

Contrasting life histories of the predatory cladocerans *Leptodora kindtii* and *Bythotrephes longimanus*

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The predatory cladocerans, Leptodora kindtii (Focke, 1844) and Bythotrephes longimanus (Leydig, 1860), express markedly different life-history traits. Leptodora produce small-bodied neonates that mature at small sizes but continue to grow throughout life. Bythotrephes produce larger neonates in both relative and absolute terms that grow rapidly to a large size at maturity whereupon they curtail somatic growth and divert resources mainly to reproduction. Despite their remarkable differences, the sets of life-history traits of both species appear to be solutions to the same basic selection pressures imposed by visually discriminating gape-limited fishes and foraging constraints imposed by prey size. Leptodora stresses pre-contact (transparency) while Bythotrephes stresses postcontact (caudal spine) modes of morphological defense against fishes. Mounting these disparate modes of defense has consequences for selection on timing and allocation to body growth that may underlie competitive imbalance between the species. Owing to the production of large-bodied neonates that grow rapidly, Bythotrephes quickly attain body sizes that both admit them to a broader prey base in size and taxonomic variety, and allow shorter prey handling times, in comparison to Leptodora. This provides Bythotrephes with a wider and more exploitable prey base from an earlier age and may explain why Leptodora has declined in density following Bythotrephes invasion into some North American lakes. The divergent sets of life-history traits expressed by Leptodora and Bythotrephes parallel two dominant life-history strategies evolved by phytoplanktivorous species of the order Cladocera.

INTRODUCTION

Life-history traits of organisms theoretically integrate across selection pressures and represent, in composite, adaptations that maximize species survival and reproductive success over an organism's life span (Stearns, 1992). Studies of life-history traits can thus provide considerable insight to the relative strength of ecological interactions that operate on fitness. Life-history analyses have proven particularly useful in illuminating the relative strengths of selection pressures acting on rotifer and crustacean zooplankton (Allan, 1976; Lynch, 1980). In reviewing life histories of phytoplanktivorous taxa of the order *Cladocera*, Lynch (Lynch, 1980) identified the existence of two dominant strategies: (1) small-bodied species (e.g. *Bosmina longirostris*) that mature early but show indeterminate somatic growth and (2) large-bodied species (e.g. *Daphnia pulex*) that delay

maturation but thereafter curtail somatic growth and commit more energy to offspring production, in relative terms, than do small-bodied cladocerans. He deduced that both strategies evolved to maximize consumption efficiency and to reduce mortality to vertebrate as well as to invertebrate predation. His insightful analysis lent considerable weight to the hypothesis that invertebrate predation has been a significant selective force, on par with vertebrate predation, in shaping local fitness measures of phytoplanktivorous *Cladocera*.

Comparatively little attention and analysis has been directed to the life-history strategies of large-bodied, carnivorous *Cladocera* (Allan, 1976; Lynch, 1980). Recent range expansions by *Bythotrephes longimanus* (*Cladocera*: Onychopoda) into North America (MacIsaac *et al.*, 2000), and across Eurasia (Grigorovich *et al.*, 1998), have spurred a variety of new studies on its ecology

providing enough literature to define adequately its life history across a representative range of ecosystems. Heightened interest in the large carnivore *Leptodora kindtii* (Cladocera: Haplopoda) has also grown appreciably in recent decades, sparked in part by collapse of *L. kindtii* densities concurrent with *B. longimanus* invasion in some North American lakes (Branstrator and Lehman, 1991; Makarewicz *et al.*, 1995; Yan and Pawson, 1997).

Despite their affiliation as Cladocera, *L. kindtii* and *B. longimanus* are otherwise taxonomically distinct. *L. kindtii* (hereafter *Leptodora*) is the sole extant species of the Haplopoda, whereas *B. longimanus* belongs to the Onychopoda along with two other freshwater taxa, *Polyphemus* and *Cercopagis*, and a variety of marine species (Richter *et al.*, 2001; Cristescu and Hebert, 2002). Researchers may still recognize two species of *Bythotrephes* (*B. longimanus* and *B. cederstroemi*) based on morphological criteria, even though recent genetic analyses suggest that the two morphological variants are members of a single, polymorphic species termed *B. longimanus* (Berg and Garton, 1994; Therriault *et al.*, 2002). The larger-bodied, more robust, *B. cederstroemi*, remains the only morphological variant of the two to have invaded North America. This study focuses on the *B. cederstroemi* variant but data from both variants are included. Hereafter, the name *Bythotrephes* refers to both or either morphological variant where distinction is relatively unimportant, otherwise the species descriptor is used.

Leptodora and *Bythotrephes* bear a number of gross morphological differences (Fig. 1). *Leptodora* has six pairs of prehensile legs called the 'trap basket' emanating from the thorax and used for prey capture; a long, segmented abdomen terminating in two small, caudal spine stylets; a bivalve carapace that shrouds only the brood chamber; a compound eye which is small in relation to body length (Branstrator and Holl, 2000) and a marked degree of body transparency. By contrast, *Bythotrephes* has four pairs of prehensile legs emanating from the thorax used to capture prey; a short, nonsegmented abdomen terminating in a long, stiff caudal spine; no bivalve carapace; a forward positioned, large compound eye implicated in aiding prey detection (Muirhead and Sprules, 2003), and occasional body and spine coloration (blue, green, brown and red). Unlike *Leptodora*, most of the total length of *Bythotrephes* is contributed by the caudal spine.

By analogy to the aforementioned life-history analysis of phytoplanktivorous Cladocera (Lynch, 1980), this study examines new and published data on several life-history traits of *Leptodora* and *Bythotrephes*. The study is guided by two primary objectives: (i) to deduce the principal selec-

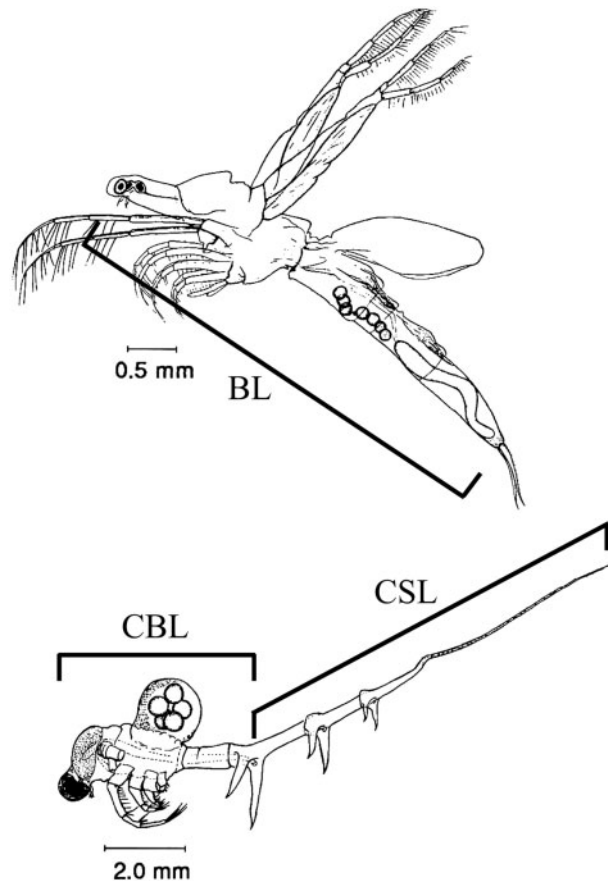


Fig. 1. Line drawings of parthenogenetically derived *Leptodora* and *Bythotrephes*. *Leptodora*'s brood chamber is shown empty, her ovaries carry preformed eggs. *Bythotrephes*' second antennae are not shown, her brood chamber holds gametogenic eggs. Darkened lines indicate length estimates in this study: BL is body length, CBL is core body length, CSL is caudal spine length. *Bythotrephes*' total length is given as the sum of CBL and CSL. Parts of this figure are reprinted from Thorp and Covich (Thorp and Covich, 2001) with permission from Elsevier.

tion pressures shaping fitness in *Leptodora* and *Bythotrephes* through comparative evaluation of their life-history traits and (ii) to explore whether fundamental differences in life-history traits of the two predatory cladocerans can provide a mechanistic basis for understanding their interspecific competitive abilities. Life-history analysis covers birth size, maturation size, ages at maturation and first parturition, somatic growth, clutch size, egg size, relative offspring weight, relative clutch weight and gametogenic egg and neonate characteristics (summarized in Table 1). Among cladocerans, the females assume the dominant roles in seasonal population dynamics and bear directly the resource tradeoffs in growth and reproduction at the core of life-history tactics. Accordingly, this analysis focuses exclusively on the females of *Leptodora* and *Bythotrephes*.

Table I: Comparative traits of *Leptodora* and *Bythotrephes*

Trait	<i>Leptodora</i>	<i>Bythotrephes</i>
Dominant fish defense	transparency (pre-contact)	caudal spine (postcontact)
Neonatal length (mm)	2 ^{2,3}	core: 1.6–2.5; spine: 4.6–6.7 ¹
Neonatal weight (µg)	2.5–5.7 ^{1,4,5,6}	core + spine: 25–98 ¹
Maturation length (mm)	5–6 ^{2,3}	core: 2.5–4.0; spine: 6.4–9.0 ¹
Maturation weight (µg)	29–46 ^{1,4,5,6}	core: 97–289; spine: 11–45 ¹
Maturation age (days)	10 at 15°C; 6 at 25°C ³	9.2 at 12.7°C; 5.4 d at 21°C ^{7,8}
First parturition age (days)	15.9 at 15°C; 8.6 at 25°C ³	14 at 12.7°C; 8.9 d at 21°C ^{7,8}
Soma growth as juvenile : adult	minor : major	major : little or none
Clutch size (number of eggs)	5–20 common ^{2,4}	2–7 common ^{9,10,11,12}
Individual egg size (mm)	~0.4 (diameter) ²	minute (unmeasured)
Relative individual offspring weight (% of adult)	8.8–15.0 ^{1,4,5,6}	34.2–36.9 ¹
Relative total clutch weight	<maternal weight ²	≥maternal weight ^{1,12,13}
Gametogenetic egg weight (µg)	10.4 ¹⁴	25.9 ¹⁴
Gametogenetic egg color	colorless ¹⁵	golden-brown ¹⁶

See text for calculations and references. All weights are dry weights. Aside from the last two entries, all entries refer to traits of females from parthenogenetic eggs and the characteristics of their parthenogenetic clutches. Most of the values given for *Bythotrephes* are based on the *B. cederstroemi* variant (Data sources: 1, this study; 2, Andrews, 1948; 3, Vijverberg and Koelewijn, 2004; 4, Vijverberg *et al.*, 2005; 5, Lehman and Cáceres, 1993; 6, Culver *et al.*, 1985; 7, Yurista, 1992; 8, Lehman and Branstrator, 1995; 9, Yan and Pawson, 1998; 10, Lehman and Lehman, 1996; 11, Ketelaars *et al.*, 1995; 12, Straile and Hälbich, 2000; 13, Lehman *et al.*, 1997; 14, Andrew and Herzig, 1984; 15, Sebestyen, 1949; 16, Jarnigan *et al.*, 2000).

METHOD

Approach

Several life-history traits were estimated directly. A weight-at-length relationship was constructed with nonpreserved *Leptodora* to estimate somatic growth trends. With *Bythotrephes*, original measurements were made of neonate weights and relative offspring weights, as well as of the partitioning of resources between body growth and reproduction. Otherwise, literature review was used to assess trait variation over the broadest geographic range available for both taxa.

Developmental stage in *Bythotrephes* is based on the numbers of pairs of lateral barbs on the caudal spine (Yurista, 1992). Stage 1 (neonate) individuals possess a single pair of lateral barbs, successive morphological stages possess 2 (stage 2) followed by 3 (stage 3) pairs, each pair being added during ecdysis events of the core body at the proximal end where the spine joins the body. Stage 3 animals continue to molt throughout life coincident with the release of neonates (Yurista, 1992). Thus, stage 3 actually represents individuals across a range of ages and molting histories. At the start of stage 3, *Bythotrephes* mature (with some exceptions, see below) and cease caudal spine growth (Yurista, 1992). To estimate the degree of postmaturation core body growth, an approach was implemented that used *Bythotrephes* collected directly from the field and that capitalized on

the synchronous timing of maturation and recruitment to stage 3. Owing to synchronicity in these two events, allometric ratios of caudal spine weight/core body weight could be used to evaluate whether adults continue to accrue core body weight postmaturation. The following decision rule was employed. Allometric ratios that decline with increasing total weight (core body plus caudal spine) indicate accrual of core body weight postmaturation. Alternatively, allometric ratios that remain fixed indicate the termination of core body growth at maturation. To test wild populations, caudal spine weight/core body weight ratios were regressed against total weights. Their least-square linear relationships were evaluated for slope significance ($\alpha < 0.05$). Because many published studies report length as opposed to weight metrics, a proxy ratio—caudal spine length/core body length—was used to query the literature to evaluate postmaturation growth trends in *Bythotrephes* populations from other ecosystems.

Procedure

Leptodora and *Bythotrephes* were collected from Pike Lake and Island Lake, respectively (St. Louis County, Minnesota, USA, 47°00' N 92°10' W). *Leptodora* were collected on 18 July and 22 August 2003; *Bythotrephes* were collected on 27 and 30 June, 25 and 29 July, 29 August and 5 September 2003. Animals were sampled by multiple casts of a Wisconsin-style net (0.5-m-diameter opening,

500- μm aperture mesh) towed from just above the sediment to the lake surface in locations of about 10-m depth in the morning hours. Samples were diluted to 1-L glass jars and returned to the laboratory. Nonpreserved specimens from the day of collection only were used for study.

Lengths were measured by ocular micrometer (Leica MZ-125). *Leptodora* was measured live from the center of the compound eye to the base of the caudal spine stylets (Fig. 1). Immediately prior to length measurements, each *Bythotrephes* was killed by piercing the heart with a needle. Core body and caudal spine length measurements of *Bythotrephes* followed established standards (Burkhardt, 1994; Fig. 1).

Weight measurements were determined on dried specimens (12 h, 60°C) by electrobalance (Cahn C-33) using dried and tared tin capsules (KHK Enterprises, Inc.). Individual measurements were recorded to the nearest microgram. Accuracy was $\pm 2 \mu\text{g}$ based on weights of empty tin capsules carried through the procedure. *Leptodora* were weighed whole with any embryos in the brood chamber being removed before weighing. *Bythotrephes* were prepared for weighing by severing the caudal spine at its junction with the core body. The core body and caudal spine were then dried and weighed separately. Care was taken to choose visibly healthy females in a barren, reproductive state for these measurements.

Gravid stage 3 *Bythotrephes* carrying embryos in the advanced, black-eye stage of development were also removed from lake collections on the day of sampling. These were placed in individual 6-mL wells of lake water without food and permitted to hatch their neonates. For clutches that emerged fully within 6 h, the mother was immediately processed, as described above, for length and weight metrics. Each of her neonates was measured for core body length and caudal spine length as described above, but dried and weighed whole. All data were analysed in SYSTAT 10.0.

RESULTS AND DISCUSSION

Contrasting organism traits

Birth size

Leptodora neonates are released from mothers almost uniformly at 2 mm body length, with little variation, suggesting strong stabilizing selection (Andrews, 1948; Costa, 1967; Manca and Comoli, 1995; Vijverberg and Koelewijn, 2004). Free-swimming neonates of 1.19 mm (Vijverberg, 1980), 1.25 mm (Mordukhai-Boltovskaia, 1958) and 1.5 mm (Costa, 1967) have been reported but are rare. Neonate body length is positively related to maternal body length but only weakly ($L_{\text{newborn}} = 0.88 + 0.14 L_{\text{adult}}$, $r^2 = 0.55$) (Vijverberg and Koelewijn, 2004).

Estimated dry weights of *Leptodora* at 2 mm body length range from 2.5 to 5.7 μg [equations (1)–(4), see below].

Bythotrephes neonates are larger and more variable in size than *Leptodora* neonates. Dry weights of neonatal *Bythotrephes* birthed from wild caught mothers range from ~ 25 to 98 μg in Island Lake (Table II), 20 to 150 μg in the Laurentian Great Lakes (Sullivan and Lehman, 1998) and ~ 10 to 65 μg in Lake Constance, Germany (Straile and Hälbich, 2000). Stage 1 *Bythotrephes* from the wild (age unknown) also range remarkably in length and dry weight (Ketelaars *et al.*, 1995; Lehman and Lehman, 1996), implying wide variation in neonatal size. One study found that stage 1 females from the same location in Lake Michigan, USA, differed by as much as $\times 4$ dry weight on average between July and September 1990 (Burkhardt, 1994).

Maturation size

Maturation size in *Leptodora* is taken to begin when parthenogenetic eggs are deposited into the brood chamber for the first time. Field and lab studies with live specimens almost uniformly find this to begin at 5–6 mm body length (Andrews, 1948; Costa, 1967; Abrusán, 2003; Vijverberg and Koelewijn, 2004). Estimated dry weights of *Leptodora* at 5.5 mm body length range from 29 to 46 μg [equations (1)–(4) see below]. Seven juvenile instars (based on ecdysis events) have been reported for *Leptodora* raised at 17.5°C (Vijverberg and Koelewijn, 2004).

Maturation size in *Bythotrephes* is difficult to score using the moment of egg entry into the brood chamber because they deposit minute eggs that are initially difficult to see. Maturity is considered to begin when embryonic development becomes significant and this generally occurs at the start of stage 3 (Yurista, 1992). Female *Bythotrephes* discontinue body growth upon maturation (see below), thus the weight of a barren stage 3 female can be used as a surrogate to estimate maturation weight. Using this proxy, data from a variety of studies show that *Bythotrephes* mature at both larger and more variable weights than do *Leptodora* (Burkhardt, 1994; Lehman and Lehman, 1996; Yan and Pawson, 1998). In Island Lake during 2003, barren stage 3 females ranged in dry weight from 108 to 326 μg (Table II). Additional variation in maturation weight in *Bythotrephes* can result from the fact that females occasionally mature and bear offspring at stages 1 and 2 (Mordukhai-Boltovskaia, 1957; Ketelaars *et al.*, 1995; Straile and Hälbich, 2000; Pothoven *et al.*, 2001, 2003).

Ages at maturation and first parturition

Few age-specific, life-history traits have been published for predatory cladocerans. This dearth may reflect the fact that they are rarely maintained in the lab. With

Table II: *Bythotrephes* dry weights (core body plus caudal spine) in μg , presented as mean \pm SD n (range), for nonpreserved specimens from Island Lake, 2003

Collection time	Stage 1	Stage 2	Stage 3	Stage 3*	Neonate
June	77.0 \pm 15.4	152.2 \pm 30.0	232.0 \pm 42.1	197.1 \pm 41.3	68.3 \pm 11.8
	24 (47–106)	24 (101–191)	23 (147–303)	12 (140–272)	36 (46–93)
July	73.0 \pm 18.7	156.1 \pm 51.6	239.2 \pm 33.3	199.0 \pm 20.1	73.5 \pm 12.1
	28 (32–108)	24 (88–272)	27 (169–326)	6 (163–221)	16 (56–98)
August–September	76.8 \pm 25.0	120.6 \pm 26.4	184.7 \pm 26.2	153.7 \pm 24.4	52.5 \pm 13.6
	28 (32–115)	25 (71–164)	26 (146–242)	15 (108–203)	43 (25–75)

Individuals were reproductively barren at the time of death. Stages 1, 2 and 3 refer to numbers of pairs of lateral barbs on the caudal spine. Stage 3* are mature females in their barren state immediately postbirthing. Neonates are the offspring birthed to stage 3* females. See methods for specific collection dates.

Leptodora, temperature-dependent development times from neonate to maturation (5.5 mm body length) have been estimated at \sim 10 days (15°C) and \sim 6 days (25°C) (Vijverberg and Koelewijn, 2004). Comparative developmental times to maturation in *Bythotrephes* (at stage 3) are 9.2 days (12.7°C) (Yurista, 1992) and 5.4 days (21°C) (Lehman and Branstrator, 1995). Times to first parturition (release of first clutch of free-swimming neonates) in *Leptodora* can be determined indirectly by adding egg development times of 5.9 days (15°C) and 2.6 days (23°C) (Vijverberg and Koelewijn, 2004) to the maturation times above, giving 15.9 days (15°C) and 8.6 days (25°C), respectively. Direct estimates of time to first parturition in *Bythotrephes* are 14 days (12.7°C) (Yurista, 1992) and 8.9 days (21°C) (Lehman and Branstrator, 1995). The comparative age statistics suggest that temperature-dependent times to maturation and first parturition are generally shorter by days in *Bythotrephes*, even when *Bythotrephes* mature at stage 3.

Somatic growth

The body weight-at-length trend for nonpreserved *Leptodora* from Pike Lake is shown in Fig. 2. June and August collections were pooled and are described statistically, with nonlinear regression, as:

$$\mu\text{g DW} = 1.018 \text{ mm}^{2.042}, r^2 = .89, n = 212 \text{ (Pike Lake)} \quad (1)$$

In comparing equation (1) to body weight-at-length relationships for nonpreserved *Leptodora* from Lake Tjeukemeer, the Netherlands:

$$\mu\text{g DW} = 0.79^{2.38}, r^2 = .95 \text{ (Vijverberg et al., 2005)} \quad (2)$$

preserved *Leptodora* from Lake Michigan, USA:

$$\mu\text{g DW} = 0.479 \text{ mm}^{2.408}, r^2 = .93, n = 67 \text{ (Lehman and Cáceres, 1993)} \quad (3)$$

and preserved *Leptodora* from Lake Erie, N. America:

$$\mu\text{g DW} = 1.560 \text{ mm}^{1.873}, r^2 = 0.99 \text{ (Culver et al., 1985)} \quad (4),$$

no major systematic biases are evident implying relatively uniform allometric trends in body weight-at-length among these ecosystems. All four trends were used to estimate natural ranges in other life-history traits.

As juveniles, *Leptodora* and *Bythotrephes* express markedly different growth schedules. *Leptodora* neonates (2 mm body length) from Pike Lake amass only 29 μg , on average, in growing to maturity (5.5 mm body length) [equation (1), Fig. 2]. By comparison, Island Lake

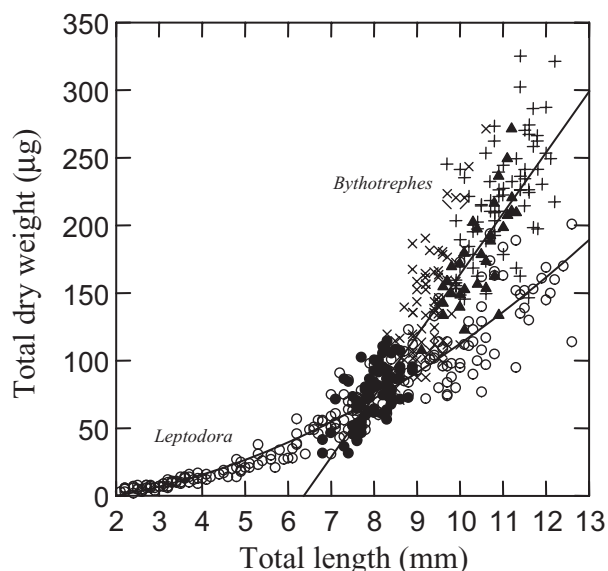


Fig. 2. Weight-at-length relationships for *Leptodora* (○) from Pike Lake [equation (1)] and *Bythotrephes* from Island Lake (total weight = 45.2 \times total length - 287.2, $r^2 = 0.81$, $n = 262$), 2003. *Bythotrephes* developmental stages are (● = 1, \times = 2, + = 3 and \blacktriangle = 3* (see methods). A nonlinear regression model was used with *Leptodora*. With *Bythotrephes*, a linear regression model gave a higher r^2 than a nonlinear model.

Bythotrephes amass on average 143 μg in growing from stage 1 to maturity (stage 3) (Fig. 2, Table II). This represents $\times 5$ more mass accrued by *Bythotrephes* in the juvenile phase over comparatively shorter temperature-dependent times. This trend highlights the emphasis placed by *Bythotrephes* on early somatic growth and is consistent with their high consumptive demand based on energetic modeling (Lehman and Branstrator, 1995; Yurista and Schulz, 1995). Elemental ratios of C : P and N : P provide further evidence for different growth rates between species. Both elemental ratios are about 40% lower in body tissues of *Bythotrephes* than *Leptodora* implying that *Bythotrephes* sustain faster relative growth rates (Sterner and Elser, 2002).

As adults, *Leptodora* and *Bythotrephes* also express markedly different growth schedules. Most somatic growth in *Leptodora* is achieved postmaturation [Equations (1)–(4)]. In Pike Lake, the longest *Leptodora* (12.6 mm body length) in 2003 weighed an estimated 180 μg , or $\sim \times 5.5$ its own back-projected dry weight at maturity [33 μg ; equation (1)]. By contrast, *Bythotrephes* not only stop accruing caudal spine weight as adults, but a variety of evidence suggests that they also stop accruing core body weight. *Bythotrephes* data from Island Lake revealed no statistically significant slopes in the ratios of caudal spine weight/core body weight when regressed against total weight (Fig. 3). This result supports the hypothesis that core body growth terminates at maturation. To test this hypothesis further, Island Lake data and published data were queried for the relationship of caudal spine length to core body length on the decision rule that a linear relationship indicates no measurable postmaturation core body growth. The Island Lake results (Fig. 4A) show tight linearity, and linearity is also evident in every published case available including *Bythotrephes* in southeastern Lake Michigan, USA, (Fig. 4B) during 1989 (Burkhardt, 1994) where the statistical relationship is strikingly similar to Island Lake specimens in Long Lake, USA, (Hoffman *et al.*, 2001); in N. American Lakes Huron, Erie and Michigan where slight deviations from linearity occur (Sullivan and Lehman, 1998); and in 19 European lakes (Straile and Hälbich, 2000) that included populations of large-bodied (*B. cederstroemi*) and small-bodied (*B. longimanus*) morphological variants.

Additional evidence for terminal core body growth in *Bythotrephes* comes from studies of populations where *Bythotrephes* mature early. In a study on Lake Michigan, USA, upwards of 75% of stage 2 females that reproduced asexually expressed little if any core body growth upon recruitment to stage 3 (Fig. 4C) (Pothoven *et al.*, 2003). In a study on Lake Constance, Germany, females

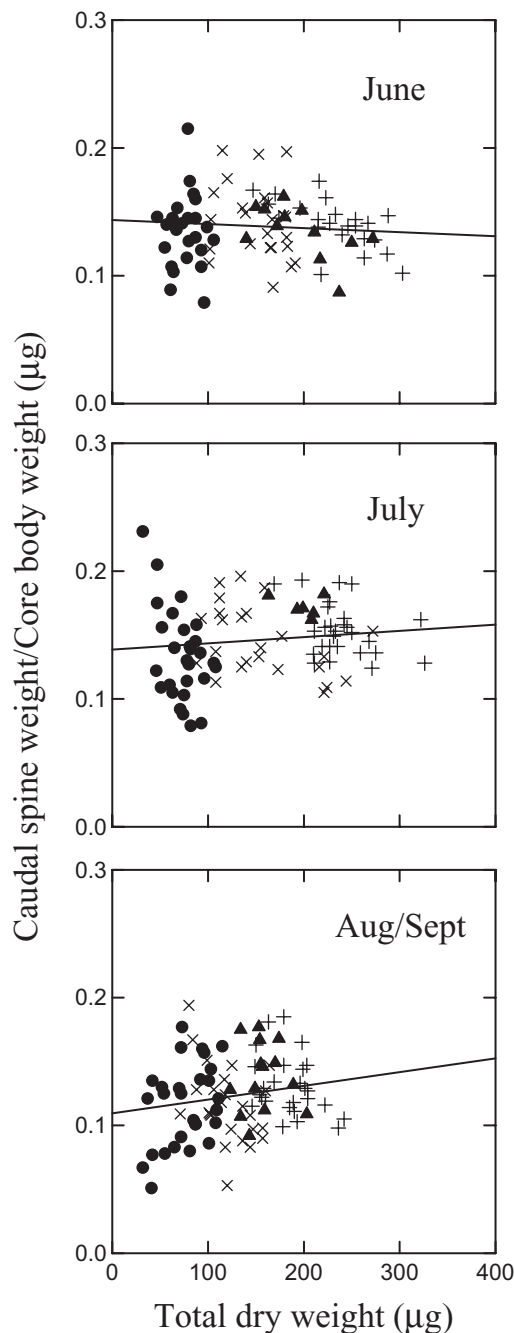


Fig. 3. Trends in *Bythotrephes* caudal spine weight/core body weight, as a function of total dry weight, for specimens from Island Lake, 2003. The slopes of least-square linear relationships were not significantly different from zero (June, $F_{1,81} = 0.60$, $P = 0.44$; July, $F_{1,83} = 1.35$, $P = 0.25$; Aug/Sept, $F_{1,92} = 3.09$, $P = 0.08$). Symbols as in Fig. 2.

matured almost uniformly at stage 2 in 1998, but most never recruited that year to stage 3 implying that females halted core body and caudal spine growth entirely once mature (Straile and Hälbich, 2000). A final piece of

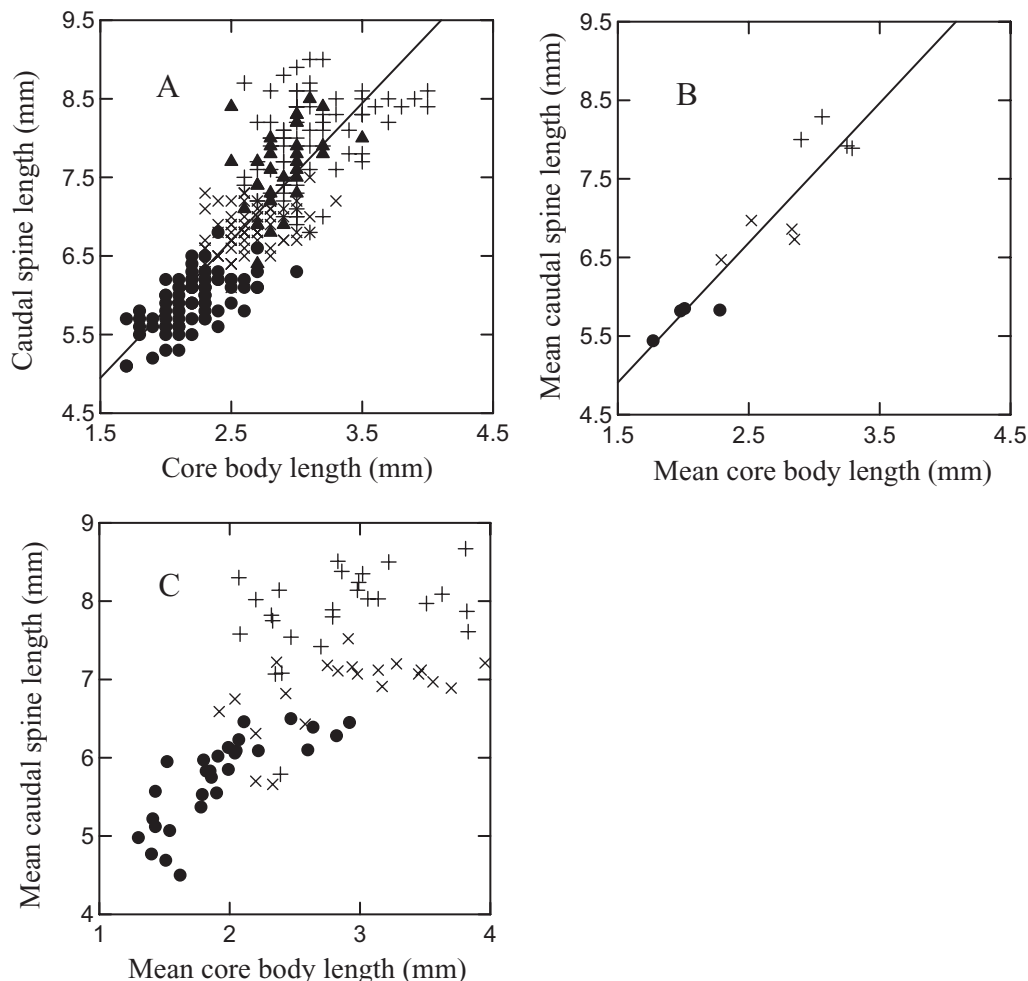


Fig. 4. Trends in *Bythotrephes* caudal spine length as a function of core body length for (A) Island Lake specimens collected in 2003 (spine length = $2.3 \times \text{body length} + 1.7$, $r^2 = 0.68$, $n = 262$), (B) Lake Michigan, USA, specimens collected in July and October 1989 based on means by stage in Table 1 reported by Burkhardt (Burkhardt, 1994) (mean spine length = $2.2 \times \text{mean body length} + 1.3$, $r^2 = 0.84$, $n = 12$) and (C) Lake Michigan specimens collected in September 2000 based on means by stage in Tables 2 and 3 reported by Pothoven *et al.* (Pothoven *et al.*, 2003). Note that axis scales are different in panel C. Symbols as in Fig. 2.

evidence for lack of postmaturation core body growth in *Bythotrephes* comes from scrutinizing the weights of females that birthed offspring in the lab in this study (Table II). They (stage 3*) had postbirth core body weights that were mid-distance, on average, between the core body weights of barren stage 2 and stage 3 individuals collected from the population at large, suggesting that *Bythotrephes* grew little, if any, in core body weight once mature. Taken together, these data provide compelling evidence that *Bythotrephes* ceases somatic growth once mature, whether this occurs at stage 3 or earlier. This pattern of resource allocation represents a major contrast in life history that distinguishes *Bythotrephes* from *Leptodora*.

Clutch size

Average clutch size of *Leptodora* in the wild can range from 3 to 18 in Lake Erie, N. America, (Andrews, 1948) as shown in Fig. 5. In Lake Tjeukemeer, the Netherlands, the average clutch size of 8-mm body length *Leptodora* ranged from ~ 10 to 20 eggs over a 3-year period (Vijverberg *et al.*, 2005). Maximum clutch size of *Leptodora* has been reported to range from 6 to 24 in Lake Erie (Andrews, 1948; Fig. 5). A lot of the variation in clutch size appears to be determined by maternal size, but some is seasonal (Fig. 5). Variation in clutch size of *Leptodora* may be partly related to the size of the feeding apparatus (trap basket) for females of similar body length (Abrusán, 2003).

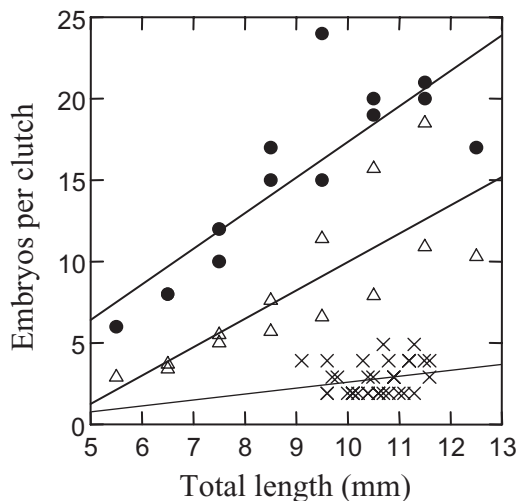


Fig. 5. Estimates of clutch size as a function of maternal total length for *Leptodora* and *Bythotrephes*. *Leptodora* data are the average (Δ) and maximum (\bullet) numbers of eggs per clutch for each of two periods (spring/summer and fall) in Lake Erie in Table 11 reported by Andrews (Andrews, 1948) based on the scoring of about 1300 individuals (average clutch size = $1.7 \times$ total length - 7.4, $r^2 = 0.61$; maximum clutch size = $2.2 \times$ total length - 4.5, $r^2 = 0.68$). For *Leptodora* of the same length and symbol, two points show seasonal variation; average clutch size was always greatest in fall while maximum clutch size was greatest in spring/summer except for the 8–9 mm size class. *Bythotrephes* data (\times) are the numbers of embryos per clutch for stage 3* mothers from Island Lake, 2003 (clutch size = $0.4 \times$ total length - 1.0, $r^2 = 0.03$).

Bythotrephes carry fewer eggs per clutch than *Leptodora* of similar total length (Fig. 5). In Island Lake, 2003, average clutch size of *Bythotrephes* ranged from 2 to 3 and maximum clutch size was 5 (unpublished data). Average *Bythotrephes* clutch sizes elsewhere range from ~2–4 in Harp Lake, Ontario, Canada, (Yan and Pawson, 1998), ~2–6 in the N. American Lakes Erie, Michigan and Huron (Lehman and Lehman, 1996), ~2–8 in Lake Michigan, USA, (Pothoven *et al.*, 2001, 2003) and ~2–7 in both the Biesbosch Reservoirs, the Netherlands (Ketelaars *et al.*, 1995) and Lake Constance, Germany (Straile and Hälbich, 2000). Maximum *Bythotrephes* clutch sizes range from 10 in Lake Constance (Straile and Hälbich, 2000) to 12 in Lakes Erie, Michigan and Huron (Sullivan and Lehman, 1998). The brood chamber of *Bythotrephes* expands throughout embryogenesis to accommodate her growing offspring.

Egg size

Like most cladocerans, *Leptodora* deposit fully provisioned parthenogenetic eggs into the brood chamber. *Leptodora* eggs are faint yellow, highly transparent and where measured vary only slightly in diameter (~0.38–0.40 mm), despite coming from a broad size range of adults and clutches (Andrews, 1948). Length conservation in the parthenogenetic eggs of *Leptodora* is consistent with

body length conservation in its parthenogenetic neonates (2 mm). Unlike *Leptodora*, *Bythotrephes* deposit tiny eggs into the brood chamber and nourish them late into development. Parthenogenetic egg diameter of *Bythotrephes* has not been reported.

Relative offspring weight

The ratio of body weight at 2 mm body length/body weight at 5.5 mm body length was used to estimate relative offspring weight for *Leptodora*. Equations (1)–(4) gave 12.7%, 9.0%, 8.8% and 15.0%, respectively. In *Bythotrephes*, the ratio of neonate total weight/stage 3* total weight with Island Lake specimens (Table II) was used to estimate relative offspring weight. Data gave 34.6%, 36.9% and 34.2% for June, July and August/September, respectively. Similar estimates for relative neonate weight of *Bythotrephes* are reported in the Laurentian Great Lakes, N. America (Sullivan and Lehman, 1998). Comparing the two species, relative neonate weight at maturity is about $\times 3$ greater in *Bythotrephes*, and the difference widens as *Leptodora* grows postmaturation.

Leptodora express minor variation in neonate size even for mothers of quite different size (see *Birth size* above). By contrast, *Bythotrephes* express major variation in neonate size that is strongly related to clutch size and maternal size (Fig. 6A). An analysis of covariance (ANCOVA) test revealed a significant, negative effect of clutch size (categorical variable) and a significant, positive effect of maternal size (main variable) on average neonate total weight (Fig. 6A). A similar relationship was revealed for Lake Erie, N. America, *Bythotrephes* (Fig. 6B) by plotting tabular data reported in Lehman *et al.* (Lehman *et al.*, 1997). A clutch size–neonate size tradeoff had been reported previously for *Bythotrephes* (Sullivan and Lehman, 1998; Straile and Hälbich, 2000) but the positive relationship between maternal weight and average neonate weight (Fig. 6) is novel. It suggests that for *Bythotrephes* broods of equivalent embryo number, larger females birth significantly heavier neonates on average. The evolutionary implication of this trend is significant because it suggests that neonate quality, if it is related to neonate body size, is controlled in part by maternal weight. A reproductive benefit of this nature may compound positive selection on accelerated, juvenile body growth in *Bythotrephes*, a trait otherwise interpreted below as a response to fish predation. Moreover, a tight neonate–maternal size relationship predicts that we might anticipate seasonal, cohort progression toward larger adults as the residual small-bodied spring mothers hatched from gametogenetic eggs, and their initial offspring, become outnumbered. This phenomenon could provide a partial explanation for the often cited observation that *Bythotrephes*

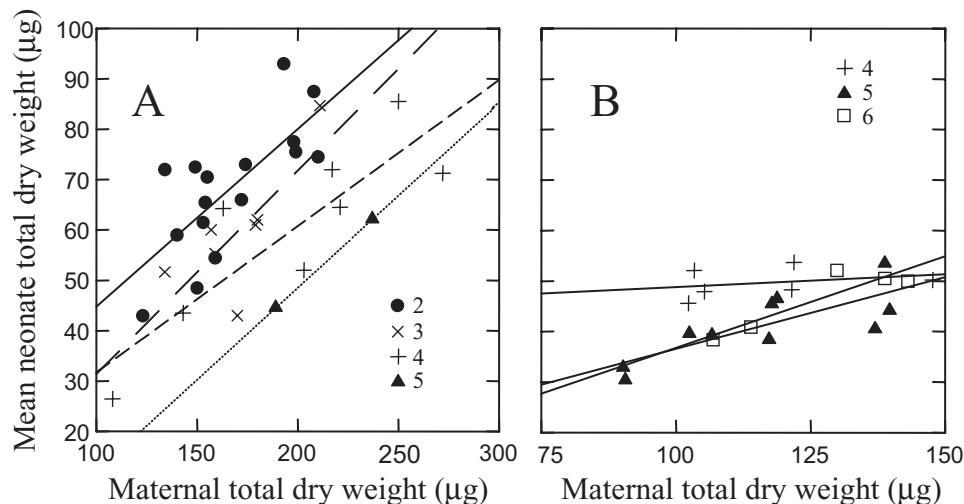


Fig. 6. *Bythotrephes* mean neonate total weight as a function of maternal total weight, immediately postbirth, for (A) stage 3* *Bythotrephes* collected from Island Lake, 2003 and (B) stage 3 *Bythotrephes* collected from Lake Erie, N. America, in Table 3 reported by Lehman *et al.* (Lehman *et al.*, 1997). Least-square regressions are graphed by clutch size, coded in panels. Slope homogeneity tests revealed that the linear trends do not have significantly different slopes within (A) ($F_{3,25}=0.2$, $P=0.88$) or within (B) ($F_{2,15}=2.5$, $P=0.11$). Subsequent analysis of covariance (ANCOVA) tests on the separate data sets revealed that within (A) linear trends are significantly different from one another at the y-intercept (categorical effect of clutch size, $F_{3,28}=9.7$, $P<0.01$) and from a slope of zero (main effect of maternal total weight, $F_{1,28}=47.3$, $P<0.01$) with an overall $r^2=0.67$. Within (B) linear trends are significantly different from one another at the y-intercept (categorical effect of clutch size, $F_{2,17}=7.4$, $P<0.01$) and from a slope of zero (main effect of maternal total weight, $F_{1,17}=17.5$, $P<0.01$) with an overall $r^2=0.67$. Note that x-axis scales differ between panels.

populations appear to transition from dominance by the small-bodied variant (*B. longimanus*) in spring to the large-bodied variant (*B. cederstroemi*) in summer (Zozula and Mordukhai-Boltovskoi, 1977; Evans, 1988).

Relative clutch weight

Leptodora partition their postmaturation growth between the soma and offspring. To compare allocation between the two pools, average dry weight of a clutch was compared to average dry weight gain in somatic tissue associated with 1 mm growth (Costa, 1967). Somatic growth was estimated by equation (1). The weight of a single clutch was estimated as the product of average, body length-specific clutch size (Fig. 5) and the dry weight of an individual neonate [4.2 µg; equation (1)]. The energetic expense of net mass accrual was assumed to be equivalent for embryonic and adult tissues. Projected results (Fig. 7) demonstrate that the smallest mothers partition net growth almost equally between the soma and offspring. Larger mothers partition progressively more net growth into offspring than the soma, however, even the largest *Leptodora* commit roughly 30% of their net growth to the soma.

Once mature, *Bythotrephes* apportion no measurable energy to somatic growth other than the cost of ecdysis. Postmaturation, net growth in *Bythotrephes* is therefore realized entirely as offspring. Fig. 8 plots total clutch weight versus a mother's barren weight based on laboratory-birthed clutches (stage 3*). The trend in Island Lake

indicates that *Bythotrephes* investment per clutch is commensurate with, or exceeds, maternal weight. Similar trends have been found in Lake Constance, Germany, with *B. longimanus* (Straile and Hälbich, 2000) and in Lake Erie, N. America, with *B. cederstroemi* (Lehman *et al.*, 1997). Results show that *Bythotrephes* commit

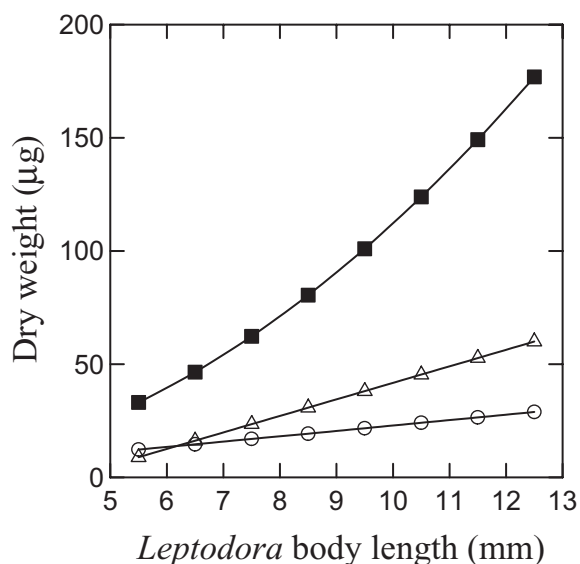


Fig. 7. Estimates of net growth allocation (in dry weight) made to body growth (○) versus offspring (△) by *Leptodora* of various sizes (■). See text for methods.

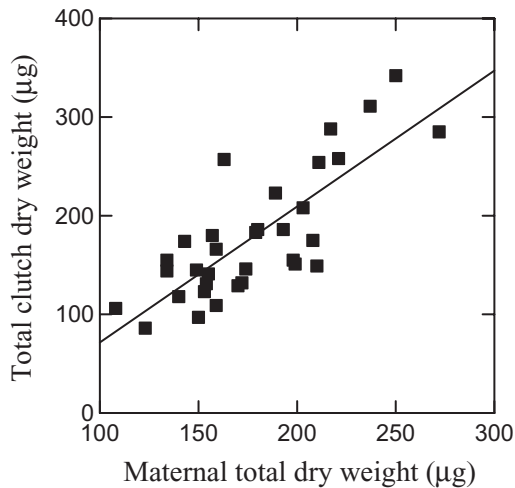


Fig. 8. *Bythotrephes* total clutch weight as a function of maternal total weight, immediately postbirth, for stage 3* specimens from Island Lake, 2003 (clutch weight = $1.4 \times$ maternal weight $- 66.2$, $r^2 = 0.62$, $n = 33$).

more total weight and relative weight (with respect to maternal weight) to offspring on a per clutch basis than do *Leptodora*.

Gametogenetic egg and neonate characteristics

Diapausing eggs of *Leptodora* are colorless and transparent (Sebestyen, 1949). They measure 0.41 mm diameter on average and have an average volume and dry weight of $36.4 \mu\text{m}^3 \times 10^6$ and 10.4 μg , respectively (Andrew and Herzig, 1984). By contrast, diapausing eggs of *Bythotrephes* are characteristically golden-brown, opaque and are larger than *Leptodora* eggs. *Bythotrephes* eggs measure 0.44–0.49 mm diameter on average (Andrew and Herzig, 1984; Jarnigan *et al.*, 2000) and have an average volume and dry weight of $60.0 \mu\text{m}^3 \times 10^6$ and 25.9 μg , respectively (Andrew and Herzig, 1984).

Developing gametogenetic neonates of *Leptodora* pass through a metanauplius stage that is rare among cladocerans. The metanauplius is transparent and presumably smaller than typical parthenogenetic neonates (Warren, 1901; Andrews, 1948). *Bythotrephes* gametogenetic neonates lack a metanauplius stage. They hatch with a caudal spine intact that has been estimated to measure 1.6 mm length (Yurista, 1992). Four *Bythotrephes* neonates that were hatched from diapausing eggs in this study weighed 8.0 μg dry weight on average. These few values indicate that *Bythotrephes* gametogenetic neonates are heavier than *Leptodora* parthenogenetic neonates (Fig. 2).

Adaptive significance of life-history traits

Life-history traits of *Leptodora* and *Bythotrephes* are profoundly different (Table I) and can be summarized as

follows. *Leptodora* mature at only a fraction of their maximum adult size. Once mature they partition net growth somewhat evenly between the soma and offspring. They emphasize large numbers of neonates per clutch that are small bodied in absolute and relative adult terms. Average egg and neonate weights vary little, despite great variation in maternal weight and clutch size. *Leptodora* accrue weight slowly compared to *Bythotrephes*. *Bythotrephes* mature at a large size (typically stage 3) and thereafter express weight gain primarily as reproductive tissue. They produce variable numbers of offspring per clutch that are individually large bodied in absolute and relative adult terms, and that already bear long caudal spines. Total weight of an individual *Bythotrephes* clutch may exceed maternal weight. Average neonate weight is highly variable and correlates with clutch size and maternal weight. Both gametogenetic eggs and offspring are larger in *Bythotrephes* than in *Leptodora*. In general, phenotypic variations in life-history traits appear to be wider in *Bythotrephes* than in *Leptodora*. Analysis of life-history traits in light of putative selection pressures suggests that constraints imposed by visually searching gape-limited predators and prey size have been more significant than constraints imposed by tactile searching gape-limited predators in the evolution of both species.

Visually searching gape-limited predators

Leptodora and *Bythotrephes* are large in comparison to most other pelagic freshwater crustaceans and are therefore highly selected targets of many fishes (de Bernardi and Giussani, 1975; Craig, 1978; Næsje *et al.*, 1987). Fish predation has undoubtedly played a major role in their evolution (Zaret, 1980). *Leptodora* has nearly perfected invisibility as a predator defense, evidenced as extreme transparency in the body proper, in parthenogenetic and gametogenetic eggs, in the metanauplius, and in the small size of the compound eye (Branstrator and Holl, 2000). Transparency is probably why sticklebacks (*Gasterosteus aculeatus*) feeding in the laboratory select *Chaoborus* over *Leptodora* of similar body length (Campbell and Knoechel, 1990) and why *Coregonus lavaretus* feeding in the wild select *Bythotrephes* over *Leptodora* (Palmer *et al.*, 2001). Two lines of evidence suggest that transparency in *Leptodora* is most effective in the juvenile instars. First, wild planktivorous fishes show no positive selection for *Leptodora* < 4 mm body length and virtually ignore *Leptodora* of 2 mm up to 3 mm body length, but the same fishes show strong selection for adult *Leptodora* (Vijverberg, 1991; Liu and Herzig, 1996; Branstrator and Holl, 2000). Second, *Leptodora* ≤ 4 mm body length demonstrate reverse migration, staying in the epilimnion by day even when fishes are present, but adult *Leptodora* under the same conditions express typical vertical

migration (Costa and Cummins, 1969; Vijverberg, 1991). Because *Leptodora* can minimize the adverse effects of fish predation by remaining inconspicuous, natural selection should favor, in addition to transparency, maturation at small sizes (Table I). Why natural selection has not resulted in decreased neonate size and maturation size even further in *Leptodora* is unclear. That *Leptodora* cannot quickly consume *Daphnia* prey until they are about 5 mm long may set the lower bounds on their maturation size (see below). Likewise, smaller birth size in *Leptodora* may be selected against on the basis of an inability to capture a broad enough spectrum of prey. Juvenile *Leptodora* eat a lot of *Bosmina* (Branstrator and Lehman, 1991) and neonatal *Bosmina* (0.2 mm body length) are already at the upper size threshold of what a 2-mm body length *Leptodora* can handle in a reasonable time (Branstrator, 1998).

The long caudal spine of *Bythotrephes* is an apparent adaptation against gape-limited fishes. There is evidence that in the wild the caudal spine may increase *Bythotrephes* survival against fishes <100 mm length (Schneeberger, 1991; Baker *et al.*, 1992; Mills *et al.*, 1992; Barnhisel and Harvey, 1995). In the laboratory, it has been shown that small fishes reject full-spine *Bythotrephes* with greater frequency than they reject no-spine or half-spine *Bythotrephes* (Barnhisel, 1991a, 1991b). Such selection by small fishes should favor *Bythotrephes* offspring with long caudal spines at birth and rapid commitment to early spine growth (Table I). Aversion conditioning can develop in fishes experienced with consuming full-spine *Bythotrephes* (Barnhisel, 1991b). This could extend the value of the caudal spine from a postcontact to a pre-contact defense if it deters learned individuals from attacking. Complete lack of ecdysis on the caudal spine of *Bythotrephes* is a trait that is atypical among crustaceans. It should decrease episodes of vulnerability and may be a direct adaptation to fish predation.

Unlike gape-limited fish, nongape-limited fish make heavy use of *Bythotrephes* as a food resource in the wild (Therriault *et al.*, 2002). Their density has been implicated in defining *Bythotrephes*' local occurrence (MacIsaac *et al.*, 2000). Thus, a critical assumption in the foregoing interpretation of *Bythotrephes*' growth strategy is that gape-limited planktivory can be dominant at times, otherwise, the negative effects of being more visible could undermine selection for rapid spine growth. Two indirect lines of evidence suggest that gape-limited planktivory on *Bythotrephes* can be strong. First, evidence suggests that fishes may have difficulties consuming the caudal spine until they reach about 100 mm length (Schneeberger, 1991; Baker *et al.*, 1992; Mills *et al.*, 1992; Barnhisel and Harvey, 1995). This represents a

significant ontogenetic window when their predation should select for rapid caudal spine investment. Second, allometric scaling dictates that juvenile fish metabolism will exceed that by adult conspecifics on a per gram basis (Peters, 1983). In one energetics study, juvenile yellow perch (0.01 g) had metabolic rates $\times 70$ adults (100 g) (Post, 1990). Thus, even when adult planktivore biomass exceeds juvenile biomass by an order of magnitude, relative selection imposed by the two groups may be comparable. Additional evidence that spine and body growth traits of *Bythotrephes* have been shaped by interactions with fish comes from Lake Constance, Germany (Straile and Hälbich, 2000). There, as fish predation strengthened during the summer, females (*B. longimanus* variant) birthed larger neonates, with longer caudal spines, that ultimately matured at larger sizes. In Lake Michigan, USA, similar switches in growth allocation were seen in a *B. cederstroemi* variant in conjunction with increased fish predation (Pothoven *et al.*, 2003). Direct estimates of consumptive demand suggest that nongape-limited size classes may dominate fish guilds sometimes (Johnson and Kitchell, 1996) but not others (Hrabik *et al.*, 2001). Hence, we should anticipate environmental gradients (temporal and spatial) in the type of selection imposed by fish predation including circumstances that favor a *Bythotrephes*-type life history. The most suitable habitat for *Bythotrephes* appears to be lakes with low planktivore biomass (MacIsaac *et al.*, 2000) or the presence of a thermal or light refuge from nongape-limited fishes (Yan *et al.*, 2001). The ecological consequences of refugia for *Bythotrephes* from nongape-limited fishes deserve more attention because such refugia could also serve to congregate small, gape-limited fishes and locally elevate their potency as a selective force on *Bythotrephes*.

The metabolic costs to *Leptodora* and *Bythotrephes* in mounting their respective morphological defenses remain largely unmeasured. Enhanced transparency in *Leptodora* may have a biochemical cost. With *Bythotrephes*, relative spine weight (caudal spine/core body) provides one proxy for estimating the cost of this defense. In Island Lake, this ratio ranged between ~ 10 – 20% in 2003 (Fig. 3). Similar estimates are reported for the Laurentian Great Lakes (Sullivan and Lehman, 1998). Compared to the core body, the caudal spine of *Bythotrephes* is clearly a minor material investment. Moreover, it becomes even less significant when distributed over an individual's lifetime considering that the distal segment is already intact at birth, spine growth terminates at stage 3, and spine segments are never molted. The only sustained energy cost to *Bythotrephes* in carrying the caudal spine may be frictional drag at low Reynold's numbers.

Tactile searching gape-limited predators

Leptodora juveniles are vulnerable to attack by both *Chaoborus* (McNaught, 1993) and *Bythotrephes* (Branstrator, 1995), and *Bythotrephes* are susceptible to cannibalism in the laboratory. Nonetheless, the effect of intraguild predation among large invertebrate predators at natural densities has been questioned because of low species densities and encounter rates (McNaught, 1993; Branstrator, 1995; Witt and Cáceres, 2004). Given our present understanding, it remains questionable whether selection pressures imposed by invertebrate predators have been significant in the life-history evolution of either *Leptodora* or *Bythotrephes*. Strong selection by invertebrates would be expected to promote perhaps larger birth size, emphasis on earlier somatic growth, delayed reproduction and heavier body armor in *Leptodora*. That said, it is possible that swarms of *Chaoborus*, *Bythotrephes* or *Mysis* could elevate their local predatory impacts high enough to alter behavioral patterns, such as vertical migration, of other invertebrate predators.

Prey size

Bythotrephes are an exception to the size-constraint paradigm under which most invertebrate predators operate (Schulz and Yursita, 1999). Dietary studies indicate that adult *Bythotrephes* show preference for large *Daphnia pulicaria* (>2 mm body length) over smaller conspecifics, and that *Bythotrephes* are able to take prey as large as *Holopedium* in the laboratory and field (Schulz and Yursita, 1999; Wahlström and Westman, 1999). This contrasts with *Leptodora* which generally takes prey <2 mm body length (Lunte and Luecke, 1990) and usually prey <1 mm body length (Herzig and Auer, 1990; Branstrator and Lehman, 1991). Natural population dynamics of putative prey taxa suggest that *Bythotrephes* take larger prey than *Leptodora* take in the wild (Lehman and Cáceres, 1993; Manca *et al.*, 2000; McNaught *et al.*, 2004). *Bythotrephes* are also quicker than *Leptodora* at dispatching prey of similar size at comparative life-history stages (Fig. 9). The greater upper size range of prey taken by *Bythotrephes* and their quicker handling times may be due in part to their larger body size. *Leptodora* neonates and adults are only a fraction of the respective weights of *Bythotrephes* neonates and adults (Fig. 2). The differences may also owe to dissimilar raptorial modes of manipulating and consuming prey.

To rend prey, *Leptodora* employ long, tapered, single-cusped mandibles that excavate (more or less scrape) tissues from between carapace valves of cladoceran prey. Portions of prey carapace are often torn, and whole animals occasionally swallowed (Zaret, 1980), but the bivalved carapace is often intact and identifiable

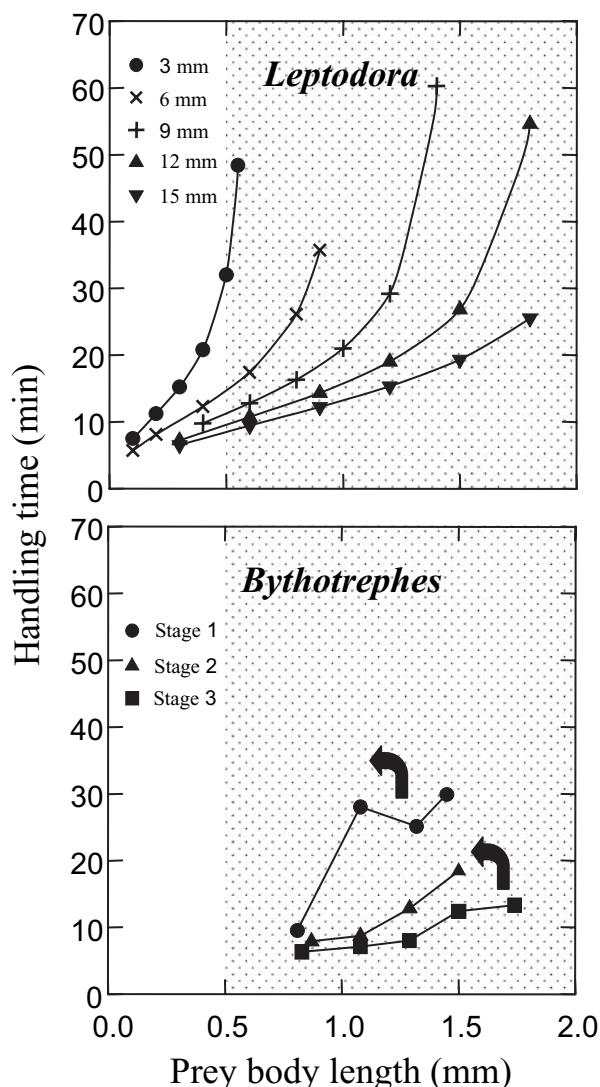


Fig. 9. Estimated trends in mean handling times of *Leptodora* (top) and *Bythotrephes* (bottom) that were fed cladoceran prey in the laboratory. *Leptodora* data are from equations (5) and (6) reported by Branstrator (Branstrator, 1998) based on *Leptodora* that were fed *Bosmina longirostris*, *Ceriodaphnia quadrangula* and *Daphnia rosea*. *Bythotrephes* data are from Table 3 reported by Burkhardt and Lehman (Burkhardt and Lehman, 1994) based on *Bythotrephes* that were fed *Daphnia pulicaria*. Each data point in the lower panel represents the mean of between 14 and 25 timed *Bythotrephes* feeding trials. *Leptodora* body lengths and *Bythotrephes* stages are coded in their respective panels. Mean dry weights of *Bythotrephes* were 95 µg (stage 1), 227 µg (stage 2) and 448 µg (stage 3). Shading on either side of 0.5 mm prey body length (x-axis) reflects the fact that this body length represents an important taxonomic division between rotifers and *Bosmina* (white) and *Daphnia* and copepods (stipulated) in many lakes. Arrows in the lower panel approximate the direction of rotational adjustment to handling times for smaller-bodied *Bythotrephes*.

when discarded (unpublished data). This excavation mechanism generally necessitates that *Leptodora* first manipulate the prey so that the ventral carapace gap faces *Leptodora*'s mouth and secondarily immobilize the

prey throughout the feeding process. Prey entrapment, manipulation and immobilization are done with thoracic appendages (trap basket) and repeated flexion of the abdomen (Browman *et al.*, 1989). Not surprisingly, there is a tight relationship between the length (volume) of the trap basket and the maximum size of prey taken by *Leptodora* (Herzig and Auer, 1990; Manca and Comoli, 1995). By contrast, *Bythotrephes* employ stout, multicusped mandibles to shred prey. Unlike *Leptodora*'s excavation repertoire, the shredding mechanism employed by *Bythotrephes* does not demand strict immobilization of prey, or that prey are entirely within the grasp of thoracic appendages, before feeding begins. Non-ingested fragments of *Daphnia* released by feeding *Bythotrephes* are typically destroyed beyond recognition. Some of the best evidence for *Bythotrephes*' distinctive ability among freshwater predatory zooplankton in being able to take relatively large prey is the fact that they can be remarkably successful cannibals on same-sized conspecifics in the laboratory (unpublished data). Despite the fastidious feeding mode of *Leptodora*, they appear to harvest less tissue per daphnid prey. Empirical estimates of the mean percent of individual *Daphnia rosea* ingested per feeding bout, based on radiotracer laboratory experiments, are 31% for *Leptodora* (Branstrator, 1998) versus 58–59% for *Bythotrephes* (Lehman, 1993). Estimates of mean percent *D. pulicaria* ingested by *Bythotrephes* using similar radiotracer tools are 59–62% and are remarkably uniform across morphological stage (Burkhardt and Lehman, 1994; Yurista and Schulz, 1995). Hence, *Leptodora* appear to be less efficient predators than *Bythotrephes* on similar sized daphnid prey both in terms of handling time (Fig. 9) and in overall tissue harvest per prey item.

The general foraging constraints associated with prey size present different challenges to *Leptodora* and *Bythotrephes*. By growing larger throughout life, *Leptodora* can reap substantial dietary gains through reduced handling time and access to a broader prey base (Fig. 9). Larger *Leptodora* also benefit reproductively by being able to carry larger clutches (Fig. 5). Natural selection based on foraging and reproductive returns should thus favor indeterminate body growth in *Leptodora* (Table I). That indeterminate body growth concurrently increases *Leptodora*'s visibility to fishes implies that foraging rewards manifested as growth and reproduction have been compensatory to increased risk from fish predation in defining *Leptodora* fitness. By contrast, neonatal *Bythotrephes* can already quickly dispense of some of the largest *Daphnia* (about 1.5 mm body length) that they might reliably encounter in their lifetime (Fig. 9). By stage 3, there appears to be only slight reductions in handling time that *Bythotrephes* could achieve through increased body

size. Hence, natural selection based strictly on foraging rewards ought to favor finite soma growth in *Bythotrephes* (Table I). Size-based reproductive benefits (Fig. 6), on the other hand, should favor indeterminate body growth in *Bythotrephes*. That body growth is finite in *Bythotrephes* suggests that reproductive returns associated with body growth are not compensatory to increased mortality risk from fishes.

To summarize, it appears that the disparate sets of life-history traits of *Leptodora* and *Bythotrephes* can be accounted for by considering the variable and simultaneous demands imposed by visually searching, gape-limited predators (fish) and foraging constraints. In the case of *Leptodora*, predator avoidance and foraging constraints impose conflicting selection on life-history allocation to somatic growth; in the case of *Bythotrephes* they appear to be complementary. Ultimately, it would be interesting to understand what selection pressures initially forged such divergent tactics, and whether taxonomic origins constrained the process. Molecular data support a sister group relationship between the Haplo-poda and the Onychopoda (Richter *et al.*, 2001), but the two groups appear to have diverged more than 8.7 million years ago (Cristescu and Hebert, 2002). Comparative biogeographic work on *Leptodora* and *Bythotrephes* across ecosystems where they are sympatric versus allopatric may provide better insights.

Life-history traits of the two predatory cladocerans reflect *r*-selected (*Leptodora*) and *K*-selected (*Bythotrephes*) strategies, where an *r*-strategist emphasizes resource allocation to total number of progeny and a *K*-strategist emphasizes highest possible individual fitness per offspring. In the case of *Leptodora*, however, generating small-bodied offspring (hence large numbers of them) is in practice also the strategy that likely maximizes individual fitness per offspring since survival is aided by small body size when visually discriminating predators are present. Consequently, it seems inappropriate to define the contrasting strategies strictly along a traditional *r*–*K* continuum.

Implications of life-history strategy for competitive ability

Variation in life-history strategy has consequences for selection on timing and allocation to body growth that may underlie competitive imbalance between *Leptodora* and *Bythotrephes*. Owing to the production of large-bodied neonates that grow rapidly, *Bythotrephes* have relatively short prey handling times and have access to large prey, such as *Daphnia*, over most of their lives (Fig. 9). By contrast, juvenile *Leptodora* cannot generally consume *Daphnia* (Branstrator and Lehman, 1991; Fig. 9). Nonetheless, the abundance of *Daphnia* is one of the best

predictors of *Leptodora* population distribution (McNaught, 1993). Hence, to reproduce, *Leptodora* would appear to bear the added constraint, over *Bythotrephes*, of growing postbirth to gain access to *Daphnia*. Thus, not only are there distinct differences in the economy of handling time, but also differences in admission to prey of large body size and taxonomic variety that contribute to potential imbalance in competitive abilities of *Leptodora* and *Bythotrephes*. The imbalance can be expressed as follows: In contrast to *Leptodora*, *Bythotrephes* have (i) more efficient prey consumption, based on handling time, over the shared portion of the prey spectrum, (ii) fewer resource constraints as juveniles in terms of prey size and taxonomic diversity, and (iii) a wider diet base, particularly as adults, through alternative prey at the upper end of the size spectrum (Fig. 9). This imbalance predicts that exploitative food competition will favor *Bythotrephes* where the prey base tends toward an abundance of large-bodied cladocerans. This may be one reason for declines in *Leptodora* densities in Lake Michigan, USA (Makarewicz *et al.*, 1995), and in Harp Lake, Ontario, Canada (Yan and Pawson, 1997), following *Bythotrephes* invasion. Imbalance predicts that *Bythotrephes* will be better suited than *Leptodora* to colonize temperate zone lakes in spring when large *Daphnia* are numerically dominant (Hoffman *et al.*, 2001). Conversely, imbalance predicts that where large *Daphnia* are rare, the exclusive prey domain of *Bythotrephes* will relax, and coexistence of the predatory cladocerans may be supported. Imbalance predicts that in lakes where only the small-bodied variant, *B. longimanus*, is resident, its small body size will compromise its access to prey at the upper end of the size spectrum, and increase prey handling times on small prey, restricting its capacity to competitively exclude *Leptodora* (Fig. 9). This may be one reason why *Leptodora* is able to persist alongside the small-bodied variant, *B. longimanus*, in Lago Maggiore, Italy (de Bernardi and Giussani, 1975; Manca and Ruggiu, 1998), and in the Biesbosch reservoirs, the Netherlands (Ketelaars *et al.*, 1995). Finally, imbalance as outlined above might be ameliorated either by fish predation that forces spatial segregation of *Leptodora* and *Bythotrephes* (Enz *et al.* 2001; Palmer *et al.*, 2001) or by an abundant, shared prey base. These mechanisms could foster coexistence of the two predatory cladocerans. It should also be pointed out that *Bythotrephes* can easily win a predatory encounter with *Leptodora* in the laboratory (Branstrator, 1995). Although such direct interaction may not be significant in the wild, it does represent a fourth ‘competitive imbalance’ between the species and one that may contribute in part to reductions in *Leptodora* densities in lakes invaded by *Bythotrephes*. Testing the relative importance

of these mechanisms in the wild will require more studies of *Bythotrephes* invasions into lakes with *Leptodora*, coupled with empirical knowledge of the density, size and taxonomic composition of prey before and during such events; information on the reproductive status (e.g. egg ratios) of *Leptodora* at the time of its population declines; and estimates of the body size (morphological variant) of the *Bythotrephes* that invade.

To conclude, the disparate sets of life-history traits of *Leptodora* and *Bythotrephes* revealed here echo remarkable parallels to life-history strategies outlined by Lynch (Lynch, 1980) for small- versus large-bodied phytoplanktivorous cladocerans, respectively. Both sets of life-history strategies reflect integrative, evolutionary responses to top-down (predation) and bottom-up (prey availability) selection pressures that might be anticipated for species such as cladocerans that are mid-positioned in aquatic food chains (McQueen *et al.*, 1986). This study and that by Lynch (Lynch, 1980) underscore the tremendous flexibility inherent in cladoceran life histories. Notably, both studies reveal a polarization in tactics guided by one of two defense modes: (i) small and inconspicuous (e.g. *Bosmina*, *Leptodora*) versus (ii) large and unwieldy (*Daphnia*, *Bythotrephes*), that ultimately has consequences for interspecific competition and the composition of zooplankton assemblages.

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REFERENCES

- Abrusán, G. (2003) Morphological variation of the predatory cladoceran *Leptodora kindti* in relation to prey characteristics. *Behav. Ecol.*, **134**, 278–283.
- Allan, J. D. (1976) Life history patterns in zooplankton. *Am. Nat.*, **110**, 165–180.

- Andrew, T. E. and Herzig, A. (1984) The respiration rate of the resting eggs of *Leptodora kindtii* (Focke 1844) and *Bythotrephes longimanus* Leydig 1860 (Crustacea, Cladocera) at environmentally encountered temperatures. *Oecologia*, **64**, 241–244.
- Andrews, T. F. (1948) The life history, distribution, growth, and abundance of *Leptodora kindtii* (Focke) in Western Lake Erie. PhD Thesis. The Ohio State University, OH, USA.
- Baker, E. A., Tolentino, S. A. and McComish, T. S. (1992) Evidence for yellow perch predation on *Bythotrephes cederstroemi* in southern Lake Michigan. *J. Gt. Lakes Res.*, **18**, 190–193.
- Barnhisel, D. R. (1991a) The caudal appendage of the cladoceran *Bythotrephes cederstroemi* as defense against young fish. *J. Plankton Res.*, **13**, 529–537.
- Barnhisel, D. R. (1991b) Zooplankton spine induces aversion in small fish predators. *Oecologia*, **88**, 444–450.
- Barnhisel, D. R. and Harvey, H. A. (1995) Size-specific fish avoidance of the spined crustacean *Bythotrephes*: field support for laboratory predictions. *Can. J. Fish. Aquat. Sci.*, **52**, 768–775.
- Berg, D. J. and Garton, D. W. (1994) Genetic differentiation in North American and European populations of the cladoceran *Bythotrephes*. *Limnol. Oceanogr.*, **39**, 1503–1516.
- de Bernardi, R. and Giussani, G. (1975) Population dynamics of three cladocerans of Lago Maggiore related to predation pressure by a planktophagous fish. *Proc. Int. Assoc. Theor. Appl. Limnol.*, **19**, 2906–2912.
- Branstrator, D. K. (1995) Ecological interactions between *Bythotrephes cederstroemi* and *Leptodora kindtii* and the implications for species replacement in Lake Michigan. *J. Great Lakes Res.*, **21**, 670–679.
- Branstrator, D. K. (1998) Predicting diet composition from body length in the zooplankton predator *Leptodora kindtii*. *Limnol. Oceanogr.*, **43**, 530–535.
- Branstrator, D. K. and Holl, C. M. (2000) Planktivory by bluegill (*Lepomis macrochirus*) on *Leptodora kindtii* in a small North American lake. *Hydrobiologia*, **437**, 101–106.
- Branstrator, D. K. and Lehman, J. T. (1991) Invertebrate predation in Lake Michigan: regulation of *Bosmina longirostris* by *Leptodora kindtii*. *Limnol. Oceanogr.*, **36**, 483–495.
- Browman, H. I., Kruse, S. and O'Brien, W. J. (1989) Foraging behavior of the predaceous cladoceran, *Leptodora kindtii*, and escape responses of their prey. *J. Plankton Res.*, **11**, 1075–1088.
- Burkhardt, S. (1994) Seasonal size variation in the predatory cladoceran *Bythotrephes cederstroemi* in Lake Michigan. *Freshw. Biol.*, **31**, 97–108.
- Burkhardt, S. and Lehman, J. T. (1994) Prey consumption and predatory effects of an invertebrate predator (*Bythotrephes*: Cladocera, Cercopagidae) based on phosphorus budgets. *Limnol. Oceanogr.*, **39**, 1007–1019.
- Campbell, C. E. and Knoechel, R. (1990) Distribution of vertebrate and invertebrate planktivores in Newfoundland lakes with evidence of predator–prey and competitive interactions. *Can. J. Zool.*, **68**, 1559–1567.
- Costa, R. R. (1967) Population dynamics and ecology of *Leptodora kindtii* (Focke). PhD Thesis. University of Pittsburgh, PA, USA.
- Costa, R. R. and Cummins, K. W. (1969) Diurnal vertical migration patterns of *Leptodora kindtii* (Focke) (Crustacea: Cladocera) in a shallow eutrophic reservoir. *Int. Rev. Hydrobiol.*, **54**, 533–541.
- Craig, J. F. (1978) A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshw. Biol.*, **8**, 59–68.
- Cristescu, M. E. A. and Hebert, P. D. N. (2002) Phylogeny and adaptive radiation in the Onychopoda (Crustacea, Cladocera): evidence from multiple gene sequences. *J. Evol. Biol.*, **15**, 838–849.
- Culver, D. A., Boucherle, M. M., Bean, D. J. *et al.* (1985) Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can. J. Fish. Aquat. Sci.*, **42**, 1380–1390.
- Enz, C. A., Heller, C., Müller, R. *et al.* (2001) Investigations on fecundity of *Bythotrephes longimanus* in Lake Lucerne (Switzerland) and on niche segregation of *Leptodora kindtii* and *Bythotrephes longimanus* in Swiss lakes. *Hydrobiologia*, **464**, 143–151.
- Evans, M. S. (1988) *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. *J. Gt. Lakes Res.*, **14**, 234–240.
- Grigorovich, I. A., Pashkova, O. V., Gromova, Y. F. *et al.* (1998) *Bythotrephes longimanus* in the Commonwealth of Independent States: variability, distribution and ecology. *Hydrobiologia*, **379**, 183–198.
- Herzig, A. and Auer, B. (1990) The feeding behaviour of *Leptodora kindtii* and its impact on the zooplankton community of Neusiedler See (Austria). *Hydrobiologia*, **198**, 107–117.
- Hoffman, J. C., Smith, M. E. and Lehman, J. T. (2001) Perch or plankton: top-down control of *Daphnia* by yellow perch (*Perca flavescens*) or *Bythotrephes cederstroemi* in an inland lake? *Freshw. Biol.*, **46**, 759–775.
- Hrabik, T. R., Carey, M. P. and Webster, M. S. (2001) Interactions between young-of-the-year exotic rainbow smelt and native yellow perch in a northern temperate lake. *Trans. Am. Fish. Soc.*, **130**, 568–582.
- Jarnigan, S. T., Swan, B. K. and Kerfoot, W. C. (2000) Fish as vectors in the dispersal of *Bythotrephes cederstroemi*: diapausing eggs survive passage through the gut. *Freshw. Biol.*, **43**, 579–589.
- Johnson, T. B. and Kitchell, J. F. (1996) Long-term changes in zooplanktivorous fish community composition: implications for food webs. *Can. J. Fish. Aquat. Sci.*, **53**, 2792–2803.
- Ketelaars, H. A. M., Wagenvoort, A. J. and Herbst, R. F. (1995) Life history characteristics and distribution of *Bythotrephes longimanus* Leydig (Crustacea, Onychopoda) in the Biesbosch reservoirs. *Hydrobiologia*, **307**, 239–251.
- Lehman, J. T. (1993) Efficiencies of ingestion and assimilation by an invertebrate predator using C and P dual isotope labeling. *Limnol. Oceanogr.*, **38**, 1550–1554.
- Lehman, J. T., Bilkovic, D. M. and Sullivan, C. (1997) Predicting development, metabolism and secondary production for the invertebrate predator *Bythotrephes*. *Freshw. Biol.*, **38**, 343–352.
- Lehman, J. T. and Branstrator, D. K. (1995) A model for growth, development, and diet selection by the invertebrate predator *Bythotrephes cederstroemi*. *J. Gt. Lakes Res.*, **21**, 610–619.
- Lehman, J. T. and Cáceres, C. E. (1993) Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Limnol. Oceanogr.*, **38**, 879–891.
- Lehman, J. T. and Lehman, D. A. (1996) Status of the non-indigenous invertebrate predator *Bythotrephes* (Crustacea: Cladocera) in Lakes Erie, Huron, and Michigan. *Portland State University Lakes Reservoirs Program*, **Publ. No. 96-8**, 7–14.
- Liu, Z. and Herzig, A. (1996) Food and feeding behaviour of a planktivorous cyprinid, *Pelecus cultratus* (L.), in a shallow eutrophic lake, Neusiedler See (Austria). *Hydrobiologia*, **333**, 71–77.
- Lunte, C. C. and Luecke, C. (1990) Trophic interactions of *Leptodora* in Lake Mendota. *Limnol. Oceanogr.*, **35**, 1091–1100.
- Lynch, M. (1980) The evolution of cladoceran life histories. *Q. Rev. Biol.*, **55**, 23–42.
- MacIsaac, H. J., Ketelaars, H. A. M., Grigorovich, I. A. *et al.* (2000) Modeling *Bythotrephes longimanus* invasions in the Great Lakes basin based on its European distribution. *Arch. Hydrobiol.*, **149**, 1–21.

- Makarewicz, J. C., Bertram, P., Lewis, T. *et al.* (1995) A decade of predatory control of zooplankton species composition of Lake Michigan. *J. Great Lakes Res.*, **21**, 620–640.
- Manca, M. and Comoli, P. (1995) Seasonal changes in size of the feeding basket of *Leptodora kindtii* (Focke) in Lago Maggiore as related to variations in prey size selection. *Limnol. Oceanogr.*, **40**, 834–838.
- Manca, M., Ramoni, C. and Comoli, P. (2000) The decline of *Daphnia hyalina galeata* in Lago Maggiore: a comparison of the population dynamics before and after oligotrophication. *Aquat. Sci.*, **62**, 142–153.
- Manca, M. and Ruggiu, D. (1998) Consequences of pelagic food-web changes during a long-term lake oligotrophication process. *Limnol. Oceanogr.*, **43**, 1368–1373.
- McNaught, A. S. (1993) The role of intraguild predation, vertebrate predation and dispersal in the organization of zooplankton communities. PhD Thesis. University of Michigan, MI, USA.
- McNaught, A. S., Kiesling, R. L. and Ghadouani, A. (2004) Changes to zooplankton community structure following colonization of a small lake by *Leptodora kindtii*. *Limnol. Oceanogr.*, **49**, 1239–1249.
- McQueen, D. J., Post, J. R. and Mills, E. L. (1986) Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.*, **43**, 1571–1581.
- Mills, E. L., O’Gorman, R., DeGisi, J., *et al.* (1992) Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. *Can. J. Fish. Aquat. Sci.*, **49**, 2009–2019.
- Mordukhai-Boltovskaia, E. D. (1957) Parthenogenic breeding of *Leptodora kindtii* (Focke) and *Bythotrephes* Leydig. *Dokl. Acad. Nauk*, **112**, 123–125.
- Mordukhai-Boltovskaia, E. D. (1958) Preliminary notes on the feeding of the carnivorous cladocerans *Leptodora kindtii* and *Bythotrephes*. *Dokl. Acad. Nauk*, **122**, 828–830.
- Muirhead, J. and Sprules, W. G. (2003) Reaction distance of *Bythotrephes longimanus*, encounter rate and index of prey risk for Harp Lake, Ontario. *Freshw. Biol.*, **48**, 135–146.
- Næsje, T. F., Jonsson, B., Klyve, L. *et al.* (1987) Food and growth of age-0 smelts, *Osmerus eperlanus*, in a Norwegian fjord lake. *J. Fish Biol.*, **30**, 119–126.
- Palmer, A., Stich, H.-B. and Maier, G. (2001) Distribution patterns and predation risk of the coexisting cladocerans *Bythotrephes longimanus* and *Leptodora kindtii* in a large lake – Lake Constance. *Hydrobiologia*, **442**, 301–307.
- Peters, R. H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Post, J. R. (1990) Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. *Can. J. Fish. Aquat. Sci.*, **47**, 554–560.
- Pothoven, S. A., Fahnenstiel, G. L. and Vanderploeg, H. A. (2001) Population dynamics of *Bythotrephes cederstroemi* in south-east Lake Michigan 1995–98. *Freshw. Biol.*, **46**, 1491–1501.
- Pothoven, S. A., Fahnenstiel, G. L. and Vanderploeg, H. A. (2003) Population characteristics of *Bythotrephes* in Lake Michigan. *J. Great Lakes Res.*, **29**, 145–156.
- Richter, S., Braband, A., Aladin, N. *et al.* (2001) The phylogenetic relationships of “predatory water-fleas” (Cladocera: Onychopoda, Haplozoa) inferred from 12S rDNA. *Mol. Phylogenet. Evol.*, **19**, 105–113.
- 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 Yursita, P. M. (1999) Implications of an invertebrate predator’s (*Bythotrephes cederstroemi*) atypical effects on a pelagic zooplankton community. *Hydrobiologia*, **380**, 179–193.
- Sebestyen, O. (1949) On the life-method of the larva of *Leptodora kindtii* (Focke) (Cladocera, Crustacea). *Acta Biol. Hung.*, **1**, 71–81.
- Stearns, S. C. (1992) *The Evolution of Life Histories*. Oxford University Press, New York.
- Sturner, R. W. and Elser, J. J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.
- Straile, D. and Hälbich, A. (2000) Life history and multiple antipredator defenses of an invertebrate pelagic predator, *Bythotrephes longimanus*. *Ecology*, **81**, 150–163.
- Sullivan, C. A. and Lehman, J. T. (1998) Character variation and evidence for spine length selection in the invertebrate predator *Bythotrephes* (Crustacea: Cladocera) from Lakes Michigan, Huron, and Erie. *Arch. Hydrobiol.* **142**, 35–52.
- Therriault, T. W., Grigorovich, I. A., Cristescu, M. E., *et al.* (2002) Taxonomic resolution of the genus *Bythotrephes* Leydig using molecular markers and re-evaluation of its global distribution. *Divers. Distrib.* **8**, 67–84.
- Thorpe, J. H. and Covich, A. P., (eds.) (2001) *Ecology and Classification of North American Freshwater Invertebrates*, 2nd edn. Academic Press, San Diego.
- Vijverberg, J. (1980) Effect of temperature in laboratory studies on development and growth of Cladocera and Copepoda from Tjeukemeer, The Netherlands. *Freshw. Biol.*, **10**, 317–340.
- Vijverberg, J. (1991) Variability and possible adaptive significance of day-time vertical distribution of *Leptodora kindtii* (Focke) (Cladocera) in a shallow eutrophic lake. *Hydrobiol. Bull.*, **25**, 85–91.
- Vijverberg, J. and Koelewijn, H. P. (2004) Effect of temperature on development and growth of the raptorial cladoceran *Leptodora kindtii* under laboratory conditions. *Freshw. Biol.*, **49**, 1415–1422.
- Vijverberg, J., Koelewijn, H. P. and van Densen, W. L. T. (2005) Effects of predation and food on the population dynamics of the raptorial cladoceran *Leptodora kindtii*. *Limnol. Oceanogr.*, **50**, 455–464.
- Wahlström, E. and Westman, E. (1999) Planktivory by the predacious cladoceran *Bythotrephes longimanus*: effects on zooplankton size structure and abundance. *Can. J. Fish. Aquat. Sci.*, **56**, 1865–1872.
- Warren, E. (1901) A preliminary account of the development of the free-swimming nauplius of *Leptodora hyalina* (Lillj.). *Proc. R. Soc. Lond., Ser. B: Biol. Sci.*, **68**, 210–218.
- Witt, A. M. and Cáceres, C. A. (2004) Potential predator-prey relationships between *Bythotrephes longimanus* and *Cercopagis pengoi* in south-western Lake Michigan. *J. Great Lakes Res.*, **30**, 519–527.
- Yan, N. D., Blukacz, A., Sprules, W. G., *et al.* (2001) Changes in zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Ontario, Canada. *Can. J. Fish. Aquat. Sci.*, **58**, 2341–2350.
- Yan, N. D. and Pawson, T. W. (1997) Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. *Freshw. Biol.*, **37**, 409–425.
- Yan, N. D. and Pawson, T. W. (1998) Seasonal variation in the size and abundance of the invading *Bythotrephes* in Harp Lake, Ontario, Canada. *Hydrobiologia*, **361**, 157–168.

- Yurista, P. M. (1992) Embryonic and postembryonic development in *Bythotrephes cederstroemi*. *Can. J. Fish. Aquat. Sci.*, **49**, 1118–1125.
- Yurista, P. M. and Schulz, K. L. (1995) Bioenergetic analysis of prey consumption by *Bythotrephes cederstroemi* in Lake Michigan. *Can. J. Fish. Aquat. Sci.*, **52**, 141–150.
- Zaret, T. M. (1980) *Predation and Freshwater Communities*. Yale University Press, New Haven.
- Zozula, S. S. and Mordukhai-Boltovskoi, F. D. (1977) Seasonal variability of *Bythotrephes longimanus* (Crustacea, Cladocera). *Dokl. Acad. Nauk*, **232**, 75–77.

