Article

Dynamics of the invasive spiny water flea, *Bythotrephes longimanus*, in Lake Simcoe, Ontario, Canada

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Abstract

The invasion of the nonindigenous zooplankter *Bythotrephes longimanus* in Lake Simcoe has the potential to impact overall ecosystem functioning, yet there is currently no information regarding the status and dynamics of its population. We used a combination of uni- and multivariate analyses to examine variation in *Bythotrephes* interannual and seasonal abundance, and life-history characteristics in Lake Simcoe from 1999 to 2007, and we explored the biotic (predators, prey) and/or abiotic (water quality, temperature) factors that may have regulated its population over this period. The mean annual abundance of *Bythotrephes* varied by an order of magnitude over the period of study and was significantly associated with epilimnetic temperature and prey and predator abundance. *Bythotrephes* typically appeared in early summer and had 2 seasonal abundance peaks, which varied in magnitude and timing within and among years. August and September Secchi depth and total phosphorus concentration predicted groups of years with similar *Bythotrephes* phenologies, lending further support to the role of water clarity as a significant component of this visual predator's habitat in its invaded range. *Bythotrephes* body size and reproductive patterns also varied seasonally, possibly reflecting the seasonal availability of cladoceran prey, predation pressure from planktivorous fish, or adaptations to avoid unfavourable conditions. Overall, a complex interaction of fish predation, food availability, temperature, and water clarity controlled the dynamics of *Bythotrephes* in Lake Simcoe. Changes to the Lake Simcoe ecosystem due to *Bythotrephes* invasion may have important consequences for the ecosystem services provided by the lake and merit further investigation.

Key words: cladoceran zooplankton, fish predation, invasive species, Lake Simcoe, life-history characteristics, population dynamics, Secchi depth, temperature

Introduction

Lake Simcoe is a valuable natural and socioeconomic resource in Ontario, Canada, providing a source of drinking water, seasonal recreational activities, a popular cold-water fishery, and a beautiful natural environment to the surrounding communities (LSEMS 2008). Expanding human pressures have impaired the structure, function, and ecological health of the Lake Simcoe watershed, however, as well as jeopardized the lake's recreational, aesthetic, and tourism potential (as reviewed in Palmer et al. 2011). Historically, Lake Simcoe water quality issues included excessive loading of phosphorus and other pollutants, growth of aquatic macrophytes and algae, and declines in late summer hypolimnetic oxygen levels leading to the recruitment failure of cold-water fish (Winter et al. 2007, Young et al. 2010). Progress has been made in recent years to reduce annual loads of phosphorus and increase late summer hypolimnetic oxygen levels (Winter et al. 2007, Young et al. 2010), but other contemporary stressors are

now also of concern, including climate change and introductions of nonindigenous species.

Crustacean zooplankton are key components of freshwater ecosystems that mediate the energy flow and recycling of nutrients among trophic levels. Invasions of nonindigenous species that negatively impact the biology and ecology of zooplankton have the potential to simultaneously influence the dynamics of multiple trophic levels (e.g., primary producers, herbivores, top predators), with cascading consequences for primary and secondary production, nutrient cycling, and water quality, and potentially impacting overall ecosystem functioning (Mack et al. 2000, Barbiero et al. 2006, Strecker et al. 2011). Historical changes in zooplankton community structure and diversity in Lake Simcoe were linked to changes in water quality and planktivorous fish abundances (Nicholls and Tudorancea 2001), but recent species invasions in the lake may also threaten zooplankton populations (J.D. Young, unpubl.). For example, zebra mussels (*Dreissena polymorpha*) became established in Lake Simcoe around 1996 (Evans et al. 2011), and their invasion coincided with significant changes in phytoplankton community composition and likely contributed to increases in water clarity (Eimers et al. 2005, Winter et al. 2011). Also of concern is the invasion of the Eurasian spiny water flea, *Bythotrephes longimanus*, which was first detected in the lake in 1993 (McNeice and Johanson 2004).

Bythotrephes longimanus (Onychopoda, Cercopagididae), hereafter *Bythotrephes*, is a large-bodied (up to 12 mm) cladoceran, with a prominent compound eye and long caudal spine (Branstrator 2005). *Bythotrephes* is a voracious predator of crustacean zooplankton, capable of altering the trophic structure of lakes (Rennie et al. 2011). Its invasion is routinely associated with reductions in the species richness of crustacean zooplankton and cladoceran standing stocks (Yan and Pawson 1997, Dumitru et al. 2001, Yan et al. 2001, 2002, Boudreau and Yan 2003, Barbiero and Tuchman 2004, Strecker et al. 2006), alterations in the behaviour of the zooplankton (Pangle et al. 2007, Young and Yan 2008, Bourdeau et al. 2011), and the displacement of native predatory invertebrates (Foster and Sprules 2009, Weisz and Yan 2011). *Bythotrephes* may compete with planktivorous fish for prey (Lehman 1991, Garton et al. 1993, Hoffman et al. 2001, Foster and Sprules 2010), diverting energy away from higher trophic levels (Dumitru et al. 2001, Strecker and Arnott 2008, Foster and Sprules 2010). Further, *Bythotrephes* may exert indirect food web effects on lower trophic levels (e.g., rotifers: Hovius et al. 2007; phytoplankton: Strecker et al. 2011).

The life history and population dynamics of *Bythotrephes* can be simultaneously influenced by both biotic and abiotic factors. For example, variations in its morphological features and body size may relate to defense against planktivorous fishes (Straile and Halbich 2000) or energetic tradeoffs related to balancing growth and reproduction (Enz et al. 2001, Branstrator 2005). The population size of *Bythotrephes* may be limited by bottom-up effects such as the availability of herbivorous crustaceans (Dumitru et al. 2001, Strecker and Arnott 2008), particularly in the spring months (Young et al. 2011), as well as top-down control by fish (Coulas et al. 1998, Jarnagin et al. 2004, Young and Yan 2008, Young et al. 2009). Temperature influences population growth rates by affecting hatching rates (Yurista 1992, Brown and Branstrator 2011), generation time (Lehman and Branstrator 1995), mode of reproduction (Straile and Halbich 2000, Manca et al. 2007), or prey consumption (Yurista et al. 2010). Because *Bythotrephes* is a visual predator (Muirhead and Sprules 2003), light availability impacts its foraging abilities (Pangle and Peacor 2009).

The invasion of *Bythotrephes* has likely impacted the structure and diversity of the zooplankton community in Lake Simcoe. For example, a preliminary analysis of *Bythotrephes* invasion to Lake Simcoe documented a decrease in cladoceran species richness and shifts in zooplankton community composition (J.D.Young, unpubl. data). In addition to these impacts on zooplankton, *Bythotrephes* may also have direct impacts on the fish community by competing with young-of-year fish for zooplankton prey, while its caudal spine may discourage predation by small fish (Garton et al. 1993, Barnhisel and Harvey 1995, Compton and Kerfoot 2004, Jarnagin et al. 2004). *Bythotrephes* seems to comprise a large portion of the summer diet of many Lake Simcoe fish (Rose 1998, Amtstaetter 2000, MacRae 2001, Johanson and Amtstaetter 2004), which may have consequences for fish condition and growth because *Bythotrephes* may provide different nutritional resources than native zooplankton prey. Such changes to the Lake Simcoe ecosystem due to *Bythotrephes* invasion would have important consequences for the recreational fisheries of, and the ecosystem services provided by, the lake.

There is currently no information on the status or dynamics of the *Bythotrephes* population in Lake Simcoe, which is vital information needed to examine its role in, and potential impacts on, the Lake Simcoe food web. In addition, the dynamics of this invader have not been well studied in its invaded range, having been examined in only a few different systems, such as the Canadian Shield lakes (e.g., Yan and Pawson 1998, Yan et al. 2001, Young et al. 2011), Great Lakes (e.g. Pothoven et al. 2001, 2003, Cavaletto et al. 2010), or constructed reservoirs in Minnesota, USA (Brown et al. 2012). The factors regulating *Bythotrephes* dynamics in Lake Simcoe may differ from other lakes due to differences in lake trophic

status, water quality, presence of other nonnative invading species, and/or the structure and complexity of the planktonic food web. Thus, increased knowledge of the population dynamics and life-history characteristics of *Bythotrephes* and its responses to environmental conditions will improve our understanding of what affects this invasive predator and provide insight into how it has adapted to its nonnative environment over time. Such information would also inform the successful management of the Lake Simcoe ecosystem. In this paper we: (1) detail the current status of the *Bythotrephes* population in Lake Simcoe through an examination of its interannual abundance and seasonal phenology; (2) identify patterns in its life history, namely body size and reproductive char-

acteristics; and (3) explore the biotic (predators, prey) and abiotic (water clarity, temperature) factors that may be regulating its population.

Study site

Lake Simcoe, located in southern Ontario, Canada (44°25′N, 79°20′W), has a surface area of 722 km², a mean depth of 14 m, and a maximum depth of 42 m (Fig. 1). The lake is composed of a "main" basin (surface area 643 km², mean depth 14 m, maximum depth 33 m) and 2 large bays: Cook's Bay at the south end (surface area 44 km², mean depth 13 m, maximum depth 15 m) and Kempenfelt Bay on the west side of the lake (surface area
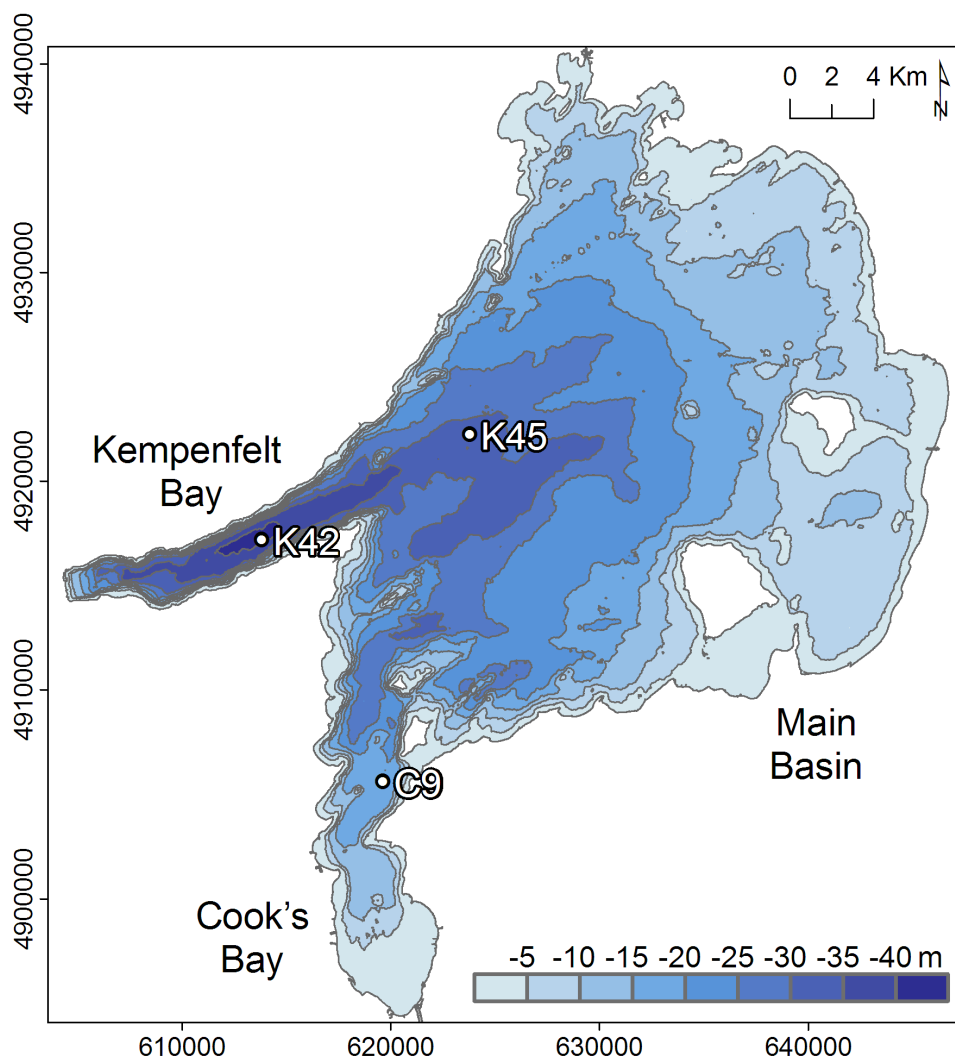

Fig. 1. Map of Lake Simcoe showing positions of 3 sampling stations: K42 in Kempenfelt Bay, C9 in Cook's Bay, K45 in the Main Basin. Bathymetry information was derived by the Ontario Ministry of Natural Resources (OMNR) from the Canadian Hydrographic Service original depth sounding field sheet, 1957, scale 1:36,000. (This map should not be relied on as a precise indicator of routes or locations, nor as a guide to navigation. The OMNR shall not be liable in any way for the use of, or reliance upon, this map or any information on this map.).

34 km^2, mean depth 20 m, maximum depth 42 m). The lake is a dimictic, hard water lake (mean calcium concentration of 41 mg L^{-1}, mean alkalinity of 116 mg L^{-1} CaCO$_3$). Recent (2004–2008) average total phosphorus (TP) concentration has ranged from 13.5–23.4 µg L^{-1} and average chlorophyll *a* concentration from 1.9–4.2 µg L^{-1} (Young et al. 2010).

Lake Simcoe's fish community is composed of a diverse assemblage of warm, cool, and cold-water fish species (Amtstaetter 2003). Those species known to consume *Bythotrephes* include lake herring (*Coregonus artedi*), lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), yellow perch (*Perca flavescens*), black crappie (*Pomoxis nigromaculatus*), pumpkinseed (*Lepomis gibbosus*), and rock bass (*Ambloplites rupestris*) (Rose 1998, Amtstaetter 2000, MacRae 2001, Johanson and Amtstaetter 2004). Black crappie is a nonindigenous species, first captured in the lake in 1987 (McNeice and Johanson 2004).

Methods

Field and laboratory methods

Personnel from the Ontario Ministry of the Environment in partnership with the Lake Simcoe Region Conservation Authority collected the *Bythotrephes*, zooplankton, and water quality samples throughout this study. Samples were taken every 2 weeks through the ice-free season (typically May to Oct) from 1999 to 2007 at 3 spatially separated stations that differed in depth and location within the lake: C9 in Cook's Bay, K42 in Kempenfelt Bay, and K45 in the main lake basin (Fig. 1).

Bythotrephes was collected at each station using a 0.75 m diameter, 3 m long, 285 µm mesh net and preserved in 5.5% sucrose formalin. In 1999, vertical net hauls were taken from 1 m above bottom to the lake surface. For all other years, vertical net hauls were taken 5 m above bottom to the lake surface at C9, and from 20 m depth to the lake surface at K42 and K45. *Bythotrephes* is not typically found in the hypolimnion during the day in stratified lakes containing lake herring (Young and Yan 2008), and thus sampling only the upper 20 m of the water column is not expected to underestimate abundance, at least during stratified months.

Bythotrephes were counted, sexed, and measured under a Leica MZ12.5 dissecting microscope using a semiautomated plankton counting system (Allen et al. 1994). Samples were often examined in their entirety for *Bythotrephes* but subsampled with a Folsom plankton splitter if abundances were high, ensuring that at least 20 individuals were counted in the smallest fraction (after Yan and Pawson 1997). Body length was measured from

the top of the eye to the anus and corrected for shrinkage in formalin using a conversion factor of 1.221 (Yan and Pawson 1998). Instar and stage of brood development were also recorded. Clutch size of parthenogenic broods was determined as the number of clear-, red-, and black-eyed embryos in gravid females. Clear-eyed embryos were dissected from the brood pouch to ensure an accurate count of parthenogenic broods. Sexually produced (i.e., resting egg) broods were determined as the number of dark-golden spheres in the brood pouch (Yurista 1992).

Crustacean zooplankton were collected at each station using a 12.2 cm diameter, 80 cm long, 80 µm mesh net, hauled from 1 m above lake bottom to the surface and preserved in 5.5% sugar formalin. For samples collected in 1999, zooplankton were enumerated following the protocol described in Nicholls and Tudorancea (2001), counting 250–300 individuals per sample. For samples collected in and after 2000, this protocol was adjusted to count at least 300 individuals per sample. All Cladocera and mature Copepoda were identified to species, where possible.

Composite water samples through the euphotic zone (lower depth determined as 2.5 times the Secchi depth) to a maximum depth of 15 m were collected with a polyvinyl chloride hose for chemical analyses at each station. TP and dissolved organic carbon (DOC) were measured in the laboratory using standard Ontario Ministry of the Environment analytical methods (Janhurst 1998). In addition, field crews measured Secchi depth and water temperature at 1 m depth intervals through the water column at each site.

Sampling of the Lake Simcoe fish community was conducted by the Lake Simcoe Fisheries Assessment Unit (LSFAU). Only warm-water fish species were sampled each year throughout our 9 year period (1999–2007); therefore, planktivorous cold-water fish species were not used in the analyses. We selected 3 warm-water fish species—pumpkinseed, yellow perch, and black crappie—because they have been found to contain *Bythotrephes* in their stomachs (Rose 1998). Fish were sampled each year in August using 1.8 m trapnets (6.4 cm mesh) set for 22 h each at randomly selected sites at least 0.5 km apart, totaling 30 net sets per year according to LSFAU protocols for the Nearshore Community Index Netting program (Sterling 1999).

Data analyses

All statistical analyses were conducted using the software package R (v 2.14.1; R Development Core Team 2011). *Bythotrephes* seasonal abundance was calculated as the mean of the 3 stations at biweekly intervals from 1999 to

2007, with station abundance being the number of female *Bythotrephes* divided by the total volume of water filtered by the net. Volumes were corrected for an average net filtration efficiency of 96% (Young 2008). Mean *Bythotrephes* annual abundance was calculated by averaging *Bythotrephes* abundance on all sampling dates from July to October for each year because it was never found in May and almost never in June and November (Fig. 2).

Multiple regression analysis was used to determine which biotic and abiotic variables best explained variation in mean *Bythotrephes* annual abundance among years. Multiple regression analysis is appropriate because *Bythotrephes* interannual abundances are unlikely to be autocorrelated (for further discussion, see Young et al. 2011). Top-down and bottom-up variables were used as predictors (Table 1). Top-down predictor variables included yearly abundance values (geometric mean annual catch rate) for the 3 warm-water fish species (pumpkinseed, black crappie, and yellow perch), while bottom-up predictor variables included mean prey

abundance (no. m^{-3}), mean Secchi depth (m), mean epilimnetic temperature (°C), mean DOC concentration (mg L^{-1}), and mean TP concentration (µg L^{-1}), averaged across all sampling dates from July to October in each year. Mean prey abundance included only herbivorous cladocerans because they seem to be the preferred prey of *Bythotrephes* (Vanderploeg et al. 1993, Lehman and Branstrator 1995, Schulz and Yurista 1999), except for *Daphnia mendotae* (Young et al. 2011). Mean prey abundance was calculated by correcting sampled lake water volumes for measured net filtration efficiency, which was estimated yearly with an impellor attached to the net's mouth. Prey abundance was log(x+1)-transformed prior to analysis to meet assumptions of normality. When the lake was not stratified, mean temperature was calculated using values from the surface to 20 m depth. Assumptions of normality and homogeneity of variances were assessed for the regression model. Collinear variables were removed from the analysis when the variance inflation factor was >10 (Quinn and Keough 2002). The most parsimonious model was determined by

Table 1. Mean (±SE) annual *Bythotrephes* abundance and top-down and bottom-up variables. Fish (top-down) abundances were calculated as geometric mean annual catch rates and bottom-up variables were averaged from July to October. PS = pumpkinseed (*Lepomis gibbosus*); BC = black crappie (*Pomoxis nigromaculatus*); YP = yellow perch (*Perca flavescens*); Prey = herbivorous cladoceran abundance; Secchi = Secchi depth; Temp = epilimnetic temperature; TP = total phosphorus concentration; DOC = dissolved organic carbon concentration.

Year	Annual *Bythotrephes* (no. m^{-3})	PS (mean annual catch rate)	BC (mean annual catch rate)	YP (mean annual catch rate)	Prey (no. m^{-3})
1999	9.5 ± 1.9	7.0	55.1	15.3	3587.7
2000	6.0 ± 1.2	15.2	26.7	17.7	1065.9
2001	10.9 ± 3.4	7.2	13.7	8.9	5107.0
2002	24.1 ± 6.7	5.6	14.0	9.2	6470.1
2003	7.6 ± 1.7	27.1	23.8	13.3	5273.7
2004	11.7 ± 2.5	17.4	2.9	17.9	3021.4
2005	29.9 ± 6.5	16.7	12.4	32.2	10356.0
2006	4.7 ± 2.4	6.6	24.9	18.2	12216.2
2007	4.3 ± 1.1	13.0	53.7	27.9	5248.2
	Secchi (m)	**Temp (°C)**	**TP (µg L^{-1})**	**DOC (mg L^{-1})**	
1999	5.8 ± 0.7	20.0 ± 0.6	9.8 ± 1.4	4.0 ± 0.2	
2000	5.5 ± 0.5	19.9 ± 0.9	14.9 ± 1.2	4.2 ± 0.2	
2001	5.7 ± 0.6	20.0 ± 0.9	14.6 ± 1.0	4.0 ± 0.2	
2002	6.8 ± 0.7	21.3 ± 0.6	17.0 ± 1.2	4.4 ± 0.3	
2003	6.3 ± 0.7	19.5 ± 1.4	16.5 ± 1.3	4.2 ± 0.3	
2004	6.3 ± 0.6	19.5 ± 0.7	17.6 ± 1.4	4.3 ± 0.2	
2005	7.3 ± 0.6	21.6 ± 0.7	14.7 ± 0.3	4.3± 0.1	
2006	7.0 ± 0.9	18.7 ± 2.1	14.4 ± 0.8	4.3 ± 0.2	
2007	7.1 ± 0.4	19.2 ± 0.5	15.2 ± 1.9	4.5 ± 0.9	

stepwise model selection using Akaike's Information Criterion (AIC), with all possible combinations of models included for comparison. Contributions of each significant predictor to the total response variance were calculated using the R library "relaimpo" (Grömping 2006).

Multivariate ordination techniques were used to distinguish *Bythotrephes* seasonal abundance patterns among years and relate these patterns to biotic and abiotic variables (after Young et al. 2011) using the R library "vegan" (Oksanen et al. 2010). Because seasonal *Bythotrephes* abundances are temporally autocorrelated (for further discussion, see Young et al. 2011), we used a canonical variates analysis (CVA), where the dependent variables were groups of years with similar seasonal *Bythotrephes* abundance patterns. Principal components analysis (PCA), followed by *K*-means clustering analysis, was used to identify the groups of years with similar *Bythotrephes* seasonal abundance patterns. Biweekly *Bythotrephes* seasonal abundances from July through October in each year were used. When *Bythotrephes* was not collected on a similar date across years, abundances were averaged between dates when necessary so that values existed for 2 sampling dates in each month for every year, totaling 8 sampling dates in each year (resulting in ~10% of values being interpolated). Mean *Bythotrephes* seasonal abundances were normalized using the maximum abundance within each year prior to PCA and *K*-means clustering. Only bottom-up predictor variables were used to explain *Bythotrephes* abundance because seasonal abundances of planktivorous fishes were unavailable. Predictor variables included biweekly values of log(x+1)-transformed mean prey abundance, mean Secchi depth, mean epilimnetic temperature, mean TP, and mean DOC. Predictor variables were collected on the same sampling dates as *Bythotrephes* in each year, or were averaged between dates when needed, as for *Bythotrephes* abundance. All predictor variables were standardized to zero mean and unit variance prior to analysis. The number of predictor variables was reduced by forward selection using the R library "packfor" (Dray 2009) and considered significant at $\alpha < 0.05$.

For analysis of life-history patterns, we calculated female body length (mm) by instar, parthenogenic clutch size, proportion of broods that were resting eggs, and proportion of the population that were males. To maximize the number of individuals collected for all life-history analyses, females were pooled across the 3 stations on each sampling date within a year. To test whether body length differed among instars or sampling dates, 2-way ANOVAs were performed for each year with "date" and "instar" as (fixed) factors. There was no indication of temporal dependence in *Bythotrephes* body lengths within years (autocorrelation function [ACF] tests; N.E. Kelly,

data not shown), thus ANOVA tests were appropriate in this instance. Multiple tests of the same hypothesis can inflate the probability of Type I error (incorrectly rejecting the null hypothesis); thus, we used the Benjamini-Hochberg correction (Benjamini and Hochberg 1995) to adjust our p values to control the false discovery rate among all 18 hypothesis tests (testing 3 *F*-ratios for each of 9 years). All ANOVAs were followed by Tukey's HSD post-hoc testing for multiple comparisons (with p values also corrected for multiple comparisons within each set of contrasts).

Parthenogenic clutch size was calculated as the mean clutch size of all females with embryos on a sampling date. For instar body length and parthenogenic clutch size, only sampling dates with ≥5 measurements were included to reduce heterogeneity of variances (Young 2008). The proportion of resting egg broods was calculated as the number of resting egg broods of the total number of broods (parthenogenic + resting egg broods) observed in females with clutches on each sampling date within each year. The proportion of males was determined as the number of males of the total number of individuals observed on each sampling date within each year.

Results

Bythotrephes annual and seasonal abundance

Bythotrephes abundance varied dramatically both among seasons and years (Fig. 2). Mean annual *Bythotrephes* abundance (±1 SE) varied from 4.3 ± 1.1 m^{-3} in 2007 to 29.9 ± 6.5 m^{-3} in 2005 (Table 1). Peak abundance (mean ±1 SE) ranged from 7.53 ± 2.16 m^{-3} in October 2007 to 77.3 ± 27.4 m^{-3} in August 2002 (Fig. 2). Peak mean epilimnetic temperature varied from year to year and coincided with peak *Bythotrephes* abundance only in 2000, 2004, and 2006. Cladoceran prey abundance was maximal in June or July most years, although it was highest in the fall in 2000, 2006, and 2007 (Fig. 2). In all years but 2007, cladoceran abundance was low when *Bythotrephes* abundance was maximal, and *Bythotrephes* abundance was low when cladoceran abundance was high or starting to increase.

Based on AIC values, the most parsimonious model for predicting interannual differences in mean annual *Bythotrephes* abundance included black crappie and yellow perch abundance, prey abundance, and epilimnetic temperature ($F_{4,4} = 180$, $p < 0.001$, adjusted r^2 = 0.98; Table 2). Secchi depth was the only collinear variable removed from the analysis (variance inflation factor = 25.75), and pumpkinseed abundance and TP were nonsignificant variables ($p > 0.3$). Black crappie abundance was significantly and negatively correlated ($p = 0.004$), and

prey abundance (p = 0.002) and epilimnetic temperature (p < 0.001) were significantly and positively correlated with mean annual *Bythotrephes* abundance. Abundance of yellow perch was not a significant predictor. Epilimnetic temperature explained the largest proportion of the total response variance, followed by black crappie, cladoceran, and yellow perch abundance, respectively (Table 2).

K-means clustering and PCA identified 4 different *Bythotrephes* seasonal phenologies, which were grouped primarily based on the month of peak *Bythotrephes* abundance and secondarily on the presence or absence of an additional seasonal population peak and low midseason abundance (Fig. 3a). For the 2000–2004 group ("July"), *Bythotrephes* abundance was highest in July and declined through November, and no second abundance peak was

observed (Fig. 2). For the 2001–2002–2006 group ("August"), highest *Bythotrephes* abundances occurred in August, and a second abundance peak was observed to occur in late September following a population low in mid-September (Fig. 2). The 1999–2005–2007 group ("October") displayed the highest *Bythotrephes* abundances in late September or early October, which were preceded by another abundance peak in August and a midseason population low in mid-September (Fig. 2). For the 2003 pattern ("September"), *Bythotrephes* abundance peaked in September, with a secondary peak in July, and the 2 peaks were separated by a population low in early August. Common to all 4 groups was low abundance (i.e., <1 m^{-3}) in May and June in all years, with *Bythotrephes* generally not collected in samples until mid-June or early July (Fig. 2).
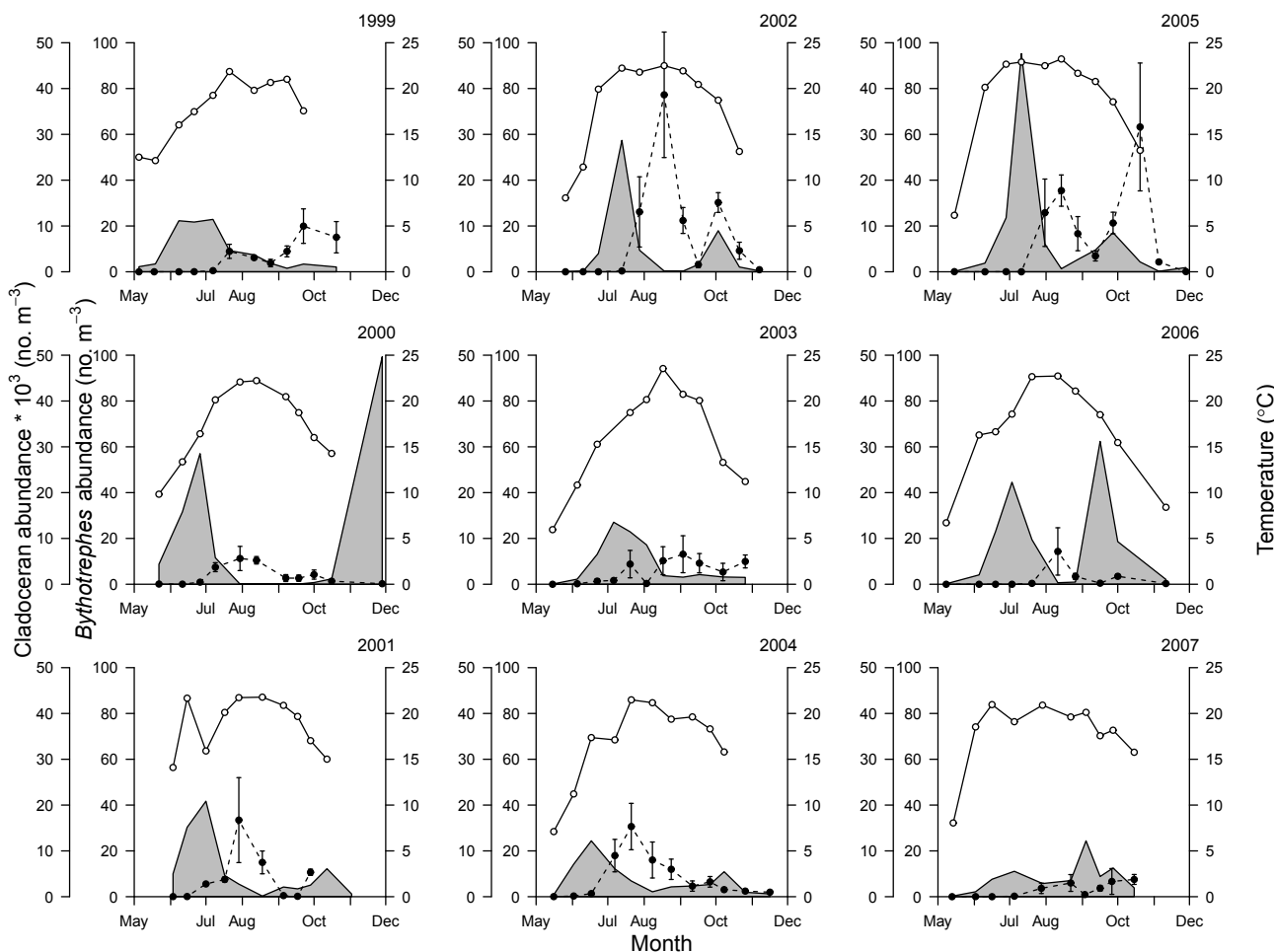

Fig. 2. Mean abundance (no. m^{-3}) of cladocerans (*10^{3}; shaded grey polygons); mean (±SE) abundance of female *Bythotrephes* (black circles, dashed line); and mean epilimnetic temperature (°C; white circles, solid line) in Lake Simcoe from 1999 to 2007. When the lake was not stratified, mean temperature was calculated using values from the surface to 20 m depth.

Table 2. Results of multiple regression analysis of mean annual *Bythotrephes* abundance with top-down and bottom-up variables for Lake Simcoe from 1999 to 2007. Bold values indicate significant results (p < 0.05). Relative importance is the contribution of each predictor variable to the total response variance. *df* = degrees of freedom; Prey = Mean annual herbivorous cladoceran abundance (no. m^{-3}); Temp = mean epilimnetic temperature (°C); BC = annual black crappie abundance (mean annual catch rate); YP = annual yellow perch abundance (mean annual catch rate).

Analysis	*F*	*df*	Adjusted r^2	p	Variable	Coefficient	t	p	Relative importance (%)
Mean annual abundance	180.0	4, 4	0.98	**<0.001**	BC	−5.44	−6.133	**0.004**	10.9
					YP	3.90	2.174	0.095	0.5
					Prey	7.72	7.146	**0.002**	10.6
					Temp	8.21	22.29	**<0.001**	77.9

CVA identified 2 variables over 3 sampling dates as significant predictors of the 4 groups of *Bythotrephes* seasonal phenologies: Secchi depth in early August (p = 0.032) and mid-September (p = 0.020), and TP in early September (p = 0.019; Fig. 3b). The first linear discriminant axis explained 82.3% of the total variance among the 4 groups of *Bythotrephes* seasonal phenologies, contrasting groups of years with high early September TP (2000, 2004) versus years with high Secchi depth in early August (1999, 2005, 2007 and 2001, 2002, 2006). The second linear discriminant axis explained 17.0% of the total variance, discriminating groups of years with high Secchi depth in mid-September (2003) from those

with high values in early August (1999, 2005, 2007, and 2001, 2002, 2006; Fig. 3b). The "July" group (2000, 2004) was positively associated with early September TP and negatively associated with early August Secchi depth. In 2000 and 2004, TP in early September was relatively high, while *Bythotrephes* abundance was at its lowest from this date onward (Fig. 4). Secchi depth in early August in these years was relatively shallow (<5 m), and *Bythotrephes* abundance was declining from its seasonal maximum at this time. The "August" group (2001, 2002, 2006) was positively associated with Secchi depth in early August and negatively associated in mid-September. In these years, Secchi depth was >5 m
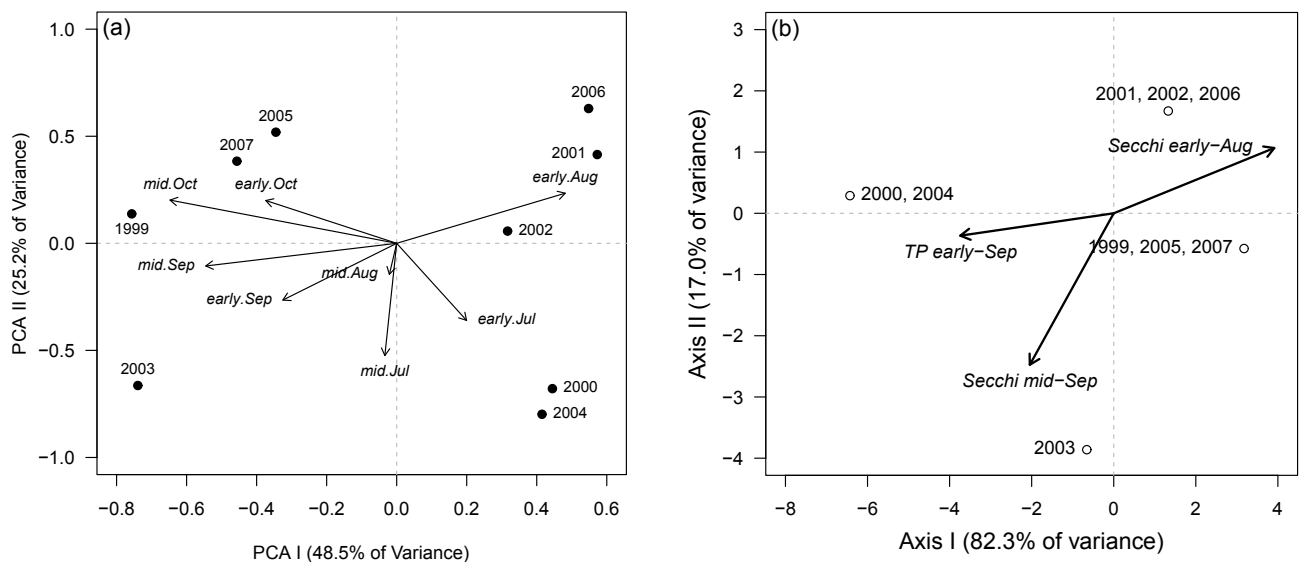

Fig. 3. Multivariate analyses for *Bythotrephes* abundance in Lake Simcoe from 1999 to 2007. (a) Principal components analysis (PCA) of the relative seasonal abundances of *Bythotrephes*. (b) Canonical variates analysis (CVA), where Secchi depth (Secchi) in early August (p = 0.032) and mid-September (p = 0.020), and total phosphorous concentration (TP) in early September (p = 0.019) were significant predictors of differences among the 4 groups of years: 2000, 2004 = "July"; 2001, 2002, 2006 = "August"; 2003 = "September"; 1999, 2005, 2007 = "October."
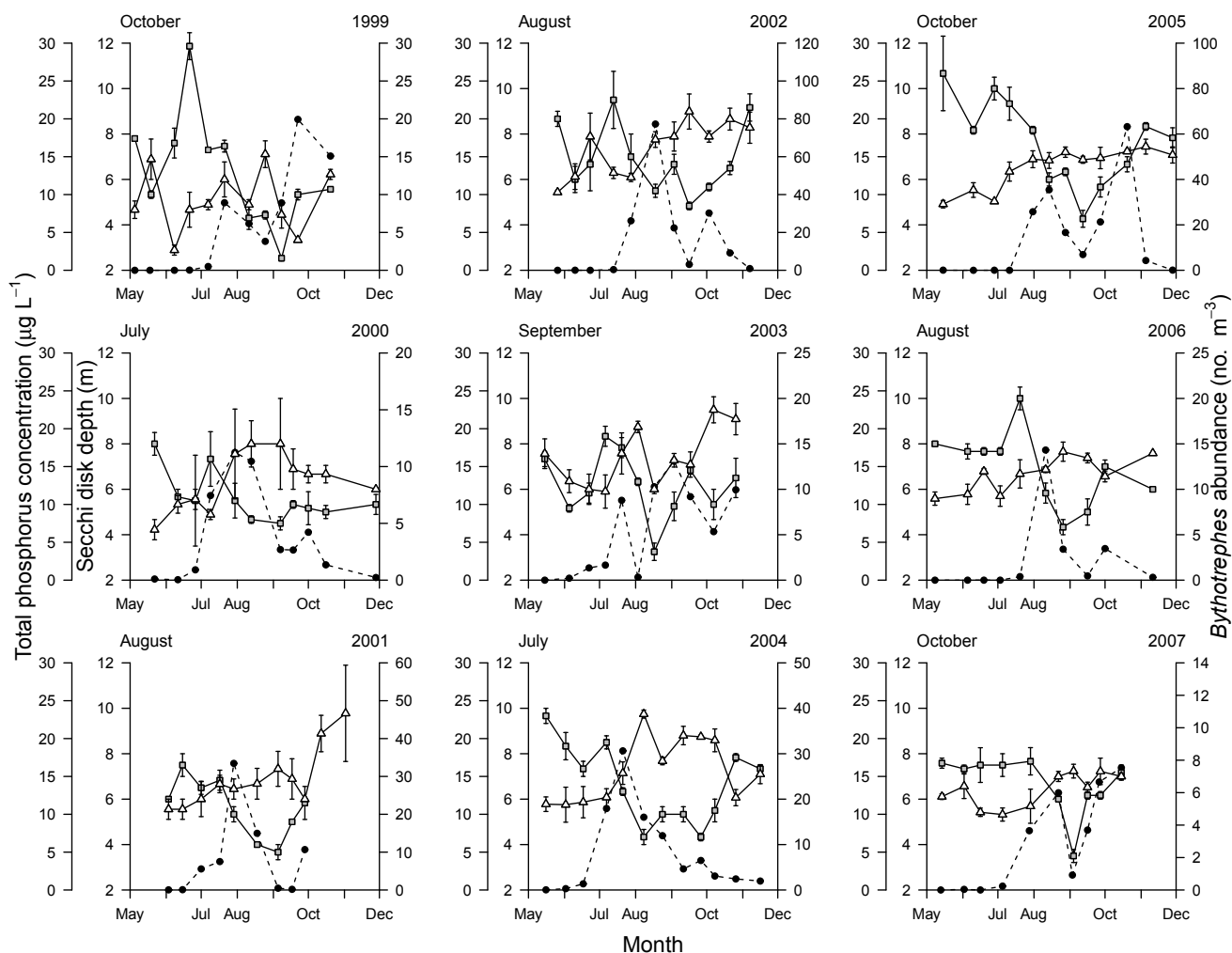
Fig. 4. Mean (±SE) total phosphorus concentrations (µg L^{-1}; white triangles, solid line); mean (±SE) Secchi depth (m; grey squares, solid line); and mean *Bythotrephes* abundance (black circles, dashed line) in Lake Simcoe from 1999 to 2007. Based on CVA results, 4 groups of years are identified by the month of peak *Bythotrephes* abundance: July, September, August, or October. The y axis range for *Bythotrephes* abundance differs among panels.

in early August and *Bythotrephes* abundance peaked, but Secchi depth was <5 m in mid-September and *Bythotrephes* abundance was at a minimum. The "September" grouping (2003) was positively associated with Secchi depth in mid-September. Secchi depth was >5 m at this time in 2003; however, *Bythotrephes* abundance was declining (Fig. 4). The "October" (1999, 2005, 2007) group had a positive association with Secchi depth in early August and a negative association with TP in early September. Early August Secchi depth was >5 m in 2005 and 2007, but not in 1999, and *Bythotrephes* abundance was near a maximum. Early September TP was relatively low or constant in these years, and *Bythotrephes* abundance was at a population low.

Life history

Bythotrephes instars I–III were typically found on all sampling dates, except at the beginning (May, June) and end (November) of the season in some years (Fig. 5); however, there were no individuals observed in instar IV throughout the study. On average, instar II individuals were (mean ± 1 SE) 0.66 ± 0.03 mm, or ~23%, larger than instar I, while instar III individuals were 0.45 ± 0.03 mm, or ~13%, larger than instar II. The body length of *Bythotrephes* varied both seasonally and among the 3 instars (Table 3; Fig. 5). In 2002, 2004, 2005, and 2006, body length differed significantly among dates and instars. There were significant Date * Instar interactions in 5 of the 9 years (1999, 2000, 2001, 2003, 2007), indicating that
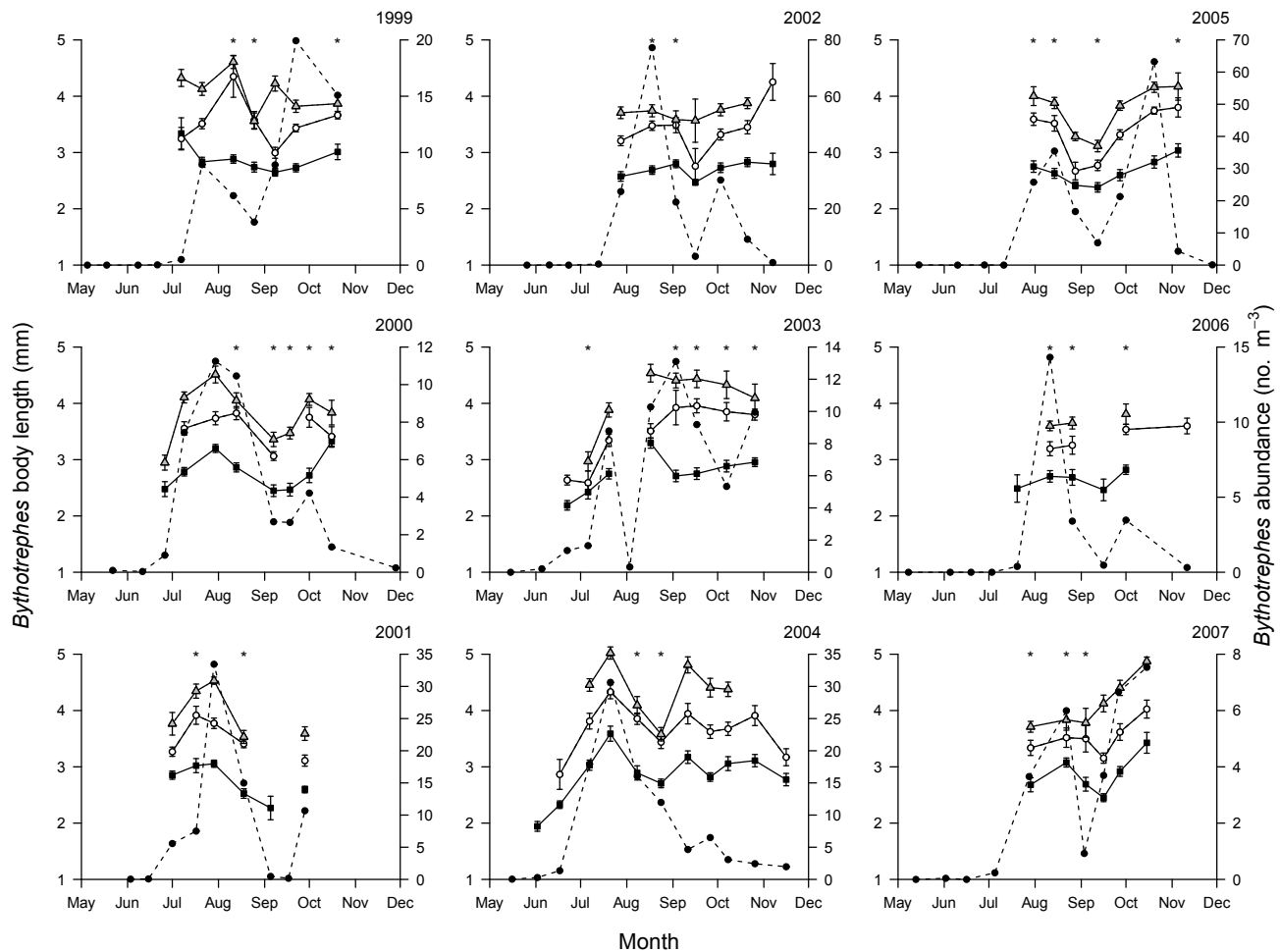
Fig. 5. Mean (±SE) *Bythotrephes* body length (mm) of instar I (black squares, solid line), instar II (white circles, solid line), and instar III (grey triangles, solid line), and mean abundance (no. m^{-3}) of *Bythotrephes* (black circles, dashed line), in Lake Simcoe from 1999 to 2007. No instar IV individuals were observed throughout the study period. Only dates with ≥5 females measured within an instar were included. Dates marked with an asterisk (*) indicate no significant difference (p' > 0.05) between instars II and III body length as determined by 2-way ANOVA and Tukey's multiple comparisons. The y axis range for *Bythotrephes* abundance differs among panels.

seasonal patterns in body length among the 3 instars were not consistent (i.e., in the same direction) across all dates within these years. Mean body length between instars I and II were significantly different on all dates in 2001, 2004, 2006, and 2007, and on all dates except one in 1999, 2000, 2002, 2003, and 2005 (Tukey's HSD, p' < 0.05). The mean body length of instars II and III did not differ significantly in August and/or September in all years, and occasionally in July, October, or November (Tukey's HSD, p' > 0.05; Fig. 5).

In years when sufficient data were available, *Bythotrephes* body length for all instars generally increased from June or July into August as the population increased in abundance. For all instars in 2000, 2002 (only instars I and

II), 2004, 2005, and 2007 (only instar I), body length was significantly larger earlier (Jul and/or early Aug) and later (around Oct) in the season than during midseason (late Aug or Sep; Tukey's HSD, p' < 0.05). In contrast, for instars II and III in 2003 and 2007, body length was significantly smaller earlier (Jun and Jul or Jul–Sep) than later (after mid-Aug or Oct) in the season (Tukey's HSD, p' < 0.05). There was no significant difference in body length over the season in 2006 (all instars) and 2002 (instar III; Tukey's HSD, p' > 0.1). *Bythotrephes* body length was largest on the same sampling dates when its seasonal abundance was highest in 2000, 2001, 2003 (instars II and III), 2004, 2005, and 2007 (Fig. 5). *Bythotrephes* body length declined as its seasonal abundance declined or was
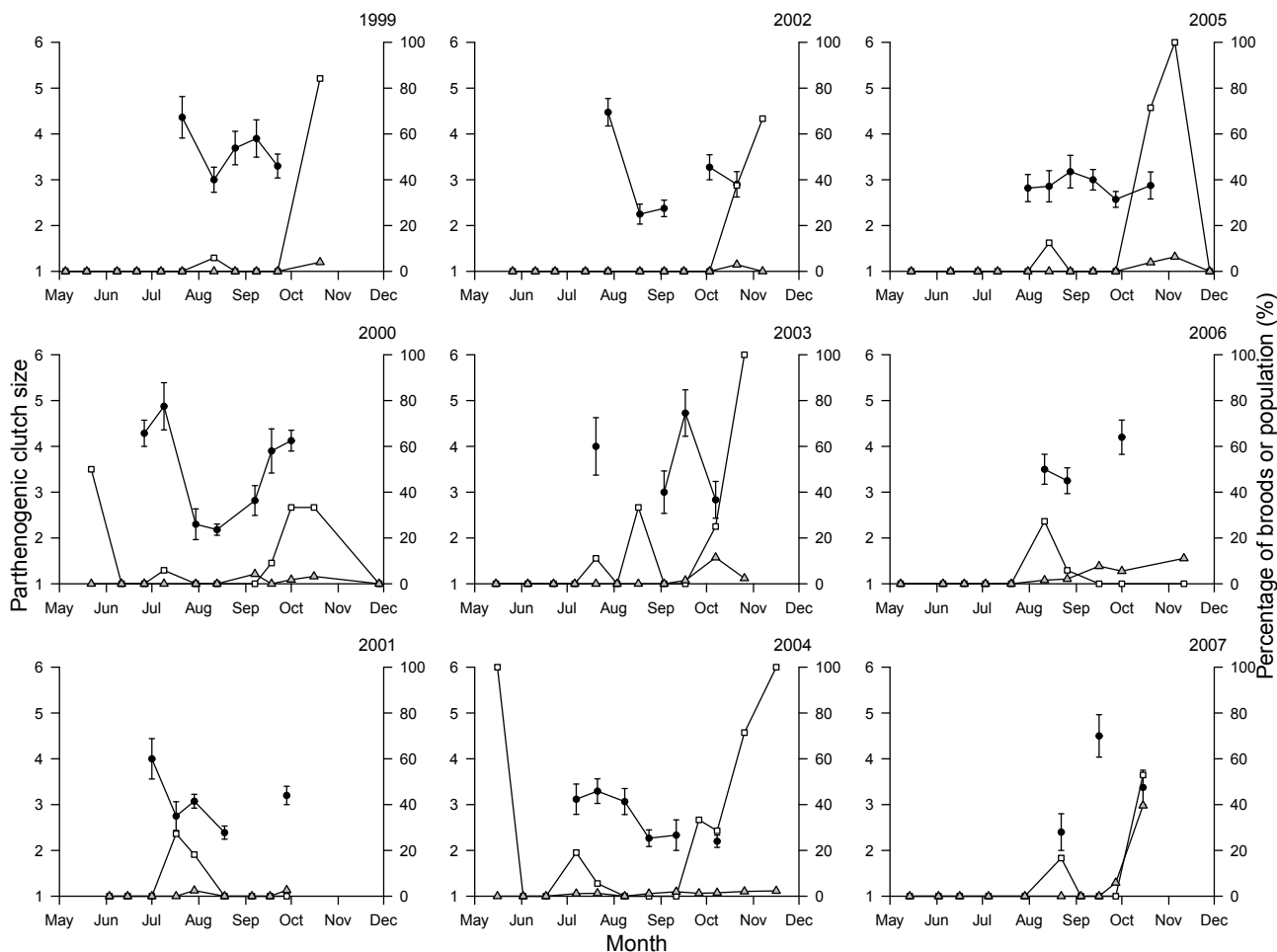
Fig. 6. Mean (±SE) *Bythotrephes* clutch size of parthenogenic broods (black circles), and percentage of resting egg broods (white squares) and males (grey triangles), in Lake Simcoe from 1999 to 2007. For clutch size, only dates where ≥5 females with embryos were collected were included.

at a midseason low in August or September for 2000, 2001, 2002 (instar II), 2004, 2005, and 2007 (instar I; Fig. 5).

Females carrying parthenogenic clutches were observed from July through September or October. In 1999, 2000, 2001, 2002, and 2004, clutch sizes were maximal in July, declined in August or September, and then increased again in all of these years but 2004. In 2005, clutch size varied little throughout July to October, ranging from 2.5 to 3 embryos per clutch. In 2003, 2006, and 2007, too few (i.e., <5) females with clutches were collected for patterns to be determined.

Resting eggs were rarely observed in some years (e.g., on only 2 sampling dates throughout the season in 1999, 2001, 2002, 2006, and 2007) but were found more frequently in others (2000, 2003, 2004, and 2005; Fig. 6). Resting egg broods were frequently observed during the summer (in all years except 2002) and fall (in all years except 2001 and 2006), but only occasionally in spring (2000, 2004; Fig. 6). In 2000 and 2004, resting egg production occurred throughout the ice-free season (spring, summer, and fall); in contrast, resting eggs were observed only in the fall in 2002 and only in the summer in 2001 and 2006. The percentage of resting egg broods was greatest in the spring (~50–100%) or fall (~40–100%), while those observed in summer did not exceed 40%. Overall, the production of resting eggs in spring and summer was unexpected, given that few males were sampled within the population on these dates (Fig. 6). Males were rare in most years, only present in late summer and fall, generally comprising <10% of the population except for October of 2007 when males comprised ~40% of the population (Fig. 6).

Table 3. Results from 2-way ANOVA comparing *Bythotrephes* body length among sampling dates and instars (I–III) in Lake Simcoe from 1999 to 2007. Only dates with ≥5 females measured within an instar were included. Bold values indicate significant results at p' < 0.05. *df* = degrees of freedom.

Year	Factor	*F*	*df*	p′
1999	Date	23.83	6, 419	**<0.001**
	Instar	201.07	2, 419	**<0.001**
	Date*Instar	4.96	12, 419	**<0.001**
2000	Date	18.85	6, 368	**<0.001**
	Instar	181.08	2, 368	**<0.001**
	Date*Instar	2.13	12, 368	**0.018**
2001	Date	57.14	4, 409	**<0.001**
	Instar	210.78	2, 409	**<0.001**
	Date*Instar	3.18	8, 409	**0.002**
2002	Date	13.27	6, 428	**<0.001**
	Instar	143.79	2, 428	**<0.001**
	Date*Instar	1.60	12, 428	0.094
2003	Date	22.59	6, 409	**<0.001**
	Instar	148.96	2, 409	**<0.001**
	Date*Instar	2.72	12, 409	**0.002**
2004	Date	30.05	7, 555	**<0.001**
	Instar	238.1	2, 555	**<0.001**
	Date*Instar	1.19	14, 555	0.288
2005	Date	37.615	6, 455	**<0.001**
	Instar	183.4	2, 455	**<0.001**
	Date*Instar	1.735	12, 455	0.064
2006	Date	3.45	3, 161	**0.021**
	Instar	61.58	2, 161	**<0.001**
	Date*Instar	0.645	6, 161	0.694
2007	Date	59.27	5, 223	**<0.001**
	Instar	146.65	2, 223	**<0.001**
	Date*Instar	2.30	10, 223	**0.018**

Discussion

Factors influencing *Bythotrephes* annual abundance

Bythotrephes longimanus has become well established in Lake Simcoe since its first detection in 1993, but it exhibits large interannual variations in abundance. Variation in *Bythotrephes* annual abundance in Lake Simcoe seems to be driven by a combination of biotic and abiotic factors. Multiple regression analysis identified predator and prey abundance and temperature in the epilimnion as significant predictors of mean annual *Bythotrephes* abundance. Years of high *Bythotrephes* abundance were predicted by low black crappie abundance, the warmest epilimnetic temperatures, and high cladoceran abundance; conversely, the lowest *Bythotrephes* abundance was predicted by the highest black crappie abundance, lowest epilimnetic temperatures, and, except for 2006, the lowest cladoceran abundances.

Top-down control of *Bythotrephes* abundance by planktivorous fish has been implicated in lakes in both its native (Straile and Halbich 2000, Palmer et al. 2001) and invaded (Coulas et al. 1998, Pothoven and Vanderploeg 2004, Pothoven et al. 2007, Young and Yan 2008, Young et al. 2009) ranges. The incorporation of *Bythotrephes* as a main prey item into the diets of large-sized fishes in Lake Simcoe is unsurprising given that *Bythotrephes* is a large, conspicuous member of the plankton community, with a prominent compound eye, bright pigmentation, and large coloured brood pouch (Barnhisel and Harvey 1995, Rivier 1998). In recent years, *Bythotrephes* may have replaced native cladocerans as the primary food resource in the summer diet of yellow perch, black crappie, pumpkinseed, and rock bass (Rose 1998). Although not examined in this study, cold-water planktivorous fish may also play a role in controlling *Bythotrephes* abundance because *Bythotrephes* has been found in the stomachs of Lake Simcoe cold-water fishes, such as lake herring (Johanson and Amtstaetter 2004), lake whitefish, and lake trout (Amtstaetter 2000, MacRae 2001). We anticipate that continued monitoring of the Lake Simcoe ecosystem will enable us to further explore the role of both warm- and cold-water fish planktivory in controlling *Bythotrephes* in the future.

Our findings agree with those of previous studies from Canadian Shield lakes that identified prey abundance as a significant factor influencing *Bythotrephes* abundance (Dumitru et al. 2001, Boudreau and Yan 2003, Strecker and Arnott 2008, Young et al. 2011). In Lake Simcoe, the highest annual *Bythotrephes* abundances occurred in 2002 and 2005, when mean annual prey abundance exceeded 6000 m⁻³. Increased food availability would allow greater population growth, allowing *Bythotrephes* to achieve the high population sizes observed in these years. In contrast, in 2006 we observed the highest annual cladoceran prey abundance but the second lowest *Bythotrephes* abundance, suggesting other factors may occasionally outweigh the positive influence of high prey availability on *Bythotrephes* abundance.

Interannual variability in epilimnetic temperature seems to have a strong impact on *Bythotrephes* abundance in Lake Simcoe, such that years when the epilimnion was warmest had the highest *Bythotrephes* abundances, while years with the lowest mean temperatures had the lowest annual *Bythotrephes* abundances. From 1999–2007, the mean annual epilimnetic temperature observed in Lake Simcoe from July through October varied from 18.7 to 21.6 °C (mean ±1 SE across all years was 19.8 ± 3.4 °C), which was higher than temperatures at which peak *Bythotrephes* population densities occurred in Lake

Michigan (i.e., 14.6 ± 0.9 °C; Cavaletto et al. 2010), but remained well within the range of *Bythotrephes* preferences and physiological tolerances (Garton et al. 1990, Kim and Yan 2010, Kerfoot et al. 2011). Temperature could be influencing *Bythotrephes* population growth by affecting hatching rates (Yurista 1992, Brown and Branstrator 2011), rates of reproduction (Yurista 1992, Burkhardt 1994, Manca et al. 2007, Brown and Branstrator 2011), feeding (Schulz and Yurista 1999, Yurista et al. 2010), and/or individual development (Lehman and Branstrator 1995). Additionally, high annual *Bythotrephes* abundance could be the result of warmer temperatures preventing cold-water planktivores from foraging into the epi- or upper metalimnion where *Bythotrephes* is likely situated (Young et al. 2009).

Bythotrephes seasonal phenology

The *Bythotrephes* seasonal abundance phenology most frequently observed in Lake Simcoe demonstrated a bimodal pattern, with an increase in summer followed by a late summer decline and a subsequent increase in the fall in most years. Four *Bythotrephes* phenologies were observed to occur among the 9 years and were grouped based on differences in the date of occurrence of peak abundance and midseason decline. Secchi depth and TP in August and September significantly predicted groups of years with differing seasonal *Bythotrephes* abundance patterns. Secchi depth discriminated among all 4 groups, while TP discriminated between only 2 of the groups ("July" and "October").

Groups of years were usually positively associated with Secchi depth at a time when it was deeper than 5 m and *Bythotrephes* abundance was increasing or at a maximum, and negatively associated when Secchi depth was shallower than 5 m and *Bythotrephes* abundance was at a minimum. This suggests that 5 m is an important Secchi depth for *Bythotrephes* abundance patterns in Lake Simcoe. The link to TP was less clear because both a positive association and high TP (the "July" group) and a negative association and low TP (the "October" group) coincided with decreased *Bythotrephes* abundance.

Secchi depth, a measure of water transparency, is affected by algae, suspended sediment, and coloured organic matter (Young et al. 2010). *Bythotrephes* is a visual predator whose reaction distance to detect prey and feeding rate is strongly affected by light intensity, decreasing rapidly below 9–10 µmol m^{-2} s^{-1} (Muirhead and Sprules 2003, Pangle and Peacor 2009); thus, variations in light penetration could have significant effects on *Bythotrephes* abundance. We currently have neither an estimate of how light intensity varies with Secchi depth in Lake Simcoe nor any information on

daytime vertical distribution of *Bythotrephes* to discern the light intensity–depth combination at which *Bythotrephes* predation is optimal in Lake Simcoe. In a previous study, Young and Yan (2008) related the presence of lake herring with *Bythotrephes* vertical position in 6 Canadian Shield lakes. They found that *Bythotrephes* median vertical position when lake herring was present was near the top of the metalimnion, roughly 2 m above the Secchi depth and 6 m above the depth at which light reached 9 µmol m^{-2} s^{-1}, a position suggested as optimal due to the decrease in *Bythotrephes* overlap with its cold-water planktivore. When lake herring was not present, *Bythotrephes* migrated close to the 9 µmol m^{-2} s^{-1} depth, which Young and Yan proposed was a trade-off for maximizing its feeding rate and avoiding warm-water predators. Because Lake Simcoe contains lake herring, *Bythotrephes* would be expected to position itself at the top of the metalimnion; however, while Secchi depths were similar, the metalimnion was much deeper in the larger Lake Simcoe (N.E. Kelly, data not shown), suggesting that variations in light penetration relative to *Bythotrephes*' vertical position could have a much greater influence on populations in Lake Simcoe than in smaller lakes. Secchi depths shallower than 5 m could affect its ability to detect and capture prey, even if sufficient prey resources were available, and could contribute to the differences in the abundance patterns observed among years. A Secchi depth threshold of 5 m observed in our study thus likely represents the depth where light is at a critical intensity for *Bythotrephes* in summer months in Lake Simcoe.

Midseason population declines in *Bythotrephes* abundance have been observed to occur in the Great Lakes (Barbiero and Tuchman 2004, Cavaletto et al. 2010), constructed reservoirs in Minnesota, USA (Brown et al. 2012), and also occasionally in Canadian Shield lakes (Young et al. 2011). Cavaletto et al. (2010) suggested that the midsummer decline in *Bythothrephes* abundance observed in Lake Michigan was driven by intense fish predation pressure, while Brown et al. (2012) suggested population crashes were due to prey limitations. In Lake Simcoe, our results suggest that poor light penetration could also be responsible for a midseason decline in *Bythotrephes* abundance, at least in some years. Additionally, while seasonal prey abundance was not a significant predictor of differences in *Bythotrephes* seasonal phenologies among years in our study, limiting food supply could be contributing to the midseason *Bythotrephes* population decline in Lake Simcoe if it occurs concurrently with periods of low light penetration. For example, years with low cladoceran abundance and low light penetration in August and/or September (i.e., 2000, 2001, 2004, or 2006) may have led to larger midseason declines or crashes in *Bythotrephes* abundance. Some of

the variations in *Bythotrephes* seasonal phenology could also be due to variability in fish predation, although we currently have no information on the seasonal abundance of warm- and cold-water planktivores.

Bythotrephes typically recruits from diapausing (resting) eggs in May (Yurista 1992, Jarnagin et al. 2004, Young 2008), yet *Bythotrephes* was not observed in pelagic samples in Lake Simcoe until June or July. The apparent absence of *Bythotrephes* in May and June may be related to low spring prey abundance because cladoceran abundance routinely did not begin increasing in the lake until June. Spring prey availability has been indicated as an important factor influencing *Bythotrephes* abundance in Muskoka lakes (Young et al. 2011). Intense predation on *Bythotrephes* in spring months could depress abundances and significantly delay the *Bythotrephes* population peak, although there is currently a paucity of information on seasonal variations in the diets of planktivorous fish in the lake. In *Bythotrephes*, resting eggs are viable for less than a year (Andrew and Herzig 1984); thus, the current year's egg bank is composed primarily of resting eggs deposited in the preceding year. Inadequate hatching conditions in the benthos in spring months, such as low dissolved oxygen levels, light levels, or temperature, may delay the onset of *Bythotrephes* emergence from resting eggs or contribute to low hatching success rates (Herzig 1985, Yurista 1997, Brown 2008, Brown and Branstrator 2011). Finally, the later season start may be an artifact of sampling offshore in a deep lake. If *Bythotrephes* begins hatching in shallow, nearshore areas (e.g., Cavaletto et al. 2010), abundances at our deep, offshore sampling stations would be below the detection limits for the sample size used in our study for these dates.

Bythotrephes life-history characteristics

Seasonal fluctuations in *Bythotrephes* body length across instars were evident in most years, possibly the result of the interplay between temperature, availability of prey, and predation by planktivorous fish (Ketelaars et al. 1995). The increase in *Bythotrephes* body length in July and August observed in some years may be related to higher epilimnetic temperatures elevating *Bythotrephes* food consumption (Burkhardt 1994, Ketelaars et al. 1995, Yurista et al. 2010). In all years, mean epilimnetic temperatures increased from 10 °C in May to 20–22 °C by August. An elevated feeding rate at higher temperatures, combined with the high availability of cladoceran prey in June and July, could explain the growth of *Bythotrephes* in July and August.

A midseason decrease in body size across instars was observed in some years, which often coincided with the decline in population abundance, and may be related to a combination of prey scarcity and planktivorous fish predation. Decreasing body size can be indicative of prey limitation (Pothoven et al. 2001, Yurista et al. 2010). Cladoceran abundance declined by 1–2 orders of magnitude from its spring population maximum by August–September in all years (except 2007), which generally preceded the decline in *Bythotrephes* body and population size. A combination of low prey availability and ineffective *Bythotrephes* predation due to poor light penetration through the water column in August and/or September could result in concurrent declines in *Bythotrephes* body length and population size. As seen in other lakes, however, predation by planktivorous fish at this time (Coulas et al. 1998, Pothoven et al. 2001, Jarnagin et al. 2004, Pothoven and Vanderploeg 2004, Young and Yan 2008, Young et al. 2009) may also be contributing to the midseason change in *Bythotrephes* body size in Lake Simcoe. The concurrent recovery of body and population size in the fall months in some years may be related to the recovery of cladoceran prey abundance and/or reduced or relaxed fish predation pressure (Pothoven et al. 2001). A longer duration of the thermal stratification phase and greater water column stability in the fall (Stainsby et al. 2011), however, combined with increases in light penetration through the water column, could also create favourable conditions increasing *Bythotrephes*' body and population size at this time.

In all years, the mean lengths of instars II and III converged on multiple dates within a season, most frequently in August and September, but also occasionally in July and October. The convergence of instar II and III body sizes has been attributed to prey scarcity (Yan and Pawson 1998), size-selective fish predation (Pothoven et al. 2001), or an energetic trade-off between growth and reproduction (Branstrator 2005, Young 2008). There is currently no evidence to support size-selective feeding by fish on *Bythotrephes*; warm-water species have not been examined and cold-water species were found not to be selective (Coulas et al. 1998, Young 2008). While cladoceran prey abundance was often low in August and September, *Bythotrephes* body sizes also converged on dates when cladoceran prey was high. The body sizes of instars II and III are often similar when active reproduction is occurring (Branstrator 2005, Young 2008). On dates when the body size of instars II and III converged, *Bythotrephes* abundance was often increasing or high, particularly for dates earlier and later in the season, and parthenogenic broods were almost always observed on these dates. Thus, the energetic tradeoff between growth and reproduction may be the factor responsible for the convergence of body sizes of instars II and III observed in Lake Simcoe.

Seasonal reproductive patterns were difficult to discern because spring dynamics were not captured due to the low numbers of *Bythotrephes* collected at this time. In most years, however, parthenogenic clutch size was lowest in August, ranging from ~2 to 3 embryos per clutch. Similar parthenogenic clutch sizes in summer have been observed previously for *Bythotrephes* in Harp Lake (Young 2008), Lake Michigan (Pothoven et al. 2001, 2003), and European lakes (Straile and Halbich 2000) and reservoirs (Ketelaars et al. 1995). Resting eggs are typically produced at the end of the *Bythotrephes* seasonal cycle (Yurista 1992), and in Lake Simcoe occurred in the fall in most years, but they were also observed to occur in spring and summer in some years. The lack of males observed in the population during the spring and summer, despite the production of resting eggs at this time may be due to a sampling artifact, such that males are rare and only occur during short periods of the season, and thus not likely to be observed in samples collected during periods of low *Bythotrephes* abundance (Ketelaars et al. 1995). The pulsed production of resting eggs throughout the spring and/or summer months could provide re-entry into the population in the fall, allowing longer seasonal persistence. Earlier seasonal production of resting eggs may also allow *Bythotrephes* to avoid periods of unfavourable growth, such as poor water clarity, low prey availability, and/or high predation rates.

Consequences of *Bythotrephes* invasion to Lake Simcoe

The primary concern regarding *Bythotrephes* invasion in Lake Simcoe is the disruption of food web pathways and energy flow through the ecosystem. The interannual variability in *Bythotrephes* abundance and seasonal variability in body size and abundance phenology observed herein could affect the Lake Simcoe food web through *Bythotrephes'* predatory impacts on zooplankton prey and the subsequent diversion of energy away from higher trophic levels (Dumitru et al. 2001, Strecker and Arnott 2008, Foster and Sprules 2010). For example, *Bythotrephes* change from large body size and abundance to smaller and less abundant midway through the season, which may allow cladoceran species a temporal refuge from predation. This could generate a pattern of classical predator–prey density cycles (e.g., Brown et al. 2012) that could result in highly variable zooplankton abundances throughout the season. Many species of fish depend on crustacean zooplankton as their primary food source, particularly during the larval stages in the summer months. In years when present in summer months, highly abundant, large-bodied *Bythotrephes* may outcompete small, gape-limited, planktivorous fish for prey (Garton et al. 1993, Barnhisel and Harvey

1995, Compton and Kerfoot 2004, Jarnagin et al. 2004), which could affect fish recruitment and biomass in Lake Simcoe. In turn, top predators (e.g., lake trout, walleye) will be impacted if the abundance of their primary or preferred prey items (e.g., lake herring, rainbow smelt) are affected by changes in the abundance or biomass of lower trophic levels. Conversely, if peak *Bythotrephes* abundance coincides with peak planktivorous fish abundance, zooplankton standing stocks could be severely reduced, which could affect water quality due to reduced herbivory.

Over the past several decades, improvements in Lake Simcoe's water quality and clarity, due to reductions in TP loading (Winter et al. 2007) and the establishment of zebra mussels in 1996 (Eimers et al. 2005, Winter et al. 2011) as well as alterations to the lake's thermal regime (Stainsby et al. 2011), may have facilitated the successful establishment of *Bythotrephes* since its invasion. In Lago Maggiore, Italy, changes in lake trophy due to phosphorus abatement, as well as lengthening of the thermal stratification phase, has been shown to increase *Bythotrephes* density and seasonal duration (Manca et al. 2007). Increasing *Bythotrephes* populations with lake reoligotrophication has been observed in other European lakes where *Bythotrephes* is native (reviewed in Therriault et al. 2002). In Lake Simcoe, continued reductions in TP loads (Winter et al. 2007, Young et al. 2010), combined with an increasing duration of thermal stratification and longer ice-free season (Stainsby et al. 2011), could result in larger *Bythotrephes* populations with a greater seasonal persistence, exacerbating its effects on the lake's food web in the future.

Conclusions

Bythotrephes has successfully established in Lake Simcoe since it was first detected in 1993. Both top-down and bottom-up variables, specifically epilimnetic temperature and predator and prey availability, were identified as significant factors associated with *Bythotrephes* annual abundance. Secchi depth and TP concentrations in the late summer and early fall predicted differences in *Bythotrephes* seasonal abundance patterns among groups of years, lending further support to the role of water clarity as a significant component of *Bythotrephes* habitat in the invaded range. *Bythotrephes* body size and reproductive patterns also varied seasonally, which could possibly reflect the seasonal availability of cladoceran prey, predation pressure from planktivorous fish, or perhaps adaptations to avoid unfavourable conditions and persist in an environment atypical of its native range (i.e., deep, clear, oligotrophic lakes; Grigorovich et al. 1998, MacIsaac et al. 2000). Overall, a complex interaction of fish predation, food availability, temperature, and water clarity controls the dynamics of *Bythotrephes* in Lake

Simcoe. Changes to the Lake Simcoe ecosystem due to *Bythotrephes* invasion may have significant consequences for the lake's ecology and the ecosystem services it provides.

Acknowledgements

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