Cannibalism by the invasive invertebrate zooplanktivore *Bythotrephes cederströmii*

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Abstract

Cannibalism (i.e., intraspecific predation) affects the population dynamics of many invertebrate species. Cannibalism by the predatory cladoceran *Bythotrephes cederströmii* has been observed and noted in laboratory settings on several occasions, but no studies have published results of cannibalism experiments or explicitly quantified *Bythotrephes* cannibalism rates. We performed two laboratory experiments that demonstrated and quantified *Bythotrephes* cannibalism. Cannibalism occurred frequently in our experiments, and cannibalism clearance rates were comparable to those for *Bythotrephes* feeding on heterospecific prey. Further, our estimates of clearance rates between conspecifics suggest that cannibalism could be an important food source during certain periods of the year, and in particular places, for which *Bythotrephes* densities are at the higher end of observed ranges. While more research is needed, our results suggest that there are conditions in which cannibalism should be included in models of *Bythotrephes* predation, including bioenergetics models predicting *Bythotrephes* consumption rates.

Keywords: Alternative prey, *Density-dependence; Intraspecific predation; Laurentian Great Lakes; Predator-prey interactions*

Introduction

Cannibalism (i.e., intraspecific predation), defined as the consumption of all or part of another conspecific individual, is ubiquitous in the animal kingdom, occurring in a wide variety of terrestrial and aquatic taxa. It can occur during multiple stages in the life cycle of an animal, and is generally associated with an asymmetry in vulnerability between the cannibal and the victim; where the victim is often at a more vulnerable life history stage than the cannibal (Elgar and Bernard 1992). Cannibalism can affect an animal's behavior, life history strategy, and reproductive success (Cushing et al. 2015) and can therefore have important ecological consequences, including stabilizing (e.g., Andersson *et al.* 2007) or destabilizing (e.g., Claessen *et al.* 2004) effects on population dynamics, lowering a cannibalistic predator's consumption of heterospecific prey (e.g., Rudolf 2008a), and promoting predator-prey coexistence (e.g., Rudolf 2007).

Rates of cannibalism can be influenced by a number of factors. Size appears to be a key factor driving the asymmetry in vulnerability in many cannibalistic species, such that increases in relative size differences among life stages increase rates of cannibalism (DeAngelis et al. 1979, Bry and Gillet 1980, Polis 1981, Claessen *et al.* 2004). Food availability may also influence cannibalism, as low food typically increases hunger levels and foraging activity (Johansson 1992, 1993, Roberts et al. 2003, Duarte et al. 2010), causing animals to expand their diets to include conspecifics (Leonardsson 1991, Rudolf 2008a, b). Cannibalism can also be density dependent, (Holling 1959, Hassell 1978, Van Buskirk 1989, Buddle et al. 2003, Richardson et al. 2010), whereby elevated conspecific density both increases encounter probabilities between individuals and reduces per capita food availability (Polis 1980, Ibánez and Keyl 2010).

Despite its general importance among diverse taxa, and suggestions of its presence, cannibalism has not been explicitly studied in *Bythotrephes cederströmii* (hereafter '*Bythotrephes*'). *Bythotrephes* is a generalist zooplanktivore, with a preference for epilimnetic prey (Pichler et al. 2021), native to European and Asian palearctic freshwaters, which has invaded North American waters in the Great Lakes region (Grigorovich et al. 1998, Yan et al. 2002; Barbiero and Tuchman 2004; Strecker et al. 2006, Kerfoot et al. 2016, Marino et al. 2019). The invasive species of the genus *Bythotrephes* introduced in the North American lakes in 1970s-early 1980s was named variously either *B. cederstroemi* (e.g., Sprules et al. 1990, Johansson et al. 1991) or *B. longimanus* (e.g., Lehman 1987, Evans 1988, Sprules et al. 1990), but has recently been identified as *B. cederströmi* (Korovchinsky and Arnott 2019). To date, references to cannibalism are anecdotal or based on unpublished laboratory observations. For instance, several workers have noted that *Bythotrephes* is cannibalistic when held in experimental containers (e.g., Zozulya 1978, Mordukhai-Boltovskoi & Rivier 1987, Vanderploeg et al. 1993, Schulz and Yurista 1999, Witt and Cáceres 2004, Branstrator 2005, Kim and Yan 2010). There is also a report of cannibalism observed *in situ* using SCUBA (K. Pangle, personal communication). There has been, however, no quantification of cannibalism rates in *Bythotrephes*, nor examination of factors that could affect cannibalism. Quantifying rates of cannibalism in *Bythotrephes* and the factors that affect them is worthwhile because of the possibility that cannibalism is an important factor contributing to *Bythotrephes'* population growth and persistence in lakes throughout Europe and North America.

There are unexplained patterns in several studies that could be elucidated with the inclusion of cannibalism by *Bythotrephes*. For example, bioenergetics and efficiency models indicate that *Bythotrephes* consumption rates often exceed zooplankton production in a number of deep oligotrophic lakes that *Bythotrephes* have invaded in north America, including the Laurentian Great Lakes (Burkhardt and Lehman 1994, Yurista and Schulz 1995, Yurista et al. 2010, Bunnell et al. 2011, Pothoven and Hook 2014) and some Canadian Shield lakes (e.g., Dumitru 2001). Abundance of conspecific prey could therefore be a particularly important factor to consider in an effort to balance estimates of prey production with predictions of *Bythotrephes* consumptive demand.

The objectives of this study were to (1) experimentally quantify rates of cannibalism in *Bythotrephes*, and to (2) examine whether three factors known to influence cannibalism: conspecific size, food availability, and conspecific density (Fox 1975, Wise 2006), affect these rates. Based on previous observations of *Bythotrephes* in the field and in laboratory settings, our expectations were that their rates of cannibalism would be comparable to their predation rates on other larger-bodied cladoceran prey (e.g., *Daphnia* and *Bosmina*). Further, based on prior theoretical and empirical work on cannibalism in general, we hypothesized that cannibalism by *Bythotrephes* would increase when: there are size (and therefore vulnerability) differences among instars, there are no other prey available, and/or conspecific densities are high. An understanding of *Bythotrephes* cannibalism rates and the factors that affect them may assist predictions of *Bythotrephes* population dynamics and their influence on food webs of the Laurentian Great Lakes and other lakes in Europe and North America.

Methods

Collection, maintenance, and description of study animal

We collected *Bythotrephes* from a 110 m depth site in Lake Michigan, offshore of Muskegon, MI (43°11′29″ N 86°32′16″ W), which is a sampling location frequently used in NOAA zooplankton surveys (e.g., Pothoven et al. 2003). Slow vertical plankton tows (i.e., <1 ms^{-1}) were performed with a conical zooplankton net with 363-μm mesh (1-m diameter, 2-m length) lowered to a maximum depth of 40m. We covered the mesh windows of the cod-end with duct tape to ensure the animals remained in water upon collection and to avoid physical damage against the cod-end mesh. Upon net retrieval, we gently poured the contents of the cod-end into a deep polypropylene cooler filled halfway with 64 μm filtered lake water to ensure the animals remained submerged. We kept animals in the shade during sorting to shield the animals from UV radiation. We used a 5-mL pipettor with the plastic tip cut to a 9-mm diameter, to capture and transfer actively swimming individuals to 60 mL glass jars (1 individual per jar) previously filled with filtered, chilled lake water. Jars were packed into coolers with icepacks and transported to Michigan State University in East Lansing, MI, where they were kept in an incubator at 20°C prior to each experiment. *Bythotrephes* were not fed during this time. A maximum of 72 hours passed between collection of individuals and use in experiments. Prior to each experiment, we classified individual *Bythotrephes* as 1st, 2nd, and 3rd instars. Instars can be easily identified, with minimal disturbance to the individual, under a dissecting scope by the number of barbs on their caudal process

(Yurista 1992). To maximize relative size differences (and hence hypothesized vulnerability) in our experiments, we used only 1st and 3rd instars in our experiments; 3rd instars can be up to five times the biomass of 1st instars (Yurista and Schulz 1995).

General methodology

We conducted two laboratory experiments with the purpose of quantifying rates of *Bythotrephes* cannibalism under a range of experimental conditions. Experiments were run using filtered (0.45 μm), aged (2 weeks) Lake Michigan water collected from the same location where the *Bythotrephes* were collected and contained in 4-L glass jars, which were used in the experiments. Because *Bythotrephes* tend to congregate in corners near the bottom of stationary containers (personal observation), we attached the jars to the outside of a large plankton wheel (87 cm wheel diameter, 122 cm row width, 8 rows, 4 jars aligned side to side per row) to prevent aggregation of individuals and thus maintain a more uniform distribution of *Bythotrephes* in the jars. Each of the experimental treatments were represented on one row of the wheel, randomly placed. Thus, each row of the wheel acted as an experimental block. The plankton wheel rotated jars top over bottom at a speed of approximately 2 minutes per revolution. We ran experiments for approximately 10 hours under controlled temperature and light conditions. We collected data on individual *Bythotrephes* by counting individual instars during transfer to the jars and by visually inspecting the contents of the jars both during and at the end of the experiment; allowing us to determine the total number of *Bythotrephes* in the jar, including the number alive and swimming and those dead at the bottom. At the end of the experiment, we removed and processed jars from the wheel row-by-row. As each row was removed from the wheel, we employed methods (see below) to stop predation.

Experiment 1

This experiment was designed first to determine *Bythotrephes* cannibalism rate and second, how instar composition and alternative prey availability could influence that rate. The experiment was a two-way factorial design, crossing two levels of instar composition (1: eight 1st instars, and 2: six 1st instars and two 3rd instars) with two levels of alternative prey availability (1: a background assemblage of zooplankton, and 2: no background zooplankton). We reasoned that rates of cannibalism should be higher in the mixed instar treatments, with 3rd instar *Bythotrephes* preferentially consuming smaller, and presumably more vulnerable 1st instars, which can be 2-5 times smaller than 3rd instars. We manipulated the presence of background zooplankton, because the lack of alternative prey could increase the hunger levels and foraging activity of *Bythotrephes* (Johansson 1991); forcing them to expand their diets to include conspecifics (Leonardsson 1991). Each treatment combination was replicated 7 times. Unfortunately, an oversight caused loss of some individuals during transfer into the experimental jars. If there were fewer than 5 individuals in a jar (which occurred in 3 of the 28 jars), we did not include these jars in our final analyses, leaving 25 of the 28 jars with 5 to 8 *Bythotrephes*, with a median of 7. We found no significant differences in initial *Bythotrephes* densities between different treatments (2-way ANOVA; Instar: $F_{1,22} = 0.15$, $P = 0.704$, Treatment: $F_{1,22} = 0.91$, $P = 0.351$, Instar*Treatment: $F_{1,22} = 1.29$ $P = 0.268$). Background zooplankton assemblage with approximate equal densities of component taxa/life stages were obtained by combining 20 subsamples with a 'thumbed' pipette in an aquarium holding natural assemblages of Lake Michigan zooplankton. These zooplankton were obtained from a vertical plankton tow from 40m depth and at the same location *Bythotrephes* were collected, with a 64 μm mesh net. Average (± s.d.) densities (ind. L^{-1}) of sample background assemblages in experimental jars were: 10.5 ± 2.1 *Daphnia mendotae*, 10 ± 2 juvenile diaptomid copepods, 6 ± 1 adult diaptomid copepods, 3.75 ± 0.7 copepod nauplii, and 2.5 ± 0.25 cyclopoid copepods. This high density of zooplankton, which greatly exceed average densities in Lake Michigan, was chosen to be conservative in examining if known prey modify any observed cannibalism. Water used in this experiment was a 75:25 mix of filtered, aged Lake Michigan water and E-pure™ ultrapure water.

The experiment was run from 11:40 to 21:40 with temperatures in the room between 21.5-21.9°C. Light intensity was 129, 37, and 4.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top, middle and the bottom of the wheel, respectively; which is in the range of light intensity where *Bythotrephes* should be capable of seeing and capturing its prey (Pangle and Peacor 2009). At the end of the experiment, as each block was removed from the wheel, sodium bicarbonate was added to each jar to narcotize the *Bythotrephes* and stop predation. The contents of each jar were then gently poured through a 64-um mesh filter, which captured intact individual *Bythotrephes* and all body parts (e.g., carapaces, spines, etc.). Intact individuals represented those that were either alive at the end of the experiment, or had died during the experiment without any obvious signs of cannibalism (i.e., missing or severely damaged body parts), and so were not included as cannibalized individuals in calculations of attack rates (see below). Individuals with signs of missing or severely damaged body parts and isolated spines (which were never consumed during cannibalism) were attributed to cannibalism. Although it was impossible to precisely quantify what proportion of a cannibalized individual was actually consumed, if only a spine was recovered, we assumed roughly 90% of that victim was consumed, as the spine can comprise up to and sometimes over 10% of adult body mass (Sullivan and Lehman 1998; Branstrator 2005). Partially cannibalized individuals with missing or severely damaged body parts were assumed to be between 10-90% consumed, with a rough average of 50% based on our observations. We note that other visible, shredded pieces of tissue were not detected in the jars.

Individual *Bythotrephes* and body parts were carefully removed from the mesh with blunt-tipped plastic forceps under a dissecting scope, and delivered to a 50-mL plastic vial filled with 95% EtOH for preservation.

Experiment 2

The second experiment was also designed to first determine *Bythotrephes* cannibalism rate and second, how instar composition and conspecific density influence that rate. We simultaneously manipulated instar composition and density in each of four treatments: (1) six 1st instars and zero 3rd instars (1.5 ind. L^{-1}); (2) six 1st instars and two 3rd instars (2 ind. L^{-1}); (3) zero 1st instars and six 3rd instars (1.5 ind. L^{-1}); and (4) zero 1st instars and twelve 3rd instars (3 ind. L^{-1}), each treatment was replicated 6 times.

The experiment was run from 10:48 to 20:35, with temperature in the room ranging between 19.0 – 21.8°C throughout the duration of the experiment. Light intensity was 129, 38, and 4.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at top, middle, and bottom of the plankton wheel, respectively. After 10 hours we removed jars from the wheel a half a block at a time, at which point we covered them in black felt as a non-destructive way to stop predation by the visually hunting *Bythotrephes* (rather than adding sodium bicarbonate as in Experiment 1). We removed the black felt of each jar individually, visually inspected the contents, and replaced the felt. Every individual in each jar was counted and categorized as 'dead-intact', 'dead with signs of attack', or 'alive'. As in Experiment 1, 'dead-intact' individuals were not used to calculate attack rates (see below). To estimate cannibalism rates, we sought a duration for which there was a sufficient number, but not too many, killed. Evaluating the number 'dead' in a non-destructive way allowed us to evaluate if 10 hours was sufficient. Because the average number dead was low (0.95 individuals per jar) we extended the experiment. Jars were placed back on the wheel, and the experiment was restarted roughly 2 hours after stopping it for an additional 10 hours of light on the wheel. At the end of this second period, individual *Bythotrephes* were counted and categorized as in Experiment 1.

Quantifying cannibalism

To quantify cannibalism, we first calculated per capita attack rates

$$a = \frac{\frac{1}{N} - \frac{1}{N_o}}{t}$$

where a is the mortality rate due to cannibalism; N is the number of individuals in the jar at the beginning of the experiment minus the number of individuals cannibalized (as distinguished from the total number dead) during the experiment; N_o is the number of living individuals in the jar at the beginning of the experiment; and t is the duration (in hours) of the experiment.

We calculated daily clearance rates (F) as

$$F = aVt$$

where V is volume of the jars, and t is the number of hours in a day (Riisgård 2001), allowing us to get the volume of water cleared of conspecifics by *Bythotrephes* per unit time per individual. Clearance rates provide the potential feeding rate of a predator on a given prey, by representing the total volume covered by a predator in a given amount of time to “clear” that volume of that specific prey. The utility of clearance rates is that they can be easily used to predict feeding rates at different prey densities.

Statistical analyses

All statistical analyses were done in R (version 4.2.1, R Core Development Team, 2015). Prior to analyses, all data were tested for normality and homoscedasticity with the Shapiro-Wilk test and the Fligner-Killeen test, respectively. In Experiment 1, we analyzed the separate and interactive effects of instar composition and background prey on daily clearance rates with 2-way mixed effects ANOVA with treatment as a fixed factor and block as a random factor. In Experiment 2, we analyzed the effects of the instar composition/density treatments on *Bythotrephes* clearance rates. We used an additive 2-way mixed effects ANOVA with treatment as a fixed factor and block as a random factor, followed by Tukey’s honestly significant difference (HSD) tests to assess post-hoc differences among treatment means for clearance rate data (Sokal and Rolhf 1995). All analyses were done on data collected at the end of day 2 of the experiment (i.e., after 20 h). For each experiment, we conducted a *post-hoc* power analysis to determine our statistical power using the package ‘pwr’(Champely et al. 2016) in R (version 4.2.1).

Results

Bythotrephes appeared generally healthy and active throughout the duration of both experiments, although a few (0.35 per jar in Experiment 1, and 0.5 per jar in Experiment 2) individuals died without any clear damage from a cannibalistic encounter. We observed several instances of cannibalism in action during our observations in which one *Bythotrephes* clearly killed a second. We also observed a number of instances where two individuals were coupled in a manner expected during a cannibalistic attack, but in which the encounters ended with seemingly no damage to the individuals (see Discussion).

In Experiment 1, *Bythotrephes* cannibalized an average (± SE) of 0.27 ± 0.05 of its conspecifics, across all jars (Fig 1a). Of those scored as cannibalized, 0.65 of 1st instars were completely consumed (only spines remained) and 0.35 were partially consumed; 0.25 of 3rd instars were completely consumed, 0.75 were partially consumed. Average (± SE) clearance rate on conspecifics across jars was 0.75 ± 0.21 $L \cdot day^{-1}$ (Fig. 1b), with a maximum clearance rate among jars of 3.4 $L \cdot day^{-1}$. We found no effects of instar composition, background prey, or their interaction on clearance rates (Table 1). In the mixed instar treatment, the average proportions of 1st and 3rd instars cannibalized across background prey treatments were 0.25± 0.07 and 0.17 ± 0.07, respectively (Fig. 1c). *Post-hoc* power analyses indicated that the design for Experiment 1 did not provide sufficient power ($\beta = 0.40$) to detect even large treatment effect sizes (e.g., ≥ 0.35; Cohen 1992).

In Experiment 2, *Bythotrephes* cannibalized an average (± SE) of 0.42 ± 0.04 of its conspecifics across all jars (Fig. 2a). Sixty percent were completely consumed as only the spine remained, and 0.40 were only partially consumed (i.e., dead individuals with signs of shredding or parts of carapace and spine remaining. Average (± SE) clearance rate due to cannibalism were 0.69 ± 0.21 L · day^{-1} and per treatment ranged from 0.19 (± 0.03) to 1.2 (± 0.2) L · day^{-1} (Fig. 2b), with a maximum clearance rate of 1.6 L · day^{-1}. Average (± SE) clearance rates in the 3rd instar/1.5 ind. L^{-1} treatment (1.2 ± 0.2) were six times higher than clearance rates in the mixed instar treatment (0.19 ± 0.03). Average (± SE) clearance rates in the 3rd instar/3 ind. L^{-1} treatment (0.52 ± 0.10) and the 1st instar treatment (0.6 ± 0.2), were intermediate to the previous two treatments (Table 2). In the mixed instar treatment, the average (± SE) proportion of 1st and 3rd instars cannibalized were 0.26 ± 0.09 and 0.42 ± 0.16, respectively (Fig. 2c). *Post-hoc* power analyses indicated that the experimental design in Experiment 2 afforded us sufficient power ($\beta = 0.82$) to detect large treatment effect sizes (e.g., ≥ 0.35; Cohen 1992), but not ($\beta = 0.47$) to detect moderate treatment effect sizes (e.g., ≥ 0.15; Cohen 1992).

Discussion

Our results indicate high rates of cannibalism in *Bythotrephes cederströmii*. Average (± SE; across jars) clearance rates were consistent between both of our experiments (0.75 ± 0.2 L · d^{-1} in Experiment 1 and 0.69 ± 0.10 L · d^{-1} in Experiment 2). These clearance rates are within the range of the average clearance rates previously reported for *Bythotrephes* feeding on *Daphnia mendotae* (0.17 ± 0.01 L · d^{-1}; Schulz and Yurista 1999), a common, and preferred prey item in lakes invaded by *Bythotrephes* (Vanderploeg et al. 1993, Schulz and Yurista 1999). The cannibalism clearance rates were also similar to those reported for *Bythotrephes* feeding on other prey, including small cladocerans (*Bosmina* spp.: 1.4 $L \cdot d^{-1}$; and *D. retrocurva* 1.2 $L \cdot d^{-1}$), and copepod nauplii (0.17 $L \cdot d^{-1}$) (Vanderploeg et al. 1993).

Conspecifics could represent an important food source for *Bythotrephes* when other prey items are at low densities or unavailable. In offshore waters of Lake Michigan, consumption requirements are a high proportion, or can exceed production, of *Bosmina* and *D. mendotae* at some points during the year, especially late in the season and occasionally as early as July or August (Pothoven and Vanderploeg 2018, Pothoven and Vanderploeg 2019). During these periods, *Bythotrephes* can reach a volumetric biomass roughly equal and greater than that of its preferred (i.e., those on which it has the highest clearance rates) cladoceran prey, *D. mendotae* and *Bosmina* (Sprules et al. 1990, Vanderploeg et al. 1993, Pangle and Peacor 2009). For example, in Lake Michigan in 2007 and 2008, *Bythotrephes* increased in density through November (and then was at lower levels in December). In the months of October and November, average *Bythotrephes* biomass density (e.g., $mg \cdot L^{-1}$) was on the same order of magnitude or exceeds that of *D. mendotae* and *Bosmina* (Vanderploeg et al. 2012). Analyzing clearance rates allows us to estimate feeding rates in the field based on experimental results; the feeding rate in mass per unit time is a product of the clearance rate and biomass density. Because both biomass density and clearance rate of conspecifics is similar to that of *D. mendotae* and *Bosmina* during certain times, our results suggest that feeding rates on conspecifics could be similar to that of *Bythotrephes*' preferred zooplankton prey, and thus conspecifics could provide an important food source for *Bythotrephes* during these times. A similar conclusion is reached for copepod prey, which in October through December have higher average densities than *D. mendotae* and *Bosmina*, but for which the clearance rates are much lower (Vanderploeg et al.

1993). In essence, when examining feeding rates using biomass density, because the clearance rates are on the same order of magnitude or larger than other prey, and the mass of individual *Bythotrephes* is far greater than those prey, calculations of feeding rates show that conspecifics could be an important resource even though densities are substantially lower.

The above analysis indicates that cannibalism could supply a substantial portion of resources to the diet of *Bythotrephes*, but ignores the temporal allocation of the resource. It is necessary to further consider whether the frequency of cannibalism in the diet would influence an individual *Bythotrephes*. For example, at the clearance rate of 0.7 $L \cdot d^{-1}$ observed in our experiment, an individual *Bythotrephes* would capture 1 conspecific in 71, 14, and 3 days when the density is 20, 100 and 500 ind L^{-1}, respectively. These densities are at the upper end of densities reported in the literature (Table S1), as described in the next paragraph. It is unclear if eating 1 conspecific in 71 days (viewed another way, 1 out of 7 *Bythotrephes* eating a conspecific every 10 days) would influence population dynamics, but it seems reasonable to assume that 1 in every 14 days, or especially 1 in every 3 days, would be important to the diet and influence a population. Some pelagic predatory crustaceans, including *Bythotrephes*, are known to have long gut residence times of up to 12-13 hours (Yurista and Schulz 1995, Murtaugh 1984, Lehman 1993, Ritz 2008). However, individuals that go long bouts between feeding (i.e., starved individuals) may retain significant amounts of material in their gut for more than three days (e.g., Murtaugh 1984).

Are *Bythotrephes* densities in natural systems high enough to influence the population dynamics based on the clearance rates found in our experiments? We performed a non-exhaustive review of the literature on *Bythotrephes* density using

Google Scholar’s Advanced Search Page to find articles with ‘abundance’ OR ‘density’ OR ‘survey’ AND ‘*Bythotrephes*’ that were dated between 1984 (date of first reported *Bythotrephes* invasion to the Laurentian Great Lakes) and the present. As with most zooplankton in deep lakes, *Bythotrephes* are found to be highly aggregated as a function of depth (e.g., Petruniak 2009, Walsh et al. 2016), and therefore densities are likely often highly variable across depths. Nevertheless, of the 44 studies we identified that reported *Bythotrephes* density, only seven reported densities as a function of depth (Table S1). Approximate average (± sd) maximum volumetric densities (ind. · m^{-3}) reported were 325 ± 600 ($n = 8$) when density was computed from water column strata, and were 105 ± 295 ($n = 33$) when density was computed from the entire water column. For those studies in which the density of different layers and the entire water column were reported, the layer with the highest density was roughly 6 ± 3 times greater than when density was computed from the entire water column, suggesting that *Bythotrephes* densities reported from entire water column estimates are likely much lower than those at certain depth strata where *Bythotrephes* is more aggregated (Table S1). Further, studies that performed stratified sampling will also underestimate maximum volumetric densities, because the strata are still likely averaging over a range of *Bythotrephes* densities (Scofield et al. 2020, Vanderploeg et al. 2015), and single strata likely only partially encompass peak densities. Taken together, *Bythotrephes* densities are frequently in the range of 100 ind. · m^{-3}, and with upper estimates in the thousands ind. · m^{-3}. Our literature survey, in combination with inferences about heterogeneity in density as a function of depth, suggest that *Bythotrephes* are often in the range in which cannibalism occurs frequently enough to influence individual, and therefore population, growth rates.

Two factors influence the estimate of cannibalism rates in the field based on the laboratory results. Our experiments ignored any satiation effects. *Bythotrephes* are a considerably large prey item, and satiation could be reached after consuming one individual. This factor reduces the estimate of cannibalism rate in the field, thus making the estimate conservative. We also only had a rough estimate of how much of the killed conspecific was actually eaten. Across both experiments, an average of 50% of the cannibalized individuals were identified by remaining spines with no bodies attached, with the remaining 50% of cannibalized individuals identified by spines with some attached and shredded carapace. Although it has been shown that *Bythotrephes* has low ingestion efficiency (59%; Burkhardt and Lehman 1994), consumption of conspecifics is likely providing a resource at a satiating level because of the very large size of conspecific prey. These two factors therefore do not diminish the inferences made above concerning the influence of cannibalism on individual and population growth rate.

The existence of cannibalism could help resolve existing discrepancies between predicted bioenergetic requirements or experimentally-determined consumption rates by *Bythotrephes* and available heterospecific prey. For example, bioenergetics and efficiency models indicate that *Bythotrephes* consumption rates derived from laboratory experiments would exceed observed zooplankton production in the deep oligotrophic lakes *Bythotrephes* often inhabit (Burkhardt and Lehman 1994, Yurista and Schulz 1995, Dumitru 2001, Yurista et al. 2010, Bunnell et al. 2011, Pothoven and Hook 2014). Because cannibalism can help overcome the effects of a limited supply of energy, it could provide *Bythotrephes* an unaccounted-for food source, which could resolve these discrepancies. More research is required to investigate if the discrepancies are encountered as a function of *Bythotrephes* density (i.e., occur when densities are sufficiently high for cannibalism to influence growth rates).

Our experiments had low statistical power to detect moderate (Experiment 2) or even large (Experiment 1) treatment effects on *Bythotrephes* cannibalism rates. It is therefore difficult to draw inferences about the effects of the three factors commonly documented to influence cannibalism rates: food availability, size, and population density. In many species, increases in relative size (and therefore vulnerability) differences among life stages increase rates of cannibalism (DeAngelis et al. 1979, Bry and Gillet 1980, Polis 1981). Our expectation was that rates of cannibalism would be highest in mixed instar treatments with 3rd instar *Bythotrephes* selectively cannibalizing 1st instars, which may have 2-5 times smaller biomass than 3rd instars, and presumably more vulnerable to attack by 3rd instars. Whereas we did find evidence in experiment 2 that 3rd instars cannibalize more than 1st instars do, they cannibalized other 3rd instars just as much, if not more, than 1st instars; suggesting either that size differences between 1st and 3rd instars may not influence vulnerability. Because *Bythotrephes* is a raptorial predator that is not gape-limited, with mouth-parts that can shred even relatively larger prey items, it is possible that size differences among instars do not play a large role in cannibalism. However, the distribution of instar types in the population could still influence the prevalence of cannibalism. For example, since 1st instars seem to attack fewer conspecifics than 3rd instars, populations with higher proportions of 3rd instars may be more likely to exhibit cannibalistic behavior.

Availability of alternative prey may also influence cannibalism, with low prey availability increasing predator hunger levels and foraging activity (Johansson 1991);

forcing them to expand their diets to include conspecific prey (Leonardsson 1991). In contrast to our expectations, we observed trends for higher cannibalism in the experimental treatments with available zooplankton prey. Due to our lack of statistical power, however, our study is inconclusive in evaluating the impact of alternative prey. Nevertheless, cannibalism by *Bythotrephes* was observed in both the presence and absence of background heterospecific prey assemblages.

Whereas the relationship between per cannibal consumption rate and population size is often positively density dependent, (Holling 1959, Hassell 1978, Van Buskirk 1989), daily attack rates in Experiment 2 did not increase with *Bythotrephes* density, (e.g., from a = 0.3 (± 0.05) at 1.5 ind. L^{-1} to a = 0.13 (± 0.03) at 3 ind. L^{-1}) suggesting that the *Bythotrephes* densities used in the experiment (i.e., 1.5 and 3 ind. L^{-1}) were at saturation. Saturation is indeed very likely, as the densities we used in our experiments were chosen to maximize encounter rates in the experiment and were high compared to natural densities which are approximately between 0.01 and 0.04 ind. L^{-1} (Pothoven et al. 2003, Pangle and Peacor 2009, Vanderploeg et al. 2012).

As noted previously (see Results), during our observations we noticed pairs of *Bythotrephes* attached to one another via thoracic appendages for minutes at a time, sometime several minutes. Sometimes these couplings ended with the individuals involved swimming away, seemingly unharmed. It is unclear whether these were unsuccessful cannibalistic attacks or some other type of interaction. Similar interactions have been observed in another large-bodied carnivorous cladoceran, *Leptodora kindtii*, and attributed to mating rather than unsuccessful cannibalistic attacks because individuals involved in these interactions were unharmed and often the same size, suggesting against vulnerability-based intraspecific predation (Browman et al. 1989).

Males are rare in the population until fall, and because we ran the experiments in August and early September, mating-associated couplings were likely to have been rare. We also note, that in several other observed couplings, one of the paired individuals was killed and partially consumed by the other.

We have demonstrated and quantified *Bythotrephes* cannibalism in a laboratory setting, with estimates that conspecifics could represent a substantial portion of the *Bythotrephes* diet during certain periods of the year in systems where *Bythotrephes* reach high densities. Given the predicted advantages of cannibalism to *Bythtorephes*, a next step is to more directly examine its importance in natural populations, as understanding its role could facilitate predicting the establishment, success, and impact of *Bythotrephes* populations.

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Literature cited

Andersson, J., Byström, P., Claessen, D., Persson, L., & De Roos, A. M., 2007. Stabilization of population fluctuations due to cannibalism promotes resource polymorphism in fish. The American Naturalist *169*: 820-829.

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: 2111-2125.

Bourdeau, P. E., Pangle, K. L., & Peacor, S. D., 2011. The invasive predator *Bythotrephes* induces changes in the vertical distribution of native copepods in Lake Michigan. Biological Invasions *13*: 2533-2545.

Bourdeau, P. E., Pangle, K. L., & Peacor, S. D., 2015. Factors affecting the vertical distribution of the zooplankton assemblage in Lake Michigan: The role of the invasive predator *Bythotrephes longimanus*. Journal of Great Lakes Research *41*: 115-124.

Branstrator, D. K., 2005. Contrasting life histories of the predatory cladocerans *Leptodora kindtii* and *Bythotrephes longimanus*. Journal of Plankton Research 27: 569-585.

Branstrator, D. K. (1995) Ecological interactions between *Bythotrephes cederstroemi* and *Leptodora kindtii* and the implications for species replacement in Lake Michigan. Journal of Great Lakes Research *21*: 670–679.

Browman, H. I., Kruse, S., & O'Brien, W. J., 1989. Foraging behavior of the predaceous cladoceran, *Leptodora kindti*, and escape responses of their prey. Journal of Plankton Research *11*: 1075-1088.

Bry, C., & Gillet, C., 1980. Reduction of cannibalism in pike (*Esox lucius*) fry by isolation of full-sib families. Reproduction Nutrition Développement *20*: 173-182.

Buddle, C. M., Walker, S. E., & Rypstra, A. L., 2003. Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). Canadian Journal of Zoology 81: 1293-1297.

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: 1281-1296.

Burkhardt, S., & Lehman, J. T., 1994. Prey consumption and predatory effects of an invertebrate predator (*Bythotrephes*: Cladocera, Cercopagidae) based on phosphorus budgets. Limnology and Oceanography 39: 1007-1019.

Butorina, L. G., 2000. A review of the reproductive behavior of *Polyphemus pediculus* (L.) Müller (Crustacea: Branchiopoda). Hydrobiologia 427: 13-26.

Champely, S., Ekstrom, C., Dalgaard, P., Gill, J., Wunder, J., & Rosario, H. D., 2016. Package'pwr'. 2015. URL: https://cran. r-project. org/web/packages/pwr/pwr. pdf (visited on 04/27/2016).

Claessen, D., A. M. de Roos, and L. Persson, 2004. Population dynamic theory of size-dependent cannibalism. Proceedings of the Royal Society B 271: 333-340.

Cohen, J., 1992. Statistical power analysis. Current Directions in Psychological Science 1: 98-101.

Cushing, J. M., Henson, S. M., & Hayward, J. L., 2015. An evolutionary game-theoretic model of cannibalism. Natural Resource Modeling 28: 497-521.

DeAngelis, D. L., Travis, C. C., & Post, W. M., 1979. Persistence and stability of seed-dispersed species in a patchy environment. Theoretical Population Biology *16*: 107-125.

Dobler, R., & Kölliker, M., 2010. Kin-selected siblicide and cannibalism in the European earwig. Behavioral Ecology 21: 257-263.

Duarte, C., Jaramillo, E., Contreras, H., & Acuña, K., 2010. Cannibalism and food availability in the talitrid amphipod *Orchestoidea tuberculata*. Journal of Sea Research 64: 417-421.

Elgar, M. A. C., & Bernard, J., 1992. *Cannibalism: ecology and evolution among diverse taxa* (No. 591.53 E53).

Evans, M.S., 1988. *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. Journal of Great Lakes Research 14: 234-240.

Fox, L. R., 1975. Factors influencing cannibalism, a mechanism of population limitation in the predator *Notonecta hoffmanni*. Ecology 56: 933-941.

Gerritsen, J., & Strickler, J. R., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Board of Canada 34: 73-82.

Getto, P., Diekmann, O., & De Roos, A. M., 2005. On the (dis) advantages of cannibalism. Journal of Mathematical Biology 51: 695-712.

Grigorovich, I. A., Pashkova, O. V., Gromova, Y. F., & van Overdijk, C. D., 1998. *Bythotrephes longimanus* in the Commonwealth of Independent States: variability, distribution and ecology. Hydrobiologia 379: 183-198.

Hassell, M. P., 1978. The dynamics of arthropod predator- prey systems. Princeton University Press, Princeton, New Jersey, USA.

Holling, C. S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91: 293-320.

Ibánez, C. M., & Keyl, F., 2010. Cannibalism in cephalopods. Reviews in Fish Biology and Fisheries 20: 123-136.

Jarnagin, S. T., 1998. Direct and indirect estimates of death rates and predator-mediated dispersal of *Bythotrephes cederstroemi*. Michigan Technological University.

Johansson, F, 1991. Foraging modes in an assemblage of odonate larvae—effects of prey and interference. Hydrobiologia 209: 79-87.

Johansson, F., 1992. Effects of zooplankton availability and foraging mode on cannibalism in three dragonfly larvae. Oecologia 91: 179-183.

Johansson, F., 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behaviour and zooplankton availability. Oikos 66: 80-87.

Johannsson, O.E., Mills, E.L. & O'Gorman, R., 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–88. Canadian Journal of Fisheries and Aquatic Sciences 48: 1546-1557.

Kerfoot, W. C., Hobmeier, M. M., Yousef, F., Lafrancois, B. M., Maki, R. P., & Hirsch, J. K., 2016. A plague of waterfleas (*Bythotrephes*): impacts on microcrustacean community structure, seasonal biomass, and secondary production in a large inland-lake complex. Biological Invasions 18: 1121-1145.

Kim, N., & Yan, N. D., 2010. Methods for rearing the invasive zooplankter *Bythotrephes* in the laboratory. Limnology and Oceanography: Methods 8: 552-561.

Korovchinsky, N.M. & Arnott, S.E., 2019. Taxonomic resolution of the North American invasive species of the genus *Bythotrephes* Leydig, 1860 (Crustacea: Cladocera: Cercopagididae). Zootaxa 4691: 125-138.

Lehman, J.T., 1987. Palearctic predator invades North American Great Lakes. Oecologia 74: 478-480.

Leonardsson, K., 1991. Effects of cannibalism and alternative prey on population dynamics of *Saduria entomon* (Isopoda). Ecology 72: 1273-1285.

Marino Jr, J. A., Peacor, S. D., Bunnell, D. B., Vanderploeg, H. A., Pothoven, S. A., Elgin, A. K., Bence, J. R., Jiao, J., & Ionides, E. L., 2019. Evaluating consumptive and nonconsumptive predator effects on prey density using field time-series data. Ecology 100: e02583.

Mordukhai-Boltovskoi, F. D. & I. K. Rivier, 1987. Predatory cladocerans Podonidae, Polyphemidae, Cercopagidae, and Leptodoridae of the world fauna. Keys to the Fauna of the USSR published by the Zoological Inst. of the Academy Sciences of the USSR, No. 148, Nauka Press, Leningrad, 183 pp. (In Russian.)

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: 135-146.

Pangle, K.L., & Peacor, S.D., 2009. Light-dependent predation by the invertebrate planktivore *Bythotrephes longimanus*. Canadian Journal of Fisheries and Aquatic Sciences 66: 1748-1757.

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: 402-412.

Persson, L., Byström, P., & Wahlström, E., 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. Ecology 81: 1058-1071.

Persson, L., Claessen, D., De Roos, A. M., Byström, P., Sjögren, S., Svanbäck, R., Wahlström, E., & Westman, E., 2004. Cannibalism in a size-structured population: energy extraction and control. Ecological Monographs 74: 135-157.

Petruniak, J., 2009. Analysis of *Bythotrephes longimanus* spatial dynamics in Harp Lake, Ontario. York University.

Pichler, A., Walters, T. L., Frischer, M. E., Nejstgaard, J. C., & Ptáčníková, R., 2021. Application of species-specific primers to estimate the *in situ* diet of *Bythotrephes* [Cladocera, Onychopoda] in its native European range via molecular gut content analysis. Journal of Plankton Research 43: 945-956.

Polis, G. A., 1980. The effect of cannibalism on the demography and activity of a natural population of desert scorpions. Behavioral Ecology and Sociobiology 7: 25-35.

Polis, G. A., 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics *12*: 225-251.

Pothoven, S. A., & Vanderploeg, H. A., 2018. Factors leading to coexistence of *Bosmina longirostris* and *Daphnia galeata mendotae* in offshore Lake Michigan. Fundamental and Applied Limnology 192: 79-89.

Pothoven, S. A., & Vanderploeg, H. A., 2019. Variable demographics and consumption requirements of *Bythotrephes longimanus* (Crustacea, Cercopagididae) along a nearshore to offshore gradient in Lake Michigan. Hydrobiologia 830: 63-75.

Pothoven, S. A., & Höök, T. O., 2014. Predatory demands of *Bythotrephes* and *Leptodora* in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 40: 106-112.

Pothoven, S. A., Fahnenstiel, G. L., & Vanderploeg, H. A., 2003. Population characteristics of *Bythotrephes* in Lake Michigan. Journal of Great Lakes Research 29: 145-156.

Pothoven, S. A., & Fahnenstiel, G. L., 2015. Spatial and temporal trends in zooplankton assemblages along a nearshore to offshore transect in southeastern Lake Michigan from 2007 to 2012. Journal of Great Lakes Research 41: 95-103.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Richardson, M. L., Mitchell, R. F., Reagel, P. F., & Hanks, L. M., 2010. Causes and consequences of cannibalism in noncarnivorous insects. Annual Review of Entomology 55: 39-53.

Riisgård, H. U., 2001. On measurement of filtration rates in bivalves—the stony road to reliable data: review and interpretation. Marine Ecology Progress Series 211: 275-291.

Roberts, J. A., Taylor, P. W., & Uetz, G. W., 2003. Kinship and food availability influence cannibalism tendency in early-instar wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 54: 416-422.

Rudolf, V. H., 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology 88: 2697-2705.

Rudolf, V. H., 2008a. The impact of cannibalism in the prey on predator–prey systems. Ecology 89: 3116-3127.

Rudolf, V. H., 2008b. Impact of cannibalism on predator–prey dynamics: size-structured interactions and apparent mutualism. Ecology 89: 1650-1660.

Schulz, K. L., & Yurista, P. M., 1999. Implications of an invertebrate predator's (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. Hydrobiologia, 380: 179-193.

Scofield, A. E., Watkins, J. M., & Rudstam, L. G., 2020. Heterogeneity in zooplankton distributions and vertical migrations: Application of a laser optical plankton counter in offshore Lake Michigan. Journal of Great Lakes Research 46: 780-797.

Sokal, R. R., & Rohlf, F. J., 1995. Biometry: the principals and practice of statistics in biological research. WH Freeman and Company, New York.

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: 346-351.

Straile, D., & Hälbich, A., 2000. Life history and multiple antipredator defenses of an invertebrate pelagic predator, *Bythotrephes longimanus*. Ecology 81: 150-163.

Strecker, A. L., Arnott, S. E., Yan, N. D., & Girard, R., 2006. Variation in the response of crustacean zooplankton species richness and composition to the invasive predator *Bythotrephes longimanus*. Canadian Journal of Fisheries and Aquatic Sciences 63: 2126-2136.

Sullivan, C. A., & Lehman, J. T., 1998. Character variation and evidence for spine length selection in the invertebrate predator *Bythotrephes* (Crustacea: Cladocera) from Lakes Michigan, Huron, and Erie. Archiv für Hydrobiologie 142: 35-52.

Van Buskirk, J., 1989. Density-dependent cannibalism in larval dragonflies. Ecology 70: 1442-1449.

Van den Bosch, F., De Roos, A. M., & Gabriel, W., 1988. Cannibalism as a life boat mechanism. Journal of Mathematical Biology 26: 619-633.

Vanderploeg, H. A., Liebig, J. R., & Omair, M., 1993. *Bythotrephes* predation on Great Lakes' zooplankton measured by an in-situ method: implications for zooplankton community structure. Archiv für Hydrobiologie 127: 1-8.

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: 336-352.

Vanderploeg, H. A., Pothoven, S. A., Krueger, D., Mason, D. M., Liebig, J. R., Cavaletto, J. F., Ruberg, S. A., Lang, G. A., & Ptáčníková, R., 2015. Spatial and predatory interactions of visually preying nonindigenous zooplankton and fish in Lake Michigan during midsummer. Journal of Great Lakes Research 41: 125-142.

Walsh, J. R., Munoz, S. E., & Vander Zanden, M. J., 2016. Outbreak of an undetected invasive species triggered by a climate anomaly. Ecosphere 7: e01628.

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: 519-527.

Yan, N. D., Girard, R., & Boudreau, S., 2002. An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. Ecology Letters 5: 481-485.

Young, J. P. W., 1978. Sexual swarms in *Daphnia magna*, a cyclic parthenogen. Freshwater Biology 8: 279-281.

Yurista, P. M., 1992. Embryonic and postembryonic development in *Bythotrephes cederstroemii*. Canadian Journal of Fisheries and Aquatic Sciences 49: 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: 141-150.

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.

Zozulya, S. S., 1978. Some aspects of the feeding behavior of *Bythotrephes longimanus* (Leydig). In: Study on behavior of aquatic invertebrates in nature. Materials from the Third All-Union symposium on the behaviour of aquatic invertebrates. *Borok* 14–15. (In Russian.)

Tables

Table 1. Results of 2-way analysis of variance (ANOVA) on the main and interactive effects of conspecific instar composition and presence/absence of background heterospecific zooplankton prey and experimental block on the clearance rates of *Bythotrephes* on conspecifics in Experiment 1.

Source	DF	SS	MS	*F*	*P*
Instar	1	0.197	0.197	0.219	0.647
Background	1	4.081	4.081	4.520	0.051
Instar*Background	1	0.336	0.336	0.373	0.551
Block	6	6.782	1.130	1.252	0.336
Residuals	15	13.543	0.903		

Table 2. Results of 1-way analysis of variance (ANOVA) on the effect of instar composition/density treatments and experimental block on the ln-transformed clearance rates of *Bythotrephes* on conspecifics in Experiment 2.

Source	DF	SS	MS	*F*	*P*
Treatment	3	8.796	2.932	5.938	**0.007**
Block	5	3.953	0.791	1.601	0.220
Residuals	15	7.407	0.494		

Table 3. Post-hoc comparisons of between treatment differences in ln-transformed clearance rates in Experiment 2. KEY: 1 – 1st instars; 3 – 3rd instars; 1&3 – Mixed 1st and 3rd instars; 3x2 – 3rd instars at double density (3.0 ind.$\cdot$L^{-1}). Pairwise comparisons that are significantly different are in bold.

Comparison	Difference	Lower	Upper	*P*
1&3-1	-0.566	-1.736	0.603	0.521
3-1	1.112	-0.057	2.282	0.065
3x2-1	0.279	-0.890	1.449	0.900
3-1&3	1.679	0.509	2.848	**0.004**
3x2-1&3	0.846	-0.324	2.015	0.203
3x2-3	-0.833	-2.002	0.336	0.213

Figure legends

Figure 1. Effects of conspecific instar composition and presence/absence of background heterospecific zooplankton prey on (a) proportion of *Bythotrephes* instars cannibalized in all replicates of each treatment, (b) daily clearance rates of *Bythotrephes* in each experimental treatment, and (c) proportion of instars cannibalized in the mixed instar (1st & 3rd) treatment, in Experiment 1. Points represent individual data points from each replicate jar, jittered to reduce overlap. Lower and upper box boundaries indicate the 25th and 75th percentiles, respectively, the line inside the box is the median, and the lower and upper error lines are the 10th and 90th percentiles, respectively. Key – Treatment indicates presence or absence of background heterospecific zooplankton assemblage; Instar represents composition of 1st and 3rd instars.

Figure 2. Effects of instar composition/density treatments on (a) proportion of *Bythotrephes* instars cannibalized in all replicates of each treatment, (b) daily clearance rates of *Bythotrephes* in each experimental treatment, and (c) proportion of instars cannibalized in the mixed instar (1st and 3rd) treatment in Experiment 2. Points represent individual data points from each replicate jar, jittered to reduce overlap. Lower and upper box boundaries indicate the 25th and 75th percentiles, respectively, the line inside the box is the median, and the lower and upper error lines are the 10th and 90th percentiles, respectively. Instar represents composition and density of 1st and 3rd instars.

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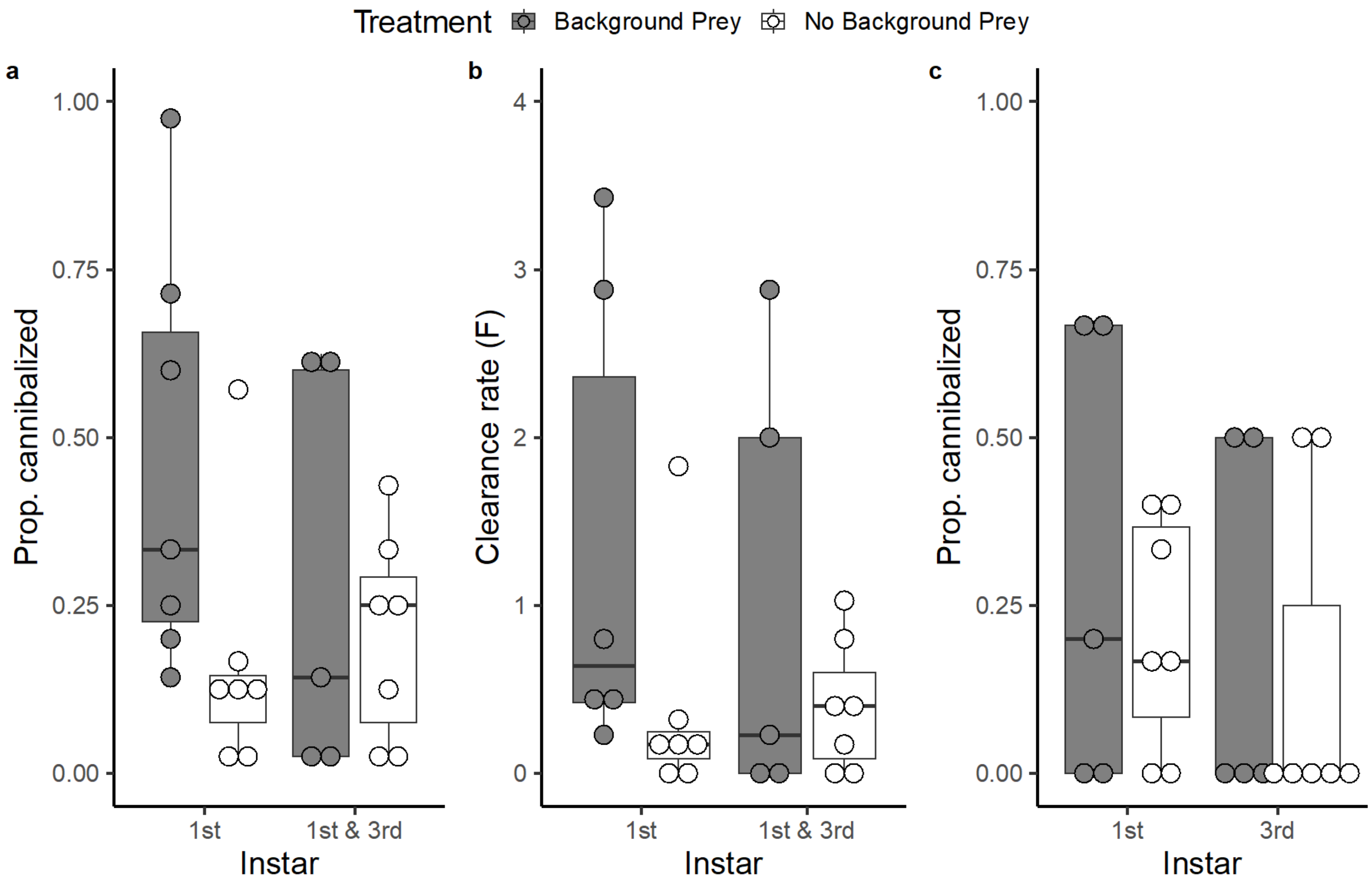
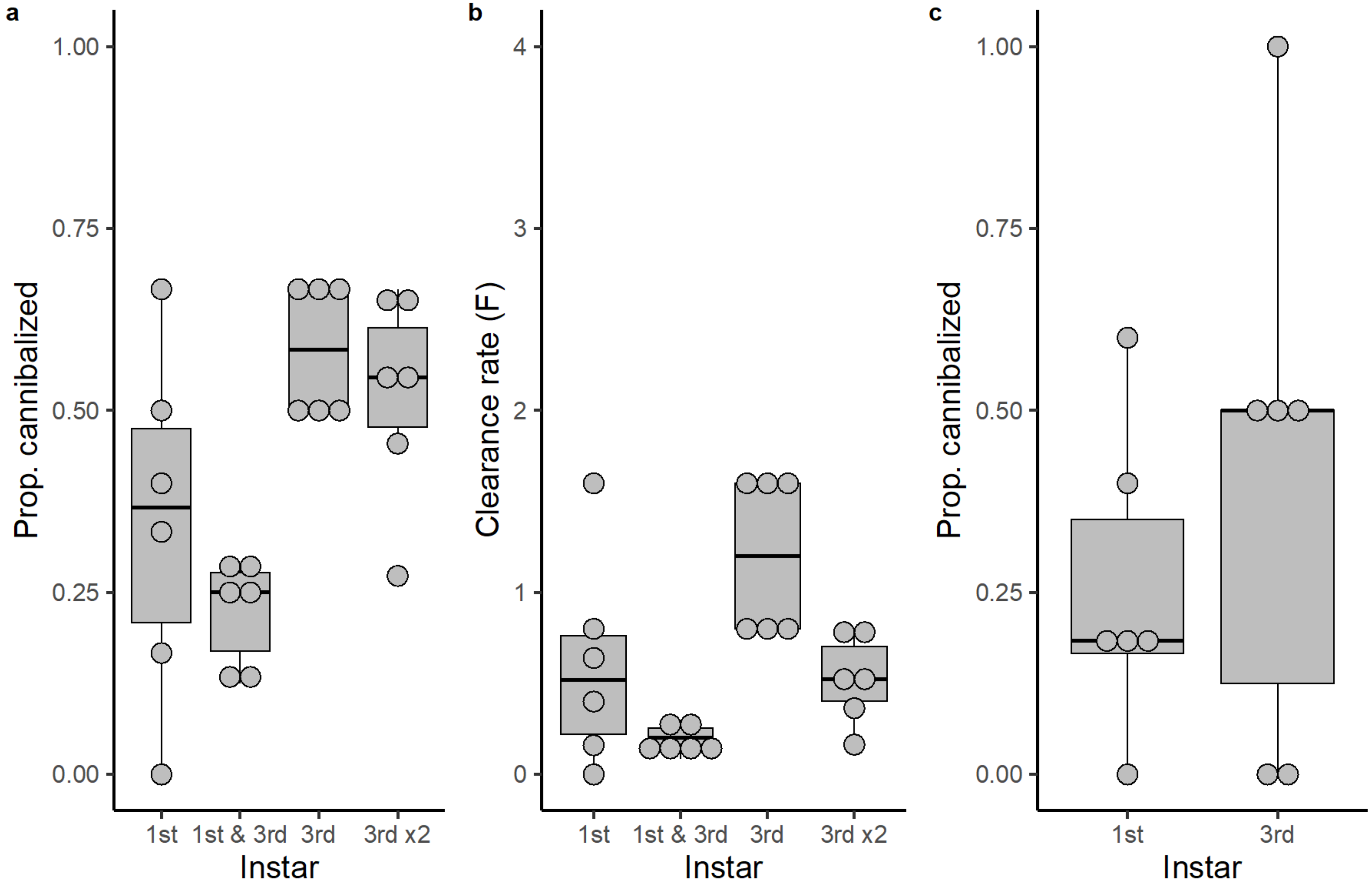


803

Figure 2


a
Prop. cannibalized
1.00
0.75
0.50
0.25
0.00
1st
1st & 3rd
3rd
3rd x2
Instar
b
Clearance rate (F)
4
3
2
1
0
1st
1st & 3rd
3rd
3rd x2
Instar
c
Prop. cannibalized
1.00
0.75
0.50
0.25
0.00
1st
3rd
Instar