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Distribution, Fecundity, and Genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in Lake Ontario

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ABSTRACT. *Two distinctive forms of cercopagids, first detected in 1998 and identified as* Cercopagis pengoi *and* C. ossiani *using taxonomic keys, were observed to co-occur in Lake Ontario.* C. ossiani *was the predominant form in western Lake Ontario in mid-June 1999 but was then replaced by* C. pengoi*-like animals over the rest of the season. Mitochondrial DNA analyses revealed that these forms were genetically identical at the ND5 gene and that they are morphologically distinctive forms of* C. pengoi. *In 1999,* Cercopagis *reached a maximum abundance of 1,759 individuals/m^3 (average abundance = 281 individuals/m^3, average biomass = 5.2 mg/m^3). In August,* Cercopagis *biomass was lowest at nearshore and embayment sites and highest at offshore sites. Body length of parthenogenetic females was lower at nearshore (1.16 mm) and embayment (1.19 mm) sites relative to offshore (1.32 mm) ones. Maximal clutch size of parthenogenetic females was 24 embryos per individual.* Cercopagis *has already spread to Lake Michigan and five Finger Lakes. Although waterfowl may disperse* Cercopagis*, these invasions likely resulted from human activities.*

INDEX WORDS: Cercopagis pengoi*, exotic species, Cladocera, biomass, genetics, dispersal, Lake Ontario.*

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INTRODUCTION

Introduction of non-indigenous species to new habitats is one of the most significant mechanisms by which humans are altering the planet (MacIsaac *et al*. 1999). Ballast water transfer between international ports has been the major dispersal vector of nonindigenous species (Cohen and Carlton 1998). The Great Lakes have been invaded by an array of ballast water-borne species over the past century, with many of the recent invaders native to the Ponto-Caspian region (Mills *et al*. 1993, Ricciardi and MacIsaac 2000). Ponto-Caspian species that now dominate foodwebs of the lower Great Lakes include zebra and quagga mussels (*Dreissena polymorpha*, *D. bugensis* (in Lakes Ontario and Erie), round gobies (*Neogobius melanostomus* in Lake Erie), the amphipod *Echinogammarus ischnus* in Lake Erie, and now the cladoceran *Cercopagis pengoi* in Lake Ontario.

Cercopagis, a pelagic zooplankter native to the Black, Azov, Aral, and Caspian seas, has invaded brackish waters of the Baltic Sea and freshwater environments in Russia and the Ukraine (Grigorovich *et al*. 2000). First reported outside of its native range by Ojaveer and Lumberg (1995) in the waters of the Baltic Sea during 1992, it now has invaded other coastal and open-water regions of the sea (Krylov *et al*. 1999). In July 1998, sport fishermen on Lake Ontario experienced difficulty retrieving fishing lines fouled by an organism initially believed to be *Bythotrephes*—a similar-looking species that is related to *Cercopagis,* that was first observed in 1988 (Makarewicz and Jones 1990). Closer examination revealed the s-shaped caudal process characteristic of *Cercopagis* (Rivier 1998). Several independent reports confirmed the existence of *Cercopagis* in Lake Ontario in 1998 (MacIsaac *et al*. 1999; Makarewicz *et al.* 1999a; Bertram, Great Lakes National Program Office, EPA, Chicago, personal communication). Based on GLNPO data, the central portion of Lake Ontario appeared to be the population epicenter during August of 1998. However, MacIsaac *et al*. (1999) and Mills (personal communication) have collected specimens from several nearshore and embayment habitats along the north and south shores of Lake Ontario and the Bay of Quinte in July, 1998. Introduction of *Cercopagis* into Lake Ontario was attributed to ballast release from ships (MacIsaac *et al.* 1999). Grigorovich *et al.* (2000) reported on the comparative biology of this species from Lake Ontario and the Baltic and Caspian seas. Reported here are the seasonal and spatial distribution, genetics and life history attributes of *Cercopagis pengoi* (Ostroumov) in Lake Ontario, and dispersal of the species during the summer and autumn of 1998 and spring, summer, and autumn of 1999.

METHODS

Offshore Seasonal Sampling (Hamlin Beach State Park)

Lake Ontario, due north of Hamlin Beach State Park (Fig. 1**,** 43° 25.110′ latitude and 77° 53.986′ longitude**)**, was sampled in 1998 and 1999 for *Cercopagis* with a double Bongo tow (571-µm nylon mesh net, 50-cm diameter, equipped with flow meters). Comparison of abundance estimates from the large mesh double Bongo net and a small mesh Wisconsin net (63-µm nylon mesh net, 50-cm diameter, equipped with a flow meter) revealed similar estimates of abundance (Table 1). Temperature profiles were measured with a SeaBird CTD. In 1999, water samples (3 m depth) for chlorophyll analysis were taken and measured fluorometrically using a Turner Model 111 Fluorometer. Approximately 800 mL aliqouts were filtered through a glass fiber filter and extracted with 90% alkaline acetone (Wetzel and Likens 1994). Secchi disk depth was determined using a black and white 20-cm disk.

In 1998, samples were taken in mid June, July, and August and then biweekly into November. Initially in 1999, biweekly sampling (5 May to 22 July 1999) was employed until *Cercopagis* abundance increased in the water column. Thereafter, a weekly sampling regime was employed (22 July to 27 September 1999) until abundance began to decrease when the biweekly sampling (27 September 1999 to 28 October 1999) regime was reinstated. Depth at the sampling site was 100 m but samples were taken vertically from 20 m to the surface—approximating the epilimnion (Table 2) during thermal stratification. The contents of each net were washed into separate catch buckets, transferred to bottles, and preserved with 10% buffered formalin. Because of the tendency of *Cercopagis* to clump together, all samples were counted totally for individuals, resting eggs, males, and asexual embryos. Enumeration of asexual embryos proved to be difficult owing to the presence of nondifferentiated embryos in many brood pouches. Often it was possible to recognize the dark eyes in the brood pouch and thus enumerate embryos. Reported here are the number of embryos per female

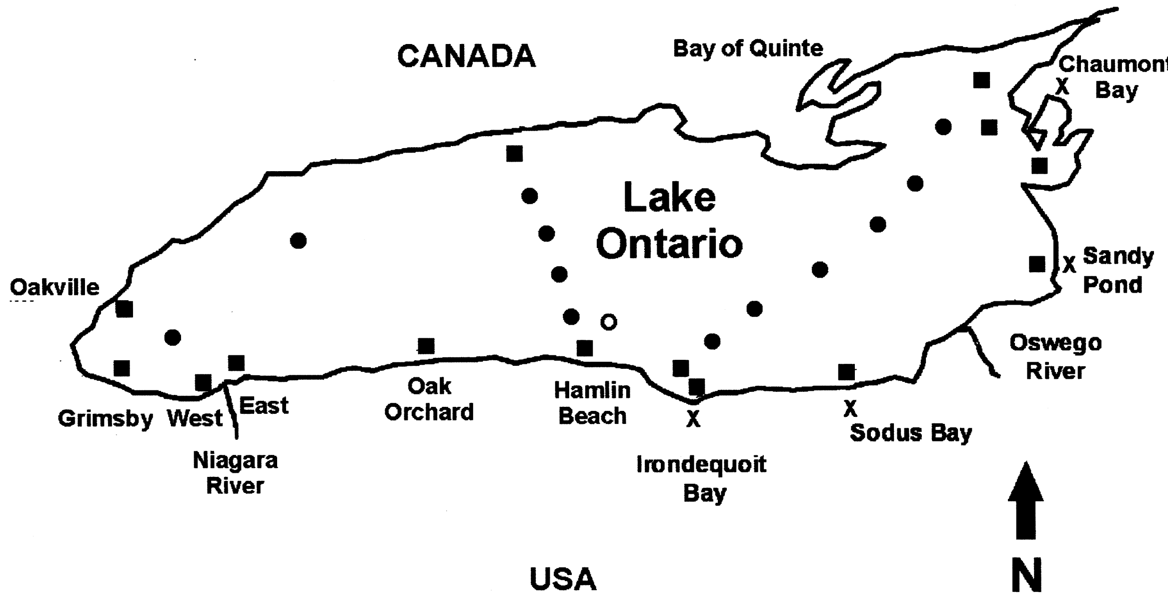

FIG. 1. **Cercopagis** *sampling sites on Lake Ontario. The open circle represents the seasonal offshore sampling site (depth = 100 m). Squares designate nearshore seasonal sampling sites (~10 m depth). Closed circles designate offshore sampling sites of the 9–13 August 1999 cruise (depth > 20 m). An "X" designates the seasonal embayment sampling sites (3–10 m depth).*

for those individuals in which it was possible to differentiate embryos. This value may underestimate fecundity since it was mainly for highly fecund females that it was not possible to resolve embryo numbers. Number of individuals counted for embryos often ranged in the hundreds at the height of the population increase in August. Body length of the first one hundred individuals enumerated in each sample was measured following Grigorovich *et al.* (2000).

TABLE 1. Comparison of Lake Ontario **Cercopagis** *abundance estimates from a double Bongo net equipped with a large mesh net (571 µm) and a Wisconsin net equipped with a small mesh net (63 µm). Values are number/m³. For the double Bongo net, the values represent the mean and the range.*

Sample Date	Double Bongo (571 µm mesh net)	Wisconsin Net (63 µm mesh net)
30 July 1999	242 (213–271)	218
1 September 1999	174 (141–207)	192
27 September 1999	64 (25–103)	31

Spatial-Temporal Sampling

"Embayment" habitats were defined as shallow (approximately 3–10 m) bay sites generally isolated from offshore waters of the main lake. Relatively shallow (approximately 10 m) sites along the shoreline, fully exposed to the main lake, were categorized as "nearshore" habitat and deeper portions of the lake (> 20 m) as "offshore." Nearshore and embayment samples were collected biweekly (once every 2 weeks) from May to October in 1998 and 1999. Nearshore samples were collected at three western locations along the south shore (Niagara River east, Niagara River west, and Oak Orchard), four eastern locations (Galloo Island, Chaumont Bay, Sandy Pond, and Sodus Bay), and one central location (Irondequoit Bay)(Fig. 1). Nearshore samples were also taken at Oakville and Grimsby, Ontario, Canada. Only fecundity data are reported from these sites. Embayment samples were collected at Chaumont Bay, Sandy Pond, Sodus Bay, and Irondequoit Bay. Twelve offshore samples were collected from EPA's R/V *Lake Guardian* from 9 to 13 August 1999 (Fig. 1).

Cercopagis was collected (153-µm mesh nylon net, 50-cm diameter, equipped with a flow meter) at

***TABLE 2.** Seasonal abundance, biomass, length, and population structure of* **Cercopagis pengoi** *in Lake Ontario in 1998 and 1999. SWT = Surface water temperature. ET = Epilimnion thickness, ND = No data, NED = No embryos differentiated. Value in parentheses indicate fecundities for 15 and 29 June at sites at Oakville and Grimsby, ON.*

Date	Average Cercopagis Abundance (#/m³)	Average Cercopagis Biomass (μg/m³)	Average Cercopagis Length (mm)	% Resting Eggs In Brood Pouch	% Males	Embryos per Female	SWT (°C)	ET (m)	Chl. *a* (μg/L)	Secchi Disk Depth (m)
1998										
14-Jun	0	0	0	0	0	0	16.8	ND	ND	ND
8-Jul	0	0	0	0	0	0	22.6	ND	ND	ND
7-Aug	0	0	0	0	0	0	22.9	ND	ND	ND
3-Sep	323	4,726	1.20	3.5	6.0	2.5	21.0	ND	ND	ND
17-Sep	141	1,777	1.10	3.1	8.5	1.8	20.7	ND	ND	ND
30-Sep	10	153	1.23	0.2	4.2	4.0	18.2	ND	ND	ND
16-Oct	6	113	1.39	0.0	18.0	3.3	14.1	ND	ND	ND
9-Nov	2	55	1.74	0.0	27.4	1.5	11.6	ND	ND	ND
1999										
28-May	0	0	0.00	0.0	0.0	0.0	16.1	3	2.2	ND
10-Jun										
15-Jun	0.3	5	1.31	0.0	0.0	5.6	16.7	3	2.8	ND
						(13.1)				
25-Jun	1	15	1.20	0.1	2.5	NED	20.4	4	3.1	ND
29-Jun						(11.3)				
7-Jul	24	398	1.29	0.7	2.2	7.2	21.9	24	1.7	7.0
22-Jul	7	107	1.23	0.0	0.2	3.2	23.3	ND	2.7	8.6
30-Jul	242	4,958	1.46	1.4	2.0	6.4	24.3	20	2.2	9.5
5-Aug	650	11,790	1.36	8.7	2.0	3.2	23.6	17	2.8	7.0
12-Aug	355	6,278	1.34	5.5	2.2	3.7	22.4	20	4.0	4.2
19-Aug	1,759	34,361	1.42	11.1	2.2	4.2	22.8	20	3.1	5.5
25-Aug	291	5,080	1.33	3.1	3.4	4.4	21.6	4	4.3	5.5
1-Sep	174	3,156	1.36	1.6	0.01	4.2	20.7	13	4.3	6.0
10-Sep	593	10,352	1.33	2.9	1.0	4.2	21.1	17	4.8	3.6
27-Sep	64	1,117	1.33	2.9	0.9	3.0	18.9	20	3.4	6.3
8-Oct	46	782	1.31	5.4	6.4	3.9	14.9	22	3.3	6.8
28-Oct	16	255	1.26	8.2	8.2	2.0	10.8	35	6.6	6.0
1999 Average	281	5,244	1.32	3.4	2.2	3.7	20.0	15.9	3.4	6.3

embayment and nearshore sites (top 10 m of the water column) and at offshore sites (top 40 m of the water column). *Cercopagis* was preserved in the field in 70% ethyl alcohol after anesthetizing samples with antacid tablets. Lengths of at least 100 individual *Cercopagis* were measured following Grigorovich *et al.* (2000). In 1998, presence or absence of *Cercopagis* was noted while in 1999 *Cercopagis* was counted using a microprojector at 20× magnification and a digitizer interfaced with a computer.

Finger Lakes *Cercopagis* Sampling

Cercopagis was sampled with a Wisconsin net (571-μm nylon mesh net, 50-cm diameter, equipped with a flow meter) during the month of August, 1999. Epilimnetic tows were taken at the deepest point in the lake.

Length-Weight Relationship

Length-dry weight regressions were developed for *Cercopagis* based on live nearshore and alcohol-preserved nearshore and offshore organisms (length range = 0.6 to 2.0 mm) collected in August, 1998 and 1999. Live organisms were sampled and kept alive for a period of up to 6 hours before measurement and drying at 60°C for 24 hours. Body length of *Cercopagis* was measured from the peak of the head to the base of the caudal process and dry weights were determined using a Sartorius BP 210D and a Cahn Electrobalance. The resulting regressions were:

Nearshore
 Alcohol preserved:
  $\ln W = 2.2309(\ln L) + 1.6585$
  $(R^2 = 0.93)$, n = 12 (1)
 Live, No preservation
  $\ln W = 1.7164 (\ln L) + 2.3703$
  $(R^2 = 0.79)$, n = 18
Offshore
 Alcohol preserved:
  $\ln W = 2.7686 + (\ln L) + 1.3690$
  $(R^2 = 0.95)$, n = 12

where W is dry weight in micrograms and L is body length in mm. All Lake Ontario biomass calculations presented here are based on the length-weight regression developed from live, nonpreserved organisms (Eq. 1).

Molecular Techniques

NADH dehydrogenase subunit 5 (ND5), a relatively rapidly evolving mitochondrial gene, was employed to screen for genetic variability within the Lake Ontario population of *Cercopagis* and to distinguish between *C. pengoi* and *C. ossiani.* This gene has been successfully employed to distinguish the genetic differentiation within the *Daphnia pulex* group (Colbourne *et al*. 1998). Total DNA was extracted from 10 ethanol preserved individuals (5 individuals of each morph), using proteinase K methods (Schwenk 1996). A 798 base pair fragment, coding for 266 amino acids, was amplified using the DpuND5 primers (5′-GGG GTG TAT CTA TTA ATT CG-3′, 5′-ATA AAA CTC CAA TCA ACC TTG-3′) designed by Colbourne *et al*. (1998) for the *Daphnia pulex* group. Each 50-µL polymerase chain reaction (PCR) contained 10 × PCR buffer, 1.5 mM $MgCl_2$, 200 µM of each of dATP, dCTP, dGTP, dTTP, 1 unit of Taq polymerase (Perkin Elmer), 0.3 µm of each primer and 2–4µL of DNA template. The PCR consisted of one cycle of one minute at 94ºC; 5 cycles of 1 min at 94ºC, 1:30 min at 45ºC, 1:30 min at 72ºC; 37 cycles of 1 min at 94ºC, 1:30 min at 50ºC, and 1:30 min at 72ºC; followed by 1 cycle of 5 min at 72ºC. The DNA product was gel-purified using the Qiaex II gene cleaning kit (Qiagen) and sequenced in both directions on an ABI 377 Automated Sequencer (Perkin-Elmer). The sequences of the ND5 gene were aligned with the Seqapp 1.9a sequence editor (Gilbert 1992).

RESULTS AND DISCUSSION

Length-Weight Relationship

Dry weight losses due to alcohol preservation were size dependent and ranged from 32% for larger organisms to 53% for smaller organisms. Over the length range observed in Lake Ontario (0.8 to 2.0 mm), the average weight of alcohol preserved organisms was 42% less than live organisms. Giguere *et al.* (1989) observed a similar average reduction in dry weight (range = 37 to 43%) and a similar size dependent relationship between length and percent reduction in weight.

Introduction into Lake Ontario

It is difficult to pinpoint the date of *Cercopagis* introduction to Lake Ontario. At the offshore sampling location north of Hamlin Beach State Park (Fig. 1), *Cercopagis* was absent in June, July, and early August of 1998. Yet *Cercopagis* was observed in 1998 on 17 June in the nearshore of Lake Ontario near Chaumont Bay and within the Chaumont Bay embayment (Fig. 1) on 29 June, in mid-July in the Bay of Quinte of Lake Ontario, and on 3 August along the northwest and northeast shores of Lake Ontario. In early September of 1998, abundance at the offshore site north of Hamlin Beach State Park reached 323 individuals/m^3 and was quickly reduced to less than five individuals/m^3 by early November (Table 2). Similar high abundances (500/m^3 in August, 1998) were observed by the Great Lakes National Program Office in Lake Ontario (P. Bertram, EPA, Chicago, personal communication) and by MacIsaac *et al*. (1999, 320/m^3).

The widespread occurrence and the relatively high densities during late summer of 1998 in Lake Ontario and the likelihood that this species prefers warm epilimnetic water (Rivier 1998) suggest that *Cercopagis* may have been introduced in the previous year. The establishment of *Cercopagis* in Lake Ontario in 1998 coincided with the lowest abundance of planktivorous *Alosa pseudoharengus* (age 1+) in the lake in 20 years (Owens *et al.* in press). Nevertheless, alewife abundance was not trivial and

FIG. 2. Lateral view of parthenogenetic females taxonomically assignable (Rivier 1998) to* Cercopagis (Cercopagis) pengoi *(*A*) and* Cercopagis (Apagis) ossiani *(*B*) from Lake Ontario. The forms are genetically indistinguishable and likely represent parthenogentic (A) and resting egg (B) generations.

predator pressure provided no apparent resistance to the establishment of *Cercopagis* in Lake Ontario. Ricciardi and MacIsaac (2000) suggest that aquatic invasions are mediated more by dispersal opportunity and favorability of abiotic conditions than by the composition of the recipient community. Zooplankton community richness may be constrained by dispersal limitation at large spatial scales (Shurin *et al.* 2000), and biotic processes at local scales (Shurin 2000).

Co-occurrence of *C. pengoi* and *C. ossiani*

Two forms of cercopagids were discovered in Lake Ontario during 1999. During spring, forms consistent with taxonomic descriptions of *C. pengoi* and *C. ossiani* (Rivier 1998) co-occurred in both northwest and south-central regions of the lake (Fig. 1). At that time, the *C. ossiani* type accounted for 72% of total abundance. This form disappeared by 29 June 1999, and only *C. pengoi*-like animals occurred during the rest of the growth season. During 2000, *C. ossiani* appeared in the Lake Ontario plankton on 5 May 2000 and remained there until 24 July 2000. Both morphs were represented by parthenogenetic females.

Genetic analysis revealed that *C. ossiani* and *C. pengoi* were genetically identical at the ND5 gene as both morphs were characterized by a single haplotype. European populations from the Black Sea, Caspian Sea and Baltic Sea are characterized by 7, 2, and 1 haplotypes, respectively (Cristescu *et al.* 2001). Lack of haplotype diversity at a polymorphic gene for the Lake Ontario populations strongly suggests that the Lake Ontario *Cercopagis* population is a single taxon, *Cercopagis pengoi*. It is possible that the North America *Cercopagis* population was founded by a very small number of individuals, most likely of Baltic Sea origin (Cristescu *et al.*

2001). Taxonomic keys indicate that *C. pengoi* and *C. ossiani* belong, respectively, to the subgenera *Cercopagis* and *Apagis* of the genus *Cercopagis* (Rivier 1998). These subgenera differ with respect to the length and structure of the caudal process. In Lake Ontario, early growth season average body lengths (±SD) for instar III parthenogenetic females of *C. pengoi* (n = 8) and *C. ossiani*-type morphs (n = 8) were 1.72 mm (0.21) and 1.41 mm (0.11), while average caudal process lengths were 9.61 (0.88) and 3.52 (0.50), respectively. *C. pengoi* differed from *C. ossiani* by its possession of a considerably longer caudal process that was more than 5.5 times the body length and terminated in a distinctive loop, whereas in *C. ossiani* the caudal process was less than 2.5 times the body length, relatively straight and lacking a loop (Fig. 2). Articular spines on the caudal process were bent posteriorly in *C. pengoi*, but anteriorly in *C. ossiani*-type morphs.

Both morphs exhibited similar spacing and development of articular spines on the caudal process (Fig. 2). The caudal process of *C. ossiani*-type morphs consisted of as many as four articular segments bearing four paired, articular spines, whereas the *C. pengoi* form had a maximum of three articular spines. Four pairs of articular spines on the caudal process, corresponding to four instars, were reported in sexually-produced individuals of *Bythotrephes* hatching from resting eggs (Zozulya 1977, Yurista 1992). During the late stage of brood development, parthenogenetic females of the two morphs were characterized by the presence of a pointed apex on the brood pouch. Average clutch size for parthenogenetic females of the *C. ossiani*-type morph (13.1 embryos per female; n = 10) was slightly but insignificantly (t-test, P = 0.41) higher than those of the *C. pengoi* morph (11.3 embryos per female; n = 16). *Cercopagis ossiani*-type animals were also observed during the early growth season in the Caspian and Baltic seas (Simm and Ojaveer 1999; I.K. Rivier, Institute of Inner Water Biology, Borok, Russia, personal communication). Morphological and reproductive peculiarities characteristic of the "first generation" that develop from dormant stages have also been demonstrated for other cladoceran taxa including *Bythotrephes*, *Daphnia pulex* and *D. cucullata* (I.K. Rivier, personal communication).

It is very likely that *C. ossiani* and *C. pengoi* represent two morphologically distinct stages of the life cycles of *C. pengoi*. The first generation of individuals (*C. ossiani*-type) may result from hatching of resting eggs, while later generations (*C. pengoi*-type) are produced by parthenogenetic reproduction (Simm and Ojaveer 1999; I.K. Rivier, personal communication). Similar morphological differences were reported between parthenogenetically and sexually produced generations of *Bythotrephes* (Zozulya 1977, Yurista 1992).

Offshore Lake Ontario— Average Length, Resting Eggs, Fecundity

Average *Cercopagis* body length increased between September (1.18 mm) and November 1998 (1.74 mm) (Table 2). Males became progressively more prevalent in the population during this period, comprising up to 27% of the population. Average body length varied little (range =1.20 to 1.46 mm) in 1999. The lack of distinct cohorts is indicative of continuous reproduction and overlapping generations of *Cercopagis*.

Males were again prevalent in the population in September 1999, and comprised 8.2% of the population during late October (Table 2). Sexual females were present but rare in the population in June and July of 1999, but did carry resting eggs. Females with resting eggs constituted 11% of the population during peak abundance on 19 August 1999, just prior to a major population decline. Sexual females decreased in late August and September, but increased thereafter to 8.2% of the population with the onset of water column turnover.

At the offshore site, average number of parthenogenetic embryos per female ranged from zero to a maximum of 7.2 in early July, though some individual females had much higher values. Females carried as many as 24 embryos during summer 1999. Females carried more parthenogenetic embyros at the nearshore stations at Oakville and Grimsby than at the offshore station in June (Table 2). In the Caspian Sea, average fecundity of parthenogenetic females was 13, while for another species, *Cercopagis micronyx*, it was reported as 20 embryos (Rivier 1998).

Offshore Seasonal Abundance

Average abundance for the 1999 study period (28 May to 28 October) was 281 individuals/m^3. *Cercopagis* was first observed at the offshore site on 10 June 1999 (Fig. 3) at a surface temperature of 16.7°C. This observation is consistent with those from the Caspian Sea, where *Cercopagis* appears between 17 to 19°C (Rivier 1998). However, this was not the first sighting in Lake Ontario in 1999.

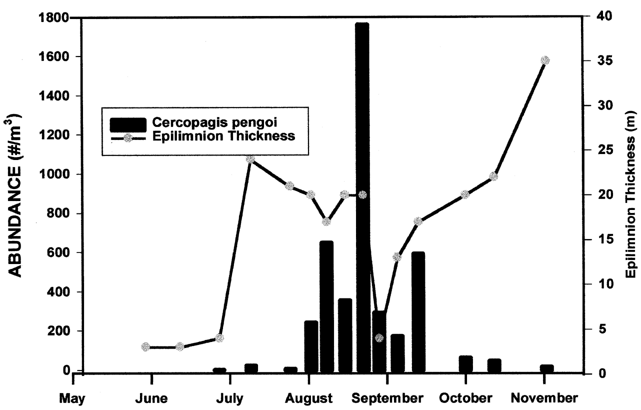

FIG. 3. Seasonal abundance of **Cercopagis pengoi** *and epilimnion thickness in Lake Ontario. Destratification began in mid-October.*

Cercopagis was observed in the nearshore of Lake Ontario near Sandy Pond on 20 May 1999 at 12.6°C. *Cercopagis* tended to appear in vertical tows earlier at nearshore sites (Sandy Pond and Chaumont Bay) in eastern Lake Ontario than other habitats.

Cercopagis abundance in offshore water remained low (less than 30 individuals/m^3) until late July, whereupon it increased rapidly and reached a peak of 1,759 individuals/m^3 on 19 August 1999 (Fig. 3). Densities of *Cercopagis* of up to 1,000/m^3 have also been observed in invaded habitats in eastern Europe (reviewed in Krylov *et al.* 1999). In the Dnieper-Bug tidal estuary, average densities range from 125 to 8,000/m^3 (Markovskii 1954), but may reach as high as 26,000/m^3 (Polishchuk and Grigoriev 1989).

Abundance in Lake Ontario declined by 83.4% the week following the population maximum. This decline was associated with upwelling of cold water and a decrease in the thickness of the epilimnion from 20 to 4 m (Fig. 3). Two weeks later, abundance rebounded to 593 individuals/m^3, but declined to only 16/m^3 on the last sampling date in late September. The fate of the population during the upwelling event is not clear, although it seems likely that animals were swept offshore considering the species' limited swimming ability. Upwelling-induced population declines were also observed along the north side of the lake during 1998 (J. Hoyle and H. MacIsaac, Ontario Ministry of Natural Resources, Glenora, ON, personal observation). In general, *Cercopagis* abundance did not correlate significantly with epilimnetic temperature or chlorophyll in 1999.

The abundance of age 1+ alewives during 1998 was the lowest in 20 years. However in 1999, the abundance index of age 1 alewife was the highest recorded since 1978 (R. O'Gorman, U.S. Fish and Wildlife, Cape Vincent, NY, personal communication). Thus, the planktivore population had relatively low and very high predation potentials during 1998 and 1999, respectively. Yearling alewife are expected to consume *Cercopagis*. A structurally and functionally similar species, *Bythotrephes*, is believed to remain at low densities in Lake Ontario owing to high alewife predation pressure (Mills *et al.* 1992). The high abundance of *Cercopagis* in the presence of large numbers of planktivorous fish is puzzling. The closely related Baltic herring (*Clupea harengus membras*) readily consumes *Cercopagis* in the Gulf of Finland (Ojaveer and Lumberg 1995), and preliminary analysis of Lake Ontario alewife stomachs indicates consumption of *Cercopagis* (Mills, personal observation). Several non-exclusive explanations may explain the high *Cercopagis* densities despite fish predation pressure. First, total alewife abundance and predation pressure may still be relatively low, despite the number of yearling fish during 1999. Second, the long, spined caudal process of *Cercopagis* may inhibit *Cercopagis* consumption by young-of-the-year (YOY) alewife. Ojaveer and Lumberg (1995) reported that YOY Baltic herring consumed copepod nauplii rather than *Cercopagis*, which were more abundant. Moreover, Barnhisel and Harvey (1995) demonstrated that *Bythotrephes*' caudal process is an effective deterrent to predation by YOY fish. *Bythotrephes* has a more robust caudal appendage than *Cercopagis*, though this structure may deter fish planktivory for the latter nevertheless. Third, high fecundity of *Cercopagis* may allow population growth to outpace consumption by alewife. Fourth, *Cercopagis* may be spatially isolated from planktivorous alewife and smelt when potential predation intensity is highest. Coulas *et al.* (1998) suggested that spatial segregation permitted coexistence of *Bythotrephes* with planktivorous lake herring (*Coregonus artedi*) in Harp Lake, Ontario. Although *Cercopagis* may be spatially separated from smelt during summer, alewife and *Cercopagis* both occupy the epilimnion during the time period (Johannsson and O'Gorman 1991; Johannsson, Sprules and Rudstam, personal observation). Consequently, it seems unlikely that *Cercopagis* has a significant spatial refuge from the major planktivore in Lake Ontario.

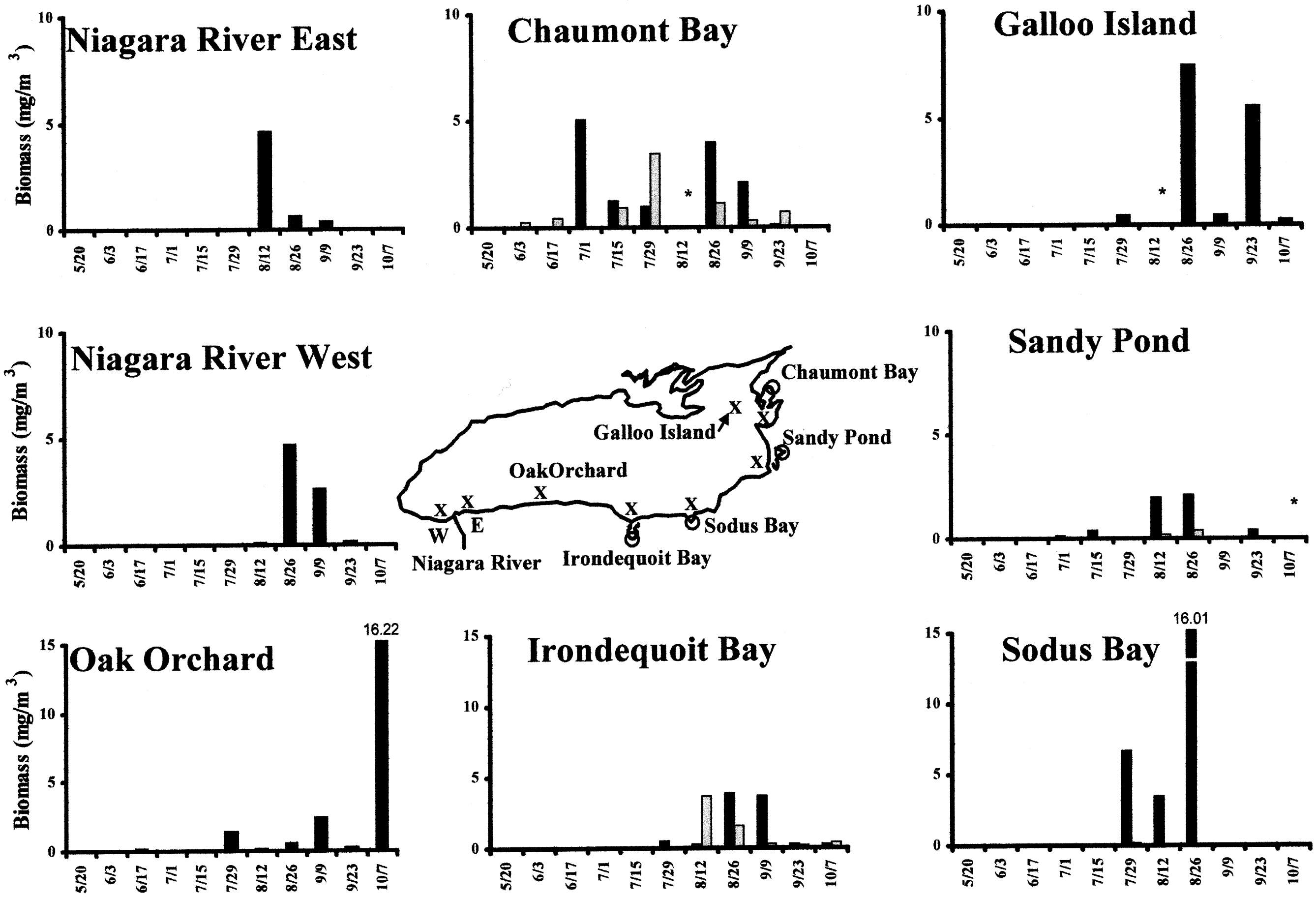

FIG. 4. Biomass of **Cercopagis pengoi** *at seven nearshore (X) and four embayment sites (O) in Lake Ontario during late May to early October, 1999. Solids black bars represent nearshore and gray bars reflect embayment habitats. Stars indicate missing data.*

Spatial and Temporal Patterns Lakewide

A maximum *Cercopagis* density of 2,334 individuals/m^3 was observed at Sodus Bay at the nearshore site on 23 August 1999 (Fig. 4). For all other sites and habitats, densities were less than 1,000 individuals/m^3 although densities of 1,183 (Galloo Island), 745 (Galloo Island), and 2,286 (Oak Orchard) individuals/m^3 were observed on 25 August, 29 September, and 7 October, respectively. May to early October densities of *Cercopagis* were highly variable and there was no significant difference at nearshore compared to embayment sites (Paired t-test, n = 10, p = 0.095). Similarly, a comparison of *Cercopagis* density at offshore and nearshore sites from 9–13 August indicated no significant difference between these habitats (ANOVA, n = 23, p = 0.32).

Cercopagis tended to appear sooner (early June) in eastern Lake Ontario (Chaumont Bay, Galloo Island, and Sandy Pond) than in western habitats along the south shore, where it generally appeared in late July and early August (Fig. 4). May through October maximum biomass in nearshore habitats was observed at Sodus Bay (16 mg/m^3) while the highest biomass in embayments was observed in Irondequoit Bay (3.7 mg/m^3).

Lakewide *Cercopagis* biomass was highly variable during August; 23 percent of all sites from all habitats had biomass levels that exceeded 6 mg/m^3 (Fig. 5). The lowest biomass during August was observed at nearshore and embayment sites; 20% of the offshore sites had biomass values between 7.0 and 9.9 mg/m^3. At the offshore sampling site north of Hamlin Beach State Park (Fig. 1), epilimnetic *Cercopagis* biomass reached 34.4 mg/m^3 on 19 August. A synoptic lake-wide comparison of the off-

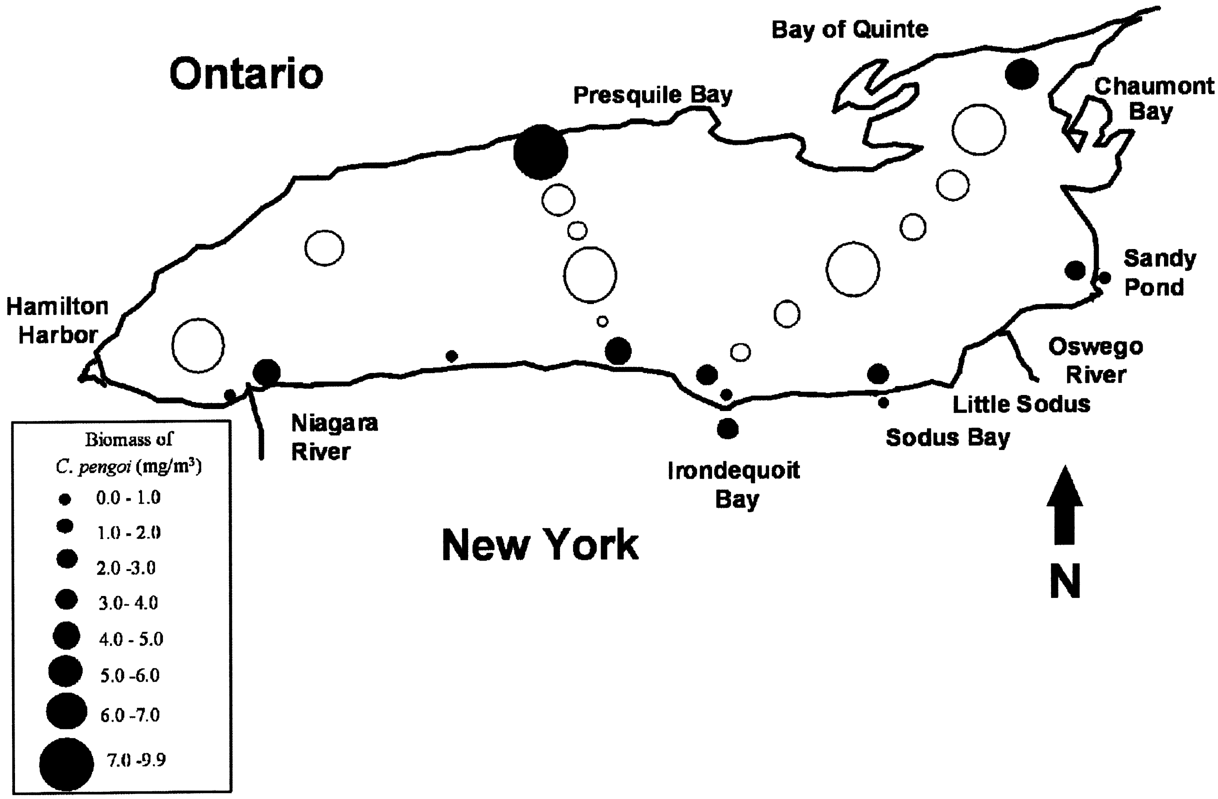

FIG. 5. **Cercopagis pengoi** ***biomass in Lake Ontario at offshore (open circles), nearshore (closed circle) habitats on 9–13 August 1999.***

shore and nearshore habitats shown in Figure 5 during 9 to 13 August indicated that *Cercopagis* biomass was significantly higher in the offshore (ANOVA, n = 23, p = 0.014).

Mean body size of *Cercopagis* tended to be higher in the offshore than in nearshore and embayment habitats in early to mid-August. Comparison of mean body size of *Cercopagis* between offshore and nearshore habitats during the 9 to 13 August period indicated that offshore organisms were significantly larger (ANOVA, n = 23, p = 0.003). Similarly, mean body lengths weighted by density for all sites and dates were lower at nearshore (1.16 mm) and embayment (1.19 mm) sites as compared to the offshore site north of Hamlin Beach State Park (1.32 mm).

Food Web

In the Baltic Sea, the entire planktivore food web was impacted by invasion of *Cercopagis pengoi. Cercopagis* constituted over 98% and 66% of the stomach contents of herring (*Clupea harengus*) and smelt (*Osmerus eperlamus*), respectively (Ojaveer and Lumberg 1995, Ojaveer 1997). Functionally similar species of planktivorous alewives and smelt (*Osmerus mordax*) inhabit Lake Ontario. The relatively high average abundance (281 individuals/m^3) of *Cercopagis* in the epilimnion of Lake Ontario suggests that this species may have a major predatory impact on zooplankton abundance and composition. Unfortunately, data demonstrating predation rate of *Cercopagis* on other zooplankton are lacking.

Even though average *Cercopagis* abundance is high (281 individuals/m^3) compared to the average abundance of *Mysis* (~4 individuals/m^3) and *Leptodora* (7 to 26 individuals/m^3), average *Cercopagis* biomass is similar to the lake biomass of these predators (Table 3). *Cercopagis* has a relatively large total length owing to its long caudal process. Body length, however, is similar to that of *Daphnia* and thus individual mass is low compared to individual *Leptodora* or *Mysis*. Consequently, *Cercopagis*'s effect on the Lake Ontario food web may not be any greater than *Mysis* or *Leptodora*

TABLE 3. Average abundance and biomass of **Mysis relicta, Leptodora kindtii, Bythotrephes** *and* **Cercopagis pengoi** *in Lake Ontario. The average represents the May-November period with the exception of* **Bythotrephes** *which is an annual average. All data are from the same site and were collected with a 571 µm mesh net from a depth of 100 m (***Mysis, Leptodora, Bythotrephes***) and* **Cercopagis** *(20 m) with the exception of Johannsson's (1992) data which were collected from a depth of 125 m with a 250 µm net at a different location on Lake Ontario. ND = No data.*

	Year	Average Abundance (ind/m^3)	Average Biomass (mg/m^3)	Maximum Abundance (ind/m^3)
Mysis relicta[1]	1984	4.0	7.2	9.2
Mysis relicta [2]	1986	4.1	ND	6.2
Bythotrephes[3] *cederstroemi*	1987	13.4	0.23	102
Leptodora[4] *kindtii*	1984	7.3	2.1	240
Leptodora[4] *kindtii*	1987	25.6	7.8	175
Cercopagis[5] *pengoi*	1999	281.4	5.2	1,759

[1]Shea and Makarewicz (1989)
[2] Johannsson (1992)
[3] Makarewicz and Jones (1990)
[4] Koapaha (1989)
[5] This study

over the course of an entire year. During the period of maximum abundance, when *Cercopagis* biomass reaches 34.3 mg/m^3, its impact on zooplankton populations is likely to be great. Moreover, *Cercopagis* is present in the epilimnion through the day and night, whereas *Mysis* is generally confined to hypolimnetic waters.

Selective feeding by *Cercopagis* on small zooplankton could adversely affect planktivorous fish by reducing abundance of their prey and have other unknown effects on the zooplankton/phytoplankton link. Because microzooplankton account for 70 to 90% of the consumption of phytoplankton in Lake Ontario (Lampman and Makarewicz 1999), its suppression by *Cercopagis* could indirectly result in an increase in abundance of phytoplankton. In summary, however, it is not yet clear whether *Cercopagis* will be an energetic link or sink.

Mechanisms of Dispersal

The mechanism of global dispersal of *Cercopagis* is most likely by ballast contamination (MacIsaac *et al.* 1999, Cristescu *et al.* 2001). The lack of genetic variability in the Lake Ontario *Cercopagis* population suggests that this population was founded by a small number of colonists. Local dispersal mechanisms potentially include transport by waterfowl, small boat traffic, or by accidental transport on contaminated fishing and sampling gear. Zooplankton may be dispersed either in plumage or through the digestive tract of waterfowl (see Maguire 1963, Charalambidou *et al.* 2000). Preliminary trials using dead waterfowl on Lake Ontario revealed that *Cercopagis* fouled the plumage of experimental lesser scaup (*Aythya affinis*), a diving duck (Matkovich, pers. observ.). Ducks could facilitate short-distance invasion of *Cercopagis* to adjacent basins. Five Finger Lakes of New York State were invaded by *Cercopagis* during 1999 (Table 4). These invasions may have been the result of either waterfowl or human-assisted dispersal. For example, it is possible that waterfowl could move *Cercopagis* females with resting eggs from Lake Ontario south to the Finger Lakes, a distance of approximately 50 km. While this dispersal mechanism cannot be discounted, particularly during periods when *Cercopagis* is abundant in epilimnetic waters, this vector is likely far less important than dispersal facilitated by humans. Higher-risk, human vectors include accidental transfers by sport or commercial fishermen, recreational boaters, or researchers. Contaminated fishing equipment appears to be a

TABLE 4. Presence of **Cercopagis pengoi** *in the Finger Lakes and Cross Lake of New York State and Lake Michigan during the summer of 1999. Conesus Lake was sampled biweekly. Lake Michigan, Cross Lake, and Canandaigua Lake were not sampled quantitatively but* **Cercopagis** *were observed on fishing line (Pearsall, Kelly, Makarewicz; pers. observ.). NO = Not observed.*

Lake	Date	Individuals/m^3
Seneca Lake	18 Aug	31.5
Cayuga Lake	25 Aug	11.6
Otisco Lake	24 Aug	29
Canandaigua Lake	17 Aug	Present
Skaneateles Lake	16 Aug	NO
Owasco Lake	25 Aug	2.1
Conesus Lake	April- Oct (biweekly)	NO
Cross Lake	4 Sep	Present
Lake Michigan		
Grand Traverse Bay	9 Sep	Present

potentially potent vector, as individual fishing lines used on contaminated lakes may accumulate hundreds of *Cercopagis* individuals (MacIsaac, pers. observ.). Moreover, commercial gill nets examined on the Black Sea during August 1999 were fouled with a film of *Cercopagis*, easily representing millions of individual organisms (MacIsaac and Grigorovich, pers. observ.). Because contaminated gill nets could facilitate invasions, separate sets of commercial or research nets should be used on invaded and uninvaded lakes.

It is not clear which, if any, of the aforementioned natural and human-assisted dispersal vectors caused the invasions of systems in the Finger Lakes. By contrast, invasion of Lake Michigan during 1999 almost certainly resulted from movement of contaminated Lake Ontario ballast water by a commercial vessel. Ships that discharge cargo at a Lake Ontario port will often load lake water as ballast prior to up-bound movement on the Great Lakes. This water is subsequently discharged at the terminal port-of-call and replaced with cargo for the out-bound voyage. This “cross-transfer” of ballast water has been identified as a potential source of nonindigenous species (Weathers and Reeves 1996). All of the dispersal vectors proposed for the Finger Lakes would be far less likely to account for invasion of Lake Michigan since both human and waterfowl “traffic” between Lake Ontario and Lake Michigan is much reduced.

Expansion of Range

Cercopagis appears to have carved a niche in the epilimnion of Lake Ontario where a potential predator, the smelt, is not prevalent in the summer, and where consumption by abundant planktivorous YOY alewife may be inhibited by the zooplankter’s caudal process. Currently, little is known about *Cercopagis’* impact on Lake Ontario or other invaded ecosystems. In the Great Lakes, exotic species have impacted ecosystem structure and function in ways we are just beginning to understand. For example, the Ponto-Caspian bivalve molluscs *Dreissena polymorpha* and *D. bugensis* have altered the food web (Makarewicz *et al.* 1999b) of western Lake Erie from a pelagic community to a benthic/pelagic system more comparable to the nearshore marine environment and have altered water chemistry of the western and central basin pelagic regions (Makarewicz *et al.* 2000). With the insertion of an abundant, predaceous cladoceran into the middle of the Lake Ontario food web, reductions would be expected in small-bodied cladoceran taxa (Lehman 1991, Yan and Pawson 1997) and, possibly, an increase in levels of hydrophobic organic compounds in piscivores because of the additional link in the food chain (Kiriluk *et al.* 1995). The potential of this organism to spread quickly and far is large. As MacIsaac *et al.* (1999) point out, asexual reproduction, high fecundity and production of resting eggs and a “sticky” caudal process promote rapid population growth, viability during unfavorable periods, and rapid dispersal.

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REFERENCES

Barnhisel, D.R., and Harvey, H.A. 1995. Size-specific fish avoidance of the spined crustacean *Bythotrephes*: Field support for laboratory predictions. *Can. J. Fish. Aquat. Sci*. 52:768–775.

Charalambidou, I.C., Ketelaars, H.A.M., and Santa-Maria, L. 2000. *Bythotrephes longimanus* (Crustacea: Onychopoda) resting eggs survive duck gut passage. *Hydrobiologia* (in press).

Cohen, A.N., and Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558.

Colbourne, J.K., Crease, T.J., Weider, L.J., Hebert, P.D.N., Hobaek, A., and Dufresne, F. 1998. Phylogenetics and evolution of a circumarctic species complex (Cladocera: *Daphnia pulex*). *Biol. J. Linnean Soc*. 65:347–365.

Coulas, R.A., MacIsaac, H.J., and Dunlop, W. 1998. Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedi*) in Harp Lake, Ontario. *Freshwater Biol*. 40:343–355.

Cristescu, M., Hebert, P.D.N., Witt, J., MacIsaac, H.J., and Grigorovich, I.A. 2001. An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. *Limnol. Oceanogr*. 46:224–229.

Giguere, L.A., St-Pierre, J.R., Bernier, B., Vezina, A., and Rondeau, J.G. 1989. Can we estimate the true weight of zooplankton samples after chemical preservation? *Can. J. Fish. Aquat. Sci.* 46:522–527.

Gilbert, D. 1992. SeqApp version 1.9a. A multiple sequence editor for Macintosh computers. INTERNET: http//fly.bio.indiana.edu.

Grigorovich, I.A., MacIsaac, H.J., Rivier, I.K., Aladin, N.V., and Panov, V.E. 2000. Comparative biology of the predatory cladoceran *Cercopagis pengoi* from Lake Ontario, Baltic Sea and the Caspian Lake. *Arch. Hydrobiol*. 149:23–50.

Johannsson, O. 1992. Life history and productivity of *Mysis relicta* in Lake Ontario. *J. Great Lakes Res*. 18:154–168.

_____, and O'Gorman, R. 1991. Role of predation, food and temperature in structuring epilimnetic zooplankton populations in Lake Ontario: 1981–1986. *Trans. Am. Fish. Soc.* 120:192–209.

Kiriluk, R.M., Servos, M.R., Whittle, M,D., Cabana, G, and Rasmussen, J.B. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. *Can. J. Fish. Aquat. Sci.* 52:2660–2674.

Koapha, J. 1989. *Leptodora kindtii*: Seasonal population abundance and food web interaction in Lake Ontario. M.S. thesis, Drake Memorial Library, SUNY Brockport, Brockport, NY.

Krylov, P.I., Bychenkov, D.E., Panov, V.E., Rodionova, N.V., and Telesh, I.V. 1999. Distribution and seasonal dynamics of the Ponto-Caspian invader *Cercopagis pengoi* (Crustacea, Cladocera) in the Neva Estuary (Gulf of Finland). *Hydrobiologia* 393:227–232.

Lampman, G.G., and Makarewicz, J.C. 1999. The phytoplankton zooplankton link in the Lake Ontario food web. *J. Great Lakes Res*. 25:239–249.

Lehman, J.T. 1991. Causes and consequences of cladoceran dynamics in Lake Michigan: The phytoplankton zooplankton link. *J. Great Lakes Res*. 17:437–445.

MacIsaac, H.J., Grigorovich, I.A., Hoyle, J.A., Yan, N.D., and Panov, V.E. 1999. Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran *Cercopagis pengoi*. *Can. J. Fish. Aquat. Sci*. 56:1–5.

Maguire, Jr., B. 1963. The passive dispersal of small organisms and their colonization of isolated bodies of water. *Ecol. Monogr.* 33:161–185.

Makarewicz, J.C., and Jones, H.D. 1990. Occurrence of *Bythotrephes cederstroemi* in Lake Ontario offshore waters. *J. Great Lakes Res*. 16:143–147.

_____, Lewis, T.W., and Halbritter, H. 1999a. *Cercopagis*: A new exotic zooplankter to Lake Ontario. *Dreissena* 10:5–7.

_____, Lewis, T.W., and Bertram, P. 1999b. Phytoplankton composition and biomass in the offshore waters of Lake Erie: pre- and post-*Dreissena* introduction (1983–1993). *J. Great Lakes Res*. 25:135–148.

_____, Lewis, T.W., and Bertram, P. 2000. Changes in Lake Erie surface water quality: Pre- and post-*Dreissena* introduction. *J. Great Lakes Res.* 26:82–93.

Markovskii, Y.M. 1954. Invertebrate fauna of the lower reaches of rivers of the Ukrainian SSR, condition of its existence and ways of use. 2. The Dnieper-Bug liman. Izdatelstvo Akad. Nauk Ukrainskoi SSR, Kiev, USSR (in Russian).

Mills, E.L., O'Gorman, R., DeGisi, J., Heberger, R.F., and House, R.A. 1992. Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after establishment of *Bythotrephes cederstroemi*. *Can. J. Fish. Aquat. Sci*. 49:2009–2019.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *J. Great Lakes Res*. 19(1):1–54.

Ojaveer, H. 1997. *Cercopagis pengoi* In Baltic Sea research network on ecology of marine invasions and introductions, INTERNET: http//www.ku.lt/nemo/mainmemo.htm.

_____, and Lumberg, A. 1995. On the role of *Cercopagis pengoi* (Ostroumov) in Parnu Bay and the NE part of the Gulf of Riga ecosystem. *Proc. Estonian Acad. Sci. Ecol*. 5 20–25.

Owens, R.W., O'Gorman, R., Eckert, T.H., and Lantry, B.F. In press. The offshore fish community of southern Lake Ontario 1972–1998. In *State of Lake Ontario*, Ed. M. Munawar. Leiden, The Netherlands: Backhuys Publishers.

Polishchuk, V.S., and Grigoriev, B.F. 1989. Zooplankton. In *The Dnieper-Bug estuarine Ecosystem,* Ed. Y.P. Zaitsev, pp. 145–159. Naukova dumka Publishers, Kiev, Ukrainian SSR. (in Russian).

Ricciardi, A., and MacIsaac, H.J. 2000. Recent mass invasions of the North American Great Lakes by Ponto-Caspian species. *Trends Ecol. Evol.* 15:62–65.

Rivier, I.K. 1998. *The Predatory Cladocera (Onychopoda: Podonidae, Polyphemidae, Cercopagidae) and Leptodorida of the World*. Leiden, The Netherlands: Blackhuys Publishing.

Schwenk, K. 1996. *Evolutionary genetics of* Daphnia *species complex: hybridism in syntopy*. Publication 2231, Netherlands Institute of Ecology, Center for Limnology, Nieuwersluis, The Netherlands.

Shea, M., and Makarewicz, J.C. 1989. Production, biomass, and trophic interactions of *Mysis relicta* in Lake Ontario. *J. Great Lakes Res*. 15:223–232.

Shurin, J. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086.

———, Havel, J.E., Leibold, M.A., and Pinel-Alloul, B. 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* 81:3062–3073.

Simm, M., and Ojaveer, H. 1999. Occurrence of different morphological forms of *Cercopagis* in the Baltic Sea. *Proc. Estonian Acad. Sci. Biol. Ecol.* 48:169–172.

Weathers, K., and Reeves, E. 1996. The defense of the Great Lakes against the invasion of nonindigenous species in ballast water. *Marine Technology* 33: 92–100.

Wetzel, R.G., and Likens, G.E. 1994. *Limnological Analysis*. New York: Springer Verlag.

Yan, N.D., and Pawson, T.W. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. *Freshwat. Biol*. 37:101–117.

Yurista, P. M. 1992. Embryonic and postembryonic development in *Bythotrephes cederstroemi*. *Can. J. Fish. Aquat. Sci*. 49:1118–1125.

Zozulya, S. S. 1977. Peculiarities of the first *Bythotrephes* generation hatched from the latent eggs. *Inform. Byul. Biol. Vnutr. Vod.* 33:34–38. [in Russian].

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