

Zooplankton life cycles: Direct documentation of pelagic births and deaths relative to diapausing egg production

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Abstract

Zooplankton demographics operate over multiple time scales corresponding to pelagic parthenogenetic generations, an overwintering stage, and an “egg bank.” Comparisons of pelagic birth and death rates with seasonal diapausing egg production provide insights into local species persistence. The spiny cladoceran (*Bythotrephes*) possesses morphological adaptations (spines and thick-walled diapausing eggs) that lessen, but do not eliminate, predation effects by fish. Because caudal spines are retained throughout life and are indigestible in fish guts, spine accumulation in sediment traps directly documents patterns of seasonal mortality. Here, we contrast deposition of spines and diapausing eggs in a recently colonized inland lake (Lake Michigamme) with deposition in a larger source lake (Lake Michigan). Direct mortality estimates at the inland lake correspond well with traditional indirect estimates from egg ratio techniques. Although spines are effective against abundant small fish in the inland lake, individuals are susceptible to ingestion by late-season young of year and larger fish. Laboratory experiments confirm that fish are responsible for spine breakage in the water column, accounting for an estimated 62–71% of seasonal mortality. Effects of late-season predation are lessened because diapausing eggs survive gut passage, yet yearly production of diapausing eggs is low in Lake Michigamme. A more balanced pelagic birth(death) to diapausing egg relationship exists in Lake Michigan, probably because egg-carrying adults find better refuge in central, deeper waters. Since spines catch on seines and diapausing eggs survive gut passage, use of bait fish and live wells promotes *Bythotrephes* dispersal.

Zooplankton studies in lakes traditionally concentrate on seasonal pelagic dynamics of local populations (N_p ; Fig. 1). Yearly population growth is treated as the consequence of a dynamic balance between instantaneous birth (b) and death (d) rates ($r = b - d$). Netting of plankton allows seasonal estimates of brood sizes and population density. Temperature-dependent regressions for developmental duration convert egg ratio measures into instantaneous birth rates (b), whereas changes in pelagic population size allow independent estimates of the realized population growth rate (r). The difference between the instantaneous birth rate and the re-

alized rate of growth provides an indirect estimate of the instantaneous death rate ($d = b - r$; Edmondson 1968; Paloheimo 1974). The indirect mortality estimates obtained from the egg ratio technique are highly variable because they combine uncertainties inherent in component parameters (DeMott 1980; Taylor and Slatkin 1981; Lynch 1982). Nonetheless, careful application of the Edmondson–Paloheimo technique allows valuable insights into the seasonal nature of processes, such as competition and predation (Hall 1964; DeMott and Kerfoot 1982; Taylor 1988).

A more recent concern is that emphasis on local pelagic demographics might provide little insight into questions of long-term persistence (multiyear continuity) at sites or dispersal of propagules between regional lakes (Shurin 2000; Berendonk and Bonsall 2002). This more expansive (meta-population) perspective argues that population demographics operate on multiple time and spatial scales (Fig. 1). Along with survivorship and fecundity of parthenogenetic generations (N_p , summer pelagic phase), there is (1) yearly diapausing egg production and hatching (N_o , overwinter component) and (2) long-term “egg bank” accumulation and persistence. Diapausing egg production and dispersal are rarely examined in as much detail as seasonal population growth, although overwintering stages might be essential to local and regional persistence. Recruitment from diapausing eggs is vital for species that do not overwinter as adults (Hairston and Munns 1984; Marcus 1984). Moreover, diapausing eggs that are resistant to consumption and desiccation can be dispersed through numerous natural vectors, including vertebrates such as birds (Proctor 1964) and fish (Mellors 1975; Jarnagin et al. 2000). Here, we examine how patterns of seasonal mortality, diapausing egg survival, and

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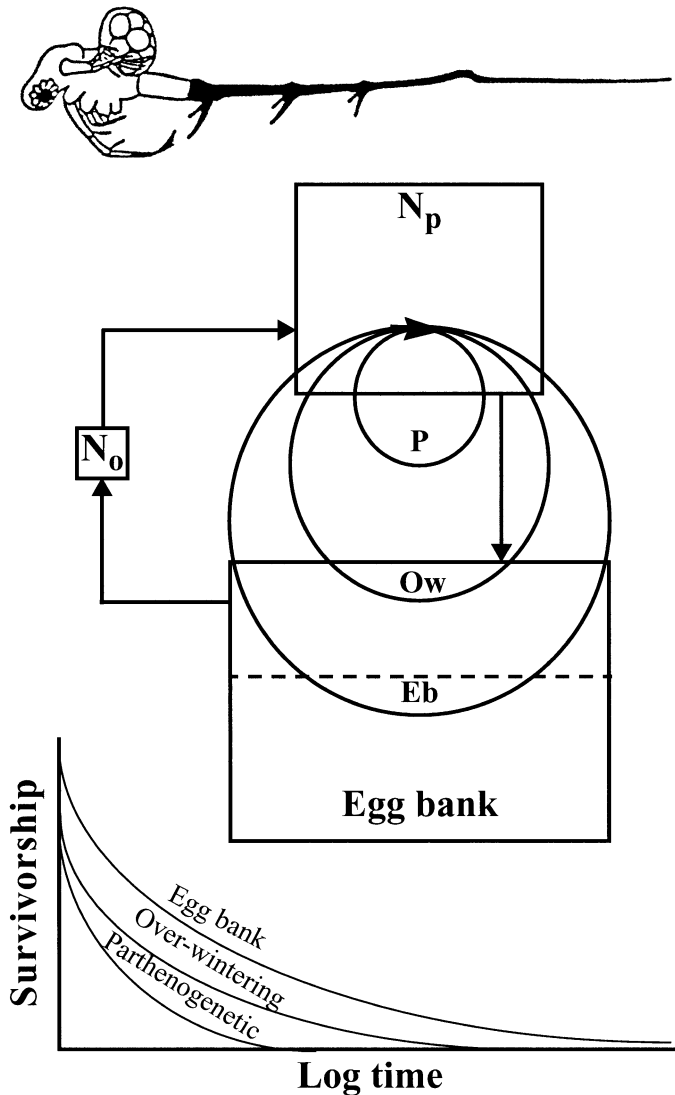


Fig. 1. Multiple time scales in *Bythotrephes* life cycle. Figure illustrates an adult with diapausing eggs. The chitinous spine is blackened to reveal the central spine, kink, and lateral barbs. Abundance N_o is the spring gametogenic *Bythotrephes* population (hatches from diapausing eggs), and N_p is the parthenogenetic *Bythotrephes* population. Diapausing eggs settle onto sediments, where some hatch in the spring. Another fraction accumulates in deep sediments, forming an "egg bank." The time scale of survivorship differs radically between parthenogenetic (P), overwintering (Ow), and the deep egg bank (Eb) generation, represented by concentric circles and survivorship curves (parthenogenetic ~ 1 –2 weeks, overwintering ~ 9 months, egg bank ~ 10 –20 yr).

dispersal of a successful exotic invader are intimately connected.

The process of increased intercontinental transport through human activities, a part of globalization, has had important impacts on modern ecosystems (Carlton and Geller 1993; Vitousek et al. 1997). Exotic species are defined as successfully reproducing, foreign species transported by humans into regions where they did not previously exist. Because they are new to the regional ecosystem and hence constitute an identifiable timeline, exotic species allow us to

quantify patterns of spread (colonization) across the landscape and to study processes that aid or limit species persistence. Mills et al. (1993) recorded 139 nonindigenous aquatic species that colonized the Laurentian Great Lakes since the early 1800s, 13 of which have had a substantial economic and ecological impact on ecosystems.

One of the most successful colonists is the spiny cladoceran, *Bythotrephes cederstroemi* (synonymous with *B. longimanus*? MacIsaac et al. 2000), probably imported from the harbor of St. Petersburg (Gulf of Finland, Baltic Sea) via ballast water during transcontinental ship transport (Berg et al. 2002). *Bythotrephes* is the only strictly freshwater genus of the family Cerocopagidae. In its native Eurasian and introduced North American range, *B. cederstroemi* (Schoedler) appears to be a stenothermic animal with a preferred temperature range of ~ 12 – 18°C (Yurista 1997), although it can tolerate temperatures in the lower 20s. The species was first reported from the Laurentian Great Lakes region in 1982–1984 and had reached Lake Huron by December 1984, Lake Ontario by September 1985, Lake Erie by October 1985, Lake Michigan by September 1986, and Lake Superior by August 1987 (see references in MacIsaac et al. 2000). The Laurentian Great Lakes now operate as a dispersal source, allowing colonization of adjacent inland lakes. Yan et al. (1992) initially reported *Bythotrephes* from 8 inland Ontario lakes in 1991, 22 in 1996 (Yan and Pawson 1997), and now >50 (Yan pers. comm.). We are aware of the species presence in four lakes on Michigan's Upper Peninsula, including Lake Michigamme. *Bythotrephes* has been reported from four additional lakes in northern Minnesota and northern Wisconsin (Jeff Gunderson pers. comm.).

The spiny cladoceran is seasonally abundant and predatory. The species is born with a rigid, barbed caudal spine of unusual size, which exceeds the body length by three to four times (Fig. 1). Individuals acquire a new pair of lateral barbs with each subsequent molt as the spine is retained throughout life. Deposition of spines into sediment traps offers a way of determining mortality schedules over a season if the settling spines remain intact. Because *Bythotrephes* does not overwinter, all individuals born will die; hence, total seasonal births will equal total deaths (Kerfoot et al. 2000).

Preliminary examination of *Bythotrephes* caudal spines from sediment traps in Lake Michigamme revealed extensive spine damage (Kerfoot et al. 2000). Damage was not anticipated given the robust nature of the spine (Keilty 1988; Hall and Yan 1997) and the shallow depth of traps. The high settling velocities of spines and the ability of lateral barbs to entangle sediments make resuspension unlikely, implying that the cause of the spine damage occurred in the water column immediately prior to deposition. Fish fecal pellets suggested that consumption was the primary cause of the observed spine damage, whereas feeding experiments demonstrated viable gut passage of diapausing eggs (Jarnagin et al. 2000). Here, we report details of pelagic demographics, size-specific information on ingestion by fish in the field, and laboratory experiments that examine the effects of gut passage on spine morphology.

Monitoring spine and diapause egg settling offered a means of directly quantifying pelagic mortality for *Bytho-*

*trephe*s and for assessing the effect of fish predation over longer time scales (Fig. 1). Although of limited taxonomic application (restricted to spine-bearing Cercopagids), the use of digestion-resistant spines and diapausing eggs offers the first opportunity to directly compare births and deaths of pelagic versus overwintering generations, extending traditional demographics. Following the initial Michigamme study, we deployed sequential sediment traps in a large source lake, Lake Michigan, to record monthly pelagic patterns of mortality (spine deposition) and to compare patterns of diapausing egg deposition with the inland lake. Consequently, we were impressed by the relatively low diapausing egg production in the inland lake relative to the large source lake. The contrasts raise questions about the precarious nature of existence in inland lakes and the factors (physical, biotic) that limit successful colonization.

Materials and methods

Life history features—The diminutive gametogenic generation (N_0 , which hatches from overwintering, fertilized diapausing eggs) has a small, kinkless spine. This distinctive generation is present from May through June. In subsequent parthenogenetic generations, the neonate is born with a long, kinked spine, which carries one pair of barbs and adds another with each instar (Fig. 1). Like *Polyphemus*, the spiny cladoceran produces parthenogenetic eggs with little yolk. The eggs develop into embryos nourished by fluids secreted from specialized cells in the floor of a completely closed brood pouch (Mordukhai-Boltovskaya 1957). The fully developed young are released as free-swimming first-instar individuals (Yurista 1992). When the environment deteriorates, sexual reproduction is initiated (see references in Burkhardt 1994). During sexual episodes, *B. cederstroemi* produces golden-brown diapausing eggs that are carried in the brood sac until released (Fig. 1). These diapausing eggs are the only eggs carried by *B. cederstroemi* that are visible to the naked eye. Because they are dark and highly visible, they can contribute to conspicuousness, making diapausing egg-bearing females more susceptible to fish predation (Mellors 1975; Zaret and Kerfoot 1975; Jarnagin et al. 2000). The diapausing eggs are dense and settle rapidly to bottom sediments, where they overwinter to establish the next season's population (Jarnagin et al. 2000).

Lake Michigamme zooplankton and sediment trap studies—To compare the expected versus observed production of spines, a series of estimates are required. First, the pelagic population abundance and demographics over time must be estimated (i.e., from egg ratio calculations). Second, the input of spines to the sediments must be monitored (sediment trap data). Third, if fish consumption produces characteristic damage to ingested spines (broken spines in fecal pellets), then the incidence of damaged spines needs to be compared with the incidence of undamaged spines in sediment traps to assess the frequency of cladoceran ingestion by fish. Here we undertake these comparisons with the aim of connecting *Bythotrephes* life histories to patterns of fish predation.

Lake Michigamme (46.5°N, 88.1°W, altitude 474 m) is a 17.6-km² multibasin lake that descends to a maximum depth

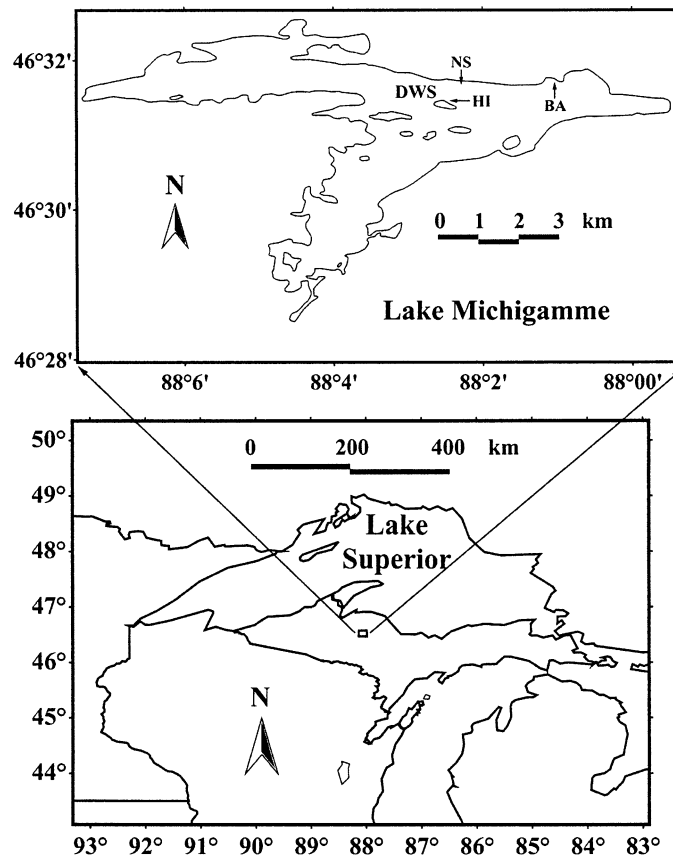


Fig. 2. Geographic location and position of sampling sites in Lake Michigamme: central basin sampling sites (DWS: physical, chemical, pelagic zooplankton, and sediment traps; HI, NS, BA: fish collection sites). HI, Harvey Island; NS, North Shore; natural beach area, BA.

of 22 m (Fig. 2). The lake is surrounded by forest and has a conductivity of 35–50 $\mu\text{S cm}^{-1}$, a methyl-orange alkalinity of 12–16 mg L^{-1} CaCO_3 , and pH 5.6–6.7. Waters are moderately to darkly stained by tannic acids. Typical midsummer Secchi disk depths range from 1.5 to 2.7 m, whereas a midsummer thermocline is present at 7–11 m. Summer epilimnetic temperatures reach a maximum of 23–26°C, whereas 5–8 m depths are typically 14–20°C (Jarnagin 1998). The lake is oligotrophic to mesotrophic, with a late summer reduction of midhypolimnetic dissolved oxygen to 4.0–4.5 mg L^{-1} .

Bythotrephes was first reported from Lake Michigamme in August 1994. The absence of prior reports in spite of frequent trolling activity (i.e., individuals snagged on lines) suggests that this was the year of invasion. Population sampling, sediment sampling, and sediment trap studies were confined to the central basin (Fig. 2). The deep-water sample site chosen for pelagic and sediment sampling (DWS) was located in the middle of the north-central basin. This site is an area of relatively uniform depth (13–15 m). Vertical temperature profiles and Secchi disk depth measurements were made as near to solar noon as possible, along with air temperature, salinity, and conductivity at 0, 5, and 10 m depths.

Littoral sites chosen for fish collection were adjacent to

DWS (HI, NS, BA). Buoys marked locations of sediment trap arrays placed at the ends of a 100-m transect running north to south at the DWS location. Sediment traps had an aspect ratio (height : diameter) of 6 and were placed in combinations of three traps within wire baskets suspended from a float and tethered on an anchored line 1 m above the sediment. Because other basins were not simultaneously studied, conclusions drawn from this study apply only to the north central basin.

Detailed pelagic sampling was conducted at the single deep-water station (DWS) during the summers of 1995 and 1996, with a follow-up in 1997. Because *Bythotrephes* are highly mobile animals that occur at low densities, several different methods of sampling were evaluated (Clarke–Bumpus horizontal tows, metered Puget Sound Net vertical tows vs. “towyo” tows; see Jarnagin 1998). On the basis of replicate variance and absolute numbers, we decided on transect (DWS) horizontal and integrated plankton tows taken with a metered 0.5-m, 350 μ m mesh Puget Sound Plankton net weight-rigged for horizontal towing. The integrated tows were oblique towyo tows that moved from the surface to depth and back. Nine replicates (three integrated tows, six vertical tows) provided estimates of seasonal density. Because vertical and integrated tows sampled different volumes of water, we volume-weighted means and variance. Propagation of errors followed Barry (1964). For detailed demographic studies, we used the long (tens of meters) horizontal tows at 1-m depth increments ($n = 13$ strata) and sampled great volumes of water for collecting numerous animals.

Bythotrephes in net tow samples were entirely enumerated to ensure large sample sizes. Each individual was classified as to instar, sex (if second instar or older), and number of parthenogenetic young or diapausing eggs in the brood sac (if sac formed). The number of parthenogenetic young usually cannot be determined until they enter the eye stage of development (Yurista 1992; Lehman et al. 1997), so we used the number of eyespots in embryos to indicate brood size. Because this interval covers only 16–25% of the total developmental time, large samples were required for accurate enumeration. Calculations followed the Edmondson–Paloheimo egg ratio method (Paloheimo 1974). The method is based on the exponential growth model: $N_t = N_0 e^{rt}$ and $r = b - d$, where N_0 is the initial (overwinter) population size, N_t is the population size at time t (days), and r is the realized rate of population growth. From measures of water column temperature and animal density, we calculated $b = \ln(E + 1)/D$, where E is the egg ratio (=number of eggs/total population size) and D is the egg developmental time (days). The rate of growth of the population was determined from successive field determinations of population density, with $r = [\ln(N_0) - \ln(N_t)]/(t_1 - t_0)$. The calculation of instantaneous mortality or death rate (d) was by difference ($d = b - r$) from the two previous variables.

The horizontal tows revealed that *Bythotrephes* were not uniformly distributed in the vertical plane (Fig. 3) because individuals tended to congregate in the 12–18°C strata. Consequently, we used an abundance-weighted mean temperature to calculate D . Two spatial models were applied: (1) without vertical migration, which assumed parthenogenetic young were vertically distributed in the same proportion as

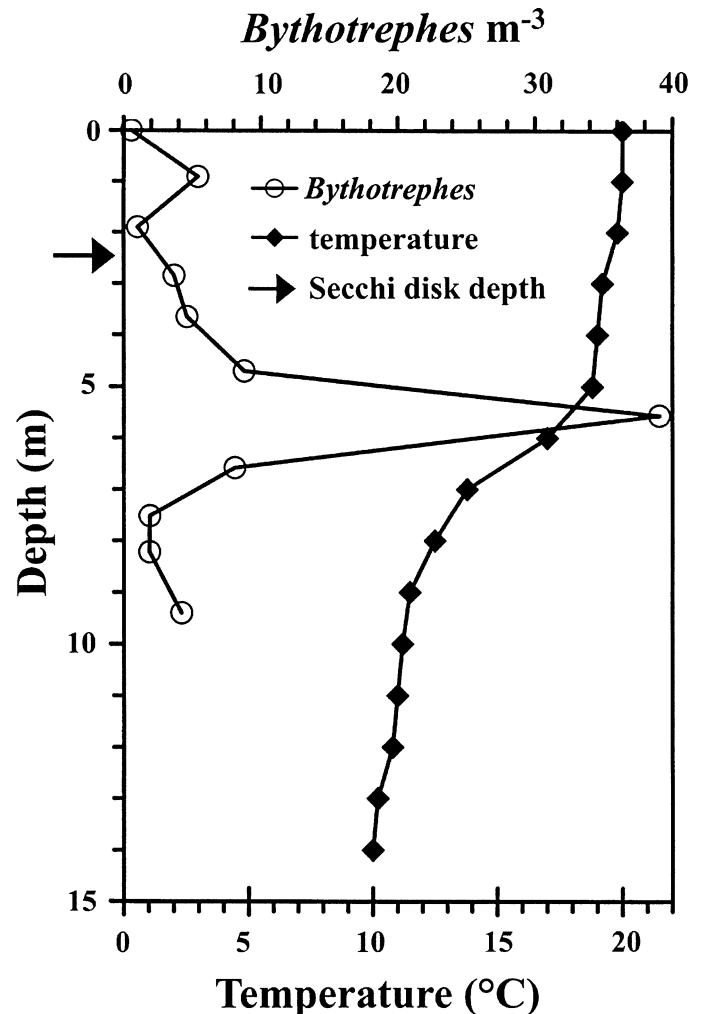


Fig. 3. Vertical distribution of *Bythotrephes* in water column (DWS, 11 July 1995) relative to temperature profile. Secchi disk depth indicated on diagram. Thirteen horizontal tows ($n = 13$) were used to determine densities and other variables used in temperature-weighted demographic calculations.

daytime abundance (depth-weighted stationary model), and (2) with vertical migration (vertical migration model), which had individuals moving up into the epilimnion during night (i.e., spread uniformly about the mean epilimnetic temperature).

Pelagic samples collected from the 116-d season in 1995 (7 June–1 October) and the 98-d season in 1996 (13 June–30 September) provided demographic estimates of spine production, mortality, and diapausing egg production. Because *Bythotrephes* do not overwinter, all individuals born would die; thus, yearly spine production could be calculated a variety of ways. Two different methods were used to estimate the seasonal number of spines deposited per square meter (seasonal mortality). The first method used the weighted mean number of *Bythotrephes* per square meter on each sample date, N_t , and d from egg ratio techniques to estimate finite daily mortality (d'). Linear interpolation of abundance between sample dates and integration of the area beneath the line estimated total mortality (linear integration mortality

method). Seasonal spine additions to a 1-m² area of sediment were multiplied by the surface area of the sediment trap (0.0081 m²) to estimate the number of spines expected per trap. The second method used the same abundance estimates multiplied by b' (finite daily birth rate from b) to estimate the number of new spines produced per day above 1 m² of sediment. Linear interpolation between sample dates allowed integration for estimates of seasonal production (linear integration birth method). Data on the number of diapausing eggs (m⁻²) allowed similar predictions for the number of diapausing eggs deposited (m⁻²). Because no lab determination of diapausing egg developmental time was done, we used published values from Lehman et al. (1997).

In addition to linear interpolation, another approach used a second-order polynomial curve fit to the population abundance estimates. The assumption with this approach is that, given sampling error, a smooth curve that describes population trends might be a more accurate estimator of the population trajectory than individual point estimates (Prepas and Rigler 1978). The polynomial regression was used to estimate population size (N_t), whereas the tangent to the curve estimated r (polynomial approach to birth method). The value b was calculated as before from pelagic brood size and developmental information.

Spike tests evaluated breakage associated with sediment and sediment trap handling. *Bythotrephes* were collected from plankton tows and killed by placing them into 1-liter containers of oxygenated water cooled to <4°C. Undamaged caudal spines were dissected from various instars and kept cool (4°C). One spike experiment involved lake sediment, in which fresh Lake Michigan sediment was filtered through 350- μ m Nitex netting and examined for fragments, which were removed. Six processed sediment subsamples, each in a 250-ml erlenmeyer flask, were then spiked with spines. Six sediment traps and 12 fish aquaria were filled with water and also spiked with known amounts of spines and diapausing eggs. Each treatment was filtered through 350- μ m Nitex netting, handled, and preserved in the same manner as field and laboratory samples.

Lake Michigan sequential sediment trap studies—Finding high mortality and low diapausing egg deposition in Lake Michigan, we wanted to compare these patterns against a large reference “source lake.” Subsequently, we deployed sequential sediment traps at four deep northern and southern basin sites (offshore) and one coastal (nearshore) site in Lake Michigan (Fig. 4) between 1998 and 2000. Given reported concentrations of *Bythotrephes* in Lake Michigan waters (Lehman 1991; Lehman and Cáceres 1993), we anticipated that deep-water sequential sediment traps would capture large numbers of settling spines and diapausing eggs, better revealing details of seasonal depositional patterns. *Bythotrephes* does not overwinter in pelagic waters of Lake Michigan, emerges from diapausing eggs in May–June, and is epilimnetic, often with a dual population maximum (July, August). The species mean depth ranges between 10 and 30 m, with only weak diel vertical migration during midsummer, although there is deep displacement during fall (Lehman and Cáceres 1993). Pelagic population dynamics were followed separately from 1998 to 2000, with the 2000 results

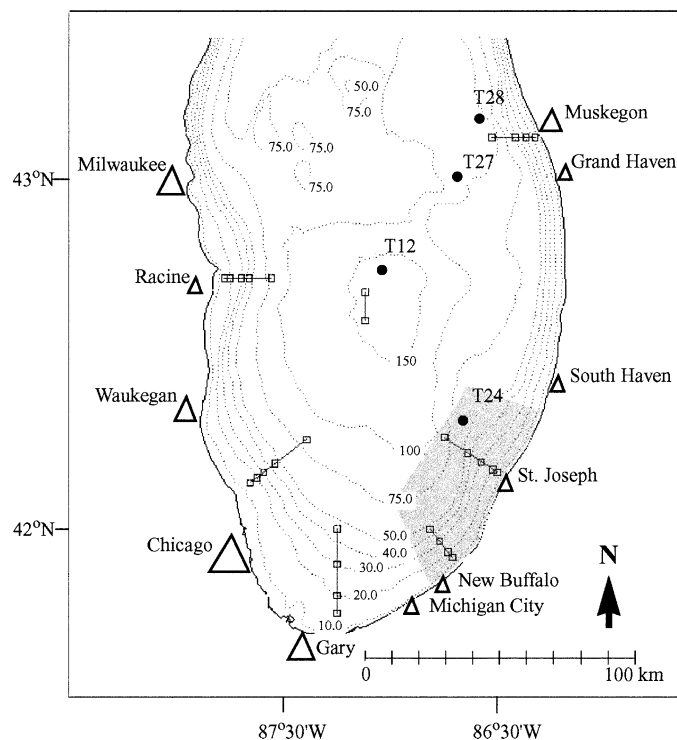


Fig. 4. Position of sequential sediment traps (solid dots) in Lake Michigan 1998–2001. Sta. T29, deep station, North Basin, is not shown. Small squares mark the position of plankton sampling stations discussed by Pothoven et al. (2003).

published recently (Pothoven et al. 2003). Mean offshore densities ranged between 278 and 570 individuals m⁻² from July to September, resembling values from spatial transects in southeastern Lake Michigan between 1987 and 1998.

The Great Lakes Environmental Research Laboratory sequencing sediment trap was cylindrical, with an inner diameter of 20 cm and an aspect ratio of 8:1 above the funnel (Eadie 1997; Muzzi and Eadie 2002). A computer-controlled carousel contained 23, 60-ml polyethylene bottles, which rotated under the funnel at preprogrammed intervals. Sampling frequency in 1999–2000 was set at 14 d (2 weeks). The traps were deployed as anchored arrays on subsurface-buoyed 10-mm steel cable. Arrays were positioned with groundlines of 200–400 m between two anchors. Retrieval was accomplished by snagging the groundlines with brass grapples, then hauling up the arrays. An acoustic release served as a backup for retrieval. The 60-ml polyethylene collection bottles were poisoned with 6 ml of chloroform and filled with distilled water immediately before deployment. Samples were sieved through 350- μ m Nitex netting to retrieve spines and diapausing eggs.

Statistics for sediment accumulation in sequential sediment traps and replication are discussed in Eadie (1997) and Muzzi and Eadie (2002). These authors determined that 20-cm traps (8:1 aspect ratio) replicated with a mean difference between pairs of 14% for sediment collection. Our own checks on spine and diapausing egg replication consisted of (1) duplicate counts of the same trap samples (counting accuracy, C.V. = 2.6% for spines; C.V. = 2.9% for eggs, $n =$

8) and (2) tallies from multiple traps at the same depth (duplicate traps, C.V. = 40.9% for spines, C.V. = 47.1% for eggs, $n = 4$). The increased variance for spine and egg counts relative to sediments probably comes from fecal pellet delivery of mixed spine and egg masses.

Laboratory fish feeding experiments—In 1995 and 1996, fish feeding experiments determined whether fish consumption of *Bythotrephes* was responsible for the observed patterns of spine damage. In 1995, yellow perch (*Perca flavescens*), bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), and smallmouth bass (*Micropterus dolomieu*) were collected by beach seine. The fish ($n = 52$) ranged in size from 46 to 155 mm total length (TL) and were selected to represent the dominant taxa present in Lake Michigan waters. Each fish was placed in an individual aquarium at 16°C in filtered, oxygenated lake water. Individual *Bythotrephes* were presented to fish with a plastic 10-ml wide-bore pipette that had the terminal end removed. Fish were starved for 24 h prior to each feeding trial and fed a mixture of zooplankton or worms following ingestion of *Bythotrephes*. Every day initially, or later every other day, bottom detritus was siphoned from each aquarium (5-mm internal diameter latex tubing) and preserved in a 5% formalin/sucrose solution. We examined only sediments from aquaria that contained fish ($n = 27$) that ate every offered *Bythotrephes*. In this way, we guaranteed that spines were consumed by fish. In 1996, we repeated the procedure, only we additionally noted the instar and brood condition of each *Bythotrephes* presented to fish.

Bythotrephes spines and fragments of spines from each sample and experiment were enumerated, analyzed for the types of damage present, and classified by age to instar. The number of diapausing eggs found and their condition was enumerated for each sample and experiment. If highly fragmented, the number of spines was estimated by the number of kinks. Each spine was tallied according to seven spine damage categories: broken at the distal end of the spine (the tip), broken at the kink, spine bent, one lateral barb missing, multiple barbs missing, broken between lateral barb pairs, and spines broken between the proximal end of the spine and the lateral barbs.

To test the hypothesis that *Bythotrephes* diapausing eggs could survive fish gut passage, 958 *Bythotrephes* that carried 113 mature diapausing eggs were fed to fish (three pumpkinseeds, range 77–140 mm TL; six yellow perch, range 81–101 mm TL) in individual aquaria. Detritus was collected over a 3-d period following consumption of a known number of eggs. These experiments complemented previously reported fish feeding trials (Jarnagin et al. 2000).

Field observations of Bythotrephes ingestion by young-of-year fish—Fish were collected by seine (10 × 1.5 m, 5-mm mesh size) on 19 July, 1 August, and 5 September 1996 from a natural beach location (BA) on the north shore of Lake Michigan (Fig. 2). Zooplankton were collected on site by the metered 0.5-m Puget Sound Plankton net rigged for horizontal towing. Additional collections of fish and zooplankton were made at two artificial beach areas on 1 August 1996 (Fig. 2; NS, North Shore; HI, Harvey Island). Collected

fish were immediately placed in plastic bags and packed in ice to stop digestion. Fish were transported to the laboratory and frozen at -10°C until dissection and gut contents were enumerated.

A subsample of 74 yellow perch (range 38–141 mm TL) from 234 collected were dissected, and stomach and lower gastrointestinal (GI) tracts were preserved separately in a 5% formalin/sucrose solution. For larger fish, scale samples taken from below the lateral line, near the tip of the pectoral fin, were checked for an annulus to determine young-of-year (YOY) or first-year status. Only the largest fish (136–141 mm) had an annulus. The stomach and lower GI tract were examined, and each *Bythotrephes* was tabulated and identified to instar, if possible. Diapausing eggs were also enumerated. The number of *Bythotrephes* ingested was plotted as a function of fish size. For larger size fish, preference for *Bythotrephes* instars was calculated by Lampert and Sommer's (1997) formulation of Chesson's Alpha index (Chesson 1978, 1983). Chesson's Alpha is based on the number of food items sampled by the consumer relative to that available in the environment. Lampert and Sommer's formulation of Alpha for instar i is $\alpha_i = (r_i/p_i)/[(r_i/p_i) + (r_j/p_j)]$, where r_i is the proportion of the item of interest in the diet, p_i is the proportion of the item in the population, and (r_j/p_j) is the relative proportion (diet/population) of all other classes. The index ranges from 0 to 1; in this case, $\alpha = 0.5$ indicates nonselective choice.

Statistics—Comparisons between expected and observed spine and diapausing egg occurrence in traps were made by Tukey honestly significant difference (HSD) pairwise tests. Spine breakage patterns from laboratory experimental tests and field gut observations were compared by multivariate analysis of variance (MANOVA). Demographic variable comparisons and nearshore versus offshore trap comparisons were made with parametric t -tests. If data were more suitable for nonparametric tests, we applied Mann-Whitney and Kruskal-Wallis tests (seasonal density estimates). Statistical tests were run on SAS version 6.09 on a UNIX platform and SYSTAT 5.2.1 on a Macintosh platform (Wilkinson 1990).

Results

Pelagic populations: Egg ratio estimates of births and deaths compared with settlement of spines and diapausing eggs into sediment traps—Towyo density estimates are compared for the 1995–1997 seasons in Fig. 5. Mean abundance (individuals $m^{-3} \pm 95\%$ confidence interval [CI]) increased a little from 1995 (6.3 ± 0.7 , $n = 106$) to 1996 (7.1 ± 0.7 , $n = 111$), then dropped substantially in 1997 (3.1 ± 0.3 , $n = 84$). Densities in 1997 were down in spring (May–June) at the time of recruitment from diapausing eggs. Individuals from the first generation (gametogenic hatchlings) were present in low numbers during June of each year, succeeded by numerically more abundant parthenogenetic individuals in subsequent generations. Discarding the first (hatching) and last (diapausing egg production) sample dates ($n = 21$) for 1995–1997, percentages of first, second, and third instars were $23.3 \pm 4.8\%$, $27.0 \pm 2.8\%$, and $50.0 \pm 5.1\%$, respectively. With the use of instar developmental times from Leh-

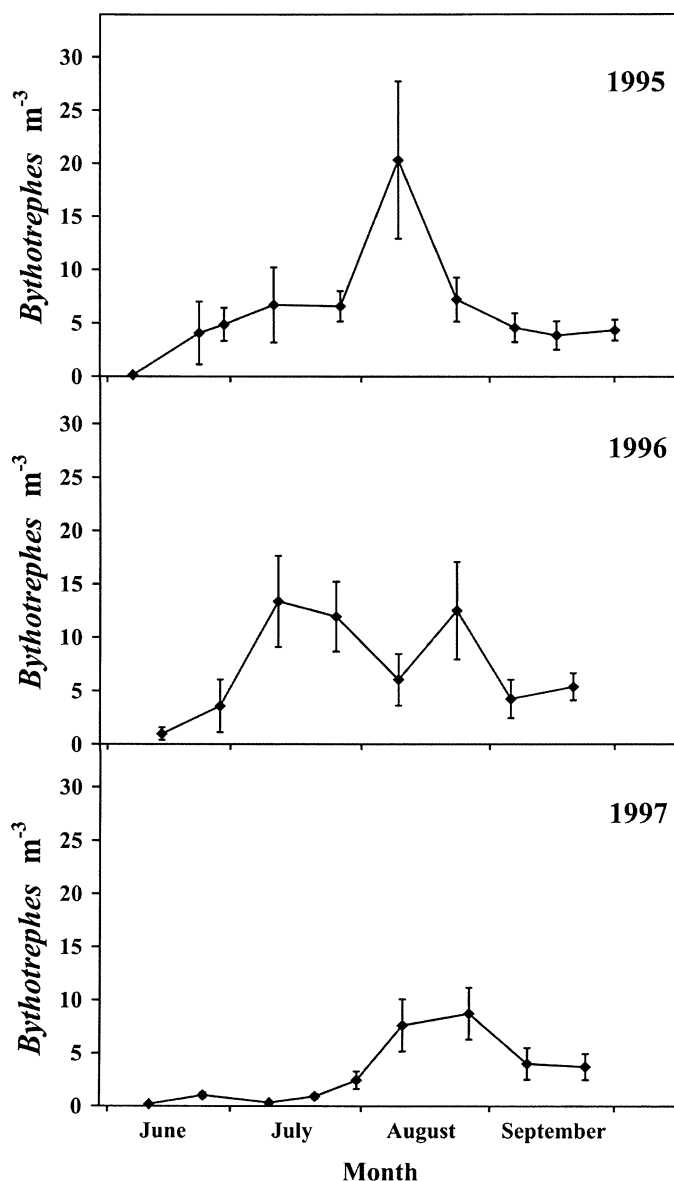


Fig. 5. Seasonal abundance of *Bythotrephes* (m^{-3}) in Lake Michigan (DWS, 1995–1997). Values are weighted means \pm 95% CI for volume-weighted replicate tows ($n = 9$; three integrated tows, six vertical tows).

man et al. (1997) (i.e., 3.5, 3.3, and 4.3 d, respectively), the proportions were similar to the expected stable age distribution: 26.8%, 24.9%, and 48.4%, respectively.

Tables 1, 2 show sample variables for 1995–1997 and estimated values for b' , r' , and d' (finite rates) for 1995–1996. Gametogenic individuals (N_g) made up only 1.9% of total *Bythotrephes* in 1995 and only 0.8% in 1996. Negative d' values occurred only during the initial sampling intervals, a spurious consequence of diapausing egg recruitment. Correcting this artifact, mean daily per capita death rates increased from 1995 ($d' = 0.15 \pm 0.02$) to 1996 (0.18 ± 0.04) and then fell in 1997 (0.10 ± 0.12) when the spiny cladoceran was less abundant. Mean parthenogenetic brood size showed evidence for midsummer food limitation as values

declined in August while the percentage of third instars bearing empty broods increased. Empty brood pouches of third-instar *Bythotrephes* suggest resource limitation (Lehman 1988) because brood size is usually correlated with food supply (Kerfoot 1974; DeMott and Kerfoot 1982; Tessier and Goulden 1982). During this interval, there was also an increased incidence of young in the brood pouches of second-instar individuals, an instar normally not reproductive. The presence of broods in second-instar individuals has been noted previously as a “rare event” (Yurista 1992). In Lake Michigan, up to 19% of all parthenogenetic young were carried by second-instar individuals for a brief period in mid-summer. Males were produced early, with a dual peak in all 3 yr (1995—27 July, 41%; 1 Oct, 59%; 1996—26 Jul, 28%; 23 Aug, 44%; 1997—21 Jul, 100%; 24 Sep, 50%), again suggesting resource decline in midsummer. In contrast, the brood size for diapausing egg-carrying females increased steadily from late July (3.5–3.7) until September–October (4.0–5.0).

The release of diapausing eggs above a 1- m^2 sediment area was calculated by the same temperature-weighted technique as for parthenogenetic births. Figure 6 gives the 1995–1996 results. Although there was a dominant autumn peak, diapausing eggs were produced throughout the summer during both years. The highest production of diapausing eggs in planktonic populations occurred late in the season as overall pelagic abundance declined, coinciding with the highest incidence of males.

As discussed (see *Materials and Methods*), there were several ways to calculate seasonal spine production (either total births or total deaths) with the use of linear or polynomial regression fits. An example of calculations is presented in Table 3 (see details of all other calculations in appendix tables in Jarnagin 1998). The predicted accumulations of spines and diapausing eggs in sediments for 1995 and 1996 calculated from egg ratio methods were compared with the actual accumulation of spines and eggs in sediment traps. A total of 66 spines and only six diapausing eggs were collected from 10 sediment traps in 1995. A total of 383 spines and only 31 diapausing eggs were collected from 18 sediment traps in 1996. That is, during both years, the ratio of overwintering eggs to births(deaths) was 0.08–0.10. Spine deposition variability per trap was used to assign a 95% confidence interval to spines collected per trap and per square meter. The results for strata-stationary and vertically migratory populations are presented in Table 4. Anomalous early-season negative d values were assigned zero values (i.e., no spines are assumed added to sediments during these intervals). Because the abundance of *Bythotrephes* is very low during the early period, the numerical effect is minor.

For 1995–1996, seasonal predictions of spine settlement from the integrated birth (b') and integrated death (d') methods were not significantly different (Tukey HSD pairwise comparisons), also indicated by 95% CI (1995: $1,080 \pm 153$ vs. $1,141 \pm 194$; 1996: $1,592 \pm 165$ vs. $1,548 \pm 194$). Polynomial fit methods produced similar to 30% lower values. Overall, egg ratio indirect estimates and sediment trap captures were within 95% CI (i.e., not significantly different). However, trap totals were consistently higher than egg ratio estimates but fell within error envelopes because of the

Table 1. *Bythotrephes* abundances and population demographics from 1995 to 1997 pelagic sampling in the central basin of Lake Michigan. During 1995, 1,131 m³ were sampled and 8,980 *Bythotrephes* collected; in 1996, 867 m³ were sampled and 6,226 *Bythotrephes* collected; in 1997, 355 m³ were sampled and 1,101 *Bythotrephes* collected.

Sample date	Mean epilimnetic temperature (°C)	Sample site (m ³)	No. <i>Bythotrephes</i> collected										Mean	
			Total	Parthenogenic	Game-togenic	3rd	2nd, male	2nd, female	1st	Bearing eye-stage parthenogenic young	<i>Bythotrephes</i> bearing eggs	Eye-stage parthenogenic young per gravid female (±95% CI)	Eggs per gravid female (±95% CI)	
1995														
07 Jun	17.4	30.0	4	0	4	1	0	0	1	2	0	0	—	—
23 Jun	26.8	25.2	93	71	22	29	0	30	34	5	0	0	4.4(0.8)	—
29 Jun	23.0	20.5	101	100	1	34	1	22	44	12	0	0	3.3(0.6)	—
11 Jul	19.5	89.0	644	644	0	330	21	180	113	54	0	0	2.9(0.2)	—
27 Jul	22.9	178.0	1171	1171	0	717	109	155	190	185	15	6	2.6(0.1)	3.5 (0.5)
10 Aug	25.4	180.1	2694	2694	0	829	111	827	929	194	6	23	2.4(0.1)	3.5 (1.3)
24 Aug	21.9	190.7	1720	1720	0	730	60	535	395	171	23	54	2.0(0.1)	3.5 (0.3)
07 Sep	19.5	181.3	1106	1106	0	429	32	208	437	51	80	160	3.5(0.3)	4.1 (0.2)
17 Sep	16.5	198.7	606	606	0	283	95	122	106	16	16	25	2.6(0.4)	4.2 (0.2)
01 Oct	14.1	37.1	841	841	0	419	193	134	95	25	5	5	4.1(0.2)	4.3 (0.2)
1996														
13 Jun	17.1	114.9	79	51	28	23	0	0	56	5	0	0	5.6(1.2)	—
27 Jun	18.1	124.3	354	352	2	206	3	46	99	48	0	0	4.0(0.3)	—
11 Jul	19.7	111.6	1448	1448	0	787	39	364	258	121	10	10	2.4(0.1)	3.6 (0.4)
26 Jul	19.7	108.0	1000	1000	0	736	50	127	87	226	22	22	2.3(0.1)	3.7 (0.2)
09 Aug	20.8	103.1	622	622	0	348	27	142	105	55	9	9	2.0(0.2)	3.7 (0.8)
23 Aug	20.9	186.7	2256	2256	0	1170	276	354	456	268	92	16	3.0(0.11)	4.4 (0.2)
05 Sep	23.0	79.8	260	260	0	147	20	38	55	21	16	5	3.0(0.4)	4.6 (0.5)
20 Sep	15.2	38.4	207	207	0	145	7	12	43	27	5	5	3.4(0.3)	5.0 (0.6)
1997														
11 Jun	22.3	54.5	11	1	10	7	0	1	3	3	0	0	7.7(0.7)	—
24 Jun	22.1	55.5	59	40	19	28	1	7	23	3	0	0	4.7(1.3)	—
10 Jul	21.9	33.2	11	11	0	8	0	3	0	2	0	0	3.5(1.0)	—
21 Jul	21.8	40.6	38	38	0	16	12	0	10	2	0	0	2.5(1.0)	—
31 Jul	22.1	35.0	86	86	0	47	1	22	16	3	0	0	3.7(0.7)	—
11 Aug	20.9	48.3	368	368	0	178	32	81	97	23	0	0	2.4(0.3)	—
27 Aug	18.3	38.7	337	337	0	200	38	73	26	17	25	25	3.0(0.3)	3.84(0.3)
10 Sep	17.0	33.2	133	133	0	52	19	22	40	7	21	21	3.3(0.4)	4.29(0.5)
24 Sep	15.2	15.6	58	58	0	19	9	9	21	0	11	11	—	4.27(0.5)

Table 2. Estimating finite b' , r' , and d' values for 1995–1996 dates. Columns for D_e and E give developmental duration and egg ratio values.

Sample date	Day of the year	Mean epilimnetic temperature	D_e (d)	E	b'	r'	d'
1995							
07 Jun	158	17.4	1.7	0.00	0.00	0.73	-0.73
23 Jun	174	26.8	1.0	0.24	0.22	0.21	0.01
29 Jun	180	23.0	1.2	0.39	0.28	0.03	0.25
11 Jul	192	19.5	1.5	0.24	0.15	0.03	0.12
27 Jul	208	22.9	1.2	0.41	0.29	0.00	0.29
10 Aug	222	25.4	1.0	0.17	0.15	0.08	0.07
24 Aug	236	21.9	1.3	0.19	0.14	-0.07	0.21
07 Sep	250	19.5	1.5	0.16	0.10	-0.03	0.13
17 Sep	260	16.5	1.9	0.07	0.04	-0.02	0.05
01 Oct	274	14.1	2.4	0.12	0.05	0.01	0.04
1996							
13 Jun	165	17.1	1.8	0.35	0.17	1.01	-0.84
27 Jun	179	18.1	1.6	0.54	0.26	0.09	0.17
11 Jul	193	19.7	1.5	0.20	0.13	0.09	0.03
25 Jul	207	19.7	1.5	0.51	0.28	-0.01	0.29
09 Aug	222	20.8	1.3	0.18	0.12	-0.05	0.17
23 Aug	236	20.9	1.3	0.35	0.22	0.05	0.17
05 Sep	249	23.0	1.2	0.25	0.19	-0.08	0.27
20 Sep	264	15.2	2.1	0.44	0.17	0.02	0.16
1987							
11 Jun	162	22.3	1.2	2.09	0.92	0.78	0.14
24 Jun	175	22.1	1.2	0.24	0.17	0.13	0.05
10 Jul	191	21.9	1.3	0.64	0.39	-0.07	0.46
21 Jul	202	21.8	1.3	0.13	0.10	0.09	0.00
31 Jul	212	22.1	1.2	0.13	0.10	0.10	0.00
11 Aug	223	20.9	1.3	0.15	0.11	0.10	0.00
27 Aug	239	18.3	1.6	0.15	0.09	0.01	0.08
10 Sep	253	17.0	1.8	0.17	0.09	-0.06	0.14
24 Sep	267	15.2	2.1	0.00	0.00	-0.01	0.01

greater variability in trap capture values. Diapausing egg production estimates from egg ratio methods were also very close to observed egg totals recovered from sediment traps in both years (significant differences indicated by different letters, Tukey HSD pairwise comparisons, $\alpha = 0.05$), with slightly higher trap estimates in 1996 (mean \pm 95% confidence level [CI]: estimated 1995, 142 ± 36 A; observed trap, 134 ± 63 A; estimated 1996, 146 ± 41 A; observed trap, 213 ± 61 B). The importance here is that for 1,400–2,600 births(deaths) $m^{-2} yr^{-1}$ in Lake Michigan, there were only 140–210 diapausing eggs produced ($m^{-2} yr^{-1}$, eggs: spines = 0.08–0.10), with the use of low-diapausing egg totals by two independent techniques (pelagic demographics, sediment trap captures).

Identifying sources of spine breakage and estimating mortality from fish predation—Spine breakage was low in laboratory aquarium and sediment trap spike tests, ranging between 1.7% and 3.6% (Table 5). In contrast, observed field spine breakage in sediment traps was unexpectedly high for both years. Comparison of the percentage of undamaged spines recovered in 1995 and 1996 sediment traps shows no significant difference between years (pooled $t_{24} = 0.47$, $P =$

0.64). Suspecting that fish were responsible for the observed breakage patterns and might serve to identify the primary cause of field mortality, we conducted laboratory fish consumption experiments (see *Materials and methods*).

Bythotrephes caudal spines that moved through the guts of fish were quantitatively passed, but highly damaged (Fig. 7). Mean spine recovery per fish was $95 \pm 5\%$ (95% CI). A total of 958 *Bythotrephes* were fed to experimental fish, and only 127 undamaged spines (13%) were recovered. The percentage of undamaged spines was even lower in dissected yellow perch guts from the field (4%; 72 of 1,555 spines, 43 guts). Gut passage tended to fold and break spines, in addition to shearing off lateral barbs, a type of damage that was unmistakable and in contrast to the condition of intact spines derived from uningested individuals that settled into traps (Jarnagin 1998; Kerfoot et al. 2000). The spines from advanced instars (second, third) suffered greater damage than the smaller, simpler spines from first instars (Jarnagin 1998). Breakage patterns for fish-fed *Bythotrephes* and sediment trap samples were similar (Fig. 8; MANOVA, $P = 0.23$; Wilk's Lambda = 0.19; $F_{16,18} = 1.4$) and distinct from bioturbation fragmentation patterns found in sediments (Jarnagin 1998).

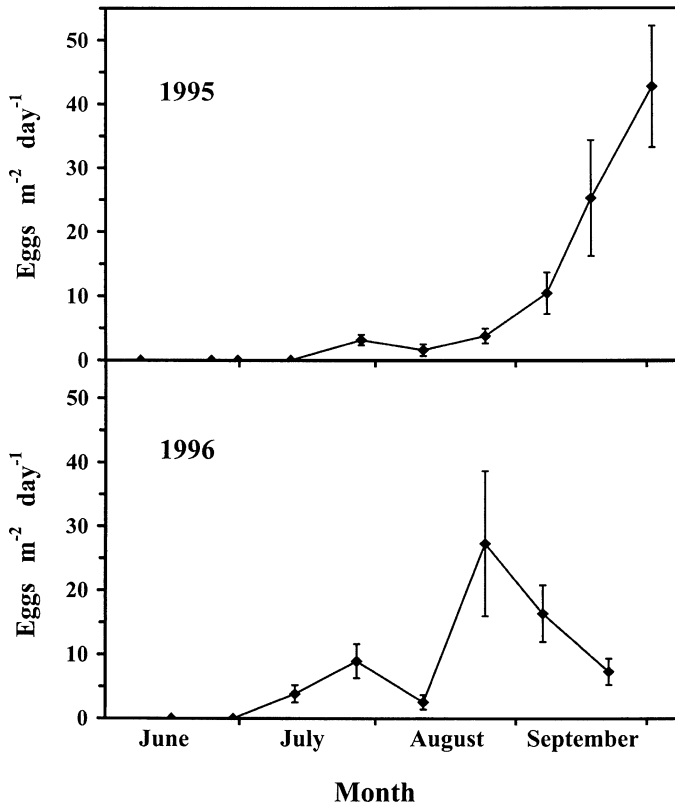


Fig. 6. *Bythotrephes* diapausing eggs ($\text{m}^{-2} \text{d}^{-1}$) in the water column (pelagic estimates, 1995–1996). Values are temperature-weighted means \pm 95% CI for tows at 13 strata ($n = 13$ tows; 1-m intervals).

Assuming 2.5% spine damage during the recovery process, because 60.3% of the spines recovered from the 1995–1996 Lake Michigan sediment trap samples were damaged, \sim 58% of spines were consumed by fish. Yet this value must also be corrected by the percentage of spines that pass through fish intact. Therefore, 62–71% ($58 + 4\%$; $58 + 13\%$) of the individuals were consumed by fish and 29–38% suffered mortality by some other cause.

Fish ingestion electivities—Most small YOY fish avoid consuming *Bythotrephes* because the spine causes considerable distress during ingestion (Barnhisel 1991a,b; Barnhisel and Kerfoot 1994 in press; Compton and Kerfoot in press). In Lake Michigan fish samples, perch <58 mm TL or >109 mm TL rarely had *Bythotrephes* in their guts. Figure 9 shows the number of *Bythotrephes* ingested by perch as a function of total length between 55 and 110 mm. Late-season YOY between 60 and 85 mm consumed up to 120 *Bythotrephes* each. Large YOY and first-year perch >84 mm contained numerous *Bythotrephes*, again up to 120 individuals each, although first-year perch would switch to larger, alternative prey.

Of the 1,171 *Bythotrephes* recovered from the 1 August 1996 yellow perch, 896 (77%) were identifiable to instar. Third-instar *Bythotrephes* made up 81% of those identified. There was no significant difference between the degree and pattern of damage to spines between yellow perch stomachs and lower GI tracts (MANOVA $P = 0.64$). For perch within the interval 58–109 mm TL, instar frequencies were compared with those in the plankton with Lampert and Sommer's (1997) formulation of Chesson's Alpha index (α_i). The 95% CI values were calculated for instar values from individual fish. Positive electivity for larger, more conspicuous, third-instar *Bythotrephes* was found (Fig. 10). Selective predation has significant implications for dispersal, in that the larger, mature *Bythotrephes* instars carry more diapausing eggs. Previous electivities run for diapause egg-carrying females also showed positive electivity (Jarnagin et al. 2000), so both traits, mature third instars and diapausing eggs, heighten electivity by foraging fishes.

Diapausing egg passage through fish guts—Along with spines, *Bythotrephes* diapausing eggs were found in fecal pellets passed by laboratory fish (Fig. 7). Of the 113 mature diapausing eggs consumed by fish, 94% survived gut passage (i.e., were recovered in apparently good condition from fecal pellets or found loose in aquarium detritus). Eighty-one percent of the total were recovered within 24 h of consumption, and 18% were recovered between 24 and 48 h following consumption. Results of hatching experiments

Table 3. Example of applying the egg ratio technique to predict 1995 season deposition of spines (m^{-2} sediment area) in the central basin of Lake Michigan.

Sample date	Day of the year	Mean <i>Bythotrephes</i> (m^{-2} , \pm 95% CI)	d' (\pm 95% CI)	Estimated spines (period ⁻¹ m^{-2} , \pm 95% CI)
07 Jun 95	158	1.6(0.8)	0.15(0.02)	0.4(0.2)
23 Jun 95	174	48.9(35.2)	0.01(0.19)	31 (79)
29 Jun 95	180	58.5(18.7)	0.25(0.03)	41 (63)
11 Jul 95	192	80.5(42.2)	0.12(0.02)	153 (59)
27 Jul 95	208	79.1(117.0)	0.29(0.01)	261 (80)
10 Aug 95	222	244.0(88.7)	0.07(0.03)	410 (142)
24 Aug 95	236	86.7(24.8)	0.21(0.03)	332 (147)
07 Sep 95	250	55.2(16.3)	0.13(0.01)	173 (52)
17 Sep 95	260	46.4(15.9)	0.05(0.01)	47 (14)
01 Oct 95	274	52.3(11.6)	0.04(0.00)	23 (9)
Total	116 (d elapsed)			1,480 (254)

Table 4. Predicted spine deposition from the egg ratio techniques versus observed sediment trap totals (m⁻² sediment area) in the central basin of Lake Michigan.

Year	Sediment trap total spines (m ⁻² , ±95% CI)	b' predicted total spines (m ⁻² , ±95% CI)	d' predicted total spines (m ⁻² , ±95% CI)	Tangent r' applied to smoothed curve
No vertical migration				
1995	1,462(608)	1,080(153)	1,141(194)	748
1996	2,625(1,161)	1,592(165)	1,548(194)	776
Vertical migration				
1995	1,462(608)	1,401(204)	1,471(234)	1,097
1996	2,625(1,161)	1,844(192)	1,803(216)	1,036
1997	—	463(47)	441(98)	—

with eggs passed through fishes guts have been published (Jarnagin et al. 2000). Generally, 40–70% of naturally dropped eggs will hatch (Yurista 1997). For Lake Michigan mature diapausing eggs fed to fishes, we found 57% initiating development and 41% hatching successfully (Jarnagin et al. 2000).

Sequential sediment traps in Lake Michigan: Seasonal patterns of spines and diapausing eggs—Studies of pelagic *Bythotrephes* populations in Lake Michigan previously confirmed that this species does not overwinter as free-swimming stages (Lehman and Cáceres 1993). During the monitoring period, individuals were more abundant at offshore sites (mean ± 1 SE; 278 ± 105 individuals m⁻² during July and 570 ± 111 individuals m⁻² during September 2000, n = 8) than at nearshore sites (137 ± 60 in July; 218 ± 94 in September, n = 7, Pothoven et al. 2003; Mann–Whitney test, P = 0.09 for July; P = 0.02 for September). The 2000 values fell within the range of abundance reported from southeastern Lake Michigan transects during 1987–1998 (Lehman 1991; Lehman and Cáceres 1993; Pothoven et al. 2001). In the southern Basin, populations were largely parthenogenetic in July, with the incidence of diapausing eggs increasing in September (Pothoven et al. 2003).

During 1998–2001, diapausing eggs and entire spines were uncommon in sediment traps out of season (February–April), although a few broken tips would settle into traps from late December to April following winter storms. Spines and diapausing eggs first appeared in abundance starting in July (Fig. 11). There was a dual peak of mortality and diapausing egg production: the first in August and the second

in late October. The late October peak coincided with fall population decline (Vanderploeg pers. comm.). Diapausing egg peaks coincided roughly with peaks in spine settlement, as site correlation ranged from weak in shallow-tethered or nearshore traps (e.g., r = 0.510, trap T12, 100 m, southern basin; n = 10, P ~ 0.1) to much stronger in deeper traps (e.g., r = 0.798, trap T29, 200 m, northern basin; n = 10, P < 0.01).

The temporal correlation between settling spines and diapausing eggs is probably enhanced in deeper traps by simultaneous arrival of both items within fecal pellets. Clumps of spines with enclosed diapausing eggs were seen in some samples, similar to ones occasionally observed in Lake Michigan. The incidence of spine breakage in Lake Michigan was also high (65%, i.e., only 213 of 603 spines were not seriously broken or stripped of lateral barbs; subsamples from traps T12, T28, and T27), with lower values during the mid-August (52% breakage) and fall decline (61% breakage). The dual peak in spine and diapausing egg deposition probably reflects the reported seasonal abundance fluctuations of pelagic populations (Lehman and Cáceres 1993) as a mid-August peak and decline, and also fall recovery followed by final population decline.

During the 3 yr of monitoring (Table 6), deep-water tallies for yearly settling ranged between 43 and 339 spines trap⁻¹ yr⁻¹ (mean ± SD, 140.2 ± 88.9, n = 13 traps), whereas tallies for the nearshore site ranged between 27 and 108 spines trap⁻¹ yr⁻¹ (68.4 ± 30.4, n = 5 traps). Total yearly egg deposition ranged between 18 and 187 eggs trap⁻¹ yr⁻¹ at offshore sites (92.2 ± 67.1, n = 13 traps) and between 1 and 21 eggs trap⁻¹ yr⁻¹ for the nearshore site (6.8 ± 8.4, n

Table 5. Sample sizes and degree of spine damage. The number of spines and fragments gives total pieces observed. The reconstructed number of spines is based on the number of kinks. Percent no damage is the number of undamaged spines divided by the reconstructed total number of spines.

Sample group	No. of sample units	No. of spines and fragments	Estimated		No. no damage	% no damage
			No. of <i>Bythotrephes</i>	No. identified to instar		
Sediment trap spike tests	6	211	208	207	205	97.2
Fish/ <i>Bythotrephes</i> aquarium spike tests	12	424	417	416	407	96.0
Lake Michigan sediment traps	26	939	423	353	138	32.6
Fish/ <i>Bythotrephes</i> aquaria	27	1,458	903	625	127	14.1
1996 yellow perch gut contents	43	2,666	1,555	1,208	72	4.6

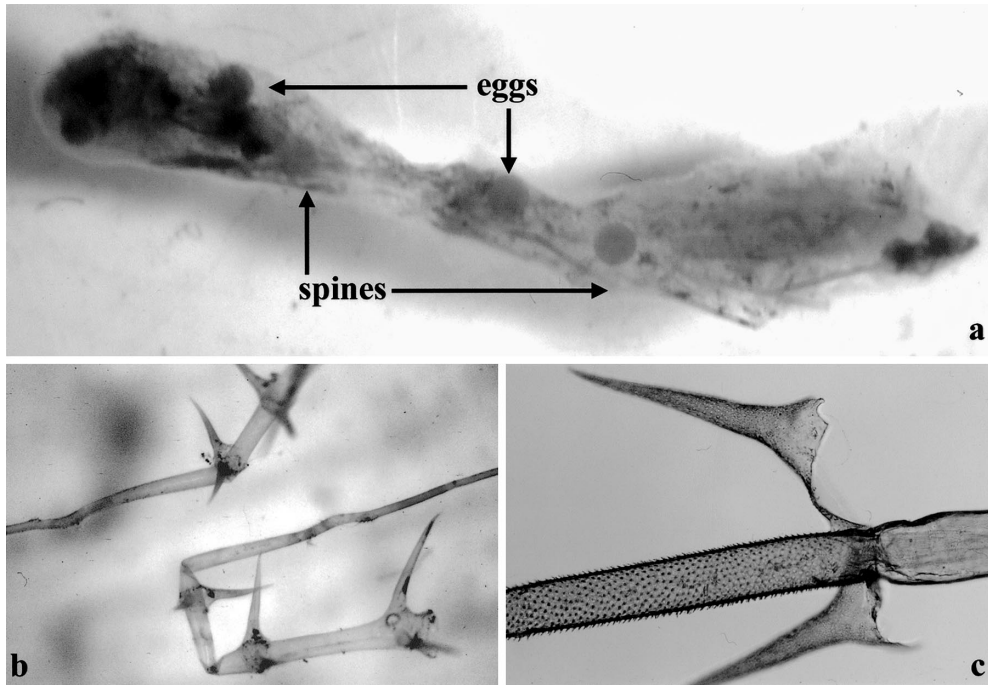


Fig. 7. Damage to spines from fish predation: (a) fecal pellet from fish/*Bythotrephes* aquarium experiment showing broken spines and enclosed diapausing eggs; (b) multiple bends in a spine from fish/*Bythotrephes* aquarium experiments (out of fecal pellet); (c) multiple barb damage (striping) in a *Bythotrephes* spine dissected from a Lake Michigan yellow perch (field collection).

= 5 traps). The number of spines and diapausing eggs captured at the nearshore site (water depth 55 m) was significantly less than the number captured in deeper, offshore (>100 m) waters (Table 6; spines, $t_{16} = 2.5, P = .02$; eggs, $t_{16} = 4.5, P = 0.001$). Relatively few diapausing eggs were deposited in coastal traps relative to spines (Table 6; eggs/spines: offshore, 0.69 ± 0.32 ; nearshore, 0.12 ± 0.16 ; $t_{16} = 5.1, P < 0.001$, with Bonferroni). Note that the mean

ratio at the nearshore site was comparable to values reported from Lake Michigan (0.08–0.10).

Therefore, during the investigated span, ~140 individuals were born and died in the water column above offshore traps, and 92 diapausing eggs were produced. Converting these totals ($m^{-2} yr^{-1}$) to make them comparable to Lake Michigan values, gives 4,463 births(deaths) $m^{-2} yr^{-1}$ and 2,935 diapausing eggs $m^{-2} yr^{-1}$.

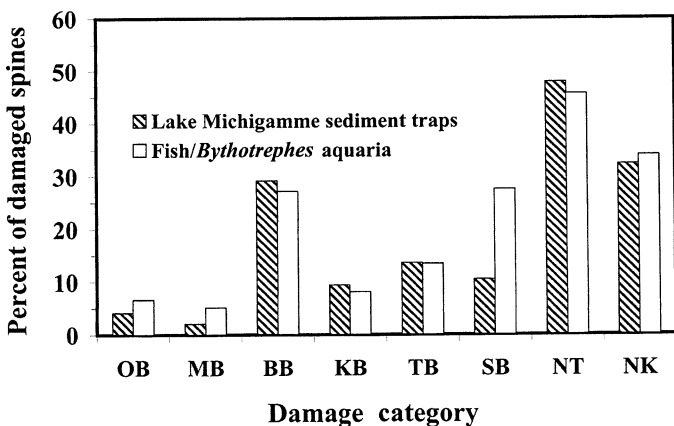


Fig. 8. Comparison of spine damage categories for the fish aquarium ($n = 545$ spines and fragments) and sediment trap samples ($n = 74$ spines and fragments). OB, one broken barb; MB, more than one broken barb; BB, broken between barbs; KB, kink broken; TB, tip broken; SB, spine bent; NT, no tip present; NK, no kink present.

Discussion

In the case of *Bythotrephes*, unique morphological traits allowed us to cross-compare indirect Edmondson–Paloheimo egg ratio estimates of mortality with a more direct technique based on deposition of spines into sediment traps. Cross-comparisons indicated that both techniques were concordant, producing moderately reliable and similar estimates of mortality and diapausing egg production. Even if the sampling in Lake Michigan missed some late-season dynamics, the coordinated sampling of plankton and settling material afforded legitimate expected versus observed cross-comparisons. Neither technique was without fault, such as curtailment of pelagic sampling by weather conditions (egg ratio) and possible benthic nephloid focusing of fecal pellets into bottom sediment traps (sediment trap technique), the latter because there were often slightly elevated totals in the deepest traps. Yet the two techniques complemented each other, confirming relatively high mortality and low diapausing egg production in Lake Michigan. Spine breakage suggested that the primary source of mortality in the recently colonized

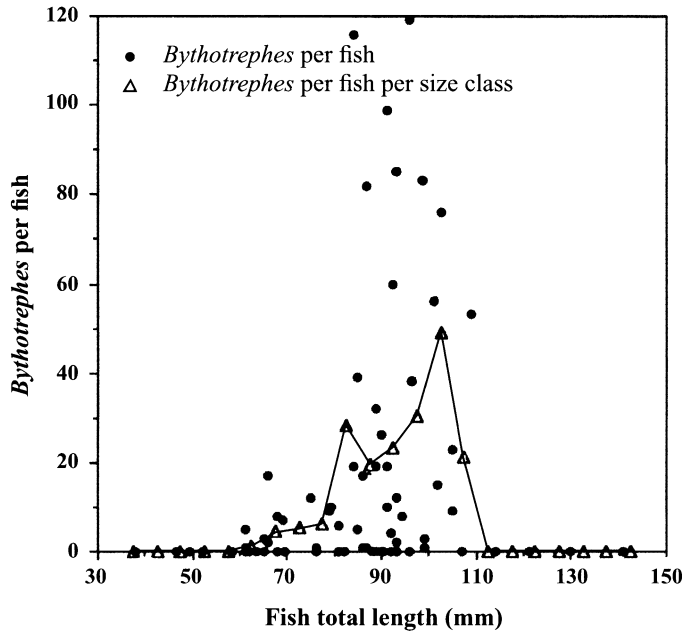


Fig. 9. Number of *Bythotrephes* consumed by yellow perch, plotted as a function of fish total length (1996 samples, $n = 74$). Dots give totals from individual fish guts, whereas triangles give means for each 5-mm size interval. Small sizes fail to consume *Bythotrephes* because of the spine, whereas larger size fish choose larger, alternative prey species.

inland lake was fish predation, a hypothesis confirmed by investigation of field breakage patterns and laboratory tests.

Fish predation has important influences on both pelagic and overwintering stages of the life history. The seasonal mean ($\pm 95\%$ CI) number of young per female in Lake Michigan (parthenogenetic phase) was 2.7 (± 0.7) for 1995 and 3.2 (± 0.8) for 1996, compared with 5.2 (± 0.3) for offshore and 4.0 (± 0.3) for nearshore Lake Michigan (Pothoven et al. 2003; t -test, $P < 0.05$ for Lake Michigan vs. Lake Michigan). In both cases, the brood sizes were less than usually seen in other freshwater cladoceran species of comparable size. Although adult body size without the spine (2 mm) is comparable to large coexisting cladocerans, *Bythotrephes* has a relatively long embryonic developmental time (~ 6 d, Yurista 1997). The relatively low number of eggs carried by *Bythotrephes* relative to similar-sized pelagic species, plus the longer developmental times, produces a lower intrinsic rate of natural increase. Yet the species is better protected against fish predation by having the spine, so there is compensation.

The spine protects instars from ingestion by the most abundant smaller fish, the early YOY stages. However, analysis of damaged *B. cederstroemi* spines recovered from sediment traps in 1995 and 1996 and from fish feeding experiments, suggests that 62–73% of the mortality in those years was from fish predation. Our results indicate that yellow perch do not begin to access *Bythotrephes* as a food source until after 55 mm TL, but the numbers consumed are substantial on an individual fish basis. Avoidance by small YOY fish is consistent with previous results from perch and rainbow trout (Barnhisel 1991b; Schneeberger 1991; Barnhisel and Kerfoot 1994). Occasional inges-

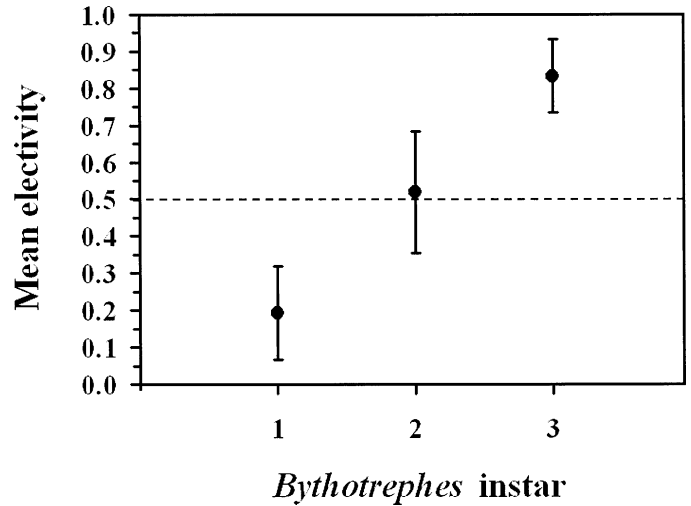


Fig. 10. Mean α_i (Lampert and Sommer's formulation of Chesson's Alpha index) for various *Bythotrephes* instar categories. Error bars indicate $\pm 95\%$ CI values from individual fish. Dashed line at $\alpha = 0.5$ indicates no electivity, whereas values > 0.5 indicate positive electivity. Values < 0.5 indicate negative electivity ($n = 23$).

tion of *Bythotrephes* by perch between 32 and 55 mm TL could result in gut puncture because, at this size, spines are twice the length of stomach dimensions (Compton and Kerfoot in press). Branstrator and Lehman (1996) also report threshold sizes of 40 and 30 mm, respectively, for alewife and bloater chub from Lake Michigan.

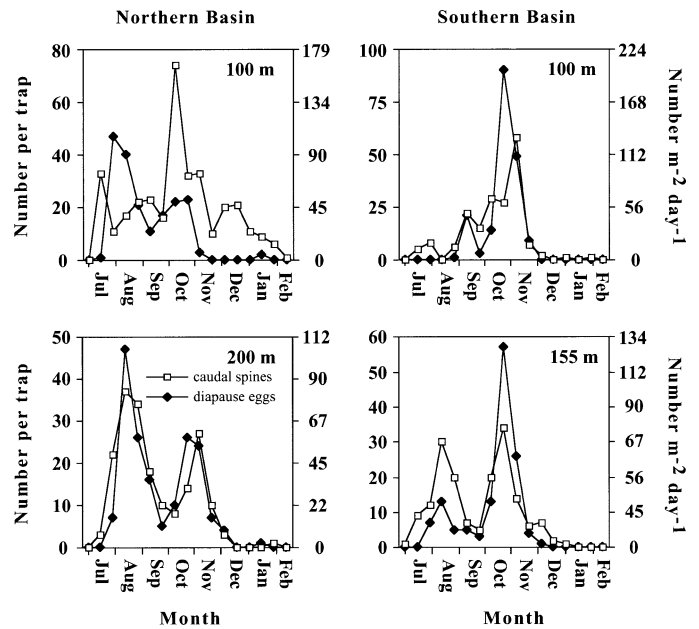


Fig. 11. The seasonal pattern for spines and diapausing eggs that settle into Lake Michigan northern (T29) and southern basin (T12) sequential sediment traps. Sequential sediment traps were tethered on the same line at different depths for each site. Counts of spines and diapausing eggs per trap are given for 2-week collections and corresponding fluxes (numbers $m^{-2} d^{-1}$). Note the high correlation between spines and eggs in the deeper traps.

Table 6. Yearly tallies for spines and diapausing eggs in Lake Michigan sequential sediment traps. If spines were broken, numbers were reconstructed from number of kinks.

Lake basin	Trap (tethered depth, m)	Site depth (m)	Collection date	No. of spines	No. of eggs	Eggs : spines
Northern	T29 (30)	260	01 Jul 00–09 May 01	74	74	1.00
	T29 (100)	260	01 Jul 00–19 May 01	160	187	1.17
	T29 (200)	260	01 Jul 00–11 May 01	186	173	0.93
Southern	T12 (30)	160	11 Jun 98–25 May 99	46	18	0.39
	T12 (30)	160	17 Jun 99–22 May 00	107	60	0.59
	T12 (100)	160	01 Jul 00–05 May 01	182	187	1.03
	T12 (155)	160	11 Jun 98–13 May 99	106	24	0.23
	T12 (155)	160	17 Jun 99–22 May 00	93	53	0.57
	T12 (155)	160	01 Jul 00–05 May 01	168	134	0.80
	T28 (30)	110	17 Jun 99–22 May 00	43	33	0.77
	T27 (30)	110	12 Jun 99–22 May 00	53	45	0.85
	T27 (30)	110	01 Jul 00–05 May 01	265	39	0.15
	T27 (105)	110	01 Jul 00–05 May 01	339	171	0.50
	T24 (30)	55	01 Jul 99–21 Oct 99	54	21	0.39
	T24 (30)	55	31 May 00–05 May 01	27	1	0.04
	T24 (30)	55	31 May 00–05 May 01	83	8	0.10
	T24 (50)	55	31 May 00–12 Oct 00	70	2	0.03
	T24 (50)	55	31 May 00–12 Oct 00	108	2	0.02

Our study emphasizes the importance of the thick, protective outer membrane of *Bythotrephes* diapausing eggs (Jarnagin et al. 2000). Saint-Jean and Pagano (1995) fed subitaneous (summer) eggs from a variety of copepods, rotifers, and cladocerans to catfish (*Heterobranchus longifilis*) and calculated gut passage survivability and viability. Hatching rates were compared with eggs removed from brood pouches. Eggs of the cladoceran species tested (*Moina micrura* and *Diaphanosoma excisum*) exhibited no viability when subjected to gut passage. Low viability was attributed to a thin outer membrane. Eggs of copepods and rotifers that survived gut passage possessed thicker outer egg membranes. By contrast, hatching success of *Bythotrephes* diapausing eggs was high following gut passage (Jarnagin et al. 2000). The evolution of the tough, dense outer membrane thus is probably an adaptation for gut passage.

Marcus and Fuller (1986) measured the settling velocity of copepod subitaneous and diapausing eggs, then calculated the density of those eggs from Stokes' equation and from density gradient centrifugation. On the basis of density gradient centrifugation (Jarnagin et al. 2000), the density of *Bythotrephes* diapausing eggs was 1.13–1.20 g cm⁻³ for mature stages, close to the value of 1.13 g cm⁻³ reported by Yurista (1997). The egg has an especially thick outer chitinous shell and a much higher density than other copepod, cladoceran, and invertebrate eggs. Settling velocities ranged between 9 and 12 mm s⁻¹, three to five times faster than most copepod and cladoceran diapausing eggs (*Bythotrephes*, 10.0 ± 0.4 mm s⁻¹, n = 150; *Daphnia retrocurva*, 2.6 ± 0.2, n = 30; *Holopedium*, 3.4 ± 0.3, n = 30; *Diaptomus*, 1.9 ± 0.2, n = 22). Hence, the thick shell insures successful gut passage through fish guts, but the high density and large size contribute to unusually high sinking speeds. In terrestrial studies, wind disperses some seeds, whereas others are dispersed by animals. The dichotomy might also apply to water bodies, as many diapausing eggs disperse via turbu-

lence and are carried far from the production site. In contrast, *Bythotrephes* diapausing eggs are heavy and fall rapidly through the water column. However, given the likelihood of ingestion by fish, they will be dispersed by animals much farther than by passive settling.

Predation by fishes in inland lakes might limit the spread of *Bythotrephes*. In Lake Michigan, *Bythotrephes* are compressed into a restricted stratum above the thermocline, have lower parthenogenetic brood sizes (resource shortage), and are subject to high fish predation in the fall. Existence seems precarious, with about 2,000 deaths(births) m⁻² yr⁻¹ compared with only 300 diapausing eggs m⁻² yr⁻¹. Our estimates of mortality in the inland lake by fish predation (62–71%) were high. In the deeper stations of Lake Michigan, egg-bearing females are spread over much greater depths (>30 m), parthenogenetic brood sizes are larger (greater resources), and there is a more balanced relationship between pelagic deaths and diapausing egg production (4,460 deaths[births] m⁻² yr⁻¹ and 2,940 diapausing eggs m⁻² yr⁻¹). At a nearshore site, the relationship seems more like that observed in Lake Michigan: lower parthenogenetic brood sizes (fewer resources) and 2,178 deaths(births) m⁻² yr⁻¹ matched against 217 diapausing eggs m⁻² yr⁻¹. Two points in the life cycle could be potential bottlenecks: (1) the restricted temperature niche in the water column for parthenogenetic generations and (2) diapausing egg production and spring hatching for the overwintering generation (Fig. 1). Low densities of first-generation individuals suggest low hatching success (9–14%, Table 1). Low production of diapausing eggs also influences the long-term development of the egg bank.

This is not the first attempt to directly monitor seasonal patterns of zooplankton mortality. For example recently, Gries and Gude (1999) utilized short-interval trapping of falling *Daphnia* remains. However, we are the first to apply “refractory” remains toward that end, including remains that

pass through fish guts intact. Fish might be limiting the success of inland lake cercopagid populations by (1) digesting nonmature diapausing eggs or (2) prematurely curtailing autumn diapausing egg production. The conspicuous nature of *Bythotrephes* in large lakes and its occurrence in larger fish guts is documented in the literature (De Bernardi and Giussani 1974; Mills et al. 1992; Branstrator and Lehman 1996). In shallow-draft, small lakes, size- or visibility-selective mortality could reduce recruitment by differentially targeting adults that carry diapausing eggs, producing a pattern similar to that observed in Lake Michigan during spring 1997. A collapse scenario seems to have played out in two of the originally colonized Minnesota inland lakes (Boulder and Fish lakes, John Lindgren pers. comm.).

The morphological adaptations (spines, thick-walled diapausing eggs) that adjust life histories to local mortality factors (fish predation) also inadvertently promote dispersal. For *Bythotrephes*, several dispersal vectors are possible. Spines can snag on nylon fish lines, gill nets, or seines. If the snagged third instars possess diapausing eggs, fisherman could unwittingly transport these eggs with their gear to inland lakes, producing a major dispersal vector proportional to seasonal fishing visitation and bait fish seining activity. Consumption by fish could also create an important dispersal vector via diapausing eggs. When females carry opaque, conspicuous diapausing eggs in the fall, they are more subject to ingestion by larger YOY fish. However, because *Bythotrephes* diapausing eggs pass through fish guts in such a highly viable condition, some contribution to the overwintering egg bank is ensured, despite ingestion. In Lake Michigan, high spine damage suggests that a sizable fraction of overwinter diapausing eggs have passed through the guts of a fish.

Mellors (1975) reported selective ingestion of *Daphnia* ephippial females by fish, although survival through fish guts and hatching was relatively poor (1.5% survival). That is, fish might act to incidentally disperse *Daphnia* diapausing eggs, but the life history could not tolerate high levels of fish predation on ephippial-carrying individuals. On the other hand, *Bythotrephes* has a high tolerance for fish predation, suggesting that fish predation is a natural part of the cercopagid life history cycle (i.e., animal-dispersed stage). Proctor (1964) discovered that a variety of crustacean eggs can be recovered in viable condition from the lower digestive tract of both wild and domestic ducks and that these eggs can be hatched successfully.

Despite incidental dispersal by birds, the primary dispersal vector is probably through bait fish (Jarnagin 1998; Jarnagin et al. 2000). So-called bait fish such as spottail shiners (60–90 mm) are known to consume *Bythotrephes* in large numbers (Hartman et al. 1992; Compton and Kerfoot in press). Ludwig and Leitch (1996) and Jarnagin et al. (2000) suggested interbasin transfer of biota via anglers' bait buckets. Diapausing eggs could be dispersed by fish or in live wells, as anglers travel between lakes in the watershed. The rapid spread of *Bythotrephes* across the landscape (MacIsaac et al. in press) suggests that this species has several dispersal options in addition to an ability to fit into existing large-lake food webs (Barnhisel and Kerfoot 1994 in press).

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