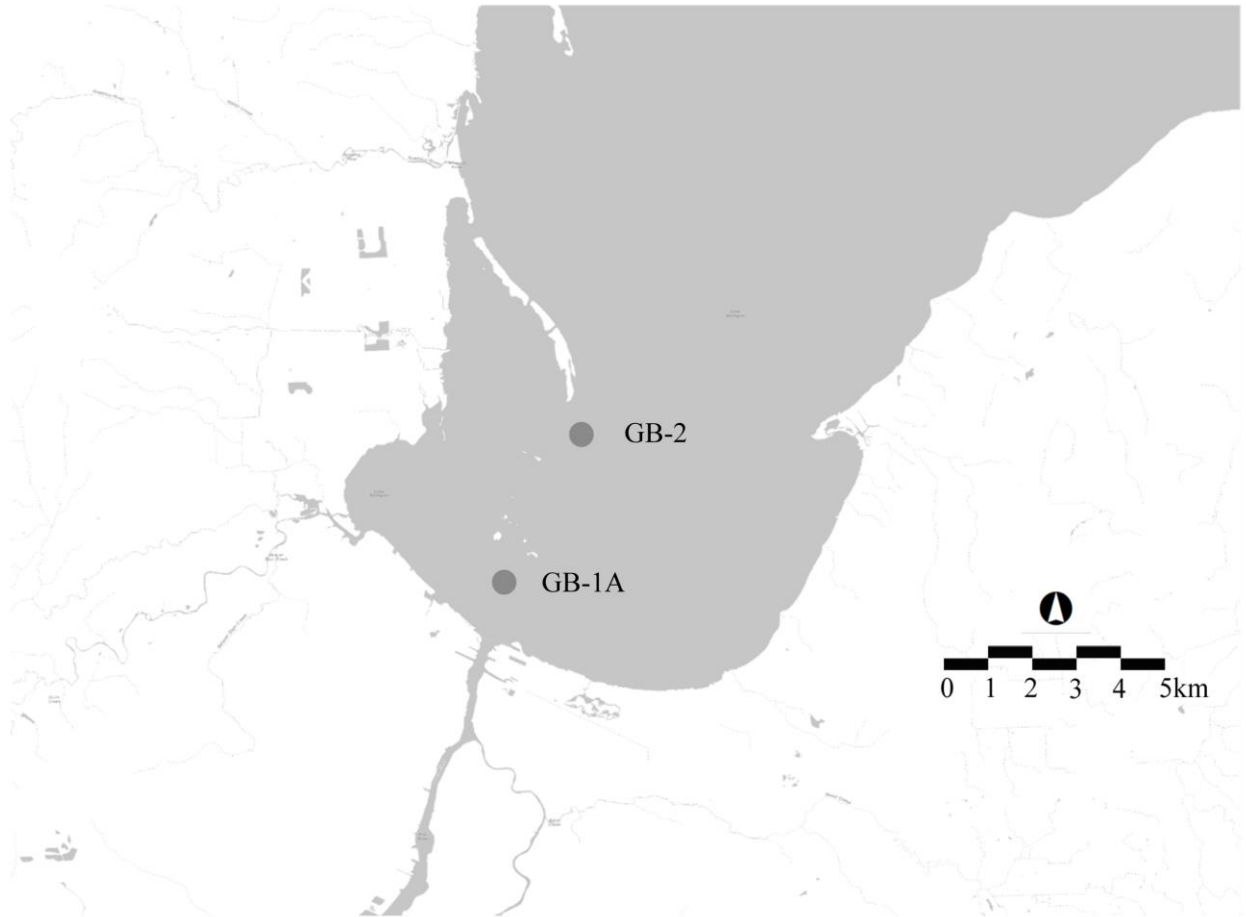
Green Bay, Lake Michigan is a highly polluted body of water. In the 20<sup>th</sup> century, paper mills became extremely popular along the Fox River. Prior to the Clean Water Act of 1972, it was legal to dump hazardous materials into the water so these paper mills took advantage of that. In the 1950's and 60's, the paper mills began using polychlorinated biphenyl (PCB) in their processes. PCB's don't degrade naturally over time and were beginning to cause problems to organisms that use the river. PCB's are dangerous because they are carcinogenic, and can cause developmental issues that negatively affect the immune system. It is recommended for pregnant women to not eat fish and for others to limit their fish intake because of the bioaccumulation of PCB's in the fish. Efforts were taken to rid the river of contaminated sediments, poor water quality and lost habitat. In 2009, a major remediation project was begun as part of the EPA Superfund, including dredging the Fox River and southern Green Bay to remove PCB contaminated sediment. Dredging involves the removal of sediments from the riverbed and brought elsewhere for safe storage. Capping, which is the process of putting sand or gravel on the riverbed to cover up the PCB's was also a method that was used in the Lower Fox River. Neither of these processes can fully rid the PCB's but they can substantially decrease the

amounts in the water. However, these PCB's are not being removed from the environment entirely, only from the aquatic one.

Southern Green Bay is a eutrophic body of water located at the mouth of the Fox River. Multiple factors contribute to the eutrophication of the water. The first is depth. The southern part of the bay at the mouth of the river is approximately 2-3m deep. Shallow depths mean wind can easily mix the water from top to bottom, thoroughly moving nutrients through the entire water column. The second is being located at the mouth of a river that is responsible for releasing loads of nutrients such as nitrogen and phosphorus into the bay. It is also a place where runoff collects and leads to nutrient loading from cultural eutrophication, the process that speeds up natural eutrophication because of human activity. Phosphorus is the limiting factor contributing to eutrophication in lakes because it cannot be found in its elemental form naturally. Blue-green algae, or cyanobacteria, can exploit nitrogen from the atmosphere but depend on an outside source for their phosphorus needs (Pote, et al., 1996). Eutrophication is inevitable in a lake when it has both shallow depths, minimal stratification and excessive nutrient loading.

Both sites in my research were in southern Green Bay. Figure 1 shows both GB1A and GB2 in southern Green Bay. GB1A is located at the mouth of the river, and GB2 is located approximately 2 miles further from the river, near Long Tail Point. The further north you go in the bay, the deeper and less polluted it gets partly because it is not being completely mixed and is diluting the nutrient loading while flowing upward towards Lake Michigan. GB2 has been shown to have more biodiversity and abundances in individual species (De Stasio, Beranek, & Schrimpf, 2018).





**Figure 1.** Map of sampling sites GB1A and GB2 in southern Green Bay (Merkle & De Stasio, Bythotrephes longimanus in shallow, nearshore waters: Interactions with Leptodora kindtii, impacts on zooplankton, and implications for secondary dispersal from southern Green Bay, Lake Michigan, 2018).

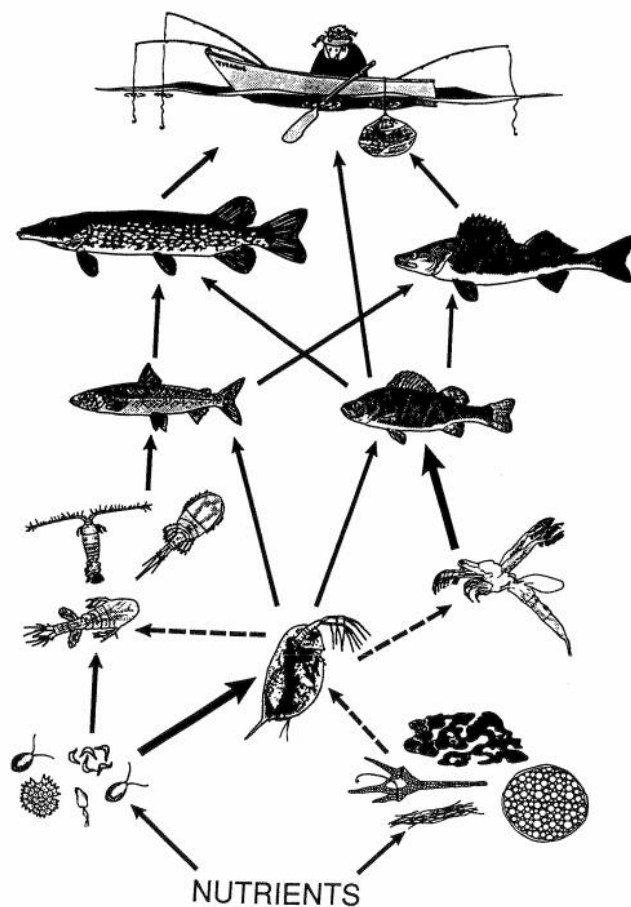
### *Invertebrate Predation in Green Bay*

Green Bay, Lake Michigan has been exposed to many challenges over the years including nutrient loading, climate change and biological invasions. Depending on the type of challenge it can have a top-down or bottom-up effect on the food web (De Stasio, Beranek, & Schrimpf,

2018). Nutrient loading leads to cultural eutrophication in the Great Lakes. The number of phytoplankton present in the water influences the abundance of zooplankton. A study comparing oligotrophic Lake Superior to eutrophic Lake Erie showed almost 9 times more crustaceans in the eutrophic Lake Erie and was related to both the temperature and chlorophyll content of the water (Patalas, 2011). This initiated a bottom-up control on the food web. Green Bay is similar to Lake Erie in that it is a eutrophic body of water. Efforts have been made to decrease the amount of phosphorus in the bay to reduce the growth of phytoplankton in the water (Qualls, Harris, & Harris, 2013). After reducing phosphorus input and the invasive introduction of the zebra mussels in Green Bay, productivity levels did not decrease as they did in other Great Lake regions, making Green Bay a unique body of water (Padilla, Adolph, Cottingham, & Schneider, 1996).

The invasive zebra mussel, *Dreissena polymorpha*, is an aquatic invertebrate that feeds on phytoplankton and has been associated with increased algal blooms of cyanobacteria (De Stasio, Beranek, & Schrimpf, 2018). In this study conducted between the years of 2000-2007, the data show that approximately 40 percent of the phytoplankton biomass was harmful cyanobacteria. Zebra mussels allow for increased light penetration which contributes to why these light-tolerant cyanobacteria can flourish (Fishman, Adlerstein, Vanderploeg, Fahnenstiel, & Scavia, 2010). Many of the zooplankton in Green Bay are algae grazers resulting in a competition with the zebra mussels. A study done in Saginaw Bay showed a decrease in the overall zooplankton biomass which was attributed to lower food availability and direct competition between the zebra mussels and zooplankton (Adlerstein, Nalepa, Vanderploeg, & Fahnenstiel, 2012).

Primary consumers are essential in the Green Bay food web. Figure 2 shows a simplified food web similar to the one found in Green Bay (Kitchell, 1992). Zooplankton are the energy transferring level between the phytoplankton and fish. Changes in these population abundances contribute to changes in vertebrate populations (Mills, Green, & Schiavone, 1987). Predatory Cladocerans such as *Bythotrephes* and *Leptodora* are important because they can control herbivorous zooplankton populations and are a source of energy for small fish which in return become prey for the larger fish.



**Figure 2.** A simplified food web diagram of interactions in Lake Mendota, Wisconsin. *Bythotrephes longimanus* is not present in this food web but can be in a similar spot as *Leptodora kindtii* (Kitchell, 1992)

### *Bythotrephes longimanus*

*Bythotrephes longimanus*, also known as the spiny water flea, is a predatory, planktonic crustacean that is typically 15 millimeters long. It is native to Northern Europe and Asia and often inhabits large, deep, temperate lakes, but have also been reported inhabiting shallow productive lakes (Grigorovich, Pashkova, Gromova, & Van Overdijk, 1998). *Bythotrephes* prefer water temperatures in the range of 10-24 °C. Anything below 4 °C or above 30 °C is considered harmful for the animal. It is theorized that they were introduced to the Great Lakes through shipping ballast water in the mid 1980's. *Bythotrephes* has an elongated tail contributing to approximately 70% of its total body length. A longer tail is an evolutionary response to reduce high levels of predation. It also aids in both the stabilization of forward motion and steering (Ketelaars & Gille, 1994). The number of spines determines the stage of the animal. Juveniles only have one spine whereas adults have three to four spines. Interestingly, in Green Bay the *Bythotrephes* only contain three spines in the adult stage, and some individuals with 2 spines do carry embryos. The animal has a large compound eye and a single pair of antennae used for swimming (Figure 3). Four total pairs of legs are attached to the body of the animal. The first pair is specialized for catching and manipulating prey. *Bythotrephes* is a predatory zooplankton feeding primarily on small-bodied cladoceran species such as *Ceriodaphnia*, *Eubosmina*, *Bosmina*, *Daphnia retrocurva*, *Daphnia pulicaria* and *Chydorus* (Vanderploeg, Liebig, & Omair, 1993). They tend to eat their prey by shredding it. A study done by Kim and Yan found that *Bythotrephes* consumed between 9-22 prey per day (Kim & Yan, 2013).

Where waters are deep, *Bythotrephes* express diel vertical migration (DVM). Vertical migration is the change of position in the water column depending on the time of day. They inhabit the deeper areas of water during the day to escape predation from fish. During the night, they move up in the water column to feed on zooplankton. In the nearshore habitat of Green Bay, *Bythotrephes* do not exhibit this pattern of vertical migration mainly because the water is too shallow. Although they can't exhibit this pattern in southern Green Bay, being in shallow waters allows for more interactions with prey due to limited space giving them the advantage when feeding.

The average lifespan of *Bythotrephes* is 12 days. They can reproduce both sexually and asexually. Sexual reproduction is used to produce diapausing, or resting, eggs while asexual reproduction produces offspring that are hatched and disperse that same summer. These resting eggs can stay in dormancy for up to 17 months and can withstand harsh conditions, for example extreme temperatures and lack of water for weeks at a time (Kim & Yan, 2013). Most resting eggs hatch after one winter and have an internal temperature cue close to 4 °C (Yurista, 1997). Along with a longer tail as an evolutionary adaptation to high predatory stresses, females can shift egg production from producing many small eggs to a few large eggs thus producing larger offspring (Straile & Halbach, 2000). This evolutionary adaptation allows for more energy going into fewer offspring resulting in a higher survival rate.



**Figure 3.** Photo of body of mature female of *Bythotrephes longimanus* (Liebig, Benson, Larson, Makled, & Fusaro, 2013).

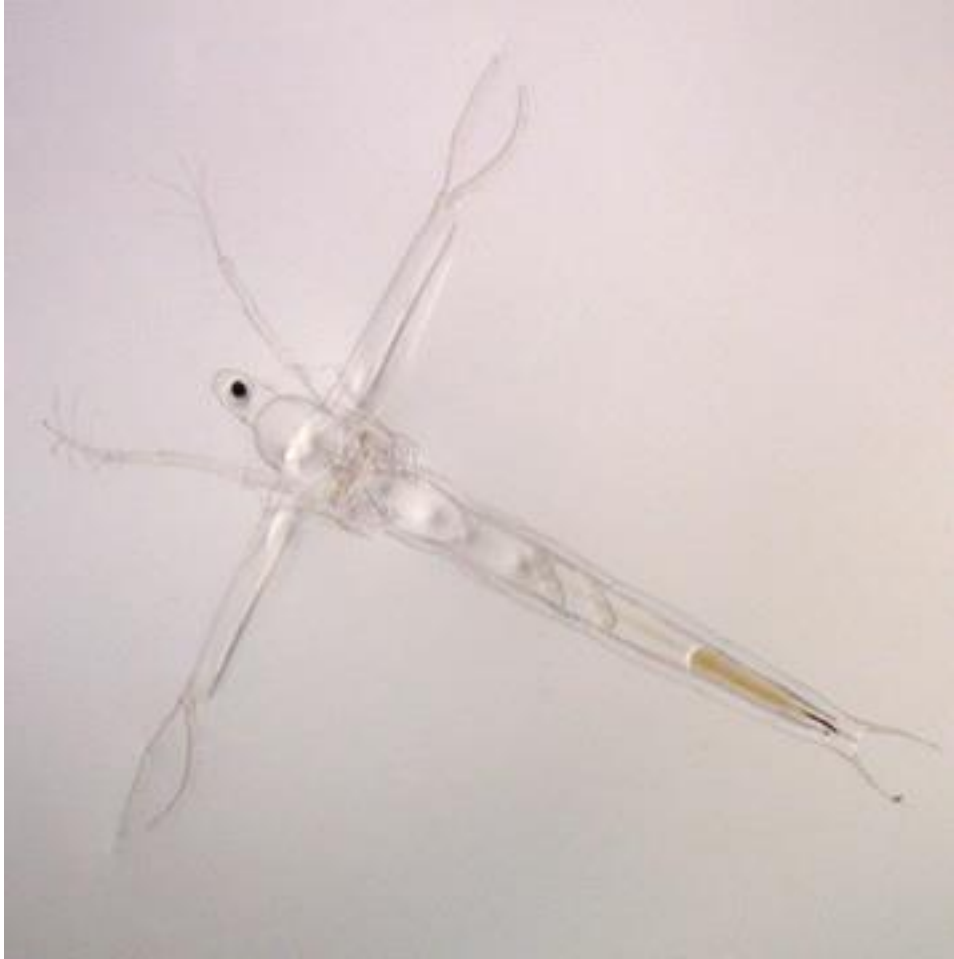
### *Leptodora kindtii*

*Leptodora kindtii* is a predatory water flea that is native to the Great Lakes in North America. On average, they grow up to 12 mm long. However, in southern Green Bay their body length averages approximately 5 mm. This smaller size potentially is due to the introduction of the invasive zooplankter *Bythotrephes*. *Leptodora* has a single compound eye and two large antennae that are used for swimming (Figure 4). On their thorax, they have six pairs of legs that are used for capturing prey that they encounter by chance (Branstrator, 2005). This is known as the ‘trap basket’. The body of *Leptodora* is 98% transparent which is a defense mechanism to avoid being eaten by fish. *Leptodora* is a key species for transferring energy through the food web because they are a primary food source for small fish.

The *Leptodora* diet is composed of multiple cladoceran species, but have also been known to consume copepods and rotifers (Herzig, 1995). The animal maneuvers the prey to have

the bivalve carapace facing the trap basket allowing for excavation of the tissues from inside the bivalve carapace (Branstrator D. K., 2005). They depend on mechanoreceptors and chance encounters to catch their prey because they do not actively search for food (Browman, Kruse, & O'Brien, 1989).

*Leptodora kindtii* reproduce both sexually and asexually and produce eggs in their brood pouch by parthenogenesis every 12 hours. There are six stages that the larvae must complete before reaching adulthood. Each stage is dependent on temperature. This typically takes three to six days to complete. The first larval stage, known as nauplii larvae, is different than most other cladocera. The pathogenic eggs from *Leptodora* hatch inside the brood pouch allowing for development and growth while still in the brood pouch. The nauplii hatched from resting eggs occur free living in the plankton giving them a disadvantage (Haney, 2013). Hatching inside the brood pouch allows the offspring to avoid exposure to the harsh conditions of the environment at the most vulnerable stage of their life.



**Figure 4.** Photograph of the body of *Leptodora kindtii* (Haney, 2013).

#### *Effects of Bythotrephes on freshwater ecosystems*

The introduction of *Bythotrephes* into the Great Lakes has negatively impacted the native zooplankton populations. Native populations not only decreased in abundance but there has also been a decline in species richness (Barbiero & Tuchman, 2004). In Harp Lake, Ontario, the average number of species detected was 9.92 species and had declined by 18% to 8 species within 6 years of *Bythotrephes* being introduced (Yan, et al., 2001). Along with a decline of



species richness, a decline in the abundances of smaller zooplankton was also exhibited in Harp Lake. The mean individual body length of the spiny water flea doubled from 0.43 mm before the invasion to 0.85 mm after the invasion. Yan et al (2001) concluded that it was the result of changes in the relative abundances of different zooplankton species in the lake.

Not only does *Bythotrephes* affect the populations of smaller zooplankton, they also affect the larger, predatory water fleas such as *Leptodora kindtii*. *Leptodora* are known to feed on similar zooplankton as *Bythotrephes*. *Bythotrephes* also compete with *Leptodora* for food and may feed on juvenile *Leptodora*, which affects their population abundances. Shallower habitats, like southern Green Bay, allows for more intense interactions between the two species. Smaller fish in Green Bay have adopted *Bythotrephes* as another source of food. However, the smallest larval fish are not able to prey upon them because of the elongated tails and the spines they possess. This, in turn, negatively affects the fish populations because the larval stages directly compete with *Bythotrephes* for prey and are not able to make this animal a viable source of energy.

## **Material and Methods**

### *Field Sites and Sampling Techniques*

Samples were collected at two sites established by previous research programs in southern Green Bay, Lake Michigan (Figure 1). GB-1A is located at N 44° 32.95', W 87° 59.89' with a depth of 1.5 meters near the mouth of the Fox River. GB2 is located at N 44° 34.82', W

87° 58.73' with a depth of 3 meters (Merkle & DeStasio, *Bythotrephes longimanus* in shallow, near shore waters: Interactions with *Leptodora kindtii*, impacts on zooplankton, and implications for secondary dispersal from southern Green Bay, 2018). GB2 is located near the tip of Long Tail Point. Both sampling sites are well-mixed due to shallow depths and mixing between the riverine inflow and the bay (Klump & LaBuhn, 2014). Sampling dates occurred biweekly from early June to late September in both 2017 and 2018.

A Clarke-Bumpus metered net sampler (0.13 m diameter and 250 micrometer mesh) was used to perform two sets of oblique tows at each site. These samples were used to calculate the overall zooplankton population at each location. An additional set of duplicate oblique tows using a regular Wisconsin type plankton net with attached flow meter (0.5 m diameter, 2.0 m length, 250 micrometer mesh) was used for the collection of *Bythotrephes longimanus* and *Leptodora kindtii* for abundance and size comparisons. The net was towed at 2 mph for either 1 or 3 minutes depending on the abundance of zooplankton and phytoplankton in the water. Samples were stored on ice to slow down metabolic processes and predation activities until returned to the laboratory for preservation.

Along with plankton tows, the surface temperature, air temperature and water clarity (i.e. Secchi depth) were recorded at each location. Temperatures used for data analysis were collected through a buoy stationed near GB1A (<http://seatemperature.info/green-bay-water-temperature.html>; accessed on 8 February 2019) Temperatures for the Spearman's rank test were averaged one week prior to the collection of zooplankton samples. Secchi depth was determined with a standard Secchi disk (20 cm in diameter) with alternating black and white quadrants. It is lowered into the water until it is no longer seen by the observer. Chlorophyll samples were also

taken from the surface at each site and transported in opaque containers to inhibit the effects of light on photopigments.

### *Laboratory*

Samples were transported to the laboratory within 3 hours of collection and were preserved for counting. Samples were filtered with a plankton sieve (63 micrometer mesh) to reduce volume in storage containers. Denatured alcohol was added to achieve at least 70% alcohol concentration for thorough preservation. Water used for Chlorophyll analysis was vacuum filtered through GFC filters until filters became clogged and had a noticeable color (at least 0.25 – 1.0 L). Filter paper was removed from the funnel and homogenized by grinding in 90% acetone using a mortar and pestle. Homogenates were centrifuged for 15 minutes at 1,500 rotations per minute. Immediately after centrifuging, total amount of acetone added was determined. Optical density of homogenates was determined using spectrophotometer (Spectronic 20. Bausch & Lomb Corp.) Measurements were taken at the wavelengths for chlorophyll a pigments and correcting for background turbidity (663nm and 750nm).

### *Counting procedures*

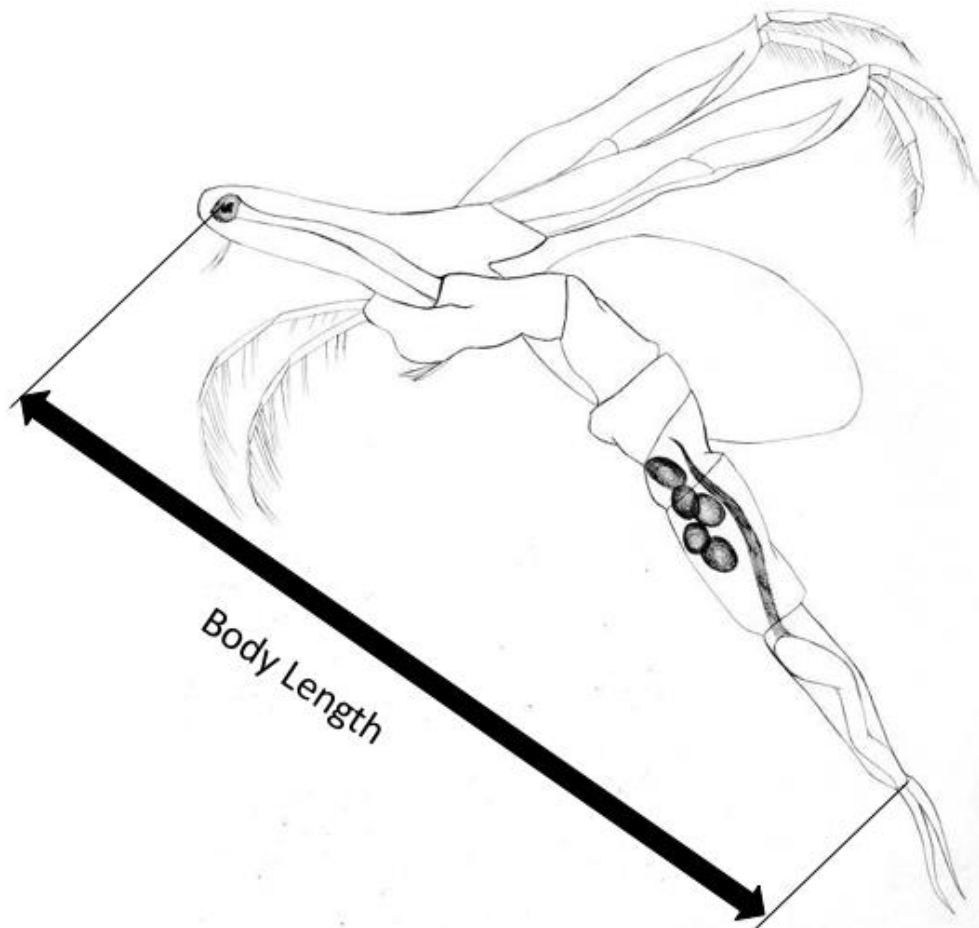
Zooplankton samples were rinsed through a mesh cup (63 micrometer mesh) to remove preservative and then diluted to obtain densities appropriate for counting. Extremely dense samples required the use of a plankton splitter resulting in half of the sample being counted. Once the sample was filtered and diluted, subsamples between 7-10 mL were taken using a P-

10000 pipette and placed into a ward zooplankton counting tray. Four subsamples from each sample were typically measured to increase accuracy of sample counts. Subsample size depended on the density of algae and zooplankton in the sample. When population abundances were low, 7-8 subsamples were counted for a better representation of the overall population. Zooplankton were counted using a dissecting microscope at 10X-50X, making it easier to identify the zooplankton. All zooplankton were identified to the species level, or the lowest taxonomic unit using Balcer et al. (Balcer, Korda, & Dodson, 1984).

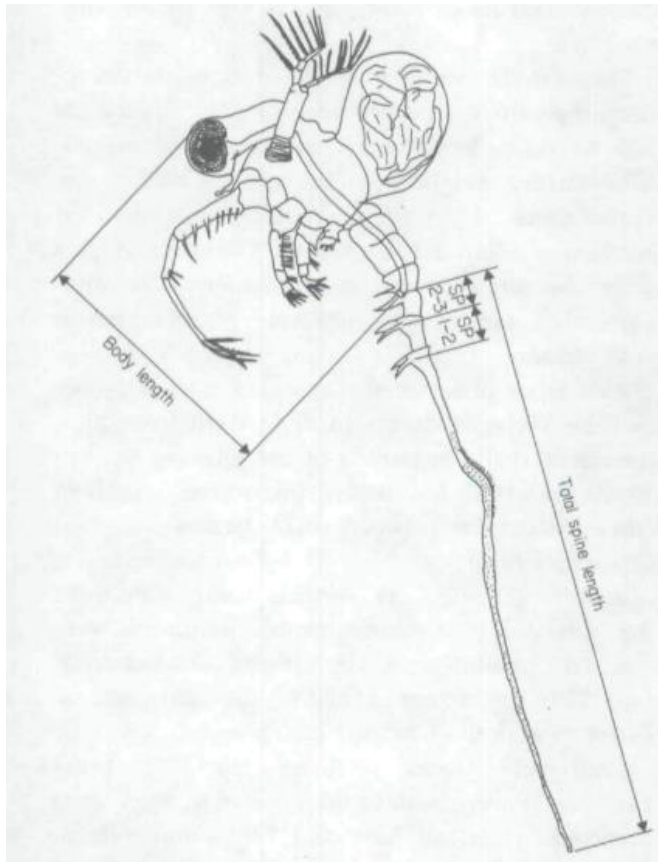
Size measurements of *Bythotrephes* and *Leptodora* were determined from preserved samples in December 2018. Specimens from samples at both locations were chosen haphazardly for size measurements of *Bythotrephes* and *Leptodora*. Preservative was removed in the same manner as for counting samples.

Approximately 20mL of water was examined until either thirty individuals from each stage were counted or the sample was finished. *Bythotrephes* were divided into three groups determined by their life stage. Each stage is correlated with the number of spines located on the tail described in the introduction. Individuals were placed in a petri dish for photodocumentation. A grid with known measurements was placed beneath the petri dish to provide a measurement scale for each image. Images were examined with Image J software (version: 2.0.0-rc-65/1.52b) to calculate the total length(mm) of the individual. *Leptodora* measurements included the entire body length from the center of the compound eye to the caudal stylet (Figure 5). *Bythotrephes* were divided into two measurements (Figure 6). Core body length was measured from the top of the compound eye to the anus. The second measurement was tail length, determined from the anus to the tip of the tail spine, as measured in a previous study done by Burkhardt et al

(Burkhardt, 1994). No correction efforts were taken on the specimens for shrinkage from preservation.



**Figure 5.** Measurements of the body length of *Leptodora kindtii* (LaMay, Hayes-Pontius, Ater, & Mihuc, 2013).



**Figure 6.** Measurements of body length and tail length parameters of *Bythotrephes* (Burkhardt, 1994).

### *Calculating Biomass/ Equations*

Data were entered into Excel spreadsheets for conversions and calculations. Since we subsampled we had to determine the whole population size in each sample. We dividing the dilution volume (in mL) by the volume of the subsample counted (mL). Most subsamples ranged from 5-10mL for each replicate. We then multiplied this number by the total number of zooplankton counted for each species in each replicate (Equation 1). This gives us the total number of zooplankton for the whole sample. By dividing this number by the total volume of

water collected in each net tow (L) we can estimate the zooplankton density (number of animals per liter; Equation 2).

$$(1) \text{ animals/sample} = (\text{Dilution volume / subsample volume}) * \text{Zooplankton Counted}$$

$$(2) \text{ Zooplankton Density (animals/Liter)} = (\text{animals/sample}) / \text{Total Tow Volume(L)}$$

The number of animals per liter can be used to calculate the total biomass of each zooplankton species. Estimates of dry weight for each zooplankton group were calculated in previous studies and used to estimate zooplankton biomass density (Table 1). By multiplying the number of animals per liter by their individual dry weight we determined their total biomass in micrograms per meters cubed ( $\text{mg/m}^3$ ) (Equation 3).

$$(3) \text{ Zooplankton Biomass} = (\text{Number of Animals per Liter} * \text{Individual Dry Weight})$$

Once individual biomasses were calculated, the replicates were averaged together to determine the number of animals at each site (GB1A and GB2). Site averages were then combined to obtain mean densities for the inner bay region on each date.

Zooplankton samples from the last two dates in August 2017 were collected by a 2m conical net, not the Clarke-Bumpus metered net sampler. The difference in tow volume was corrected by dividing the number of animals per liter by 3. The procedure for correction was taken from Merkle and De Stasio (Merkle & De Stasio, 2018).

**Table 1.** Individual dry weights of predatory and herbivorous zooplankton in southern Green Bay (Richman, Bailiff, Mackey, & Bolgrien, 1984).

Species	Individual Dry Weight (ug)
Calanoid Adult	6.13
<i>Acanthocyclops/ Diacyclops</i>	24.02
<i>Mesocyclops</i>	24.02
Cyclopoid Copepodites	3.08
<i>Alona</i>	5.14
<i>Bosmina longirostris</i>	11.41
<i>Eubosmina coregoni</i>	11.21
<i>Ceriodaphnia</i>	11.46
<i>Chydorus</i>	7.08
<i>D. g. Mendotae</i>	9.98
<i>D. longiermis</i>	78.6
<i>D. pulicaria</i>	154.01
<i>D. retrocurva</i>	33.32
<i>D. schodleri</i>	33.38
<i>Leptodora</i>	84.56
Stage 1 <i>Bythotrephes</i>	63
Stage 2 <i>Bythotrephes</i>	254



Stage 3 <i>Bythotrephes</i>	496
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### *Statistical Analysis*

We did not test for normality within the data instead we used nonparametric tests (Kruskal-Wallis test and Spearman's rank correlation). Statistical analysis were run using PAST (Paleontological Statistics Package, version 3.23; (Hammer & Harper, 2001).) Biomass data were calculated using Microsoft Excel (Version 15.30 (170107)).

## **Results**

### Population Dynamics

*Bythotrephes* - Patterns of biomass change for *Bythotrephes* were similar in the two years examined, but biomass in 2017 was generally higher than in 2018 (Figures 7 & 8). There was a slight increase in biomass each year during two periods throughout summer. The biomass of female *Bythotrephes* in 2017 exhibited two distinct increases in abundance. The first was in mid-June where biomass rose to nearly 20 mg/m<sup>3</sup>. The second was from early to mid-August where biomass approached 13 mg/m<sup>3</sup>. The biomass of juvenile *Bythotrephes* also increased close to 10 mg/m<sup>3</sup> during this second peak but did not increase during the first peak of the summer. Peaks occurred for both female and juvenile *Bythotrephes* in early and late-July during 2018. Female

*Bythotrephes* biomass reached  $\sim 1.5 \text{ mg/m}^3$  in early July and  $6.5 \text{ mg/m}^3$  in late July 2018. A collapse of total biomass, close to  $0 \text{ mg/m}^3$ , in mid-July is consistent between the two years. Along with a consistent collapse of biomass, *Bythotrephes* displayed a late summer bloom in August for both years. Biomass of male *Bythotrephes* was extremely low in 2017. Only two dates were male *Bythotrephes* present in the samples and densities were less than  $0.015 \text{ mg/m}^3$ . No male *Bythotrephes* were observed during 2018; however, we can confirm there were males present in the population because we encountered female *Bythotrephes* containing resting eggs in their brood pouch. Female *Bythotrephes* are the major contributor to the population's biomass in both years whereas the juvenile and male *Bythotrephes* contribute a small portion of the total population (Figures 9 & 10).

*Leptodora* – *Leptodora* populations differed in both biomass and patterns between 2017 and 2018 (Figures 11 and 12). *Leptodora* exhibited low population abundances, less than  $1 \text{ mg/m}^3$ , from June to July in 2017 (Figure 11). Biomass increased from  $\sim 0.5 \text{ mg/m}^3$  to  $8 \text{ mg/m}^3$  in the time span of a month during July. Two weeks after its highest recorded biomass, they experienced their lowest recorded value,  $0.5 \text{ mg/m}^3$ . Abundances recovered and increased to about  $4.5 \text{ mg/m}^3$  in mid-August. An oscillating pattern of *Leptodora* biomass was present in 2018 where every two weeks there was a reciprocal change in abundance (Figure 12). Biomass began at  $0 \text{ mg/m}^3$  in early June and increased to  $4.25 \text{ mg/m}^3$  by early July. Density decreased to  $1 \text{ mg/m}^3$  in late July and rose back up to  $4 \text{ mg/m}^3$  two weeks later. Biomass then decreased to less than  $0.5 \text{ mg/m}^3$  in mid- August. The oscillation pattern continued through the last recorded dates; however, during the period of increase abundances tripled to  $13 \text{ mg/m}^3$  compared to

approximately 4 mg/m<sup>3</sup> on previous dates. Biomass of *Leptodora* decreased to 1 mg/m<sup>3</sup> by the end of September.

*Zooplankton* - The biomass of zooplankton differed between 2017 and 2018 (Figure 13 &14).

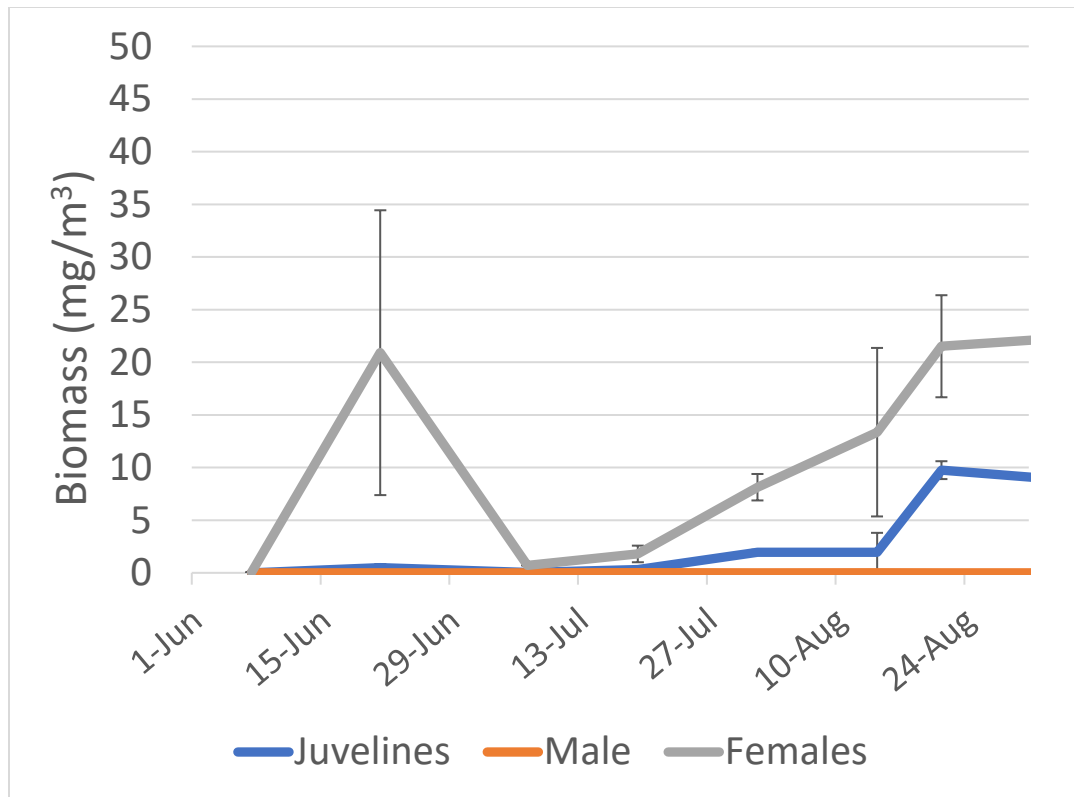
Zooplankton were divided into three major groups: calanoids, cyclopoids, and cladocerans.

Cladoceran biomass was generally higher than for the other two groups in both years. On the first sampling date in 2017 cladoceran levels at were 1762 mg/m<sup>3</sup>, while cyclopoid and calanoid levels were 175 mg/m<sup>3</sup> and 2.5 mg/m<sup>3</sup> respectively (Figure 13). Cladocerans exhibited a decline to 554 mg/m<sup>3</sup> in late-June 2017, and increased to 1212 mg/m<sup>3</sup> one month later. The later months of summer showed a steady decline in cladoceran biomass. Cyclopoid levels remained consistent throughout the summer and ranged from 150-350 mg/m<sup>3</sup>. Calanoid levels were consistently less than 12 mg/m<sup>3</sup> throughout the duration of the summer. Starting cladoceran biomass was much lower in 2018 (337 mg/m<sup>3</sup>) than in 2017 (1762 mg/m<sup>3</sup>) (Figure 14). However, there was a decline in early July similar to that in 2017, diminishing the cladoceran biomass to a mere 46 mg/m<sup>3</sup> in 2018. There were mid-July increases of all three zooplankton groups in 2018 compared to just cladocerans in 2017. High levels of cyclopoids were only recorded on the mid-July data in 2018. Cladocerans continued to increase from 744 mg/m<sup>3</sup> to 885 mg/m<sup>3</sup> over the next two weeks and cyclopoids decreased from 832 mg/m<sup>3</sup> to 307 mg/m<sup>3</sup>. By mid-August, levels for all three groups had returned to biomass values similar to early summer and remained low throughout September.

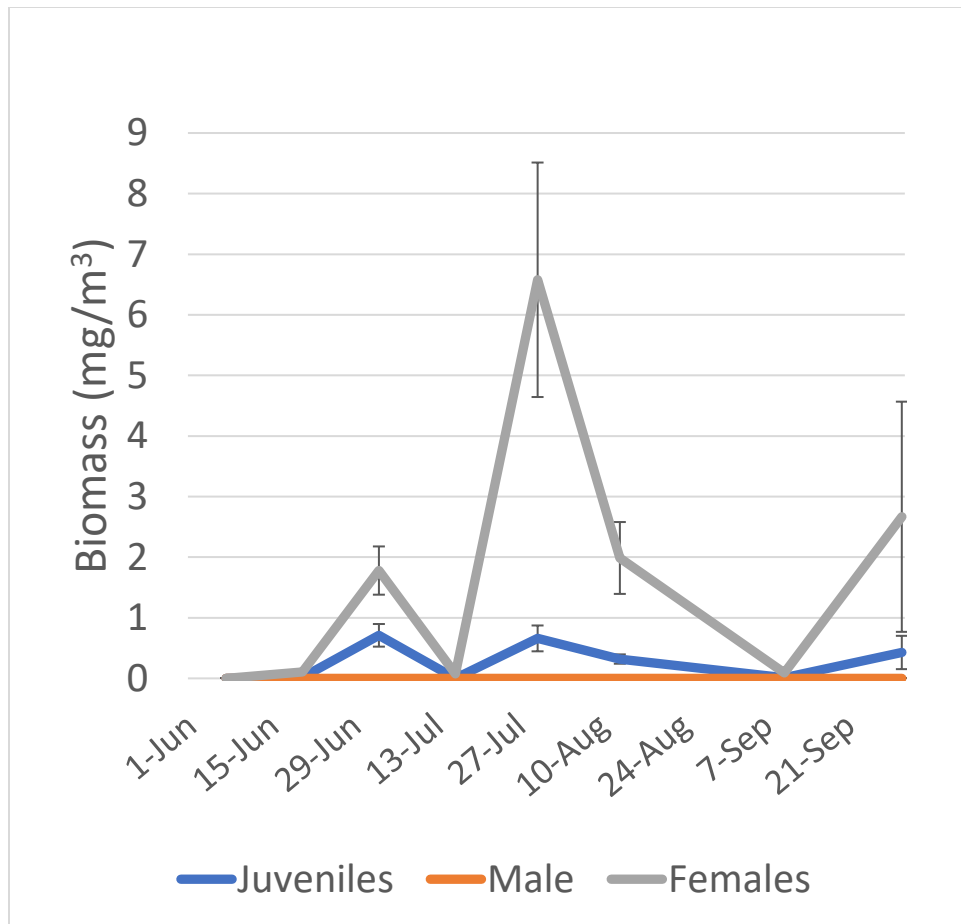
Total zooplankton biomass displayed a trend of decreasing values in late June of both years followed by an increase to peak values in late-July (Figure 15 &16). The total biomass of

zooplankton was consistent between the two years during this peak but differ in the distribution across the zooplankton groups. The majority of zooplankton biomass was due to cladocerans in 2017 compared to 2018 where the biomass was distributed more evenly between the three groups. Calanoid levels were exceedingly low in 2017, reaching a maximum of only 12 mg/m<sup>3</sup> in the middle of June. The biomass of both calanoids and cyclopoids were significantly higher in 2018 during this mid-July increase.

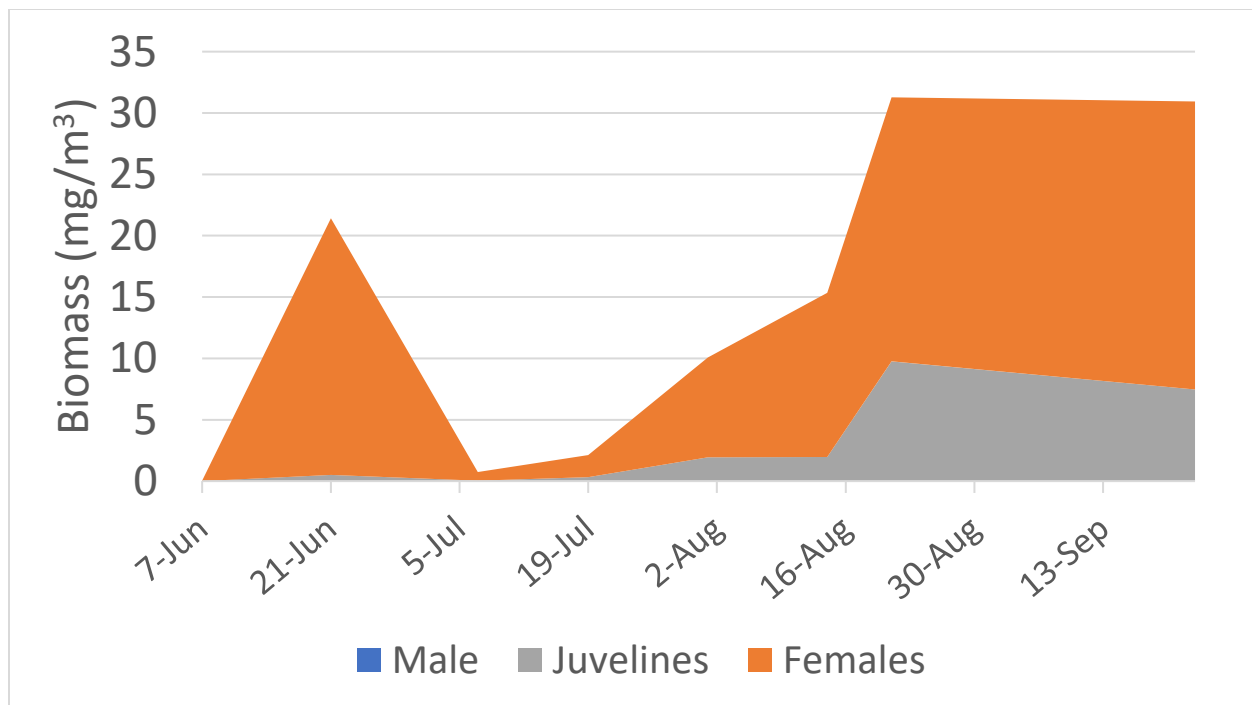
Reciprocal population dynamics were present between the biomass of *Bythotrephes* and *Leptodora* during the years 2017 (Figure 17) and 2018 (Figure 18). *Bythotrephes* were more abundant than *Leptodora* in 2017. However, the role of the dominant species switches in 2018 where *Leptodora* were more abundant than *Bythotrephes*. This data can be compared to similar results found in 2015 and 2016 by Merkle and De Stasio, 2018.



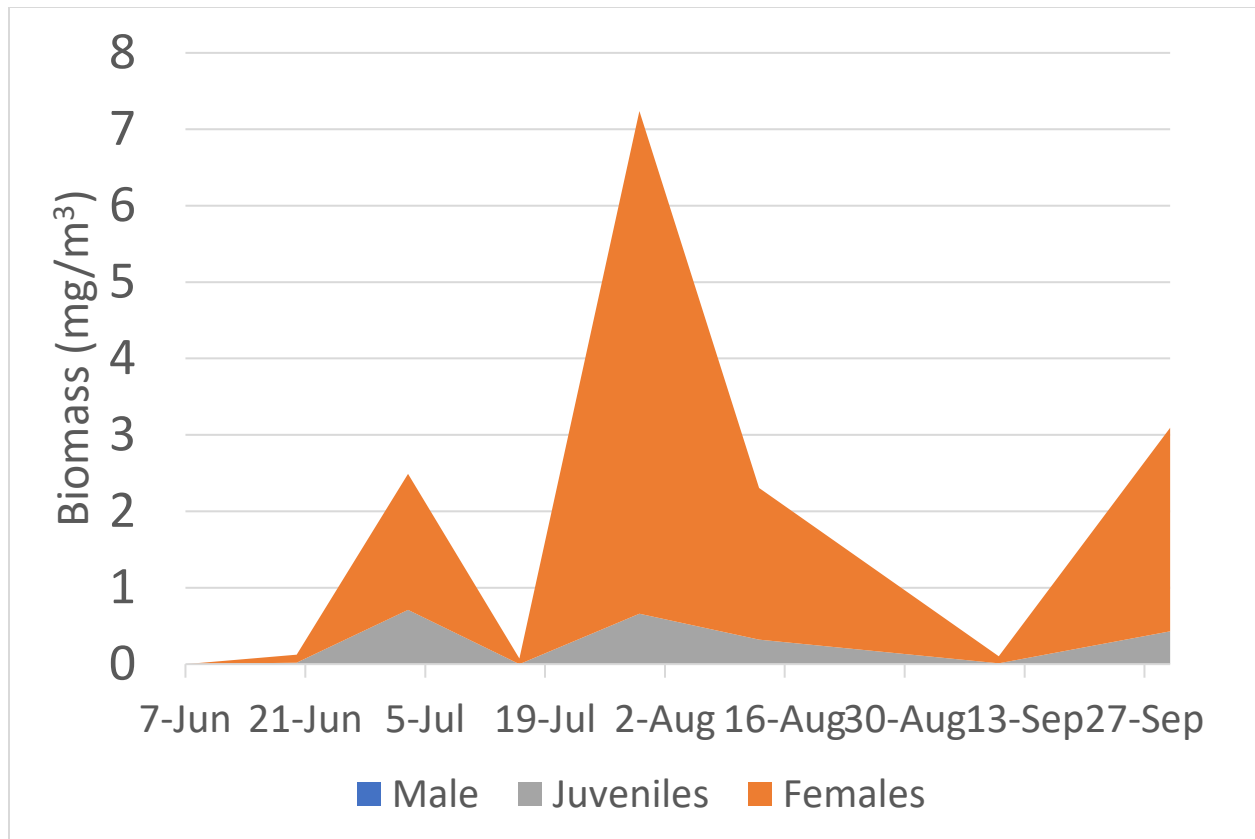
**Figure 7.** Mean biomass ( $\text{mg/m}^3 \pm 1 \text{ SE}$ ) of *Bythotrephes* at two sites in southern Green Bay in 2017.



**Figure 8.** Mean biomass ( $\text{mg/m}^3 \pm 1 \text{ SE}$ ) of *Bythotrephes* in southern Green Bay in 2018.

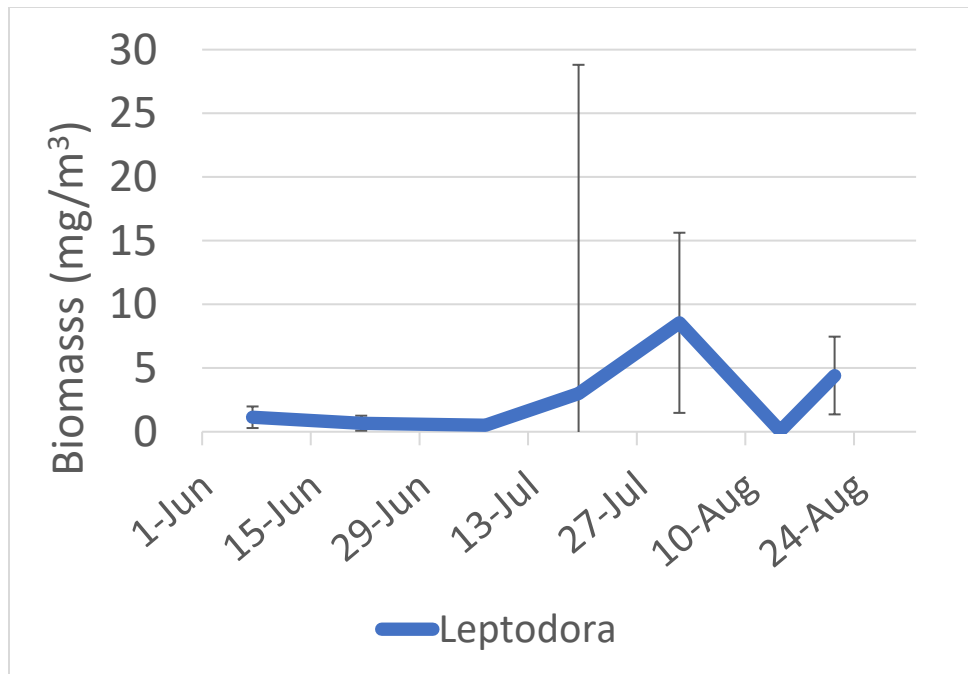


**Figure 9.** Distribution of the mean biomass (mg/m<sup>3</sup>) within the *Bythotrephes* population in southern Green Bay in 2017.

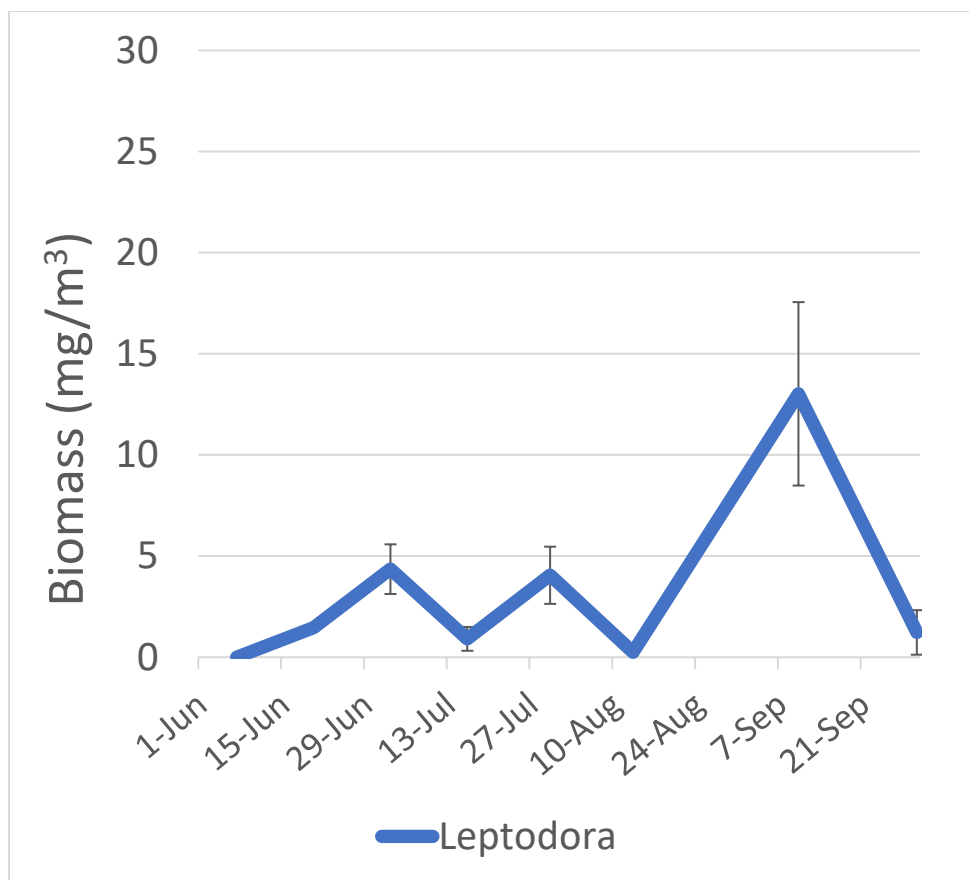


**Figure 10.** Distribution of the mean biomass (mg/m<sup>3</sup>) within the *Bythotrephes* population in southern Green Bay in 2018.

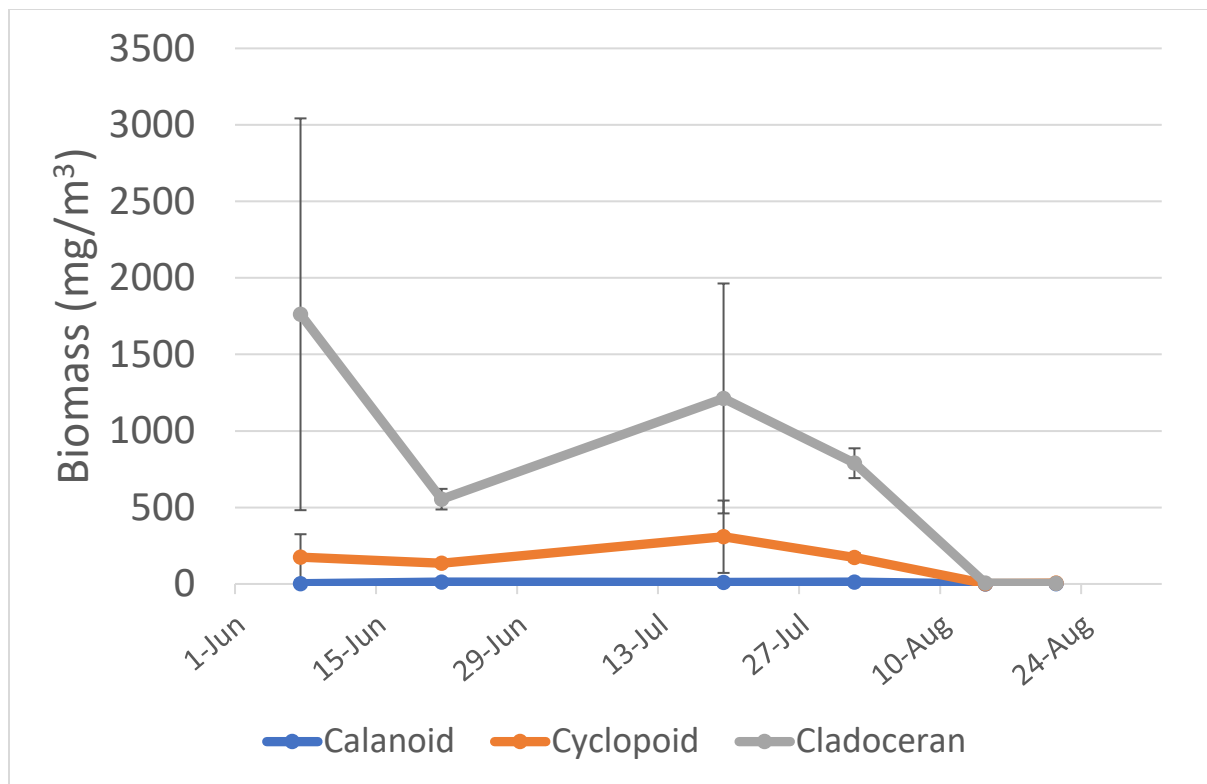




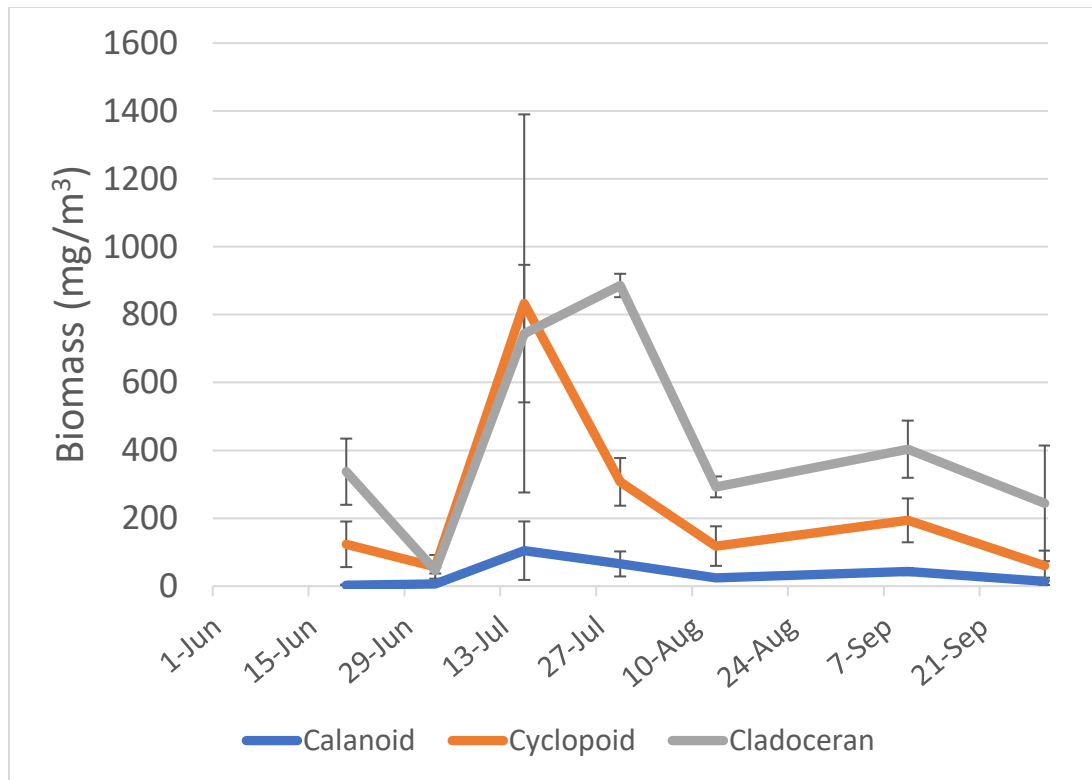
**Figure 11.** Mean biomass ( $\text{mg/m}^3 \pm 1 \text{ SE}$ ) of *Leptodora* at two sites in southern Green Bay in 2017.



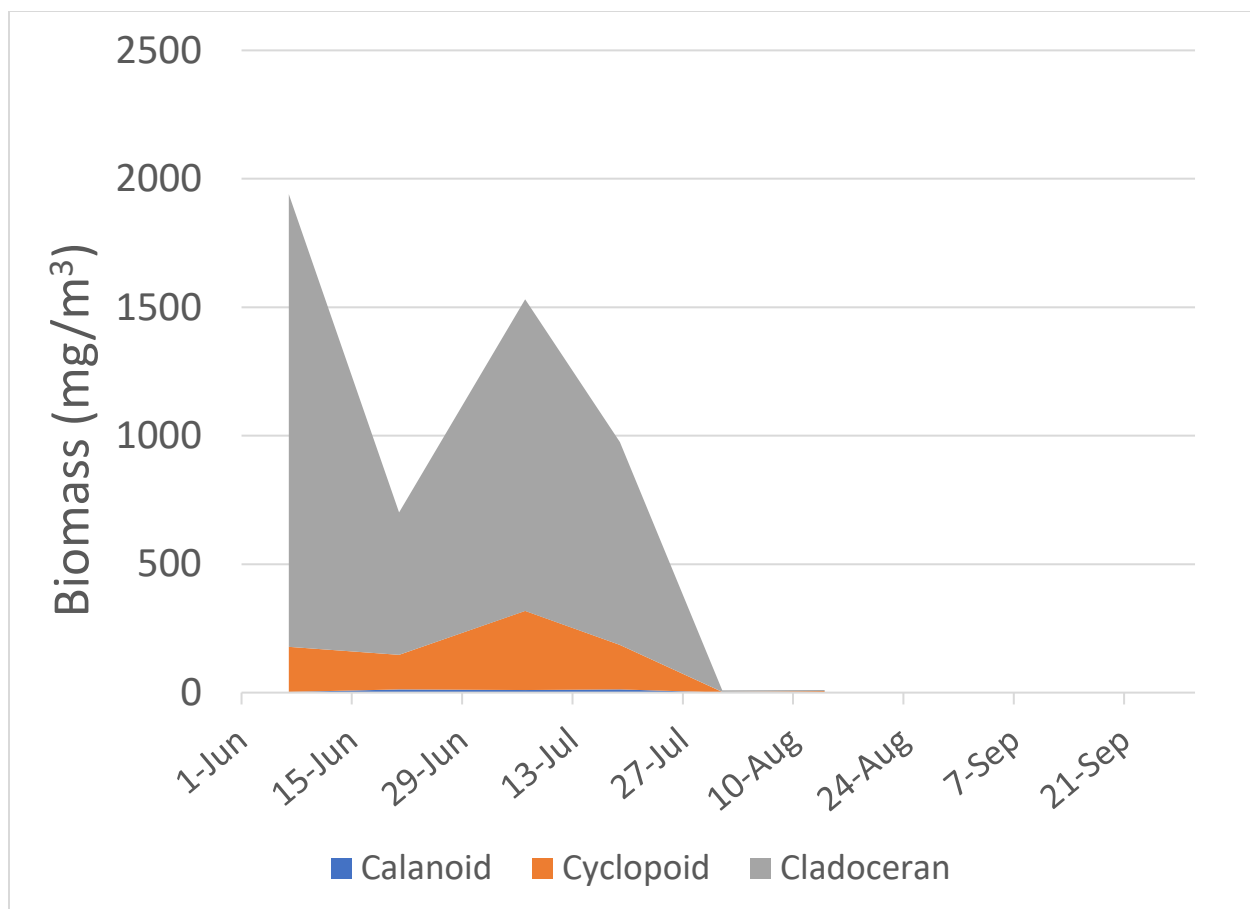
**Figure 12.** Mean biomass ( $\text{mg/m}^3 \pm 1 \text{ SE}$ ) of *Leptodora* at two sites in southern Green Bay 2018.



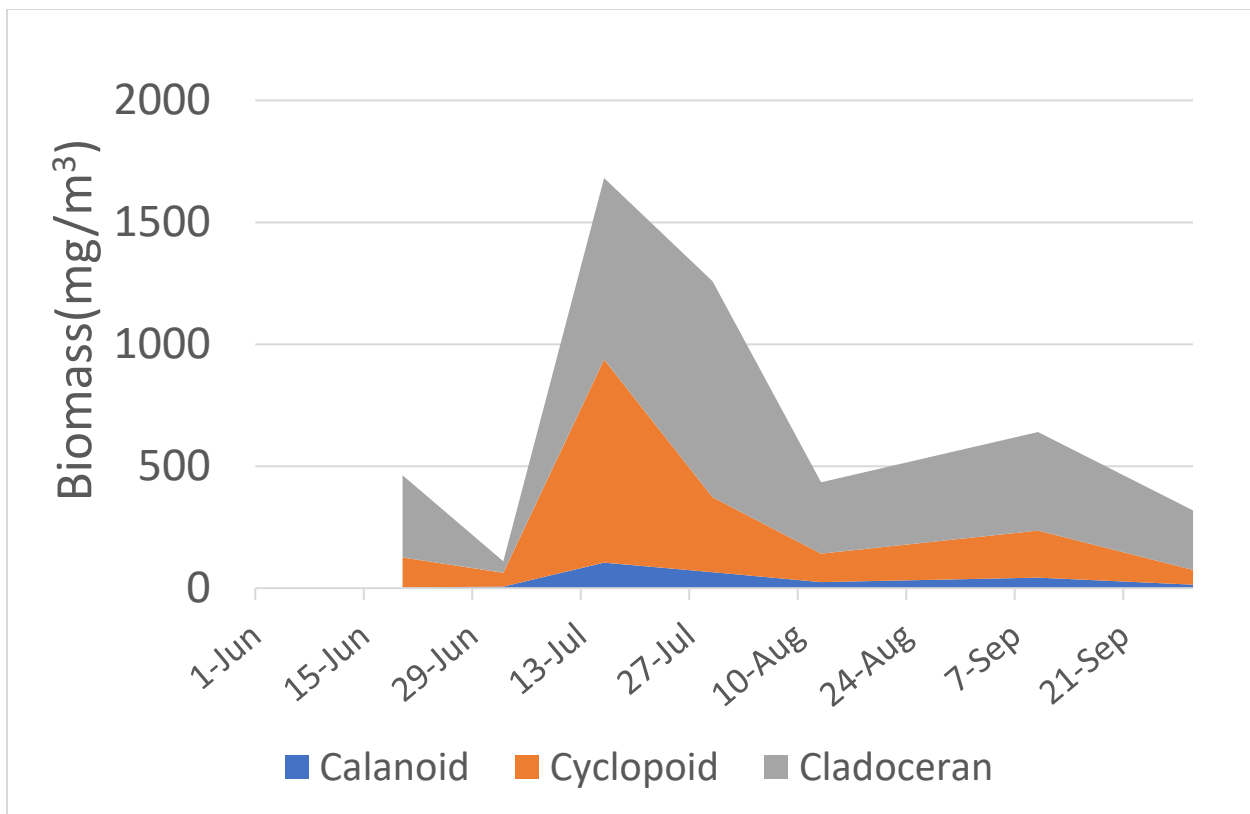
**Figure 13.** Mean biomass ( $\text{mg/m}^3 \pm 1 \text{ SE}$ ) of zooplankton at two sites in southern Green Bay in 2017. Zooplankton divided into three groups: calanoid, cyclopoid and cladoceran.



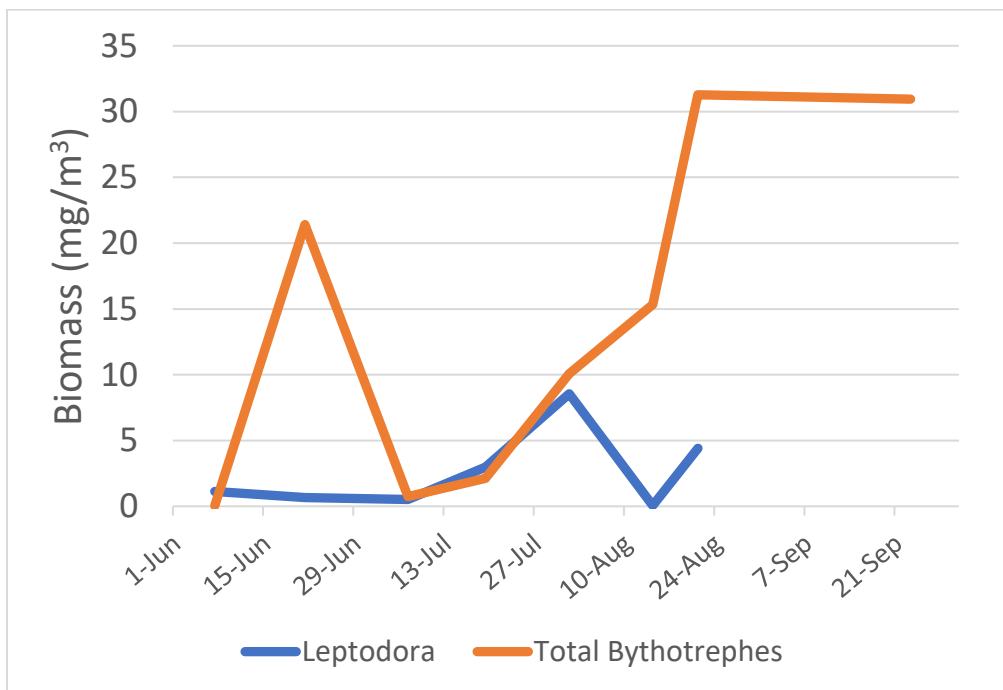
**Figure 14.** Mean biomass ( $\text{mg/m}^3 \pm 1 \text{ SE}$ ) of zooplankton at two sites in southern Green Bay in 2018. Zooplankton divided into three groups: calanoid, cyclopoid and cladoceran.



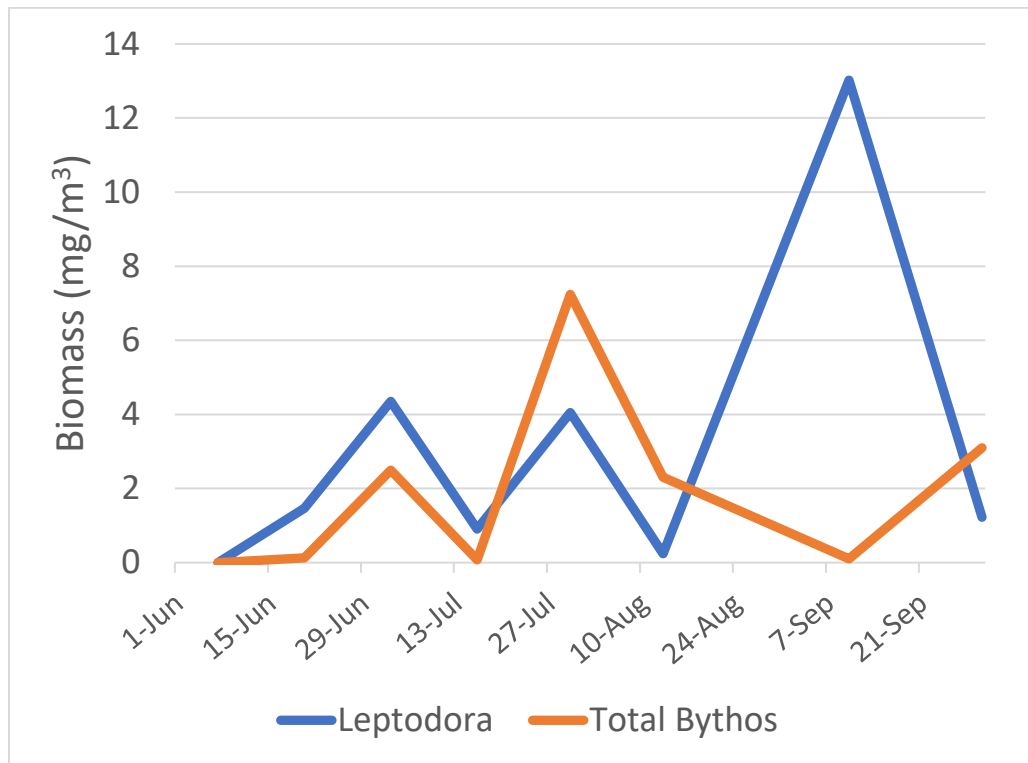
**Figure 15.** Mean biomass (mg/m<sup>3</sup>) of total zooplankton at two sites in southern Green Bay in 2017. Data were not collected in September.



**Figure 16.** Mean biomass (mg/m³) of total zooplankton at two sites in southern Green Bay in 2018.



**Figure 17.** Mean biomass ( $\text{mg}/\text{m}^3$ ) of *Bythotrephes* and *Leptodora* at two sites in southern Green Bay in 2017.



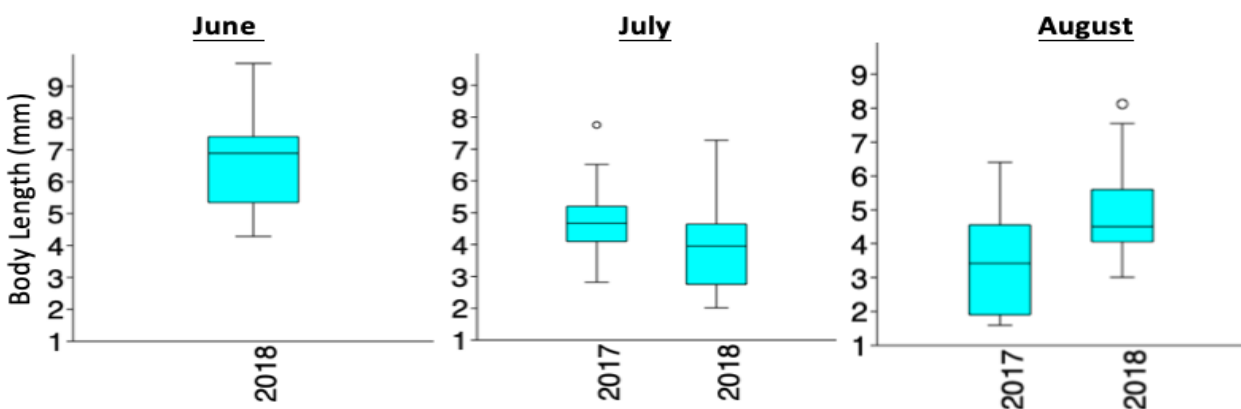
**Figure 18.** Mean biomass ( $\text{mg}/\text{m}^3$ ) of *Bythotrephes* and *Leptodora* at two sites in southern Green bay in 2018.

### Body Size Dynamics

Body sizes of *Leptodora* and Stage 3 *Bythotrephes* showed significant changes between years for multiple months examined (Table 2). The body length of *Leptodora* was significantly longer in 2017: however, variability during 2018 was greater. There was a reciprocal pattern during the month of August compared to July. *Leptodora* body length in 2017 was significantly longer than it was in 2018, and the median was 1mm greater than in 2017. Body lengths varied

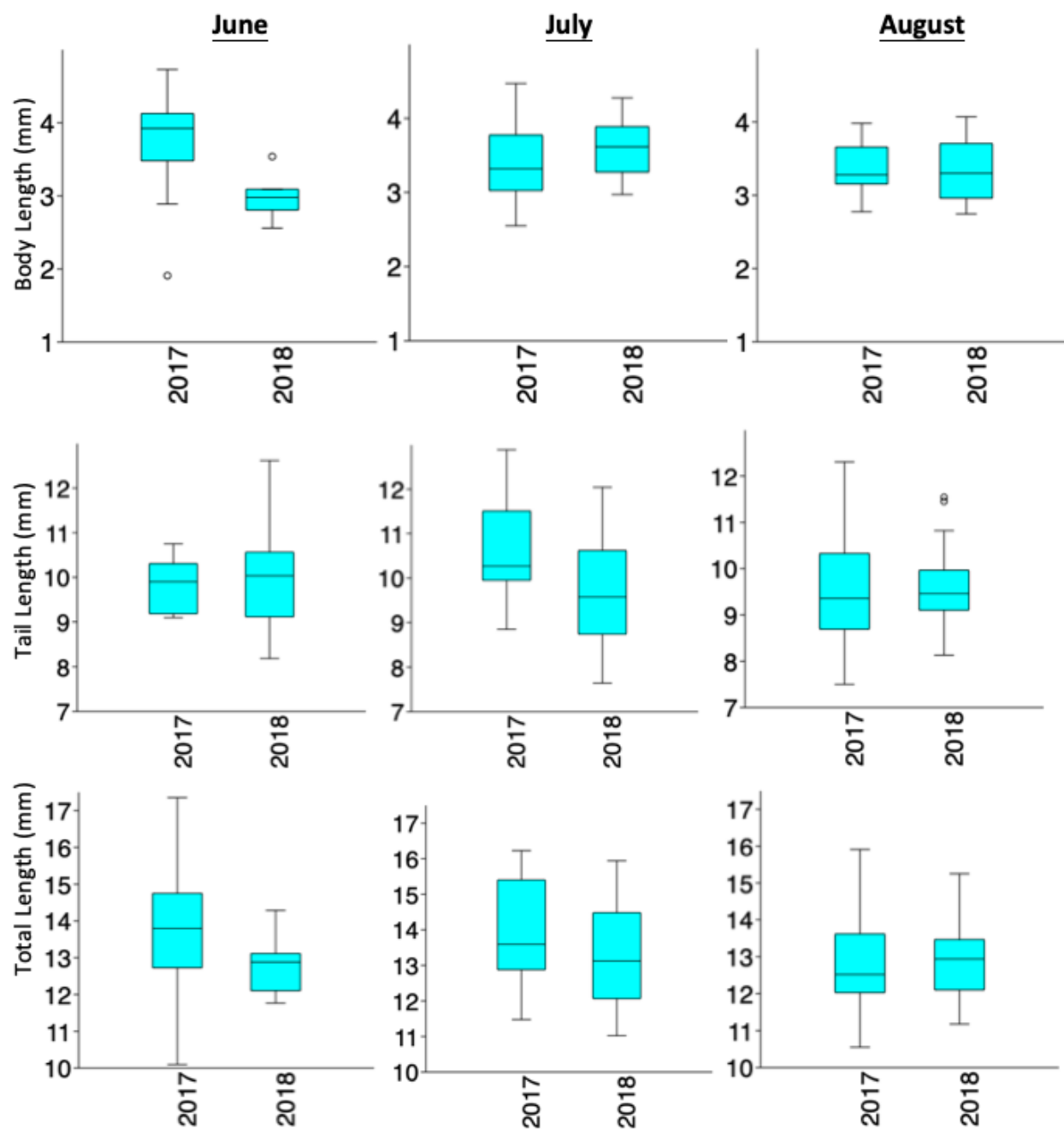
throughout the three months of 2018 (Figure 19). Body size in June 2018 was almost double the length in July and August.

The body length of *Bythotrephes* was significantly larger in June 2017 than in June 2018, by 1mm (Figure 20). There was no significant difference in the tail length of *Bythotrephes* between the years, resulting in an overall significant difference in the total length with a p-value of 0.00085 (Table 2). The body length of *Bythotrephes* was greater during July 2018 than it was during July 2017. Although *Bythotrephes* had a smaller body size in July 2017 they had a longer tail length, with the median being 0.7mm greater than in July 2018.



**Figure 19.** Body length (mm) of *Leptodora* at two sites in southern Green Bay in the months of June, July and August in the years 2017 and 2018.





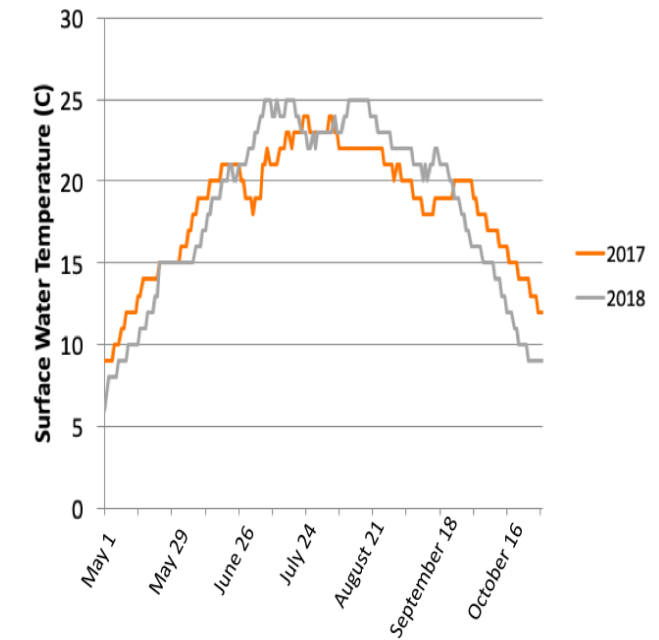
**Figure 20.** Size measurements (mm) of tail length, body length and total length of *Bythotrephes* at two sites in southern Green Bay during June, July and August of 2017 and 2018.

**Table 2.** Kruskal-Wallis p-values of body length, tail length and total length in adult *Bythotrephes* and *Leptodora* at two sites in southern Green Bay between the months of June-August in 2017 and 2018.

Month	Category	P value	Significant Difference
June	Body Length (B)	0.00085	yes
June	Tail Length (B)	0.727	no
June	Total Length (B)	0.036	yes
July	Body Length (B)	0.021	yes
July	Tail Length (B)	0.0038	yes
July	Total Length (B)	0.063	no
August	Body Length (B)	0.426	no
August	Tail Length (B)	0.471	no
August	Total Length (B)	0.63	no
July	Body Length (L)	0.0033	yes
August	Body Length (L)	0.0049	yes

## Temperature

Temperatures varied throughout the summers of 2017 and 2018, with highest temperatures peaking in late July and early August (Figure 21). From early May to mid-June, temperatures in 2017 were approximately 1° C higher than in 2018. Temperatures decreased about 3-4°C for a short period of time in early July 2017 before continuing to rise to their peak of 23.5°C two weeks later. In contrast, July 2018 temperatures increased to a peak of 25 °C for a two-week period before experiencing a drop of 3° C down to temperatures similar to those in 2017. The period of colder temperatures lasted for approximately two weeks in 2018 whereas in 2017 it was less than one week. After temperatures decreased in July 2018 they returned to 25°C for 1.5 weeks before beginning a steady decline in late August. Temperatures declined during late August in both 2017 and 2018, followed by a slight increase in temperatures before declining again in October. This was the last increase in temperature for both years. June 2018 had warmer temperatures than in 2017 throughout the summer months, June- early September. June 2017 had warmer temperatures in the spring and fall months, May and late September.

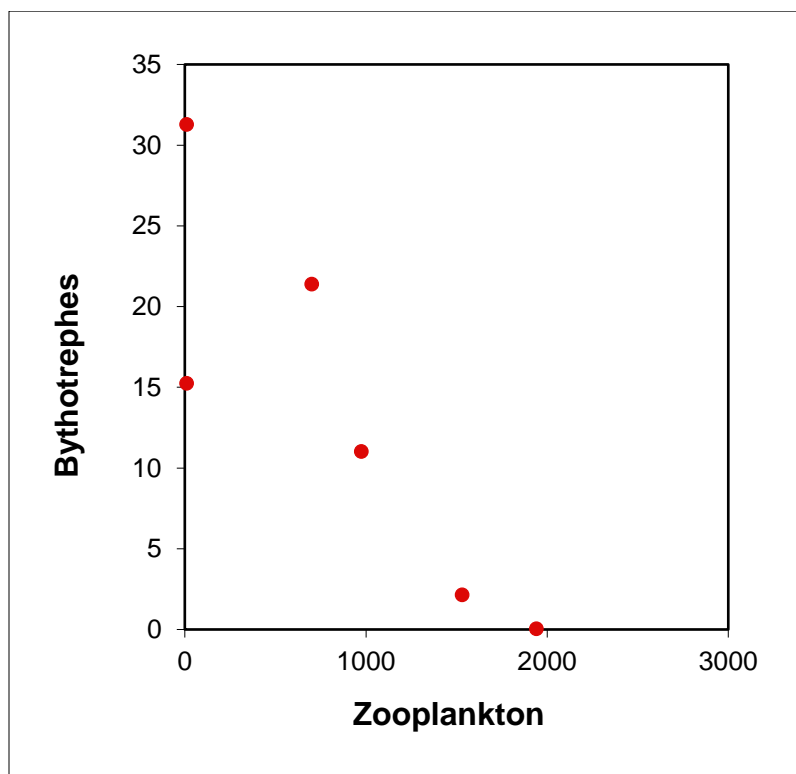


**Figure 21.** Surface water temperature during May-October in 2017 and 2018 in southern Green Bay, Lake Michigan.

### Correlations among variables

A Spearman's rank correlation was used to measure the strength and direction of association between pairs of variables. Ten different tests were run comparing different relationships (Table 3). Individual tests were used to examine *Bythotrephes* dynamics by comparing the biomass of *Bythotrephes* to the biomass of *Leptodora*, temperature, and total zooplankton biomass. The biomass of *Leptodora* was compared to temperature and total zooplankton biomass along with the biomass of *Bythotrephes*. Each scenario was run for each year 2017 and 2018. Of the ten tests, nine did not exhibit a significant correlation between the two variables. The relationship between the biomass of *Bythotrephes* and the total zooplankton biomass in 2017 was the only test where there was a significant relationship (Figure 22). The

Spearman's Rho coefficient was -0.8285 with a p-value of 0.0333, indicating in a negative correlation between the two variables.



**Figure 22.** Spearman's Rho scatterplot comparing total *Bythotrephes* biomass to total zooplankton biomass at two sites in southern Green Bay in 2017.

**Table 3.** Spearman's Rank correlation coefficients and p-values comparing pairs of variables in southern Green Bay. Significance was determined against an alpha value of 0.05.

Comparison	Year	Spearman's Rho	p-value	Significance
<i>Bythotrephes</i> compared to:				
<i>Leptodora</i>	2017	0.1428	0.7131	No
<i>Leptodora</i>	2018	0.4047	0.368	No
Temperature	2017	0.3928	0.3956	No
Temperature	2018	0.0476	0.9348	No
Total Zooplankton	2017	-0.8285	0.0333	Yes
Total Zooplankton	2018	0.0714	0.8396	No
<i>Leptodora</i> compared to:				
Total Zooplankton	2017	0.3143	0.563	No
Total Zooplankton	2018	-0.1785	0.7131	No
Temperature	2017	0.142	0.7139	No
Temperature	2018	1	0	No

### **Discussion**

*Bythotrephes longimanus* and *Leptodora kindtii*

Dynamics of an ecosystem can change significantly within a short period of time. *Bythotrephes* populations vary from year to year and can affect the population dynamics of other species inhabiting Green Bay. The biomass of *Bythotrephes* affects *Leptodora* biomass throughout multiple years in the bay. In years that have high *Bythotrephes*, the biomass of *Leptodora* decreases because of the predation pressures inflicted on them or the direct competition for resources (Lehman & Caceres, 1993). When comparing the biomass of *Bythotrephes* from 2018 against other years, it is most similar to numbers and patterns in 2016 (Merkle & DeStasio, 2018). Both years experienced a lower biomass of *Bythotrephes* than in 2015 or 2017. However, the past four years reveal a similar pattern in *Bythotrephes* biomass over the summer. There is a decrease in abundance around the middle of July and a slight increase in the population towards the end of the summer (DeStasio, Beranek, & Schrimpf, 2018). During low years of *Bythotrephes* biomass, predation pressure on *Leptodora* are also lower, allowing *Leptodora* populations to flourish. Lower predation on *Leptodora* means not as many individuals are being consumed in their juvenile stage. This allows them to reach sexual maturity resulting in a higher percentage of mating and producing offspring.

The body size of *Bythotrephes* can be associated with the size of prey that can be ingested. A larger body size allows for selection of larger prey and a faster ingestion rate (Burkhardt & Lehman, 1994). Juvenile *Bythotrephes* have been recorded taking three times longer than an adult to ingest a cladoceran prey item such as *Daphnia pulicaria*. The body length of *Bythotrephes* was shorter in 2017 than in 2018 in the month of July. We can look at *Leptodora* as a prey item for *Bythotrephes* and determine how the body length of *Bythotrephes* can impact the population of *Leptodora* and total zooplankton. The body length of *Leptodora* may have been longer during July 2017 because *Bythotrephes* had an upper limit on the size of prey they could

ingest, giving larger *Leptodora* an advantage. A similar reciprocal pattern occurred in July of 2018 when the body size of *Bythotrephes* was larger, resulting in a greater amount of small *Leptodora*. The shorter median body length of *Leptodora* may have been a result of having fewer adults in the population because *Bythotrephes* were feeding on them more efficiently.

### *Predatory Zooplankton and Herbivorous Zooplankton*

Predatory zooplankton such as *Bythotrephes* and *Leptodora* have been shown to control the population abundance and size structure of herbivorous zooplankton in lake ecosystems (Lunte & Luecke, 2008; Walsh, Lathrop, & Zanden, 2017). Zooplankton population biomass in southern Green Bay has consistently ranged between 1,000 mg/m<sup>3</sup> and 1,500 mg/m<sup>3</sup> over the last two decades (DeStasio, Beranek, & Schrimpf, 2018). Both years, 2017 and 2018, have numbers within this range, supporting the theory of a relatively consistent zooplankton population in southern Green Bay. By using a Spearman's rank test, we demonstrated a significant negative relationship between the total biomass of *Bythotrephes* and total zooplankton biomass in 2017 (Fig. 22). This negative relationship between *Bythotrephes* and total zooplankton biomass likely occurs because a larger population size of *Bythotrephes* requires greater consumption, taking more zooplankton out of the population (Merkle & DeStasio, 2018). The higher levels of *Bythotrephes* present in 2015 and 2017 indicate that *Bythotrephes* is directly impacting the population dynamics of herbivorous zooplankton in Green Bay. In addition to the effect of *Bythotrephes* biomass on prey population dynamics, temperature likely also influences the consumption rate of *Bythotrephes*. A study done by Mordukhai-Boltovskaia (1958) showed that



temperature affects the consumption rate of *Bythotrephes*. They found that *Bythotrephes* consumed 9 prey/day in the temperature range of 10-15°C compared to 25-30 prey/day at 15-20°C (Mordukhai- Boltovskaia, 1958; Merkle & DeStasio, 2018). This increase in prey consumption rates with increasing temperature suggests that temperature differences among years may also indirectly affect total zooplankton biomass.

*Bythotrephes* are not the only variable affecting the zooplankton populations. In years where *Bythotrephes* are lower in abundance, different predators may inflict mortality on the populations of herbivorous zooplankton causing the total zooplankton biomass to remain consistent over the years. *Leptodora* consumption rates were low in 2015 when *Bythotrephes* consumption rates were extremely high. The next year there was a significant increase in consumption rates for *Leptodora* which resulted in them having more of an impact on the zooplankton populations while the abundance of *Bythotrephes* had decreased (Merkle & De Stasio, 2018)

Both *Bythotrephes* and *Leptodora* were lower in 2018 than in previous years. When both *Bythotrephes* and *Leptodora* are low, we may need to account for unchanging total zooplankton biomass by taking into consideration the impact of fish predation. Fish data from 2015-2017 displayed a steady recruitment rate for Walleye Young of the Year (YOY) in Green Bay, with trawl catch rates of 10-13 fish/hour. However, in 2018 recruitment for Walleye YOY increased almost six-fold, to an average of 77 fish/per trawl hour averaged over areas near our two sampling sites. A high recruitment of fish likely means a high consumption rate of all zooplankton, including *Bythotrephes* and *Leptodora* (unpublished data, S. Hogler, Wisconsin Department of Natural Resources, *personal communication*). Since *Bythotrephes* levels were low

and *Leptodora* populations weren't significantly higher, we can conclude that Walleye YOY was a potential factor that kept the zooplankton populations from increasing in 2018.

### *Factors Influencing the biomass of Bythotrephes*

There are multiple factors to look at when determining what is driving the population dynamics of *Bythotrephes* in Green Bay. The first is temperature. *Bythotrephes* flourish in temperatures between 10°C and 24°C (Berg & Garton, 1988). Previous studies have shown a direct correlation between *Bythotrephes* and temperature, with *Bythotrephes* abundances decreasing as temperatures rise (Garton, Berg, & Fletcher, 1990). Consistent with these trends, temperatures were cooler in 2017 than they were in 2018 and the biomass of *Bythotrephes* was higher in 2017. Abundances in late June 2017 were high for female *Bythotrephes* when temperatures were at 21°C. The biomass of *Bythotrephes* continued to remain low throughout summer while temperatures were at their peak and began to rise as temperatures cooled down. The patterns therefore are consistent with the hypothesis that temperature can be an important factor affecting *Bythotrephes* dynamics.

Fish predation is the second factor that can impact the population dynamics of *Bythotrephes*. Locations where *Bythotrephes* can express vertical migration leads to more relaxed predation pressures from fish. For example, middle and northern Green Bay have a deeper and more transparent water column. Evidence shows that *Bythotrephes* exhibit a diel vertical migration pattern in this type of environment (unpublished data, B. DeStasio). Areas such as southern Green Bay where the water is not deep enough to permit this type of behavior force a more intense interaction between the species, resulting in higher potential predation

pressures on *Bythotrephes*. A higher recruitment rate of fish in 2018 likely diminished the populations of *Bythotrephes*, similar to patterns observed in earlier studies of Lake Michigan (Lehman & Caceres, 1993).

We can conclude from our data that *Bythotrephes* have a direct effect on the food-web in southern Green Bay. The populations of *Bythotrephes* can be affected by temperature and fish predation which alters their consumption rates on herbivorous zooplankton populations. Higher consumption rates of *Bythotrephes* results in a negative correlation with zooplankton.

*Bythotrephes* also exhibit a constant pattern throughout each year with a mid-summer decline and an increase near the end of summer. We have also concluded that there is an alternating pattern in biomass between *Bythotrephes* and *Leptodora*. Lower abundances of *Bythotrephes* allows for *Leptodora* and juvenile fish to feed more on zooplankton, making the biomass of zooplankton more consistent over the years.

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I hereby reaffirm the Lawrence University Honor Code.

Arianna Neumeyer