

Comparing annual population growth estimates of the exotic invader *Bythotrephes* by using sediment and plankton records

Roland I. Hall¹ and Norman D. Yan

Ontario Ministry of Environment and Energy, Aquatic Science Section, Dorset Research Centre,
POB 39, Dorset, Ontario POA 1E0

Abstract

The annual population growth of the exotic invader *Bythotrephes cederstroemi* was calculated from the spatial distribution and rate of accumulation of its diagnostic caudal processes in the sediments of Harp Lake, Ontario. To our knowledge, this is the first use of the sediment record to quantify the annual population growth of a zooplankton species on a whole-lake scale with confidence estimates. In 1994, 553 ± 254 (95% C.L.) animals m^{-2} were produced in Harp Lake, an estimate statistically indistinguishable from that developed independently from the plankton data and temperature-dependent growth models (459 animals m^{-2}). When annual population growth estimates will suffice, the sediment record offers several advantages. It requires less fieldwork than do plankton-based approaches and requires the quantification of the means and variances of fewer parameters. It also can provide population growth estimates for the past. For example, the sediment record indicated that one-third of all *B. cederstroemi* ever produced in Harp Lake predated the start of our plankton records in 1994. The sediment record may have other uses. The breakage of caudal processes may provide clues to the rates of fish predation on *B. cederstroemi*, suggesting, for example, that 40% of the Harp Lake *B. cederstroemi* were eaten by fish in 1994.

Bythotrephes cederstroemi Schoedler (Cercopagidae, Onychopoda) is a large, predaceous, Palearctic cladoceran zooplankton that successfully invaded each of the Laurentian Great Lakes during the mid-1980s (reviewed by Garton et al. 1993). Soon thereafter, the invader spread inland from the Great Lakes. Yan et al. (1992) reported *B. cederstroemi* in eight lakes in southern Ontario and three lakes in Minnesota. Since 1993, *B. cederstroemi* has been reported from eight other lakes in Ontario, bringing its known distribution in the province to 16 inland lakes in five tertiary watersheds. Given its European distribution in lakes that range widely in size, hardness, acidity, color, trophic status, and fish assemblages (Nilsson and Pejler 1973; Hobaek and Raddum 1980; Naesje et al. 1987), there is little doubt that *B. cederstroemi* will continue to spread across North America.

If sufficiently abundant, *B. cederstroemi* can change the behavior, standing stocks, and size composition of its zooplankton prey (Lehman and Caceres 1993). Hence, the inevitable spread of *B. cederstroemi* in temperate North America is of concern because the invader might indirectly alter water clarity (Lehman 1988), fish yields (Warren and Lehman 1988), and contaminant partitioning (Fontaine and Stewart 1992), primarily through its effects on zooplankton (Lehman and Caceres 1993; Yurista and Schulz 1995; Lehman and Branstrator 1995). Unfortunately, we have no knowledge at present of the impacts of *B. cederstroemi* on inland lakes and their food webs.

¹ Present address: Department of Biology, University of Regina, Regina, Saskatchewan S4S 0A2.

Acknowledgments

We thank Trevor Pawson for assistance and advice in the laboratory and field, and for preparing Figs. 1 and 3. Martyn Futter generously provided statistical advice. R.I.H. was supported by a NSERC postdoctoral fellowship. Peter Dillon, John Smol, and Gary Sprules provided helpful comments on an earlier draft. We thank the two anonymous reviewers for their constructive comments.

To predict the significance of the invasion, we must quantify the linkages between *B. cederstroemi* and its prey. Information on the bioenergetics, prey preferences, and population growth of the predator are required. Knowledge of the bioenergetics (Yurista 1992; Yurista and Schulz 1995; Lehman and Branstrator 1995) and prey preferences of *B. cederstroemi* (Vanderploeg et al. 1993; Schulz and Yurista 1995; G. Sprules pers. comm.) is growing rapidly. Here, our intent is to provide a first estimate of the population growth of *B. cederstroemi* in inland waters. We operationally define population growth as the accrual of numbers of animals per unit time.

Estimates of two parameters are needed to calculate population growth over a time interval—the abundance of all developmental stages during the interval and their duration of development (Rigler and Downing 1984). Because both of these parameters are difficult to estimate with accuracy at present, few population growth calculations of *B. cederstroemi* exist.

Temporal and spatial distribution patterns must be known in order to estimate abundance. The latter is not routinely quantified; hence, confidence bounds for abundance often cannot be constructed. This lack of attention to spatial heterogeneity is an old problem for zooplankton population biologists (Prepas and Rigler 1978; Lynch 1982). However, this problem may be particularly severe for *B. cederstroemi* because there is anecdotal evidence of significant spatial heterogeneity for the invader at several scales, including the 1-10-m scale (C. Charon pers. comm.) and the 25-100-m scale (N. Hutchinson pers. comm.).

The duration of developmental stages is also difficult to estimate because cohorts of *B. cederstroemi* are not discernible in the field. In such situations development times of zooplankton are usually estimated from temperature-dependent growth models (Rigler and Downing 1984). Data needed to construct such models exist for embryonic *B. cederstroemi* (Yurista 1992), but very few data are available for

postembryonic, free-living stages (Lehman and Branstrator 1995). Furthermore, the assumption that temperature is the sole determinant of growth for embryonic *B. cederstroemi* needs testing. Unlike most cladocera, *B. cederstroemi* deposits tiny, yolk-free eggs in brood pouches, bathing embryos in nutritive secretions during development. Hence, both maternal nutritional status and temperature might influence embryonic development in nature. Of course, both temperature and food influence the growth and development of the feeding stages of zooplankton (Lynch 1980), but temperature- and food-dependent models of growth have not been developed for the free-living stages of *B. cederstroemi*. In summary, critical gaps in knowledge currently hamper calculations of the population growth of *B. cederstroemi* with traditional, plankton-based approaches.

There may be a nontraditional solution to this problem if annual population growth estimates will suffice. Population growth may be calculated from the accumulated deposition of the distinctive caudal processes of *B. cederstroemi* to lake sediments. Our primary objective is to employ the sediment record to quantify the population growth of *B. cederstroemi* in Harp Lake, a recently invaded lake in south-central Ontario, Canada. We compare this sediment-based population growth calculation to an estimate developed by conventional means, i.e. using temporal and spatial plankton data combined with a temperature-dependent growth model for *B. cederstroemi* (Yurista 1992; Lehman and Branstrator 1995).

We can estimate *B. cederstroemi* population growth from the rate of accumulation of its caudal processes in lake sediments if we can date the sediments sampled, numerically link population growth with the abundance of caudal processes, assume (whatever the cause of mortality) that the caudal processes are deposited in lake sediments in a recognizable state, demonstrate that the caudal processes remain recognizable after deposition, and quantify the pattern of caudal process deposition on a whole-lake scale.

The first three of these assumptions are not a concern in this study. *B. cederstroemi* first appeared in the plankton of Harp Lake in 1993. During the early stages of colonization, the total sedimented pool of *B. cederstroemi* caudal processes grows relatively rapidly; hence, the difference between late autumn and early spring densities of caudal processes in bulk sediments can provide the annual population growth increment. Consequently, the sediments need not be dated. Second, each animal can contribute only one caudal process at most to the sediment record because *B. cederstroemi* produces only a single caudal process during its life, adding articular segments to it at most juvenile moults (Yurista 1992; terminology of the caudal process and fragments follows Martin and Cash-Clark 1995). Third, intact *B. cederstroemi* caudal processes or recognizable fragments of them are found in the lower intestine of numerous fish species (Schneeberger 1991). Hence, identifiable portions of the caudal processes are assumed to survive gut passage.

Here we address the last two assumptions. We determine what proportion of the sedimented caudal processes can be detected after a summer's incubation under simulated hypolimnetic conditions. We also quantify the spatial distribution of caudal processes in the sediments of Harp Lake in the early spring and late fall of 1994. Once the spatial dis-

tribution of caudal processes in the sediments and their degree of preservation is known, annual population growth is readily estimated.

We have four objectives: to determine if the caudal processes of *B. cederstroemi* or their fragments remain recognizable after a season of incubation under simulated hypolimnetic conditions; to describe the spatial distribution of the caudal processes in the sediments of Harp Lake; to calculate the annual population growth of *B. cederstroemi* in the lake from the abundance of caudal processes in the sediments; and to compare population growth estimates generated independently from sediment and plankton data, as well as the strengths and weaknesses of each method.

Site description

Harp Lake is a single-basin lake with an area of 71.4 ha, a mean depth of 12.4 m, and a maximum depth of 37.5 m. It is a soft-water (conductivity, 35 $\mu\text{S cm}^{-1}$), nonacidic (pH 6.3), oligotrophic lake (total phosphorus, 8 $\mu\text{g liter}^{-1}$) used primarily for recreation. Although the lake is ringed by cottages, the catchment is forested. Dillon et al. (1987) and Molot and Dillon (1991) provided additional details on the geologic setting, acid-base chemistry, and trophic state of the lake.

The zooplankton of Harp Lake have been sampled on a biweekly basis during the ice-free season since 1977 (Yan 1986). The lake supports a rich zooplankton fauna because of its well-oxygenated hypolimnion and presence of glacial relict copepods. Twenty-four crustacean taxa have been identified >10 times since the record began (Yan et al. 1996). The zooplankton community was stable (Yan et al. 1996) before the *B. cederstroemi* invasion.

Bythotrephes cederstroemi was first detected in summer 1993, 2 yr after it was reported in the much larger Peninsula Lake, immediately downstream (Yan et al. 1992). Given the historical regularity of the Harp Lake sampling, the invasion probably did not precede our detection by more than a year.

Methods

Sediment sampling and analysis- Thirty-six sites were selected by means of a stratified random sampling design (Krebs 1989). With no foreknowledge of the spatial distribution of caudal processes in the sediments, we divided the lake into three regions with approximately equal areas of three depth zones (0-9, 9-23, and 23-38 m; Fig. 1). Four sample sites were randomly positioned within each of the resulting nine depth zone/lake region strata. A 37th site was located at the deepest spot in the lake. This site was the main sampling station from which historical water and plankton samples had been collected (Yan 1986; Dillon et al. 1987).

Surface-sediment samples were collected twice in 1994 at each site, once on 25 May or 2 June, then again on 10 or 11 October. The spring period was selected to precede the appearance of *B. cederstroemi* in the plankton, the fall period to follow its disappearance (Fig. 2).

Unconsolidated lake sediments were sampled using an Ekman box corer (15 X 15 cm). To prevent the loss of caudal

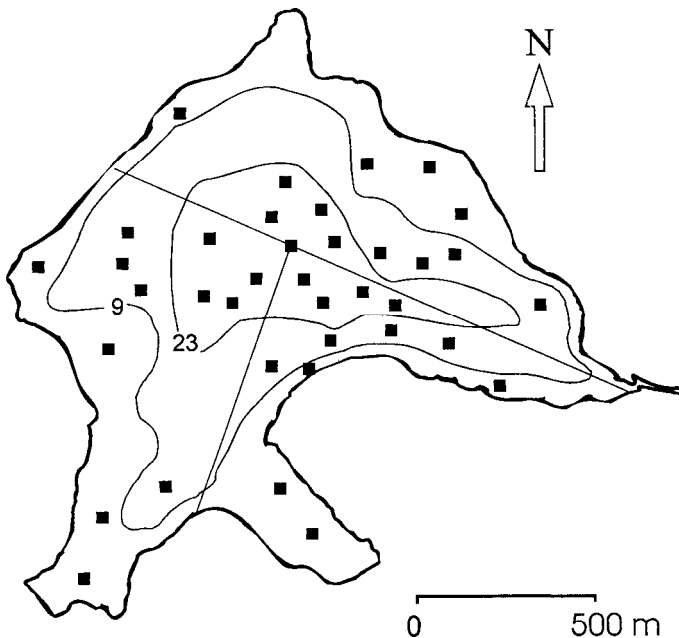


Fig. 1. Bathymetric chart of Harp Lake showing the location of the three lake regions, the three depth zones, and the 37 sediment sampling sites.

processes during sampling, we controlled the drainage of water from the surface of the corer by lifting it into the boat inside a water-filled bucket and keeping similar water levels in the Ekman box corer and bucket. Water from inside the Ekman was then slowly siphoned onto 250- μm mesh to collect any caudal processes suspended above the sediments. We used 250- μm mesh because the distance between the tips of the smallest set of paired articular spines on the caudal processes of Harp Lake *B. cederstroemi* exceeds 250 μm . Once the overlying water was drained, we removed the top 3 cm of the sediment. All samples were stored in polyethylene jars at 4°C in the dark until they were enumerated 2.5–11 months after collection.

The surface 3-cm layer represents the past 5–10 years of deposition in Harp Lake, based on radiometric (^{210}Pb) dating (Evans et al. 1986; P Dillon unpubl. data). Exponential declines in ^{210}Pb activities in surface sediments were characteristic of a depositional environment with little sedimentary mixing (Binford 1990). Additionally, that caudal processes were never found in sediments below 3-cm depth indicates they were not mixed into deeper sediments.

Bythotrephes cederstroemi caudal processes apparently preserve well in sediments from the Laurentian Great Lakes (Keilty 1988). However, several agents can contribute to the degradation of plankton remains in lake sediments, including mechanical or abrasional forces, chemical dissolution, and fragmentation, digestion and decomposition by biota. Consequently, most organisms do not leave sedimentary records from which rates of population growth can be readily calculated (Kerfoot 1995).

To determine the proportion of caudal processes of *B. cederstroemi* that could be recovered after a season of incubation under simulated hypolimnetic conditions, we performed

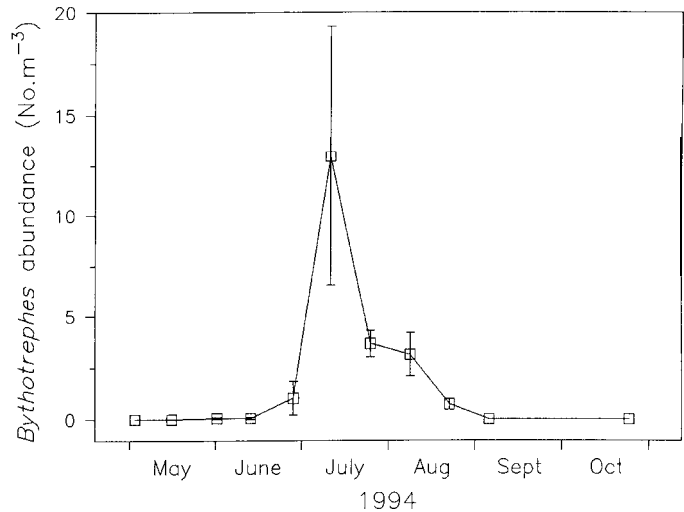


Fig. 2. Abundance of *Bythotrephes cederstroemi* (arithmetic mean \pm 1 SE, $n = 10$ per date) in the plankton of Harp Lake during 1994.

a “spike-recovery” experiment. We collected deep (>5 cm), caudal process-free sediment samples from four sites in the lake that differed in overlying water depth (5–35.5 m) and sediment type [organic sediment (gyttja) to sand]. A known number (Table 1) of heat-killed, physically intact *B. cederstroemi* with one-, two-, or three-articular class caudal processes were added to duplicate 500-ml polyethylene jars from each site. Each jar contained, by volume, two-thirds sediment and one-third filtered (250 μm) water from the lake. The jars were incubated for 4.5 months in the dark at 4°C to simulate lake bottom conditions. The duration of incubation exceeded the 1994 *B. cederstroemi* growing season (Fig. 2). The overlying water in the jars never became anaerobic. Live benthic invertebrates, including chironomids, *Pontoporeia*, and *Mysis relicta*, were retrieved from the jars when the experiment was terminated. Caudal processes were observed on the sediment surface at the end of the experi-

Table 1. Data from the spike-recovery experiment showing the number of one-, two-, and three-articular class *Bythotrephes cederstroemi* individuals added and the number of caudal processes retrieved after incubating them in caudal process-free, aerobic Harp Lake sediment at 4°C in the dark for 4.5 months.

Sample	Sedi- ment type	No. ind. added (articular class)			No. caudal processes retrieved (articular class)			% Broken tips	% recovered
		1	2	3	1	2	3		
1A	Gyttja	5	3	8	5	3	7	0	93.8
1B	Gyttja	4	3	9	4	2	7	2	93.8
2A	Gyttja	5	4	7	4	4	5	1	87.5
2B	Gyttja	3	4	9	2	3	8	0	81.2
3A	Gyttja	4	4	8	3	2	8	0	81.2
3B	Gyttja	4	4	9	3	4	9	1	100.0
4A	Sand	3	5	8	4	6	3	2	93.8
4B	Sand	5	6	5	3	4	4	0	68.8

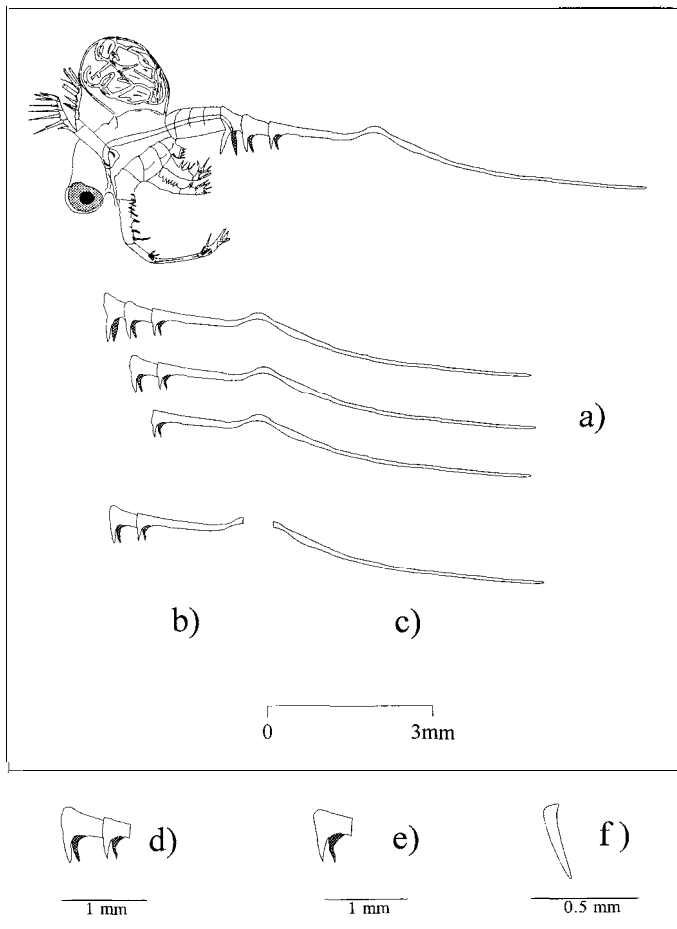


Fig. 3. Sketch of *Bythotrephes cederstroemi* illustrating common sites of fragmentation of caudal processes retrieved from sediment samples: [a.] intact one-, two-, and three-articular class caudal processes; [b.] caudal process (with paired articular spines) broken beyond the characteristic kink; [c.] caudal-process tip; [d.] isolated articular segment; [e.] paired articular spines; [f.] individual articular spine. The number of *B. cederstroemi* represented by caudal processes and fragments = $a + b + (c - b)$, if $c - b > 0$. Terminology follows Martin and Cash-Clark (1995). Modified from Burkhardt (1994).

ment, suggesting that these organisms caused minimal bioturbation.

To retrieve and enumerate *B. cederstroemi* caudal processes from the lake-sediment and spike-recovery samples, we enhanced their visibility by adding 1 ml of red dye (10 g liter⁻¹ Eosin B, 10 g liter⁻¹ Biebricht Scairet) to each sample at least 4 h before processing. Samples were then sieved through 250- μ m mesh, and caudal processes and their fragments (Fig. 3) were identified and enumerated at 10X magnification using a Nikon SM-Z10 microscope.

We performed a repeated measures ANOVA followed by Tukey's HSD multiple comparisons test to quantify the spatial and temporal distribution of caudal processes in the sediments. In particular, we determined if sampling season (spring vs. fall), depth zone, and lake region explained variability in caudal process abundances. Data from the main

station were excluded from this analysis because they could not be assigned to a unique lake region (Fig. 1). This analysis also permitted us to select the most appropriate method of estimating the mean and variance of the population growth estimates on a whole-lake scale, i.e. to select the most appropriate strata for calculating the descriptive statistics.

Bythotrephes cederstroemi population growth during 1994 was calculated from the difference between the abundance of caudal processes in pairs of fall and spring samples at each site. Caudal process abundances in the spring samples were used to estimate the population growth prior to 1994. We assume that most of the pre-1994 population growth was in 1993, the year *B. cederstroemi* was first observed in the lake.

Plankton sampling and analysis—With no foreknowledge of the spatial distribution of *B. cederstroemi* in the plankton of the lake, we used a stratified random sampling design. We visited the lake during daylight hours at regular intervals on 11 occasions between 5 May and 21 September 1994. By early September, *B. cederstroemi* had disappeared from the plankton. We returned to the lake in late October and confirmed the absence of *B. cederstroemi* from the plankton. On each visit one station was randomly located in each of the three depth zones in the three regions of the lake (Fig. 1). The main station was also visited, providing 10 stations per visit.

At each of the 10 stations a single vertical haul from 2 m above the lake bottom to the surface was taken with a 0.75-m-diameter closing tow net with a 1-m-long cylindrical closing section over a 1.5-m-long cone. Both sections were constructed of 285- μ m mesh with a porosity of 55%, providing an open area ratio (porosity X filtering area/mouth area) for the net of 5.2:1. The net was equipped with a Rigosha flowmeter. Filtration efficiencies averaged 88% and were used in the calculation of sample volumes. A total of 54.2 m³ of lake water (range, 47.4–63.5) was sampled in the 10 vertical hauls during each visit to the lake.

To assess the vertical distribution of *B. cederstroemi*, we combined 1994 and 1995 data. The closing net was used to collect separate vertical hauls through the epi-, meta-, and hypolimnion of the lake at five open water stations on a single date in July 1994 and on a biweekly basis from late June to the end of August 1995 at the main station.

All samples were examined for *B. cederstroemi* with a semiautomated counting system (Allen et al. 1994). Individuals were counted, sexed, and sized. The numbers of pairs of articular spines on the caudal process were recorded following Burkhardt's (1994) nomenclature. The caudal process was categorized as kinked or straight to determine whether the individual had emerged from gametogenic or parthenogenic eggs (Yurista 1992). We recognized five stages of development of parthenogenic broods following Yurista's (1992) nomenclature: females with no brood pouches, early brood pouches, large embryos with unpigmented eyes, red-eyed embryos, and black-eyed embryos. Clutch sizes of red-eyed and black-eyed broods were recorded. The incidence and clutch sizes of resting egg broods were logged sepa-

Table 2. Summary of caudal-process data from the spike-recovery experiment and spring and fall sediment samples taken from Harp Lake during 1994.

Caudal process class and summary statistics	Spike-recovery exp.	Spring samples	Fall samples
No. intact one-articular class caudal processes	28	56	134
No. intact two-articular class caudal processes	28	41	125
No. intact three-articular class caudal processes	51	17	55
No. caudal processes with breakage	6	85	254
No. animals represented	113	199	568
% Breakage	5.3	42.7	44.7
Min No. animals sample ⁻¹	—	0	2
Max No. animals sample ⁻¹	—	37	48
Sample size	8	37	37

rately. Data were managed in a relational database by using ORACLE (Pawson and Yan 1993).

To estimate the population growth of *B. cederstroemi* from the plankton data, we restricted our attention to animals produced by parthenogenesis because only a single gametogenic female (with a straight caudal process) was observed during 1994. The 1994 population growth of parthenogenic animals (P in animals m^{-2}) was estimated as

$$P = \bar{z}NSD_p^{-1}. \quad (1)$$

\bar{z} is the mean lake depth (in meters), N is the abundance of parthenogenic neonates on a whole-lake scale (in neonates m^{-3}), and S is the length of the 1994 *B. cederstroemi* season (in days). The season was assumed to be the 84-d interval from 15 June to 7 September, i.e. from the sampling visit before to the visit after the observation of *B. cederstroemi* of parthenogenic origin in the water column (Fig. 2). Their development time from parturition to primiparity (in days) is calculated as $D_p = 0.268/(0.00178T - 0.0069)$ (from Lehman and Branstrator 1995), where T is the temperature.

To select the most appropriate method to estimate N , we determined the spatial distribution of animals in the lake. We submitted counts of *B. cederstroemi* from all stations and dates to a randomized block ANOVA to determine which among sampling date, region, and depth zone of the lake accounted for significant variability in abundances. The main station data were excluded from this analysis because they could not be assigned to a unique lake region (Fig. 1).

Results

Spike-recovery experiment—Entire, heat-killed *B. cederstroemi* were used in the spike-recovery experiment, but only their caudal processes were retrieved from the jars. All soft body parts had disappeared during the 4.5-month incubation. In contrast, the retrieved caudal processes showed no signs of dissolution under the simulated hypolimnetic conditions of dark and cold, despite the presence of both macro- and microbiota in the sediments. A small percentage of the caudal processes were broken when enumerated (mean, 5.3%; range, 0-13%; Table 2).

Caudal processes from nearly all animals added to each jar were recovered (mean, 87.5%; Table 1). This high rate

of recovery indicates that our search image and retrieval methods for caudal-process fragments were sound. The recovery of caudal processes ranged from 69 to 100% (Table 1). The sample with the lowest recovery was full of fungal hyphae that surrounded many caudal processes, perhaps obscuring some from view. We included the data from this sample because we also observed fungal hyphae in the regular sediment samples.

Caudal process preservation and distribution in sediments—Caudal processes and fragments were well preserved in all sediment samples, exhibiting no visible signs of dissolution. However, many caudal processes were broken. Several classes of caudal-process fragments were retrieved, including intact one-, two- and three-articular class caudal processes, caudal processes (with paired articular spines) that were broken beyond their characteristic kink, caudal-process tips (the portion beyond the kink), isolated articular segments, paired articular spines, and individual articular spines (Fig. 3). On average, 43% of the spring population and 45% of the fall population of caudal processes were broken (Table 2). The spike-recovery experiment proved that most caudal processes were not broken during sample processing.

The number of animals (or their intact caudal processes) represented by caudal-process fragments in each sample was calculated as the sum of intact caudal processes (Fig. 3a) plus the number of caudal-process tips (Fig. 3c) retrieved in excess of caudal processes that were broken beyond their kink (Fig. 3b). Counts of caudal-process remains indicated that 199 *B. cederstroemi* were present in the spring samples and 568 were present in the fall samples (Table 2).

Caudal processes were roughly three times as abundant in the fall than in spring sediments in 1994 (Tables 2-4). Sediments therefore accumulated fossil remains of *B. cederstroemi* during the 1994 growing season. This result suggests that caudal processes can be used to estimate population growth during the year.

Caudal processes counts varied from site to site in the lake, from 0-37 per sample in spring to 2-48 per sample in fall (Table 2, Fig. 4). The variability was not attributable to the region of the lake sampled, but there were significant differences among depth zones (Table 3). Sites in the near-shore depth zone (0-9 m) collected on average twice as

Table 3. Summary of inferential statistics used to quantify the spatial and temporal distribution of *Bythotrephes cederstroemi* and its remains in the sediments and plankton of Harp Lake during 1994. Sediment data were analyzed with a repeated-measures ANOVA followed by Tukey's HSD multiple comparisons test. Plankton data were analyzed with a randomized block ANOVA.

Variable	Sediment data*			Plankton data				
	F	value	P	df	F	value	P	df
Sampling date†	25.08		<0.001	1	3.63		0.014	4
Depth zone	4.41		0.020	2	0.49		0.62	2
Region	0.21		0.808	2	0.66		0.52	2

* Interaction terms for depth zone × sampling date and region × sampling date did not account for significant variation ($\alpha = 0.05$) in the dataset.

† Sampling date refers to the spring vs. fall samples for the sediment data and biweekly sampling for the plankton data during the *Bythotrephes* season only (15 June-7 September 1994).

many caudal processes as did sites in the two deeper zones in both spring and fall (Fig. 4; Tables 3, 4).

Sediment-based B. cederstroemi population growth-We calculated *B. cederstroemi* population growth from the estimated abundances of animals deposited on the sediments by weighting the mean abundance of caudal processes in the three depth zones by the area of each zone (Table 4), assuming a recovery efficiency of 87.5% (Table 1). Errors were calculated as 95% C.L. following Krebs (1989).

From the spring caudal-process counts, we estimated pre-1994 *B. cederstroemi* population growth at 295 ± 159 animals m^{-2} . The difference between the fall and spring data provided a 1994 population growth estimate of 553 ± 254 animals m^{-2} . Therefore, about twice as many *B. cederstroemi* were produced in the lake in 1994 as in all previous years since the invasion.

Plankton-based B. cederstroemi population growth-The abundance of neonates was calculated as the product of the total densities of *B. cederstroemi* in the water column averaged over the season ($2.799 m^{-3}$), the proportion that were female (0.94) and carrying parthenogenic broods (0.56), and the mean clutch size of red-eyed and black-eyed broods (3.02 embryos clutch $^{-1}$). The resultant value (4.44 neonates m^{-3}) was apportioned among the epi-, meta-, and hypolimnia based on the average daytime distribution of animals among these layers (i.e. 80, 18, and 2%, respectively). Hence, we estimated there were 3.51, 0.84, and 0.08 animals m^{-3} on average in the epi-, meta-, and hypolimnion of the lake during the 1994 *B. cederstroemi* season.

The average temperatures in the epi-, meta- and hypolimnia during the 1994 *B. cederstroemi* season were 20.9, 12, and 5°C. From Yurista (1992, figure 6) and Lehman and Branstrator (1995), this provides hypothesized values of development times from parturition to primiparity of 8.85, 18.74, and 137.63 d. Production in the hypolimnion was ignored because these waters supported a tiny proportion of the population (2%), with estimated development times exceeding the length of the season. Neonates were replenished a calculated 9.49 times in the epilimnion and 4.48 times in the metalimnion during 1994.

Table 4. Summary of the area and the mean and standard error of *Bythotrephes cederstroemi* caudal-process abundances (based on an 87.5% rate of caudal-process recovery) in pre-1994 and 1994 sediment samples from three depth zones of Harp Lake used to calculate annual population growth and 95% C.L.s.

Depth zone (m)	Area (ha)	Mean abundance (caudal processes m^{-2})		SE (caudal processes m^{-2})	
		Pre-1994	1994	Pre-1994	1994
0-9	30.00	406.35	744.97	60.72	111.71
9-23	27.60	224.34	452.91	42.04	34.57
23-36	13.78	195.36	336.02	13.41	22.50
Whole lake	71.38	295.24	553.09	75.06	119.08

Harp Lake has a mean depth of 12.4 m. Hence, following Eq. 1, the plankton-based population growth estimate in 1994 was 459 animals m^{-2} . This value corresponds closely to the mean sediment-based estimate for the year (553 animals m^{-2}), and the difference between the estimates is within 17% of the sediment-based value. On the basis of the 95% C.L. about the sediment-based mean (299-807 animals m^{-2}), the plankton- and sediment-based population growth estimates are statistically indistinguishable. The 95% C.L.s include a relatively broad range of values ($\pm 54\%$ of the mean), but they are comparable to errors for plankton-based numerical abundance estimates of other cladocerans (which typically range from 240 to $>80\%$ of the mean-George and Edwards 1974; Makarewicz and Likens 1979; Swift and Hammer 1979).

Discussion

Accurate estimates of *B. cederstroemi* population growth are essential to calculate its impacts on aquatic food webs (Lehman and Caceres 1993). There are no published esti-

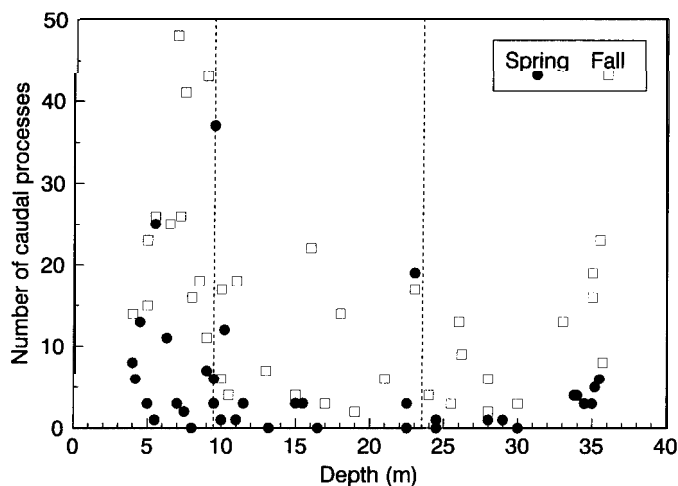


Fig. 4. Relationship between depth of overlying water and the number of caudal processes collected from the sediments of Harp Lake at the 37 sites in spring and fall 1994. Vertical dashed lines indicate boundaries between the three depth zones.

mates of the mean and variance of *B. cederstroemi* population growth in North American lakes because of the difficulty of estimating the distributional characteristics of the parameters needed for plankton-based calculations. To our knowledge, this study provides the first whole-lake annual *B. cederstroemi* population growth estimates with measures of confidence. Use of the sediment record permitted such estimates.

Lake sediments have rarely been used to quantify annual zooplankton population growth. Most species leave remains that are difficult to identify, and few investigators have linked population growth in plankton to rates of deposition and preservation of animal remains in lake sediments (Kerfoot 1995). Confirming Keilty's (1988) observation, we have shown that *B. cederstroemi* leave recognizable fossils in lake sediments—their caudal processes. The caudal processes were well preserved under simulated hypolimnetic conditions, and were largely retrievable after one growing season. Furthermore, the close agreement between annual *B. cederstroemi* population growth estimated independently from the plankton and sediment records indicates that caudal processes preserve a quantitative record of recent *B. cederstroemi* population growth in lakes. Therefore, the sediment record can provide the data needed to calculate annual population growth if the spatial distribution of caudal processes in the sediments is quantified.

In fact, for annual population growth estimates, the sediment-based approach has several advantages. First and most importantly, all the data needed for calculating population growth and the associated error were readily obtainable in two visits to the lake (i.e. the distribution, abundance, and recoverability of caudal processes). For plankton-based estimates, there are still critical knowledge gaps, especially concerning the influence of nutrition and temperature on embryonic and postembryonic growth rates (Yurista 1992; Lehman and Branstrator 1995), as well as the diurnal vertical distribution of free-living animals. Indeed, because temperature-dependent models of growth are based on very few data, we could not calculate confidence limits for the plankton-based population growth estimate.

Second, the sediments "sample" continuously, functioning as ongoing accumulators of data. Because lake sediments integrate temporal information, they may capture evidence of temporal patterns missed by traditional weekly or fortnightly plankton sampling programs. Continuous sampling may be especially critical during the summer, when epilimnetic *B. cederstroemi* populations may be turning over each week.

Third, sediment-based population growth estimates may integrate spatial patterns. Freshwater zooplankton are distributed heterogeneously at several spatial scales (Pinel-Aloul 1995) and *B. cederstroemi* is no exception. Both lake-scale (25-100 m or larger), wind-driven patchiness and smaller (meter)-scale behavioral patchiness have been described anecdotally (N. Hutchinson and C. Charon pers. comm.). The sediments can integrate ephemeral patchiness across the growing season, whereas massive sampling would be required to describe these patterns in the plankton as they occurred. For example, between 13 July and 26 August 1994, when *B. cederstroemi* was abundant in the plankton,

the variance/mean ratio for our 10 vertical hauls indicated that we needed between 8 and 25 samples on different dates to estimate the mean abundance of the population in the lake within 25% (Prepas 1984).

Because sediments serve as both spatial and temporal accumulators of data, field sampling required far less time and effort to estimate annual population growth from the sediments than from the plankton. In this study, the mean and variance of *B. cederstroemi* population growth was determined from 74 sediment samples collected during two visits to the lake. In contrast, we collected twice as many samples on a fortnightly basis to describe the daytime spatial and vertical distribution of *B. cederstroemi* in the plankton. However, the total time required for sorting the plankton and sediment samples was nearly equal. No plankton samples were collected at night, so the nocturnal vertical distribution in 1994 remains unknown. Furthermore, because we sampled only on a biweekly basis, it is possible that we missed the population peak (Fig. 2). Population growth estimates based on plankton methods and temperature-dependent growth models are extremely sensitive to these missing data.

Bythotrephes cederstroemi caudal processes will probably leave a reliable long-term record in lake sediments. In this study, caudal processes and their fragments showed no signs of dissolution after an 11-month incubation under simulated hypolimnetic conditions. Keilty (1988) demonstrated that caudal processes could be retrieved at least 4 years after they were deposited in Lake Michigan sediments. Of greater significance, Nilssen and Sandoy (1990) recorded remains of the related *B. longimanus* from the bottom of a 22-cm-deep sediment core from Lake Gulspettvann in Norway. Hence, it is a good assumption that caudal processes of *B. cederstroemi* should preserve in lake sediments for decades to centuries in many North American lakes. Consequently, it may be possible at any time to use the sediment record to assess the invasion dates and long-term impacts of *B. cederstroemi* on zooplankton communities. Plankton-based methods, in contrast, must be initiated immediately upon invasion by *B. cederstroemi* or else they miss the starting point, and sampling programs must be maintained thereafter.

At present, the sediment-based approach is most useful during the early stages of invasion by *B. cederstroemi* because, as we have shown, annual increments can be determined from bulked sediments. In some lakes, varved sediments permit accurate sediment dating at annual intervals, so our methods could be used to estimate annual population growth long after the invasion. However, the abundances of *B. cederstroemi* caudal processes are considerably lower (e.g. 550 m⁻²) than the pollen, algae, and herbivore fossils routinely investigated by paleoecologists (Warner 1990). Hence, our approach will not be adaptable to long-term paleoecological studies of *B. cederstroemi* dynamics until larger bore coring and core-sectioning equipment are developed.

If annual population growth estimates will not suffice, the plankton-based method must be used. In theory, plankton-based methods can be used to calculate the population growth of any recognizable life stage, as well as genders, articular classes, and gametogenic vs. parthenogenic animals. To date, the sediment-based method cannot provide this information because a large proportion (45%) of caudal

processes are fragmented when retrieved, and the various stages cannot as yet be identified from the sizes or appearances of the fragments (Fig. 3).

If we assume that the caudal processes of *B. cederstroemi* are broken when the animals are ingested by fish, then our data suggest that a significant portion of the mortality of *B. cederstroemi* is attributable to fish. In the lake sediment samples, 45% of the caudal processes were broken. In contrast, only 5% of caudal processes were broken in the spike-recovery samples. All samples were processed identically, so the difference is not a methodological artifact. Benthic macroinvertebrates from the lake survived the incubation period in the spike-recovery jars; therefore, the difference in breakage between the laboratory and field sediments is probably not attributable to the actions of benthos. The major difference between the laboratory and field samples is that we added intact *B. cederstroemi* to laboratory samples, whereas the field sediments collect whatever animals or their fragments rain down from the water column. Any fragmentation of caudal processes caused by the feeding of fish did not influence our spike-recovery samples, but could certainly have affected the field collections.

Differences in heterogeneity between the sediment and plankton records are consistent with the hypothesis that fish consume a significant amount of the *B. cederstroemi* produced. *B. cederstroemi* caudal processes were preferentially deposited in the nearshore (0-9 m) depth zone of Harp Lake (Fig. 4), but no such distribution was evident in the plankton (Table 3). Planktivorous fish may, in part, concentrate *B. cederstroemi* remains in the nearshore sediments because they are more abundant in the littoral vs. the pelagic zone of the lake (R. Coulas and W. Dunlop pers. comm.). Once established, *Bythotrephes* is a preferred prey item for many fish species (Fitzmaurice 1979; Bur and Klarer 1991; Schneeberger 1991). Several fish species common in Harp Lake are known to consume *B. cederstroemi*, including yellow perch (*Perca flavescens*) (Bur and Klarer 1991; Schneeberger 1991), lake herring (*Coregonus artedii*), smallmouth bass (*Micropterus dolomieu*), and lake trout (R. Coulas pers. comm.). In Lake Michigan, fish planktivory may depress nearshore *B. cederstroemi* abundances (Lehman and Caceres 1993). Consequently, fish predation and defecation are a plausible cause of the elevated caudal-process abundances in the nearshore region relative to the distribution of live *B. cederstroemi* in the plankton. If caudal-process fragmentation is an index of fish predation, our data suggest that 40% (45% in sediment samples minus 5% in spike-recovery samples; Table 2) of all *B. cederstroemi* that are deposited in the sediments died as a result of fish predation.

Sediment caudal-process records may have one additional use—namely, to document the presence of the invader in particular lakes and its dispersal. After the 1994 growing season, caudal processes were collected from the sediments at all 37 sites in Harp Lake (Fig. 4). Therefore, collection of just a few sediment samples at any time of the year may be adequate to correctly establish the presence or absence of *B. cederstroemi* in lakes, shortly after the initial invasion. Hence, programs designed to track the spread of this invader should consider lake sediments as a prime source of data.

References

- ALLEN, G., N. D. YAN, AND W. T. GEILING. 1994. ZEBRA2-zooplankton enumeration and biomass routines for APIOS: A semi-automated sample processing system for zooplankton ecologists. Ont. Min. Environ. Energy Rep.
- BINFORD, M. W. 1990. Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lake sediment cores. J. Paleolimnol. 3: 253-267.
- BUR, M. T., AND D. M. KLARER. 1991. Prey selection for the exotic cladoceran *Bythotrephes cederstroemi* by selected Lake Erie fishes. J. Great Lakes Res. 17: 85-93.
- BURKHARDT, S. 1994. Seasonal size variation in the predatory cladoceran *Bythotrephes cederstroemi* in Lake Michigan. Freshwater Biol. 31: 97-108.
- DILLON, P. J., R. A. REID, AND E. DE GROESBOIS. 1987. The rate of acidification of aquatic ecosystems in Ontario, Canada. Nature 329: 45-48.
- EVANS, H. E., P. J. DILLON, P. J. SCHOLER, AND R. D. EVANS. 1986. The use of $\text{Pb}^{210}/\text{Pb}$ ratios in lake sediments for estimating atmospheric fallout of stable lead in south-central Ontario, Canada. Sci. Total Environ. 54: 77-93.
- FITZMAURICE, P. 1979. Selective predation on Cladocera by brown trout, *Salmo trutta* L. J. Fish Biol. 15: 521-525.
- FONTAINE, T. D., AND D. J. STEWART. 1992. Exploring the effects of multiple management objectives and exotic species on Great Lakes food webs and contaminant dynamics. Environ. Manag. 16: 225-229.
- GARTON, D. W., D. J. BERG, A. N. STOECKMANN, AND W. R. HAAG. 1993. Biology of recent invertebrate invading species in the Great Lakes: The spiny water flea, *Bythotrephes cederstroemi*, and the zebra mussel, *Dreissena polymorpha*, p. 63-84. In B. N. McKnight [ed.], Biological pollution: the control and impact of invasive exotic species. Indiana Acad. Sci.
- GEORGE, D. G., AND R. W. EDWARDS. 1974. Population dynamics and production of *Daphnia hyalina* in a eutrophic reservoir. Freshwater Biol. 4: 445-465.
- HOBAK, A., AND G. G. RADDUM. 1980. Zooplankton communities in acidified lakes in south Norway, p. 1-132. In Acid precipitation—Effects on forests and fish. SNSF Proj. IR 75/80.
- KEILTY, T. J. 1988. A new biological marker layer in the sediments of the Great Lakes: *Bythotrephes cederstroemi* (Schödler) spines. J. Great Lakes Res. 14: 369-371.
- KERFOOT, W. C. 1995. *Bosmina* remains in Lake Washington sediments: Qualitative heterogeneity of bay environments and quantitative correspondence to production. Limnol. Oceanogr. 40: 211-225.
- KREBS, C. J. 1989. Ecological methodology. Harper and Row.
- LEHMAN, J. T. 1988. Algae biomass unaltered by food-web changes in Lake Michigan. Nature 332: 537-538.
- , AND D. K. BRANSTRATOR. 1995. A model for growth, development, and diet selection by the invertebrate predator *Bythotrephes cederstroemi*. J. Great Lakes Res. 21: 610-619.
- , AND C. E. CACERES. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. Limnol. Oceanogr. 38: 879-891.
- LYNCH, M. 1980. The evolution of cladoceran life histories. Q. Rev. Biol. 55: 24-42.
1982. How well does the Edmondson-Paloheimo model approximate instantaneous birth rates? Ecology 63: 12-18.
- MAKAREWICZ, J. C., AND G. E. LIKENS. 1979. Structure and function of the zooplankton community of Mirror Lake, New Hampshire. Ecol. Monogr. 49: 109-127.
- MARTIN, J. W., AND C. CASH-CLARK. 1995. The external morphology of the onychopodid 'cladoceran' genus *Bythotrephes* (Crustacea, Branchiopoda, Onychopoda, Cercopagidae), with

- notes on the morphology and phylogeny of the order Onychopoda. *Zool. Scripta* 24: 61-90.
- MOLOT, L. A., AND P. J. DILLON.** 1991. Nitrogen/phosphorus ratios and the prediction of chlorophyll in phosphorus-limited lakes in central Ontario. *Can. J. Fish. Aquat. Sci.* 48: 140-145.
- NASJE, T. E., B. JONSSON, L. KLYVE, AND O. T. SANDLUND. 1987. Food and growth of age-0 smelts, *Osmerus eperlanus*, in a Norwegian fjord lake. *J. Fish. Biol.* 30: 119-126.
- NILSSEN, J. P., AND S. SANDOY.** 1990. Recent lake acidification and cladoceran dynamics: Surface sediment and core analyses from lakes in Norway, Scotland and Sweden. *Phil. Trans. R. Soc. Lond. Ser. B* 327: 299-310.
- NILSSON, N.-A., AND B. PEJLER.** 1973. On the relation between fish fauna and zooplankton composition in north Swedish lakes. *Inst. Freshwater Res. Drottningholm Rep. No. 53*, p. 53-77.
- PAWSON, T. W., AND N. D. YAN. 1993. Zooplankton data and sample archive database design for the Dorset Research Centre. *Ont. Min. Environ. Energy Rep.* 38 p.
- PINEL-ALLOUL, B.** 1995. Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia* 300/301: 17-42.
- PREPAS, E. E.** 1984. Some statistical methods for the design of experiments and analysis of samples, p. 266-335. *In* J. A. Downing and F. H. Rigler [eds.], *A manual on methods for the assessment of secondary productivity in fresh waters*. IBP Handbook 17, 2nd ed. Blackwell.
- AND E. H. RIGLER. 1978. The enigma of *Daphnia* death rates. *Limnol. Oceanogr.* 23: 970-988.
- RIGLER, E. H., AND J. A. DOWNING.** 1984. The calculation of secondary productivity, p. 19-58. *In* J. A. Downing and F. H. Rigler [eds.], *A manual on methods for the assessment of secondary productivity in fresh waters*. IBP Handbook 17, 2nd ed. Blackwell.
- SCHNEEBERGER, P. J.** 1991. Seasonal incidence of *Bythotrephes cederstroemi* in the diet of yellow perch (ages 0-4) in Little Bay de Noc, Lake Michigan, 1988. *J. Great Lakes Res.* 17: 281-285.
- SCHULZ, K. L., AND P. M. YURISTA.** 1995. Diet composition from allozyme analysis in the predatory cladoceran *Bythotrephes cederstroemi*. *Limnol. Oceanogr.* 40: 821-826.
- SWIFT, M. C., AND U. T. HAMMER. 1979. Zooplankton population dynamics and *Diatomus* production in Waldsea Lake, a meromictic lake in Saskatchewan. *J. Fish. Res. Bd. Can.* 36: 1430-1438.
- VANDERPLOEG, H. A., J. R. LIEBIG, AND M. OMAIR.** 1993. *Bythotrephes* predation on Great Lakes zooplankton measured by an in situ method: Implications for zooplankton community structure. *Arch. Hydrobiol.* 127: 1-8.
- WARNER, B. [ED.].** 1990. *Methods in Quaternary ecology*. Geol. Assoc. Can.
- WARREN, G. J., AND J. T. LEHMAN. 1988. Young-of-the-year *Coregonus hoyi* in Lake Michigan: Prey selection and influence on the zooplankton community. *J. Great Lakes Res.* 14: 420-426.
- YAN, N. D. 1986. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian Shield lakes. *Can. J. Fish. Aquat. Sci.* 43: 788-796.
- , W. I. DUNLOP, T. W. PAWSON, AND L. E. MACKAY. 1992. *Bythotrephes cederstroemi* (Schoedler) in Muskoka Lakes: First records of the European invader in inland lakes in Canada. *Can. J. Fish. Aquat. Sci.* 49: 422-426.
- , W. KELLER, K. M. SOMERS, T. W. PAWSON, AND R. E. GIRARD. 1996. The recovery of crustacean zooplankton from acid and metal contamination: comparing manipulated and reference lakes. *Can. J. Fish. Aquat. Sci.* 53: 1301-1327.
- YURISTA, P. M.** 1992. Embryonic and postembryonic development in *Bythotrephes cederstroemi*. *Can. J. Fish. Aquat. Sci.* 49: 1118-1125.
- , AND K. L. SCHULZ. 1995. Bioenergetic analysis of prey consumption by *Bythotrephes cederstroemi* in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 52: 141-150.

Submitted: 17 October 1995

Accepted: 7 May 1996

Amended: 9 October 1996