Effects of the non-indigenous cladoceran *Cercopagis pengoi* on the lower food web of Lake Ontario

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SUMMARY

1. In North America, the invasive predatory cladoceran *Cercopagis pengoi* was first detected in Lake Ontario. We explored the impact of *Cercopagis* on the lower food web of Lake Ontario through assessments of historical and seasonal abundance of the crustacean zooplankton, by conducting feeding experiments on the dominant prey of the invader, and by estimating its food requirements.
2. Between 1999 and 2001, a decrease in the abundance of dominant members of the Lake Ontario zooplankton community (*Daphnia retrocurva*, *Bosmina longirostris* and *Diacyclops thomasi*) coincided with an increase in the abundance of *Cercopagis*. *Daphnia retrocurva* populations declined despite high fecundity in all 3 years, indicating that food limitation was not responsible. Chlorophyll *a* concentration generally increased, concomitant with a decline in the herbivorous cladoceran zooplankton in the lake.
3. Laboratory experiments demonstrated that *Cercopagis* fed on small-bodied species including *D. retrocurva* and *B. longirostris*.
4. Consumption demand of mid-summer populations of *Cercopagis*, estimated from a bioenergetic model of the confamilial *Bythotrephes*, was sufficient to reduce crustacean abundance, although the degree of expected suppression varied seasonally and interannually.
5. Predatory effects exerted by *Cercopagis* on the Lake Ontario zooplankton, while initially very pronounced, have decreased steadily as the species became established in the lake.

Keywords: *Cercopagis*, food web, Lake Ontario, non-indigenous species, predation

Introduction

Over the past 15 years the Laurentian Great Lakes, as well as many inland lakes in North America, have experienced a wave of invertebrate invasions from Eurasia (see Ricciardi & MacIsaac, 2000; Ricciardi, 2001). Unlike exotic species invasions of the Great Lakes in the early twentieth century (Mills *et al.*, 1993), recent invaders became established at low- and mid-

trophic levels and have dramatically altered energy flow and contaminant movement through the lakes (Dermott *et al.*, 1999; Ryan *et al.*, 1999; reviewed in Shuter & Mason, 2001). The most recent invader to establish itself in Lake Ontario is the predaceous zooplankter *Cercopagis pengoi* (Ostroumov) (MacIsaac *et al.*, 1999; Makarewicz *et al.*, 2001a). Within 3 years of being reported in Lake Ontario, *C. pengoi* invaded Lake Michigan (Charlebois, Raffenberg & Dettmers, 2001) and Lake Erie (Therriault *et al.*, 2002), as well as many inland lakes in New York (e.g. Seneca, Cayuga, Otisco, Canandaigua, Owasco and Cross) and Michigan (e.g. Muskegon) (Makarewicz *et al.*, 2001a; Therriault *et al.*, 2002).

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Cercopagis pengoi is now one of the most abundant predaceous zooplankters in Lake Ontario, although its maximum offshore density has decreased each year since colonisation from a mean peak abundance of 1759 m^{-3} in 1999 to 355 m^{-3} in 2001 (Makarewicz *et al.*, 2002). In general, *Cercopagis* appears in the zooplankton community at low density (< 30 m^{-3}) in late June and does not achieve maximum abundance until late July. Peak abundance at both nearshore and offshore sites in Lake Ontario occurs between late July and mid-August (Makarewicz *et al.*, 2002). Two closely related forms, *C. pengoi* and *C. ossiani*, occur in Lake Ontario (Makarewicz *et al.*, 2001a). Sequencing of the mitochondrial ND5 gene revealed that these forms are characterised by a single haplotype, and that only the ancestral species, *C. pengoi*, is actually established in the lake (Makarewicz *et al.*, 2001a). The morphotypes probably represent progeny produced via sexual (*C. ossiani*) and asexual reproduction (*C. pengoi*) (Simm & Ojaveer, 1999; Makarewicz *et al.*, 2001a). Similar morphological differences have been reported for confamiliar *Bythotrephes* (Zozulya, 1977; Yurista, 1992).

Cercopagis pengoi is a predatory cladoceran that preys on zooplankton by physically tearing the integument of the prey and ingesting the contents (Mordukhai-Boltovskoi, 1968). Rivier (1998) inferred that *C. pengoi* fed on nauplii, copepodids and adult calanoid copepods. Field evidence from Lake Ontario demonstrated that invasion by *C. pengoi* was correlated with the decline in abundance of juvenile cyclopoids in the epilimnion (Benoit *et al.*, 2002). Research on the confamilial *Bythotrephes* provides insight on the possible impacts that *C. pengoi* might have on the food web. For example, in Harp Lake, Ontario, long-term analyses of zooplankton community structure pre- and post-*Bythotrephes* invasion revealed a significant decline in crustacean zooplankton diversity, particularly of small-bodied taxa (Dumitru, Sprules & Yan, 2001; Yan, Girard & Boudreau, 2002). Similarly, small- and mid-sized *Daphnia* spp. declined after invasion of Lake Michigan by *Bythotrephes* (Lehman & Caceres, 1993). Schulz & Yurista (1999) suggested that *Bythotrephes* preferred larger prey [e.g. *Daphnia pulicaria* (Forbes)], while the smaller *C. pengoi* would probably be limited to consumption of smaller species by virtue of its smaller size. Because small-bodied cladocerans and cyclopoid copepods have historically dominated the zooplankton community of Lake Ontario, invasion

by *C. pengoi* may be expected to impact zooplankton diversity and community composition (O'Gorman, Bergstedt & Eckert, 1987; Johannsson, Mills & O'Gorman, 1991; Lampman & Makarewicz, 1999).

The goal of this study was to identify the predatory impact of *C. pengoi* on lower trophic levels of the Lake Ontario community by combining studies of seasonal and historical abundance of the zooplankton and phytoplankton, laboratory studies on feeding, and bioenergetic estimates of consumption requirements.

Methods

Seasonal field sampling

Procedures and locations for sampling the zooplankton followed Makarewicz *et al.* (2001a). In general, samples were taken due north of Hamlin Beach State Park (43°25.110′ latitude and 77°53.986′ longitude), Lake Ontario, New York, U.S.A. Samples were collected from two stations (30- and 100-m depth) between 07.00 and 10.00 hours. Diel studies indicated that *C. pengoi* did not migrate below 20 m. Sampling was conducted every 2 weeks in spring and autumn and weekly during the summer when *C. pengoi* abundance increased.

Zooplankton samples were collected using vertical hauls taken from 20 m to the surface. *Cercopagis pengoi* was collected using a flow-metered double Bongo net (571-µm mesh net, 50-cm diameter). The entire sample was counted because of the tendency of *C. pengoi* spines to tangle, which would have prevented unbiased subsampling. The remainder of the zooplankton community was collected using a Wisconsin net (63-µm mesh net, 50-cm diameter) equipped with a flow meter. Both samples were preserved in 10% buffered formalin. Before counting, zooplankton samples were mixed thoroughly and diluted individually to obtain 150–350 organisms per subsample. Three replicate 10-mL subsamples were withdrawn using a Hensen–Stemple pipette. Zooplankton taxonomy largely followed Balcer, Korda & Dodson (1984) although other keys were also consulted (e.g. Edmondson, 1959; Rivier, 1998). Cladocerans, adult cyclopoid copepods and large rotifers were identified, and the number of individuals and eggs per species were counted using a dissecting microscope and a multichambered glass counting cell (Gannon, 1971). Length measurements were made on the first 20

individuals of each species encountered per sample. Calanoid copepods, cyclploid nauplii and copepodids were counted but not identified to species. Historical abundance data were analysed with the non-parametric comparison ANOVA method of Kruskal–Wallis followed by a multiple comparison test (Dunn's Test, see Siegal & Castellan, 1988; Zar, 1999).

Phytoplankton samples were collected with a water bottle in August 2000 at a depth of 3 m and immediately preserved with Lugol's iodine and formalin solution. Counting procedures followed Makarewicz, Bertram & Lewis (1998).

During 2001, the vertical distribution of potential prey items of *C. pengoi* was established at the offshore location by performing zooplankton tows at fixed depth intervals (0–20, 20–40, and 40–60 m) with a closing net (17-cm diameter, 63-μm mesh) equipped with a flow meter. The diel distribution of zooplankton was assessed by collecting replicate ($n = 3$) samples at 1-m intervals from the surface to 20 m between 1300 and 1400 and between 2200 and 2330 on 27 July 2001. Samples were collected, using a submersible water pump at a rate of 1 L sec^{-1} into filter tubes (0.3-m length and 12-cm diameter, 153-μm mesh net). Samples were counted in entirety for *C. pengoi* and for *D. retrocurva* (Forbes). The Kolmogorov-Smirnov test, which is sensitive to differences in the general shapes of two distributions, was used to evaluate diel differences in zooplankton abundance.

Laboratory feeding experiments

Laboratory feeding experiments, using *C. pengoi* collected daily at Hamilton Harbour, were conducted on the two dominant cladocerans in Lake Ontario. Short net hauls (210-μm mesh, 0.5-m diameter) were used to collect zooplankton, which were rinsed into 1.5-L containers containing lake water to minimise stress during transport to the laboratory. Free (i.e. spine unattached to conspecifics or detritus) and apparently healthy (i.e. swimming well) *C. pengoi* individuals were isolated and removed from samples using either a wide mouth pipette or fine forceps and placed singly within an environmental chamber containing filtered lake water (Whatman glass microfibre 934 AH filter, 1.5-μm) for a 24-hour acclimation period (Yurista & Schulz, 1995). Prey species [*Bosmina longirostris* (Muller) and *D. retrocurva*)] were also collected from Hamilton Harbor, Lake Ontario. Individual prey

species separated into monocultures were placed into 2-L containers filled with aerated, filtered lake water and fed dried *Chlorella* daily (<1 mg L^{-1}). Every second day, prey monoculture water volumes were reverse filtered to 25% of the total initial volume using a 40-μm Nitex mesh filter and brought back up to volume with the addition of freshly-collected, filtered lake water.

Experiments were conducted in an environmental chamber at 18 °C and 1.78 μE m^{-2} s^{-1} light intensity (24-hour light) using third instar, parthenogenic females of *C. pengoi* in 1.5-L vessels. Within the environmental chamber, experimental containers were placed in an open-top box allowing only diffuse overhead light. Healthy prey (40 per vessel, $n = 5$) were randomly added to containers filled with filtered lake water and a single *C. pengoi*. Prey density (26 000 m^{-3}) approximated the average total zooplankton abundance observed in western Lake Ontario in 2000. Replicated controls lacking *C. pengoi* were also run for each treatment. After 12 h, the contents were concentrated by reverse filtration (using 40-μm Nitex mesh) and observed using a dissecting microscope to assess predator and prey mortality, as well as animal condition. Prey individuals found trapped within the water surface film were considered as live after the experimental period.

Energetic requirements of Cercopagis

Cercopagis pengoi and *Bythotrephes* are confamilial and have similar morphological features, feeding behaviours and ecological niches. Both species grab prey with enlarged antennae and physically tear the integument and ingest the contents of prey organisms (Mordukhai-Boltovskoi, 1968; Rivier, 1998). Owing to the paucity of physiological data and the similarity in feeding behaviour, a bioenergetics model developed for *Bythotrephes* (Yurista & Schulz, 1995) was employed to estimate *C. pengoi* consumption demand. With appropriate model adjustments based upon the proportional body mass of the two species, the model assumed that, like third instar *Bythotrephes*, third instar *Cercopagis* will consume 105% of its dry weight in carbon per day. Consumption rates, particularly of predators, approach or exceed 100% of dry weight per day for several species (Yurista & Schulz, 1995). For example, the copepod *Mesocyclops edax* (Forbes) consumed 100% of its dry weight per day (Brandl &

Fernando, 1975) and *Polyphemus*, a predatory clado-ceran closely related to *Cercopagis* and *Bythotrephes*, consumed 86% of its dry weight per day (Monakov & Sorokin, 1972). *Bosmina*, a herbivore, may consume as much as 170% per day at high food concentrations (Urabe, 1991).

The number of prey required to fulfill the energetic demand of a single *C. pengoi* (predation rate) was calculated by dividing the consumption demand (μgC day^{-1}) by the mean weight, in carbon, of prey. Zooplankton weights were calculated by utilising the median lengths and the associated length : weight regressions for Great Lakes zooplankton of Culver *et al.* (1985), as well as length : weight relation-ships for Lake Ontario populations of *D. retrocurva*, *B. longirostris* and *D. thomasi* (Forbes) (Johannsson & O'Gorman, 1991) and *Cercopagis* (Makarewicz *et al.*, 2001b). Carbon was assumed to make up 50% of dry weight (Salonen *et al.*, 1976; Makarewicz & Likens, 1979).

To evaluate further the impact of *C. pengoi* on the zooplankton in Lake Ontario, an alternate approach, using the physiological method of Winberg assessed predation pressure as the relationship between con-sumption rate of *C. pengoi* (C_i) and production rate of its potential prey (P_{hz}) (Telesh, Bolshagin & Panov, 2001). Predation pressure (C_i/P_{hz}) exerted by the *C. pengoi* population at peak abundance was consid-ered as a measure of the *per capita* effect of the invader on the plankton. The overall impact (*I*) of *C. pengoi* on the zooplankton in Lake Ontario in 1999 through 2001 was calculated as:

$$I = (N_i/N_z)(C_i/P_{hz}),$$

where N_i/N_z is the relation of population density of *C. pengoi* (N_i) to total crustacean zooplankton abun-dance (N_z). The parameter (*I*) is a dimensionless value which can vary in the range $0 \leq I \leq 1$ (Telesh *et al.*, 2001).

Daphnia retrocurva and *B. longirostris* production in the upper 20 m was estimated by the egg-ratio method (Paloheimo, 1974) using the egg develop-ment-temperature relationship from Belehradeks's equation (Cooley, Moore & Geiling, 1986). Production for each species was calculated by multiplying the number of new recruits during the interval between sampling periods (*B*) by the mean dry weight for individuals of each species during the same period. Individual weight was calculated with the length :

weight relationship derived for Lake Ontario taxa (Johannsson & O'Gorman, 1991). Estimates of *D. thomasi* production followed the empirical model that Shuter & Ing (1997) developed, in part, with data from Lake Ontario. The model emphasises that the temperature experienced by the organism can account for variation in daily weight-specific production (production : biomass ratio). The biomass of *D. thom-asi* on each sampling day was calculated by summing the biomass of each development stage. Mean indi-vidual weight for each stage was assumed constant at 0.9 μg for nauplii, 1.9 μg for copepodids and 3.2 μg for adults (Johannsson & O'Gorman, 1991).

To assess other effects of *Cercopagis* on the lower food web of Lake Ontario, we measured chlorophyll *a* concentration. In 1999, between 500- and 750-mL aliquots of water were filtered through a glass-fibre filter; the chlorophyll was extracted with 90% alkaline acetone (Wetzel & Likens, 1994) and measured with a Turner Model 111 fluorometer (Turner Instrument Company, Carpinteria, CA, U.S.A.). During 2000–2001, chlorophyll *a* concentration and temperature were measured with a Seabird SEALOGGER CTD (Model SBE 25, SeaBird, Inc., Bellevue, WA, U.S.A.) equipped with a WETStar fluorometer (standard range 0.03–75 μg L^{-1}). The WETStar fluorometer (Wetlabs, Philomath, OR, U.S.A.) was factory calibrated and confirmed with the Turner Model 111 in the laborat-ory. Chlorophyll measurements taken with the Sea-Bird CTD were averaged from 20 m to the surface.

Results

From July until September 2001, the numerically dominant cladocerans, *B. longirostris* and *D. retrocurva*, were found predominantly (88 and 92%, respectively) in the upper 20 m, while 42% of adult *D. thomasi* were observed there (Table 1). Juvenile copepodids were also predominantly (70%) observed in the upper 20 m of the lake.

The dominant zooplankters displayed different patterns of vertical distribution over the course of a day. Night and day distributions of *Daphnia* and *Cercopagis* were significantly different ($P \leq 0.05$, Kolmogorov–Smirnov test). For example, *Daphnia* was restricted to the epilimnion at night, with a maximum abundance at 8 m (Fig. 1); at midday its maximum abundance was observed at 12 m (i.e. below the thermocline). Conversely, maximum *C. pengozi*

Table 1 Vertical distribution of potential *Cercopagis pengoi* prey from July to September 2001. Values represent the percent of the population observed in the top 20 m of Lake Ontario of the 60 m sample
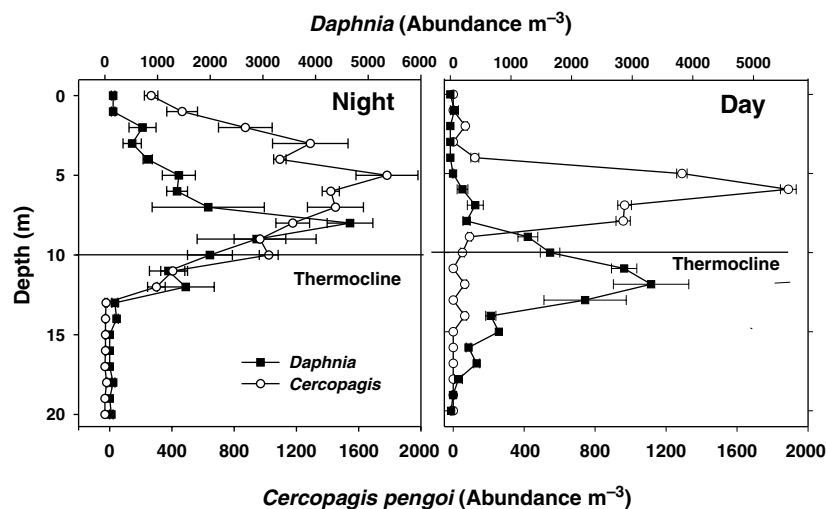
Date	Epilimnion thickness (m)	*Cercopagis pengoi* (Number m^{-3})	Percent of individuals in the upper 20 m			
			Bosmina longirostris	*Daphnia retrocurva*	*Diacyclops thomasi*	Copepodids
17 July	2.0	0.8	97.4	94.5	57.0	94.0
25 July	15.0	16.3	97.4	100.0	40.4	83.0
1 August	3.0	3.9	74.6	82.1	28.2	68.5
8 August	12.0	354.0	60.7	84.4	7.4	26.0
15 August	6.6	188.0	97.2	98.0	78.0	92.0
28 August	7.3	16.6	99.3	99.3	84.0	99.0
5 September	22.0	3.4	81.6	87.8	4.7	42.0
12 September	26.0	0.6	96.2	92.4	33.0	57.0
Average	11.7	72.3	88.0	92.3	41.6	70.2

abundance occurred in the epilimnion, with peak abundances at noon and midnight only 1 m apart (i.e. 5 and 6 m, respectively).

Historically, the crustacean zooplankton community of Lake Ontario has been composed chiefly of small cladocerans and cyclopoid copepods, with the summer community dominated by *D. retrocurva*, *B. longirostris* and *D. thomasi*. While the abundance of these three species in offshore waters varied across years, each has experienced a major decline following establishment of *C. pengoi* in the lake (Fig. 2). For example, mean August abundances of each species were significantly lower (*P*≤0.05, Kruskal–Wallis ANOVA) during the 1999 through 2001 interval than during 1986–91 and 1990–95 (Fig. 2).

Seasonal patterns of abundance also support the hypothesis of zooplankton suppression by *Cercopagis*. Dramatic declines in three common members of the zooplankton community were coincident with peak abundance of *C. pengoi* (Figs 3 and 4). For example, during the summer of 1999, the abundance of *C. pengoi* at the offshore location increased quickly in late July and reached a maximum of 1759 m^{-3} on 19 August (Fig. 3). *Daphnia retrocurva* achieved a peak abundance of 4650 m^{-3} on 30 July and declined sharply to 120 m^{-3} during the *C. pengoi* population maximum. The decline in *Daphnia* abundance was not attributable to food limitation, as its instantaneous birth rate did not decline during this time (Table 2). In the week following the *C. pengoi* peak, however, *D. retrocurva* abundance increased steadily, culminating in a maximum of 5170 m^{-3} on 9 October. *Bosmina longirostris* achieved its greatest abundance of 32 000 m^{-3} on 7 July and steadily decreased to 125 m^{-3} during the *C. pengoi* population maximum. Unlike *Daphnia*, however, *Bosmina* abundance did not rebound following the

Fig. 1 Vertical distribution of *Daphnia retrocurva* and *Cercopagis pengoi* in Lake Ontario during the day (13.00 to 14.00 hours) and night (22.00 to 22.30 hours), 27 July 2001.
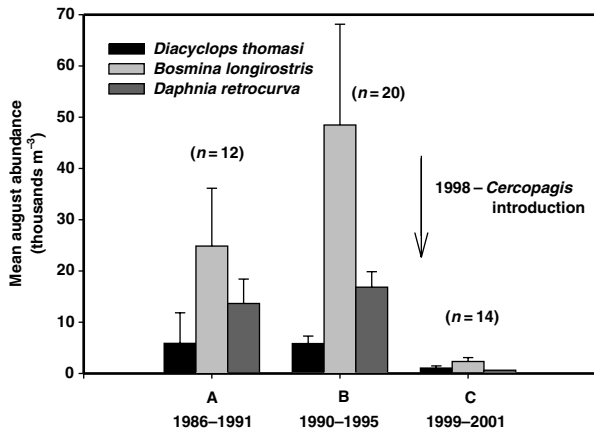
Fig. 2 Average (+1 SE) August abundance of three dominant zooplankton before and after the appearance of *Cercopagis* in Lake Ontario. Data sources: 1986–91, 100-m site from Makarewicz (1991), 1990–95 from Johannsson *et al.* (1998) and 1999–2001, 100-m site from this study. The 1986–91 study and the present study employed the same sampling equipment and technique, including the same sampling locations, depth (0–20 m), mesh net (64 μm), sampling time and sampling months. The 1990–95 of Johannsson *et al.* (1998) data also represent offshore data taken with a Wisconsin net (0.5-m diameter, 65-μm mesh) on the north side of Lake Ontario (sampling depth of 0–20 m during unstratified periods or 1 m above the thermocline to the surface).

decrease of *C. pengoi*. The instantaneous birth rate of *Bosmina* was below the replacement rate prior to, during, and after the *C. pengoi* population increase

(Table 2). *Diacyclops thomasi* (adults + juveniles) abundance in the upper 20 m steadily decreased from a maximum in spring to a minimum in August. *Diacyclops* abundance increased during autumn and reached nearly 10 000 m^{-3} at the end of the sampling season. Declines in zooplankton abundance at the nearshore station were similar to those at the offshore station in both time and magnitude, despite a 300% difference in *C. pengoi* abundances at these locations (Fig. 4).

The inverse patterns of abundance observed between *Cercopagis* and the three dominant zooplankton taxa during 1999 were largely repeated in 2000 and 2001. During 2000, dominant zooplankton species were in decline or at low abundance whenever *Cercopagis* density exceeded approximately 200 m^{-3} (Figs 3 and 4). For example, *D. retrocurva* abundance remained low (<600 m^{-3}) at the nearshore and offshore sites when *Cercopagis* was abundant, despite relatively high birth rates (e.g. Table 2). When *Cercopagis* decreased, *D. retrocurva* increased (Figs 3 and 4). Similarly, the abundance of *Bosmina* (nearshore and offshore) and *Diacyclops* (offshore only) peaked before and after the summer increase in *Cercopagis*.

During 2001, the density of *C. pengoi* offshore was significantly lower than in the previous 2 years (*P* ≤ 0.05, Kruskal–Wallis ANOVA). In contrast, the 2001 nearshore density of *C. pengoi* was not significantly lower than in 1999 and 2000 (*P* = 0.42,
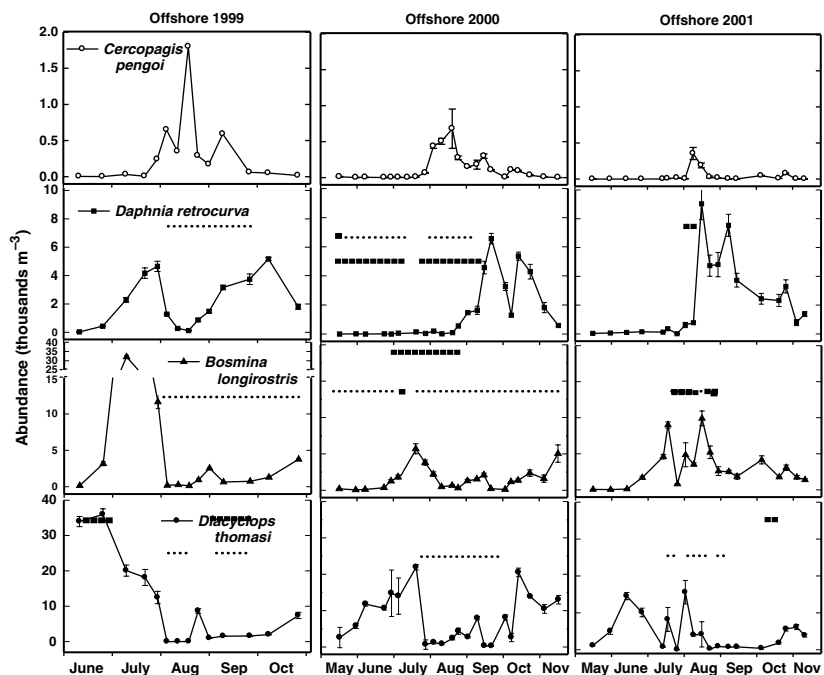

Fig. 3 Seasonal abundance of *Cercopagis pengoi, Daphnia retrocurva, Bosmina longirostris* and *Diacyclops thomasi* in the upper 20 m at offshore stations of Lake Ontario, 1999 to 2001. Values are mean abundance ±SE. Horizontal dotted line indicates time period when consumption (bioenergetic estimates) demands of *Cercopagis* (μgC m^{-3} day^{-1}) surpass production by each species.

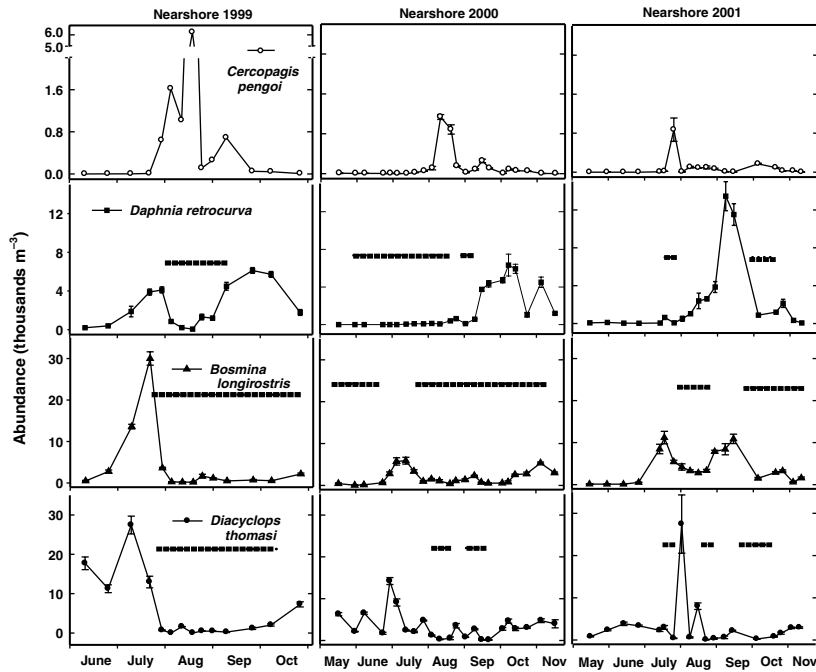**Fig. 4** Seasonal abundance of *Cercopagis pengoi, Daphnia retrocurva, Bosmina longirostris* and *Diacyclops thomasi* in the upper 20 m at nearshore stations of Lake Ontario, 1999–2001. Values are mean abundance ±SE. Horizontal dotted line indicates time period when consumption (bioenergetic estimate) demands of *Cercopagis* (μgC m^{-3} day^{-1}) surpass production by each species.

Kruskal–Wallis ANOVA) despite much lower peak densities. Despite a relatively high birth rate over the whole summer period (Table 3), the population of *D. retrocurva* did not increase markedly until the week after the *C. pengoi* population maximum (Fig. 3). At the nearshore site, *D. retrocurva* began a slow increase in abundance after the peak in *Cercopagis* abundance (Fig. 4). As in 2000, *Bosmina* density was lower during the period when *Cercopagis* was abundant and consumption exceeded production. No obvious relationship existed between *Cercopagis* and *Diacyclops* abundance in 2001.

An inverse relationship was observed between the abundance of herbivorous cladocerans, mainly *D. retrocurva* and *B. longirostris*, and chlorophyll *a* concentration. This relationship was stronger in 1999 ($r = -0.69$, $P = 0.01$) and 2000 ($r = -0.59$, $P < 0.01$) than during 2001 ($r = -0.10$, $P = 0.70$). The highest chlorophyll concentration occurred during algal blooms in late spring and during the mid-summer depression of the herbivorous Cladocera associated with *Cercopagis* population maxima (Fig. 5).

Predation experiments and energetic requirements

Laboratory experiments provided corroborative evidence that *C. pengoi* preyed on the two dominant Cladocera, *B. longirostris* and *D. retrocurva*. Clear evidence of predation (e.g. detached heads or postabdomen) was often evident in trials involving *Daphnia* and *Bosmina*. *Cercopagis pengoi* consumption rates on *Bosmina* and *Daphnia* averaged 2.8 *Cercopagis*$^{-1}$ day^{-1} (Table 4). This value closely approximates the bioenergetic model estimate for *D. retrocurva* (2.1–4.7 *Cercopagis*$^{-1}$ day^{-1}) but is lower than the estimate (7.1 *Cercopagis*$^{-1}$ day^{-1}) for *B. longirostris* (Table 4).

We estimated the daily consumption demand of *C. pengoi* by multiplying the estimated consumption need of an individual, determined from Yurista & Schulz (1995), by zooplankton abundance (e.g. Fig. 6). At the offshore location in 1999 and 2000, consumption demand of the *C. pengoi* population exceeded production of the major cladoceran and cyclploid copepod taxa 55 and 65%, respectively, of the time (Fig. 3). In 1999, for example, offshore consumption of *C. pengoi* exceeded production of *D. retrocurva*, *B. longirostris* and *D. thomasi* during August and September, and extended into October for *B. longirostris* (Fig. 3). During 2001, offshore consumption exceeded production of these three taxa only 23% of the time. There were similar patterns of nearshore consumption and production (Fig. 4). Calculated values of the overall impact of *C. pengoi* on the zooplankton community were high at the offshore and nearshore stations in 1999, substantially lower in 2000, and were nearly undetectable in 2001 (Table 5).

Table 2 Instantaneous birth rate of *Daphnia retrocurva* and *Bosmina longirostris* prior to and during the *Cercopagis pengoi* abundance peak at the offshore station in 1999–2001

	Date	*Daphnia retrocurva*	*Bosmina longirostris*
1999			
Prior to peak	8 July	0.326	0.012
	22 July	0.267	0.021
	30 July	0.323	0.017
	Average	0.305	0.017
During peak	5 August	0.365	0.011
	12 August	0.334	0.008
	19 August	0.316	0.014
	25 August	0.288	0.002
	Average	0.326	0.009
2000			
Prior to peak	12 July	0.274	0.000
	19 July	0.224	0.009
	27 July	0.331	0.004
	Mean	0.276	0.004
During peak	3 August	0.216	0.010
	10 August	0.318	0.025
	19 August	0.359	0.011
	24 August	0.275	0.012
	30 August	0.266	0.017
	Average	0.287	0.015
2001			
Prior to peak	17 July	0.394	0.016
	25 July	0.432	0.017
	1 August	0.407	0.008
	Average	0.411	0.014
During peak	8 August	0.357	0.011
	15 August	0.203	0.014
	Average	0.280	0.012

Table 3 Instantaneous birth rate of *Daphnia retrocurva* and *Bosmina longirostris* prior to and during the *Cercopagis pengoi* abundance peak at the nearshore station in 2001

	Date	*Daphnia retrocurva*	*Bosmina longirostris*
Prior to peak	26 June	0.235	0.000
	13 July	0.261	0.008
	17 July	0.311	0.020
	Average	0.269	0.010
During peak	25 July	0.432	0.010
	1 August	0.370	0.010
	8 August	0.361	0.011
	15 August	0.322	0.010
	22 August	0.178	0.010
	29 August	0.259	0.011
	Average	0.320	0.010

majority of individuals in Lake Ontario was found within the warm uppermost 20 m of water both by day and night, with no evidence of diurnal vertical migration. These results contrast with those from the Caspian Sea, where vertical migration into deeper water has been reported (Rivier, 1998). This difference in behaviour may reflect differences in the genetic composition of the Caspian and Lake Ontario populations (Cristescu *et al.*, 2001; Makarewicz *et al.*, 2001a).

In the laboratory, *C. pengoi* preyed on *D. retrocurva* and *B. longirostris*. Predation rates of *D. retrocurva* determined experimentally were similar to those calculated from bioenergetic modelling, while experimental estimates for *B. longirostris* were lower than those from bioenergetic modelling. Consumption rates may be low in our experiments, as prey organisms caught in the surface film may not be readily available to predators.

Discussion

Cercopagis pengoi is restricted to the epilimnion and apparently does not migrate below the thermocline in Lake Ontario. Ojaveer *et al.* (2001) also noted that the
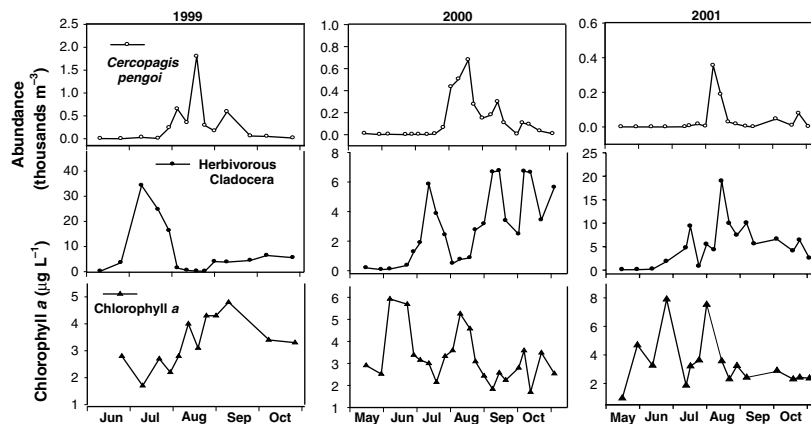

Fig. 5 Seasonal abundance of *Cercopagis pengoi* and herbivorous Cladocera (*Bosmina, Daphnia, Holopedium*) and chlorophyll *a* concentration at the offshore location, 1999–2001. Please note scale changes.

Table 4 Laboratory determined and bioenergetics derived consumption rates of *Cercopagis pengoi* on dominant Lake Ontario cladoceran zooplankton

	Consumption rate (Number $Cercopagis^{-1}$ day^{-1})
Laboratory	
Daphnia retrocurva	2.8
Bosmina longirostris	2.8
Bioenergetic	
Daphnia retrocurva*	4.7
Daphnia retrocurva†	2.1
Bosmina longirostris*	7.5
Bosmina longirostris†	7.1

*Weight calculated from the length–weight relationship developed for Lake Ontario zooplankton (Johannsson & O'Gorman, 1991) based on length data from this study.
†Based on the median length and length–weight relationships of Great Lakes' species (Culver *et al.*, 1985).

Cercopagis pengoi predation rates based on bioenergetic modelling indicate that abundance of this exotic predator could sharply reduce much of the Lake
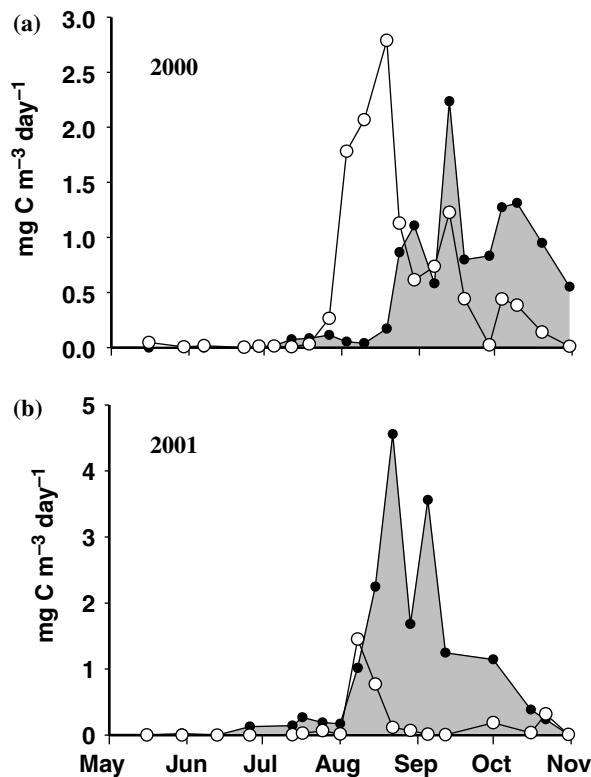

Fig. 6 Daily consumption demand of *Cercopagis pengoi* (open circles) and daily production of herbivorous cladocerans (filled area) at the offshore location of Lake Ontario in 2000 (a) and 2001 (b). *Cercopagis* consumption was estimated from the bioenergetics model of Yurista & Schulz (1995).

Table 5 Predatory Impact (*I*) of *Cercopagis pengoi* on the zooplankton community of Lake Ontario during the periods of peak abundance from 1999 to 2001

Station	Year	Impact (*I*)
Offshore	1999	0.85
	2000	0.02
	2001	<0.001
Nearshore	1999	0.73
	2000	0.06
	2001	<0.001

The parameter (*I*) is a dimensionless value that varies in the range 0–1, from no to high predatory impact (Telesh *et al.*, 2001; also see Methods).

Ontario crustacean population within a few days. This result is consistent with both the seasonal and the long-term (pre- and post-invasion) Lake Ontario data. For example, the abundance of *Daphnia*, *Bosmina* and *Diacyclops* was low whenever *C. pengoi* abundance was high, although these prey species often maintained high birth rates. Conversely, high prey abundance typically occurred only when *C. pengoi* was absent or scarce (<200 m^{-3}; Fig. 7).

Historical data are consistent with the hypothesis of predatory suppression of major zooplankton taxa in Lake Ontario. A comparison of zooplankton abundance, pre- and post-*C. pengoi* invasion, indicates that the August abundance of the dominant Lake Ontario zooplankton (*D. retrocurva, B. longirostris* and *D. thomasi*) has declined significantly after the invasion. A similar result has been observed in the Gulfs of Riga and Finland in the Baltic Sea, where abundances of herbivorous cladocerans (*Bosmina* spp., *Daphnia* spp.) and rotifers declined significantly after *C. pengoi* invaded that basin (Ojaveer *et al.*, 2000; Telesh *et al.*, 2001). Overall, the calculated impact (*I*) of *C. pengoi* on the herbivorous zooplankton community was greatest in 1999, when *C. pengoi* was very abundant, and declined progressively in 2000 and 2001 when *C. pengoi* abundance was much lower (Table 5).

Observed interannual and seasonal changes in herbivorous crustacean abundances may be attributable, in part, to artifacts of the sampling design rather than to the effect of a new predator in the system. However, we are aware of no data that support this scenario for either *D. retrocurva* or *B. longirostris* in Lake Ontario. In fact, our studies on Lake Ontario suggest the opposite. The dominant Lake Ontario Cladocera, *B. longirostris* and *D. retrocurva*, were restricted to the
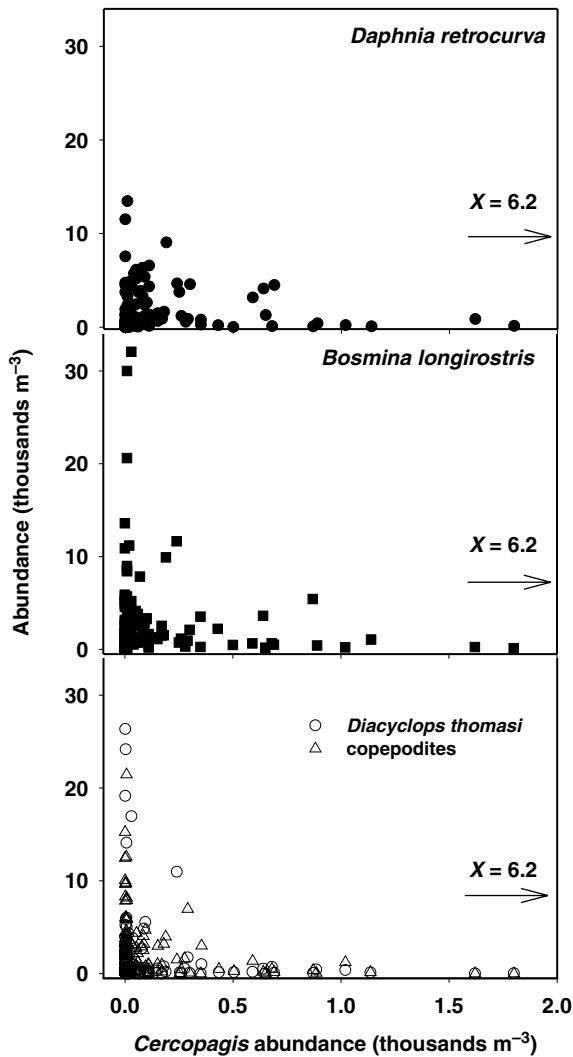
Fig. 7 Simultaneous abundance of *Cercopagis pengoi* and *Daphnia retrocurva*, *Bosmina longirostris*, *Diacyclops thomasi* and copepodites in Lake Ontario between 1999 and 2001 ($n = 111$). The highest value of *Cercopagis* abundance ($X = 6200$ m^{-3}, represented by the arrow) was left off of the graph to improve resolution at the majority of data points; corresponding abundance values of other zooplankton were: 60 m^{-3} for *D. retrocurva*; 180 m^{-3} for *B. longirostris*; and 100 and 0 m^{-3} for *D. thomasi* and copepodites, respectively.

upper 20 m of Lake Ontario throughout the summer of 2001 (Table 1).

Unlike *Bosmina* and *Daphnia*, the majority of the Lake Ontario *Diacyclops* population resided below the upper 20 m on five of eight sampling dates during 2001 (Table 1). This observation may be a result of a preference for deeper water during summer stratification (Wilson & Roff, 1973) or a diurnal vertical migration pattern deeper than that of the Cladocera

(Barbierio, Schact & Dimartino, 2000). Alternatively, this pattern may be a direct response to predation from *C. pengoi*, whether it be consumption of individuals in the epilimnion or predator avoidance (Benoit *et al.*, 2002). Clearly, the abundance of *D. thomasi* in Lake Ontario is influenced by several factors, including predation by *C. pengoi* (Benoit *et al.*, 2002, this study) and by thermal structure. For example, on 19 August 1999 at the offshore site, *D. thomasi* abundance was <30 m^{-3} in the upper 20 m. The following week on 25 August an upwelling event reduced the thickness of the epilimnion from 20 to 4 m (Makarewicz *et al.*, 2001a). On that day, *D. thomasi* abundance in the upper 20 m of the lake increased by a factor of 300, only to decrease again the following week (Fig. 3) when the upwelling event ended. Major changes in *Daphnia* and *Bosmina* abundance were not observed with variation in the thermal structure.

Changes in the abundance of Cladocera may have been related to the increase, beginning in 1994, of the planktivorous three-spine stickleback [*Gasterosteus aculeatus* (Linneaus)] population in Lake Ontario (Hangelin & Vuorinrn, 1988; Ibrahim & Huntingford, 1989; Bolger, Bracken & Dauod, 1990). Stickleback abundance peaked in 1996 and decreased thereafter prior to *C. pengoi* invading the system in 1998 (Owens *et al.*, 2002). Sticklebacks in Lake Ontario are generally associated with the nearshore, but some individuals will disperse into the pelagic zone and congregate in the metalimnion (Manzer, 1976; R. O'Gorman, pers. comm.). Although we cannot completely dismiss the impact of sticklebacks on the zooplankton community, its presence in the metalimnion and decline in numbers, prior to the decrease in herbivorous cladoceran, suggests that it was not responsible for observed changes in abundances of dominant epilimnetic Cladocera.

Our seasonal and interannual data indicate a strong but variable top–down effect of *C. pengoi* on Lake Ontario's zooplankton community. Microzooplankton in this lake have historically accounted for between 70 and 90% of phytoplankton consumption (Lampman & Makarewicz, 1999). Consequently, if microzooplankton are suppressed by *C. pengoi*, an increase in phytoplankton biomass might be anticipated. In 1999 and 2000, when consumption rates of *C. pengoi* greatly exceeded production rates from major herbivorous cladocerans (e.g. Fig. 6a), phytoplankton populations peaked in mid-summer (Fig. 5). During August 2000,

the edible size fraction of phytoplankton [<10 μm greatest axial linear dimension (GALD)] of the herbivorous cladocerans, comprised approximately 52% portion of the Lake Ontario phytoplankton community. Phytoplankton composition data was not available in 1999. Significant inverse relationships between herbivorous Cladocera and chlorophyll concentrations were observed in 1999 and 2000, but not 2001. In 2001, when maximum *C. pengoi* populations were approximately 20 and 65% lower than their maxima in 1999 and 2000, respectively, and *C. pengoi* consumption rates were low compared with production of herbivorous cladocerans (Fig. 6b), a response in the phytoplankton population was not apparent. *Cercopagis* predation on crustacean zooplankton populations in Lake Ontario, especially on *Bosmina* and *Daphnia*, thus appear to cascade down the food web to increase phytoplankton abundance. This observation does not rule out the potentially important role that protozoans and rotifers may play in controlling phytoplankton (Vanderploeg *et al.*, 2002), as our sampling scheme did not include these organisms.

Cercopagis pengoi has the ability to reduce dramatically the summer abundance of Lake Ontario zooplankton. Thus, it may be a competitor with planktivorous fish for energy obtained from zooplankton, potentially inducing a significant bottleneck to productivity of the fish community. For example, if the long caudal appendage of *C. pengoi* reduces its vulnerability to fish planktivory, then competition for zooplankton may result in less food for developing fish and produce a bottleneck in recruitment (Shuter & Mason, 2001). Even if zooplankton production can pass to fish through *C. pengoi*, fish production may ultimately decline because of lengthening of the food web (i.e. a reduced ecological efficiency). Alternatively, production of some fish species which exploit *Cercopagis* may increase, as has happened in the Gulf of Riga (Ojaveer *et al.*, 2000). Further investigation on feeding behaviour of planktivores on the introduced *Cercopagis* is warranted.

In summary, field, laboratory, bioenergetic and physiologic data support the contention that *C. pengoi* feeds on and suppresses abundances of small-bodied herbivorous zooplankton in Lake Ontario. During periods when *Cercopagis* effectively suppresses other zooplankton, phytoplankton abundance increases proportionally.

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