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Joelle D. Young, Angela L. Strecker & Norman D. Yan

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Increased abundance of the non-indigenous zooplanktivore, *Bythotrephes longimanus*, is strongly correlated with greater spring prey availability in Canadian Shield lakes

Joelle D. Young · Angela L. Strecker · Norman D. Yan

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Abstract The non-indigenous zooplanktivore, *Bythotrephes longimanus*, is a large Palaearctic cladoceran that is spreading rapidly in the Great Lakes watershed in North America. As a voracious predator, *Bythotrephes* can reduce herbivorous cladoceran abundance and diversity; however, the variables that affect its abundance are not well understood. To determine what bottom-up factors are associated with the abundance and seasonal dynamics of established

Bythotrephes populations, two *Bythotrephes* datasets from lakes in south-central Ontario, Canada, were analysed using multiple regression and multivariate analyses: a multi-lake dataset of nine lakes sampled in 2003 and a multi-year dataset of one of these lakes, Harp Lake, sampled from 1994–1998 and 2001–2004. Bottom-up variables tested were Secchi disk depth, epilimnetic temperature, cladoceran (prey) density, total phosphorus, dissolved organic carbon and Chlorophyll *a*, as well as maximum depth for the multi-lake dataset. In both analyses and datasets, springtime abundance of herbivorous cladocerans was consistently found to be a significant factor associated with *Bythotrephes* (June–September) abundance; *Bythotrephes* annual abundance was significantly and positively associated with mean May and June prey abundance, along with mean Secchi disk depth for the multi-lake dataset, and groups of lakes or years with similar *Bythotrephes* seasonal abundance patterns were predicted by June prey abundance. Additionally, prey availability was the dominant contributor towards changes in weekly *Bythotrephes* birth rates calculated for two of the study lakes. Our study suggests that prey availability influences *Bythotrephes* abundance, which provides evidence that *Bythotrephes* establishment success is affected by the abundance of its prey.

J. D. Young · N. D. Yan
Biology Department, York University, Toronto,
ON M3J 1P3, Canada

Present Address:
J. D. Young (✉)
Water Monitoring Section,
Ontario Ministry of the Environment, Toronto,
ON M9P 3V6, Canada
e-mail: joelle.young@ontario.ca

A. L. Strecker
Department of Biology, Queen's University, Kingston,
ON K7L 3N6, Canada

Present Address:
A. L. Strecker
School of Aquatic and Fishery Sciences,
University of Washington, Seattle,
WA 98105, USA

N. D. Yan
Dorset Environmental Science Centre,
Ontario Ministry of the Environment,
Dorset, ON P0A 1E0, Canada

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Introduction

Bythotrephes longimanus is a Palaearctic cladoceran that was first detected in the Great Lakes in the early 1980s (Johannsson et al. 1991) and has since invaded >140 North American lakes (Branstrator et al. 2006; Weisz and Yan 2010; Muirhead and MacIsaac 2011). The invader is a voracious and active predator that consumes a large number of zooplankton each day, with a preference for herbivorous cladocerans (Vanderploeg et al. 1993; Burkhardt and Lehman 1994; Wahlström and Westman 1999; Grigorovich et al. 1998). Consequently, zooplankton species richness and abundance, particularly of cladocerans, have declined in invaded lakes in which *Bythotrephes* is abundant (Yan et al. 2002; Boudreau and Yan 2003; Barbiero and Tuchman 2004; Strecker et al. 2006). However, *Bythotrephes* abundance exhibits considerable variability among and within lakes, and, as we do not currently understand the key factors controlling its abundance, we cannot predict the degree of impact *Bythotrephes* will have in individual lakes.

The population dynamics of a cladoceran species are directly driven by bottom-up and/or top-down regulation (e.g., Hall 1964; Lampert et al. 1989; Luecke et al. 1990). Given that *Bythotrephes* is a voracious predator, prey availability would likely be an important bottom-up regulator of its abundance. Dumitru et al. (2001) and Strecker and Arnott (2008) observed that *Bythotrephes* consumption rates on occasion exceeded prey production rates, i.e., prey could limit *Bythotrephes* production. Because *Bythotrephes* is mostly situated in the metalimnion during the day (Young and Yan 2008) and is primarily a visual feeder, the depth of light penetration would affect its feeding rates (Muirhead and Sprules 2003; Pangle and Peacor 2009), and consequently its abundance. This may explain why *Bythotrephes* is most commonly present, and often most abundant, in clear, oligotrophic lakes, which are also deep (MacIsaac et al. 2000; Therriault et al. 2002; Branstrator et al. 2006; Manca et al. 2007; Weisz and Yan 2010). Warmer water temperatures might increase *Bythotrephes* abundance, as *Bythotrephes* per capita birth rates are temperature dependent (Yurista 1992), and population maxima can coincide with peak summer temperatures (Rivier 1998; Brown 2006).

The primary top-down regulator of *Bythotrephes* is predation from both warm- and cold-water planktivorous fish (Coulas et al. 1998; Jarnagin et al. 2004). Macroinvertebrate predators are likely unimportant predators of *Bythotrephes* (Foster and Sprules 2010), although it can be consumed by *Mysis relicta* (Nordin et al. 2008). In contrast, it has been suggested that *Bythotrephes* was eliminated by planktivorous fishes in some European lakes when fish densities were sufficiently large (Langeland 1978; Stenson 1978; Nilsson 1979). In North American lakes, planktivory by cold-water fish species, such as *Coregonus artedii* (cisco or lake herring) or *Osmerus mordax* (rainbow smelt), and the warm-water *Perca flavescens* (yellow perch) were implicated in up to 50% of *Bythotrephes* mortality in Harp Lake, Ontario, and Lake Michigamme, Michigan (Hall and Yan 1997; Jarnagin et al. 2004). Additionally, a refuge initially hypothesized to afford *Bythotrephes* protection from cisco (Yan and Pawson 1998; Yan et al. 2001) now seems unlikely to exist in most Canadian Shield lakes (Young et al. 2009).

A variety of *Bythotrephes* abundance patterns among and within lakes have been observed. After establishment, *Bythotrephes* can be virtually absent in some lakes or years while in others it is very abundant (Cairns et al. 2007). Seasonal *Bythotrephes* patterns can also vary enormously from lake to lake or year to year within the same lake, ranging from sustained stable densities, to single or multiple population peaks (e.g., Yan and Pawson 1998). It is currently not clear what regulates these *Bythotrephes* abundance patterns, which is unfortunate given that impacts on prey appear to vary with *Bythotrephes* abundance (Boudreau and Yan 2003). Our objective was to identify the bottom-up variables that are associated with mean *Bythotrephes* annual abundance and seasonal abundance patterns in established *Bythotrephes* populations. We focussed on bottom-up variables that could affect *Bythotrephes* abundance because of the difficulty in acquiring accurate temporal data on fish abundances in multiple lakes.

Methods

Nine lakes in south-central Ontario, Canada, with established *Bythotrephes* populations were sampled (Table 1). The lakes were oligo- to meso-trophic with

Table 1 Mean annual *Bythotrephes* abundance (± 1 standard deviation), and bottom-up variables for (a) the multi-lake dataset, and (b) the multi-year (Harp Lake) dataset

	Annual <i>Bytho</i> (no. m ⁻³)	pH	TP ($\mu\text{g L}^{-1}$)	DOC (mg L ⁻¹)	Chla ($\mu\text{g L}^{-1}$)	Secchi depth (m)	Spring temp (°C)	Summer temp (°C)	Spring prey (no. m ⁻³)	Summer prey (no. m ⁻³)	Max depth (m)	Surface area (ha)	Year <i>Bytho</i> detected
(a)													
Bernard	6.1 \pm 5.1	7.13	9.56	3.4	1.95	3.75	13.1	20.8	7129.6	5.62	47.9	2057.7	1998
Fairy	1.4 \pm 1.3	6.95	6.98	5.9	0.83	2.43	15.4	22.1	17377.2	7126.4	69.5	711.5	1990
Harp	3.9 \pm 3.9	6.98	7.22	6.7	2.31	3.52	17.6	22.4	4515.5	2746.8	37.5	71.7	1993
Lake of Bays	2.7 \pm 2.3	6.97	3.38	5.1	2.08	4.22	13.9	22.0	2076.4	784.6	70.1	6904.1	1995
Mary	1.7 \pm 1.0	6.96	7.21	6.6	2.48	2.38	15.1	22.0	11487.1	6854.7	56.4	1065.4	1990
Muskoka	1.7 \pm 1.0	7.02	5.50	5.5	3.96	2.82	15.1	22.1	3310.0	5821.9	66.5	12206.0	1989
Peninsula	9.0 \pm 5.4	7.14	9.00	6.1	2.08	3.29	16.0	22.3	43626.4	18707.8	34.1	864.8	1991
Skeleton	0.3 \pm 0.4	6.94	3.82	2.6	0.49	7.38	12.9	21.3	32.7	1435.9	64.7	2155.5	1998
Vernon	4.1 \pm 3.5	6.75	7.90	7.1	2.02	2.50	17.1	21.4	12863.5	3972.7	37.2	1505.1	1991
(b)													
1994	2.2 \pm 3.7	6.29	6.80	3.79	2.10	4.20	15.7	21.3	1297.6	909.5			
1995	1.8 \pm 1.6	6.36	6.19	4.08	2.41	4.10	20.0	20.6	2538.4	3451.0			
1996	0.3 \pm 0.2	6.28	5.44	4.13	3.40	3.55	11.6	21.2	82.6	1496.0			
1997	0.8 \pm 0.6	6.32	5.63	3.67	1.88	4.46	12.9	20.0	282.9	1735.9			
1998	3.4 \pm 4.3	6.45	5.98	3.52	2.62	4.93	19.5	21.3	2790.1	2961.5			
2001	2.6 \pm 2.4	6.33	5.36	4.03	2.68	4.65	16.8	21.4	802.6	1023.3			
2002	2.5 \pm 3.2	6.43	6.04	3.75	1.17	4.36	16.5	22.3	579.9	2185.2			
2003	3.4 \pm 3.4	6.42	6.35	3.92	1.80	4.49	15.3	21.7	2207.45	2005.23			
2004	3.0 \pm 3.7	6.44	5.90	4.06	1.89	4.38	18.5	20.7	1929.92	2301.63			

Annual *Bytho* = mean June to September *Bythotrephes* abundance, TP = total phosphorus, DOC = dissolved organic carbon, Chla = Chlorophyll *a*, Secchi depth = mean ice-free (all dates sampled) Secchi disk depth, Spring temp = Mean May and June epilimnetic temperature, Summer temp = Mean July to September epilimnetic temperature, Spring prey = Mean May and June herbivorous cladoceran abundance, Summer prey = Mean July to September herbivorous cladoceran abundance, Max depth = maximum depth, Year *Bytho* detected = the year that *Bythotrephes* was first detected in each lake, pH, TP, DOC and Chla are from July 14 for the multi-year dataset and are ice-free means for the multi-year dataset

circumneutral pH and planktivorous fish communities consisting of yellow perch, cisco and/or rainbow smelt (Strecker et al. 2006).

To test for factors that affect *Bythotrephes* annual and seasonal abundance, two datasets were compiled containing information on *Bythotrephes* abundance and potential bottom-up factors (zooplankton abundance, temperature profiles, Secchi disk depth and water chemistry). A *multi-lake dataset* consisted of data from the nine lakes sampled in 2003 as part of a study on the effect of *Bythotrephes* on zooplankton communities (Strecker et al. 2006; Strecker and Arnott 2008). A *multi-year dataset* consisted of nine years of data (1994 to 1998 and 2001 to 2004) from Harp Lake. Harp Lake has been monitored through the ice-free season by the Ontario Ministry of the Environment (OMOE) since 1977. *Bythotrephes* was first observed in Harp Lake in routine zooplankton samples in 1993 (Yan and Pawson 1997), and an intense and independent *Bythotrephes* monitoring program was initialized on the lake by the OMOE in 1994 (Yan and Pawson 1998) that has continued through most ice-free seasons ever since. In addition, we collected weekly samples of *Bythotrephes* and temperature profiles in Harp Lake in 2003 and in Peninsula Lake in 2004 so that per capita birth rates could be calculated. Harp Lake was chosen due to its long term *Bythotrephes* sampling record, and Peninsula Lake was chosen because the *Bythotrephes* seasonal abundance in 2003 differed substantially from the pattern typical of Harp Lake.

Sample collection

The nine lakes comprising the multi-lake dataset were sampled every two weeks over a five day period. From June to August, *Bythotrephes* were collected at 5 stations, a deep lake station as well as 4 other stations <1 km apart, while in September, *Bythotrephes* were collected only at the deep station. At each station, *Bythotrephes* were collected from 5 m off the lake bottom to the lake surface with a 400- μm mesh, 0.5-m diameter mouth, 2.5-m net (Strecker et al. 2006). From May to September at the deep station, samples of zooplankton were collected and vertical temperature profiles (at 1-m increments) and Secchi disk depth were measured. Zooplankton were collected separately from the epilimnion, metalimnion

and hypolimnion with a conical closing net that had 110- μm mesh and 0.5-m diameter mouth (Strecker and Arnott 2008). The epilimnion was defined as the surface layer where temperature decreased by less than 1°C m^{-1} and the metalimnion was the layer where temperature changed more than 0.2°C m^{-1} . Once in the middle of the summer (during the week of July 14), water samples for the purpose of chemical analyses were collected at the deep station from the epilimnion with a 2.5-cm diameter integrated tube sampler. In 7 of the lakes, the 'deep station' was the deepest position in the lake; however, this was inaccessible for Muskoka Lake and Lake of Bays thus they were sampled at a secondary deep spot that was not much shallower.

For the multi-year dataset, *Bythotrephes* were collected in Harp Lake every 1–4 weeks at 10 stations following a protocol designed by Yan and Pawson (1998). *Bythotrephes* were collected at each station from 2–3 m above the lake bottom to the lake surface using a 2.5-m net with a 0.75-m diameter mouth and 285- μm mesh. Every two weeks at the deepest spot in the lake, Secchi disk depth and temperature profiles (at 1-m increments) were measured, and zooplankton and water chemistry samples were collected. Zooplankton were sampled with a 80- μm mesh, 12.5-cm diameter net in hauls from 5 depths to surface, with the haul lengths selected so that the combined composite represented all strata in proportion to their volume (Yan and Pawson 1997). Bathymetrically weighted composite water samples were collected through a weighted tygon tube via a peristaltic pump as described in Girard and Reid (1990) and Ingram et al. (2006).

For the calculation of accurate per capita birth rate of a species, many gravid animals must be assessed frequently (De Mott 1980); therefore, two of the study lakes were sampled weekly from May to October. Harp Lake was sampled in 2003 at 10 stations and Peninsula Lake was sampled in 2004 at 15 stations, with the number of stations determined after examination of pilot studies of spatial variance (Young 2008). On each sample date, temperature profiles and *Bythotrephes* were collected using methods outlined above for Harp Lake.

Sample processing

Bythotrephes and zooplankton samples were enumerated with a semi-automated, zooplankton

enumeration and measuring system called ZEBRA (Allen et al. 1994). Multi-year *Bythotrephes* samples were examined entirely and multi-lake samples were subsampled with a Folsom plankton splitter when *Bythotrephes* appeared abundant in a sample (>32 *Bythotrephes* present). Sex and instar of *Bythotrephes* were identified and clutch size of broods containing embryos with red- or black-eyed pigmentation was recorded. For each sampling date, *Bythotrephes* abundance was calculated as a mean of all stations, with station abundance being the number of female *Bythotrephes* divided by the total volume of water filtered by the net. In the multi-year samples, volumes were corrected with a filtration efficiency of 95% (Young 2008). *Bythotrephes* instar and embryo density used in the birth rate analyses were calculated similarly to female abundances.

Zooplankton samples were enumerated following a protocol described in Girard and Reid (1990), where subsamples of a known volume were generated with a Folsom plankton splitter and a minimum of 350 individuals were identified and enumerated. As herbivorous cladocerans are the favoured prey of *Bythotrephes*, a sum of their densities (i.e., of genera *Daphnia*, *Bosmina*, *Eubosmina*, *Holopedium*, *Chydorus* and *Diaphanosoma*) was used as the variable representing *Bythotrephes* prey. *Bythotrephes* primarily occupies the epi- and metalimnion, and thus will only overlap with prey in these layers (Young and Yan 2008). Therefore, prey abundance was treated differently for the two datasets due to differences in zooplankton collection. For the multi-lake dataset in which individual thermal layers were sampled for zooplankton separately, only epi- and metalimnion prey were included. In the multi-year dataset in which zooplankton were volume-weighted to include all thermal layers, *Daphnia mendotae* was excluded from prey abundance as it is known to migrate into the hypolimnion during the day to avoid overlap with *Bythotrephes* (Lakes Michigan and Erie, Pangle et al. 2007; Harp Lake, Young and Yan 2008). To meet assumptions of normality in the following analyses, all prey abundances were transformed using $\log(x + 1)$.

Water samples were analysed for total phosphorus (TP), Chlorophyll a (Chla), dissolved organic carbon (DOC) and pH at the OMOE's Dorset Environmental Research Centre following standard OMOE (2003) methods.

Data analyses

Mean *Bythotrephes* annual abundance

Multiple regression analyses were performed to determine which bottom-up variables most parsimoniously explained variation in mean *Bythotrephes* annual abundance among lakes (multi-lake dataset) and among years (multi-year dataset). For each dataset, the best subsets procedure in SigmaStat (version 3.1) was used to calculate all possible models (not including interactions). The most parsimonious model was chosen as the one with the smallest Akaike's Information Criterion corrected for small sample sizes (AIC_c; Johnson and Omland 2004). A Kolmogorov–Smirnov normality test and a constant variance test were used to assess assumptions for the regression models and all passed with $P > 0.05$.

Mean *Bythotrephes* annual abundance was calculated by averaging *Bythotrephes* abundance on all sample dates from June to September for each lake or year. The predictor variables for the multi-lake regression were log-transformed mean spring (all sample dates in May and June) and summer (all dates in July to September) prey abundance, mean spring and summer temperature, mean ice-free (all dates sampled) Secchi disk depth, mid-summer TP, and maximum depth. The predictor variables for the multi-year regression were mean spring and summer prey abundance, mean spring and summer temperature, and mean ice-free Secchi disk depth, TP and Chla. pH was not included as it did not vary greatly between lakes or dates (Table 1), and was >6 in all lakes, a level of acidity that should not affect *Bythotrephes* abundance (Natalie Kim, York University, unpublished toxicity data). No collinearity among variables was detected as variance inflation factors were always <10 (Quinn and Keough 2002).

When the dependent variable in a multiple regression is species abundance data, there is a risk that the data are autocorrelated, as abundance on one date would depend on previous dates. However, it is unlikely that mean *Bythotrephes* annual abundance would be autocorrelated, as *Bythotrephes* overwinter as resting eggs. Resting egg production in one year may affect the following year's initial *Bythotrephes* abundance, but other processes such as reproduction should quickly take over, making it unlikely that mean annual abundance would be affected.

Seasonal *Bythotrephes* abundance

Multivariate analyses were used to determine which bottom-up variables could predict differences in seasonal *Bythotrephes* abundance patterns for each dataset. Because *Bythotrephes* abundances collected every few weeks would be autocorrelated, it would not be appropriate to use redundancy analyses with seasonal *Bythotrephes* abundance as the dependent variable. Instead, canonical variates analyses (CVA) were used where the dependent variables were groups of lakes (multi-lake dataset) or years (multi-year dataset) with similar seasonal *Bythotrephes* abundance patterns. Predictor variables for the multi-lake CVA were maximum depth, biweekly values for Secchi disk depth, epilimnetic temperature and log-transformed prey abundance, and mid-summer (July 14) DOC and TP. Predictor variables for the multi-year CVA were monthly means for Secchi disk depth, epilimnetic temperature, log-transformed prey abundance, DOC and TP. Monthly means were used for the multi-year predictor variables because they were sampled on different dates from year to year and not at the same time as *Bythotrephes*. Predictor variables were first checked for normality using the Kolmogorov–Smirnov test. Variables that were not normally distributed (i.e., $P > 0.05$; only variables from the multi-lake dataset: Secchi disk depth in mid July and early September and prey abundance in early June and early August) were not included in the multivariate analyses as they violated this assumption. The rest of the variables were tested with a Monte Carlo permutation test (with 999 permutations) by manual selection to determine if a significant amount of variation was explained ($P < 0.05$) (ter Braak and Šmilauer 2002).

To identify the groups of lakes or years with similar seasonal abundance patterns for the CVAs, we first grouped those with very low abundance (≤ 1 *Bythotrephes* m^{-3}), which were Skeleton Lake for the multi-lake dataset, and 1996 and 1997 for the multi-year dataset. For the rest of the lakes or years, groups were generated with a principal components analysis (PCA) and hierarchical cluster analyses, where the response variables were relative seasonal *Bythotrephes* abundances. For the multi-lake dataset, all biweekly seasonal abundances from June to September for each lake were used as they were collected within 5 days of each other. For the multi-year

dataset, *Bythotrephes* were not always collected on a similar date each year; therefore, abundances were averaged between dates when needed so that values existed for similar dates twice a month from end of June to mid September. Because data were only collected monthly in 2001, this year was excluded from the seasonal multi-year analysis. The cluster analyses used were single, median, centroid, average and weighted average linkages with Euclidean distances where lakes or years were grouped when $\geq 50\%$ similarity. Cluster analyses were performed in MiniTab 15, normality tests were done in SigmaPlot 3.1 and multivariate analyses were performed in Canoco 4.5.

Contributions to per capita birth rates

To identify whether temperature, prey availability or predation were contributing to per capita birth rate changes over time (i.e., how much birth rates were increasing or decreasing from one date to the next), partial differentials were applied to the three variables in the following equation for per capita birth rate, $b = R \ln(1 + P_e P_a)$ (Polishchuck 1995). This equation is the same as the Edmondson-Paloheimo model and thus relies on the same assumptions. R (d^{-1}) is the inverse of the temperature-dependent embryo development rate, P_e is the proportion of embryos to adult (i.e., second and third instar) *Bythotrephes*, P_a is the proportion of adult vs. all *Bythotrephes*, and thus $P_e P_a$ is the ratio of embryos to all *Bythotrephes*. b was only calculated for dates when the number of females carrying embryos was greater than 6, where sample sizes varied from 7 to 33 in Harp Lake and 6 to 292 in Peninsula Lake. To approximate the rate of change in the per capita birth rate, db/dt (d^{-2}), for each sample date, separate polynomials were fit to birth rates on three consecutive sample dates (i.e., a sample date and the sample dates before and after), differentiated and solved for the sample date (Polishchuck 1995).

The interpretation of this method was based on how much the partial derivative of each variable (d^{-2}) contributed to db/dt . A greater contribution from R (i.e., $\text{Con}R$) suggests that temperature was affecting the changes in per capita birth rates, as embryo development rate in *Bythotrephes* is primarily temperature dependent (Yurista 1992). When $\text{Con}P_e$ provides the major contribution, prey

availability was assumed to be the most important factor, as resources affect the proportion of mature females reproducing in cladocerans (Hall 1964; Goulden and Hornig 1980). A contribution from P_a with or without P_e (i.e., $ConP_a$ and/or $ConP_e$) suggests that per capita birth rates were changing due to a combination of factors known to affect cladocerans: predation by fish that select larger over smaller females (P_a) and/or females with clutches, especially larger ones, over those without clutches (P_e) (Gliwicz and Pijanowska 1989; Polishchuck 1995).

Results

Mean annual *Bythotrephes* abundance

In the multi-lake dataset, mean *Bythotrephes* annual abundance ± 1 standard deviation ranged from 0.3 ± 0.4 (in Skeleton Lake) to 9.0 ± 5.4 (in Peninsula Lake) *Bythotrephes* m^{-3} (Table 1a). Based on AIC_c values, the most parsimonious model for predicting among lake differences in mean annual abundance included abundance of spring prey, mean Secchi disk depth and maximum depth as factors (adjusted $R^2 = 0.80$; $F_{3,5} = 11.40$; $P = 0.01$). Spring prey and Secchi depth were both significantly and positively correlated with mean annual *Bythotrephes* abundance, while maximum depth was not a significant predictor (Table 2a).

In the multi-year dataset, mean annual *Bythotrephes* abundance ± 1 standard deviation varied from 0.3 ± 0.2 (in 1996) to 3.4 ± 4.3 (in 1998) and 3.4 ± 3.4 (in 2003) *Bythotrephes* m^{-3} (Table 1b). The most parsimonious model for predicting among year differences only included the abundance of spring prey (adjusted $R^2 = 0.67$; $F_{1,7} = 17.25$;

$P = 0.004$) as a significant and positive factor (Table 2b).

Seasonal *Bythotrephes* abundance

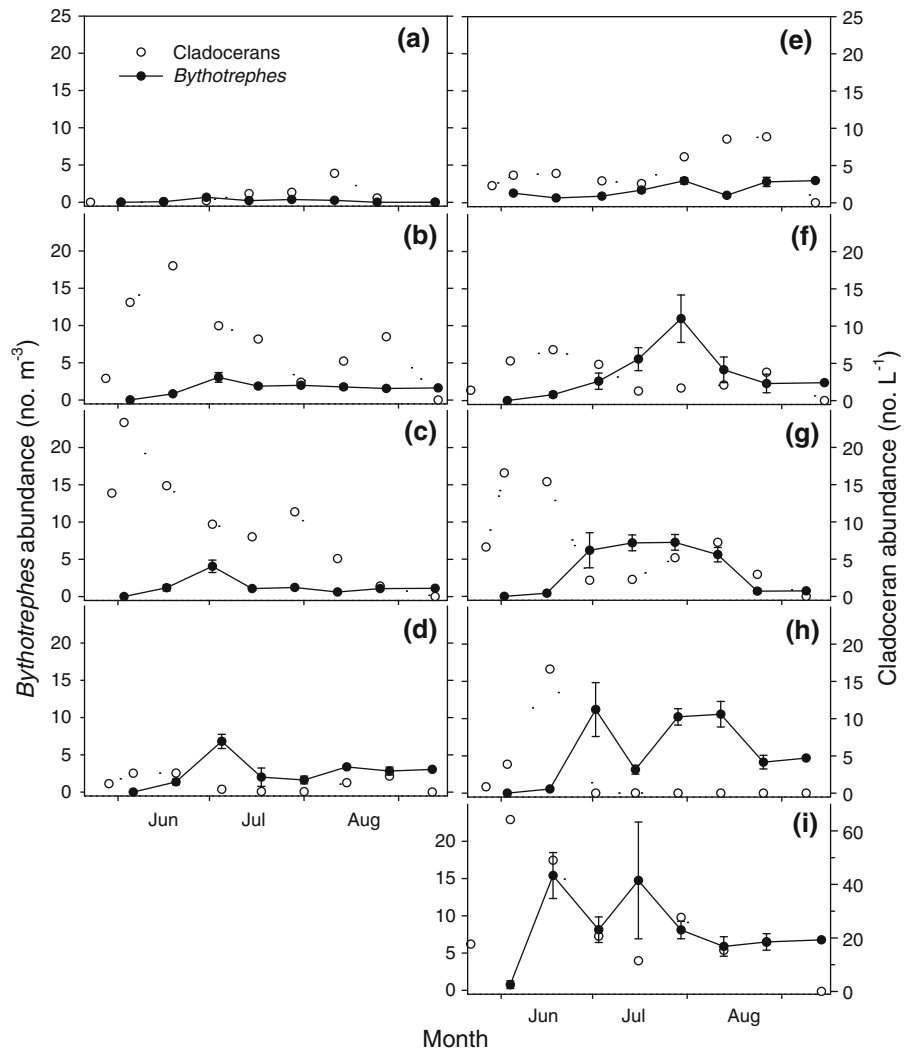
In the multi-lake dataset, *Bythotrephes* seasonal abundance patterns varied substantially (Fig. 1) and did not cluster consistently into similar groups using the different cluster analyses. The four groups suggested by the PCA best summarized the results of the cluster analyses and thus were used in the CVA: (1) Peninsula Lake, (2) Fairy and Mary lakes and Lake of Bays, (3) Bernard and Vernon lakes, and (4) Muskoka and Harp lakes (Fig. 2a). Prey abundance in mid June was the only variable that was marginally significant at predicting these groups on Axis 1 of the multi-lake CVA ($P = 0.06$; Fig. 2b). Skeleton Lake had a strong negative association with June prey along Axis 1, and both prey and *Bythotrephes* abundance were very low in this lake (Fig. 1a). Peninsula Lake had a strong positive association with June prey, and had very high prey and *Bythotrephes* abundances in early June (Fig. 1i). Bernard and Vernon lakes also had a positive association with June prey abundance; prey abundances were relatively high in June in both lakes and *Bythotrephes* abundance was relatively high from the end of June to the middle of August (Fig. 1g, h). The remaining two groups only had a weak association with June prey abundance. Harp and Muskoka lakes had low but somewhat contrasting prey and *Bythotrephes* abundances in comparison to the other lakes, with *Bythotrephes* peaking later in the season (Fig. 1e, f). Although Fairy Lake, Lake of Bays and Mary Lake had similar relative seasonal *Bythotrephes* abundance patterns, their prey abundance patterns were different; June prey abundance was very high in Fairy and Mary lakes but very low in Lake of Bays (Fig. 1b, c, d).

Table 2 Results of multiple regression analyses of mean annual *Bythotrephes* abundance with bottom-up variables for (a) nine lakes in the multi-lake dataset and (b) nine years for the multi-year (Harp Lake) dataset

Dataset	DF _{res,reg}	Adjusted R^2	F ratio	P value	Variable	Coefficient	t value	P value
(a)	3,5	0.80	11.40	0.01	Spring prey	3.97	3.32	0.02
					Secchi depth	1.76	2.86	0.04
					Max depth	-0.08	-2.20	0.08
(b)	1,7	0.67	17.25	0.004	Spring prey	1.81	4.15	0.004

Significant results ($P < 0.05$) are in bold. Variables are defined in the footnote of Table 1

Fig. 1 Seasonal abundance of *Bythotrephes* and its prey in the multi-lake dataset lakes: **a** Skeleton Lake, **b** Mary Lake, **c** Fairy Lake, **d** Lake of Bays, **e** Lake Muskoka, **f** Harp Lake, **g** Lake Vernon, **h** Bernard Lake and **i** Peninsula Lake. Prey abundance is of herbivorous cladocerans in the epi- and metalimnion, and is on a different scale for Peninsula Lake due to high densities. Error bars represent one standard error



The multi-year *Bythotrephes* seasonal abundance patterns were very similar in most years (Fig. 3), and the results of the cluster analyses and the PCA (Fig. 4a) consistently produced the same three groups: (1) 1996 and 1997, (2) 1998, and (3) 1994, 1995 and 2002–2004. The multi-year CVA identified June prey abundance as a significant predictor of the three groups on Axis 1 ($P = 0.04$) (Fig. 4b). 1996 and 1997 had a strong negative association with June prey, and both years had very low prey and *Bythotrephes* abundance (Fig. 3c, d). 1994, 1995 and 2002–2004 had a positive association with June prey abundance, and all years had higher June prey abundances with a mid-summer peak in *Bythotrephes* abundance (Fig. 3a, b, f–h). 1998 had a strong

association with June prey, and June prey abundance was very high in the spring in this year, although *Bythotrephes* abundance did not peak until autumn (Fig. 3e).

Per capita birth rates

In the early spring of 2003 in Harp Lake, too few *Bythotrephes* were collected (Fig. 3g) to accurately calculate per capita birth rates (De Mott 1980); however, low densities and the absence of red- and black-eyed embryos suggested that birth rates were also very low. On the other hand, in Peninsula Lake in 2004, *Bythotrephes* abundance and per capita birth rates were the highest in early spring, with birth rates

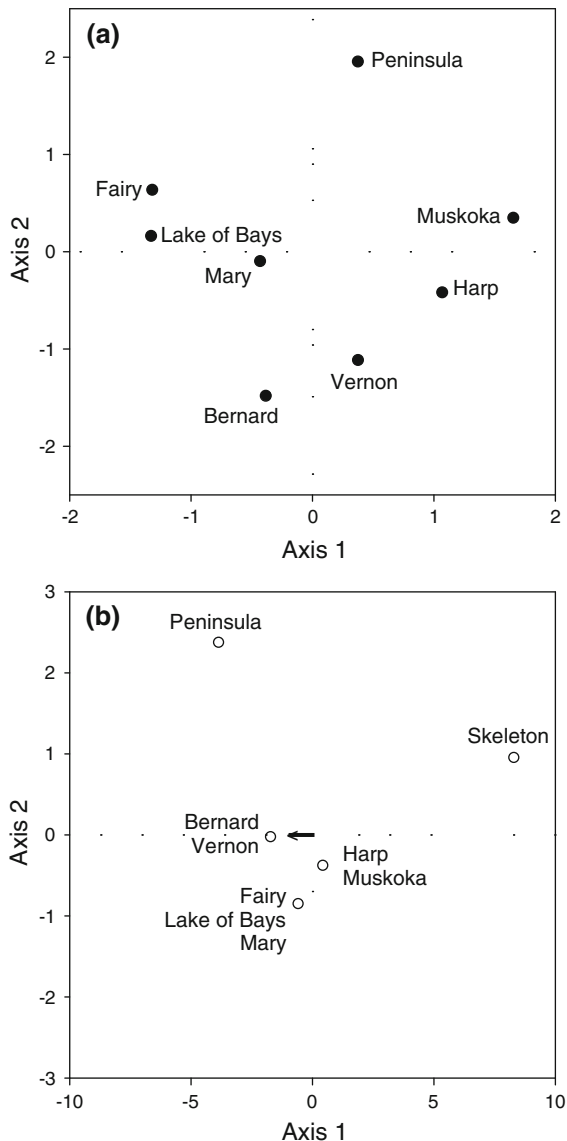


Fig. 2 Multivariate analyses for the multi-lake dataset lakes. **a** Principal components analysis of the relative seasonal abundances for the eight lakes that had mean abundance >1 *Bythotrephes* m^{-3} (i.e., not including Skeleton Lake), and **b** Canonical variates analysis of the five groups of lakes where mid-June prey abundance (black arrow) was the only variable that was marginally significant ($P = 0.06$). The magnitude of the mid-June prey abundance arrow has been increased by a factor of 3 so that it could be more visible

at 0.1 day^{-1} as early as 20 May, increasing to a maximum of 0.2 day^{-1} on 10 June (Figs. 5, 6b). *Bythotrephes* per capita birth rates were the highest in Harp Lake on 10 July (Fig. 6a), preceding the population peak (Fig. 3g).

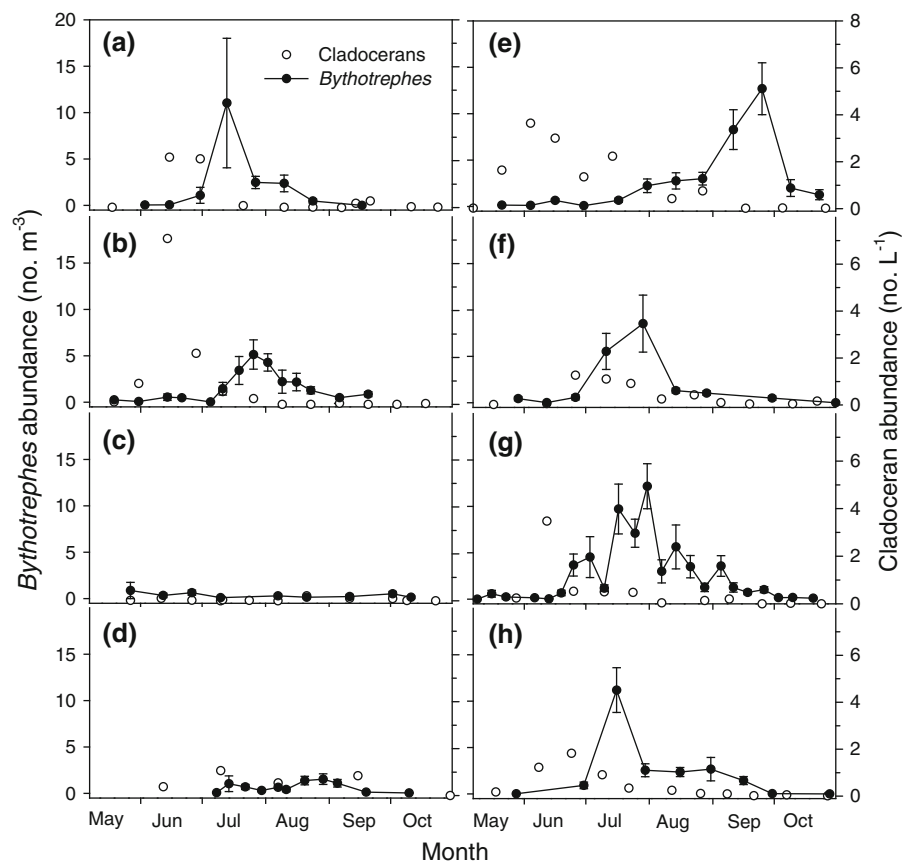
P_e was almost always the main contributor to the positive and negative changes in per capita birth rates in both Harp and Peninsula Lake (Fig. 6), suggesting that prey availability was the primary factor affecting *Bythotrephes* per capita birth rates. There was often an additional, smaller contribution from P_a , making it difficult to differentiate whether prey availability or predation were driving the contribution from P_e , but suggesting that predation was sometimes responsible such as in mid July in Harp Lake when per capita birth rates decreased considerably. R , and thus temperature, also contributed to per capita birth rate changes, most prominently in the spring in Peninsula Lake.

Discussion

In all analyses and datasets, the abundance of prey in the spring was consistently found to be a significant factor associated with *Bythotrephes* annual and seasonal abundance. In the multiple regressions, spring prey abundance had a significant and positive association with mean annual *Bythotrephes* abundance, as well as Secchi disk depth for the multi-lake dataset. In the CVAs, prey abundance in June was the only significant variable that was associated with groups of lakes or years with similar seasonal *Bythotrephes* abundance patterns, although some groups did not appear to be significantly predicted by spring prey suggesting other unmeasured factors were involved. Lastly, prey availability appeared to be the most common and dominant contributor to changes in per capita birth rates in Harp and Peninsula lakes, while temperature and predation were also important on some dates.

The multiple regressions on the multi-lake and multi-year datasets both suggested that greater prey abundance in the spring contributed to greater mean annual *Bythotrephes* abundance. The CVAs showed a very similar trend, where groups of lakes or years that appeared to be significantly different were those with both high *Bythotrephes* abundance and June prey abundance compared with groups with both very low *Bythotrephes* and June prey abundance. Lakes in the multi-lake dataset that had the greatest *Bythotrephes* abundance reached maximum abundance by mid (e.g., Peninsula Lake) or late (e.g., Bernard and Vernon Lake) June. In the lakes in this study,

Fig. 3 Seasonal abundance of *Bythotrephes* and its prey in Harp Lake for **a** 1994, **b** 1995, **c** 1996, **d** 1997, **e** 1998, **f** 2002, **g** 2003 and **h** 2004. *Bythotrephes* sampling in 1999–2001 was infrequent and thus these years were not included in seasonal analyses. Prey abundance is of herbivorous cladocerans (excluding *Daphnia mendotae*) and was volume-weighted to represent the whole water column. Error bars represent one standard error



Bythotrephes overwinters as resting eggs that begin hatching in May (Young 2008). A greater availability of prey in the early months of *Bythotrephes* emergence would allow for higher per capita birth rates, leading to increased population growth. Additionally, *Bythotrephes* clutch sizes in the spring are much larger than the summer, making very high birth rates possible (Straile and Hälbig 2000; Young 2008). In Peninsula Lake in 2004, which had a very similar early spring *Bythotrephes* abundance peak to 2003, per capita birth rates were highest in June, and prey availability was the greatest contributor on 3 June. *Bythotrephes* in European Lake Constance (Straile and Hälbig 2000) and Lago Maggiore (Manca et al. 2007) have a similar population dynamic to Peninsula Lake. The early spring *Bythotrephes* abundance peaks in these lakes were also attributed to earlier onsets of exponential growth (Manca et al. 2007) and high springtime per capita birth rates (Straile and Hälbig 2000).

In most years in Harp Lake, *Bythotrephes* abundance had a later peak than the other lakes, which

occurred mid-summer and resembled the Rybinsk reservoir in Russia (Rivier 1998). Prey abundance in Harp Lake routinely did not start increasing until June, suggesting a consistent insufficiency of prey to support a spring bloom of *Bythotrephes* thus potentially explaining the delayed *Bythotrephes* peak. Interestingly, prey abundance in 1998 began increasing in May and reached a maximum in early June, yet *Bythotrephes* abundance did not peak until autumn, indicating a factor other than prey availability affected *Bythotrephes* abundance in this year. We suggest that the discrepancy is attributable to a dramatically reduced pool of resting eggs in the spring of 1998. The *Bythotrephes* egg bank for a current year consists mainly of the eggs deposited the preceding year, as *Bythotrephes* resting eggs are only viable for approximately three-quarters of a year (Andrew and Herzig 1984). Due to the low *Bythotrephes* abundances in 1996 and 1997, resting egg production and sediment deposition were likely very low preceding 1998, thus explaining the unique *Bythotrephes* seasonal pattern in 1998.

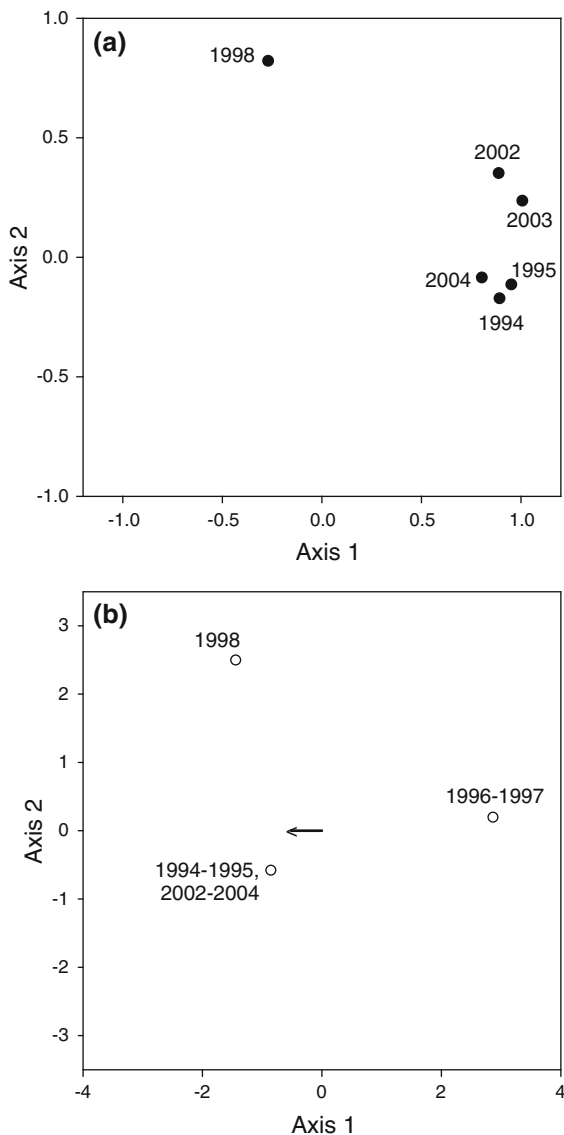


Fig. 4 Multivariate analyses for the Harp Lake multi-year dataset. **a** Principal components analysis of the relative seasonal abundances for all years that had mean abundance >1 *Bythotrephes* m^{-3} (i.e., not including 1996 and 1997), and **b** Canonical variates analysis of the three groups of years where June prey abundance (black arrow) was the only significant variable ($P = 0.04$)

Aside from the size of the *Bythotrephes* egg bank, additional factors not used in our analyses could account for the unexplained variation in the multiple regressions and the weak associations with June prey for some groups in the CVAs. For example, *Bythotrephes* abundance in Mary and Fairy Lake was relatively low, even though spring prey abundance

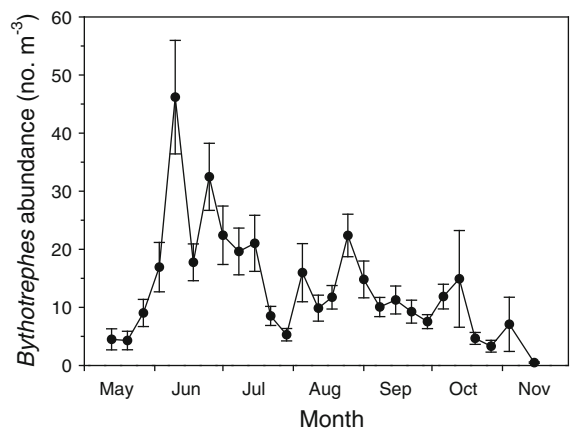


Fig. 5 *Bythotrephes* seasonal abundance in Peninsula Lake 2004. Error bars represent one standard error

was as high, if not higher, than other lakes with higher *Bythotrephes* abundances. Planktivory of *Bythotrephes* in Mary and Fairy Lake could potentially be responsible for the unexpectedly low abundances; however, there is not enough information on fish abundance for these lakes to examine this possibility.

In Harp Lake, information on consumption of *Bythotrephes* by cisco in 1995 (Coulas et al. 1998) and 2003 (Young et al. 2009) indicate that cold-water planktivory had little effect on *Bythotrephes* abundance in the spring but contributed to *Bythotrephes* summer population dynamics. In the spring of 1995 and 2003, very few *Bythotrephes* were observed in cisco stomachs, and thus cold-water planktivory did not appear to play a role in delaying the increase in *Bythotrephes* abundance. However, during the summer, non-trivial numbers of *Bythotrephes* were observed in cisco stomachs in both years, indicating that cisco was at least in part responsible for the late-summer *Bythotrephes* population crashes. After the *Bythotrephes* main population decline in 2003, per capita birth rates remained relatively constant but the population size continued to fall, most likely due to an increasing per capita consumption by cisco once *Bythotrephes* became abundant (Young et al. 2009). In this study, predation also appeared to contribute to the change in per capita birth rates in July and August. Through the analysis of broken tail spines in the sediments, Hall and Yan (1997) estimated an annual loss of *Bythotrephes* to fish of 40% in Harp Lake in 1995, which may be an underestimate as the percentage of tail spines that remained intact while

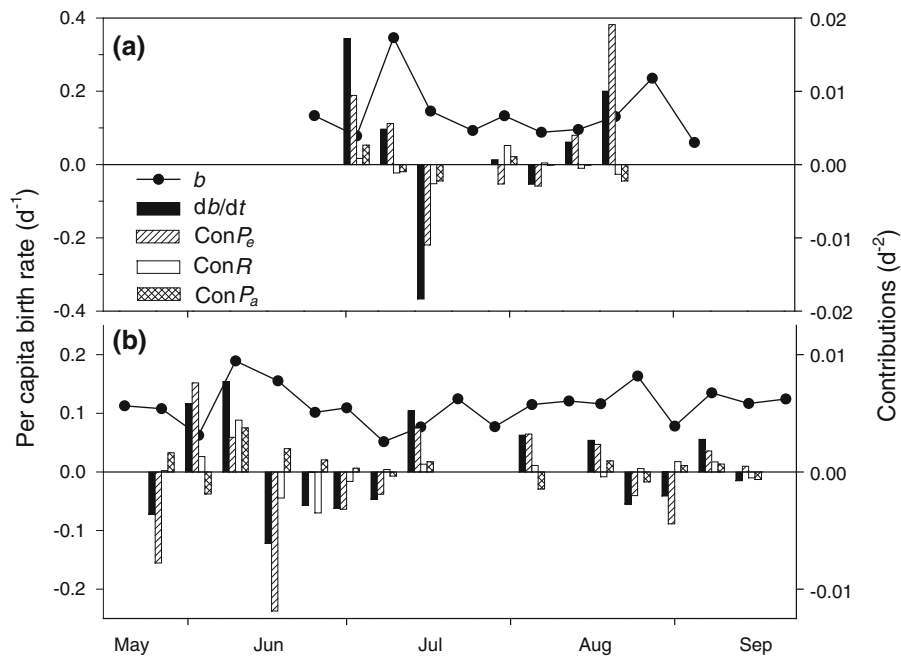


Fig. 6 *Bythotrephes* birth rate analysis for **a** Harp Lake 2003 and **b** Peninsula Lake 2004. On the lefthand y-axis is the per capita birth rate, b . On the righthand y-axis is the rate of change in the per capita birth rate, db/dt , along with $ConP_e$ representing the contribution of food availability, $ConR$ representing temperature and $ConP_a$ with or without $ConP_e$ representing predation. Theoretically, the sum of the contributions (SumCon) should add up to db/dt ; therefore, dates with

$0.5 > \text{SumCon}:db/dt > 2$ were not presented (Polishchuck 1995). db/dt was approximated for each sample date by fitting separate polynomials to birth rates on three consecutive sample dates (i.e., a sample date and the sample date before and after), differentiating it and solving for the sample date (Polishchuck 1995). Please note that the scale of the y-axes differ between **a** and **b**

passing through fish was not considered, and could range from 4 to 13% (Jarnagin et al. 2004). Recent modelled estimates of death rates of *Bythotrephes* in Harp Lake were as high as 0.19 day^{-1} (Wittman et al. 2011).

Along with cold-water planktivory, prey availability also appeared to affect *Bythotrephes* summer abundance in Harp Lake. Around the population crash in both 1995 and 2003, *Bythotrephes* consumption exceeded prey production (Dumitru et al. 2001; Strecker and Arnott 2008), indicating that prey were limiting. *Daphnia* abundance often follows a similar trend with population size declining soon after the clear-water phase, due primarily to the lack of edible phytoplankton, but also due to predation (Lampert et al. 1989; Luecke et al. 1990). Additionally, prey availability continued to contribute to changes in birth rates through the summer. Given the apparent effect of prey availability on *Bythotrephes* abundance during the summer, we might have expected summer prey abundance to be associated with *Bythotrephes*

abundance in our analyses but it was not. This discrepancy could be explained by the fact that a relationship between *Bythotrephes* and prey abundance might be weakened in the summertime due to *Bythotrephes* consumption on its prey.

The importance of *Bythotrephes* as a visual predator was indicated from the results of the multi-lake multiple regression, as the combination of increased prey in the spring and light availability affected its mean annual abundance. Similar to many fish planktivores, *Bythotrephes* uses light for efficient finding and capturing of prey (Muirhead and Sprules 2003). The light levels at which it achieves its maximum feeding rate are $\geq 100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Pangle and Peacor 2009), usually the top 3–5 m of our study lakes (JDY, unpublished data) similar to Secchi disk depth. During the day, most *Bythotrephes* are deeper than this (Young and Yan 2008); therefore, greater light penetration would be expected to have a direct positive effect on its feeding rate. This might also at least partially explain why *Bythotrephes*

is more often found in clear lakes (Weisz and Yan 2010).

Our study has suggested the importance of spring prey on *Bythotrephes* abundance, as well as reinforced previous studies (e.g., Pangle and Peacor 2009) on the role that light plays in *Bythotrephes* predation. It is also evident that other factors not measured in this study may also have an effect on *Bythotrephes* abundance, such as resting egg abundances and planktivorous fish predation. Understanding the factors that are associated with the abundance of an invasive species provides insight into the invasion process and helps to identify and target systems that are susceptible to successful establishment of an invasive species. Recent work has identified that an Allee effect exists for *Bythotrephes* (e.g., Wittman et al. 2011). If prey availability affects *Bythotrephes* abundance in established populations as suggested in our study, it might also be an important factor at the low abundances that occur when a species is first introduced, which is when an Allee effect would be operating. Therefore, our study suggests the hypothesis that *Bythotrephes* establishment success is affected by the availability of its prey foodbase.

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