

**DETERMINING THE ROLE OF FISH PLANKTIVORY ON SPINY WATER FLEA  
(*BYTHOTREPES LONGIMANUS*) PRODUCTION IN UPPER GREAT LAKES**

by

Kevin Keeler

A thesis submitted  
in partial fulfillment of the requirements  
for the degree of  
Master of Science  
School of Natural Resources and Environment  
at the University of Michigan  
February 2014

Thesis Committee:

Professor James S. Diana, co-chair

Adjunct Professor David B. Bunnell, co-chair

This page left intentionally blank

## **Abstract**

Aquatic invasive species pose a threat to the stability of food webs. The Great Lakes invasion of the spiny water flea *Bythotrephes longimanus* has reduced densities of more easily captured zooplankton (cyclopoid copepods and cladoceran species) for prey fishes. As a readily available prey item, *Bythotrephes* has been incorporated into fish diets. Therefore the ability of fish to effectively control *Bythotrephes* biomass by high consumption rates could potentially impact fish and zooplankton communities. I compared estimates of *Bythotrephes* production to consumption by fish in lakes Michigan and Superior. Comparisons were made in one day in April, July and September in the northern basin of Lake Michigan at near (18-m), intermediate (46-m), and offshore depths (110-m). Similar comparisons were made between September and November at similar depths in the Apostle Islands area of Lake Superior. Alewife and cisco were the dominant consumers respectively in Lake Michigan and Superior. In September, consumption by fishes in Lake Michigan exceeded production (up to 178 %) at nearshore and intermediate sites, while at offshore sites, consumption was less than 15 % of *Bythotrephes* production. In Lake Superior, consumption exceeded production (up to 842%) at all offshore sites each month but only in November at the intermediate site. Contrasting Lake Michigan, nearshore consumption of *Bythotrephes* by fishes was nonexistent in Lake Superior. Although consumption exceeded production on multiple occasions in Lake Michigan, *Bythotrephes* never declined following excessive consumption indicating a lack of control. However, control occurred twice at the offshore Lake Superior site in September and October. To explore factors other than fish consumption, a generalized additive model was employed for data from both lakes. Only epilimnetic temperature was included in the most parsimonious model explaining biomass changes of *Bythotrephes*. Overall, control by biotic (fish consumption) processes was limited, and abiotic (temperature) processes appeared to have a stronger influence on invasive

*Bythotrephes* dynamics. These analyses demonstrate the need to identify not only the interactions between invasive species and other biota, but also the physical parameters of lakes that could regulate their populations.

## **Acknowledgments**

A majority of funding was provided by the Great Lakes Restoration Initiative from the Environmental Protection Agency. The Rackham Graduate School and School of Natural Resources and Environment provided travel funding for conferences and I thank the family of Karl F. Lagler for awarding me additional research support. I am grateful for my advisors Jim Diana and David “Bo” Bunnell for guidance and positive comments throughout this research. Laboratory and field assistance was received from Patty Armenio, Margi Chriscinske Bruce Davis, John French III, Justin Mychek-Londer, Eric Nelson, Lynn Ogilvie, Brian O’Malley, Elizabeth Puchala, and Nicole Watson. Volunteer assistance was provided by Kelly McClure and Ryan Oleynik. The crews of the R/V Grayling, Sturgeon, Kiyi, and Barney Devine aided in collections of fish, zooplankton, and other essential data. Collectively, I thank the wonderful people at the U.S. Geological Survey-Great Lakes Science Center in Ann Arbor, MI, and the Ashland, WI station. Statistical assistance and insight was given by Jean Adams. Technical advice and general comments were given from Dave Warner, Dan Yule, Steve Pothoven, and Chuck Madenjian. The Diana laboratory group and Barb Diana were helpful and welcoming throughout the entire process of acclimating to graduate school. It was a pleasure to teach alongside Lynn Carpenter, Erin Burkett, and fellow graduate student instructors in the general ecology laboratory. Finally, I thank my wife Colleen for encouragement during this experience.

## **Table of Contents**

	<b>Page</b>
Abstract.....	ii
Acknowledgments.....	iv
List of Tables.....	vi
List of Figures.....	vii
Introduction.....	1
Materials and Methods.....	6
Results.....	18
Discussion.....	22
Tables and Figures.....	31
Literature Cited.....	42
Appendices.....	53

## List of Tables

	<b>Page</b>
Table 1. Regressions used to predict dry weights of invertebrates in Lake Michigan and Lake Superior.....	31
Table 2. Sizes used to separate fish species in Lake Michigan and Lake Superior into different size classes.....	32
Table 3. Total length (mm) to weight (g) regressions from collected fish in Lake Michigan 2010 and Lake Superior 2011 .....	33
Table 4. Prey and predator energy densities (J/g) used for bioenergetics modeling of fishes in Lake Michigan and Lake Superior .....	34
Table 5. Summary of the 10 generalized additive models with the lowest corrected Akaike's Information Criterion (AIC <sub>c</sub> ) values used to explain <i>Bythotrephes</i> biomass ( $\mu\text{g}/\text{m}^2$ ) at two Lake Michigan sites (2010) and one Lake Superior site (2011).....	35

**List of Figures**

	<b>Page</b>
Figure 1. Maps of sampling sites and nearby port cities for Lake Michigan in top inset and Lake Superior in bottom left inset. ....	36
Figure 2. Seasonal changes in dry weight biomass (mean±SE) of collected <i>Bythotrephes</i> (mg/m <sup>2</sup> ) compared between Lake Michigan sites of Frankfort (FF -a, b, and c) and Sturgeon Bay (SB-d, e, and f) and Lake Superior site in the Apostle Islands (AI-g, h, and i) across depths (m) and months. ....	37
Figure 3. Overall proportion (mean±SE) of <i>Bythotrephes</i> (dry weight) in diets of fishes by size class from a) Lake Michigan and b) Lake Superior.....	38
Figure 4. Ratio of fish community consumption of <i>Bythotrephes</i> to production in Lake Michigan offshore of Frankfort, MI, and Sturgeon Bay, WI, and Lake Superior at the Apostle Islands, WI. ....	39
Figure 5. Proportion of instances when estimated consumption by fish on <i>Bythotrephes</i> equaled or exceeded 100% of production of <i>Bythotrephes</i> across depths at Lake Michigan sites (a) and the single Lake Superior site (b). ....	40
Figure 6. Most parsimonious ( $\Delta AIC$ less than 2) generalized additive model with explanatory variable smoothed epilimnetic temperature best explaining <i>Bythotrephes</i> biomass ( $\mu\text{g}/\text{m}^2$ ). Biomasses and temperatures from Lake Michigan (F=Frankfort, MI, S=Sturgeon Bay, WI) and Lake Superior (A=Apostle Islands, WI). ....	41



## **Introduction**

Aquatic invasive species have dramatically altered the dynamics of many food webs throughout the world (Lodge 2001, Strayer 2010). Yet understanding how they influence interactions between trophic levels can be especially difficult given the complexity within systems (Vitousek et al. 1997). The Laurentian Great Lakes underwent a number of biological invasions that systematically restructured their food-webs (Christie 1974, Mills et al. 1993, Ricciardi & MacIsaac 2000). Ultimately several invasive taxa such as alewife *Alosa pseudoharengus* (Wells 1970, Madenjian et al. 2002), sea lamprey *Petromyzon marinus* (Smith & Tibbles 1980), and zebra *Dreissena polymorpha* and quagga mussels *Dreissena rostriformis bugensi* (Schloesser & Nalepa 1994, Nalepa et al. 2009) became dominant and altered the flow of energy. Due to these potentially negative impacts, both scientists and managers require an understanding of the trophic interactions of invasive species, including its primary predators, as well as the direct and indirect effects they have on prey (Yan et al. 2011).

The spiny water flea *Bythotrephes longimanus* (previously *Bythotrephes cederstroemi*- hereafter *Bythotrephes*) is a predatory cladoceran that arrived in the Great Lakes via ballast water from trans-Atlantic shipping (Sprules et al. 1990). Since the first documented occurrence in Lake Huron in 1984 (Bur et al. 1986, Makarewicz 1988), its spread to each Great Lake was uninhibited, reaching Lake Superior in 1987 (Cullis & Johnson 1988), as well as numerous inland lakes (Yan et al. 1992, Yan & Pawson 1997) via anthropogenic and biotic routes. As a primarily epilimnetic predator, the Great Lakes zooplankton community experienced direct and indirect effects from the *Bythotrephes* invasion. First, numerous easily captured cladoceran and cyclopoid species markedly declined in abundance, became extremely rare, or were extirpated due to consumption by *Bythotrephes* (Lehman 1991, Lehman & Cáceres 1993, Dumitru et al.

2001, Yan et al. 2002, Barbiero & Tuchman 2004). Interestingly, *Bythotrephes* in Europe exerted the same top-down effect on *Daphnia* species, demonstrating the widespread impacts that can occur (Manca et al. 2000). More recent research revealed that *Bythotrephes* also influenced zooplankton communities from multiple lakes indirectly in several ways (non-consumptive effects). Experimentally, karimones released by *Bythotrephes* in the epilimnion altered the daily vertical migration (DVM) of native zooplankton (Pangle & Peacor 2006). Lake Michigan, Lake Erie, and Lake Huron zooplankton exhibited declines (Barbiero & Tuchman 2004) and possibly avoided predation from *Bythotrephes* by moving deeper into the water column (Bunnell et al. 2012), but experienced colder temperatures, and models predict lowered production and abundance (Pangle et al. 2007).

In addition to its effects on zooplankton, *Bythotrephes* also influences the planktivorous fish community as a competitor for herbivorous zooplankton and as a prey item itself. Models predicting their consumption have revealed that *Bythotrephes* can at times consume more zooplankton than the entire prey fish community (Hoffman et al. 2001, Bunnell et al. 2011). Furthermore, *Bythotrephes* consumption can limit prey availability to young-of-the-year fish, preferential to easily captured prey items (Link 1996, Hoffman et al. 2001). *Bythotrephes* also tend to prefer large *Daphnia* species, thus reduced abundances have a negative energetic impact on prey fish that must consume smaller sized prey (Schulz & Yurista 1999). One less-studied and potentially positive impact on prey fish is that as zooplankton move deeper to avoid *Bythotrephes* predation during the day, increasing prey densities are available for planktivorous fish in the meta- and hypolimnion (sensu Pothoven & Vanderploeg 2004, Vanderploeg et al. 2012). Its long spine and large compound eye make *Bythotrephes* a conspicuous zooplankter that is often consumed by numerous juvenile and adult fish species not limited by gape. Great

Lakes consumers include non-native planktivores such as juvenile (Branstrator & Lehman 1996) and adult (Keilty 1990) alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax* (Barnhisel & Harvey 1995), as well as native planktivores species such as bloater *Coregonus hoyi* (Branstrator & Lehman 1996), lake whitefish *Coregonus clupeaformis* (Barnhisel & Harvey 1995), and cisco *Coregonus artedii* (Barnhisel & Harvey 1995), and native benthivores such as deepwater sculpin *Myoxocephalus thompsonii* (Evans 1988) and slimy sculpin *Cottus cognatus* (Mychek-Londer unpublished data and this study), and invasive round goby *Neogobius melanostomus* (Barton et al. 2005).

Given the multiple and likely overall negative impacts of *Bythotrephes* on zooplankton and prey fishes, a pivotal research goal should be to determine whether fish predation can control or limit its production. Control is a commonly used word in the ecological literature, and its definition can widely vary. Carpenter et al. (1985) suggested that consumers control prey when changing their species composition, biomass, or productivity. Other research focused on more strict definitions using either declines in the entire zooplankton community by mass balance (Dettmers & Stein 1992), or consumption of some percentage of production (Rudstam et al. 1994a) as appropriate control. I defined control by 1) more consumption than production of a species and subsequently 2) decline of that species following excessive consumption. Evidence for the first criterion of my definition was provided by Pothoven et al. (2007) in the nearshore environment (10-m depth) of Lake Michigan where *Bythotrephes* lacked deepwater refuges from fish (Pothoven et al. 2001, 2003). Therefore, nearshore planktivorous fish communities, particularly those dominated by alewife (Pothoven et al. 2013), might promote heavy predation on the invader and limit its potential impact on the zooplankton community. This result suggests

that *Bythotrephes* is less controlled in deepwater habitats because *Bythotrephes* can migrate into refuges in the metalimnion or deeper waters (Lehman & Cáceres 1993).

Aside from top-down consumptive effects of fish, other factors are also likely to influence distribution and abundance of *Bythotrephes*. For example, one biotic factor is the availability of its preferred prey items (herbivorous cladocerans, cyclopoid adults, and calanoid and cyclopoid copepodites) because they should increase *Bythotrephes* production, and ultimately its density. Abiotic drivers such as epilimnetic water temperature should also affect production because *Bythotrephes* can consume more prey and grow faster at higher temperatures (Yurista & Schulz 1995, Yurista et al. 2010). When temperatures exceed 23 °C, however, production should decrease because respiratory enzymes become inactive preventing oxygen consumption (Yurista 1999) suggesting a lethal mechanism for this species in natural systems. Therefore temperatures provide abiotic environmental maximum and minimum constraints limiting *Bythotrephes* populations. It is possible that a multitude of factors contribute to *Bythotrephes* dynamics, neither consumption nor temperature alone, and that a combination of abiotic and biotic variables can better explain changing food webs in invaded lakes. Taking variables such as temperature regimes and planktivore composition into account can aid in determining which lakes will continue to be inundated with this invasive species as well as which lakes are candidates for future colonization.

The overall goal of this work was to determine if fish can affect *Bythotrephes* production via planktivory. Specifically, I evaluated which species consumed more *Bythotrephes* than were produced, whether control of *Bythotrephes* existed, and if other biotic and abiotic processes have greater explanatory power than planktivory for *Bythotrephes* population dynamics. In answering the first objective, I used field sampling and laboratory analyses to document consumption of

*Bythotrephes*. Next, I used models of fish consumption to determine whether planktivorous and benthivorous fishes consumed more *Bythotrephes* compared to their production across three near to offshore transects, including two in Lake Michigan and one in Lake Superior. Control of *Bythotrephes* by fish consumption was determined to exist when 1) more *Bythotrephes* were consumed in a location than were produced, and 2) declines of *Bythotrephes* occurred in subsequent months after excessive consumption by prey fish. Lastly, I attempted to determine if fish consumption or any other biotic (prey items) and abiotic (temperature) variables influenced *Bythotrephes* biomass across lakes.

Previous examples of excessive *Bythotrephes* consumption suggested where control via planktivory could occur. I hypothesized that 1) predation by alewife would have the largest impact on *Bythotrephes* in the Lake Michigan nearshore, consistent with previous work (Pothoven et al. 2007, Pothoven et al. 2013). 2) Lake Superior consumption would be highest in deeper waters offshore because diets of offshore populations of cisco are comprised of up to 63% *Bythotrephes* (Gamble et al. 2011a). 3) Consumption in both lakes would exceed production of *Bythotrephes* prior to fall increases in *Bythotrephes* densities typically seen with this species and similar taxa. 4) Among the abiotic and biotic variables in the statistical models, I hypothesized that a combination of planktivory and available prey biomass would best explain *Bythotrephes* biomass changes given the ability for fish to exert top-down control and the positive relationship found with *Bythotrephes* and their prey in Canadian Shield Lakes (Young et al. 2011).

## **Materials and Methods**

### **Sampling Design**

To explore factors influencing *Bythotrephes*, I combined field sampling, laboratory enumeration of zooplankton and fish diet analysis, and bioenergetics and statistical modeling. Three sites were sampled along transects at nearshore (18m), intermediate (46m), and offshore (110m) depths. Lake Michigan samples were taken in the northern basin offshore of Frankfort, MI (44.52°, -86.26°) and Sturgeon Bay, WI (44.75°, -87.28°) in 2010 aboard the R/V Grayling and Sturgeon (Figure 1). Lake Superior samples were taken offshore of Stockton Island (46.94°, -90.51°) in the Apostle Islands National Lakeshore in 2011 aboard the R/V Kiyi (Figure 1). The temporal frequency of sampling differed between lakes. In Lake Michigan, fish were sampled in April, July, and September, whereas zooplankton were sampled monthly from April to October. In Lake Superior, fish and zooplankton were sampled in April, September, October, and November.

### **Zooplankton Sampling and Processing**

Zooplankton samples were collected identically in each lake to estimate density and biomass of *Bythotrephes*, as well as other zooplankton. At each depth, whole-water column samples were collected (starting 1 m above the bottom of the lake) during the day using a set of replicate tows with a 153- $\mu$ m mesh, 0.5-m diameter net fitted with a flowmeter, and retrieved at a speed of about 0.5 m/s. A 5 minute antacid bath was used to relax zooplankton bodies for future measurement and biomass determination prior to fixation in 5% sucrose formalin.

For both lakes, laboratory enumeration and measurements followed USEPA zooplankton processing protocol (Anonymous 2003) and as described in Bunnell et al. (2012). The entire

sample was enumerated completely to estimate density and biomass of large taxa such as *Bythotrephes*, *Leptodora kindtii*, *Mysis relicta*, and *Cercopagis pengoi*. All adults were identified to species (except for *Bosmina* species). Copepodites (immature copepods) were identified to species except *Leptodiaptomus* species. Samples were split with a Folsom plankton divider to estimate densities of smaller and more numerous crustacean zooplankton. Samples were split until the number of zooplankton identified within each of those subsamples equaled between 200 and 400 total individuals (the smallest subsamples known as the ‘A’ and ‘B’ samples). Less abundant species (i.e., those whose counts summed to less than 40 in the ‘A’ and ‘B’ splits) were counted in the ‘C’ split (whose split fraction equaled the sum of the ‘A’ and ‘B’ splits). Only large (i.e., *Limnocalanus macrurus*, *Senecella calanoides*, *Epischura lacustris*) and/or rare (i.e., not typically seen at that time of year or depth) taxa were counted in the ‘D’ split (whose split fraction equaled the sum of the ‘A’, ‘B’, and ‘C’ splits). Split-specific densities for each taxon were averaged, with a weighting based on the proportion of each total sample represented by the split.

Zooplankton measurements were applied to length-weight regressions to estimate biomass by dry weight (Table 1). The first 20 individuals in each taxon and life-stage were measured with an ocular micrometer under a dissecting microscope (Leica Wild M8). Specimens from the cladocera order, primarily *Daphnia* species and *Bosmina longirostris*, were measured from either the top of their head, or the front of their rostrum to the base of the caudal spine or the distalmost part of their carapace (Dumont et al. 1975, Bottrell et al. 1976). Calanoid and cyclopoid copepods (adults) and copepodites (immature) were measured from the anterior-most part of the cephalosome to the distal end of the caudal ramus (Pace & Orcutt 1981, Doubek & Lehman 2011). *Mysis* were measured by the antennal scale length, and then converted to a

total length measurement for biomass (Grossnickle & Beeton 1979, Shea & Makarewicz 1989). Biomass estimations for aquatic insects, e.g. Chironomid species, were made from head capsule width measurements (Smock 1980).

### ***Bythotrephes* Production Estimates**

Similar to other collected zooplankton, regressions were applied to *Bythotrephes* to estimate biomass which, in turn, was used to estimate production. First, each individual *Bythotrephes* was classified to instar (based on the number of barbs on the spine), and for each instar that occurred, up to twenty individuals were measured. Lengths were converted to weights by measuring individuals from the proximal end of its spine to the base of the kink of the spine (Garton & Berg 1990), or where spinules were located in sexually-produced individuals (Rivier & Dumont 1998). A Seabird electronic bathythermograph (BT, CTD) was used at most of the collection sites to estimate the vertical temperature profile. In the nine cases where Seabird was not used, surface temperatures from Great Lakes Coastal Forecasting System were utilized to estimate temperature (Schwab & Bedford 1999). Epilimnetic temperatures were then calculated from the ratio of Great Lakes Coastal Forecasting System surface temperatures to known epilimnetic temperatures (0.89;  $R^2=0.68$ ). Given that the epilimnion is the preferred depth for *Bythotrephes* (Lehman & Cáceres 1993), I calculated the mean epilimnetic temperature, or mean temperature of the top 20 m when not stratified. I estimated *Bythotrephes* production from my own biomass estimates using  $\log P/B_{\text{daily}} = \alpha + \beta T$ : where P = production (g/ day), B = biomass (g /day), T = temperature (°C),  $\alpha = -1.725$  and  $\beta = 0.044$  (Shuter & Ing 1997). Although the coefficients from Shuter & Ing (1997) were developed for herbivorous cladocerans, the predicted production estimate was not different from egg-ratio production estimates (Foster & Sprules 2009). Because the egg-ratio production model requires bi-weekly collections, I considered the



Shuter & Ing (1997) model an appropriate replacement given the sampling design. All production estimates were calculated on an areal ( $\text{g} \cdot \text{m}^{-2} \text{d}^{-1}$ ) basis to facilitate comparisons with consumption of *Bythotrephes* by fish.

Post-hoc analysis for day and night estimates of *Bythotrephes* densities using the previously described gear revealed that day samples were biased low. Specifically, samples pooled from both Lake Huron in 2012 (n=9) and Lake Superior in 2011 (n=7) revealed estimated biomasses (mean $\pm$ SD) from night samples to be  $2.06 \pm 0.90$  times greater than those estimated from day samples (paired t-test,  $t_{16} = -4.97$ ;  $p < 0.001$ ). To conduct the most robust test of *Bythotrephes* control, I multiplied the daytime estimates of *Bythotrephes* biomass by 2.06, which thereby increased estimated *Bythotrephes* production.

### **Fish Sampling**

To estimate consumption of *Bythotrephes* by the fish community, fish were collected at sites where zooplankton were also sampled. Gears used for fish included bottom trawl and midwater trawl with acoustics. Bottom trawls were used because many benthivores and planktivores are associated with the lake bottom during some part of daylight hours. I used “Yankee style” trawls with a 12-m headrope that fished for 10-20 minutes per tow, depending on the lake, and collected individuals within 1 m of the bottom at each site. Upon retrieval, collected fish were sorted by species and size class (Table 2), measured (TL, mm), weighed (nearest 0.1 g), and up to 20 fish per species and size-class were frozen for later diet analysis. Benthic fish densities (#/ha) were estimated by the area swept as a function of time on bottom, vessel speed and width of net, then averaged for the two replicate tows. Densities of deepwater sculpin, slimy sculpin, and round goby were always estimated from bottom-trawl collections.

Pelagic estimates of fish densities were required because some species and life-stages are not fully vulnerable to the bottom trawl. As a result, I also conducted nighttime stepped-oblique midwater trawls (equipped with netmind sensors to estimate fishing depth) and used an echosounder to acoustically estimate fish density in every 5 m of water column (excluding 1 m above the bottom and below the hull of the vessel). Acoustics data were collected with Biosonics DT-X split beam echosounder version 4.0 with 38 and 120 kHz transducers following previous guidelines for Lake Michigan (Warner et al. 2008, Parker-Stetter et al. 2009, Rudstam et al. 2009, and Warner et al. 2009) and Lake Superior (Rudstam et al. 2009). Acoustic densities were apportioned to species using a combination of midwater trawl species and size composition data and *in situ* target strength (TS) information derived from analysis in Echoview © 4.6 following the approaches outlined by Warner et al. (2008, 2009) for Lake Michigan and Yule et al. (2007) and Myers et al. (2009) for Lake Superior. Mean mass of fish was estimated by predicting length from TS using Rudstam et al. (2003), then predicting mass from length (rainbow smelt) or predicting mass directly from TS (bloater) using Fleischer et al. (1997). Acoustics estimates (> 1 m off of lake bottom) did not overlap with bottom trawls (lake bottom to 1 meter off bottom) and therefore the combination of these gears (so long as they were fished during the same time of day) avoided double-counting. Any collected fish in midwater trawls underwent the same processing protocol as the bottom trawls and were saved for diet analysis.

Fish were sampled with all gears in both lakes, but there were differences in some of the methodology beyond months of fish sampling aside from those previously mentioned. Bottom trawl duration was 10 minutes or less in Lake Michigan during the day, but trawls in Lake Superior occurred for 20 minutes during both day and night. Species apportionment for acoustics differed between the lakes. In Lake Michigan acoustic densities <40 m below the

surface were apportioned using midwater trawl data with Netmind mensuration gear exclusively, while acoustic densities  $\geq 40$  m below the surface were apportioned using mean TS. If mean TS for an acoustic cell was  $< -45$  dB, targets were assumed to be large rainbow smelt. If mean TS was  $\geq -45$  dB, targets were assumed to be large bloater for Lake Michigan and cisco for Lake Superior. In Lake Superior at depths greater than 50 m during April, October, and November and greater than 30 m in September, targets were classified as ciscoes (bloater, shortjaw cisco, and kiyi). When low sample sizes from Lake Superior midwater trawls in a month made acoustics difficult to apportion species, the combined species composition from midwater and bottom trawls was used as a surrogate. Because fish collection in Lake Michigan occurred either during the day (bottom trawls) or at night (midwater trawls and acoustics), I used only the highest density estimates to characterize maximum planktivore density between the two collection methods (acoustic: bottom trawl selection; 76% for alewife, 92% rainbow smelt, 50% bloater; bottom trawls were used exclusively for sculpin species) that could account for maximum consumption. Contrasting this in Lake Superior, both trawling methods were deployed at night so that their estimates could be summed.

### **Fish Diet Analysis**

To reveal *Bythotrephes* consumption by the fish community, diets from fish in each lake were analyzed. After thawing, each fish was sexed (if mature), weighed (nearest 0.1 g), and measured for TL (nearest 1 mm). To account for possible ontogenetic changes in diet, alewife, bloater, cisco, rainbow smelt, and lake whitefish were summarized by small and large size classes (Table 2) based upon tracking histograms of seasonal modal length changes for each fish species. An excision was made from the anus to the esophagus, and stomachs, from pyloric caeca to esophagus, were removed and placed in 70% ethanol for preservation until processing.

Up to 15 individuals were processed for diets in a given species, size class, depth, month, and site when available. To process stomachs, each was placed in a watch glass with contents removed under a dissecting microscope. All prey individuals were identified to species or, if digestion inhibited identification, a higher taxonomic level. Each individual prey taxon was enumerated and up to 10 individuals per species were measured for each fish sample. Length-weight regressions (same as zooplankton processing; see Table 1) were then applied so that diet proportion by weight could be estimated.

*Bythotrephes* had a separate enumeration/identification procedure due to retention of its spines and possible overestimation of recent consumption (Parker-Stetter et al. 2001, Parker-Stetter et al. 2005, Storch et al. 2007). Only “tissued” spines (those spines with some degree of attached body tissue to the proximal end) and/or bodies with eye spots were considered a countable prey item. If “tissued” spines were found accompanying spineless bodies with eye-spots, then spines along with bodies having eye-spots were combined to count as one individual, and not two separate ones.

In Lake Michigan samples, the entire contents of an individual stomach were enumerated and identified unless there were a high number of diet items (i.e., >200), and then the stomach was sub-sampled. If sub-sampled, stomach contents were placed in a known volume of water (usually 100 ml), suspended in the water with a magnetic stirrer, and then a known volume was removed with a pipette. Stomach contents were processed in 10% volumetric sub-samples, and when at least 100 prey items were counted, the entire sample was extrapolated (sensu Pothoven et al. 2009, Gamble et al. 2011a, 2011b). Prior to any subsampling, large prey items (*Bythotrephes*, *Mysis*, *Diporeia*, larval fish, and chironomid species) were first enumerated completely and measured for each fish. This was done in part to avoid *Bythotrephes* spines, or

other large species, from compromising the integrity of the sub-sampling procedure. In Lake Superior samples, I used a modified sub-sampling procedure given the large stomachs of cisco and lake whitefish and resultant high number of prey items. First, I enumerated and measured all large prey items (*Bythotrephes*, *Mysis*, *Diporeia*, larval fish, and chironomid species) from an individual fish. With the remaining smaller diet items, however, I pooled up to 5 of the individual diets from a given fish species/size class that were collected from the same tow, following the protocol of Gamble et al. (2011a, 2011b). The processing of these pooled diet items followed the same sub-sampling routine as the Lake Michigan procedure (counting prey in the 10% subsample volume increments).

### **Fish Consumption Estimates**

Daily consumption ( $\text{g/m}^2$ ) of *Bythotrephes* was estimated for every species, at every site and date, when *Bythotrephes* was identified in at least one diet. Two methods of estimating consumption were used: bioenergetics modeling and daily ration modeling. Bioenergetics models for alewife, bloater, lake whitefish, round goby, and rainbow smelt within Wisconsin Sea Grant-Fish Bioenergetics 3.0 software were used to estimate consumption using each of the localized lake parameters. No changes were made from the original data compilation (Hanson et al. 1997), except for modifications to the bloater and generalized coregonid model where the mass dependence coefficient for swimming speed at all temperatures (RK4) was changed from 0.025 to 0.25 (Rudstam et al. 1994b) and the lake whitefish model where the respiration coefficient (RA) was changed from 0.0018 to 0.00138 (Madenjian et al. 2006a, 2013). For deepwater and slimy sculpin, a daily ration model was utilized (Mychek-Londer & Bunnell 2013) as bioenergetics models for these species have not been parameterized. Ninespine

stickleback *Pungitius pungitius*, which consumed  $<0.01$  *Bythotrephes* by dry weight and lacked a species specific bioenergetics model, did not receive a consumption estimate.

Where possible, inputs compiled for bioenergetics models were measured directly from collected individuals and sites. Temperature at each site, fish weights (Table 3), and individual diet proportions by species/size class were quantified as inputs into the model. Inputs such as energy densities of prey and predators were applied from previous research (Table 4).

Temperatures for bioenergetics model input were calculated from temperature profiles from SeaBird CTD. To estimate temperatures experienced by benthivores, I used lake hypolimnetic temperature. Estimated temperature experienced by planktivores was calculated as a single mean temperature weighted by density of a given species and size class in each 5-m vertical stratum of the water column.

Estimated proportion of maximum consumption (p-value) for bioenergetics models was derived from field data where possible or from previous studies. For a given species, I tracked modal length from size distributions across the sampling year to estimate growth of size classes through time. First, length-weight regressions were used to estimate beginning and end weight over a known time period. These were used to estimate p-value required to achieve this growth. This approach was possible for alewife (both size classes), Lake Michigan bloater (both size classes), and Lake Michigan and Superior rainbow smelt (both size classes).

When histograms could not be used to estimate fish growth, I relied on growth rates or p-values from previous studies. For round goby in Lake Michigan, I assumed a daily growth rate from previous research (Taraborelli et al. 2010, Lynch & Mensinger 2013). For cisco, lake whitefish, and bloater in Lake Superior, I applied conservative p-values associated with

maintenance ration because I was unable to track growth through length frequency, and the high likelihood of each species consuming large proportions of *Bythotrephes* (Gamble et al. 2011a, 2011b).

For deepwater and slimy sculpins, a daily ration model was used:

$$\text{daily ration (dry g prey consumed)} = \bar{S} / 100 \times 24 \text{ h} \times r (h - 1) \times \text{FDW}$$

where  $\bar{S}$  = index of fullness (g) as a function of body size, 24 = hours in a day,  $r$  = the slope coefficient from the gastric evacuation experiments, and FDW = fish dry weight (g) (Mychek-Londer & Bunnell 2013). This model was developed for temperatures  $\leq 6^\circ \text{C}$  and benthic temperatures during months of *Bythotrephes* consumption never exceeded this temperature.

Although  $\bar{S}$  was derived from Lake Michigan sculpins collected from January to May, I applied these estimates given that fish size, rather than season, appears to drive variability in index of fullness (Kraft & Kitchell 1986, Mychek-Londer & Bunnell 2013). Daily ration of the fish was applied to a wet: dry weight ratio for slimy sculpin (0.216) or deepwater sculpin (0.210) (Mychek-Londer & Bunnell 2013). Spoonhead sculpin consumed very low proportions of *Bythotrephes* (<0.01 by dry weight), so I chose not to estimate their consumption because no bioenergetics or daily ration model exists.

In each instance of *Bythotrephes* consumption by an individual species and size class, the daily consumption of an average individual was multiplied by the maximum density (#/ha) of fish on that date and site to achieve a potential population consumption estimate (total wet g consumed/m<sup>2</sup>). Biomass of *Bythotrephes* consumed per m<sup>2</sup> was converted to dry weight by applying a 0.12 dry weight ratio (Lehman & Cáceres 1993). After population consumption was modeled for a given species, size class, depth, and date, the consumption from all species were

summed to obtain a fish community consumption estimate that was compared to daily *Bythotrephes* production at that site, depth, and date.

### **Determining Biotic and Abiotic Influences on *Bythotrephes***

Control was determined based on fish consumption and *Bythotrephes* population declines, however additional evaluations were conducted to explain *Bythotrephes* changes. Statistical models were used to explore how abiotic and biotic factors along with fish consumption could explain variability in population dynamics of *Bythotrephes*. Pooling across both lakes, I developed a generalized additive model (GAM) (Wood 2006) within R 2.14.2 (R Core Team 2013) using the mgcv package (Wood 2011) to explore the relative explanatory power of epilimnetic water temperature, preferred zooplankton prey availability, bottom depth, site, and consumption by the fish community. *Bythotrephes* biomass in the month following estimated fish consumption was utilized as the response variable and transformed (natural log) to normalize its distribution. Depth was fit as either a linear covariate or a 3-level categorical variable. Site was fit as a 3-level categorical variable. Zooplankton prey of *Bythotrephes* (cladocerans, Schulz & Yurista 1999, cyclopoid adults, Dumitru et al. 2001, and calanoid and cyclopoid copepodites, Dumitru et al. 2001) was fit as a linear covariate and equaled the average biomass between the month when fish consumption was estimated and the following month (when *Bythotrephes* biomass was the response variable). Epilimnetic temperature (either collected from Seabird bathythermograph on dates when *Bythotrephes* were collected or estimated using Great Lakes Coastal Forecasting System) was similarly averaged over the same two months as zooplankton prey. Because epilimnetic temperature could be non-linearly related to *Bythotrephes* biomass (Yurista 1992), each model that included temperature was fit with either linear or spline smoothed temperature variables. My model assumed that these three response



variables (consumption, zooplankton prey, and temperature) were deterministic of future *Bythotrephes* biomasses. There were a total of 40 candidate models, and I calculated Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ) to select the most parsimonious model (Burnham & Anderson 2002). If  $\Delta AIC_c$  for a given model was less than 2, then those models were considered equivalent to the top-ranked model in terms of explanatory power.  $W_i$  determined weight of evidence in a model indicating the probability that the model was best given the data and set of candidate models (Burnham & Anderson 2001).

## **Results**

### ***Bythotrephes* Biomass**

In Lake Michigan, each instar of *Bythotrephes* was collected from July through October with few individuals collected in April and June. The biomass ( $\text{mg}/\text{m}^2$ ) varied between sites and depths. Highest overall abundances occurred in Sturgeon Bay (Figure 2). Temporal patterns differed between sites. For both sites, biomass was generally highest in September or October. Biomass typically increased from July through October at all depths in Sturgeon Bay, but Frankfort abundance and biomass declined across all depths in August. The only depth at which any *Bythotrephes* were found there in August was 110 m ( $9.58 \text{ mg}/\text{m}^2$  and  $2.30 \text{ mg}/\text{m}^2$ ). Within each site, biomass varied across depths: highest biomass occurred at the offshore depth for Sturgeon Bay ( $265.74 \text{ mg}/\text{m}^2$ ), whereas highest biomass was at an intermediate depth for Frankfort ( $85.96 \text{ mg}/\text{m}^2$ ). Trends for estimated production (corrected for day sampling bias) were similar to those of biomass, with highest production for Sturgeon Bay at 110 m ( $23.7 \text{ mg}/\text{m}^2$ ) in October. However, highest production in Frankfort was at 18 m ( $6.98 \text{ mg}/\text{m}^2$ ) in July, while maximum biomass there occurred at 46 m in October.

In Lake Superior, *Bythotrephes* was sampled from September through November at every depth (Figure 2 g, h, i), and was not found in April. Biomass generally decreased over time at all depths. Biomasses and densities for offshore samples (110-m) were generally lower in September and October than for nearshore samples (18 & 46-m). The highest biomass was in October at 18 m ( $88.6 \text{ mg}/\text{m}^2$ ) (Figure 2 g). Lake Superior *Bythotrephes* had highest production estimates in September (2.4, 3.3, and  $2.6 \text{ mg}/\text{m}^2$  with increasing depth intervals) as well as nearshore in October ( $2.90 \text{ mg}/\text{m}^2$ ). For months when *Bythotrephes* were collected, lowest production estimates were in November for all depths.

### **Fish Consumption of *Bythotrephes***

A total of 1160 planktivorous and benthivorous fishes collected from Lake Michigan during April, July, and September 2010 were analyzed for diet content (alewife n=345, bloater n=126, rainbow smelt n=189, round goby n=94, slimy sculpin n=266, deepwater sculpin n=140). Although numerous prey items were consumed (appendix tables 1-12), all species and size classes consumed some *Bythotrephes* throughout the year (Figure 3a), although the highest mean proportion of *Bythotrephes* (dry weight) was only 0.16. Pooling across months and depths, the species and size classes with diet proportions of at least 0.10 for *Bythotrephes* were large alewife (0.16), large rainbow smelt (0.15), and small bloater (0.16). Benthivorous round goby (0.07), slimy sculpins (0.05), and deepwater sculpin (<0.01), as well as small alewife (0.07), small rainbow smelt (0.05), and large bloater (<0.01) consumed marginal proportions of *Bythotrephes*.

A total of 685 planktivorous and benthivorous fishes were collected from Lake Superior during April, September, October, and November 2011 (rainbow smelt n=236, cisco n=101, lake whitefish n=161, bloater n=73, spoonhead sculpin n=114). Like Lake Michigan, diets varied by species and size classes (appendix tables 13-17). *Bythotrephes* was consumed by all species (Figure 3b), but was a rarer diet item for all but large cisco (0.43), small cisco (0.18), and small bloater (0.18).

### **Comparing Fish Consumption to *Bythotrephes* Production**

In Lake Michigan, my modeling and daily ration estimates indicated that most of the production of *Bythotrephes* was consumed by alewife with significant contributions from rainbow smelt and round goby in some instances (Figure 4 a-f). The ratio of consumption to production reached or exceeded 1.0 in 3 of 12 comparisons, but only in the nearshore zone in

July at Sturgeon Bay and September at both sites (Figure 4, 5a, and Appendix Tables 18-23). Consumption by alewife alone exceeded production of *Bythotrephes* in July at Sturgeon Bay. In September, consumption by several planktivores exceeded production at each nearshore site (Figure 4a, 4d). Across all months, highest consumption to production ratios primarily occurred nearshore (Figure 4a, d), somewhat lower ratios at intermediate depths (Figure 4b, e) and ratios near zero offshore (Figure 4c, f). In nearshore Lake Michigan, consumption exceeded production for 75% of my estimates (Figure 5a). Consumption in intermediate and offshore sites never exceeded production with the greatest ratio only reaching 0.14 in Sturgeon Bay in September.

In Lake Superior, consumption exceeded production due to cisco with minor contributions from other species. When it was present, cisco was the predominate consumer (Figure 3b). Consumption exceeded production in November at 46 m and September, October, and November at 110 m in Lake Superior (Figure 4g, h, Appendix Tables 24-25). Small and large cisco consumed between 1.4% and 839% of *Bythotrephes* production. The only other species to consume at least 5% of *Bythotrephes* production on a given site/day were small bloater (8%) and large lake whitefish (8.1%). Production was exceeded by consumption in four out of nine instances where *Bythotrephes* were sampled (Figure 5b) and consumption at the 110-m site always exceeded production. Conversely, at the intermediate depth, *Bythotrephes* production was exceeded by consumption at intermediate depths (46-m) only during November (Figure 5b). Nearshore (18-m) consumption of *Bythotrephes* was never observed and therefore production was never exceeded (Figure 5b).

## **Control of *Bythotrephes***

To determine whether *Bythotrephes* was controlled by fish planktivory, I evaluated whether *Bythotrephes* declined in the month following consumption exceeding production at a given depth and site. There were three instances for control to possibly occur in Lake Michigan at 18 m, but no control was supported as *Bythotrephes* biomass increased in the following month. For Lake Superior, there was one instance at 46 m and three instances at 110 m when control could possibly occur. Because December zooplankton samples were not collected, control could not be ascertained for November consumption estimates. Hence, only two cases of control could be evaluated (110 m in September and October) and both met control criteria as indicated by subsequent declines in *Bythotrephes* biomass.

## **Statistical Modeling**

AIC<sub>c</sub> model selection revealed a single model with a smoothed temperature variable as the most parsimonious with substantial support and weight of evidence (Table 5). Across both lakes, highest *Bythotrephes* biomass occurred at temperatures near 15°C, and the model predicted a non-linear relationship between *Bythotrephes* and temperature with *Bythotrephes* biomass increasing between 10 and 15°C, and then declining to the lowest values at ~22°C (Figure 6). Three other models had relatively low  $\Delta$  AIC<sub>c</sub> values (2.6-3.4), and each included temperature plus one additional variable (consumption by fish, preferred zooplankton prey, or sampling site) with weights of evidence from 16-10%. Overall, temperature had the greatest explanatory power for *Bythotrephes* dynamics in Lake Michigan and Lake Superior.

## Discussion

Numerous fish species in Lake Michigan and Lake Superior consumed *Bythotrephes*. Fitting with my first hypothesis, of the fish in Lake Michigan that consumed *Bythotrephes*, alewife at nearshore depths had the largest proportions in their diet. Fitting with my second hypothesis for Lake Superior, cisco consumed the largest proportions of *Bythotrephes* at deeper depths. Regardless of consumption, control of *Bythotrephes* was inconsistent throughout the lakes. Control of *Bythotrephes* was supported in none of the 12 possible instances in Lake Michigan. While consumption was higher than *Bythotrephes* production in some instances, populations of *Bythotrephes* never declined following this high consumption indicating a lack of control. Conversely, control of Lake Superior *Bythotrephes* was evident in both possible cases offshore, but never at intermediate depths countering my third hypothesis of control at all deeper depth locations in Lake Superior. While the estimates of consumption indicated that control of *Bythotrephes* by fishes was supported only in offshore depths of Lake Superior, the results of the GAM indicated that temperature was the best explanatory abiotic or biotic variable determining *Bythotrephes* changes across depths as well as lakes. These results countered my fourth hypothesis, that planktivory by fishes or resource limitation via *Bythotrephes* prey availability would facilitate *Bythotrephes* biomass in Lake Michigan and Lake Superior.

Of the explanatory variables analyzed in the GAM, temperature best explained *Bythotrephes* biomass changes. Previous research found that *Bythotrephes* mortality increased with increasing temperatures (Garton et al. 1990). In their laboratory experiments, mortality increased after exposure to temperatures above 15°C. My wild collected *Bythotrephes* biomasses were always highest at 15-16 °C, with lower values below 10°C and lowest values above 20°C, suggesting a narrow range of optimal temperature for production. Other field

studies have argued that temperatures above 24°C can negatively impact *Bythotrephes* abundance (Compton & Kerfoot 2004) or can even limit its North American distribution (Kerfoot et al. 2011). These decreases in biomass at higher temperatures could be linked to *Bythotrephes* physiological stress. Temperatures above 23°C limit respiratory and enzyme activity for *Bythotrephes* (Yurista 1999) which could lead to increased mortality and reduced production. Below these lethal temperatures, however, warmer epilimnetic temperatures (15-18°C) increase consumption by *Bythotrephes* (Yurista et al. 2010) and the length of their body and spine (Miehls et al. 2013). Other explanatory variables such as fish consumption or prey availability were not included in the most parsimonious model. Yet in relation to prey availability, Pangle & Peacor (2010) found that temperature, and not resource availability, regulated the growth rate of *Daphnia* species, another cladoceran. Overall temperature extremes appear to limit *Bythotrephes* via physiological stress and this stress likely reflects the lower biomasses I observed when temperatures were below 10°C and above 20°C.

There are two main caveats that should be taken into account when interpreting the GAM results. First, temperature was the most parsimonious explanatory variable, and it appears unlikely that, within the context of the AIC results, consumption by fish and prey availability were important explanatory variables. However, the second highest weight of evidence in the GAM models was a combination of temperature and consumption. Warmer temperatures do occur in late summer when previously gape-limited fishes become large enough to consume *Bythotrephes*. My results indicated that high temperatures correspond with decreased biomass of *Bythotrephes*, and that consumption was highest when *Bythotrephes* biomass was also high. Furthermore, my bioenergetics-derived estimation of consumption from the alewife population in Lake Michigan (the species that consumed most of *Bythotrephes* production) indicated a

positive correlation with temperature. But this positive correlation with temperature did not occur for cisco (the species which consumed most of *Bythotrephes* production in Lake Superior). In total, although consumption could have been a contributing factor to *Bythotrephes* population dynamics based on its inclusion in the second ranked GAM model, and the bioenergetics modeling, its effects were less direct than temperature. The second caveat to take into account is that not every other variable could have been included in the GAM. For example, fishhook water flea *Cercopagis pengoi* biomass was not included as it was ephemeral, occurred only in Lake Michigan, and only in Frankfort waters. Therefore, the presence or absence of *Cercopagis* in GAM models would have been a poor predictor of *Bythotrephes* biomass. While *Cercopagis* did occur when *Bythotrephes* was either low or absent, the probable combination of increased predation from fish on *Bythotrephes* and thus release from predation for *Cercopagis* (Witt & Cáceres 2004) or competitive interactions (sensu Pichlova-Ptácniková & Vanderploeg 2009) between the two invasive predatory cladocerans is a more probable explanation of their limited overlap. Whether consumption by fish or another factor caused densities of *Bythotrephes* to decrease concurrently with *Cercopagis* increases suggests that a complicated relationship exists and merits further research.

Consumption of *Bythotrephes* by planktivorous and benthivorous fishes varied with depth in Lake Michigan. Alewife, rainbow smelt, and round goby were the largest overall consumers of *Bythotrephes*. High alewife consumption of *Bythotrephes* was consistent with studies by Pothoven et al. (2007) and Storch et al. (2007) in Lake Michigan. Also overall consumption by all fishes was lower when offshore in deeper waters. Rainbow smelt consumed *Bythotrephes* primarily at nearshore depths. Previous research found that *Bythotrephes* comprised between 25 (Storch et al. 2007) and 27% (Lantry & Stewart 1993) of rainbow smelt diets. Mills et al. (1995)



documented rainbow smelt as shifting towards a diet including *Bythotrephes* when available in Lake Ontario. Lastly, the consumption of pelagic *Bythotrephes* by benthic round goby in the nearshore was somewhat unexpected given their respective habitat differences. However, Barton et al. (2005) indicated that round goby consumption of *Bythotrephes* represented active searching for prey in the water column, not just in benthos. Schaeffer et al. (2005) also frequently found *Bythotrephes* (86% frequency of occurrence) in diets for small (50-79 mm) round gobies in the 27-46-m depth range in Lake Huron. Each of these non-native fish species are typically associated with pelagic or benthic habitats, but each demonstrated an ability to consume a primarily epilimnetic zooplankton.

Fish consumption of *Bythotrephes* in Lake Superior contrasted with Lake Michigan. In Lake Superior, consumption of *Bythotrephes* never occurred at nearshore depths. But similar to Lake Michigan, *Bythotrephes* was a diet item for numerous species. Cisco, rainbow smelt, bloater, lake whitefish, and spoonhead sculpin were all consumers of *Bythotrephes* in Lake Superior. My finding that cisco dominated the consumption of *Bythotrephes* at intermediate and offshore depths was corroborated by Gamble et al. (2011a, 2011b), who reported that diets of cisco in Lake Superior were comprised of *Bythotrephes* in both the summer (63%) and fall (37%), with fall diets switching to a predominance of *Mysis* (63%). Young et al. (2009) suggested that once *Bythotrephes* become abundant in smaller Ontario lakes, cisco search for them as a prey item. My fall cisco diets at 110 m included at least 78% *Bythotrephes* consumption by large individuals and variable (0-87%) consumption by small individuals, suggesting that *Bythotrephes* remain a preferred prey item for cisco. Cisco is a key predator of *Bythotrephes* in Lake Superior given its high proportions in its diets, its high ratio of

consumption to *Bythotrephes* production, and conclusion that cisco was associated with control in Lake Superior.

Evidence of control by cisco in Lake Superior was limited to the offshore site in September and October. It was possible that they also controlled *Bythotrephes* in November at intermediate depths (46-m) and offshore depths (110-m), but thus could not be confirmed due to a lack of sampling in December. Furthermore, in Lake Superior, the low density of *Bythotrephes* offshore contrasts reports from Keweenaw Bay of higher offshore densities (Barnhisel & Kerfoot 2004). However, my result was corroborated by another Lake Superior study that revealed *Bythotrephes* attained a lower overall biomass at sites deeper than 30 m (Sierszen et al. 2011). Once *Bythotrephes* increase in abundance, cisco selectivity of *Bythotrephes* remains high even when densities of this prey decline (Young et al. 2009). Therefore, whenever there is any overlap between the species, consumption is likely to be high. Cisco remain pelagic in the water column (Yule et al. 2007, 2008), as well as at intermediate to offshore depths (Muir et al. 2013). The combination of cisco preferring epilimnetic *Bythotrephes* and remaining high in the water column over deeper waters provides an explanation as to why consumption was greater than production at these offshore locations and not nearshore where spatial overlap could potentially be higher. The offshore habitat selection of Lake Superior cisco could explain the consistent lack of nearshore consumption and higher nearshore biomasses of *Bythotrephes*.

While consumption was greater than *Bythotrephes* production in some instances, there are several possible explanations why control could have existed in the Lake Michigan nearshore, but was never detected. First, fish consumption was generally greater than *Bythotrephes* production at this depth, and even though *Bythotrephes* are known to remain epilimnetic in the water column, they likely have limited refuge from predation relative to the 46

m or 110 m where planktivorous fish likely occur in deeper water than epilimnetic (Lehman & Cáceres 1993). Although this nearshore overlap between *Bythotrephes* and fish would suggest that control could occur through excessive consumption, control was not detected. Second, the planktonic nature of *Bythotrephes* could influence my biomass estimates at our fixed sampling sites. Relatively slow planktonic swimming speeds (Muirhead & Sprules 2003) as well as lake currents (Watson 1974, Churchill et al. 2004, Compton & Kerfoot 2004) have been shown to affect zooplankton populations by upwelling occurrences that can transport zooplankton to new locations. Zooplankton such as *Bythotrephes* are likely equally susceptible to these occurrences. Third, the monthly sampling frequency might be too long to measure the response of zooplankton to excessive consumption. Because *Bythotrephes* typically exhibit a 2-week life cycle (i.e., time from neonate to primiparity) shorter-term declines caused by fish consumption could have been missed in my study. Together, the caveats indicate the potential difficulty in detecting the effect of various abiotic and biotic factors on *Bythotrephes* population dynamics when sampling occurred monthly at fixed sites, such as the Lake Michigan nearshore where my bioenergetics modeling suggested that predation could be regulating *Bythotrephes* population dynamics.

One other issue related to sampling is that *Bythotrephes* were collected using a zooplankton net during the day. Due to the reaction time (Muirhead & Sprules 2003), and possible light sensitivity (Pangle & Peacor 2009) of *Bythotrephes*, a day:night correction factor was used to account for possible net avoidance. Based on the greater abundance ( $1.88X \pm 0.76$ ; mean  $\pm$ SD) and biomass ( $2.06X \pm 0.90$ ; mean  $\pm$ SD) of *Bythotrephes* collected at night, *Bythotrephes* appeared to be avoiding nets. While there is confidence in the correction factor due to the sample size (n=16), it could have affected my conclusions regarding whether control

occurred. To explore the effect of this correction factor, I compared my results in each lake to two scenarios: 1) no application of the correction factor and 2) increasing the correction factor to an even higher estimate (2.96, which adds the highest SD to the mean correction factor). These changes would only affect the first prerequisite for control (i.e., whether consumption exceeded production). If I did not use this correction factor, then consumption would exceed production for 75% of the collections at 18 m, 50% at 46-m, and 0 % at 110 m in Lake Michigan. However control would still not have occurred in Lake Michigan because significant declines were not observed following these time periods. Completing the same exercise of ignoring the correction factor caused estimated consumption in Lake Superior to exceed production 66% of the collections at 46 m and 100% at 110 m. But the number of instances of control would not change. Increasing the correction factor to an even higher estimate resulted in consumption exceeding production only 25% of the collections at 18 m, 0% at 46 m, and 0% at 110 m in Lake Michigan but still control would not exist. Increasing the correction factor for Lake Superior would cause consumption to exceed production in only 33% of the instances for both 46 m and 110 m. Furthermore, because these excesses occurred in November, our previous conclusion that control existed in September and October would no longer be supported in Lake Superior. Considering these scenarios and the disparity between day and night sampling, future collections of *Bythotrephes* should take place at night to avoid any potential bias of daytime net avoidance.

Another set of caveats existed with estimating consumption from bioenergetics modeling. Limited periodic fish sampling prevented estimation of growth rates more frequently and growth estimates over shortened time periods would be a more appropriate method for estimating p-value and thus fish consumption. Secondly, estimated high consumption values above those of production did not always result in control. These results are similar to those of other

bioenergetics studies and comparisons where zooplankton production was exceeded by predatory demand of pelagic planktivorous fishes in Lake Ontario (Rand et al. 1995). Similarly Rand & Stewart (1998) found that up to 100% of alewife could be consumed by salmonines in Lake Ontario. Rudstam et al. (1994b) also found varying degrees of consumption, and even when consumption was high, they did not find corresponding declines in zooplankton. Finally, Bunnell et al. (2011) reported consumption by *Bythotrephes* alone should exceed zooplankton production in Lake Huron, yet zooplankton did not always decline in the month following excessive consumption. Given these estimates of large proportions or even the biomass of entire populations being potentially consumed, high values of consumption do not always translate into measurable declines in the prey population. Whether these results are due to poorly estimated modeling or sampling efforts, it suggests that better estimates of prey and predator abundances are needed in such endeavors involving fish consumption of various prey items.

This study represents a complementary look at both biotic and abiotic factors that could influence invasive *Bythotrephes*. Across both lakes, epilimnetic temperature was the most important explanatory variable contributing to *Bythotrephes* biomass changes. Therefore temperature regimes could play a greater role in predicting *Bythotrephes* future success. Numerous fish consumed *Bythotrephes*, yet the ability of these species to control *Bythotrephes* was limited. Consumption primarily by cisco, along with other native and non-native species, at offshore depths in Lake Superior resulted in a few instances of control of *Bythotrephes*. In the Lake Michigan nearshore, *Bythotrephes* were consumed primarily by non-native species alewife, rainbow smelt, and round goby. But even when consumption was greater than production, control did not occur in Lake Michigan. Top-down control via fish consumption of *Bythotrephes* appeared to be unlikely based on these results. However, given their consumption of

*Bythotrephes*, alewife in Lake Michigan and cisco in Lake Superior could still influence *Bythotrephes*, regardless of the inability to consistently control this invasive zooplankton. While my definition of control was based on consumption, it is likely not the main driver of *Bythotrephes* dynamics and results indicated population changes are more interconnected to abiotic factors. This study indicates the difficulty in determining a sole deterministic factor for invasive species dynamics, and attempting to control or limit their proliferation requires an understanding of a multitude of variables. Efforts in understanding *Bythotrephes* should focus not only on which species consume them or what lake they inhabit, but at what depths they are consumed, and what temperatures a given population experiences. This work demonstrates the importance in acknowledging the complexity of lake food webs while attempting to understand biotic and abiotic factors contributing to energy transfers.

Table 1: Regressions used to predict dry weight of invertebrates in Lake Michigan and Lake Superior.

Taxa	Length-weight regression	Source
<i>Bythotrephes longimanus</i>	$10^{1.428(\log \text{ spine length, mm}) + 1.670}$	Garton & Berg (1990)
<i>Cercopagis pengoi</i>	$e^{2.37 + 1.716(\log \text{ body length, mm})}$	Makarewicz et al. (2001)
Calanoid species	$e^{2.46(\log \text{ length, mm}) + 1.05}$	Pace & Orcutt (1981)
<i>L. macrurus</i>	$e^{3.01(\log \text{ length, mm}) + 0.71}$ (April) $e^{3.01(\log \text{ length, mm}) + 0.71}$ (May) $e^{3.78(\log \text{ length, mm}) + 0.54}$ (June) $e^{3.01(\log \text{ length, mm}) + 0.71}$ (July) $e^{1.85(\log \text{ length, mm}) + 2.78}$ (August) $e^{0.6218(\log \text{ length, mm}) + 2.6197}$ (September) $e^{0.6218(\log \text{ length, mm}) + 2.6197}$ (October)	Doubek & Lehman (2011)
Cyclopoid species	$e^{3.23(\log \text{ length, mm}) + 2.2266}$	Pace & Orcutt (1981)
<i>Mesocyclops edax</i>	$e^{3.97(\log \text{ length, mm}) + 1.66}$	Rosen (1981)
Chironomid	$e^{2.32(\log \text{ length, mm}) - 5.279}$	Smock (1980)
<i>Dreissena</i>	$FW = 37 \text{ length}^2 - 2.64 \text{ length} + 0.058207$ $DW = 0.5 \times DW$	Hillbricht-Ilkowska & Stanczykowska (1969) Sprung (1993)
<i>Diporeia</i>	$0.0067 \times (\text{length, mm})^{3.0232}$	Winnell & White (1984)
<i>Mysis</i>	$(6.18 \times \text{antennal length}) + 0.5$ $e^{2.86(\log \text{ length, mm}) - 6.1709}$	Grossnickle & Beeton (1979) Shea & Makarewicz (1989)
Cladoceran species	$e^{2.56(\log \text{ length, mm}) + 1.51}$	Rosen (1981)
<i>Daphnia mendotae</i>	$e^{2.56(\log \text{ length, mm}) + 1.51}$	Dumont et al. (1975)
<i>Bosmina</i>	$e^{2.53(\log \text{ length, mm}) + 2.71}$	Bottrell et al. (1976)

Table 2: Sizes used to separate fish species in Lake Michigan and Lake Superior into different size classes.

Lake	Species Common Name	Size Class, mm total length (TL)	
		Small	Large
Michigan	Alewife	<110	≥110
	Bloater	<120	≥120
	Rainbow Smelt	<90	≥90
Superior	Cisco	<260	≥260
	Bloater	<240	≥240
	Rainbow Smelt	<90	≥90
	Lake Whitefish	<160	≥160



Table 3: Total length (mm) to weight (g) regressions from collected fish in Lake Michigan 2010 and Lake Superior 2011.

Lake	Species	Length (mm) to weight (g) regression
Michigan	Alewife	$= 8.06^{-6} \text{ Total length}^{2.98}$
	Bloater	$= 5.16^{-6} \text{ Total length}^{3.06}$
	Rainbow Smelt	$= 2.96^{-6} \text{ Total length}^{3.11}$
	Round Goby	$= 2.85^{-6} \text{ Total length}^{3.36}$
	Slimy Sculpin	$= 3.48^{-6} \text{ Total length}^{3.30}$
	Deepwater Sculpin	$= 3.09^{-6} \text{ Total length}^{3.23}$
Superior	Cisco	$= 3.00^{-6} \text{ Total length}^{3.18}$
	Bloater	$= 4.12^{-5} \text{ Total length}^{2.68}$
	Rainbow Smelt	$= 5.89^{-7} \text{ Total length}^{3.46}$
	Lake Whitefish	$= 1.68^{-6} \text{ Total length}^{3.27}$

Table 4: Prey and predator energy densities (J/g) used for bioenergetics modeling of fishes in Lake Michigan and Lake Superior.

Taxa	Energy Density Value (J/g) or Equation	Source
<i>Bythotrephes</i>	1674	Lantry & Stewart (1993)
Calanoid	2300	Cummins & Wuycheck (1971)
Cladocerans	2412	Cummins & Wuycheck (1971)
Cyclopoid	2300	Cummins & Wuycheck (1971)
<i>Diporeia</i>	4185	Stewart & Binkowski (1986)
Dipteran	2746	Cummins & Wuycheck (1971)
Insect	3138	Lantry & Stewart (1993)
Bivalves/ <i>Dreissena</i>	2427	Schneider (1992)
<i>Mysis</i>	4604	Stewart & Binkowski (1986)
Unidentified Fish	4435	Lantry & Stewart (1993)
Alewife	Small-4493 (April), 4059 (July), 4703 (September) Large-5665 (April), 4184 (July), 5741 (September)	Madenjian et al. (2006b)
Rainbow Smelt	$3730.6 + (111.73 \times \text{Wet Weight, g})$	Lantry & Stewart (1993)
Round Goby	4600	Lee & Johnson (2005)
Cisco	6517	Pangle et al. (2004)
Bloater	$(22.5 \times \text{Total Length, mm}) + 2397$	Pothoven et al. (2012)
Lake Whitefish	$5211 + (2.543 \times (\text{Wet Weight, g}))$	Madenjian et al. (2006a)

Table 5: Summary of the 10 generalized additive models with the lowest corrected Aikaike's Information Criterion ( $AIC_c$ ) values used to explain *Bythotrephes* biomass ( $\mu\text{g}/\text{m}^2$ ) at two Lake Michigan sites (2010) and one Lake Superior site (2011). Each model was ranked according to its  $\Delta AIC_c$  value and its corresponding Aikaike weight ( $w$ , given the probability that a given model is best). Model variable abbreviations were: Temp=epilimnetic temperature ( $^{\circ}\text{C}$ ), Cons=consumption on *Bythotrephes*, Zpprey=preferred zooplankton prey available to *Bythotrephes*, Site=one of the three study sites, and Depth=depth at each site. Subscript f indicates a categorical variable.

Model Rank	Model of Explanatory Variables	$AIC_c$	$\Delta AIC_c$	$w$	$R^2$
1	s(Temp)	43.711	0	0.561	0.839
2	s(Cons) + s(Temp)	46.263	2.552	0.157	0.846
3	s(Temp) + s(Zpprey)	47.006	3.295	0.108	0.840
4	Site <sub>f</sub> + s(Temperature)	47.107	3.396	0.103	0.870
5	s(Cons) + s(Temp) + s(Zpprey)	50.113	6.402	0.023	0.847
6	Depth <sub>f</sub> + s(Temp)	50.440	6.729	0.019	0.844
7	Site <sub>f</sub> + s(Cons) + s(Temp)	51.444	7.733	0.012	0.872
8	Site <sub>f</sub> + s(Temp) + s(Zpprey)	51.593	7.882	0.011	0.871
9	Depth <sub>f</sub> + s(Cons) + s(Temp)	54.190	10.479	0.003	0.851
10	Depth <sub>f</sub> + s(Temp) + s(Zpprey)	55.181	11.470	0.002	0.857

Figure 1: Maps of sampling sites and nearby port cities for Lake Michigan in top inset and Lake Superior in bottom left inset. Sampling sites are indicated by enclosed circles and local port cities are open squares.

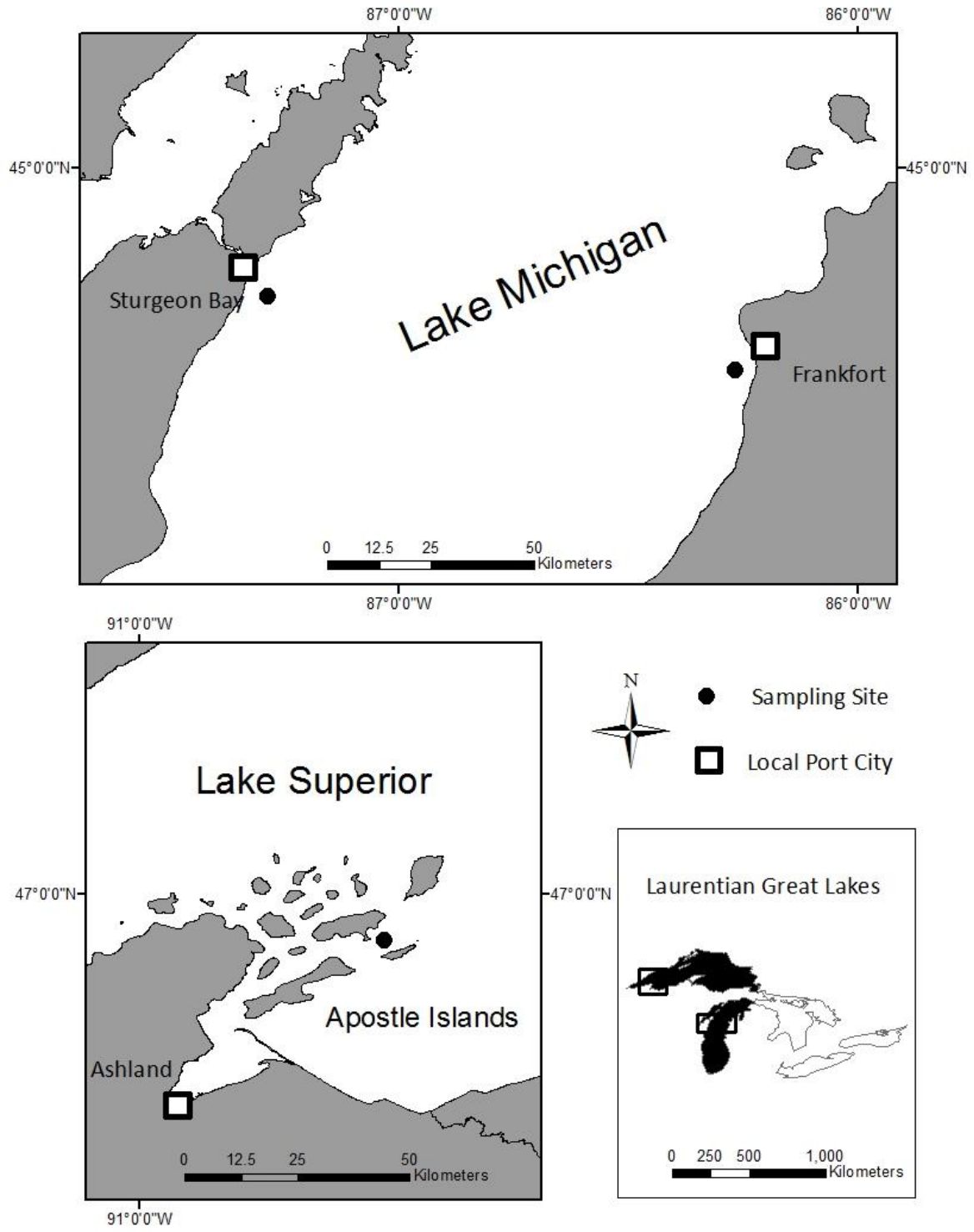


Figure 2: Seasonal changes in dry weight biomass (mean $\pm$ SE) of daytime collected *Bythotrephes* (mg/m<sup>2</sup>) compared between Lake Michigan sites of Frankfort (FF -a, b, and c) and Sturgeon Bay (SB-d, e, and f) and Lake Superior site in the Apostle Islands (AI-g, h, and i) across depths (m) and months.

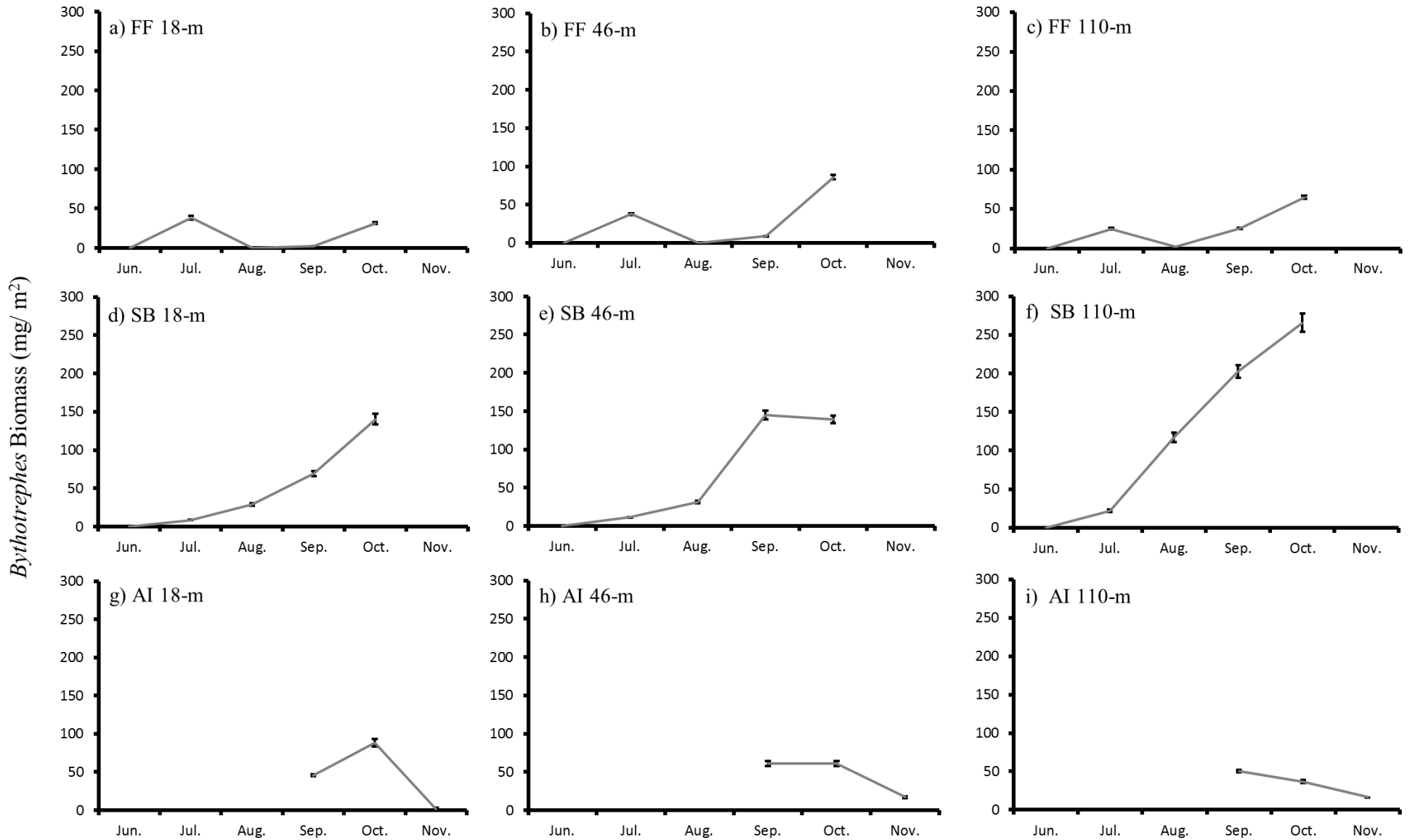


Figure 3: Overall proportion (mean $\pm$ SE) of *Bythotrephes* (dry weight) in diets of fishes by size class from a) Lake Michigan and b) Lake Superior. LW=lake whitefish, SS=slimy sculpin, DWS=deepwater sculpin, Spoon=spoonhead sculpin, and RG=round goby.

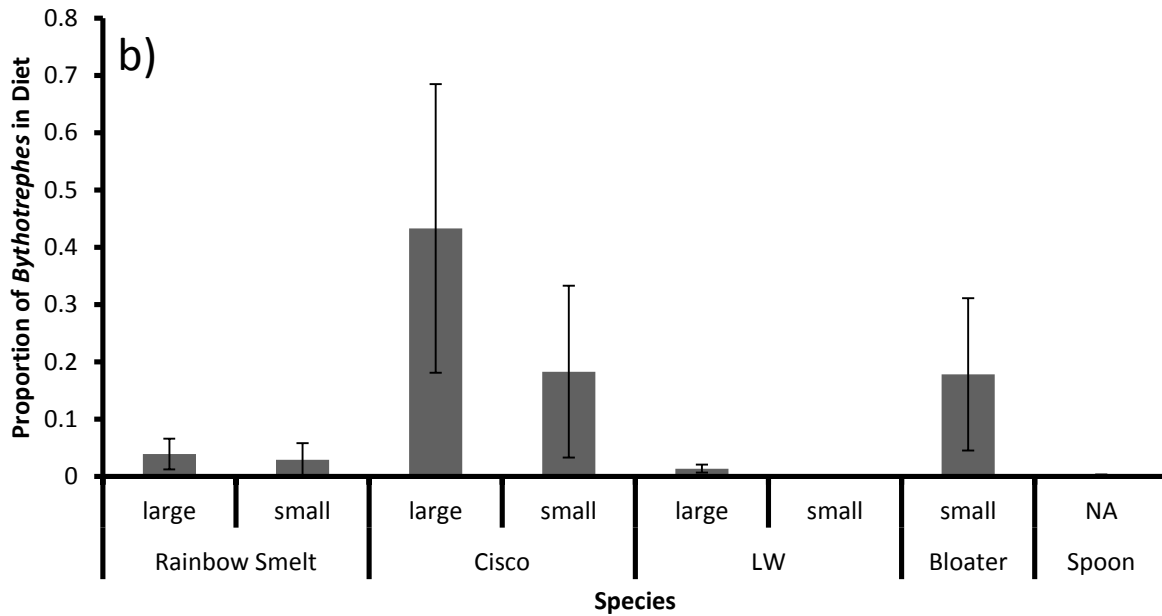
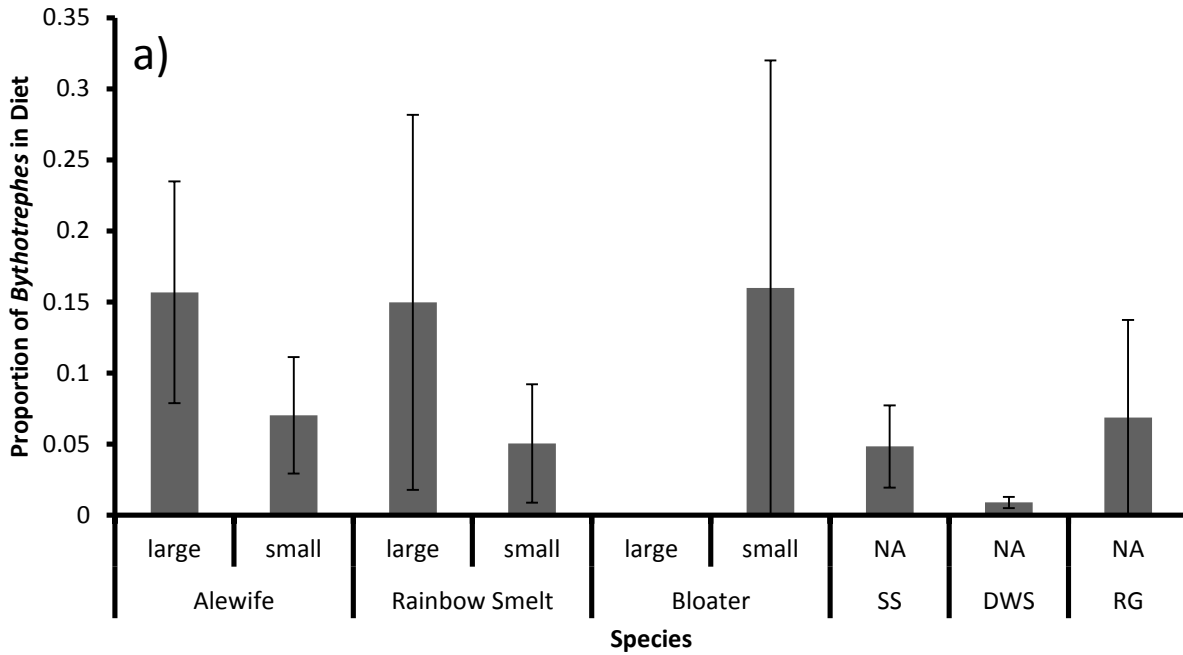


Figure 4: Ratio of fish community consumption of *Bythotrephes* to production in Lake Michigan offshore of Frankfort, MI (upper graphs), and Sturgeon Bay, WI (middle graphs), and Lake Superior at the Apostle Islands, WI (lower graphs). Ratios meeting or exceeding one are indicated by an asterisk. *Bythotrephes* were never consumed by fish at the 18-m location in Lake Superior.

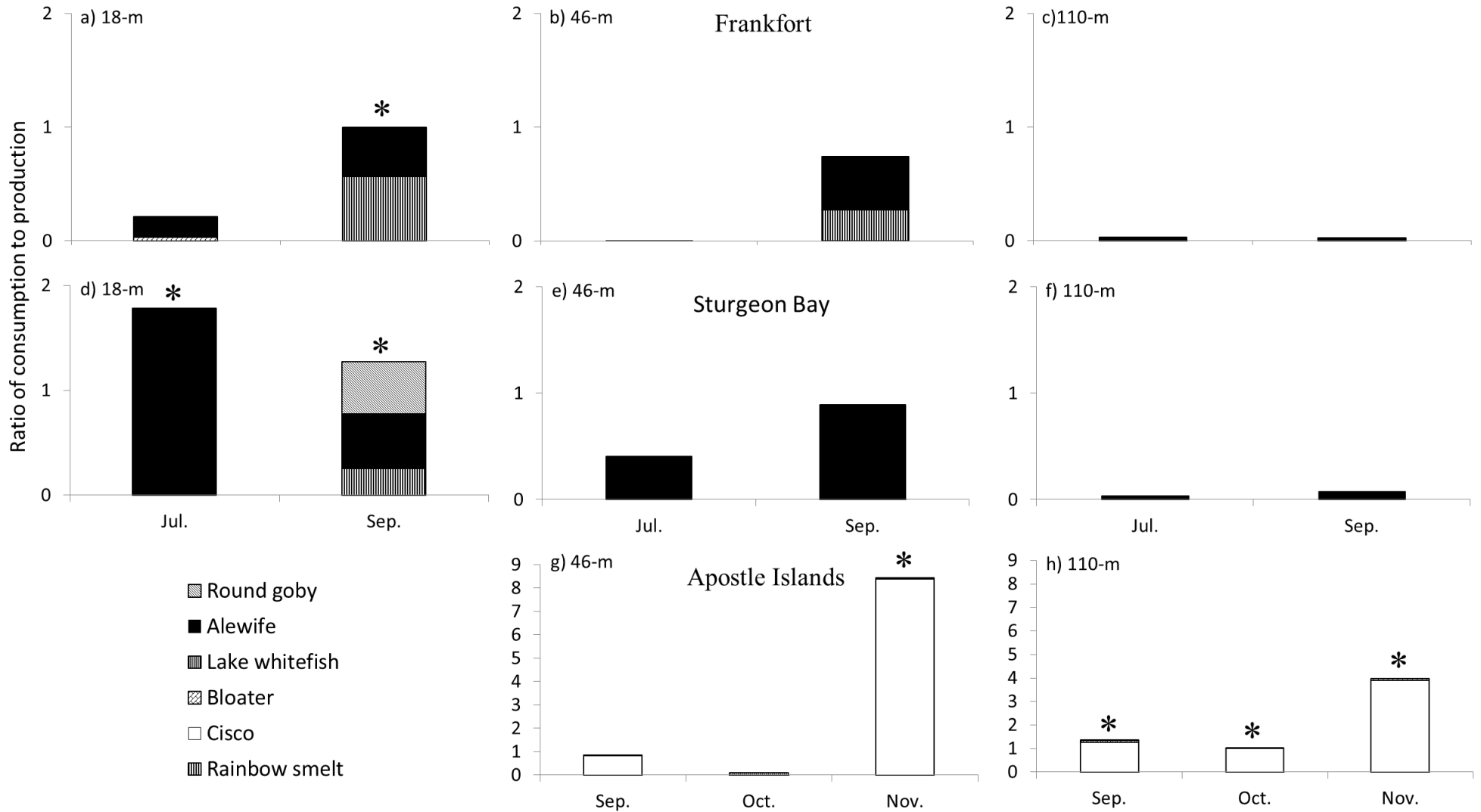


Figure 5: Proportion of instances when estimated consumption by fish on *Bythotrephes* equaled or exceeded 100% of production of *Bythotrephes* across depths at Lake Michigan sites (a) and the single Lake Superior site (b). Number (n) of comparisons listed above each bar.

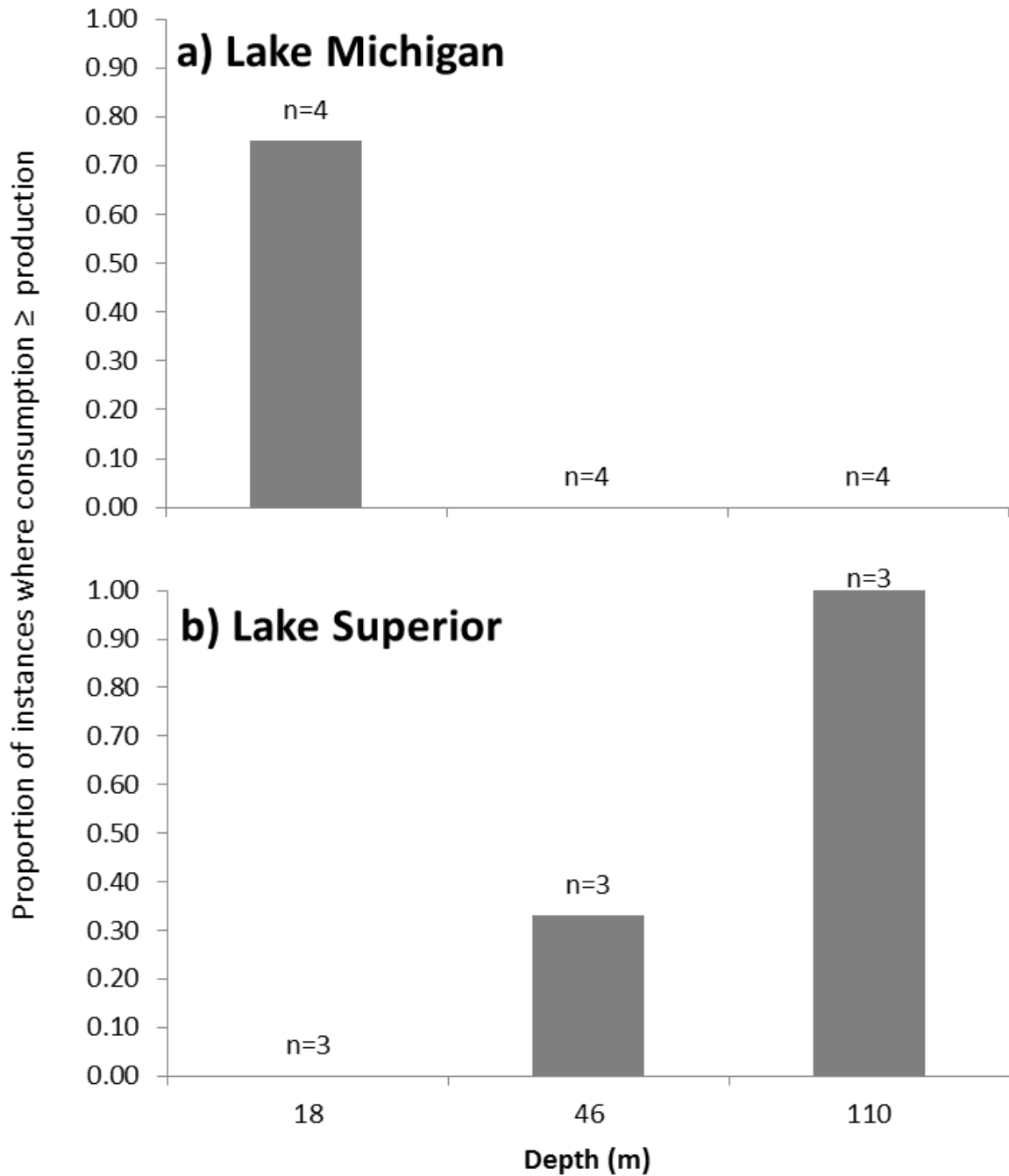
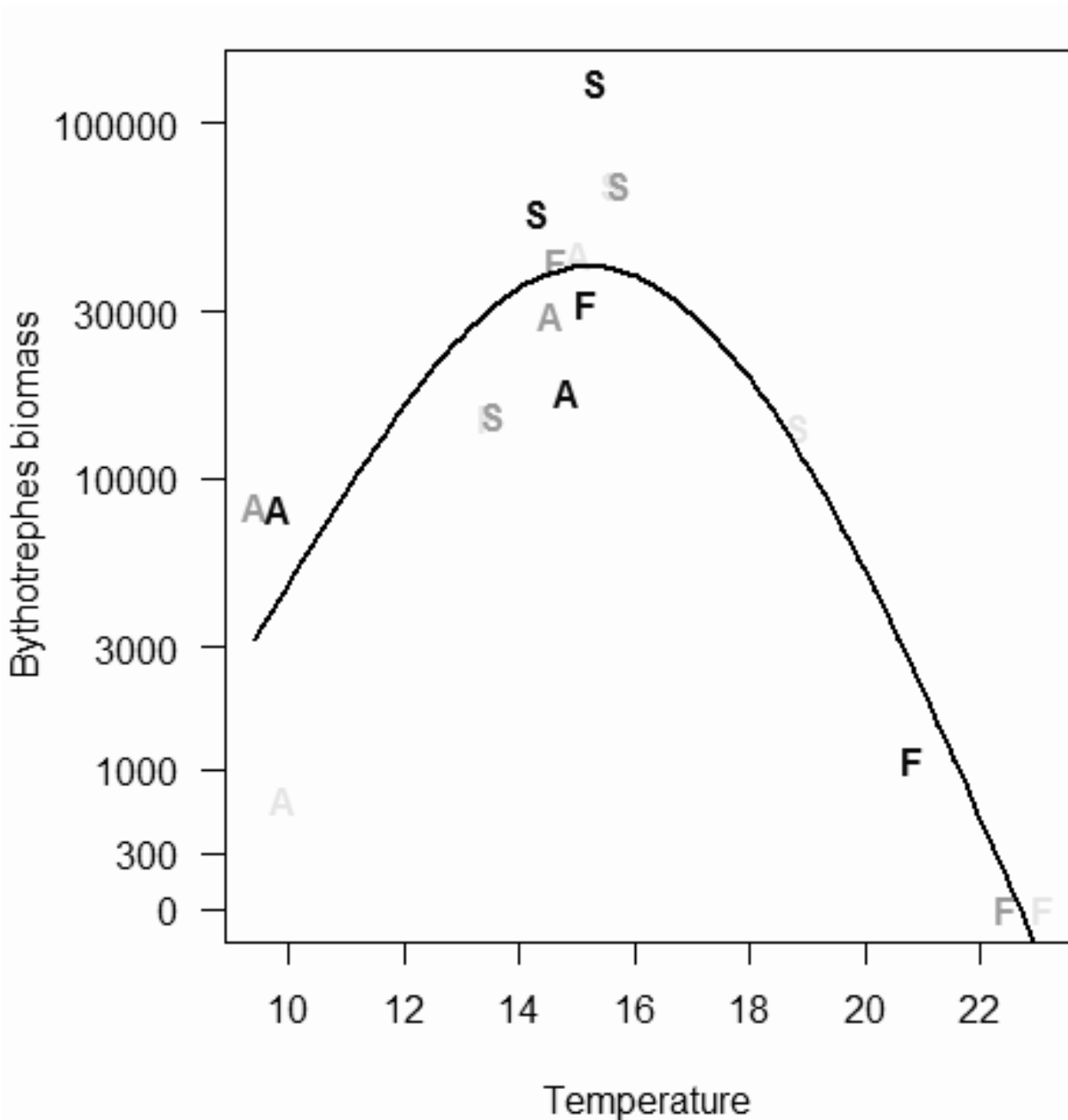




Figure 6: Most parsimonious ( $\Delta AIC_c$  less than 2) generalized additive model with explanatory variable smoothed epilimnetic temperature best explaining *Bythotrephes* biomass ( $\mu\text{g}/\text{m}^2$ ).

Biomasses and temperatures from Lake Michigan (F=Frankfort, MI, S=Sturgeon Bay, WI) and Lake Superior (A=Apostle Islands, WI). Near to offshore depths represented by light to dark hues.



## Literature Cited

- Anonymous. 2003. Standard Operative Procedure for Zooplankton Analysis. U.S. Environmental Protection Agency, Great Lakes National Program Office (2003) Report LG403.
- Barbiero, R. P., & Tuchman, M. L. 2004. Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. Canadian Journal of Fisheries and Aquatic Sciences, 61(11), 2111-2125.
- Barnhisel, D. R., & Harvey, H. A. 1995. Size-specific fish avoidance of the spined crustacean *Bythotrephes*: field support for laboratory predictions. Canadian Journal of Fisheries and Aquatic Sciences, 52(4), 768-775.
- Barnhisel, R.D., & Kerfoot, C.W. 2004. Fitting into food webs: behavioral and functional response of young lake trout (*Salvelinus namaycush*) to an introduced prey, the spiny cladoceran (*Bythotrephes cederstroemi*). Journal of Great Lakes Research, 30, 300-314.
- Barton, D. R., Johnson, R. A., Campbell, L., Petruniak, J., & Patterson, M. 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002–2004. Journal of Great Lakes Research, 31, 252-261.
- Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., & Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology, 24.
- Branstrator, D. K., & Lehman, J. T. 1996. Evidence for predation by young-of-the-year alewife and bloater chub on *Bythotrephes cederstroemi* in Lake Michigan. Journal of Great Lakes Research, 22(4), 917-924.
- Bunnell, D. B., Davis, B. M., Warner, D. M., Chriscinske, M. A., & Roseman, E. F. 2011. Planktivory in the changing Lake Huron zooplankton community: *Bythotrephes* consumption exceeds that of Mysis and fish. Freshwater Biology, 56(7), 1281-1296.
- Bunnell, D. B., Keeler, K. M., Puchala, E. A., Davis, B. M., & Pothoven, S. A. 2012. Comparing seasonal dynamics of the Lake Huron zooplankton community between 1983–1984 and 2007 and revisiting the impact of *Bythotrephes* planktivory. Journal of Great Lakes Research, 38(3), 451-462.
- Bur, M. T., Klarer, D. M., & Krieger, K. A. 1986. First records of a European cladoceran, *Bythotrephes cederstroemi*, in Lakes Erie and Huron. Journal of Great Lakes Research, 12(2), 144-146.
- Burnham, K. P., & Anderson, D. R. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife research, 28(2), 111-119.

- Burnham, K. P. & Anderson, D. R. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer, New York.
- Carpenter, S. R., Kitchell, J. F., & Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. *BioScience*, 35(10), 634-639.
- Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. *Journal of the Fisheries Board of Canada*, 31(5), 827-854.
- Churchill, J.H., Kerfoot, W.C., & Auer, M.T. 2004. Exchange of water between the Keweenaw Waterway and Lake Superior: characteristics and forcing mechanisms. *J. Great Lakes Res.* 30 (Suppl. 1):55–63.
- Compton, J. A., & Kerfoot, C.W. 2004. Colonizing inland lakes: consequences of YOY fish ingesting the spiny cladoceran (*Bythotrephes cederstroemi*). *Journal of Great Lakes Research*, 30, 315-326.
- Cullis, K. I., & Johnson, G. E. 1988. First evidence of the cladoceran *Bythotrephes cederstroemi*, Schoedler in Lake Superior. *Journal of Great Lakes Research*, 14(4), 524-525.
- Cummins, K. W., & Wuycheck, J. C. 1971. Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* 18:1-158.
- Dettmers, J. M., & Stein, R. A. 1992. Food consumption by larval gizzard shad: zooplankton effects and implications for reservoir communities. *Transactions of the American Fisheries Society*, 121(4), 494-507.
- Doubek, J. P., & Lehman, J. T. 2011. Historical biomass of *Limnocalanus* in Lake Michigan. *Journal of Great Lakes Research*, 37(1), 159-164.
- Dumitru, C., Sprules, W. G., & Yan, N. D. 2001. Impact of *Bythotrephes longimanus* on zooplankton assemblages of Harp Lake, Canada: an assessment based on predator consumption and prey production. *Freshwater Biology*, 46(2), 241-251.
- Dumont, H. J., Van de Velde, I., & Dumont, S. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, 19(1), 75-97.
- Evans, M. S. 1988. *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. *Journal of Great Lakes Research*, 14(2), 234-240.
- Fleischer, G. W., Argyle, R. L., & Curtis, G. L. 1997. In situ relations of target strength to fish size for Great Lakes pelagic planktivores. *Transactions of the American Fisheries Society*, 126(5), 786-794.

- Foster, S. E., & Sprules, W. G. 2009. Effects of the *Bythotrephes* invasion on native predatory invertebrates. *Limnology and Oceanography*, 54(3), 757-769.
- Gamble, A. E., Hrabik, T. R., Stockwell, J. D., & Yule, D. L. 2011a. Trophic connections in Lake Superior part I: the offshore fish community. *Journal of Great Lakes Research*, 37(3), 541-549.
- Gamble, A. E., Hrabik, T. R., Yule, D. L., & Stockwell, J. D. 2011b. Trophic connections in Lake Superior part II: the nearshore fish community. *Journal of Great Lakes Research*, 37(3), 550-560.
- Garton, D. W., & Berg, D. J. 1990. Occurrence of *Bythotrephes cederstroemi* (Schoedler 1877) in Lake Superior, with Evidence of Demographic Variation within the Great Lakes. *Journal of Great Lakes Research*, 16(1), 148-152.
- Garton, D. W., Berg, D. J., & Fletcher, R. J. 1990. Thermal tolerances of the predatory cladocerans *Bythotrephes cederstroemi* and *Leptodora kindtii*: relationship to seasonal abundance in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(4), 731-738.
- Grossnickle, N. E., & Beeton, A. M. 1979. Antennal scale length as a measure of relative size in the opossum shrimp, *Mysis Relicta* Loven. *Crustaceana*, 36(2), 141-146.
- Hanson, P. C., Johnson, T. B., Schindler, D. E., & Kitchell, J. F. 1997. Fish bioenergetics 3.0. University of Wisconsin, Sea Grant Institute. Center for Limnology.
- Hillbricht-Ilkowska, A., & Stanczykowska, A. 1969. The production and standing crop of planktonic larvae of *Dreissena polymorpha* (Pall.) in two Mazurian lakes. *Pol. Arch. Hydrobiol*, 16(29), 193-203.
- Hoffman, J. C., Smith, M. E., & Lehman, J. T. 2001. Perch or plankton: top-down control of *Daphnia* by yellow perch (*Perca flavescens*) or *Bythotrephes cederstroemi* in an inland lake? *Freshwater Biology*, 46(6), 759-775.
- Keilty, T. J. 1990. Evidence for alewife (*Alosa pseudoharengus*) predation on the European cladoceran *Bythotrephes cederstroemi* in northern Lake Michigan. *Journal of Great Lakes Research*, 16(2), 330-333.
- Kerfoot, W. C., Yousef, F., Hobmeier, M. M., Maki, R. P., Jarnagin, S. T., & Churchill, J. H. 2011. Temperature, recreational fishing and diapause egg connections: dispersal of spiny water fleas (*Bythotrephes longimanus*). *Biological Invasions*, 13(11), 2513-2531.
- Kraft, C. E., & Kitchell, J. F. 1986. Partitioning of food resources by sculpins in Lake Michigan. *Environmental Biology of Fishes*, 16(4), 309-316.

- Lantry, B. F., & Stewart, D. J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. *Transactions of the American Fisheries Society*, 122(5), 951-976.
- Lee, V. A., & Johnson, T. B. 2005. Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). *Journal of Great Lakes Research*, 31(2), 125-134.
- Lehman, J. T. 1991. Causes and consequences of cladoceran dynamics in Lake Michigan: Implications of species invasion by *Bythotrephes*. *Journal of Great Lakes Research*, 17(4), 437-445.
- Lehman, J. T., & Cáceres, C. E. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Limnology and Oceanography*, 38(4), 879-891.
- Link, J. 1996. Capture probabilities of Lake Superior zooplankton by an obligate planktivorous fish—the lake herring. *Transactions of the American Fisheries Society*, 125(1), 139-142.
- Lodge, D. M. 2001. Responses of lake biodiversity to global changes. In future scenarios of global biodiversity (ed. F. S. Chapin III, O. E. Sala & E. Huber-Sannwald), pp. 277–312. New York: Springer
- Lynch, M. P., & Mensinger, A. F. 2013. Temporal patterns in growth and survival of the round goby *Neogobius melanostomus*. *Journal of fish biology*, 82(1), 111-124.
- Madenjian, C. P., Fahnenstiel, G. L., Johengen, T. H., Nalepa, T. F., Vanderploeg, H. A., Fleischer, G. W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, E.S., Lavis, D.S., Roberston, D.M., Jude, D.J., & Ebener, M. P. 2002. Dynamics of the Lake Michigan food web, 1970-2000. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(4), 736-753.
- Madenjian, C. P., O'Connor, D. V., Pothoven, S. A., Schneeberger, P. J., Rediske, R. R., O'Keefe, J. P., Bergstedt, R.A., Argyle, R.L., & Brandt, S. B. 2006a. Evaluation of a lake whitefish bioenergetics model. *Transactions of the American Fisheries Society*, 135(1), 61-75.
- Madenjian, C. P., Pothoven, S. A., Dettmers, J. M., & Holuszko, J. D. 2006b. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(4), 891-902.
- Madenjian, C. P., Pothoven, S. A., & Kao, Y. C. 2013. Reevaluation of lake trout and lake whitefish bioenergetics models. *Journal of Great Lakes Research*. 39(2). 358-364.

- Makarewicz, J.C., 1988. Phytoplankton and zooplankton in Lake Erie, Lake Huron, and Lake Michigan: 1984, Volume 1- Interpretive Report. U.S. Environmental Protection Agency GLNPO Report No. 3 (EPA-905/3-88-001).
- Makarewicz, J. C., Grigorovich, I. A., Mills, E., Damaske, E., Cristescu, M. E., Pearsall, W., LaVoie, M.J., Keats, R., Rudstam, L., Hebert, P., Halbritter, H., Kelly, T., Matkovich, C., & MacIsaac, H. J. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov)(Crustacea, Cladocera) in Lake Ontario. *Journal of Great Lakes Research*, 27(1), 19-32.
- Manca, M., Ramoni, C., & Comoli, P. 2000. The decline of *Daphnia hyalina galeata* in Lago Maggiore: a comparison of the population dynamics before and after oligotrophication. *Aquatic sciences*, 62(2), 142-153.
- Miehls, A. L., McAdam, A. G., Bourdeau, P. E., & Peacor, S. D. 2013. Plastic response to a proxy cue of predation risk when direct cues are unreliable. *Ecology*, 94(10), 2237-2248.
- Mills, E. L., Leach, J. H., Carlton, J. T., & Secor, C. L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research*, 19(1), 1-54.
- Mills, E. L., Adams, C., O'Gorman, R., Owens, R. W., & Roseman, E. F. 1995. Planktivory by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) on microcrustacean zooplankton and dreissenid (*Bivalvia: Dreissenidae*) veligers in southern Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(5), 925-935.
- Muir, A. M., Vecsei, P., Pratt, T. C., Krueger, C. C., Power, M., & Reist, J. D. 2013. Ontogenetic shifts in morphology and resource use of cisco *Coregonus artedii*. *Journal of fish biology*, 82(2), 600-617.
- Muirhead, J., & Sprules, W. G. 2003. Reaction distance of *Bythotrephes longimanus*, encounter rate and index of prey risk for Harp Lake, Ontario. *Freshwater Biology*, 48(1), 135-146.
- Mychek-Londer, J. G., & Bunnell, D. B. 2013. Gastric evacuation rate, index of fullness, and daily ration of Lake Michigan slimy (*Cottus cognatus*) and deepwater sculpin (*Myoxocephalus thompsonii*). *Journal of Great Lakes Research*.
- Myers, J. T., Jones, M. L., Stockwell, J. D., & Yule, D. L. 2009. Reassessment of the predatory effects of rainbow smelt on ciscoes in Lake Superior. *Transactions of the American Fisheries Society*, 138(6), 1352-1368.

- Nalepa, T. F., Fanslow, D. L., & Lang, G. A. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia spp.* to the invasive mussel *Dreissena rostriformis bugensis*. *Freshwater Biology*, 54(3), 466-479.
- Pace, M. L., & Orcutt Jr, J. D. 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. *Limnology and Oceanography*, 822-830.
- Pangle, K. L., Sutton, T. M., Kinnunen, R. E., & Hoff, M. H. 2004. Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. *Transactions of the American Fisheries Society*, 133(5), 1235-1246.
- Pangle, K. L., & Peacor, S. D. 2006. Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. *Freshwater Biology*, 51(6), 1070-1078.
- Pangle, K. L., Peacor, S. D., & Johannsson, O. E. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, 88(2), 402-412.
- Pangle, K. L., & Peacor, S. D. 2009. Light-dependent predation by the invertebrate planktivore *Bythotrephes longimanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(10), 1748-1757.
- Pangle, K. L., & Peacor, S. D. 2010. Temperature gradients, not food resource gradients, affect growth rate of migrating *Daphnia mendotae* in Lake Michigan. *Journal of Great Lakes Research*, 36(2), 345-350.
- Parker-Setter, S. L., Rudstam, L. G., Mills, E. L., & Einhouse, D. W. 2001. Retention of *Bythotrephes* spines in the stomachs of eastern Lake Erie rainbow smelt. *Transactions of the American Fisheries Society*, 130(5), 988-994.
- Parker-Setter, S. L., Witzel, L. D., Rudstam, L. G., Einhouse, D. W., & Mills, E. L. 2005. Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62(1), 145-152.
- Parker-Setter, S. L., Rudstam, L. G., Sullivan, P. J., & Warner, D. M. 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. *Great Lakes Fish. Comm. Spec. Pub.*, 09-01.
- Pichlova-Ptacnikova, R., & Vanderploeg, H. A. 2009. The invasive cladoceran *Cercopagis pengoi* is a generalist predator capable of feeding on a variety of prey species of different sizes and escape abilities. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, 173(4), 267-279.

- Pothoven, S. A., Fahnenstiel, G. L., & Vanderploeg, H. A. 2001. Population dynamics of *Bythotrephes cederstroemii* in south-east Lake Michigan 1995–1998. *Freshwater Biology*, 46(11), 1491-1501.
- Pothoven, S. A., Fahnenstiel, G. L., & Vanderploeg, H. A. 2003. Population characteristics of *Bythotrephes* in Lake Michigan. *Journal of Great Lakes Research*, 29(1), 145-156.
- Pothoven, S. A., & Vanderploeg, H. A. 2004. Diet and prey selection of alewives in Lake Michigan: seasonal, depth, and interannual patterns. *Transactions of the American Fisheries Society*, 133(5), 1068-1077.
- Pothoven, S. A., Vanderploeg, H. A., Cavaletto, J. F., Krueger, D. M., Mason, D. M., & Brandt, S. B. 2007. Alewife planktivory controls the abundance of two invasive predatory cladocerans in Lake Michigan. *Freshwater Biology*, 52(3), 561-573.
- Pothoven, S. A., Vanderploeg, H. A., Ludsins, S. A., Höök, T. O., & Brandt, S. B. 2009. Feeding ecology of emerald shiners and rainbow smelt in central Lake Erie. *Journal of Great Lakes Research*, 35(2), 190-198.
- Pothoven, S. A., Bunnell, D. B., Madenjian, C. P., Gorman, O. T., & Roseman, E. F. 2012. Energy density of bloaters in the upper Great Lakes. *Transactions of the American Fisheries Society*, 141(3), 772-780.
- Pothoven, S. A., Höök, T. O., Nalepa, T. F., Thomas, M. V., & Dyble, J. 2013. Changes in zooplankton community structure associated with the disappearance of invasive alewife in Saginaw Bay, Lake Huron. *Aquatic Ecology*, 1-12.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rand, P. S., Stewart, D. J., Lantry, B. F., Rudstam, L. G., Johannsson, O. E., Goyke, A. P., Brandt, S. B., O’Gorman, R. & Eck, G. W. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(7), 1546-1563.
- Rand, P. S., & Stewart, D. J. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(2), 318-327.
- Ricciardi, A., & MacIsaac, H. J. 2000. Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. *Trends in Ecology & Evolution*, 15(2), 62-65.
- Rivier, I. K., & Dumont, H. J. F. 1998. The predatory Cladocera (Onychopoda: Podonidae, Polyphemidae, Cercopagidae) and Leptodorida of the world. Guides to the identification of the micro-invertebrates of the continental waters of the world. Backhuys Publishing, Leiden, The Netherlands.



- Rosen, R. A. 1981. Length-dry weight relationships of some freshwater zooplankton. *Journal of Freshwater Ecology*, 1(2), 225-229.
- Rudstam, L. G., Aneer, G., & Hildén, M. 1994a. Top-down control in the pelagic Baltic ecosystem. *Dana*, 10, 105-129.
- Rudstam, L. G., Binkowski, F. P., & Miller, M. A. 1994b. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. *Transactions of the American Fisheries Society*, 123(3), 344-357.
- Rudstam, L. G., Parker, S. L., Einhouse, D. W., Witzel, L. D., Warner, D. M., Stritzel, J. L., Parrish, D.L. & Sullivan, P. J. 2003. Application of in situ target-strength estimations in lakes: examples from rainbow-smelt surveys in Lakes Erie and Champlain. *ICES Journal of Marine Science: Journal du Conseil*, 60(3), 500-507.
- Rudstam, L. G., Parker-Stetter, S. L., Sullivan, P. J., & Warner, D. M. 2009. Towards a standard operating procedure for fishery acoustic surveys in the Laurentian Great Lakes, North America. *ICES Journal of Marine Science: Journal du Conseil*, 66(6), 1391-1397.
- Schaeffer, J. S., Bowen, A., Thomas, M., French III, J. R., & Curtis, G. L. 2005. Invasion History, Proliferation, and Offshore Diet of the Round Goby *Neogobius melanostomus* in Western Lake Huron, USA. *Journal of Great Lakes Research*, 31(4), 414-425.
- Schloesser, D. W., & Nalepa, T. F. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(10), 2234-2242.
- Schneider, D. W. 1992. A bioenergetics model of zebra mussel, *Dreissena polymorpha*, growth in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(7), 1406-1416.
- Schulz, K. L., & Yurista, P. M. 1999. Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. *Hydrobiologia*, 380(1-3), 179-193.
- Schwab, D. J., & Bedford, K. W. 1999. The Great Lakes forecasting system. *Coastal and Estuarine Studies*, 157-174.
- Shea, M. A., & Makarewicz, J. C. 1989. Production, biomass, and trophic interactions of *Mysis relicta* in Lake Ontario. *Journal of Great Lakes Research*, 15(2), 223-232.

- Shuter, B. J., & Ing, K. K. 1997. Factors affecting the production of zooplankton in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(2), 359-377.
- Sierszen, M. E., Kelly, J. R., Corry, T. D., Scharold, J. V., & Yurista, P. M. 2011. Benthic and pelagic contributions to *Mysis* nutrition across Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(6), 1051-1063.
- Smith, B. R., & Tibbles, J. J. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(11), 1780-1801.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, 10(4), 375-383.
- Sprules, W. G., Riessen, H. P., & Jin, E. H. 1990. Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. *Journal of Great Lakes Research*, 16(3), 346-351.
- Sprung, M. 1993. The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. zebra mussels: Biology, impacts, and control, 39-54.
- Strayer, D. L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, 55(s1), 152-174.
- Stewart, D. J., & Binkowski, F. P. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. *Transactions of the American Fisheries Society*, 115(5), 643-661.
- Storch, A. J., Schulz, K. L., Cáceres, C. E., Smyntek, P. M., Dettmers, J. M., & Teece, M. A. 2007. Consumption of two exotic zooplankton by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) in three Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(10), 1314-1328.
- Taraborelli, A. C., Fox, M. G., Johnson, T. B., & Schaner, T. 2010. Round goby (*Neogobius melanostomus*) population structure, biomass, prey consumption and mortality from predation in the Bay of Quinte, Lake Ontario. *Journal of Great Lakes Research*, 36(4), 625-632.
- Vanderploeg, H. A., Pothoven, S. A., Fahnenstiel, G. L., Cavaletto, J. F., Liebig, J. R., Stow, C. A., Nalepa, T.F., Madenjian, C.P., & Bunnell, D. B. 2012. Seasonal zooplankton dynamics in Lake Michigan: Disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *Journal of Great Lakes Research*, 38(2), 336-352.
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, 21(1), 1-16.

- Warner, D. M., Kiley, C. S., Claramunt, R. M., & Clapp, D. F. 2008. The influence of alewife year-class strength on prey selection and abundance of age-1 chinook salmon in Lake Michigan. *Transactions of the American Fisheries Society*, 137(6), 1683-1700.
- Warner, D. M., Schaeffer, J. S., & O'Brien, T. P. 2009. The Lake Huron pelagic fish community: persistent spatial pattern along biomass and species composition gradients. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(8), 1199-1215.
- Watson, N. H. F. 1974. Zooplankton of the St. Lawrence Great Lakes-species composition, distribution, and abundance. *Journal of the Fisheries Board of Canada*, 31(5), 783-794.
- Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. *Limnology and Oceanography*, 556-565.
- Winnell, M. H., & White, D. S. 1984. Ecology of shallow and deep water populations of *Pontoporeia hoyi* (Smith) (Amphipoda) in Lake Michigan. *Freshwater Invertebrate Biology*, 118-138.
- Witt, A. M., & Cáceres, C. E. 2004. Potential predator-prey relationships between *Bythotrephes longimanus* and *Cercopagis pengoi* in southwestern Lake Michigan. *Journal of Great Lakes Research*, 30(4), 519-527.
- Wood, S. N. 2006. *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC.
- Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)* 73(1):3-36.
- Yan, N. D., Dunlop, W. I., Pawson, T. W., & MacKay, L. E. 1992. *Bythotrephes cederstroemi* (Schoedler) in Muskoka lakes: first records of the European invader in inland lakes in Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(2), 422-426.
- Yan, N., & Pawson, T. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. *Freshwater Biology*, 37(2), 409-425.
- Yan, N. D., Girard, R., & Boudreau, S. 2002. An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. *Ecology Letters*, 5(4), 481-485.
- Yan, N. D., Leung, B., Lewis, M. A., & Peacor, S. D. 2011. The spread, establishment and impacts of the spiny water flea, *Bythotrephes longimanus*, in temperate North America: a synopsis of the special issue. *Biological Invasions*, 13(11), 2423-2432.

- Young, J. D., Loew, E. R., & Yan, N. D. 2009. Examination of direct daytime predation by *Coregonus artedii* on *Bythotrephes longimanus* in Harp Lake, Ontario, Canada: no evidence for the refuge hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(3), 449-459.
- Young, J. D., Strecker, A. L., & Yan, N. D. 2011. Increased abundance of the non-indigenous zooplanktivore, *Bythotrephes longimanus*, is strongly correlated with greater spring prey availability in Canadian Shield lakes. *Biological Invasions*, 13(11), 2605-2619.
- Yule, D. L., Adams, J. V., Stockwell, J. D., & Gorman, O. T. 2007. Using multiple gears to assess acoustic detectability and biomass of fish species in Lake Superior. *North American Journal of Fisheries Management*, 27(1), 106-126.
- Yule, D. L., Stockwell, J. D., Black, J. A., Cullis, K. I., Cholwek, G. A., & Myers, J. T. 2008. How systematic age underestimation can impede understanding of fish population dynamics: lessons learned from a Lake Superior cisco stock. *Transactions of the American Fisheries Society*, 137(2), 481-495.
- Yurista, P. M. 1992. Embryonic and postembryonic development in *Bythotrephes cederstroemii*. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(6), 1118-1125.
- Yurista, P. M., & Schulz, K. L. 1995. Bioenergetic analysis of prey consumption by *Bythotrephes cederstroemi* in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(1), 141-150.
- Yurista, P.M. 1999. A model for temperature correction of size-specific respiration in *Bythotrephes cederstroemi* and *Daphnia middendorffiana*. *Journal of Plankton Research* 21:721-734
- Yurista, P. M., Vanderploeg, H. A., Liebig, J. R., & Cavaletto, J. F. 2010. Lake Michigan *Bythotrephes* prey consumption estimates for 1994-2003 using a temperature and size corrected bioenergetic model. *Journal of Great Lakes Research*, 36, 74-82.

**Appendices:**

	<b>Page</b>
Appendix Table 1: Frankfort, MI planktivore diet proportions (dry weight) collected 18-m April, July, and September 2010.....	55
Appendix Table 2: Frankfort, MI benthivore diet proportions (dry weight) collected 18-m April, July, and September 2010.....	56
Appendix Table 3: Frankfort, MI planktivore diet proportions (dry weight) collected 46-m April, July, and September 2010.....	57
Appendix Table 4: Frankfort, MI benthivore diet proportions (dry weight) collected 46-m April, July, and September 2010.....	58
Appendix Table 5: Frankfort, MI planktivore diet proportions (dry weight) collected 110-m April, July, and September 2010.....	59
Appendix Table 6: Frankfort, MI benthivore diet proportions (dry weight) collected 110-m April, July, and September 2010.....	60
Appendix Table 7: Sturgeon Bay, WI planktivore diet proportions (dry weight) collected 18-m April, July, and September 2010.....	61
Appendix Table 8: Sturgeon Bay, WI benthivore diet proportions (dry weight) collected 18-m April, July, and September 2010.....	62
Appendix Table 9: Sturgeon Bay, WI planktivore diet proportions (dry weight) collected 46-m April, July, September 2010.....	63
Appendix Table 10: Sturgeon Bay, WI benthivore diet proportions (dry weight) collected 46-m April, July, September 2010.....	64
Appendix Table 11: Sturgeon Bay, WI planktivore diet proportions (dry weight) collected 110-m April, July, September 2010.....	65
Appendix Table 12: Sturgeon Bay, WI benthivore diet proportions (dry weight) collected 110-m April, July, September 2010.....	66
Appendix Table 13: Stockton Island, WI planktivore diet proportions (dry weight) 18-m April, September-November 2011.....	67
Appendix Table 14: Stockton Island. WI planktivore diet proportions (dry weight) collected 46-m April, September-November 2011.....	68

**Appendices continued:**

	<b>Page</b>
Appendix Table 15: Stockton Island, WI benthivore diet proportions (dry weight) collected 4-m April, September-November 2011.....	69
Appendix Table 16: Stockton Island, WI planktivore diet proportions (dry weight) collected 110-m April, September-November 2011.....	70
Appendix Table 17: Stockton Island, WI benthivore diet proportions (dry weight) collected 110-m April, September-November 2011.....	71
Appendix Table 18. Comparison of 18-m Lake Michigan fish consumption and production of <i>Bythotrephes</i> in July 2010.....	72
Appendix Table 19. Comparison of 18-m Lake Michigan fish consumption and production of <i>Bythotrephes</i> in September 2010.....	73
Appendix Table 20. Comparison of 46-m Lake Michigan fish consumption and production of <i>Bythotrephes</i> in July 2010.....	74
Appendix Table 21. Comparison of 46-m Lake Michigan fish consumption and production of <i>Bythotrephes</i> in September 2010.....	75
Appendix Table 22. Comparison of 110-m Lake Michigan fish consumption and production of <i>Bythotrephes</i> in July 2010.....	76
Appendix Table 23. Comparison of 110-m Lake Michigan fish consumption and production of <i>Bythotrephes</i> in September 2010.....	77
Appendix Table 24. Comparison of 46-m Lake Superior fish consumption and production of <i>Bythotrephes</i> in 2011.....	78
Appendix Table 25. Comparison of 110-m Lake Superior fish consumption and production of <i>Bythotrephes</i> in 2011.....	79

Appendix Table 1: Frankfort, MI planktivore diet proportions (dry weight) collected 18-m April, July, and September 2010.

Month	Species	Size	Prey Species									
			Class									
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerrans	<i>Mysis</i>	<i>Diporeia</i>	Dipterans	Fish	<i>Dreissena</i>
April	Alewife	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
July	Alewife	Large	0.48	0.27	0.02	0.07	<0.01	0	0	0.15	0	<0.01
		Small	0.29	0.56	0.06	0.02	<0.01	0	0	0.06	0	<0.01
	Bloater	Large	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
		Small	0.63	0.21	<0.01	0.03	<0.01	0	0	0.11	0	0
	Rainbow Smelt	Large	0.14	0.10	<0.01	0.12	0	0	0	0.30	0.33	0
		Small	<0.01	0.73	0.02	0.03	<0.01	0	0	0.12	0.09	<0.01
September	Ninespine Stickleback	-	<0.01	<0.01	<0.01	0.95	0	0	0	0.04	<0.01	0
		Alewife	Large	NA	NA	NA	NA	0	NA	NA	NA	NA
	Small		0.13	0.18	<0.01	0.58	<0.01	0	0	0.10	0	<0.01
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0.69	0	0	0	0	0	0	0.31	0	0
Small		0.69	0.02	<0.01	0.28	0	0	0	0	0	0	

Appendix Table 2: Frankfort, MI benthivore diet proportions (dry weight) collected 18-m April, July, and September 2010.

Month	Species	Size	Prey Species										
			Class	<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb.	Cladocerans	<i>Mysis</i>	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish
<b>April</b>	DWS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	SS	-	0	0.02	0	0	0	0	0	0	0.02	0.45	0
	RG	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>July</b>	DWS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	SS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	RG	-	0	0	0.05	0.34	0	0	0	<0.01	0	0.51	
<b>September</b>	DWS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	SS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	RG	-	0	0	<0.01	0.05	0	0	<0.01	0.02	0	0.77	



Appendix Table 3: Frankfort, MI planktivore diet proportions (dry weight) collected 46-m April, July, and September 2010.

Month	Species	Size	Prey Species										
			Class	<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	<i>Dreissena</i>	<i>Cercopagis</i>
April	Alewife	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0	0.43	0	<0.01	0	0	0	0.57	0	0	0
		Small	0	0.82	0.08	0	0	0	0	0.11	0	0	0
July	Alewife	Large	0.12	0.44	0.05	0.10	0	0	0	0	0.29	0	0
		Small	0	0.95	0.04	<0.01	0	0	0	0	0	0	0
	Bloater	Large	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA
		Small	0	0.47	0.03	0.44	0	0	0	0	0.07	0	0
	Rainbow Smelt	Large	NA	NA	NA	NA	0	NA	NA	NA	NA	NA	NA
		Small	0	0.46	<0.01	0.35	0	0	0	0	0.05	0	0.10
September	Alewife	Large	0.70	0.12	0.01	0.05	<0.01	0	0	0	0.11	0	0
		Small	0.08	0.16	0.09	0.55	<0.01	0	0	0	0.02	0.03	0
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.59	<0.01	0.36	0	0	0	0	0.05	0	0
	Rainbow Smelt	Large	0.31	0.02	<0.01	0.47	0	0	0	0.18	0	0	<0.01
		Small	0.98	<0.01	0	0.01	0	0	0	0	0	0	0
Ninespine Stickleback	-	<0.01	0.17	<0.01	0.30	0	0	0	0.41	0.09	0	0	



Appendix Table 5: Frankfort, MI planktivore diet proportions (dry weight) collected 110-m April, July, and September 2010.

Month	Species	Size	Prey Species										
			Class										
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish	<i>Dreissena</i>	<i>Cercopagis</i>
<b>April</b>	Alewife	Large	0	0.66	<0.01	<0.01	0	0	0.33	0.01	0	0	0
		Small	0	0.92	<0.01	<0.01	0	0	0.07	<0.01	0	0	0
	Bloater	Large	0	0.60	<0.01	<0.01	0	0	0.40	<0.01	0	<0.01	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	1	0	0	0	0	0	0	0	0	0
<b>July</b>	Alewife	Large	0.08	0.61	<0.01	0.26	0	0	0	0.05	0	0	0
		Small	0	0.46	0	<0.01	0	0	0.54	0	0	0	0
	Bloater	Large	<0.01	0.05	0.03	<0.01	0	0	0.83	0.04	0.05	<0.01	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.21	0	0.71	0.08	NA	NA	NA	NA	NA	NA
<b>September</b>	Alewife	Large	0.04	0.21	<0.01	0.05	<0.01	0	0.70	<0.01	0	<0.01	<0.01
		Small	<0.01	0.68	0.17	0.14	<0.01	0	0	0	0	<0.01	0
	Bloater	Large	0	<0.01	0	<0.01	0	<0.01	0.99	0	0	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.21	0	0.71	0	0	0	0	0	0	0



Appendix Table 7: Sturgeon Bay, WI planktivore diet proportions (dry weight) collected 18-m April, July, and September 2010.

Month	Species	Size	Prey Species									
			Class									
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	Mysis	Dipterans	Fish	<i>Dreissena</i>
April	Alewife	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
July	Alewife	Large	0.20	0.40	0.29	0.09	0	0	0	<0.01	0	<0.01
		Small	0.02	0.75	0.15	0.08	0	0	0	0	0	<0.01
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.81	0.17	0.02	0	0	0	0	0	<0.01
September	Ninespine Stickleback	-	0	0	1	0	0	0	0	0	0	0
	Alewife	Large	0.35	0.51	0.04	0.07	<0.01	0	0.01	0.02	0	0
		Small	0.09	0.54	0.06	0.26	0.02	0	0	0.03	0	<0.01
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0.43	0.27	0.01	<0.01	0	0	0	0.03	0.25	0
		Small	0.07	0.92	0.02	<0.01	0	0	0	0	0	0
	Ninespine Stickleback	-	0	0.35	0.01	0.07	0	0	0	0.46	0	0

Appendix Table 8: Sturgeon Bay, WI benthivore diet proportions (dry weight) collected 18-m April, July, and September 2010.

Month	Species	Size	Prey Species								
			Class								
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish	<i>Dreissena</i>
<b>April</b>	DWS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
	SS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
	RG	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
<b>July</b>	DWS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
	SS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
	RG	-	0	0	0	0	0	0	0	1	0
<b>September</b>	DWS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
	SS	-	NA	NA	NA	NA	NA	NA	NA	NA	NA
	RG	-	0.43	0	0.02	0.31	0	0	0.10	0	0.01

Appendix Table 9: Sturgeon Bay, WI planktivore diet proportions (dry weight) collected 46-m April, July, and September 2010.

Month	Species	Size	Prey Species									
			Class									
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish	<i>Dreissena</i>
April	Alewife	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0	0.73	0.03	0	0	0	0.24	0	0	0
		Small	0.03	0.82	0.04	<0.01	0	0	0.10	0	0	<0.01
July	Alewife	Large	0.22	0.48	0.05	0.14	<0.01	0	0.10	0.02	0	0
		Small	0.11	0.51	0.10	0.19	<0.01	0	0.01	0.07	0	<0.01
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.69	0.12	0.01	0	0	0.18	0	0	0
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
September	Alewife	Large	0.31	0.61	0.04	0.04	<0.01	0	0	<0.01	0	0
		Small	0.02	0.78	0.10	0.07	0.02	0	0	<0.01	0	0
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0.62	<0.01	0	<0.01	0	0	<0.01	0	0.37	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ninespine Stickleback	-	0	<0.01	0.24	0.51	0	0	0	0.08	0.16	0	





Appendix Table 11: Sturgeon Bay, WI planktivore diet proportions (dry weight) collected 110-m April, July, and September 2010.

Month	Species	Size	Prey Species									
			Class									
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish	<i>Dreissena</i>
April	Alewife	Large	0	0.83	<0.01	<0.01	0	0	0.16	0.01	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	0	0.60	0	<0.01	0	0	0.40	0	0	<0.01
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0	0.99	0	<0.01	0	0	0	0	0	0
		Small	0	0.75	0	0	0	0	0.25	0	0	0
July	Alewife	Large	0.05	0.34	0.01	0.02	<0.01	<0.01	0.57	0.01	0	<0.01
		Small	<0.01	0.40	<0.01	0.16	0	0	0.41	0.03	0	<0.01
	Bloater	Large	0	0.03	<0.01	<0.01	0	0	0.86	0.10	0	<0.01
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0	0.05	0	<0.01	0	<0.01	0.82	0.01	0.11	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
September	Alewife	Large	0.07	0.42	<0.01	<0.01	<0.01	0	0.49	0.02	0	0
		Small	0.17	0.51	0.22	0.08	0.02	0	0	0	0	<0.01
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.29	0.46	0.25	0	0	0	0	0	0



Appendix Table 13: Stockton Island, WI planktivore diet proportions (dry weight) 18-m April, September-November 2011.

Month	Species	Size Class	Prey Species									
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	<i>Sphaerium</i>	<i>Dreissena</i>	
April	Cisco	Large	0	0.99	<0.01	0	0	0	0	0	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
September	Cisco	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.95	0	0.05	0	0	0	0	0	0
October	Cisco	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.76	0	0.24	0	0	0	0	0	0
November	Cisco	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.90	<0.01	0.10	NA	NA	NA	NA	NA	NA

Appendix Table 14: Stockton Island. WI planktivore diet proportions (dry weight) collected 46-m April, September-November 2011.

Month	Species	Size Class	Prey Species									
			<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	<i>Sphaerium</i>	<i>Dreissena</i>	
April	Cisco	Large	0	0.99	<0.01	0	0	0	0	0	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0	<0.01	0	0	0.22	0.70	0.07	0	0	0
		Small	0	0.34	0.07	0	0.03	0.56	0	0	0	0
September	Cisco	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0.62	0.13	<0.01	0.25	0	0	<0.01	0	0	0
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0.77	0.08	0	0	0	0.15	0	0	0	0
	Rainbow Smelt	Large	0.16	<0.01	<0.01	0.09	0.03	0.72	<0.01	<0.01	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
October	Cisco	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0.04	<0.01	0	0.95	0	0.01	0	0	0	0
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0.91	0.04	0	0.05	0	0	0	0	0	0
	Rainbow Smelt	Large	0.03	0.08	0	0.05	<0.01	0.84	0	0	0	0
		Small	0	0	0	1	0	0	0	0	0	0
November	Cisco	Large	0.94	0	0	0.06	0	0	0	0	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Rainbow Smelt	Large	0	0	0	0	0	1	0	0	0	0
		Small	0	0.52	<0.01	0.27	0	0.20	0	0	0	0

Appendix Table 15: Stockton Island, WI benthivore diet proportions (dry weight) collected 46-m April, September-November 2011.

Month	Species	Size	Prey Species										
			Class	<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish	<i>Sphaerium</i>
April	Spoon	-	0	0	0	0	0	1	0	0	0	0	0
	LW	Large	0	<0.01	<0.01	<0.01	0	0.39	0.27	0.07	0.13	0.13	<0.01
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
September	Spoon	-	<0.01	<0.01	0	<0.01	0	0.96	0.02	0.01	0	0	0
	LW	Large	0.04	0	0	0.08	0	0.31	0.51	0.06	0	0.03	0
		Small	0	<0.01	0	0.11	0.08	0.03	0.83	<0.01	0	0.01	<0.01
October	Spoon	-	<0.01	0	<0.01	<0.01	0	0.98	0	<0.01	0	0	0
	LW	Large	0.06	0	<0.01	0.05	0	0.47	0.31	0.04	0	0.06	0
		Small	0	0	0	0.50	0	0	0.49	<0.01	0	0	0
November	Spoon	-	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	LW	Large	0.02	<0.01	<0.01	0.01	0	0.25	0.55	0.06	0	0.11	0
		Small	<0.01	0.04	0.03	0.17	0	0.10	0.62	0.03	0	0.01	0

Appendix Table 16: Stockton Island, WI planktivore diet proportions (dry weight) collected 110-m April, September-November 2011.

Month	Species	Size	Prey Species										
			Class	<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	Pred. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	Fish	<i>Dreissena</i>
April	Cisco	Large	0	1	<0.01	0	0	0	0	0	0	0	0
		Small	0	0.60	0.03	0.06	<0.01	0.03	0.29				
	Bloater	Large	0	0.57	0	<0.01	0	0	0.42	0	0	0	0
		Small	0	0.60	0.03	0.06	<0.01	0.03	0.29				
	Rainbow Smelt	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Small		0	1	0	0	0	0	0	0	0	0	0	
September	Cisco	Large	0.78	0.17	0	0.04	0	0	0	0	0	0	0
		Small	0.64	0.10	<0.01	0.25	0	0	0	0	0	0	0
	Bloater	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0.33	0.67	0	0	0	0	0	0	0	0	0
	Rainbow Smelt	Large	<0.01	<0.01	0	<0.01	0	0	0.91	0	0	0	0
		Small	0.23	0.77	0	0	0	0	0	0	0	0	0
October	Cisco	Large	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0.87	0.05	0.08	0	0	0	0	0	0	0	0
	Bloater	Large	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Small	0	0.03	0	0	0	<0.01	0.97	0	0	0	0
	Rainbow Smelt	Large	0.05	<0.01	0	<0.01	0	0	0.95	0	<0.01	0	0
		Small	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
November	Cisco	Large	0.96	0	0	0.04	0	0	0	0	0	0	0
		Small	0	0.92	0.08	0	0	0	0	0	0	0	0
	Bloater	Large	0	0	0	0	0	0	1	0	0	0	0
		Small	0.02	0.15	<0.01	0.10	0	0	0.73	0	0	0	0
	Rainbow Smelt	Large	<0.01	0.09	0	0.06	0	<0.01	0.85	0	0	0	0
		Small	0	0.19	<0.01	0.62	0	0.06	0.12	0	0	0	0

Appendix Table 17: Stockton Island, WI benthivore diet proportions (dry weight) collected 110-m April, September-November 2011.

Month	Species	Size	Prey Species									
			Class	<i>Bythotrephes</i>	Calanoid	Cyclopoid	Herb. Cladocerans	<i>Diporeia</i>	<i>Mysis</i>	Dipterans	<i>Sphaerium</i>	Fish
<b>April</b>	Spoon	-	0	0.04	0.04	<0.01		0.85	0.03	<0.01	0	0.04
	LW	Large	NA	NA	NA	NA		NA	NA	NA	NA	NA
		Small	NA	NA	NA	NA		NA	NA	NA	NA	NA
<b>September</b>	Spoon	-	<0.01	<0.01	0	<0.01		0.84	0.12	0.03	0	0
	LW	Large	<0.01	<0.01	0	<0.01		0.65	0.32	0.01	0.01	<0.01
		Small	NA	NA	NA	NA		NA	NA	NA	NA	NA
<b>October</b>	Spoon	-	<0.01	<0.01	<0.01	<0.01		0.90	0.09	<0.01	0	0
	LW	Large	<0.01	0	0	<0.01		0.88	0.10	<0.01	<0.01	0
		Small	NA	NA	NA	NA		NA	NA	NA	NA	NA
<b>November</b>	Spoon	-	<0.01	<0.01	0	<0.01		0.93	0.04	<0.01	0	0.03
	LW	Large	0	<0.01	0	<0.01		0.68	0.20	0.04	0.08	0
		Small	NA	NA	NA	NA		NA	NA	NA	NA	NA

Appendix Table 18: Comparison of 18-m Lake Michigan fish consumption and production of *Bythotrephes* in July 2010.

Month	Site	Species	Size Class Weight (g) TL (mm)	P-value Yearly from mode <sup>1</sup>	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Species Population <sup>2</sup> (# ha <sup>-1</sup> ) Acoustics (A) Bottom (B)	Population Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	<i>Bythotrephes</i> Production <sup>3</sup> (mg·m <sup>-2</sup> ·day <sup>-1</sup> )
July	Frankfort	Alewife	Small 5.92 93.45	0.35	0.29	37.89	188.22 (A)	0.71	1.48	6.98
			Large 19.70 139.88	0.43	0.48	60.4	94.11 (A)	0.56		
		Rainbow Smelt	Small 0.60 50.69	0.99	0.006	1.462E-10	470.55 (A)	6.9x10 <sup>-12</sup>		
			Large 4.98 99.86	0.61	0.14	0.34	8.08 (B)	0.00027		
	Sturgeon Bay	Bloater	Small 7.55 103.56	0.28	0.63	20.38	96.9 (B)	0.20		
			Large 6.36 95.67	0.31	0.02	1.86	54.69(A)	0.010	1.98	1.11
		Alewife	Small 22.86 147.05	0.28	0.21	51.37	381.13 (B)	1.97		
			Large							

<sup>1</sup> Seasonal P-value was estimated from modal size changes of fish caught from April to September.

<sup>2</sup> Population estimates selected the largest value to determine if in any scenario consumption was greater than production.

<sup>3</sup> Temperature used for *Bythotrephes* production selected the mean epilimnetic temperature determined as optimal location for the species.



Appendix table 19: Comparison of 18-m Lake Michigan fish consumption and production of *Bythotrephes* in September 2010.

Month	Site	Species	Size Class Weight (g) TL (mm)	P-value Yearly from mode	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Species Population (# ha <sup>-1</sup> ) Acoustics (A) Bottom (B)	Population Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	<i>Bythotrephes</i> Production (mg·m <sup>-2</sup> ·day <sup>-1</sup> )
Sept.	Frankfort	Alewife	Small 0.76 46.90	0.35	0.13	3.82	229.02 (A)	0.087	0.20	0.20
		Rainbow Smelt	Small 0.65 52	0.99	0.69	10.42	57.25 (A)	0.060		
			Large 9.60 123.32	0.61	0.69	4.77	114.51 (A)	0.055		
	Sturgeon Bay	Alewife	Small 5.12 88.94	0.31	0.09	7.68	4427.68 (A)	3.40	8.65	6.82
			Large 23.23 147.86	0.28	0.35	88.17	15.71 (B)	0.14		
		Rainbow Smelt	Small 0.61 50.82	0.47	0.07	0.48	1475.89 (A)	0.070		
			Large 9.89 124.5	0.38	0.43	5.60	2951.79 (A)	1.65		
		Round Goby	- 1.53 50.78	0.46	0.43	4.10	8260.05 (B)	3.38		

Appendix Table 20: Comparison of 46-m Lake Michigan fish consumption and production of *Bythotrephes* in July2010.

Month	Site	Species	Size Class Weight (g) TL (mm)	P-value Yearly from mode	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Species Population (# ha <sup>-1</sup> ) Acoustics (A) Bottom (B)	Population Consumption (mg·m <sup>-2</sup> day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> day <sup>-1</sup> )	<i>Bythotrephes</i> Production (mg·m <sup>-2</sup> day <sup>-1</sup> )
July	Frankfort	Alewife	Large 19.70 139.88	0.33	0.12	19.54	13.37(A)	0.026	0.027	6.20
		Slimy Sculpin	- 5.34 74.54	NA	0.06	NA	27.44 (B)	0.00083		
	Sturgeon Bay	Alewife	Small 6.36 95.67	0.31	0.11	11.75	20.40(A)	0.024	0.40	0.99
			Large 22.86 147.05	0.27	0.22	52.2	71.49(A)	0.37		
		Slimy Sculpin	- 3.25 64.13	NA	0.001	NA	172.66 (B)	6.7x10 <sup>-5</sup>		

Appendix Table 21: Comparison of 46-m Lake Michigan fish consumption and production of *Bythotrephes* in September 2010.

Month	Site	Species	Size Class Weight (g) TL (mm)	P-value Yearly from mode	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Species Population (# ha <sup>-1</sup> ) Acoustics (A) Bottom (B)	Population Consumption (mg·m <sup>-2</sup> day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> day <sup>-1</sup> )	<i>Bythotrephes</i> Production (mg·m <sup>-2</sup> day <sup>-1</sup> )
Sept.	Frankfort	Alewife	Small 0.76 46.90	0.32	0.08	1.86	483.46 (A)	0.090	0.69	0.93
			Large 31.09 163.06	0.33	0.70	26.97	127.22 (A)	0.34		
		Rainbow Smelt	Small 0.65 52.00	0.90	0.98	13.98	35.12 (A)	0.049		
			Large 9.60 123.32	0.31	0.32	6.74	295.68 (A)	0.20		
		Slimy Sculpin	- 2.98 62.45	NA	0.05	NA	289.55(B)	0.0053		
		Sturgeon Bay	Alewife	Small 5.12 88.94	0.31	0.02	1.88	1332.82(A)	0.25	12.85
	Large 23.23 147.86			0.27	0.31	75.06	1659.97(B)	12.45		
	Rainbow Smelt		Large 9.89 124.5	0.41	0.62	4.30	267.97 (A)	0.12		
	Slimy Sculpin		- 2.20 57.01	NA	0.26	NA	469.46(B)	0.038		

Appendix Table 22: Comparison of 110-m Lake Michigan fish consumption and production of *Bythotrephes* in July 2010.

Month	Site	Species	Size Class Weight (g) TL (mm)	P-value Yearly from mode	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Species Population (# ha <sup>-1</sup> ) Acoustics (A) Bottom (B)	Population Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	<i>Bythotrephes</i> Production (mg·m <sup>-2</sup> ·day <sup>-1</sup> )
July	Frankfort	Alewife	Large 19.70 139.88	0.20	0.079	12.75	73.30 (A)	0.093	0.11	3.36
		Bloater	Large 42.06 181.54	0.29	0.0009	0.065	367.52 (A)	0.0024		
		Deepwater Sculpin	- 6.60 92.00	NA	0.03	NA	10.7 (B)	0.00020		
		Slimy Sculpin	- 5.34 74.54	NA	0.11	NA	232.69 (B)	0.013		
	Sturgeon Bay	Alewife	Small 6.36 95.67	0.27	0.0033	0.28	130.96 (A)	0.0036	0.052	1.65
			Large 22.86 147.05	0.17	0.05	7.17	65.72 (A)	0.047		
		Slimy Sculpin	- 3.25 64.13	NA	0.008	NA	407.59 (B)	0.0013		

Appendix Table 23: Comparison of 110-m Lake Michigan fish consumption and production of *Bythotrephes* in September 2010.

Month	Site	Species	Size Class Weight (g) TL (mm)	P-value Yearly from mode	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Species Population (# ha <sup>-1</sup> ) Acoustics (A) Bottom (B)	Population Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> ·day <sup>-1</sup> )	<i>Bythotrephes</i> Production (mg·m <sup>-2</sup> ·day <sup>-1</sup> )
Sept.	Frankfort	Alewife	Small 0.76 46.90	0.32	0.001	0.035	3621.33 (A)	0.013	0.068	2.93
			Large 31.09 163.06	0.20	0.03588	17.55	31.55 (B)	0.055		
		Deepwater Sculpin	- 5.75 88.17	NA	0.0012	NA	21.88 (B)	0.000013		
		Slimy Sculpin	- 2.98 62.45	NA	0.0007	NA	258.47 (B)	0.000067		
	Sturgeon Bay	Alewife	Small 5.12 88.94	0.27	0.16	12.25	1002.587(A)	1.23	1.28	17.96
			Large 23.23 147.86	0.17	0.07	3.09	111.57 (B)	0.034		
		Deepwater Sculpin	- 16.19 121.57	NA	0.025	NA	97.31 (B)	0.0023		
Slimy Sculpin		- 2.20 57.01	NA	0.057	NA	712.78 (B)	0.013			

Appendix Table 24: Comparison of 46-m Lake Superior fish consumption and production of *Bythotrephes* in 2011.

Month	Species	Size Class Weight (g) TL (mm)	P-value	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption per fish (mg dry weight day <sup>-1</sup> )	Species Population <sup>4</sup> (# ha <sup>-1</sup> )	Population Consumption Total (mg·m <sup>-2</sup> day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> day <sup>-1</sup> )	<i>Bythotrephes</i> Production <sup>5</sup> (mg·m <sup>-2</sup> day <sup>-1</sup> )
Sept.	Rainbow Smelt	Large 9.73 121.50	0.26	0.15	3.99	115.21	0.046	5.75	6.74
	Cisco	Small 115.37 244.66	0.15	0.62	362.35	150.40	5.450		
	Bloater	Small 76.66 218.00	0.58	0.77	144.42	0.44	0.006		
	Lake Whitefish	Large 337.25 346.38	0.41	0.04	37.46	66.67	0.250		
Oct.	Rainbow Smelt	Large 10.59 124.51	0.26	0.03	0.91	62.22	0.006	0.37	3.75
	Cisco	Small 123.55 250.00	0.46	0.04	17.95	29.91	0.054		
	Bloater	Small 68.98 209.58	0.58	0.91	274.47	0.11	0.003		
	Lake Whitefish	Large 256.98 318.66	0.29	0.06	57.96	52.27	0.303		
Nov.	Cisco	Large 421.75 368.00	0.46	0.94	1884.82	29.84	5.624	5.64	0.68
	Lake Whitefish	Large 40.46 181.04	0.18	0.02	2.96	65.64	0.019		
		Small 13.05 128.10	0.14	<0.01	0.02	19.45	<0.001		

<sup>4</sup>Population estimates combined bottom and midwater trawl with acoustic apportionment.<sup>5</sup>Temperature used for *Bythotrephes* production selected the mean epilimnetic temperature determined as optimal location for the species as well as biomass correction factor from night zooplankton collections

Appendix Table 25: Comparison of 110-m Lake Superior fish consumption and production of *Bythotrephes* in 2011.

Month	Species	Size Class Weight. (g) TL (mm)	P-value	<i>Bythotrephes</i> proportion in diet	<i>Bythotrephes</i> Consumption/fish (mg dry weight day <sup>-1</sup> )	Fish Population (# ha <sup>-1</sup> )	Population Consumption Total (mg·m <sup>-2</sup> day <sup>-1</sup> )	Community Consumption (mg·m <sup>-2</sup> day <sup>-1</sup> )	<i>Bythotrephes</i> Production (mg·m <sup>-2</sup> day <sup>-1</sup> )
Sept.	Rainbow Smelt	Small 0.15 36.5	0.49	0.23	0.61	31.30	0.0019	7.10	5.36
		Large 9.72 121.50	0.26	<0.01	0.09	49.61	0.00045		
	Cisco	Small 115.37 244.66	0.14	0.64	411.78	102.46	4.22		
		Large 194.25 288.29	0.19	0.78	1048.68	24.11	2.53		
	Bloater	Small 76.66 218.00	0.51	0.33	54.72	62.75	0.34		
	Lake Whitefish	Large 337.25 346.38	0.41	<0.01	0.02	11.35	0.00002		
Oct.	Rainbow Smelt	Large 10.59 124.51	0.26	0.05	1.40	43.73	0.0061	2.51	2.49
	Cisco	Small 123.55 250.00	0.18	0.87	579.50	43.18	2.50		
	Lake Whitefish	Large 256.98 318.66	0.27	<0.01	0.49	2.25	0.00011		
Nov.	Rainbow Smelt	Large 14.37 136.00	0.26	<0.01	0.11	34.05	0.00036	2.58	0.66
	Cisco	Large 421.75 368.00	0.47	0.96	1937.26	13.05	2.53		
	Bloater	Small 76.34 217.67	0.51	0.02	5.49	94.46	0.052		