

Assessing the impact of a recent predatory invader: The population dynamics, vertical distribution, and potential prey of *Cercopagis pengoi* in Lake Ontario

Hugues P. Benoit¹ and Ora E. Johannsson

Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, 867 Lakeshore Road, Burlington, Ontario, Canada L0R 2H2

David M. Warner

Cornell Biological Field Station, Department of Natural Resources, Cornell University, Bridgeport, New York 13030

W. Gary Sprules

Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, Canada L5L 1C6

Lars G. Rudstam

Cornell Biological Field Station, Department of Natural Resources, Cornell University, Bridgeport, New York 13030

Abstract

The predatory impacts of *Cercopagis pengoi*, a planktivorous cladoceran first observed in Lake Ontario in 1998, were assessed by examining patterns in the distribution and population dynamics of macrozooplankton. Specifically, we determined the vertical distribution of *C. pengoi* in Lake Ontario with respect to other zooplankton species and possible biotic and abiotic controlling factors and used seasonal time series of potential prey species, both before and after *C. pengoi* invasion, to make inferences about predatory impacts of *C. pengoi*. The highest abundances of *C. pengoi* generally occurred at the bottom of the epilimnion or at the top of the metalimnion, and strong diel vertical migration was not observed. The vertical distribution of cyclopoid and calanoid nauplii and copepodids was deeper in 1999 than had historically been observed, which suggest possible avoidance of *C. pengoi* or localized predatory depletion. Seasonal analyses of normalized biomass size spectra from the Bay of Quinte supported an impact of *C. pengoi* on organisms <0.1 μg dry weight. The hypothesized predatory effect on juvenile copepods was supported by an analysis of seasonal time series, where we observed that high abundances of *C. pengoi* coincided with marked decreases in these groups. Consequently, the presence of *C. pengoi* likely decreases the production of juvenile copepods both through direct predation and through a shift of copepod vertical distribution to colder waters. Among the cladocerans, only *Bosmina longirostris* abundance declined in the presence of *C. pengoi* in the analysis of seasonal time series.

The transfer of ballast water between ports has served as an important vector, facilitating the invasion of many aquatic species to new habitats (Carlton and Hodder 1995). Such is thought to be the case for *Cercopagis (Cercopagis) pengoi*, a Ponto-Caspian predatory onychypod cladoceran (Rivier 1998). It has recently colonized the Baltic sea (Ojaveer and Lumberg 1995) and was first detected at relatively low abundances (<325 m^{-3}) in Lake Ontario in 1998 (MacIsaac et al. 1999). Abundances in parts of the lake the following year

reached over 2,000 m^{-3} , and it had increased its range, colonizing Lake Michigan and five of the New York State Finger Lakes (Makarewicz et al. 2001; Ojaveer et al. 2001). The rapid increase in both lakewide abundance and range raises great concerns for the degree and impact of *C. pengoi*'s invasion into North America.

North American lakes have previously been colonized by a related cercopagid, *Bythotrephes* sp., which has proved to be an important predator on smaller zooplankton, altering the macrozooplankton community (Yan and Pawson 1997). The greater abundances and propensity for population growth (egg production) exhibited by *C. pengoi* (Grigorovich et al. 2000; Makarewicz et al. 2001) suggest that it may have a considerable impact. This impact is compounded by the possession of a long caudal appendage that is five to eight times the body length (i.e., 6–10 mm), with a distinctive terminal loop (Grigorovich et al. 2000). This appendage may prevent predation by smaller planktivorous fish, although larger fishes are able to consume them (Baltic herring, Ojaveer and Lumberg 1995; alewife, D. M. Warner pers. comm.). Consequently, at high abundances, *C. pengoi* may be a strong competitor with many species of fish during their pelagic early life history stages.

¹ Current address: Fisheries and Oceans Canada, Gulf Fisheries Center, 343 avenue Université, P.O. Box 5030, Moncton, New Brunswick, Canada E1C 9B6 (BenoitH@dfo-mpo.gc.ca).

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Despite the potentially important role that *C. pengoi* may play in ecosystems, detailed information on that role is limited, with the exception of some observations from the Baltic Sea (Gulf of Riga and Gulf of Finland), which it invaded in 1992. In the Baltic Sea *C. pengoi* are consumed by several fish species, sometimes constituting a majority of herring (*Clupea harengus*) diets, although young-of-year herring select against them (Ojaveer and Lumberg 1995; Ojaveer et al. 2000). Preliminary studies suggest that *C. pengoi* diet in those systems consists of about 60% juvenile copepods, 20% rotifers, and 20% podonids (E. Gorokhova pers. comm., also cited in Uitto et al. 1999), although long-term patterns in zooplankton abundance suggest a negative effect on *Bosmina* sp. but not on other species (Ojaveer et al. 1998, 2000). In North America, two recent studies in Lake Ontario have documented the horizontal spatial distribution of *C. pengoi*, along with some descriptions of population characteristics (Ojaveer et al. 2001; Makarewicz et al. 2001). Ojaveer et al. (2001) also present data on its vertical distribution (collected at a 20 m resolution) that suggest that *C. pengoi* is mainly found in the epilimnion and that it does not undergo diel vertical migrations. But data on predation impacts on zooplankton in Lake Ontario are still lacking. To fully understand the ecological importance of *C. pengoi* in Great Lakes food webs, better information on prey types and sizes, as well the degree of temporal and spatial (vertical and horizontal) overlap with potential prey, measured at finer resolutions, is required.

The objectives of our research were (1) to determine the vertical distribution of *C. pengoi* in Lake Ontario with respect to other zooplankton species and possible biotic and abiotic controlling factors and (2) to use time series of potential prey species to make inferences about predatory impacts of *C. pengoi*. The vertical distribution of zooplankton species was used to make predictions about predator-prey relationships involving *C. pengoi*. We assessed these hypotheses using biomonitoring data from the Bay of Quinte (Lake Ontario, North America). In these analyses, potential prey and trophic relationships were identified between periods before and after *C. pengoi* using two complementary methods: a body-size based approach, using normalized biomass size spectra (e.g., Sprules and Munawar 1986), and seasonal time series of species abundances.

Methods and materials

Data for this study were obtained from three sources for Lake Ontario: a 1999 study of the vertical distribution of zooplankton in the open waters, historical data from an open-water monitoring program, and seasonal zooplankton data from an ongoing biomonitoring program in the Bay of Quinte. Sampling methodology differed among the studies with each summarized below. Rotifers were not collected during any of the studies.

Vertical distribution study (Lake Ontario, 3–6 August 1999)—Discrete-depth zooplankton samples were taken to study the vertical distribution of *C. pengoi* in relation to the rest of the community and to other vertically stratified biotic (chlorophyll *a*) and abiotic (temperature, light) variables. A

Table 1. Station locations, depths, and time periods sampled for the vertical distribution study, 3–5 August 1999. Time periods: M = morning, A = afternoon, N = night.

Date	Latitude	Longitude	Station depth (m)	Series
3 Aug 99	43°18.44'N	79°41.16'W	43	A, N
4 Aug 99	43°29.29'N	79°17.43'W	116	M, A, N
5 Aug 99	43°25.63'N	78°33.56'W	112	M, A, N

different station was sampled on each of 3 days in order to maximize the variation in *C. pengoi* abundance among samples (Table 1). Separate vertical series were collected for the morning (0900–1200 h), afternoon (1600–1900 h) and night (2200–0100 h) at each station. Each sampling series comprised 10 equally spaced zooplankton samples collected from 3- to 30-m depth using a submersible pump. Each sample consisted of 390 liters of water filtered through a 110- μ m mesh net prior to preservation. Further samples were taken from 30–60 m and 60–100 m (station depth permitting) using a metered 40-cm diameter, 64- μ m mesh closing net. Exceptions to this methodology occurred for the night samples on 3 and 4 August, where pump samples were taken down to 18 m, and a closing-net collection was used to sample zooplankton over the 20–30 m depth range.

Vertical profiles of temperature and chlorophyll *a* (using fluorescence as a surrogate) were collected using a conductivity-temperature-depth (CTD) meter with a mounted fluorometer. Fluorometer readings were calibrated using measured chlorophyll *a* concentrations (determined using the GF/C filtration/acetone extraction and grinding method described by Strickland and Parsons 1968). The temperature profiles were used to calculate water density, and a criterion of 0.08 kg m⁻³ m⁻¹ was chosen as the minimum density gradient to delineate epilimnion depth (e.g., Johannsson et al. 1998).

Light transmission (corrected for variation in incident light) was measured for each daytime vertical series at 1-m intervals down to 20 m. Light extinction coefficients, calculated as the slope of the relationship between depth (m) and log₁₀-light (μ mol s⁻¹ m²), did not differ statistically among stations (-0.115 ± 0.015 [mean \pm SD], ANCOVA, $P > 0.10$). Thus light-at-depth varied strictly with incident light, which was measured continuously at 5-min intervals using a sensor mounted at the ship's highest point.

The long-term biological monitoring program on Lake Ontario (Bioindex)—This program was run by Fisheries and Oceans Canada from 1981 to 1995, with weekly sampling (April–October) of the lower trophic levels at two permanent stations (see Johannsson et al. 1998 for details). Biweekly sampling continued at one of the stations (41, 43°43.00'N, 78°01.36'W, depth = 130 m) in 1996 and 1997. This station is generally considered to be representative of the conditions and zooplankton community development in the pelagic zone of central Lake Ontario (Neilson and Stevens 1986; Johannsson and Minns 1987). For the current study, we used data collected during the thermally stratified summer period

for 1995–1997 to give a recent historical perspective of the macrozooplankton community. Samples consisted of duplicate epilimnetic and metalimnetic net tows collected using a metered 50-cm diameter, 64- μ m mesh closing net.

Project Quinte (Bay of Quinte, Northeastern Lake Ontario)—Zooplankton have been collected continuously at three stations since 1979, in biweekly samples from May to September/October (see Cooley et al. 1986 for details on the sampling; Johnson and Hurley 1986 for details on Project Quinte). These stations include one in the upper bay (Belleville, 44°09.15'N, 77°20.79'W, depth = 5 m), one midbay (Haybay, 44°05.58'N, 77°04.21'W, 12 m), and one at the mouth of the bay, leading into Lake Ontario (Conway, 44°02.73'N, 76°53.90'W, 32 m). With a 41-liter Schindler-Patalas trap (75- μ m mesh), three depths are sampled at Belleville (1, 2, 3 m), four at Haybay (1, 2, 3, 6 m), and eight at Conway (1, 3, 5, 8, 10, 15, 20, 25 m). A single sample is constructed and analyzed for each station date.

Sample processing—All zooplankton samples were preserved in 4% buffered formalin. Identification and enumeration were conducted by a single enumerator, ensuring consistency among studies. A minimum of 400 individual zooplankters was enumerated from each sample using the stratified (subsampling) counting system described in Cooley et al. (1986). Subsampling was not used to enumerate *C. pengoi*. Body length measurements were made on the first 40–70 individuals encountered of each taxon. These were converted to body weight using published length–weight relationships (cf. Appendix 1 of Johannsson et al. 2000). Although there is some variation in the relationships for *C. pengoi* (e.g., Grigorovich et al. 2000; Makarewicz et al. 2001; Ojaveer et al. 2001), this was not a concern given the distinctly greater weight of *C. pengoi* relative to other zooplankters and our consideration of abundance rather than biomass.

Data analysis—vertical series—Preliminary analyses of the data from the 1999 vertical series showed that the majority of the biomass of *C. pengoi* and the rest of the zooplankton community was located above 30 m. Most species had single distinct modes of abundance in the top 20 m and densities at 30 m comprised only 0.6–2.8% of the summed 3–30 m densities. The only exceptions were *Limnocalanus macrurus* and *Leptodiaptomus sicilis*, two deep-water calanoid copepods that occurred at relatively low abundances and did not overlap much with the rest of the community. Consequently, we focused our analyses on the data collected by the pump sampler (top 30 m), where we have the greatest vertical resolution. However, zooplankton collected via vertical net hauls (20–30 m) during the first two evenings of the study were also included in vertical distribution plots and used in comparing abundances of organisms in the epilimnia and metalimnia.

We used direct (redundancy analysis [RDA]) and indirect (principal components analysis [PCA] followed by correlation of the factors to environmental variables) ordination techniques to examine relationships within the macrozooplankton community and with the environmental variables

in the vertical series. Linear ordination methods were used because the lengths of the environmental gradients were generally short and typically related linearly/monotonically to zooplankton abundance (Legendre and Legendre 1998). We used forward selection in the RDA to select and test (via randomizations) the environmental variables that significantly correlated with the community data, reporting the explained variance and statistical significance for both marginal effects (environmental variables considered singly) and conditional effects (additional variables to the model). However, because true community structure and gradients resulting from “unmeasured” factors may not be expressed in the constrained ordination, and because our primary interest was examining the relationship among species with environmental correlations as a secondary objective, we present graphically only the results from the indirect ordination.

Each sample was included as a separate sampling unit in the ordination (i.e., each depth, for each vertical series). Zooplankton abundances were normalized by $\log_{10}(n + 1)$ transformation and centered for the PCA, and displayed using a correlation biplot (Legendre and Legendre 1998). The environmental variables (temperature, fluorescence, incident light) were standardized prior to analysis. Because light extinction coefficients were consistent throughout the study, we used incident (surface) light as a surrogate for light-at-depth, thus avoiding problems due to the strong collinearity with temperature. Only axes with eigenvalues greater than the average of all eigenvalues were interpreted.

Data analysis—Bay of Quinte: seasonal and historical comparisons—Following the practice of Sprules and Munawar (1986), normalized biomass size spectra (NBSS) were created for biweekly samples during 1997–2000, providing appropriate seasonal and “historical” resolution with which to consider shifts in the size distribution of macrozooplankton subjected to *C. pengoi* predation.

Results

Vertical distributions—Peak abundances of *C. pengoi* consistently occurred at the bottom of the epilimnion or top of the metalimnion, with only one exception, 4 August (night), which had a second peak in the hypolimnion (Fig. 1). This pattern was consistent even on 5 August, when the epilimnion was twice as deep as on previous days. *C. pengoi* were found at all depths sampled; however, by 30-m depth, few individuals were collected. The majority of the zooplankton community occurred below the peak in *C. pengoi* abundance (Fig. 1) and was composed primarily of juvenile copepods, representing an average of 64.5% of the zooplankton population at peak densities for each profile (range: 45.5–92.2%). Consequently, a better description of the vertical distribution of the remaining zooplankton species can be obtained from the PCA analysis (below).

Only two environmental variables were important in influencing the vertical distribution of macrozooplankton, as determined using forward selection in the RDA. Temperature had the largest impact (marginal and conditional effect, $\lambda = 0.37$, $F = 40.7$, $P < 0.005$), followed by fluorescence (marginal effect, $\lambda = 0.14$; conditional effect, $\lambda = 0.07$, F

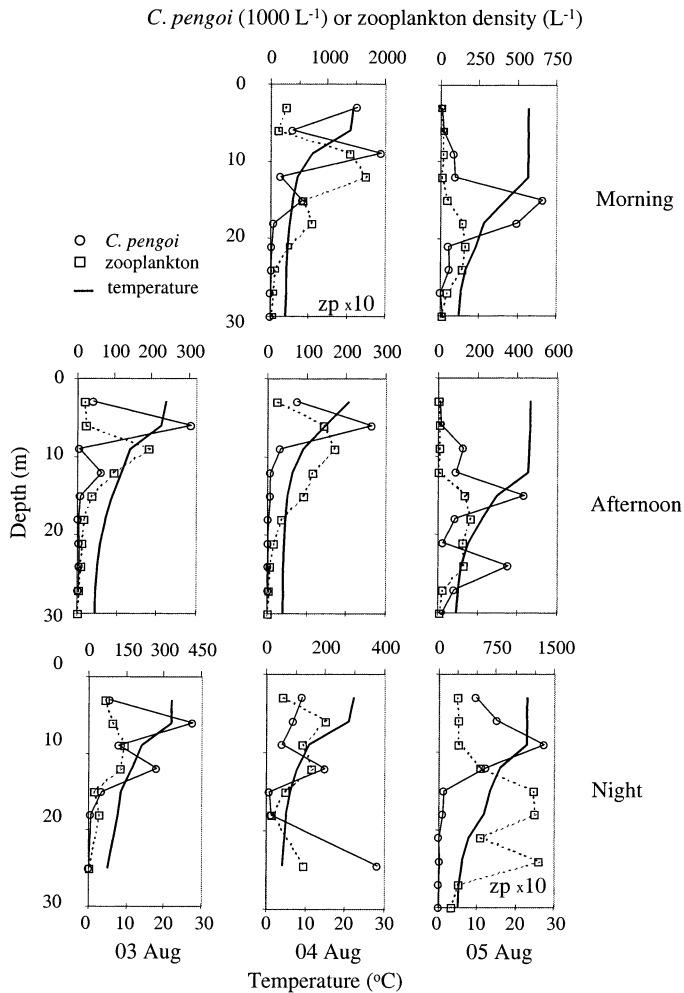


Fig. 1. Vertical profiles for abundances of *C. pengoi* and the entire macrozooplankton community, as well as for temperature in August 1999. Each panel represents a separate vertical series for each sampling day (3–5 August, from left to right) and for each period of the day (morning, afternoon, and night, from top to bottom. See text for details). Note that abundances of *C. pengoi* are in numbers $1,000 \text{ L}^{-1}$ (i.e., m^{-3}), whereas those of the zooplankton community are generally in numbers L^{-1} so that the two could be plotted on the same axis. As indicated on the panels, the only exceptions are for 4 August (morning) and 5 August (night) where the zooplankton community is plotted in numbers 10 L^{-1} .

= 8.83, $P < 0.005$). Generally the vertical distribution of fluorescence (depth of the peak and breadth) varied mostly among stations (Fig. 2a). Consistent associations with *C. pengoi* or the community as a whole (Fig. 1) were not apparent from these plots, although species specific associations may exist (see results of the ordination analysis below). Incident light (Fig. 2b), which varied widely as a result of strong changes in cloud cover, was the third variable to enter the RDA and was generally unimportant in separating the species considered ($F = 1.20$, $P = 0.35$).

The first two PCA axes were sufficient to explain a large portion of the variance in the species abundance data (axis 1, $\lambda_1 = 0.469$, 46.9% cumulative percentage explained variance; axis 2, $\lambda_2 = 0.281$, 75.0%) (Fig. 3). The first axis

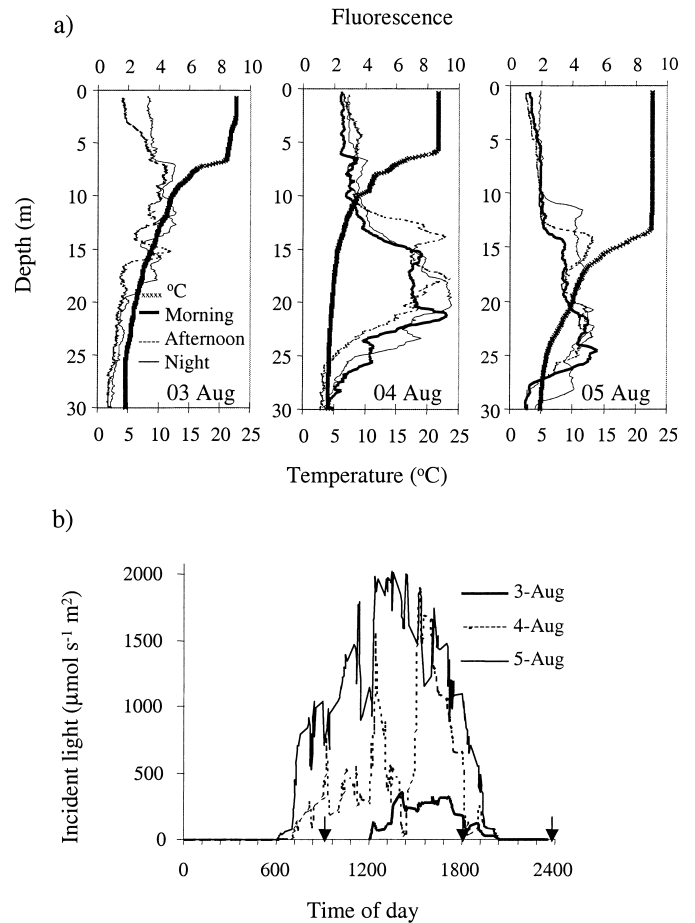


Fig. 2. (a) Vertical profile of fluorescence for each sampling day (separate panels) of the 1999 vertical series, with an average temperature profile for that day added for reference. Separate fluorescence profiles are plotted for morning, afternoon, and night series. (b) Incident light (recorded via a light sensor equipped with an electronic data logger) as a function of the time of the day (24 hour clock). Arrows indicate approximately the midpoint in time for each of the three daily vertical series. Note also that data collection for incident light began at noon on 3 August, which is why incident light begins with a value of zero at that time.

separated species based on the average depth distribution (Table 2), which explains why the axis correlated most strongly with temperature ($r = 0.85$) and fluorescence ($r = -0.49$). Species that loaded positively on that axis were found predominantly in the epilimnion or the top of the metalimnion. The second axis appears to separate species based on how much their depth distribution changed as a result of the deepening of the epilimnion on the third day (Table 2). The gradient ranged from distribution changes that were characterized by a slight deepening of the minimum depth of occurrence (calanoid juveniles) to species whose entire distribution shifted downward (*Eubosmina* and *Bosmina*). This axis did not correlate strongly with the environmental variables (temperature, -0.31 ; fluorescence, -0.20).

Overall, the results of the ordination show a negative correlation (calanoid nauplii) or no correlation (cyclopoid nauplii) between *C. pengoi* and zooplankton whose small body

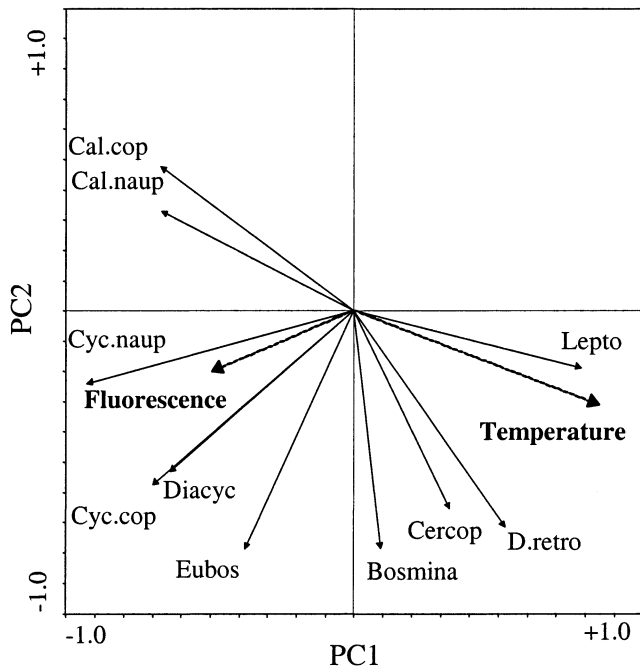


Fig. 3. Correlation biplot for the indirect ordination (PCA followed by correlation with the two statistically significant environmental variables: temperature and fluorescence) for the August 1999 vertical series. Vectors pointing in the same or complete opposite (180°) direction indicate strong positive and negative correlation, respectively. Vectors at right angles (90°) to one another indicate no correlation. When vectors are projected onto the axes, the length of the resulting line indicates the degree of correlation with that axis. Abbreviations used: Bosmina, *Bosmina longirostris*; Cercop, *Cercopagis pengoi*; D.retro, *Daphnia retrocurva*; Eubos, *Eubosmina* sp.; Lepto, *Leptodora kindtii*; Diacyc, *Diacyclops thomasi*; Cyc.naup and Cyc.cop, cyclopoid nauplii and copepodids (same convention used for calanoid copepods).

size would make them most vulnerable to predation by an invertebrate planktivore (Dodson 1974; Yan and Pawson 1997). Interestingly, the species with the most similar vertical distributions as *C. pengoi* include both larger species (*Daphnia retrocurva*) that are unlikely to be eaten by *C. pengoi*, based on their body size, and intermediate sized species (*Bosmina longirostris*) that may be vulnerable for only a portion of their life history.

As suggested in the RDA, incident light also does not significantly separate *C. pengoi* or the community as a whole, based on their vertical distributions (Figs. 1, 2b). However, when species are considered individually, many appear to move vertically over the diel cycle (Fig. 4). The failure of the RDA to separate taxa is likely because of the overriding influence of temperature and fluorescence in the RDA and because the diel movements of taxa are often of low to moderate amplitude and in the same direction for most taxa. *Diacyclops thomasi*, cyclopoid copepodids, *Daphnia retrocurva*, *Eubosmina* sp., and to a lesser extent *Bosmina longirostris* all show higher relative abundances in the epilimnion during the night. The opposite is true of *Leptodora kindtii*. On the other hand, the nauplii and the calanoid copepodids do not show any apparent diel movements. Al-

Table 2. Average depth* distribution (\pm SE) \dagger , and percentage change \ddagger in the mean depth of each species following the wind event in the early morning of 5 August. Table is sorted by increasing mean depth.

Species	Average depth (m)	Standard error	Percentage change
<i>Leptodora kindtii</i>	6.2	0.7	39
<i>Daphnia retrocurva</i>	8.4	1.6	47
<i>Cercopagis pengoi</i>	10.1	1.5	45
<i>Bosmina longirostris</i>	11.0	1.4	47
<i>Eubosmina</i> sp.	13.3	1.8	47
<i>Diacyclops thomasi</i>	13.9	1.9	43
Cyclopoid copepodids	13.9	1.6	41
Cyclopoid nauplii	17.0	1.6	38
Calanoid nauplii	19.8	1.3	19
Calanoid copepodids	21.9	1.5	16

* Mean depths were calculated for each series as an average weighted by the density of the species at each depth. An overall average of all of the mean depths estimated for each of the eight vertical series is presented in this table.

\dagger Standard error for the average of the eight mean depths (i.e., for each vertical series).

\ddagger An overall average depth was calculated for the five series collected from 3 and 4 August, as well as a separate average for the three series from 5 August (following the wind event). The value presented here represents how much deeper the species were on the last day of the study.

though some vertical movement was observed on 5 August, *C. pengoi* does not demonstrate consistent strong vertical migration, as many of the other taxa do. Interestingly, on the night of 5 August, when *C. pengoi* was relatively and

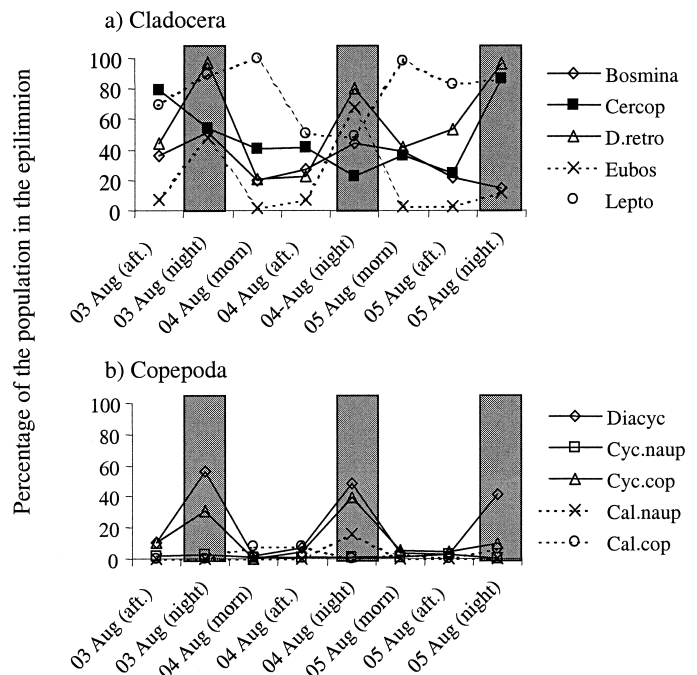


Fig. 4. Percentage of the populations (by density) found in the epilimnion for the major macrozooplankton species encountered for each 0–30 m vertical series (August 1999). Abbreviations for species names are the same as for Fig. 3. Shaded bars have been added to further highlight the night samples.

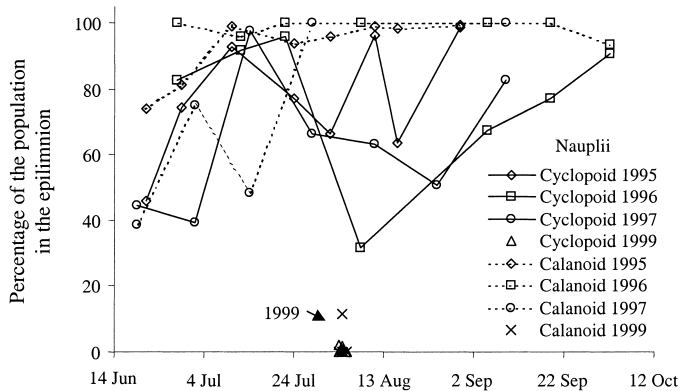


Fig. 5. Seasonal time series of the percentages (by density) of the surface water (epilimnion and metalimnion) copepod naupliar populations found in the epilimnion at station 41 (BioIndex) in 1995–1997. Percentages were calculated for each taxon on each date as the population abundance in the epilimnion divided by the abundance in the epilimnion and metalimnion combined, multiplied by 100. Similarly calculated percentages for the August 1999 vertical series study conducted in the open water of west-central Lake Ontario are plotted as a contrast.

numerically most abundant in the epilimnion, the diel migration of many of the other species appeared to be reduced in amplitude even though the epilimnion was deeper.

Because copepod nauplii occur in the size ranges hypothesized to be most vulnerable to invertebrate predation, their vertical distribution in August 1999 was compared with that observed in the past in Lake Ontario to determine whether there have been changes since the arrival of *C. pengoi*. Copepod nauplii in August 1999 occurred much deeper than they had in recent history for any time during the summer period (Fig. 5). Similar analyses for other zooplankton taxa did not show such striking patterns (data not shown).

Based on the observations from the August 1999 study and available information from the Baltic Sea (Uitto et al. 1999; Ojaveer et al. 2000), we hypothesized that juvenile copepods and possibly also similarly sized organisms (e.g., small cladocerans, such as *Ceriodaphnia* sp., *Bosmina longirostris*, and *Chydorus sphaericus*) represent the most likely prey for *C. pengoi*. We examined this hypothesis using seasonal time series from Bay of Quinte biomonitoring data collected during the past 5 yr.

Seasonal patterns and determination of potential prey—*Cercopagis pengoi* was discovered in 1999 for the first time at two stations in the Bay of Quinte. Individuals first appeared at Conway at low densities in 1999 on 16 June, with strong population growth from 14 July up to a peak of about 300 individuals m^{-3} on 11 August (Fig. 6, top left panel). A peak of 130 individuals m^{-3} was observed at Belleville on the same date (not included in the figure). Abundances declined rapidly thereafter at both stations, although individuals were observed well into October at Conway. Similar seasonal patterns were observed in other parts of the lake (Makarewicz et al. 2001). In 2000, the *C. pengoi* population first appeared at Conway on 19 July and reached a peak of about 600 individuals m^{-3} on 2 August (Fig. 6). Population

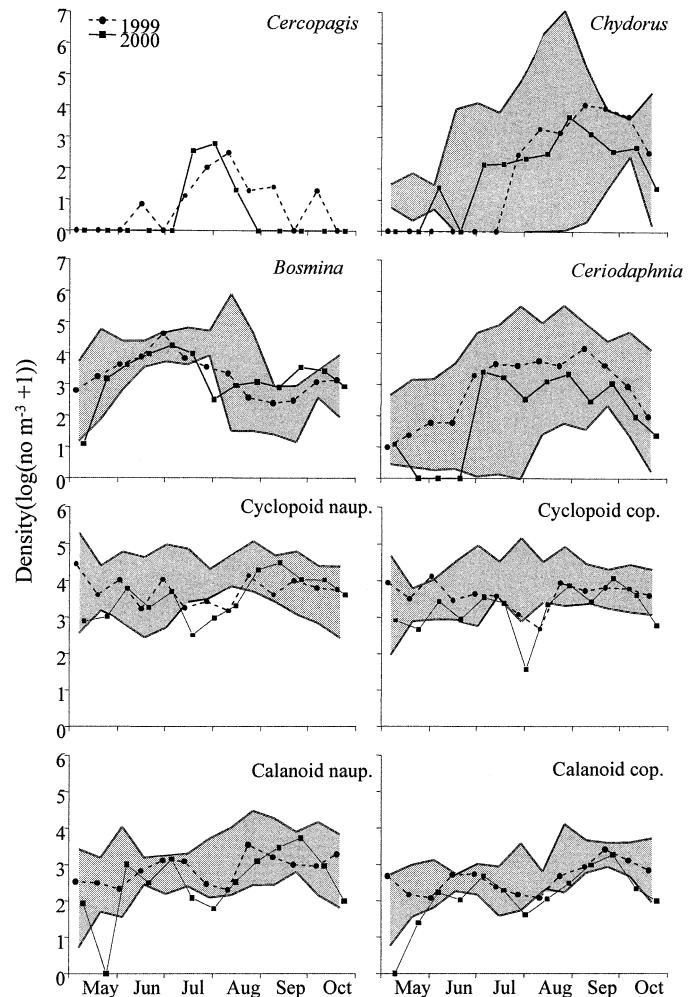


Fig. 6. Seasonal population dynamics (1999–2000) of *Cercopagis pengoi*, *Chydorus sphaericus*, *Bosmina longirostris*, *Ceriodaphnia* sp., and cyclopid and calanoid nauplii and copepod populations at Conway (Bay of Quinte). The shaded area represents the mean of the 1995 to 1998 (before *Cercopagis pengoi*) abundances ± 2 standard deviations (i.e., 95% confidence range). Note the logarithmic axes.

density rapidly declined to 18 individuals m^{-3} on 16 August and then disappeared. At Belleville, *C. pengoi* was only found on 30 August (227 individuals m^{-3}). Although *C. pengoi* were not observed at the midbay station (Haybay) in 1999, they were observed on three occasions at relatively low abundance in 2000 (1 August, 78.05 m^{-3} ; 15 and 29 August, 9.76 m^{-3}). Because the Conway station had the greatest abundance and occurrence of *C. pengoi*, we focus the analyses that follow on data collected from that station. We use data collected at Hay Bay to contrast with the results from Conway because the *C. pengoi* presence at Hay Bay was relatively small.

Individual *C. pengoi* generally weighed more than 10 μg and appear in the right-hand tail of the NBSS for 1999 and 2000 (Fig. 7a,b). Macrozooplankton of these sizes, specifically large individuals of the cladoceran species *Daphnia galeata mendotae*, were only observed once before in the

previous two years (19 August 1997) (Fig. 7c,d). We also observed a pronounced decrease in the biomass of smaller organisms ($<0.15 \mu\text{g}$) varying roughly inversely with densities of *C. pengoi* in 1999 and 2000. Such a dip in the left-hand portion of the NBSS was not observed at any time from 1995 to 1998 (Fig. 7: in order to conserve space only data from 1997 and 1998 are presented).

We tested the statistical significance of the hypothesized *C. pengoi* impact by considering the biomass of zooplankters smaller than $0.1 \mu\text{g}$ (those most affected according to Fig. 7). We conducted a general linear model (GLM) analysis using the following model:

$$\begin{aligned} \log_{10}(\text{biomass}) &= \beta_0 + \beta_1 \cdot \text{week} + \beta_2 \cdot \text{year} + \beta_3 \cdot \text{Cercopagis} \\ &+ \beta_4 \cdot \text{Cercopagis} \cdot \text{week} + \beta_5 \cdot \text{Cercopagis} \cdot \text{year} + \varepsilon \end{aligned}$$

where biomass is the total biomass of zooplankters weighing less than $0.1 \mu\text{g}$, week represents the individual weeks presented in Fig. 7 (same for 'year'), and *Cercopagis* is the presence/absence of the predator. The only significant factor in the model was the presence/absence of *C. pengoi* (Table 3), which suggests that the decrease in small zooplankton concomitant with the presence of that predator was not due solely to chance.

A similar analysis was then conducted on the individual size categories considered in Fig. 7 as an exploratory measure to roughly delineate the sizes of zooplankton inferred to be affected by *C. pengoi*. The biomass of organisms in each category was analyzed separately using the following model:

$$\begin{aligned} \log_{10}(\text{biomass}) &= \beta_0 + \beta_1 \cdot \text{week} + \beta_2 \cdot \text{year} + \beta_3 \cdot \text{Cercopagis} + \varepsilon \end{aligned}$$

Given the exploratory nature of the analysis and that the main goal was to rank the importance of the relationship between *C. pengoi* and biomass among categories, we did not apply a Bonferroni correction to the type I error rate. As in the previous analysis, the effects of week and year were not statistically significant ($P > 0.05$) in all cases considered. Overall a significant effect of *C. pengoi* on the biomass of zooplankton was inferred for all size categories smaller than $0.13 \mu\text{g}$, but not in any of the larger categories (Table 4). Although this does not mean that impacts on organisms larger than that weight are not occurring, we were only able to statistically discern impacts up to that weight.

Taking $0.1 \mu\text{g}$ as an estimate of the weight at which we infer significant *C. pengoi* predatory impacts, we find that for Conway the nauplii populations, especially the calanoids, are most vulnerable (Table 5). Some of the small-bodied cladocerans, namely *Ceriodaphnia* sp., *Chydorus sphaericus*, and *Bosmina longirostris*, may also have some vulnerable individuals in their populations.

The seasonal dynamics of the organisms identified as most vulnerable supports a hypothesized predatory impact of *C. pengoi* on the juvenile copepods (Fig. 6). The abundance of those organisms over the period when *C. pengoi* is abundant is at the lowest since 1995. The seasonal dynamics also suggests that *Bosmina longirostris* is affected (Fig. 6). During

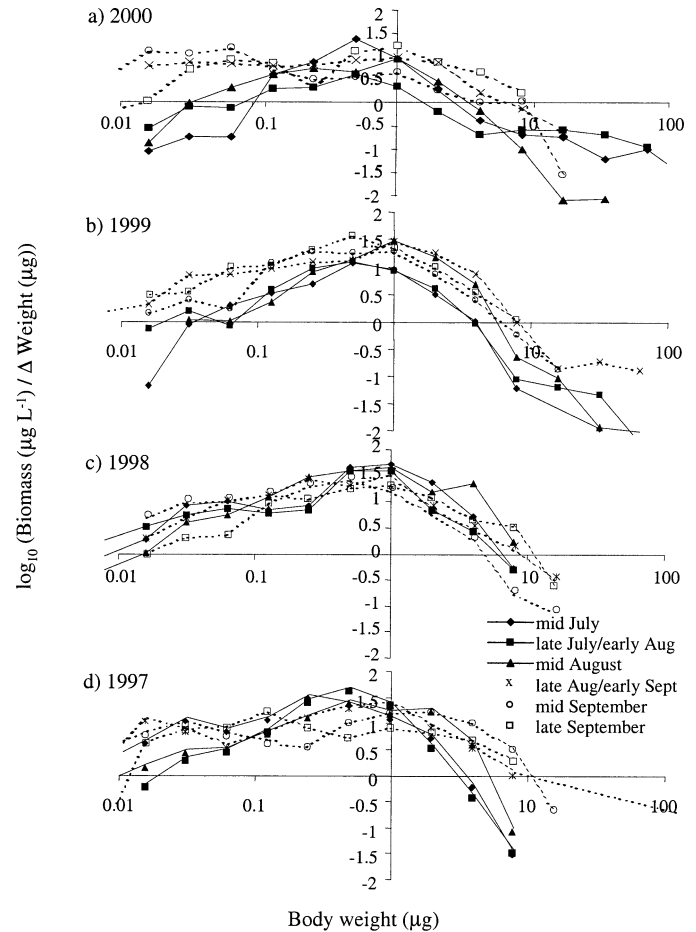


Fig. 7. Normalized biomass size spectra for the macrozooplankton community at Conway in (a) 2000, (b) 1999, (c) 1998, and (d) 1997. Solid lines represent the data from mid-July until mid-August, when *C. pengoi* were abundant in 1999 and 2000. The data from late August and September, when *C. pengoi* was present but at low density (1999) or not present at all (2000), are represented by dashed lines. Similar symbols represent similar sampling dates across the four panels. Note that spectra are plotted for only six dates, when *C. pengoi* was present, to avoid clutter; however, the general patterns observed are consistent for dates prior to July and for October (data not shown). Normalized biomass size spectra for 1995 and 1996 (not shown) were similar to those in 1997 and 1998.

the period when *C. pengoi* was most abundant (mid-July to late August), abundances of nauplii, copepodids, and *B. longirostris* were at the lowest observed in the last six years for that time period. Furthermore, the timing of the peak abundance of *C. pengoi* in both 1999 and 2000 corresponded with the maximum declines in their potential prey species. Similar patterns were not observed for the other two small-bodied cladoceran taxa, *Ceriodaphnia* sp. and *Chydorus* sp. (Fig. 6), which show considerably more interannual variability in population dynamics, precluding us from detecting a decline coinciding with the presence of *C. pengoi*.

As a result of the relatively small presence of *C. pengoi* at Hay Bay, we compared the size structure of the zooplankton community there with that at Conway in order to further confirm that the patterns observed at Conway were likely

Table 3. Results of a general linear model for the total biomass of zooplankton smaller than 0.1 μg individual weight.*

Station	Source	df	MS (type III)	F	P
Conway	Week†	6	0.072	0.89	0.528
	Year†	3	0.068	0.84	0.496
	<i>Cercopagis</i>	1	0.970	12.05	0.004
	<i>Cercopagis</i> × Week	3	0.015	0.19	0.902
	<i>Cercopagis</i> × Year	1	0.134	1.66	0.220
Haybay	Week†	6	0.259	3.70	0.023
	Year†	3	0.254	3.63	0.042
	<i>Cercopagis</i>	1	0.012	0.17	0.686
	<i>Cercopagis</i> × Week	3	0.045	0.64	0.601
	<i>Cercopagis</i> × Year	1	0.005	0.07	0.800

* The analysis was conducted separately on the Conway and Haybay stations. The weight category was chosen by a visual assessment of the inferred *C. pengoi* impact in Fig. 7a, b.

† Analysis was performed for the same weeks and years presented in Figs. 7 and 8.

attributable to *C. pengoi*. The NBSS from Hay Bay in 1999 (no *C. pengoi* present) and in 2000 (present but at relatively low abundance) do not display the same depletion of small-bodied zooplankton as observed at Conway (Fig. 8). There is no discernable pattern in the NBSS from Hay Bay both within and among years. This is supported by a GLM analysis in which the impact of *C. pengoi* was not statistically significant ($P = 0.69$) and was much less important than the variability in biomass due to differences among weeks or years (Table 3). Similarly, the 1999 and 2000 abundances of juvenile copepods and *B. longirostris* did not drop below the 95% confidence interval of the 1995–1998 abundance estimates during the midsummer period (data not shown). It is important to note, however, that the production of zooplankton at Hay Bay is somewhat greater than at Conway, and consequently a predatory effect, if present, may be less discernable. Nonetheless, while the lack of an impact at Hay Bay does not confirm outright that the impacts observed at

Table 4. Results of a general linear model used to analyze the total biomass of zooplankton in the individual body weight categories at Conway. A separate analysis was conducted for each category, although results are only displayed for body weight categories 1.0 μg or smaller. Only the results for the effect of *C. pengoi* are presented because the effects of week and year were not statistically significant ($P > 0.05$) in all cases considered here and were not significant in the analysis presented in Table 3.

Weight category (μg)	Source	df	MS (type III)	F	P
0.016	<i>Cercopagis</i>	1	1.035	4.63	0.046
0.032	<i>Cercopagis</i>	1	0.621	8.57	0.009
0.063	<i>Cercopagis</i>	1	1.067	11.66	0.003
0.126	<i>Cercopagis</i>	1	0.190	1.99	0.177
0.251	<i>Cercopagis</i>	1	0.354	2.57	0.128
0.501	<i>Cercopagis</i>	1	0.392	3.23	0.090
1.000	<i>Cercopagis</i>	1	0.172	2.03	0.172

Table 5. Proportion of the Conway zooplankton species populations inferred to be vulnerable to *C. pengoi* due to an individual body weight of 0.1 μg or smaller. Also presented are the minimum and maximum individual weights recorded for each species at Conway. All information presented is for the 1997–2000 period.

Species	Minimum weight (μg)	Maximum weight (μg)	Percentage of population 0.1 μg or smaller
<i>Bosmina longirostris</i>	0.09	3.2	<0.1
<i>Eubosmina</i> sp.	0.30	8.3	0
<i>Daphnia retrocurva</i>	0.26	16.0	0
<i>Ceriodaphnia</i> sp.	0.04	2.2	0.8
<i>Chydorus sphaericus</i>	0.06	1.7	1.3
Cyclopoid nauplii	0.008	0.3	1.3
Calanoid nauplii	0.009	0.4	52.5
Cyclopoid copepodites	0.18	6.1	0
Calanoid copepodites	0.54	9.6	0

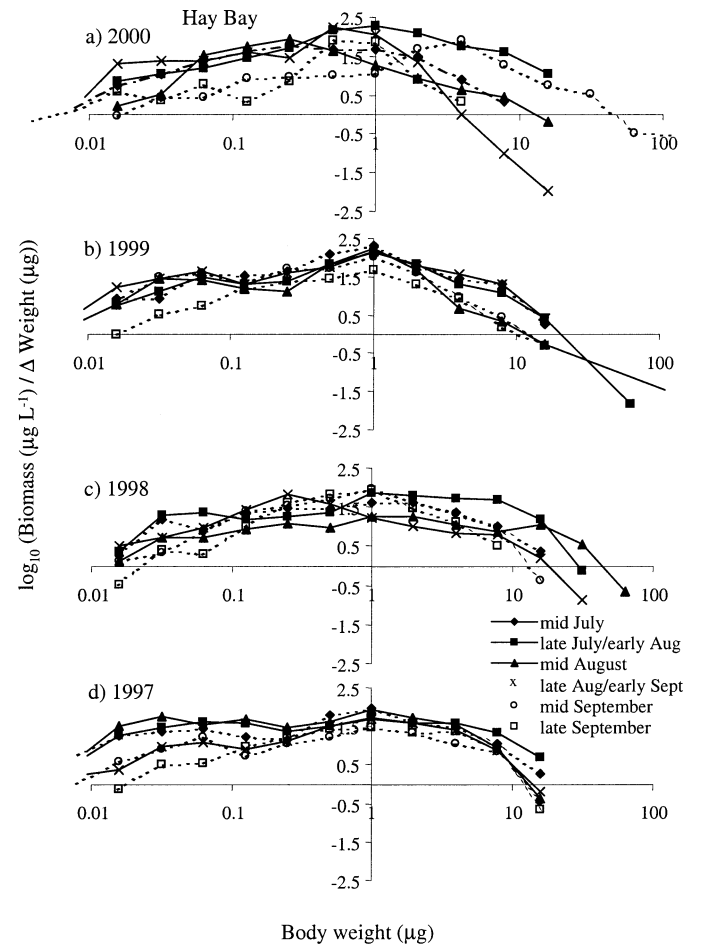


Fig. 8. Normalized biomass size spectra for the macrozooplankton community at Haybay in (a) 2000, (b) 1999, (c) 1998, and (d) 1997. Legend as in Fig. 7. Note that *C. pengoi* were observed at Haybay on three occasions at low abundances in 2000: 1 August at 78.05 m^{-3} , 15 August at 9.76 m^{-3} , and 29 August at 9.76 m^{-3} . They were not observed at that station in 1999. Normalized biomass size spectra for 1995 and 1996 (not shown) were similar to those in 1997 and 1998.

Conway were due to *C. pengoi*, it does support that contention.

Finally we wish to note certain pieces of anecdotal information that support our contention that the impacts we report are likely due to *C. pengoi*. We considered other sources of size-selective predatory mortality, but none proved consistent with the impacts observed. *Leptodora kindii*, a predatory zooplankton, was at relatively high abundance in 1999 but not in 2000 when the strongest impacts on juvenile copepods were observed (O. E. Johannsson unpubl. data). Planktivory by alewives has likely increased in recent years due to what appears to be a large year class in 1998 and a relatively large year class in 1999, based on age-1 surveys (Bob O'Gorman, U.S. Geological Survey pers. comm.). However only young-of-the-year (YOY) fish are expected to have a strong seasonal pattern to planktivory rates, and by end of July–August, YOY alewives would feed more on larger copepods and cladocerans than nauplii and *Bosmina* sp. (Urban and Brandt 1993). Furthermore, apparent year-class strength of alewife cannot explain why the greatest impacts on small-bodied zooplankton occurred in 2000. Finally, *Mysis relicta* is an important planktivore in Lake Ontario, but mysid planktivory is restricted to water depths below the thermocline due to their avoidance of temperature and light during the summer (Johannsson et al. 1994).

Discussion

The determination of direct and indirect predatory impacts requires knowledge of the types and sizes of potential prey, as well as the spatiotemporal overlap with predators. We have attempted to address these components and have relied heavily on the biomonitoring data from the Bay of Quinte to determine prey types based on size and species, as well as temporal overlap. Only with such seasonally explicit, long-term monitoring data, which precedes the invasion of *C. pengoi*, were we able to confidently infer predatory impacts and distinguish them from seasonal variability.

Generally, we infer that *C. pengoi* can be a voracious predator on the smaller fraction of the zooplankton community, particularly in the shallower strata. The depletion of small-bodied copepods suggests that in August, when *C. pengoi* reaches high abundances, it may compete with the pelagic early life history stages of fish with late or protracted spawning periods (e.g., alewife, emerald shiner, centrarchids, gizzard shad) (Seifert 1972; Graham and Sprules 1992). However, the juveniles of most fish species should be feeding on larger zooplankton by that time, and as such, a direct competitive impact is not expected to be great. Rather, the impacts on fish are expected to be indirect, since recruitment and production of larger copepod stages would be affected. Interestingly, strong effects on juvenile copepods were not observed in the Baltic Sea (Ojaveer et al. 1998, 2000). However, zooplankton species composition in the Baltic is partly driven by a large-scale hydrodynamic pattern affecting salinity (Viitasalo et al. 1994), and these effects may be masking or overriding shorter term seasonal changes in the zooplankton community caused by invertebrate predation.

Results from the vertical distribution study indicate that

the vertical distributions of *Bosmina longirostris* and *C. pengoi* are correlated, which suggests that there is no active avoidance or local depletion. We cannot comment on the vertical overlap between *C. pengoi* and *Chydorus* sp. or *Ceriodaphnia* sp., since these species were not found in the August 1999 open-lake samples. According to the NBSS data, the body sizes of vulnerable individuals of the small-bodied cladocerans represent only a small portion of the population for these taxa. This may explain why the dramatic differences in the historical vertical distribution observed for copepod nauplii, which are of the sizes most vulnerable to predation, were not observed for *Bosmina longirostris*.

Although they were not collected in our studies, we suspect that rotifers, which fall into the body sizes most vulnerable to predation by *C. pengoi*, are also strongly affected (Uitto et al. 1999). These organisms provide a vital link in the microbial loop and represent an important fraction of secondary production in pelagic areas of the lower Great Lakes (e.g., Johannsson et al. 2000).

Generally we found that the bulk of the *C. pengoi* population occurred at the bottom of the epilimnion or the top of the metalimnion. Other studies (Krylov et al. 1999; Uitto et al. 1999; Ojaveer et al. 2001) have observed a more epilimnetic distribution, although this may partly be due to a coarser sampling regime using plankton tows rather than discrete-depth pump samples. In our study the vertical position of *C. pengoi* appears to have important ramifications to its inferred main prey. Although we cannot determine whether this effect is a result of depletion in the epilimnion due to predation, or predator avoidance, it is clear the bulk of the juvenile copepod population occurred in much colder waters in August 1999 than in 1995–1997. The position of organisms within the vertical dimension affects temperature-dependent metabolic rates, which translate into impacts on growth and development rates (i.e., stage durations), as well as reproductive characteristics (e.g., Shuter and Ing 1997). There are, therefore, important implications to production at the individual, population, and community levels (Shuter and Ing 1997; Stockwell and Johannsson 1997) given that water temperature can vary by up to 15°C between the epilimnion and the bottom of the metalimnion in Lake Ontario (Johannsson et al. 1998).

Given the recent nature of the invasions, coupled with the general lack of information on the ecology of *C. pengoi*, there is a need for the rapid dissemination of even basic predictions as to its impact on the pelagic food web. Although there is an urgent need for research focused on the prevention of such biological invasions (Ricciardi and MacIsaac 2000), knowledge of predicted impacts may alter other management actions in the ecosystem in the longer term (e.g., phosphorus control, fish stocking, etc.). Given its propensity for population growth, coupled with strong direct and indirect impacts on smaller zooplankton, *C. pengoi* has the potential to dramatically affect pelagic secondary production in the systems that it has invaded. What remains to be determined is the extent of those impacts to its competitors and predators when mediated through the Lake Ontario food web.

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