Perch or plankton: top-down control of *Daphnia* by yellow perch (*Perca flavescens*) or *Bythotrephes cederstroemi* in an inland lake?

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SUMMARY

1. Seasonal termination of the vernal clear-water phase in Long Lake, Grand Traverse Co., Michigan coincided with severe size-selective predation on juvenile *Daphnia pulicaria* from 0.8 to 1.8 mm in length. This could be caused by predation by age-0 yellow perch (*Perca flavescens*) or by the exotic predatory zooplankter *Bythotrephes cederstroemi*.
2. During the initial decline of *Daphnia*, Ivlev's electivity coefficient for yellow perch from 15.0 to 20.0 mm in length was 0.50 for copepods and −0.75 for *D. pulicaria*.
3. Bioenergetics modelling of both yellow perch and *Bythotrephes* demonstrates that, during the initial *Daphnia* decline, *Bythotrephes* consumed 1.5–5 times greater total mass than yellow perch. Furthermore, models in which *Bythotrephes* consumed juvenile *Daphnia* were more consistent with the timing of the *Daphnia* decline than those in which yellow perch consumed juvenile *Daphnia*.
4. The invasion of *Bythotrephes* into Long Lake seems to be a significant perturbation, introducing effects that propagate throughout the food chain. *Bythotrephes* created a possible bottleneck for age-0 yellow perch in late June by suppressing *Daphnia*.

Keywords: bioenergetics, *Bythotrephes*, *Daphnia*, perch, trophic cascades

Introduction

The seasonal clear water phase typical of many inland lakes has been attributed to intense grazing by herbivorous zooplankton (Lampert, 1978; Edmondson & Litt, 1982; Lampert *et al.*, 1986). An extended period of unusual water clarity has been associated with a trophic cascade (Hrbácek, 1962; Carpenter, Kitchell & Hodgson, 1985; Carpenter *et al.*, 1987; Brett & Goldman, 1997), in which piscivores prey on planktivorous fish, thereby releasing grazers from predation and permitting a clear water phase. Subsequently, intense feeding by planktivorous fish reduces grazer numbers, truncating the clear water phase. A sudden decline in grazing zooplankton, especially *Daphnia*, has usually been attributed to predation by plankti-

vorous fish such as minnows (Carpenter & Kitchell, 1988) and yellow perch (*Perca flavescens* (Mitchill)) (Mills, Forney & Wagner, 1987), but also to predation by *Cyclops* (Lampert, 1978) and a combination of starvation and fish predation (Lampert *et al.*, 1986).

A clear water phase has been a regular feature in Long Lake, Grand Traverse County, Michigan (B. Lishawa, unpublished). At such times, Secchi disk transparency ranges from 10 to 19 m. *Daphnia pulicaria* Forbes is dominant during the clear water phase, reaching a density exceeding 5800 m^{-3}. Recent surveys of yellow perch in Long Lake indicate that most age classes are growing faster than the average for Michigan lakes (Michigan Department of Natural Resources, 1997). Perch data seem consistent with a trophic cascade interpretation, wherein *D. pulicaria* is the primary food, and the clear water phase ends when perch reduce the density of *D. pulicaria*. This could be similar to findings in Oneida Lake, New York, where control of *Daphnia* populations by age-0

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yellow perch has been documented (Mills *et al.*, 1987).

Long Lake hosts a second planktivore: *B. cederstroemi* Schoedler (Crustacea: Cladocera). *Bythotrephes* probably invaded Long Lake from nearby Lake Michigan, transported in bait buckets or boat wells. *Bythotrephes* is a voracious predator of mid-sized *Daphnia* (Lehman, 1988; Lehman, 1991; Lehman & Cáceres, 1993; Yan & Pawson, 1997). *Bythotrephes* may also compete for mid-size *Daphnia* with age-0 fish (Lehman, 1991).

The presence of two planktivorous predators, yellow perch and *Bythotrephes*, begged the question of the cause of the seasonal decline of *Daphnia* in Long Lake. This can be approached through bioenergetics models, which permit quantitative evaluation of distribution and abundance of prey, growth-determining metabolic processes of predators, key environmental factors and related changes in predation pressure within a framework that can be projected through time (Kitchell, Steward & Weininger, 1977).

Yellow perch probably thrive when both *Diaptomus* and mid-size *Daphnia* are plentiful from the time larvae start to feed until the fish become benthivorous (Hansen & Wahl, 1981; Confer & Lake, 1987; Mills, Sherman & Robson, 1989). Previous studies suggest that yellow perch switch from *Diaptomus* to *Daphnia* at 25–37 mm total length (Mills & Forney, 1981; Mills, Confer & Ready, 1984; Post & McQueen, 1988). If *Daphnia* are scarce, perch seek alternate food, including benthos and smaller zooplankton, which causes reduced growth (Mills & Forney, 1981). Further, fish larvae have a relatively high metabolic rate compared with adults (Post, 1990), and energy stores can be quickly depleted, making them particularly vulnerable to starvation (Lasker, 1975). Starvation has been implicated as a probable cause of recruitment failure if proper food is limited (Hunter, 1981; Miller *et al.*, 1988). Therefore, *Daphnia* abundance may be critical for successful recruitment.

Maintaining *Bythotrephes* in laboratory cultures to determine prey consumption rate has been difficult (Burkhardt, 1994; Yurista, 1992), and estimates from the field and laboratory vary widely. In the laboratory, it has been estimated that *Bythotrephes* can consume 25–30 prey day^{-1} at maximum (Mordukhai-Boltovskaya, 1958). In the field, ingestion rate has

been estimated for Lake Huron and Saginaw Bay at 0.4 and 18% of their body mass daily, respectively (Vanderploeg, Liebig & Omair, 1993), corresponding to many fewer than 25 prey day^{-1}. Bioenergetic analysis based on the carbon budget has yielded results more similar to the maximum, laboratory rate than the field rate. Early instars were estimated to consume 150% and adults 118% of their body mass daily (Yurista & Schulz, 1995).

Modelling trophic interactions requires assumptions regarding prey preference. In the absence of reproducible data on consumption rate and prey preference there has been no resolution of whether either *Bythotrephes* or fish exert top–down control on *Daphnia*. While bioenergetics models support arguments that *Bythotrephes* can suppress *Daphnia* (Lehman & Cáceres, 1993; Burkhardt & Lehman, 1994; Burkhardt, 1991; Lehman & Branstrator, 1995; Lehman, Bilkovic & Sullivan, 1997), clearance rates calculated from experiments have been more conservative (Sprules, Riessen & Jin, 1990; Vanderploeg *et al.*, 1993).

This paper reports our analysis of the interaction between yellow perch, *Bythotrephes* and *Daphnia* in Long Lake. The study used a sampling design recommended for age-0 fish–zooplankton interactions (Wanzenböck, Whiteside & Mehner, 1997). The design integrated size distribution, abundance, and vertical distribution of major zooplankton taxa and production, life history, vertical distribution and development rate of *Daphnia* with diet, growth, distribution and bioenergetics of fish and *Bythotrephes*.

Methods

Site description. Long Lake is a mesotrophic, multiple basin, kettle lake (Lat. 44°43′ N, Long. 85°85′ W, length 6.6 km, width 3.2 km, maximum depth 27 m, mean depth 8.1 m) within the Platte River catchment (Fig. 1). About 52% of Long Lake by area is less than 5 m in depth. Only 2.9% of lake surface overlies depths greater than 15 m. Although the littoral zone is large, it is sandy and both submergent and emergent macrophytes are rare. Catchment soils are mostly loamy sands with calciferous bedrock. In 1982, yellow perch, walleye (*Stizostedion vitreum vitreum* (Mitchill)) and various Centrarchidae were dominant members of the fish community (Michigan Department of Natural Resources, unpublished).
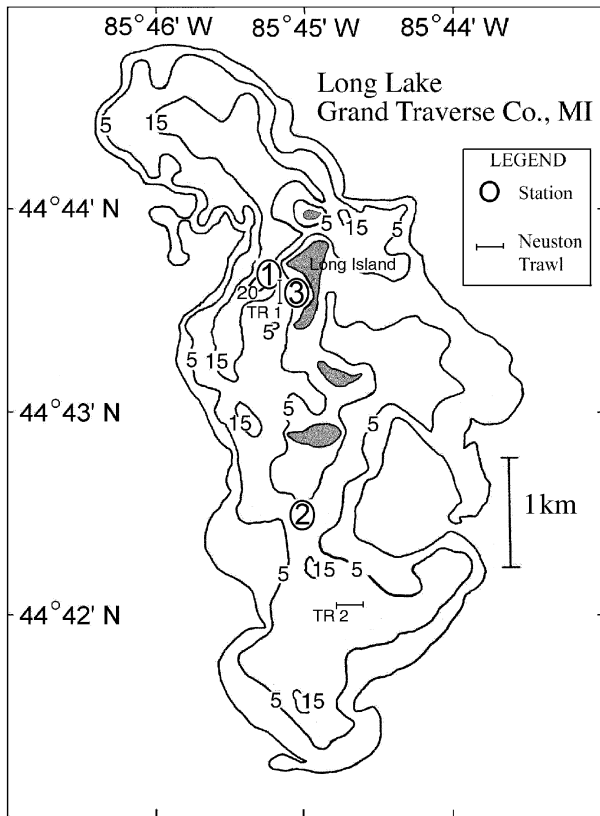
parthenogenic females was determined by counting embryos with red or black pigmented eyes. Resting eggs were also recorded. *Daphnia* clutch size was recorded; loose eggs and embryos were also counted.

Clutch size and body length of all *Daphnia* in three representative vertical tows, 15 May, 20 June and 20 September, were recorded. Length was measured from the mid-point of the eye to the base of the tail spine using a calibrated ocular micrometer. Presence of eggs or embryos, as well as the clutch size, was recorded for fecund females.

Chlorophyll *a* was detected by fluorescence using a fluorimeter (Turner TD700) equipped with excitation and emission filters suitable for distinguishing chlorophyll *a* from phaeopigments. Fluorescence measurements were calibrated to chlorophyll *a* concentration by reference to acetone blank fluorescence and fluorescence of standard chlorophyll *a* (Sigma-Aldrich Chemical, St Louis, MI, U.S.A.) diluted in 90% v/v acetone.

Bythotrephes and age-0 yellow perch were removed from neuston tows. *Bythotrephes* were scored for generation, body length, spine length, sex, clutch size, stage of embryonic development and mass. Distinct generations were determined by following cohorts through time. Length measurements were as defined by Burkhardt (Sullivan & Lehman, 1998; Fig. 1). Embryonic development was determined by the number of barb pairs and the development stage of the brood sack. First instar (one-barb) and adult female (four-barb stage for animals hatched from resting eggs or three-barb otherwise) animals were either freeze-dried or oven-dried at 60 °C for 24 h, desiccated at room temperature for 24 h, then weighed (± 1 μg; Cahn 29 electrobalance). Body mass or spine mass was determined by weighing the respective tissue. Spines were removed under a dissecting microscope by severing them with a razor at the proximal end of the scleritized spine tissue.

Larval fish were identified to species (Auer, 1982), blotted, weighed (± 0.01 mg wet mass; Mettler H33) and measured (± 0.25 mm, total length). Gut contents of selected fish were examined, the entire undifferentiated gut was removed, the contents dispersed in a Petri dish, prey items identified to the closest relevant taxon, counted and measured. Copepod length was reported as length of the metasome, *Daphnia* length was measured from mid-point of the eye to the base of the tailspine, and all other measurable lengths were recorded as the longest dimension of the organism.

The electivity coefficient of Ivlev (1961) was used to compare gut contents to nocturnal mean volumetric abundance of taxa calculated from vertical tows taken 5 m to surface. Potential values range from −1, indicating complete rejection of food item, to + 1 for exclusive selection of a food item. Copepods unidentifiable because of digestion, but mainly Calanoida, were combined with *Diaptomus* to calculate a single electivity coefficient.

Daphnia birth and death rate

Estimation of birth rate. The mean rate of egg development for *Daphnia* was estimated from the vertical distribution of eggs and embryos and mean stratum temperature. Three strata were considered: 0–5, 5–15 and 15–24 m, based on vertical net collections. Mean inventories ($N\ m^{-2}$) of eggs and embryos in the 0–5 m stratum during Day or Night on each date were calculated directly from the replicate 5 m tows at Stations 1, 2 and 3. Mean inventories ($N\ m^{-2}$) in the 5–15 m stratum during Day or Night on each date were calculated as the difference between $N\ m^{-2}$ from 0 to 15 m tows and $N\ m^{-2}$ from 0 to 5 m tows. Mean inventories ($N\ m^{-2}$) in the 15–24 m stratum were calculated as the difference between $N\ m^{-2}$ from 0 to 24 m tows and $N\ m^{-2}$ from 0 to 15 m tows.

The relative proportion of eggs and embryos in the various strata, f (eggs), was calculated. Mean temperature in each stratum was calculated from Whitney TC-5 measurements at 1-m vertical intervals. Development rate ($1/D$, day^{-1}) in each stratum was calculated from temperature by (Pastorok, 1978; Edmondson & Litt, 1982)

$$1/D = 0.000411 \cdot T^2 + 0.0108 \cdot T^2 - 0.0163 \qquad (1)$$

The mean development rate for each vertical distribution (Day or Night) was calculated as

$$\text{Day-}1/D(\text{or Night-}1/D) = \Sigma(1/D \cdot f(\text{eggs})) \qquad (2)$$

The Daytime period was calculated as the number of h between sunrise and sunset at the latitude of Long Lake, using the algorithm reported by Fee (1990). The mean development rate was calculated on a 24-h basis by scaling the individual Day and Night (1/D) mean estimates, when both were available:

$$
\begin{aligned}
\text{24h-}1/D = &(1/D)\text{day} \cdot (\text{day-hours}/24) \\
&+ (1/D)\text{night} \cdot (\text{night-hours}/24)
\end{aligned} \qquad (3)
$$

In the absence of Night-1/D estimates, the Day-1/D estimates were adopted without modification. Based on the estimated egg development rate, the mean concentration (N m^{-3}) of *Daphnia*, and the mean egg ratio (E, eggs/female) on each sampling date, birth rate (b, day^{-1}) was calculated as (Paloheimo, 1974):

$$b = \ln(E+1)/D \qquad (4)$$

Estimation of death rate. Net intrinsic population growth rate (r, day^{-1}) was calculated from successive estimates of population abundance:

$$r = \ln[N(t)/N(0)]/\Delta t \qquad (5)$$

Death rate (d, per day) was calculated by difference from:

$$d = \text{ave-}b - r \qquad (6)$$

where ave-b is the average birth rate (= (initial + final)/2) over the interval used to calculate r. The rate of mortality on *Daphnia* implied by the calculated death rate was estimated as

$$\textit{Daphnia killed } m^{-3} \, day^{-1} = d \, \textit{Daphnia } m^{-3} \qquad (7)$$

Yellow perch bioenergetics model. The consumption rate of age-0 yellow perch was derived from a bioenergetics model (Kitchell *et al.*, 1974; Kitchell *et al.*, 1977) using the empirical and projected growth rate. The model asserts that *per capita* growth rate is a function of consumption (C), respiration (R), egestion or faecal loss (F) and excretion or urine loss (U), calculated as *per capita* intrinsic rates (day^{-1}) (Kitchell *et al.*, 1977).

$$dB/B \, dt = C - (R + F + U) \qquad (8)$$

Consumption is a function of maximum feeding rate, body mass, metabolic rate and temperature (Kitchell *et al.*, 1977; Eq. 2). Respiration is a function of body mass, temperature, activity rate, specific dynamic action and consumption (Kitchell *et al.*, 1977; Eq. 3). Both egestion and excretion are functions of consumption and temperature (Kitchell *et al.*, 1977; Eq. 4). The model includes three adjustments of parameter values to account for differences between adult and young-of-year fish metabolism (Post, 1990; Table 1). Field tests of the model demonstrate that it can describe growth accurately (Rice & Cochran, 1984; Post, 1990).

The perch model is underdetermined mathematically, and requires a scaling factor, prey availability or P, to reconcile the model outcome with empirical data. P represents the proportion (0–1.0) of prey accessible for consumption. In order to be consistent with previous applications of this modelling approach, P was used to scale the ration to fit the observed growth curve. P-values were initially fit so that, for each sampling date, the difference between the observed and predicted wet mass was zero. A daily series of P-values was then generated using an exponential function fit to the initial P-values using a least sum of squares method. This series was used to generate daily growth increments. Population consumption per cubic metre was derived by multiplying the consumption for perch of average individual mass, B, by perch density per cubic metre.

Sampling by neuston net became an ineffective capture method for age-0 yellow perch after 29 May. Perch growth was consequently projected by the

Table 1 Mean volumetric abundance (N m^{-3}) of all taxa in Long Lake, *Daphnia* egg ratio and birth rate, and *Bythotrephes* average clutch size, summer 1998. Volumetric abundance was calculated by averaging the deepest diurnal tow available at Stations 1 and 2 for all taxa except *Bythotrephes* before 6 June. Volumetric abundance for *Bythotrephes* before June 6 was calculated from nocturnal neuston tows

Date	*Daphnia*	Egg ratio	Birth rate	*Diaptomus*	Cyclopoids	*Chaoborus*	*Bythotrephes*	Clutch size (SD)
25 April	4290	0.15	0.019	800	730	0	0	
2 May	5810	0.08	0.011	310	500	4	4	–
9 May	4820	0.04	0.007	4380	1100	4	10	8.7 (1.6)
15 May	4990	0.07	0.014	4010	2250	10	6	9.4 (2.7)
22 May	4040	0.10	0.018	4040	2370	1	21	5.4 (0.9)
29 May	2670	0.38	0.047	3420	1620	14	30	5.9 (1.2)
6 June	380	0.60	0.080	2020	560		20	
12 June	3	0.90	0.102	1160	430		26	
20 June	0.1	4.96	0.295	1350	340		4	3.0 (1.4)
20 September	491	0.31	0.062	11900	1700		6	

model to determine whether perch could have been the primary cause of the decline in *Daphnia*. The simulation was performed by appending empirical perch weights from Long Lake with weights of Oneida Lake perch from 1976 (Mills & Forney, 1983). The Oneida Lake time series was appended starting on June 8, the date on which Long Lake perch were projected to reach a mean wet body mass equal to the initial body mass reported in the Oneida Lake time series (47 mg), growing at a rate appropriate to the prey availability measured in late May.

Consumption rate at the population level was determined by multiplying the density of age-0 fish by the individual consumption expressed in carbon mass. Three limiting assumptions were made: first, there was no fish mortality after 29 May; second, the maximum *per capita* consumption rate was predicted by the fish body growth trajectory from Oneida Lake; and third, perch consumed only *Daphnia*. These assumptions assured that the estimated consumption by the fish population would be the maximum plausible. Wet mass was converted to dry mass by a factor of 0.19 (Mills & Forney, 1983) and dry mass was converted to C by a factor of 0.50 (Salonen *et al.*, 1976; Makarewicz & Likens, 1979).

Comparing simulated perch predation against expected *Daphnia* mortality permitted a test of the hypothesis that perch could account for the population decline in *D. pulicaria*. The number of *Daphnia* killed m^{-3} day^{-1} between sample dates was calculated from mean population density of *Daphnia* multiplied by the per capita death rate for the time interval. To calculate perch consumption in terms of *Daphnia* eaten m^{-3}, the bioenergetically derived consumption rate was divided by the average weight of prey consumed. First, a hypothetical consumption rate was calculated for perch feeding on juvenile *Daphnia* (0.8 mm length) and compared with the empirical *Daphnia* death rate. Secondly, the mean length and weight of *Daphnia* consumed were calculated by using the empirical length-mass relationship for *Daphnia* to find the mean body mass necessary to satisfy simultaneously the mortality rate expressed in numbers and in biomass.

The calculated consumption rate was transformed into the death rate (day^{-1}) by dividing the predicted number of *Daphnia* eaten m^{-3} day^{-1} by total number of *Daphnia* m^{-3}. The *Daphnia* population was mod-

elled assuming exponential growth, where *r* was equal to birth rate minus derived death rate based on yellow perch predation.

Bythotrephes bioenergetics model. A bioenergetics model for *Bythotrephes* was adapted from the set of equations and parameter values reported by Lehman *et al.* (1997). The model observes mass balance and was used to derive a population level consumption rate by providing empirical values for temperature, neonate and adult female mass and population density. Total predation is calculated as a function of growth (dC/dt), respiration (R), ingestion efficiency (IE) and assimilation efficiency (AE). Respiration is an exponential function of temperature, growth is an exponential function of age. Ingestion efficiency is the ratio of prey biomass ingested to the biomass of prey killed. Assimilation efficiency is the fraction of prey biomass ingested that is not subsequently egested. Parameters and equations were unaltered for model implementation.

The abundance-weighted mean development rate was calculated from the proportion of *Bythotrephes* found in the 0–5, 5–15 and 15–24 m strata and the amount of time spent in each stratum:

$$d_{\mathrm{Mean}} = \Sigma[D(T)_i f_i](\mathrm{day\ h}/24) + \Sigma[D(T)_i f_i] \\ (\mathrm{night\ h}/24) \qquad (9)$$

where $D(T)_i$ is development as function of stratum temperature in stratum *i*, f_i the frequency of *Bythotrephes* found in stratum *i*, and day *h* the number of h between sunrise and sunset for a particular sampling date. Because development and respiration are both nonlinear functions of temperature, the mean temperature experienced by a population does not predict accurately the mean metabolic rate. Thus, equivalent mean daily temperature referenced to development rate (Tequiv) of *Bythotrephes* was calculated. 'Tequiv' is the equivalent temperature required to reproduce the weighted mean development rate for the population, calculated as in Eq. 9. Tequiv values were used to estimate a conservative bound for *Bythotrephes* predation.

A similar test to that carried out for yellow perch was performed, comparing simulated *Bythotrephes* predation against expected *Daphnia* mortality in order to test the hypothesis that *Bythotrephes* could account for the population decline in *D. pulicaria*. Again, for

simplicity and reference calculation, we assumed that the predator, *Bythotrephes*, consumed only *Daphnia*.

Results

Limnological conditions. Long Lake warmed gradually from 25 April to 29 May (Fig. 2). The warming trend was interrupted temporarily between 29 May and 6 June, when a strong mixing episode cooled and deepened the epilimnion. During these 2 weeks, average weekly air temperature fell from 17.7 °C the previous week to 12.6 °C and 16.2 °C, respectively. Subsequently, the lake continued to become warm. Dissolved oxygen reciprocated the pattern exhibited by temperature over the sampling period (Fig. 2). By 29 May, the depths of the lake were becoming anoxic, but the mixing episode replenished them with oxygen. By 20 September, the lake had become anoxic below 15 m.

Chlorophyll *a* increased throughout the summer from 0.31 (25 April, Station 2) to 1.83 μg L^{-1} (20 September, Station 2). No consistent pattern was observed between stations. Secchi depth was maximal on 9 May. The depth at which 1% of surface PAR remained from 24 April to 15 May was approximately 24 m. On 6 June, after the cooling episode, Secchi depth and the limit of penetration of 1% surface PAR declined.
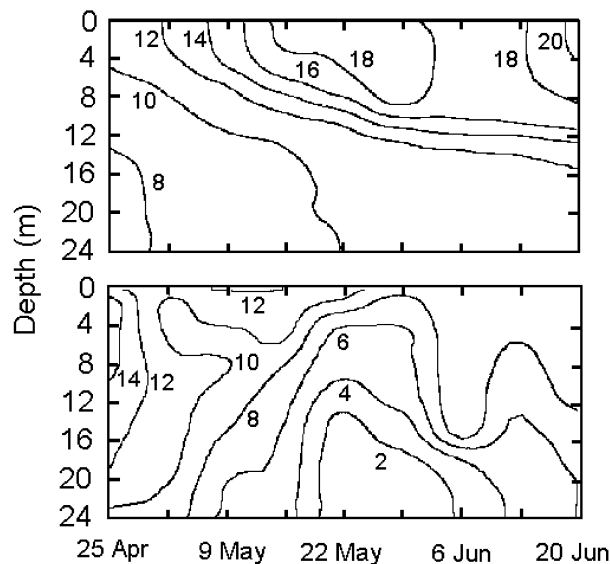

Fig. 2 Isopleths of temperature (top) and dissolved oxygen (below) of Long Lake 1998.

Zooplankton community and dynamics. Long Lake was populated mainly by *D. pulicaria*, *Diaptomus minutus* Lilljeborg and *Diaptomus oregonensis* Lilljeborg, Cyclopoida and *Chaoborus*. In September 1998, other taxa present at low density included *Bosmina longirostris* (O.F. Mueller), *Diaphanosoma birgei* Korinek, *Leptodora kindtii* Focke and various rotifers. In samples collected in September 1997, two specimens of *Daphnia ambigua* Scourfield were found and *Diaptomus* dominated the water column. Rare taxa in 1997 included Cyclopoida, *Epischura lacustris* S.A. Forbes, *D. birgei*, *B. longirostris*, *Chydorus*, *Ceriodaphnia* and *Asplanchna*.

Comparisons of abundance were performed using paired *t*-tests on logarithmically transformed data from vertical tows. If the abundance in the sample was zero for one or both members of the pair, the data were excluded. For all inventory data (N m^{-2}) from 0 to 5 m vertical tows, results were statistically indistinguishable among all stations. Furthermore, diurnal 0–15 m tows from Stations 1 and 2 were indistinguishable for all dates. Egg ratio data for *Daphnia* from 0 to 15 m and 0–24 m tows on dates when both strata were sampled were also indistinguishable. A significant difference was found between daytime and nighttime inventories calculated from 0 to 15 m vertical tows (Stations 1 and 2 combined) for both cyclopoid copepods and *Chaoborus* ($P = 0.025$ and $P = 0.007$, respectively). A significant difference was also found between the inventories calculated from 0 to 15 m and 0–24 m vertical tows for cyclopoids ($P = 0.047$).

Mean concentrations (combined day and night) of *Diaptomus* C1-C6, cyclopoid C1-C6, and *Bythotrephes* were indistinguishable between 0 and 15 m and 0–24 m collections. The mean concentration of *Daphnia* (N m^{-3}) estimated from 0 to 24 m tows was greater than that estimated from 0 to 15 m tows ($P = 0.031$), on all dates except 29 May, when concentration was indistinguishable between depth strata. This result is confounded by diel migration, because all 0–24 m tows were daytime collections except 29 May, for which both day and night collections existed.

Based on the statistical inferences and conclusions, abundance for each taxon was estimated using the following data groupings. All diurnal 0–5 m vertical tows inventories from Stations 1, 2 and 3 were pooled by dates, as were nocturnal 0–5 m tows for Stations 1 and 2. All diurnal 0–15 m inventories were pooled by date, and nocturnal 0–15 m inventories were also

pooled by date. The diurnal and nocturnal 0–24 m concentration estimates for 29 May were pooled. Mean concentrations (N m^{-3}) were estimated from 0 to 24 m tows when possible. In the absence of a 0–24 m tow, we pooled diurnal 0–15 m tows from Stations 1 and 2. On 25 April, concentrations were estimated from the only data available, 0–15 m diurnal vertical tows at Stations 1 and 2.

Daphnia pulicaria was numerically dominant (4000 m^{-3}) from 25 April to 22 May (Table 1), *Diaptomus* was dominant thereafter. *Daphnia* declined by about one half the following week and by 12 June had become rare (3 m^{-3}). By September, *Daphnia* remained rare. The highest birth rate was observed on 20 June. Potential bias in birth rate estimates from egg predation or egg inviability was undetectable; there were no statistical differences (χ^2 analysis, $P = 0.1$) in egg:embryo ratio among all dates (mean proportion embryos = 0.20, SD = 0.03, $n = 9$ dates) except for 12 June, when the average proportion of

embryos was elevated (0.29). *Daphnia* clutch size also changed over time (Fig. 3). Comparison of 15 May and 20 June samples indicated fewer juveniles present on 20 June, despite larger clutches in existing females. Comparison of 15 May and 20 September samples also shows a larger proportion of juveniles on 15 May, although the 20 September sample contained a larger proportion of juveniles than did 20 June.

Three trends were observed in the size distribution of *Daphnia*. First, average length increased significantly from 15 May to 20 June as the dominant stage switched from juveniles to adults (Table 2). The average size of *Daphnia* on 15 May was 1.44 mm, on 20 June it was 2.65 mm. Secondly, length distribution changed from unimodal to bimodal as juveniles disappeared from the population (Fig. 4). Thirdly, the lesser of the two modes shifted down in size, as juveniles were increasingly scarce, from 1.0 (6 June) to 0.8 mm (20 June).

As juvenile *Daphnia* were removed, the proportion of females bearing eggs increased, which increased the overall egg : female ratio (Table 1). The proportion of females bearing ephippia was 0.00 from 25 April to 22 May, but increased to 0.08 on 29 May then 0.12 on 6 June, and fell again to 0.04 and 0.00 on 12 June and 20 June, respectively, suggesting an episode of food limitation.

Diaptomus and cyclopoid copepods declined coincident with *Daphnia* during late May and June (Table 1). Unfortunately, because adults were rare in samples throughout May, it was not possible to calculate birth and death rates or clutch size variation for these populations as for *Daphnia*.

Zooplankton diel migration. Diel vertical migration by *Daphnia* was detected on 9 and 15 May (Fig. 5) by Schindler trap. By day, the majority of *Daphnia*
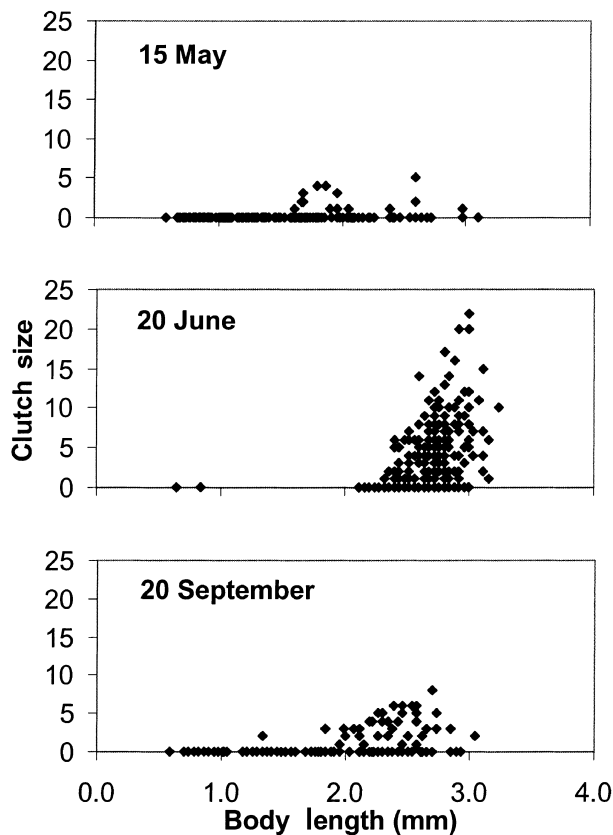
Fig. 3 *Daphnia* body length and clutch size measured in number of eggs or embryos per total number of females for 15 May, 20 June and 20 September.

Table 2 Minimum, maximum and mean length of *D. pulicaria* in Long Lake 1998

| Date | Length | | | | |
	Minimum (mm)	Maximum (mm)	Mean (mm)	SE	n
15 May	0.57	3.11	1.44	0.08	302
22 May	0.75	2.51	1.55	0.13	140
29 May	0.71	3.04	1.84	0.16	143
6 June	0.71	2.06	1.72	0.06	283
20 June	0.64	3.24	2.65	0.14	343
20 September	0.64	3.00	1.64	0.10	162
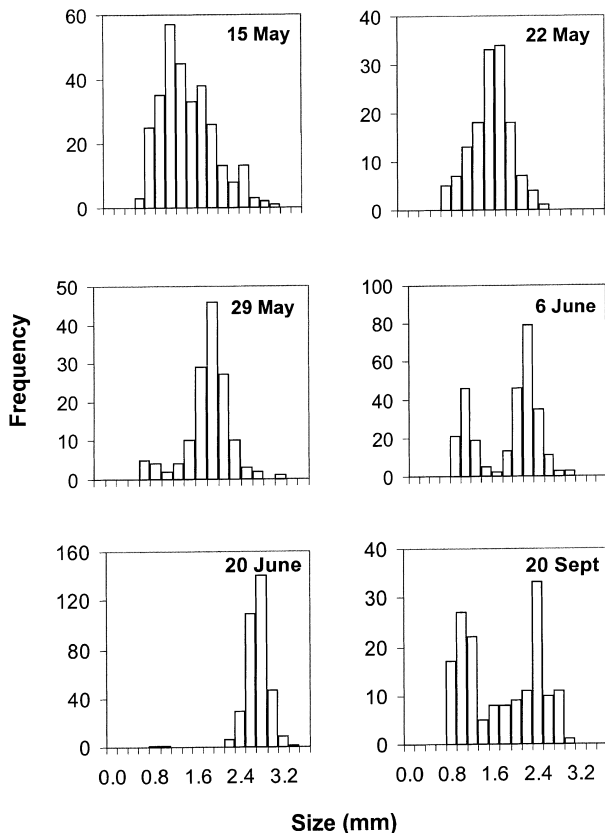
Fig. 4 Size distribution of *D. pulicaria* in Long Lake from 15 May to 20 June 1998.
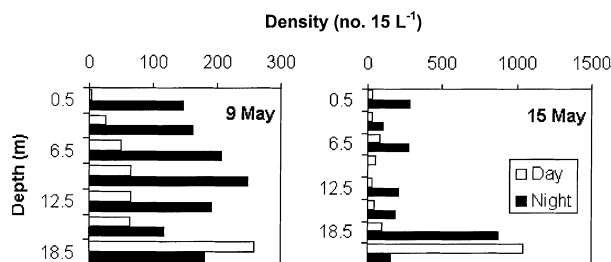
Fig. 5 Diel migration patterns in *Daphnia* from 9 and 15 May. Abundance is given as number of zooplankton per 15 L.

strated the same migration patterns as the rest of the population.

Bythotrephes were too rare to be sampled by Schindler trap. Instead, migration patterns were observed in vertical tows. The population was concentrated below 5 m during daytime sampling. From 15 May to 20 September, over 90% of *Bythotrephes* were found below 5 m, except on 29 May, when over 80% were found below 5 m. During night, particularly in early May, a greater abundance of *Bythotrephes* was found in shallow water. On 9 May, 33% of the population was found below 5 m. By 29 May, 82% remained below 5 m, even at night. *Bythotrephes* became confined to deeper strata through the summer and eventually became scarce, except at Station 1. *Daphnia* were generally distributed deeper than *Bythotrephes* during the day, but demonstrated diel migration. Thus, their distributions overlapped more extensively at night.

Clear water phase. Historical Secchi disk records (Fig. 6) show that from 1992 to 1998, vernal Secchi depths of 8–10 m were common. Typically, the clear water phase began in late April. The maximum Secchi depth measured was 18.9 m (1997). In 1998, an early clear

resided in the deepest strata sampled, 18.5 m. On 15 May, more than 1000 *Daphnia* were in the 18.5 m sample. Collections from shallower water also contained less than 100 animals. Nocturnal samples show migration up the water column, with the majority of *Daphnia* between 8 and 12 m. Similarly, daytime samples from 9 May show the distribution of *Daphnia* to be highly stratified. Nocturnal samples on 9 May indicate a uniform distribution in the water column. Fecund females on 9 and 15 May demon-
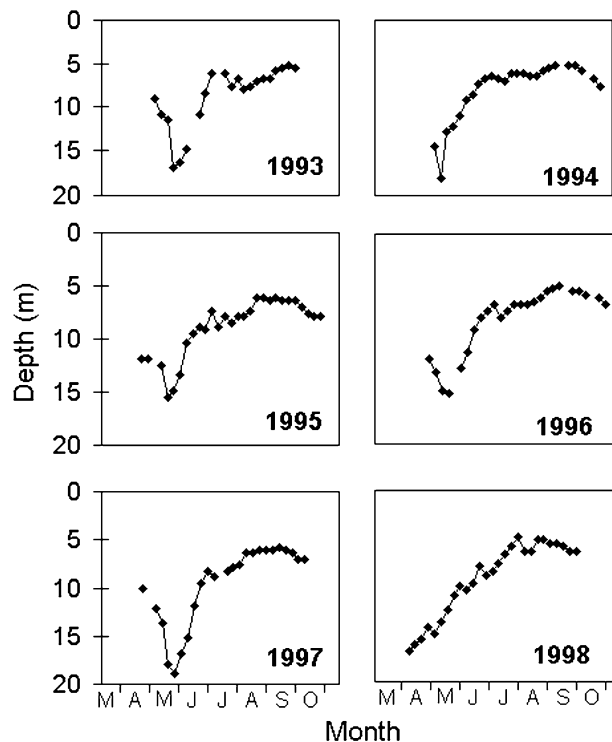

Fig. 6 Secchi disk profiles for Long Lake 1993–98.

water phase occurred, with a maximum depth of 16.8 m on 25 April, approximately 3 weeks ahead of the record in 1993 and 1996, when maximum Secchi disk depth was similar (17.1 m and 15.1 m, respectively) on 29 May. On 20 June, chlorophyll *a* increased above 1.0 µg L^{-1}, whereas in previous weeks it had been approximately 0.6 µg L^{-1}. Also, Secchi depth decreased to less than 10 m and *Daphnia* became extremely rare. Based on these distinct, correlative changes, we defined the clear water phase in Long Lake as the period with Secchi transparency exceeding 10 m. Thus, average length of the clear water phase from 1993 to 1998 was 8 weeks.

Abundance, growth and diet of age-0 yellow perch. Age-0 yellow perch were taken in neuston samples from 2 to 29 May. Perch on 2 and 9 May were at hatching length (5–6 mm total length); by 29 May, average total length increased to 14.7 mm (Table 3). Average wet mass per yellow perch increased exponentially from 0.3 to 18.6 mg by 29 May (Table 3). The greatest density of yellow perch was observed on 16 May, just after the major hatching period, at 2.21 m^{-3} (Table 3), and declined afterwards to approximately 0.2 m^{-3} by 22 May.

On 29 May, yellow perch 15–21 mm in size favoured *Diaptomus* and other copepods as prey (Table 4). These taxa composed over 80% of all prey found in the stomachs. *Daphnia pulicaria* were rarely found (3.3%) compared with unidentifiable copepods (60.9%) and *Diaptomus* (32.1%). Based on Ivlev's equation, age-0 yellow perch showed strong selection against *Daphnia*, cyclopoids and Chaoborus and strong selection for *Diaptomus* (Table 4). *Diaptomus* and other copepods found in perch guts had mean lengths of 0.41 and 0.53 mm, respectively. *Daphnia* were the largest food items, averaging 1.25 mm, but still significantly smaller than the average *Daphnia* size, 1.84 mm ($P = 0.006$).

Mass, abundance and distribution of Bythotrephes. Individuals of the one-barbed, first (G1) generation of *Bythotrephes*, hatched from over-wintered resting eggs, were an order of magnitude smaller in mass than 1-barbed *Bythotrephes* of the third (G3) generation (Table 5). Compared with *Bythotrephes* of the Great Lakes, dry mass by instar of *Bythotrephes* in 1997 was intermediate between those sampled in Lake Erie and Lake Huron (Bilkovic & Lehman, 1997), and more variable within instars (Table 5). Maximum body

Table 3 Mean length, wet mass and volumetric abundance of age-0 yellow perch in Long Lake

Date	Length (mm)	SD	Wet mass (mg)	SD	n	Average abundance (N m^{-3})
2 May 98	6.00	–	0.3	–	1	0.01
9 May 98	6.62	0.66	0.7	0.2	101	0.57
15 May 98	8.28	1.39	1.4	0.9	196	2.21
22 May 98	10.39	2.44	5.0	3.5	18	0.17
29 May 98	14.66	3.07	18.6	14.8	27	0.20

Table 4 Mean length of age-0 yellow perch sampled for gut contents ($n = 5$), number of prey found in the digestive tract, length of prey and electivity coefficient for 29 May

Average perch length (mm)	Prey in gut	Average number in gut	Average length (mm)	Ivlev's electivity coefficient
17.1	Copepod	22.4	0.41	Combined
	Diaptomus	11.8	0.53	0.50
	Daphnia pulicaria	1.2	1.25	−0.75
	Cyclopoid	1.0	0.48	−0.85
	Others	0.4	1.00	n/c

'n/c' indicates value not calculated.

Table 5 Comparison of the mean total dry mass of *Bythotrephes* from the Great Lakes in 1993 (Bilkovic & Lehman, 1997; Table 1) with that in Long Lake by stage (S) or instar (I), and generation (G) when known

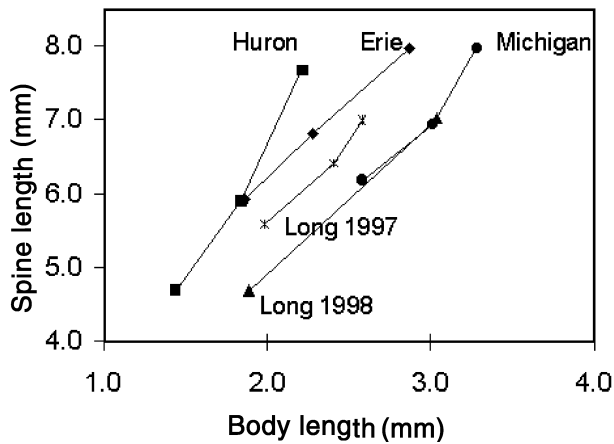| Lake	Stage	n	Dry mass (µg)	CV (%)
Long Lake 1997	S1	22	63.1	47.4
	S2	17	114.3	30.3
	S3	5	144.2	14.8
	S4	4	306.5	13.2
Long Lake 1998	I1 (G1)	116	1.9	31.6
	I4 (G1)	46	64.4	33.4
	I1 (G3)	60	24.9	102.0
	I3 (G3)	99	207.7	36.9
Lake Erie	S1	18	42.6	5.4
	S2	31	97.8	4.1
	S3	11	120.8	3.1
	S4	12	202.8	5.8
Lake Huron	S1	8	78.0	17.8
	S2	32	174.3	4.9
	S3	14	268.2	10.1
	S4	36	506.7	4.3
Lake Michigan	S1	10	133.9	4.0
	S4	6	621.6	9.7

Fig. 7 Comparison of mean body lengths and spine lengths of *Bythotrephes* by instar stage from Lakes Erie, Huron, Michigan in 1996 (Sullivan & Lehman, 1997) and Long Lake in 1997 and 1998.

weights are reached at late brood stage, stage 4 (Bilkovic & Lehman, 1997), when the four-barb or three-barb females are near parturition and are carrying embryos at the black-eye stage of development. G1, stage 4 females weighed 89.4 µg on 15 May. By 21 June, G3, stage 4 females weighed 378.5 µg.

Morphology of Long Lake *Bythotrephes* was intermediate between populations in Lakes Erie and Michigan (Fig. 7). Total spine lengths were shorter, 7 mm, than those found in the Great Lakes, 8 mm. Spine length thus does not appear to be constant among all lakes, but ratio of body length to spine

length for 3-barb animals produced by parthenogenesis appears to be constant at about 0.40.

Abundance of *Bythotrephes* increased from 4 m^{-3} (2 May) to a maximum of 30 m^{-3} on 29 May, and subsequently declined (Table 1). In May, neuston tows taken near the surface at night yielded estimates of *Bythotrephes* abundance that exceeded concentrations in vertical tows at deep stations by factors ranging from 100 to 3. Vertical tows revealed that, in May, *Bythotrephes* was initially found in the warm upper epilimnion, which then contributed to a large proportion of total lake volume. In June, *Bythotrephes* effectively vanished from shallow water and so vertical tows in deep water were more representative; data indicated that *Bythotrephes* were abundant only in the lower strata. Accordingly, we calculated *Bythotrephes* abundance from the large volume neuston collections during May, and then from vertical net collections in June.

Bioenergetics model for P. flavescens. During May, perch growth averaged 0.24 day^{-1}, ranging from 0.12 on 2 May to 0.34 on 15 May. Predation simulations comparing derived consumption rates to hypothetical prey size indicated that perch feeding on juvenile *Daphnia* 0.8 mm in length could not account for *Daphnia* mortality between 22 May and 6 June (Table 6). To account for the numbers of *Daphnia* killed in May, perch would have had to consume only very small *Daphnia* from 15 to 22 May, and only large

Table 6 Results of predation simulations with age-0 yellow perch and *Bythotrephes* bioenergetics models. 'Σ Predation' = population level consumption calculated from the models, '*Daphnia* death rate' = number of *Daphnia* expected to die based on birth and death rate analyses, 'Consumption' = number of 0.8 mm length *Daphnia* consumed by each predator, '*Daphnia* mass' = mean mass of individual *Daphnia* consumed by each predator feeding at *Daphnia* mortality level, '*Daphnia* length' = mean length of individual *Daphnia* consumed by each predator feeding at *Daphnia* mortality level

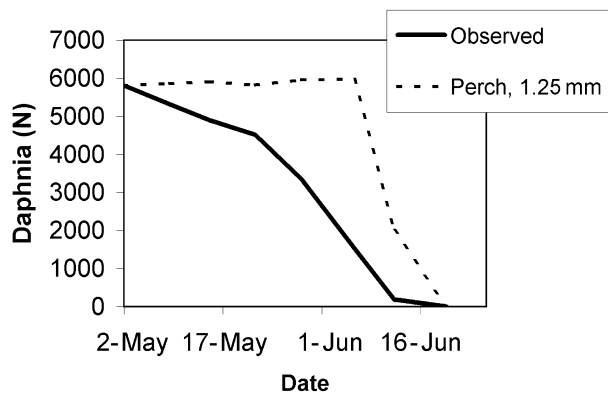| Time interval	Σ Predation (µg C m^{-3} day^{-1})	*Daphnia* death rate (N m^{-3} day^{-1})	Consumption (N m^{-3} day^{-1})	*Daphnia* mass (µg C)	*Daphnia* length (mm)
Age-0 perch bioenergetics model					
15–22 May	649	207	563	0.3	0.53
22–29 May	143	307	124	2.1	0.97
29 May–6 June	455	470	395	1.0	0.77
6–12 June	1080	169	937	0.2	0.43
12–20 June	1956	1	1697	0.0	0.07
Bythotrephes bioenergetics model					
15–22 May	213	207	184	0.97	0.76
22–29 May	695	307	603	0.44	0.59
29 May–6 June	755	470	655	0.62	0.66
6–12 June	515	169	447	0.33	0.54
12–20 June	362	1	314	0.00	0.12

Fig. 8 Simulated population decline of *Daphnia* with the assumption that age-0 yellow perch consumed only *Daphnia* 1.25 mm in length.

juvenile *Daphnia* from 22 to 29 May. By 6 June, perch would have to consume *Daphnia* smaller than *Daphnia* size at birth in order to account numerically for *Daphnia* mortality.

Thus, the only credible model for top–down control of *Daphnia* by yellow perch is that perch exclusively consumed juvenile *Daphnia* after 29 May. If perch were consuming only *Daphnia* of the mean size actually found in their guts on 29 May (1.25 mm), no decline in *Daphnia* would have been observed until 10 June (Fig. 8). *Daphnia* death rates, calculated on the assumption that perch were feeding on *Daphnia* 1.25 mm in length, suggested that the *Daphnia* population should have remained constant or increased slightly until 10 June, at which point a sharp decline would have occurred.

During 1998, *P*-values were less than 0.2 until 12 May. The *P*-value remained low during the entire sampling period, but increased to 0.35 for fish growing from 22 to 29 May.

Bioenergetics model for Bythotrephes. The observed dry mass of three-barb females carrying embryos without pigmented eyes was compared with the dry mass predicted by the bioenergetics model. The first (G1) generation's growth trajectory was not modelled accurately by the bioenergetics model; average predicted mass was 77% of that observed. For subsequent generations (G2, G3), however, the model appears to provide relatively accurate predictions; predicted mass was 108% of that observed.

Calculated prey consumption by *Bythotrephes* was the greatest from 29 May to 12 June and greater

than the *Daphnia* death rate for all dates (Table 6). The maximum daily value for total predation was 1020 μg C m^{-3} day^{-1} on 29 May. The consumption rate per unit biomass was intermediate between that calculated by Yurista & Schulz (1995) and Vanderploeg *et al.* (1993), averaging 0.93, 0.78 and 0.64 day^{-1}, respectively, for one, two and three-barb instars from 2 May to 20 June.

Calculated mean length of *Daphnia* consumed (Table 6) suggests *Bythotrephes* predation was consistent with the observed size distribution of *Daphnia*. The bimodal distribution (Fig. 4) suggests that *Bythotrephes* were feeding on animals 0.8–1.0 mm in length, less than the mean length of *Daphnia* for all dates sampled. Assuming *Bythotrephes* was consuming the available food, modelled by setting predation from *Bythotrephes* equal to the total number of *Daphnia* dying week^{-1}, the calculated mean length of *Daphnia* consumed from 15 May to 12 June (Table 6, column 5) was consistent with the selected sizes inferred from the field data. After 12 June, *Daphnia* abundance and total mortality were too low to support *Bythotrephes*' requirements for prey.

Discussion

Length data and egg ratio data evaluated together suggest that Long Lake *Daphnia* populations were affected by predation throughout most of the study. *Daphnia* size data suggest severe, size selective predation on juveniles during late May and early June 1998 (De Bernardi & Guissani, 1975; Zaret, 1980). By 20 June, *Daphnia* in the size range preferred both by *Bythotrephes* and age-0 yellow perch were absent (Hansen & Wahl, 1981; Burkhardt & Lehman, 1994). The size distribution of *Daphnia* indicated that mortality was concentrated in the smallest individuals. It is therefore likely that gape-limitation was a factor in *Daphnia* predation. Birth rate and average clutch size increased in mid-June while the *Daphnia* populations decreased, indicating that an accelerated death rate was crucial in the dynamics. Ephippial production by *Daphnia* increased in late May and early June, indicating the population was food-stressed at the start of its decline. The proportion of females that became gametogenic was small (maximum = 0.12 on 6 June, dropping back to zero by 20 June), however, and in any event does not account for the strikingly bimodal size distribution and marked increase in partheno-

genic birth rate. Thus, the most probable explanation for the *Daphnia* decline was predation by age-0 fish or an invertebrate, not starvation or predation by adult fish.

Diet analysis suggests that age-0 perch could not be a primary cause of *Daphnia* decline in Long Lake. Gut contents of yellow perch on 29 May were dominated by *Diaptomus*, with few *Daphnia* present. Perch showed strong electivity for *Diaptomus* and strong electivity against *Daphnia*. Thus, diet data suggest that age-0 yellow perch were not a major factor in the decline of *Daphnia*. Similarly, copepods composed over 90% of the diet in Oneida Lake, New York for yellow perch of 15 mm length (Wahl *et al.*, 1993), and cyclopoids composed 64.2% while *Daphnia* only composed 0.5% of the diet of 17 mm yellow perch in Lake St George, Ontario (Post & McQueen, 1988). The relative availability of suitably sized prey may explain the preference of perch. Hansen & Wahl (1981) found that Oneida Lake yellow perch under 28 mm show strong preference for *Daphnia* 0.5 mm in length, similar to the mean size of *Diaptomus* and copepods consumed by perch in Long Lake. No *Daphnia* found in the gut of sampled yellow perch was so small, most probably because of the increasing rarity of juvenile *Daphnia*.

Bioenergetics modelling indicated age-0 yellow perch density was too low, and observed growth too small, to permit perch to cause the decline in *Daphnia*, even if perch ate *Daphnia* exclusively. Population modelling of *Daphnia*, with the assumption that perch were eating *Daphnia* of the mean size (1.25 mm) estimated for 29 May, indicated that the *Daphnia* decline began too early in the season to attribute it to predation by yellow perch. The model suggests that predation by perch could have contributed to the demise of an already declining population of *Daphnia* in early to mid June, but age-0 yellow perch could not solely have accounted for the decline. Further, prey availability values suggest that perch were close to starvation from the time of hatching until 15 May. Post (1990) calculated observed growth rates for increasing prey availability (*P*-value) for a larval fish of 10 mg, which corresponds to average wet mass on 25 May for Long Lake. Post (1990) suggested that a *P*-value of 0.2 was representative of maintenance ration; any *P*-value < 0.2 produced negative growth, or starvation, in age-0 perch. *P*-values were less than 0.2 until 12 May, although at that time perch weighed

one-tenth of the value used in Post's model. The increase in *P*-value during late May suggests perch that managed to recruit into larger size classes gained access to more food in the form of *Diaptomus* and, occasionally, *Daphnia*. By 6 June, available food, estimated as the total number of *Daphnia* dying week^{-1}, fell too low to bioenergetically support the rate of perch growth (Table 6). This represents a possible bottleneck in growth for the perch population, hypothetically growing at *P* equal to 1.0.

Instead, field and model data suggest *Bythotrephes* was the more probable agent. *Daphnia* appeared to be an important food resource for *Bythotrephes*. Peak *Bythotrephes* density coincided with the beginning of the *Daphnia* decline; *Bythotrephes* began to decline after *Daphnia* declined. Because *Daphnia* birth rate was low, modest acceleration in the death rate was sufficient to alter *Daphnia* population dynamics. The rapid increase in the population of *Bythotrephes*, caused by the large clutches in G1 and G2 females, short maturation time of under a week (the unpublished instar analyses of Hoffman & Lehman) and iteroparous reproduction by G2 and G3 females (G1 females had disappeared by the time the larger G2 females comprised most of the population), was probably a factor, as well. While iteroparity is common in *Daphnia* (Threlkeld, 1987), it had not been previously reported in Great Lakes populations of *Bythotrephes*.

The bioenergetics model demonstrates that *Bythotrephes* predation is a credible explanation for the decline in *Daphnia*. Predation by *Bythotrephes* can account entirely for the death observed in the *Daphnia* population; moreover, the mean length of *Daphnia* consumed according to the bioenergetics model was consistent with the observed size distribution of *Daphnia*.

The perch bioenergetics model has known biases. First, by assuming no mortality in perch, exclusive prey preference for *Daphnia* and maximum consumption rates after 29 May, we intentionally estimated consumption rates at the maximum value plausible. Although prey preference data for Long Lake perch indicated that *Daphnia* comprised a small portion of the diet in late May, Mills & Forney (1981; Table 1) found that it was not unusual for *Daphnia* to comprise 95% of young perch (26–31 mm TL) diet. Because yellow perch should have attained such a length in Long Lake during June, we considered that the assumption was biologically reasonable. Secondly, the assumption that perch were growing at a

temperature equal to that of the upper epilimnion may also have overestimated consumption rate. However, the lake was relatively isothermal from 10 m to the surface in late June and September, and that zone represented most of the volume of the lake. Adjusting model parameters (e.g. P) to fit empirical data does not correct bias, but it gives a frame of reference to evaluate the potential range of predation on *Daphnia* by age-0 yellow perch.

Oneida Lake data were used to establish a biologically realistic scenario that projected perch growing at maximum rate. Data for Oneida Lake in 1976 seemed biologically consistent with Long Lake. First, like Long Lake, the pelagic zone of Oneida Lake is dominated by large bodied *Daphnia* (*D. pulex* Leydig emend. Richard), its primary planktivore is age-0 yellow perch, and its primary piscivore is walleye (Mills *et al.*, 1989). Secondly, it is improbable that perch were food limited that year; consumption by Oneida Lake yellow perch in 1976 never exceeded 27% of the production by *D. pulex* and fish density was low (Mills & Forney, 1983). Thirdly, Oneida Lake perch sampled at the start of this Oneida Lake time series were approximately 18 mm in length and 47 mg wet mass; the Long Lake perch sampled on 30 May were 16–21 mm in length and 30.2–62.1 mg wet mass.

Oneida Lake temperature is similar to Long Lake, early August temperature is approximately 24 °C (Mills *et al.*, 1989), epilimnion temperature for Long Lake during similar periods ranges from 22 to 25 °C. Stratification patterns differ between the two lakes. Oneida Lake is generally homothermal (Mills *et al.*, 1989), whereas Long Lake is generally stratified during the summer months.

Similarities in mass and growth bolster confidence that the bioenergetic model derived for Great Lakes populations of *Bythotrephes* was appropriate for the Long Lake population. Dry mass of the Long Lake population was between that found in Lakes Erie and Huron, and the magnitude of order difference in mass between the G1 and G3 generations is consistent with Burkhardt's (1994) finding that Lake Michigan *Bythotrephes* exhibited seasonal variation in dry mass by as much as a factor of five within single instar stages. Further, the mass-specific rate derived from the model declined with increasing instar stage, similar to observations made by Yurista & Schulz (1995) and consistent with allometric expectation explicit in the growth equations.

The *Bythotrephes* bioenergetics model also has known biases. The assumption that *Bythotrephes* exclusively consumes *Daphnia* may overestimate its contribution to *Daphnia* mortality. Models based on C and P budgets have yielded an expectation of strong prey preference for *Daphnia* (Lehman & Branstrator, 1995), whereas mesocosm experiments have yielded weak prey preference for *Daphnia* (Sprules *et al.*, 1990) and suggested it to be a generalist predator (Vanderploeg *et al.*, 1993). However, mesocosm experiments have been inconsistent with mass-balance models in determining consumption rate (Yurista & Schulz, 1995). Allozyme evidence has been offered that *Bythotrephes* consumes calanoids, cyclopoids and *Daphnia*, lending support to the generalist hypothesis (Yurista & Schulz, 1995), but the use of allozymes in diet studies has been criticized and discounted (Giller, 1984; Giller, 1986; Sunderland, 1988). The best hypothesis at present is that *Bythotrephes* is an opportunistic predator, feeding primarily on *Daphnia* when it is abundant, and switching to an alternate diet when *Daphnia* is scarce.

The trophic impact of *Bythotrephes* appears to ripple throughout the food chain. Effects propagate down the food chain depressing *Daphnia* and perhaps releasing some phytoplankton from grazing, across its own trophic level by competing with age-0 perch, and also up the food chain, reducing food resources for walleye and adult yellow perch. If perch in Long Lake were following the typical ontogenetic sequence, and grew by June to a size at which they switch from copepods to *Daphnia*, food availability would have been severely limited. Possible responses by yellow perch include an early niche shift to feeding on benthic invertebrates, reduced growth and increased mortality. Perch recruitment may be further reduced by food limitation early in life. At the observed size of perch in Long Lake on 12 May (1.1 mg), the calculated P-value of 0.2 is below maintenance ration. Perch may be exposed to a period of starvation, greatly increasing the risk of mortality in the population, either from cannibalism by adults (Tarby, 1974) or from reduced burst speed, which increases vulnerability to predation (Webb & Corolla, 1981; Miller *et al.*, 1988). If a bottleneck to recruitment occurred in Year-One, the few surviving perch might grow exceedingly well because of a low density of conspecifics.

In Long Lake, perch dynamics and biomass are consistent with the idea of a recruitment bottleneck in

Year-One. Perch are heavier than the average for Michigan lakes in all year classes after Year-One (Michigan Department of Natural Resources, 1997). Walleye, which feed on perch, are growing slower than the state average, suggesting food limitation.

The framework for this study combined zooplankton sampling, age-0 fish sampling, direct feeding analyses and bioenergetics modelling to investigate relationships between zooplankton, planktivorous invertebrates and planktivorous vertebrates. By integrating field data through modelling, we could test a hypothesis with several different lines of evidence. In this case it helped to resolve two competing hypotheses for a natural phenomenon, and has potential to do so in other cases.

Acknowledgements

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