

Prey consumption and predatory effects of an invertebrate predator (*Bythotrephes*: Cladocera, Cercopagidae) based on phosphorus budgets

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Abstract

Phosphorus excretion rates, ingestion efficiency, and P content of *Bythotrephes* at different developmental stages are used to estimate predation rates indirectly from metabolic needs. A growth model is developed to predict P content and weight of this invertebrate planktivore throughout its life. P consumption required to complete one parthenogenic life cycle of the predator is estimated from metabolic rates and weight measurements of individual instars. Based on P requirements and prey stoichiometry, empirical ingestion efficiency of 59%, and assimilation efficiency of 85%, each *Bythotrephes* consumes the equivalent of 14 *Daphnia* per day on average and can inflict mortality equal or greater in magnitude to *Daphnia* recruitment rates during midsummer in offshore waters of Lake Michigan, particularly when predator population abundance exceeds 400 individuals m⁻².

Bythotrephes cederstroemi, a predaceous cladoceran native to northern Europe and Asia, invaded the Laurentian Great Lakes in the mid-1980s (Lange and Cap 1986; Bur et al. 1986; Berg and Garton 1988). Within 1 yr after it appeared in Lake Michigan in 1986 (Lehman 1987; Evans 1988), *Bythotrephes* became well established in offshore waters, reaching peak abundances by midsummer (Lehman 1991). Coinciding with the successful invasion of the predator were declines in the three dominant *Daphnia* species (Lehman 1988, 1991). Changes to the herbivorous zooplankton were attributed to direct mortality imposed on *Daphnia* by *Bythotrephes*. Sprules et al. (1990) suggested alternatively that most of the observed decline in the *Daphnia* population should be attributed to predation by planktivorous fish.

The potential predatory impact of *Bythotrephes* depends on prey consumption rates. One way to estimate consumption is to rely on experimental rates of predation in the laboratory or in enclosure experiments in situ. An alternative approach is to calculate the nutrient requirements for maintenance and growth.

Literature reports of prey consumption rates for *Bythotrephes* vary considerably. Mordukhai-Boltovskaia (1958) reported 25–30 prey d⁻¹ to be the maximum consumed by *Bythotrephes*. Sprules et al (1990) and Vanderploeg et al. (1993) used much lower rates to calculate the potential impact of *B. cederstroemi* on *Daphnia*. More precise estimates of prey consumption are required to assess the impact of the exotic cladoceran on the zooplankton community of the Laurentian Great Lakes. However, studies of predation by *Bythotrephes* are complicated by a number of factors. The animals are difficult to maintain in laboratory culture (Mordukhai-Boltovskaia 1958; Yurista 1992; Burkhardt 1991). To avoid cannibalism, the predators must be kept in separate containers, and large vessels are required to simulate natural prey densities. It is difficult, moreover, to monitor cause and time of death of *Bythotrephes* in field enclosures. Cannibalism of adults on their offspring, frequently observed in the laboratory, adds further complication to enclosure experiments. Because of the multitude of challenges to direct predation experiments and their subsequent extrapolation to nature, this study adopted an alternative approach. We use mass balance equations to estimate prey consumption from metabolic requirements to test the null hypothesis that this invertebrate predator could not impose enough mortality to influence population dynamics of *Daphnia* in Lake Michigan.

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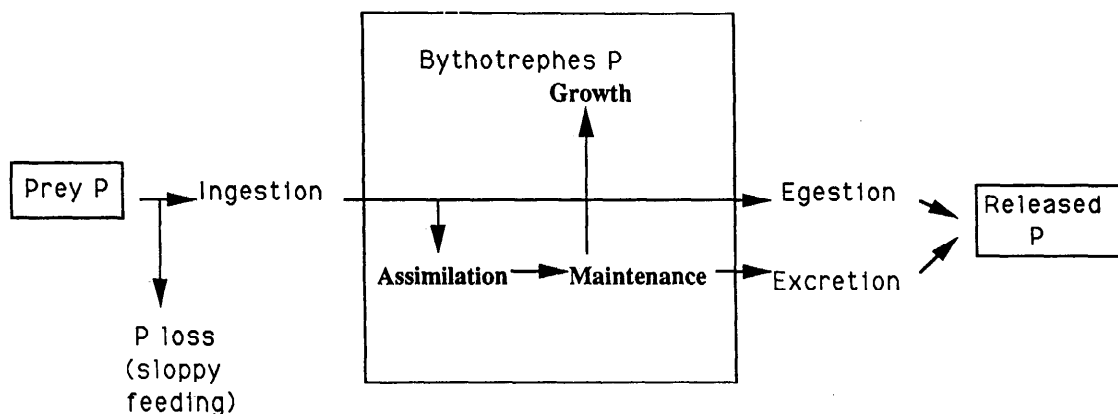


Fig. 1. P turnover by *Bythotrephes*.

Materials and methods

P content and P excretion rate—We collected *Bythotrephes* with a 1-m Puget Sound closing net of 130- μ m mesh aperture from 20-m vertical hauls in southeastern Lake Michigan during two research cruises on 16–19 July and 30 July–3 August 1990. The sampling station ($z = 100$ m) was located 36 km offshore Grand Haven, Michigan, at 43°N, 86°40'W. All P excretion experiments commenced on shipboard within 15 min after collecting the plankton samples. Animals were rinsed three times in Lake Michigan water and transferred individually to tissue culture wells by grasping their chitinous spine with forceps. Each well contained 2.5 or 5.0 ml of GF/F-filtered lake water (FLW) maintained in shipboard incubations at 10, 16, or 19°C.

Animals were incubated in the dark for 10–12 h and monitored microscopically for damage or abnormal behavior at 3-h intervals. Gender and reproductive stage of the animals were recorded. At the end of incubation, the animals were placed on Teflon, immediately frozen on dry ice, and later freeze-dried for analysis of dry weight (DW) and P content. Two milliliters from each incubation vessel were transferred to borosilicate tubes and frozen for subsequent analysis. The increase in SRP (Strickland and Parsons 1972) in experimental wells compared to FLW controls was measured in 2-ml spectrophotometer cells (5-cm pathlength). The rate of SRP release by *Bythotrephes* is termed P excretion rate.

Individual freeze-dried animals were weighed, placed in borosilicate tubes containing 2 ml of 1% $K_2S_2O_8$ solution, and autoclaved for 60 min. Samples were then diluted 1:1 with deionized water and P was estimated as SRP.

P ingestion efficiency—Feeding experiments were performed both shipboard and ashore at room temperature of $\sim 20^\circ\text{C}$. We placed *Bythotrephes* collected during 15–20 July and 30–31 July 1991 in tissue culture wells containing 2 ml of FLW and kept them without food for at least 24 h before feeding experiments. All experiments were accomplished within 2 d after collection. In 258 individual feeding trials, we applied forceps to the tail spines of *Daphnia pulex* and offered them to *Bythotrephes*. The entire process of feeding was observed microscopically, and the loss of shredded prey during feeding was recorded. The time interval between accepting prey and final drop of debris was considered prey handling time. After each successful feeding trial, *Bythotrephes* was removed and the content of the incubation vessel transferred to borosilicate tubes for TP analysis (1% $K_2S_2O_8$).

Only barren *Daphnia* females, ranging in size from 0.64 to 1.96 mm (eye to base of tail spine), were used in feeding experiments. P content was related to body length of *D. pulex* by nonlinear regression. Ingestion efficiency (IE) of P was calculated from P_{prey} (P content of experimental *Daphnia* calculated from regression) and P_{debris} (P content of debris detected in the incubation vessel after feeding):

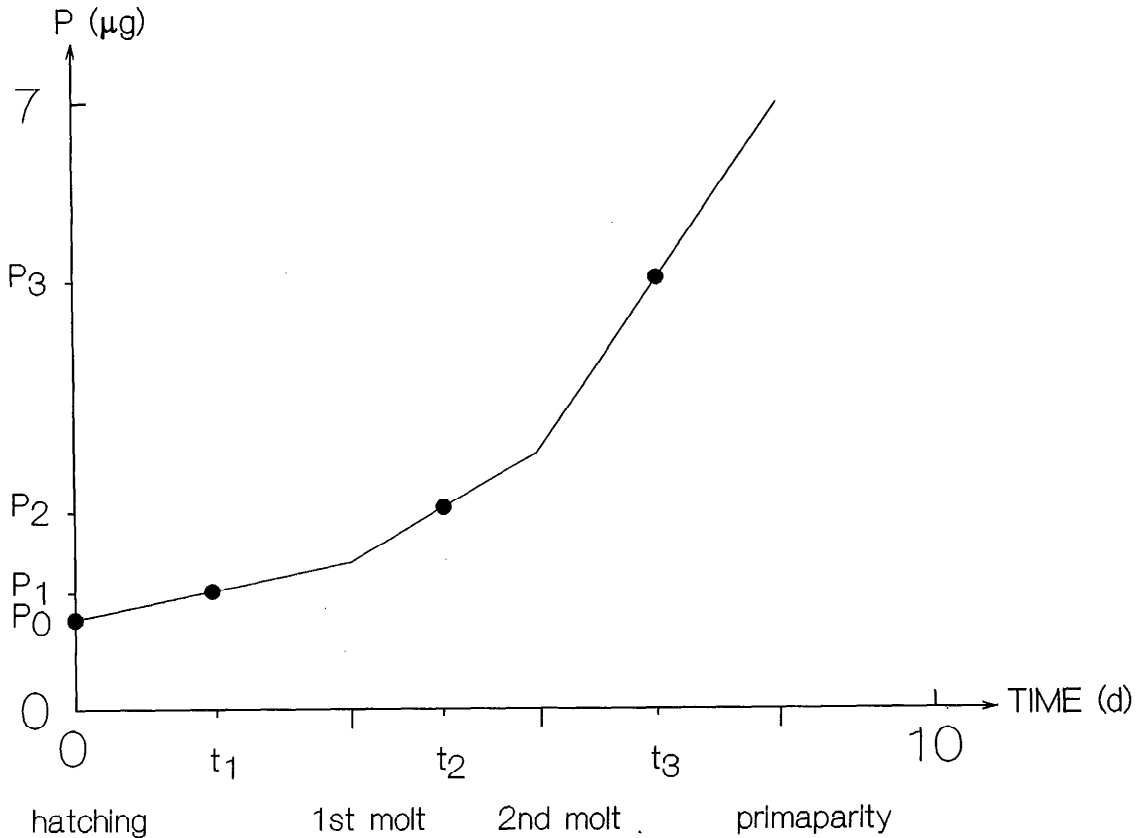


Fig. 2. Graphical model of *Bythotrephes* growth. Development time on the horizontal axis represents one complete life cycle of parthenogenic females. Mean P contents at instar midpoint ages are indicated.

$$IE = (P_{\text{prey}} - P_{\text{debris}}) / P_{\text{prey}} \quad (1)$$

Direct measurement of assimilation efficiency (AE) for *Bythotrephes* feeding on *Daphnia* (Lehman 1993) has established that $AE = 85\%$ ($SE = 2\%$).

Calculation of prey consumption rates—P turnover by *Bythotrephes* is illustrated schematically in Fig. 1. Loss of debris during feeding causes only a fraction of prey P to be ingested. P which passes the digestive tract without participating in metabolism contributes as egestion to released P. Assimilation is defined as the fraction of P absorbed through the wall of the intestine. Assimilated P is used for maintenance and growth; P released via metabolism is termed excretion.

Data for *Bythotrephes* collected between 30 July and 3 August 1990 were chosen for calculations of prey consumption rates. As indi-

cated in Fig. 2, W_i and P_i represent mean DW and P contents by instar for animals at times (t_i) midway between two molts. The third instar represents mature parthenogenic females.

P content of *Bythotrephes* as a continuous function of age, $P(t)$, can be described as

$$P(t) = P_0 + \int_0^t [CR(W) \cdot IE \cdot AE - E(T, W)] dt \quad (2)$$

P_0 is P content of neonates at hatching ($\mu\text{g P}$), $CR(W)$ is P consumption rate ($\mu\text{g P d}^{-1}$) as a function of body mass, and $E(T, W)$ is average P excretion rate ($\mu\text{g P d}^{-1}$) as a function of weight and temperature.

All statistical analyses were performed with SYSTAT 5.0. QBASIC (DOS 5.0) was used for computer simulations. Biases caused by logarithmic transformation were corrected in re-

Table 1. P content as percentage of dry weight for the three instars of *Bythotrephes cederstroemi* collected in July 1990. Standard deviations in parentheses.

Instar	P content (%)	Wt (μg)	n
1	1.42(0.37)	75(18)	62
2	1.28(0.35)	161(41)	65
3	1.07(0.34)	398(143)	59

gressions by the residual mean square (RMS) (Bird and Prairie 1985). Thus, the error term $\exp(\text{RMS}/2)$ was introduced when logarithmic equations were back-transformed to original units.

Results

P content—P content of *Bythotrephes* as a function of DW was calculated by nonlinear regression ($r^2 = 0.917$, $n = 186$) of P content (P, μg) against W (μg), yielding

$$P = 0.047 W^{0.741}. \quad (3)$$

Weight-specific P content of juvenile *Bythotrephes* (instar 1) was 1.42% (SD = 0.37, $n = 62$) but decreased significantly ($P < 0.001$) with increasing body size. For adult animals (instar 3), P constituted on average 1.07% (SD = 0.34, $n = 59$) of DW (Table 1).

P excretion rate—Soluble reactive P (SRP) concentrations in experiments typically ranged from 1 to 3.5 μM . All values were above the detection limit and within the linear range of the standard curve. Figure 3 shows weight-specific P excretion rate plotted against individual DW at 10, 16, and 19°C. Size-specific P excretion rates varied inversely with DW at all temperatures. The results for 10 and 16°C are from samples collected on 16 July 1990. Due to logistic limitations, P excretion experiments at 19°C were conducted on 31 July 1990. Animals on that date tended to be larger, owing to an increase in average body size of *Bythotrephes* over summer (Burkhardt 1994). Despite differences in average DW between the two dates, there is sufficient overlap in size to permit comparison of excretion rates at the different treatments.

Temperature had a significant positive effect on P excretion rates at any given body size (ANCOVA, $P < 0.001$), but size effects on P excretion (slopes of regression lines) were not detectably different with temperature (Fig. 3).

Table 2. P excretion [P_{ex} , $\mu\text{g P (mg DW)}^{-1} \text{d}^{-1}$] and turnover times measured for *Bythotrephes* at 10 and 16°C. Dry weights are of animals collected 16 July 1990. Standard deviations in parentheses.

T (°C)	Instar	P_{ex}	Turnover time (d)	DW (μg)	
				DW (μg)	n
10	1	3.4(1.1)	3.7(1.3)	77(23)	18
	2	2.6(0.6)	4.8(1.9)	155(40)	11
	3	1.7(0.8)	6.8(2.9)	439(160)	18
16	1	4.4(1.1)	3.1(0.8)	75(19)	16
	2	3.7(0.9)	3.6(0.9)	159(44)	25
	3	2.3(0.8)	5.3(2.5)	408(123)	25

Average P excretion rates and corresponding DW for each instar at 10 and 16°C are listed in Table 2.

P excretion, weight, and temperature can be related in the general form

$$E = \alpha \exp(kT)W^\beta, \quad (4)$$

which we solved by nonlinear regression of the data shown in Fig. 3 ($n = 157$, $r^2 = 0.945$): $\alpha = 0.484$ (SE = 0.071), $k = 0.043$ (SE = 0.006), $\beta = -0.384$ (SE = 0.029). Weight-specific P excretion rate (E_w , $\mu\text{g P mg DW}^{-1} \text{h}^{-1}$) thus varies with temperature (T , °C) and body weight (W , μg) as

$$E_w = 0.484 \exp(0.043T)W^{-0.384}. \quad (5)$$

Daily mass of P excreted per animal (E , $\mu\text{g P d}^{-1}$) is

$$E = 0.0116 \exp(0.043T)W^{0.616}. \quad (6)$$

Of 275 *Bythotrephes* collected for possible use in experiments, 14.9% died within the first 6 h of incubation. An additional 17.5% of the animals appeared to be damaged, displaying atypically slow swimming activities, differences in the movement of left and right second antennae, or other types of abnormal behavior likely to be caused by cryptic mechanical injuries not immediately apparent when animals were isolated from net collections. Bias potentially introduced by using damaged or weakened animals was minimized by excluding the corresponding cases a priori from analyses, and our data are based solely on vigorous specimens.

No significant differences in P excretion rates were detected when incubating the animals in vessels of different size (ANOVA, $P > 0.05$), and the data were pooled.

P ingestion efficiency—*D. pulicaria* was typ-

ically accepted by *Bythotrephes* within seconds. The predator grasped the prey with its large first thoracic legs, placed it near the mandibles between its pairs of thoracic legs, and began shredding it. Within minutes after being grasped, ingested parts of the shredded *Daphnia*, in particular its black eye and green gut contents, could be identified in the anterior part of the intestine. Although *Bythotrephes* appears capable of orienting its prey in any desired position, *Daphnia* was generally oriented with its head at the mouth of the predator and its ventral side directed inward; few adjustments were necessary to hold *Daphnia* in a favorable position. Small pieces of the shredded prey, including parts of thoracic appendages and antennae, were dropped during feeding. Typically, feeding ended with the release of a large piece of debris, after which *Bythotrephes* exhibited some cleaning behavior to assure complete discard of prey remains.

We divided *D. pulicaria* into five size classes ranging from <1.0 mm (min size, 0.64 mm) to >1.6 mm (max size, 1.96 mm) to investigate effects of prey size relative to the size of *Bythotrephes*; feeding results (Table 3) are reported by *Bythotrephes* instar.

Burkhardt (1991) found that P content of *D. pulicaria*, P_D (μg), can be calculated from *Daphnia* body length, L (mm):

$$P_D = 0.124L^{2.162}. \quad (7)$$

Equation 7 was used to estimate the amount of P offered to *Bythotrephes* in feeding experiments. P_{in} , the quantity of prey P ingested, can be calculated as

$$P_{in} = P_D - P_{debris} + P_{ex}. \quad (8)$$

P_{debris} is P content of debris dropped by *Bythotrephes* as a result of "sloppy feeding," and P_{ex} is P excretion during the experiment.

Ingestion efficiency IE was calculated as

$$IE = P_{in}/P_D. \quad (9)$$

Due to the brief incubation (typically <15 min for instars 2 and 3) and reduced P excretion rate after more than 24 h of starvation, the term P_{ex} is small compared to P content of *Daphnia*. We quantified the impact of the excretion term on calculations of IE by incubating 28 *Bythotrephes* after successful feeding trials for a time interval equal to the prey han-

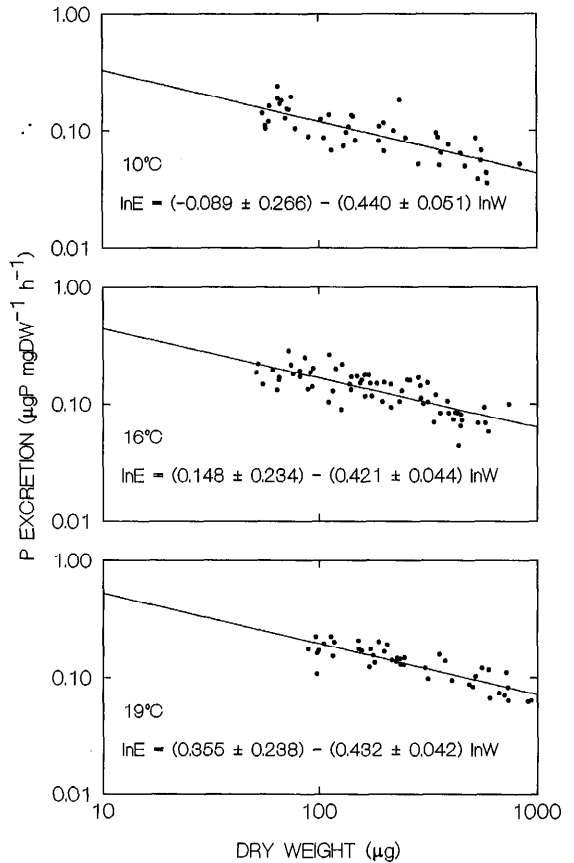


Fig. 3. Size-specific P excretion rates and individual dry weights of *Bythotrephes* at 10, 16, and 19°C. Linear regressions are shown for log-transformed data.

Table 3. Feeding by *Bythotrephes* instars on *Daphnia pulicaria* of various mean length. Time—mean handling time (min); IE—mean P ingestion efficiency. Standard error of the mean (SE) in parentheses.

<i>Bythotrephes</i> instar	<i>Daphnia</i> size class (mm)	Length (mm)	Time (min)	IE	n
1	<1.0	0.81(0.02)	9.5(0.9)	0.51(0.02)	20
	1.0–1.2	1.08(0.02)	28.0(2.9)	0.57(0.02)	16
	1.2–1.4	1.32(0.02)	25.1(1.6)	0.53(0.03)	20
	1.4–1.6	1.45(0.01)	29.9(2.8)	0.58(0.03)	14
2	<1.0	0.87(0.02)	7.9(0.9)	0.49(0.03)	18
	1.0–1.2	1.08(0.01)	8.7(0.7)	0.57(0.03)	19
	1.2–1.4	1.29(0.02)	12.8(1.6)	0.53(0.04)	16
	1.4–1.6	1.50(0.01)	18.4(2.0)	0.53(0.02)	25
3	<1.0	0.83(0.03)	6.3(0.8)	0.46(0.04)	21
	1.0–1.2	1.08(0.01)	7.1(0.8)	0.58(0.02)	23
	1.2–1.4	1.29(0.01)	8.0(0.5)	0.56(0.02)	25
	1.4–1.6	1.50(0.01)	12.4(1.2)	0.59(0.02)	20
	>1.6	1.74(0.02)	13.3(1.3)	0.59(0.03)	21

Table 4. Parameters used to calculate P consumption rates CR_i, where $i = 0$ corresponds to a neonate and $i = 1, 2, 3$ correspond to instar averages. W_i is body mass ($\mu\text{g DW}$), P_i is P content ($\mu\text{g P}$), t_i is average age of each instar, IE is ingestion efficiency, and AE is assimilation efficiency.

	$i = 0$	$i = 1$	$i = 2$	$i = 3$
W_i (μg)	73	102	195	495
P_i (μg)	1.03	1.36	2.31	4.95
t_i (d)	0	1.6	4.3	6.8
IE (%)	—	59	59	59
AE (%)	—	85	85	85

dling time. SRP concentration in the incubation vessel was measured to estimate P release during the feeding experiments. The amount of P excreted was, on average, 4.1% (SE = 0.4, $n = 28$) of the P content of the *Daphnia*. This result compares to 3.7% (SE = 0.2) predicted for excretion rates from the regression model (Eq. 6).

P ingestion efficiencies, not corrected for P_{ex} , and prey handling times are presented in Table 3. On average, almost half of prey P is lost during feeding. When all data are pooled, P ingestion efficiency calculated by Eq. 9 for *Bythotrephes* feeding on *D. pulicaria* is 55% (SD = 12, $n = 240$). If allowance is made for P_{ex} , IE equals 59%. Within each size class, P ingestion efficiency is not significantly different among *Bythotrephes* of the three developmental stages (ANOVA, $P > 0.05$). Each instar feeds least efficiently on the smallest *Daphnia* (<1 mm), but we observed no significant differences in IE when we offered *Daphnia* of larger size to any *Bythotrephes* instar.

Prey of any given size are handled most quickly by adult *Bythotrephes* (instar 3). Animals of the second and third instar exhibit a continuous increase in handling time with size of the *Daphnia* (ANOVA, $P < 0.001$). In contrast, a stepwise increase in handling time between size class 1 (<1.0 mm) and size class 2 (1.0–1.2 mm) was observed for juvenile *Bythotrephes*. The first instar spent about three times longer feeding on prey >1 mm than on *Daphnia* of the smallest size class. Larger prey size did not result in significant differences in either handling time or P ingestion efficiency (ANOVA, $P > 0.05$). Average DW of *Bythotrephes* used in feeding experiments was 95 μg (instar 1), 227 μg (instar 2), and 448 μg (instar 3). Thus, the animals were intermediate with respect to seasonal size variation in 1991 and

were similar in body mass to specimens collected on 30 July–3 August 1990 (Burkhardt 1994). Behavioral observations during feeding experiments indicate that even juvenile *Bythotrephes* can grasp and shred *D. pulicaria* longer than 1.4 mm when the prey are offered with forceps. However, *D. pulicaria* of the largest size class is almost as big as the core body of juvenile *Bythotrephes* and the prey appear to be difficult to handle. Twenty percent of instar 1 and 15% of instar 2 rejected *D. pulicaria* >1.2 mm or dropped the prey during handling within the first 2 min. In contrast, all but two feeding trials were successful (97%) when we offered *Daphnia* <1.2 mm to pre-adult instars.

Prey consumption rates—Parameters used to calculate P consumption rates are summarized in Table 4. Based on measured development times of *Bythotrephes* at 12°C and a temperature-dependent development model (Yurista 1992), development time of animals collected on 31 July 1990 was calculated at 18.6°C, the mean epilimnetic temperature. Postembryonic rates of development were scaled to temperature in proportion to Yurista's (1992) model for embryonic development. Primarity at 18.6°C is predicted to be reached after 8.2 d

First approximation of P consumption rates was obtained by assuming an allometric relationship between CR and W:

$$\text{CR} = a \cdot W^b \quad (10)$$

Equation 2 was solved by numerical integration after substituting Eq. 6 and 10:

$$P(t + \Delta t) = P(t) + [a \cdot W^b \cdot \text{IE} \cdot \text{AE} - 0.116 \cdot \exp(0.043T) \cdot W^{0.616}] \Delta t \quad (11)$$

with $T = 18.6^\circ\text{C}$ and $\Delta t = 0.1$ d. Parameters a and b were varied in factorial combination to minimize least-squared residual errors of the model to empirical data. Negative correlation exists between the parameters so alternative combinations give similar fits to data, but residuals were minimized with $b = 0.89795$ and $a = 0.02203$. Relative differences between predicted and observed mean P contents were -1.5% for the first instar, -1.7% for the second, and +0.2% for the third.

ΣP , the P content of prey consumed by *Bythotrephes*, was calculated as

$$\Sigma P = \sum_{j=1}^k CR_j \Delta t_j \quad (12)$$

where k equals the number of time intervals Δt_j from neonate to primiparity. The mean rate of P consumption throughout life (CR, $\mu\text{g P d}^{-1}$) can then be defined as

$$CR = \Sigma P / D \quad (13)$$

where $D (= \Sigma \Delta t_j)$ is generation time. Average P content of prey consumed by each instar can be calculated as well.

Handling time increased substantially when *Bythotrephes* juveniles were offered *D. pulicaria* > 1.0 mm (Table 3). The greatest increase in handling time by second instar animals occurred at *Daphnia* sizes > 1.4 mm. Although first and second instars could feed on prey > 1.4 mm, an increased percentage of unsuccessful feeding trials (prey rejected or lost during handling) suggests that the first two instars may elect smaller prey in nature. In contrast, adult *Bythotrephes* readily accepted *D. pulicaria* up to 1.96-mm body length. To provide a rudimentary model of increased prey size during life, we assumed that the three instars feed on *D. pulicaria* of average size 1.0 mm in instar 1, 1.2 mm in instar 2, and 1.6 mm in instar 3. As we explain in the next section, these figures probably provide a conservative estimate of the numerical impact of the predator on *Daphnia* populations in Lake Michigan.

On the basis of the relationship between P content and body length (Eq. 7), $P_D(1) = 0.124 \mu\text{g}$, $P_D(2) = 0.184 \mu\text{g}$, and $P_D(3) = 0.343 \mu\text{g}$ represent the average P content of *D. pulicaria* of 1.0-, 1.2-, and 1.6-mm body length, respectively. These values were used to convert P consumption (CR, $\mu\text{g P d}^{-1}$) into prey consumption (PR, prey d^{-1}):

$$PR_i = CR_i / P_D(i). \quad (14)$$

Table 5 lists results from the growth model. PR represents the number of *D. pulicaria* of specified size which *Bythotrephes* must consume per day to satisfy its metabolic requirements. Average consumption rates are presented for each developmental stage and from hatching to primiparity. Daily P demands increase during postembryonic development. Because larger *Daphnia* have been used to convert P requirements into prey consumption

Table 5. Average rates of phosphorus consumption (CR) and prey consumption (PR) predicted from the simulation growth model. Results are shown for the three developmental stages of *Bythotrephes* collected in July 1990. Instar 1-3 refers to the entire life cycle of parthenogenic females from hatching to primiparity.

Instar	CR ($\mu\text{g P d}^{-1}$)	Nominal prey length (mm)	PR (prey d^{-1})
1	1.25	1.0	10
2	2.36	1.2	13
3	6.04	1.6	18
1-3	3.18	1.0-1.6	14

rates of adult *Bythotrephes*, increased CR does not translate linearly into big differences in PR between instars, and average consumption throughout life is roughly 14 prey d^{-1} .

Lehman and Cáceres (1993) report birth rates (b) for *Daphnia* species in Lake Michigan ranging from 0.035 to 0.162 d^{-1} (mean = 0.086, SE = 0.012, $n = 11$). Total numbers of new recruits added to *Daphnia* populations can thus be estimated by

$$dN_D/dt = bN_D(t) \quad (15)$$

where $N_D(t)$ is *Daphnia* m^{-2} . Predatory mortality imposed on the *Daphnia* populations at or near these rates would be sufficient to suppress population increases independent of any additional sources of natural mortality.

To evaluate the maximum potential impact of consumption by *Bythotrephes* on the *Daphnia* populations, we considered the magnitudes of consumption that could be supported if each predator killed 14 *Daphnia* d^{-1} ; we used abundance data reported by Lehman and Cáceres (1993). Both upper- and lower-bound estimates of the rate of new *Daphnia* recruitment were calculated by Eq. 15, with $b = \text{mean} \pm 2 \text{ SE}$. Thus, if consumptive demands by the *Bythotrephes* population equaled or exceeded the rate of prey renewal, the predator would be theoretically capable of cropping all natural recruitment. Results (Fig. 4) indicate that mid-summer consumptive demand by *Bythotrephes* equals or exceeds the yield possible by harvesting all new *Daphnia* production. By late summer, however, the waning *Bythotrephes* population inflicts rates of mortality that are too low to suppress *Daphnia* unless additional sources of mortality contribute to *Daphnia* losses.

Another way to evaluate predatory effects of

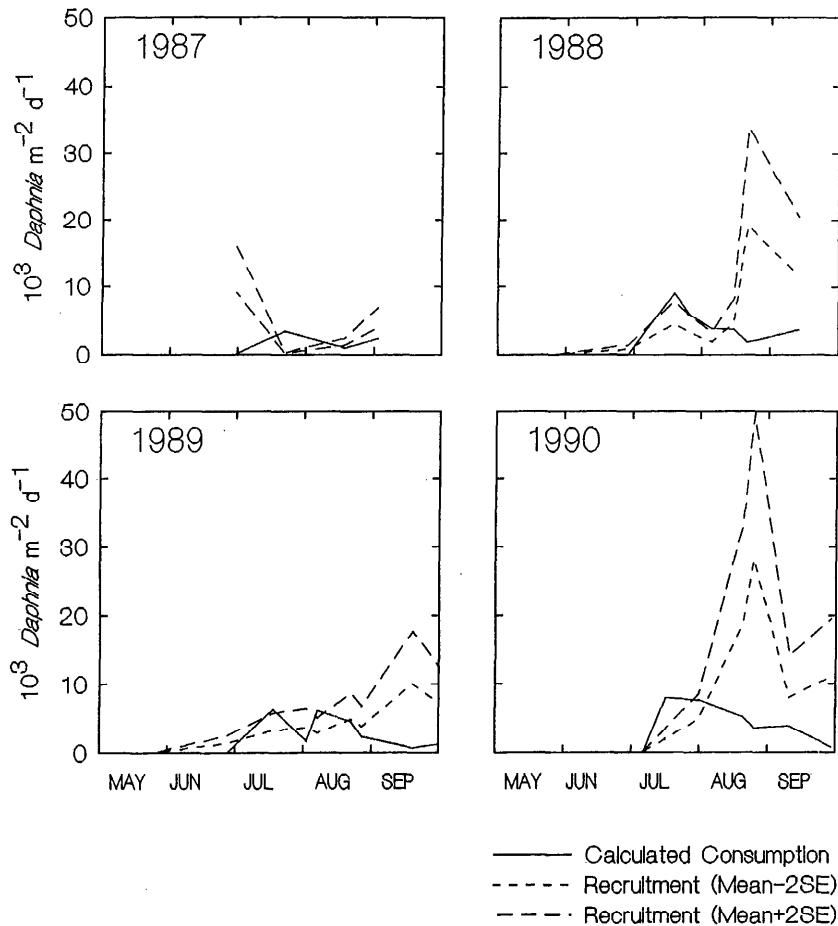


Fig. 4. Rates of consumption of *Daphnia* by *Bythotrephes*, calculated from metabolic P demands, together with upper- and lower-bound estimates of *Daphnia* population renewal.

Bythotrephes is to estimate the population densities of *Daphnia* which could exist at equilibrium with ambient abundances of the predator, given model rates of consumption and *Daphnia* population renewal. If actual field densities of *Daphnia* exceed these equilibrium values, mortality imposed by *Bythotrephes* alone would be insufficient to offset population growth rates. If abundances lie on or below the equilibrium line, however, consumptive demand by *Bythotrephes* alone would equal or exceed *Daphnia* recruitment so that all prey recruitment could potentially be cropped by the invertebrate predator. Figure 5 reports simultaneous abundances of *Daphnia* spp. and *Bythotrephes* at inshore (20 m) and offshore

(100 m) reference stations along 43°N from 1987 to 1992 for epilimnion temperatures >15°C ($n = 82$). Comparison of data with model prediction indicates that *Daphnia* populations (here, mainly *D. galeata mendotae*) have been consistently suppressed whenever *Bythotrephes* populations reach ~400 individuals m^{-2} .

Discussion

P content—Diets of carnivorous and herbivorous zooplankton differ stoichiometrically owing to lower P contents of phytoplankton compared with zooplankton (Behrendt 1990). Zooplankton exhibit little intraspecific variation in P content, whereas interspecific vari-

ability is high (Hessen and Lyche 1991). Mean P content ranges almost 7-fold, from 0.38% of DW in *Eudiaptomus gracilis* to 2.6% in *Scapholeberis mucronata*. Our results indicate that P:DW ratios of *B. cederstroemi* vary with size of the animals. Mean P content of juveniles (1.42% DW = 75 μg) was 33% higher than adults (1.07%, DW = 398 μg). This trend is consistent with P measurements of *Daphnia magna* by Hessen (1990), who measured 1.64% P:DW ratios in animals <100 μg DW, compared to 1.27% in adults. He suggested that decreasing P:DW ratios throughout life were a result of decreasing RNA contents in adults. Differences in lipid contents may also affect P:DW ratios. Based on a literature survey, Andersen and Hessen (1991) calculated 1.43% (SD = 0.27) P:DW for several *Daphnia* species. Similar P:DW for juvenile *Bythotrephes* indicates that carnivorous Cladocera may contain as much P as herbivores.

P excretion rates—During 1990 in Lake Michigan, mean DW of *Bythotrephes* instars ranged from 71 μg (instar 1, 16 July 1990) to 636 μg (instar 3, 10 September 1990) (Burkhardt 1994). This difference in individual body mass corresponds to a decrease in size-specific P excretion rates by a factor of 2.3 at constant temperature (Eq. 5). Adults consistently contain about five times as much mass as juveniles (Burkhardt 1994). As a result, individual P excretion rate (Eq. 6) increases by a factor of 2.7 from juvenile to adult, whereas weight-specific P excretion rate (Eq. 5) is approximately halved. Changes in ambient summer temperature influence P excretion to a lesser degree. Between 16 July and 30 September 1990, mean epilimnetic temperatures ranged between 15.5 and 21.3°C, resulting in a maximum difference of 30% in weight-specific P excretion rates.

Because *Bythotrephes* is difficult to maintain in laboratory cultures and starvation may cause decreases in P excretion rates (Johannes 1964; Le Borgne 1979), animals were not acclimated to experimental temperatures. However, two of the treatments (16 and 19°C) differed by not more than 1.6°C from mean epilimnetic temperature at the time of collection. The degree to which P excretion rates at 10°C would change after long-term acclimation cannot be estimated from this study, but the effect of temperature on P excretion is less extreme than

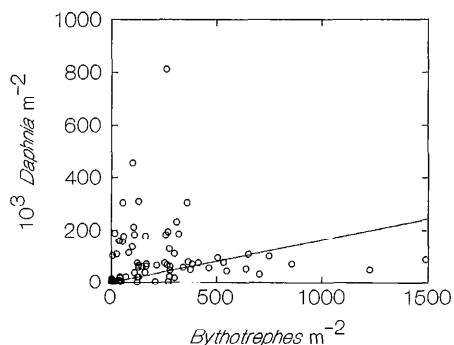


Fig. 5. Simultaneous abundances of *Daphnia* and *Bythotrephes* in Lake Michigan, 1987–1992, at $T > 15^\circ\text{C}$. The line represents the equilibrium *Daphnia* population consistent with ambient *Bythotrephes* abundance, a ration of 14 *Daphnia* d^{-1} , and birth rates of 0.086 d^{-1} .

differences due to variation in body mass. Thus, the use of 10°C data without acclimation probably does not introduce a large error in calculations of P excretion rates from Eq. 5 and 6.

In this study, the products of P release by *Bythotrephes* were analyzed as SRP, which may include both inorganic and organic P (Strickland and Parsons 1972). Peters and Lean (1973) characterized the P release products of *Daphnia rosea* and *Diaptomus minutus* and concluded that only ~10% of released soluble P was organic. The bulk of released P, analyzed by gel filtration, appeared to be orthophosphate. These results are consistent with studies by Ferrante (1976) with natural zooplankton collections. We therefore assume that measurements of SRP release closely approximate excretion of mineralized P.

Burkhardt (1991) tested the effect of duration of incubation on P excretion rate by measuring SRP release by *Bythotrephes* over successive short-term incubation intervals. Mean rates measured in 10–12-h incubations underestimate initial rates by at most 25% and are the result of a gradual and continuous decrease in P excretion that Burkhardt ascribed to lack of food during the incubation. To the extent that our values for P excretion may represent slight underestimates, our calculated consumption rates by *Bythotrephes*, and hence its predatory effects, would be slightly larger.

P ingestion efficiency—Feeding by pelagic invertebrates often involves losses during handling and ingestion. Lampert (1978) reported

losses up to 17% measured as C while *Daphnia pulex* feeds on diatoms. Carnivorous zooplankton lose even greater proportions of their prey by sloppy feeding. About 25% of prey C was lost by the marine amphipod *Calliopius laeviusculus* before ingestion (Dagg 1974, 1976). IE was independent of temperature but increased with increasing size of the predator. Losses of prey body contents could exceed 35% for small amphipods. Brandl and Fernando (1975) measured IE = 37% (i.e. 63% loss of prey biomass) in experiments with *Mesocyclops* feeding on *Ceriodaphnia*. *Bythotrephes* ingests, on average, 55–59% of the P in its prey, depending on whether simultaneous excretion losses are counted. Slightly lower ingestion efficiencies of P ingestion by *Bythotrephes* appears to be largely unaffected by the body length of *D. pulicaria*. Even juveniles exhibit IE > 50% when feeding on prey almost as large as themselves.

Prey handling times of typically <15 min are similar to those of predatory copepods (Brandl and Fernando 1974, 1975). Dagg (1974) reported 15–40 min for prey ingestion by *Calanus*, indicating that longer feeding times are not uncommon. Even though the smallest *Bythotrephes* can shred and handle prey of almost its own body size, the marked increase in handling time of juveniles feeding on *Daphnia* > 1.0 mm and the increased percentage of larger prey rejected or dropped by preadult instars may indicate their preference for smaller prey.

Prey consumption rates—Mordukhai-Boltovskaia (1958) did not detect any obvious relation between prey consumption rates and size of *Bythotrephes* in the first few days of life. However, the size of her experimental animals varied little. The animals in Lake Michigan exhibit great variation in body size during life as well as on a seasonal basis. Dry weights of *Bythotrephes* collected in 1990 varied by a factor of more than 5 within each instar and were positively correlated with ambient water temperature (Burkhardt 1994). Neonates weighed as little as 10 μg at hatching in June 1990, whereas the largest adults in early August and September exceeded 1,000 μg DW. Results from our growth model indicate a severalfold increase in daily P demands of adults compared to juveniles. Similarly, rates of P con-

sumption must vary seasonally due to variation in mean body mass. Larger animals assimilate more P individually, and large size coincides with warm temperatures which enforce increased metabolic activities and faster growth, thereby increasing food demands. Mordukhai-Boltovskaia reported a marked effect of temperature on feeding. At temperatures above 15°C maximum prey consumption rates of >25 were recorded, but the rate dropped to 9 prey d^{-1} at 10–15°C. Combined effects of size and temperature may account for some of the differences in prey consumption rates predicted by different investigators.

Calculations of prey consumption rates of *Bythotrephes* in Lake Michigan apply to parthenogenic females. Males were excluded from measurements. Size differences exist between females produced parthenogenically and gametogenically (Yurista 1992), but the latter were not present in summer or fall samples. Losses of P due to molting have not been included in calculations of P requirements. Our data are representative of *Bythotrephes* in Lake Michigan during summer when the number of males in the sample is small (<5%), mean epilimnetic temperatures reach 19–20°C, and *Daphnia* is present.

The growth model shown in Eq. 11 is relatively robust. Different combinations of the allometric constants for CR (Eq. 10) yield similar fits to empirical data, and corresponding consumption rates vary by <10%. The model thus exhibits low sensitivity to errors that may arise from the approximation of the precise CR function.

Rates of prey consumption predicted by our model are consistent with observed capabilities of the predator. At the average prey handling time of 13.3 min by adult *Bythotrephes* (Table 3), animals would spend 4 h d^{-1} feeding on their estimated ration of 18 *Daphnia*, thus leaving plenty of time for searching and other components of their time budgets. Personal observations of an adult *Bythotrephes* which consumed 12 *D. pulicaria* offered during 3 h demonstrate that the animals are capable of ingesting the predicted numbers of prey.

The mass balance approach developed here can help to evaluate the results of predation experiments. For instance, Vanderploeg et al. (1993) added *Bythotrephes* to plankton assem-

blages from Saginaw Bay and from Lake Huron and reported ingestion rates of 0.18 and 0.004 d⁻¹ by weight, respectively. They concluded from their results that the predatory impact of *Bythotrephes* may be more modest for Lake Michigan than Lehman (1991) had indicated. Model analysis suggests, however, that the measured ingestion rates are lower than should be expected. Vanderploeg et al. (1993) reported experimental temperatures and body masses of their experimental animals: $T = 23.5^{\circ}\text{C}$, $W = 130 \mu\text{g DW}$ for the Saginaw Bay experiment; $T = 21.9^{\circ}\text{C}$, $W = 137 \mu\text{g DW}$ for the Lake Huron experiment. On the basis of Eq. 3, these animals would contain 1.73 and 1.80 $\mu\text{g P}$, respectively, and at experimental temperatures would be losing P by excretion at 0.639 and 0.616 $\mu\text{g P d}^{-1}$ (Eq. 6). A maintenance ration (MR, $\mu\text{g P d}^{-1}$) for the animals under these conditions can be calculated as the ingestion rate necessary to support the required excretion losses (i.e. no growth):

$$\text{MR} = P_{\text{ex}}/(\text{IE} \cdot \text{AE}). \quad (16)$$

MR values for the two experiments are 1.27 and 1.23 $\mu\text{g P d}^{-1}$, respectively, or 0.73 and 0.68 d⁻¹, referenced to body P contents. The required maintenance levels are at least severalfold higher than the predation rates reported by Vanderploeg et al., suggesting that *Bythotrephes* may have fed poorly in the experimental chambers because the reported ingestion rates are far too low for healthy, growing animals. This analysis underscores the potential biases of enclosure-based predation estimates applied to large invertebrate planktivores like *Bythotrephes* and highlights the need for independent assessments of their accuracy.

Our growth models and data indicate a monotonic increase in weight which is truncated at primiparity when neonates are released from the dorsal brood pouch. Most *Bythotrephes* do not survive primiparity in the laboratory, but we do not know what fraction of the population is iteroparous in nature. Multiple clutches do not alter calculations of consumption rates by instar, however, because the release of offspring results in a weight loss to levels similar to animals at their second molt (Lehman unpubl. data).

Conversion from metabolic demand for P to prey consumption rates depends on P contents and sizes of prey. Selectivity for prey by size cannot be predicted by mass balance. Lehman (1991) reported an increase in average body size of *D. pulicaria* from 1.165 mm in 1985, before the arrival of *Bythotrephes*, to 1.588 mm in 1987, after it had become established. If the shift reflected size-selective predation by *Bythotrephes*, it would indicate that the animals have their strongest impact on *Daphnia* <1.6 mm in body size. From observed abundances and biomasses of *Daphnia* species in offshore Lake Michigan (Lehman and Cáceres 1993) and the mean P content reported by Andersen and Hessen (1991) for *Daphnia* (1.43% P:DW), mean P content per daphnid from 1987 to 1990 was 0.202 $\mu\text{g P}$ (SD = 0.040, $n = 52$ dates). This is considerably smaller than the P content of 1.6-mm *D. pulicaria* (= 0.343 μg). Consequently, if adult *Bythotrephes* consumed *Daphnia* of average size in the population, predicted PR would be higher by 70% than the values we used to produce Fig. 4. The impact of the higher predation rate would be further exaggerated by the fact that adult instars tend to dominate the age structure of field populations. In Lake Michigan, 3-barb (adult) females represented 53% (SD = 24%, $n = 75$) of the animals in populations sampled from 1987 to 1990.

Offsetting these higher predation estimates is the possibility that *Bythotrephes* consumes alternative prey, and we may overestimate the impact of predation by assuming that the consumption is directed against *Daphnia* alone. Vanderploeg et al. (1993) reported that *Bythotrephes* used in Saginaw Bay experiments ate *Bosmina*, *Eubosmina*, *Chydorus*, and *Ceriodaphnia* in addition to *Daphnia*. The predator elected Cladocera and strongly elected against copepods. *Daphnia* accounted for 60.4% of the diet, and all Cladocera together accounted for 95.9%. In the offshore waters of Lake Michigan, alternative cladoceran prey are rare, and *Daphnia* accounts for 91% (SD = 18%, $n = 35$) of the total cladoceran biomass from July to September (1987 to 1990). Thus, the possibility of *Bythotrephes* supplementing its diet with prey other than *Daphnia* is limited. We believe, therefore, that the use of 1.6-mm *Daphnia* to convert P demand to prey con-

sumption rates by adult *Bythotrephes* represents a conservative estimate of the numerical impact of the predator on the *Daphnia* populations in Lake Michigan.

D. pulicaria was used as a representative prey item for several reasons. Laboratory feeding experiments indicated that *Bythotrephes* readily eats it. Mordukhai-Boltovskaia (1958) reported that the escape movements of copepods spared them from capture by *Bythotrephes* in laboratory experiments; in comparison to copepods, escape movements by *Daphnia* are slow, and we have observed successful captures. Because *D. pulicaria* was the largest of the three species of *Daphnia* originally present in Lake Michigan, using it as a representative for computing numerical predation estimates guaranteed that our estimates would be conservative. Finally, the decline in *Daphnia* abundance and changes in size structure after the invasion of *Bythotrephes* suggested that the invertebrate predator had been an important influence, a conclusion strengthened by our estimates of consumption rates. Indeed, we recognize that *Daphnia* populations alone may at times be insufficient to sustain *Bythotrephes* demand during midsummer, and we anticipate that occasional production of *Bythotrephes* males and resting eggs during summer months may be a symptom of food limitation.

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