Distribution and Population Characteristics of *Cercopagis pengoi* in Lake Ontario

Henn Ojaveer[1,*], Linda A. Kuhns[2], Richard P. Barbiero[3], and Marc L. Tuchman[4]

[1]*Estonian Marine Institute*
Viljandi Rd 18^b
11216 Tallinn, Estonia

[2]*Grace Analytical Lab*
536 S. Clark Street 10th Floor
Chicago, Illinois 60605

[3]*DynCorp I&ET Inc.*
6101 Stevenson Avenue
Alexandria, Virginia 22304

[4]*Great Lakes National Program Office*
United States Environmental Protection Agency
77 W. Jackson Boulevard
Chicago, Illinois 60604

ABSTRACT. *The spatial and vertical distribution of a recent exotic species, the predatory cladoceran* Cercopagis pengoi, *was studied in Lake Ontario in September 1999. Only typical forms of the species* C. pengoi, *characterized by a relatively long tail with an S-bend and claws with straight or backwardly bent tips, were found. Structure of the* Cercopagis *population was rather uniform over the lake, consisting mainly (over 90%) of parthenogenetic females. Median epilimnetic abundance and biomass was 295/m³ (max. = 2,544/m³) and 13.4 mg DW/m³ (max. = 113.3 mg DW/m³), respectively.* Cercopagis *contributed a median of 15.8%, and at maximum 73.8%, of the total crustacean zooplanktonic biomass (exclusive of nauplii). Abundances showed a significant positive relationship with distance from shore (r² = 0.34, p < 0.01), but distribution was independent of the depth and temperature of the epilimnion.* Cercopagis *did not exhibit any diurnal vertical migration patterns: over 90% of the individuals stayed either in the epilimnion or within the metalimnion during the day and night. The proportion of individuals, both live specimens and carcasses of dead individuals, in cooler layers was negligible (< 3%). The following weight (W) – body length (L) relationship was developed during the study: ln(W) = 2.98*ln(L) – 6.42 (r² = 0.85, p < 0.001).*

INDEX WORDS: *Cercopagis pengoi, cladoceran, crustacean zooplankton, Lake Ontario, non-indigenous species.*

INTRODUCTION

During the last decades, the modification of aquatic ecosystems by human activities has increased considerably, as evidenced, for example, by a rise in unintended releases of non-indigenous species. If successfully established, these species can effect substantial changes in the structure and functioning of aquatic ecosystems and may lead to severe ecological, as well as economic, consequences (Mills *et al.* 1993, Niermann *et al.* 1994, Carlton 1999, Ketelaars *et al.* 1999, Rutherford *et al.* 1999, Nalepa *et al.* 1999).

Mills *et al.* (1993) reported the establishment of 139 exotic species in the Great Lakes since the 1800s, most of those species being native to Eurasia (55%). Of these, however, they claimed that a relatively small number—only 9%—had a substantial

---
[*]Corresponding author: E-mail: henn@sea.ee

influence upon the Great Lakes ecosystem. Most of the recent important invaders to the Great Lakes, such as *Dreissena* spp., *Neogobius melanostomus*, *Gymnocephalus cernuus*, and *Echinogammarus ischnus*, are native to the Ponto-Caspian basin (Ricciardi and Rasmussen 1998). These authors have identified 17 additional Ponto-Caspian invertebrates that have recent invasion histories and the likely potential to be introduced to the Great Lakes.

The latest exotic species to invade the Great Lakes region, first observed in Lake Ontario in 1998, is the predatory cladoceran *Cercopagis pengoi* (MacIsaac *et al.* 1999). This species had previously invaded several sub-basins of the NE part of the Baltic Sea (Ojaveer and Lumberg 1995, Krylov *et al.* 1999) and expanded its distribution area toward the south and north in 1999 (Zmudzinski 1999; E. Leppäkoski, Åbo Akademi University, Turku, Finland, pers. comm.). *C. pengoi* has caused substantial changes in the diet of several fish species in the Baltic and by fouling fishing gear has caused direct economic loss for fishers.

Although substantial ecological impacts in the Great Lakes due to *C. pengoi* have not been documented as of yet, ecosystem effects associated with another recent invader similar to *C. pengoi*, the predatory cladoceran *Bythotrephes cederstroemi*, have been seen in the Great Lakes. These include, among others, disappearance or dramatic decline in the abundance of small-sized crustacean zooplankton species and changes in zooplankton community dominance (Yan and Pawson 1997, Lehman and Caceres 1993), alterations in the structuring factor of the indigenous zooplankton community (Lehman 1991), and changes in the diet of commercial fish species (Mills *et al.* 1992).

In this paper, the primary goal was to assess the distribution pattern, and characteristics and structure of the newly-established *C. pengoi* population in Lake Ontario. In addition, an individual weight-body length conversion formula for *C. pengoi* was developed for calculating population biomass.

METHODS

Samples were collected on board the U.S. Environmental Protection Agency (U.S. EPA) R/V *Lake Guardian* in Lake Ontario during 14 to 19 September 1999. Vertical tows through the epilimnion layer, the depth of which was determined from temperature profiles taken using a Seabird STE-911 CTD, were taken with a metered 153-µm mesh net at a total of 24 stations (Fig. 1). In order to study possible diur-
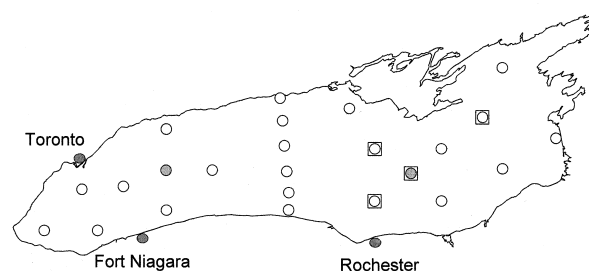

FIG. 1.   Location of sampling stations in Lake Ontario. Filled circles denote stations of migration study of C. pengoi*; stations where* C. pengoi *was found in 1998 are indicated by squares.*

nal vertical migration (DVM) of *C. pengoi*, zooplankton tows were performed at fixed depth intervals (0–20, 20–40, 40–60, 60–80 and 80–100 m) by means of a closing net. DVM samples were taken at 6 a.m., 12 p.m., 6 p.m., and 12 a.m. at two offshore stations (Fig. 1). After collection, samples were narcotized with soda water and preserved with sucrose formalin solution (Haney and Hall 1973). All individuals of *C. pengoi* were removed from each sample under a dissecting microscope and enumerated. To enumerate the rest of the crustacean community (excluding nauplii), samples were split with a Folsom plankton splitter and four stratified aliquots examined per sample. For biomass calculations, length measurements were made on the first twenty individuals encountered of each species per sample, including *C. pengoi*, and biomass computed using length-weight relationships found in the literature. In the case of *C. pengoi*, the relationship developed in this study was used. Body length of *C. pengoi* was measured from the tip of the head to the tip of the third articular spine. The laboratory analyses were performed 1 to 4 months after field sampling.

Comparisons were made of the body size and fecundity of sexual females between 1998 and 1999, using samples generated from the U.S. EPA Great Lakes National Program Office (GLNPO) summer survey in 1998. For these comparisons, individuals were measured from stations at which *C. pengoi* was found in 1998. In that year, *C. pengoi* was found at four stations in the eastern basin of the lake (Fig. 1; see also Barbiero *et al.* in press). Zooplankton tows from Lake Ontario were taken between 5 to 7 August in 1998, and were made with both a 64 µm mesh net to a depth of 20 m, and with a 153 µm mesh net to the shallower of 100 m or 2 meters from the bottom at each station. A Mann-Whitney Rank

Sum test failed to find significant differences in body length between individuals collected using the different mesh sizes (α = 0.05), so these data were pooled in subsequent analyses. All measurements were done by the same individual (HO). To compare body lengths of individuals of different instars collected in 1998 and 1999, the nonparametric Mann-Whitney Rank Sum Test was used. All statistical tests were conducted using Sigmastat 2.0.

To develop a body length-dry weight relationship, 233 *C. pengoi* individuals were sorted according to body lengths (min. = 0.95 mm, max. = 2.55 mm). Individuals were dried for 48 hours at 60°C and held over silica gel for 2 hours prior to weighing. Up to 8 specimens of similar body lengths were grouped together. Dry mass was determined using a Cahn C-33 microbalance with a precision of 1 µg. Both body length and dry weight were ln-transformed to stabilize variance, and the relationship between them determined using least squares regression. It is understood that some shrinkage typically occurs after preservation with formaldehyde (Kapiris *et al.* 1997, Yan and Pawson 1997). The length-weight relationship developed here, however, was specifically intended to be used with preserved individuals. It should be recognized, though, that some underestimation is possible due to loss of mass upon preservation (Campbell and Chow-Fraser 1995, and references therein).

RESULTS

The *Cercopagis* community of Lake Ontario in September 1999 was represented by a typical morphological form of the species *Cercopagis pengoi*, characterized by possession of a relatively long tail with characteristic S-bend and claws with straight or backwardly bent tips. The tail length to body length ratio averaged 4.68 (SD = 0.56, n = 100). The structure of the *C. pengoi* community was uniform over the lake, with parthenogenetic females contributing over 95% of all individuals. Sexual females and males together constituted less than 5% of the population.

Medians of epilimnetic abundance and biomass of *C. pengoi* were 295/m^3 (interquartile range = 541/m^3, max. = 2,544/m^3, n = 24) and 13.4 mg DW/m^3 (interquartile range = 25.0 mg DW/m^3, max. = 113.3 mg DW/m^3, n = 24), respectively. The median percent contribution of *C. pengoi* to the zooplankton community was 15.8% on a dry weight basis (max. = 73.4%) and 0.6% on an abundance basis (max. = 5.7%) (Fig. 2). Abundance and bio-
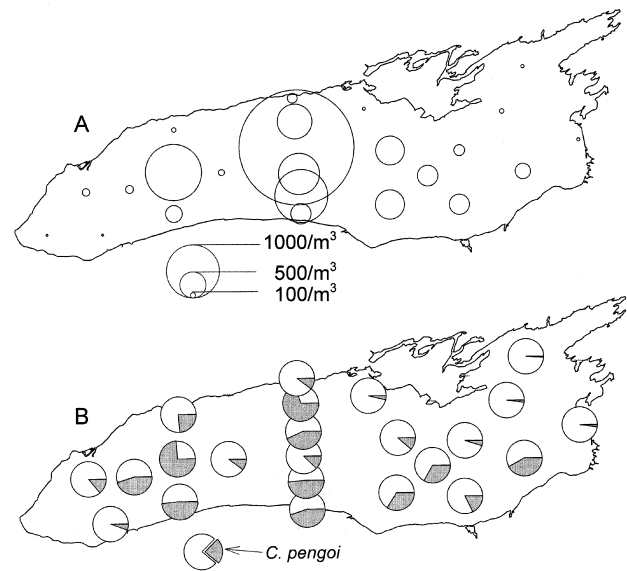

FIG. 2.   A.) *Abundance of* C. pengoi *(individuals/m^3); and B.) Percent contribution of* C. pengoi *to crustacean zooplanktonic biomass (excluding nauplii) in the epilimnion of Lake Ontario, September, 1999.*

mass of *C. pengoi* tended to be higher in the central region of the lake than in coastal areas; least squares regression revealed a significant relationship between abundance and distance from shore (r^2 = 0.34, p = 0.0015; Fig. 3). However, a significant relationship was not observed between percent contribution of *C. pengoi* to the total zooplankton
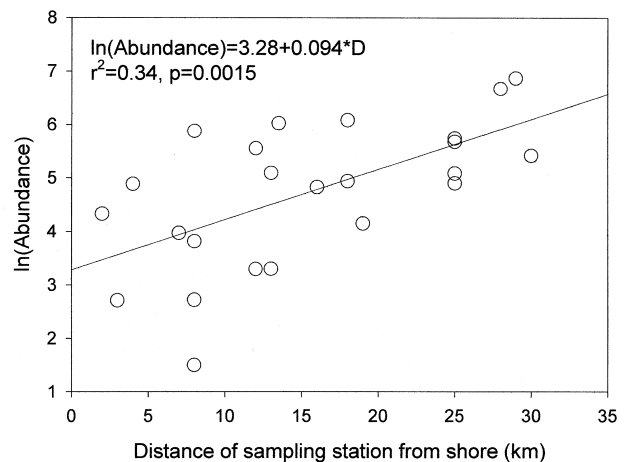

FIG. 3.   *Relationship between ln-transformed epilimnetic abundance of* C. pengoi *and distance of sampling station from shore (km) in Lake Ontario.*
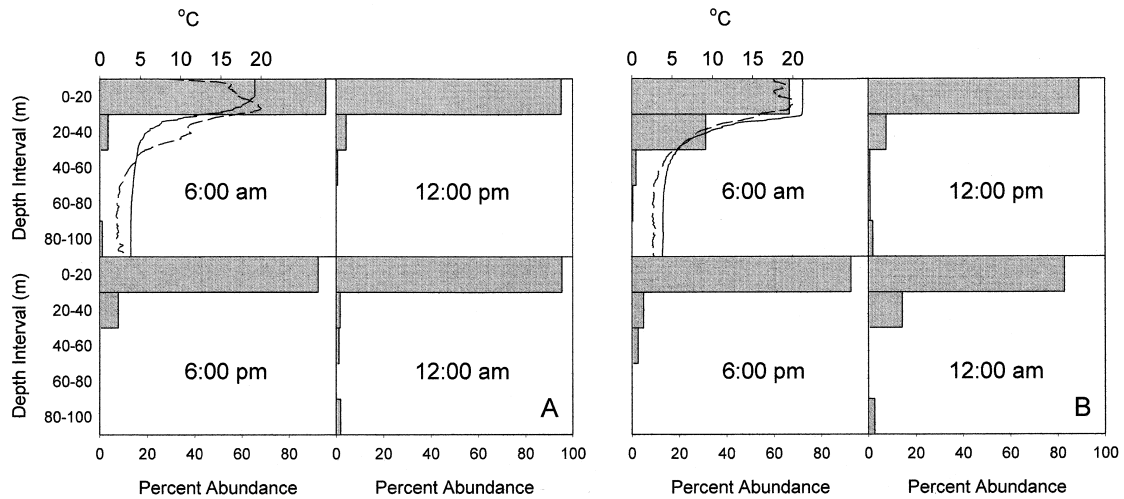
FIG. 4. *Depth distribution of* C. **pengoi** *during migration study at A.) Western station; and B.) Eastern station. Lines denote: (—) temperature, °C; and (---)* in vivo *chlorophyll (relative units).*

biomass and distance from shore ($\alpha = 0.05$). Similarly, significant relationships were not found between abundance and either depth or mean temperature of the epilimnion ($\alpha = 0.05$).

Vertical distribution of *C. pengoi* exhibited similar patterns at both stations of the migration study. The majority of individuals were found within the warm uppermost 20 m water layer during both day and night; no DVM was evident. However, relatively more individuals were distributed in the 20 to 40 m stratum at the eastern station than at the western station (Fig. 4). This difference could be explained in part by depth of the epilimnion, which was substantially thicker at the eastern (20 m) than the western (12 m) station. However, it also appears that *C. pengoi* can occur rather abundantly within the metalimnion. At both stations, less than 3% of the *C. pengoi* population occurred in deeper (> 40m) water layers.

A relatively high proportion of *C. pengoi* individuals without any detectable body fluidum, including lack of a large pigmented eye, most likely representing individuals dead at the time of collection, was observed in deeper water layers—up to 100% of the total count within a depth interval. However, absolute densities remained at rather low levels, at most 7/m³, suggesting that sinking of dead *C. pengoi* to deeper water layers is probably not intense in Lake Ontario.

Comparisons of body lengths of females by instar between 1998 and 1999, using a Mann-Whitney

Rank Sum Test, showed statistically significant differences between years for instar three females, both sexual and parthenogenetic (P = <0.001 in both cases), while lengths of earlier instars were not significantly different ($\alpha = 0.05$; Fig. 5). The larger body size of sexual females in 1998 was accompanied by increased fecundity (usually 2 eggs in brood pouch), whereas only 4.9% of sexual females carried 2 eggs in 1999.
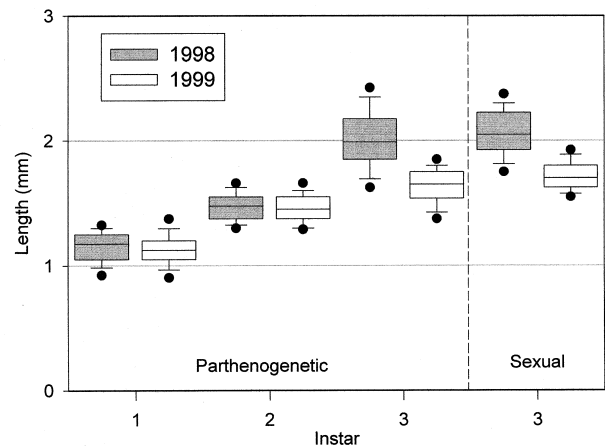

FIG. 5. *Comparison of body length (mm) of sexual and parthenogenetic females by instar in Lake Ontario in 1998 and 1999. Boxes denote 25th and 75th percentile, interior lines denote median, whiskers denote 10th and 90th percentiles, points indicate 5th and 95th percentiles.*
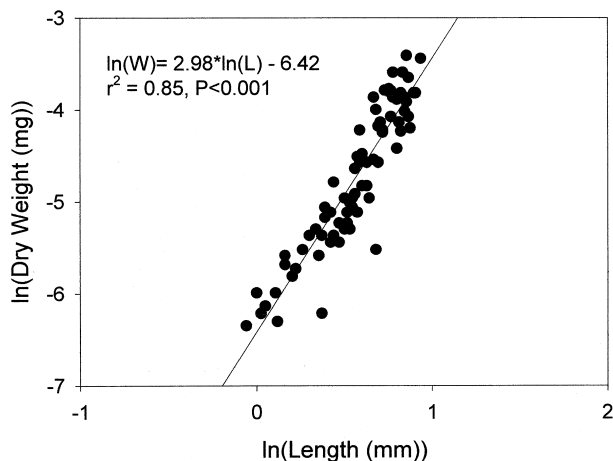
$$\ln(W)= 2.98 * \ln(L) - 6.42$$
$$r^2 = 0.85, P<0.001$$

FIG. 6.   Relationship between ln-transformed dry weight (W, mg) and body length (L, mm) for C. pengoi *in Lake Ontario.*

Dry weight of females of extreme body lengths (min. = 0.88 mm; max. = 2.58 mm, respectively) differed by 24.7 times. A regression formula for ln-transformed body length (L)—dry weight (W) relationship, developed during the study and used for *Cercopagis* biomass calculations, is given in Figure 6.

DISCUSSION

In the *Cercopagis* population of Lake Ontario in late summer only typical *C. pengoi* individuals were found, having a long tail spine with a characteristic S-bend and claws with straight or backwardly bent tips, a finding consistent with results from the Baltic Sea. In both water bodies, the occurrence of individuals with morphological features deviating from the typical *C. pengoi* was reported in spring and early summer. The most prominent difference from the typical *C. pengoi* form is the relatively short caudal process without an S-bend, and forwardly bent tips of the claws. According to Mordukhai-Boltovskoi and Rivier (1987), those are characteristic of *C. (Apagis) ossiani.* Simm and Ojaveer (1999) hypothesized that these atypical specimens probably represent the first parthenogenetic generation of the species *C. pengoi* hatched from resting eggs, and the morphology of subsequent generations are characteristic of typical representatives of *C. pengoi.* This suggestion is consistent with another recent study conducted by Makarewicz *et al.* (2001) who used mitochondrial DNA analyses to show that *C. ossiani*

and *C. pengoi* are morphologically distinctive forms of a single species.

The maximum population abundance of *C. pengoi* observed in this study ($2,544/m^3$) is substantially higher than has been observed in other invaded basins (maximum values frequently below $600/m^3$ with outstanding densities up to $1,800/m^3$: Krylov *et al.* 1999 and references therein, Uitto *et al.* 1999). In 1998, in the first year of identification in Lake Ontario, *C. pengoi* reached maximum densities of $322/m^3$ in coastal areas of the western part of the lake in late August (~5 km offshore between Oakville and Grimbsy, Ontario: MacIsaac *et al.* 1999) and $465/m^3$ in upper water layers (< 20 m) in open areas of the eastern part of the basin in the first week of August (Barbiero *et al.* in press). However, *C. pengoi* densities were probably substantially underestimated in that first study in comparison with those of this study, since samples were collected from the bottom to the surface (sampling depth < 27 m, MacIsaac *et al.* 1999), while *C. pengoi* inhabits mainly the warmer upper water layers. Thus, environmental conditions of Lake Ontario both in 1998 (western coastal areas) and 1999 (open basin) supported relatively high densities of *Cercopagis.* Also, the maximum proportion of *C. pengoi* in the zooplankton community of Lake Ontario (73%, dry wt. basis) was remarkably larger than those documented in the Baltic Sea. According to Ojaveer *et al.* (1998), during its population maximum *C. pengoi* made up about 25% of the total mesozooplankton (individuals 0.2 to 2.0 mm in length) biomass (wet wt.) in the Gulf of Riga. However, in that study body weight of *C. pengoi* was assumed to be equal to that of the smaller cladoceran *Podon*, and therefore was probably substantially underestimated. In 1998, *Cercopagis* population abundances remained at relatively low levels in the Baltic Sea. In that year, the species made up a maximum of 15% of the total zooplankton biomass in the Gulf of Riga (M. Simm, Estonian Marine Institute, Tallinn, Estonia, pers. comm.). Therefore, relatively larger scale and more pronounced ecosystem effects caused by the *C. pengoi*, initially on plankton communities, but eventually through food-web interactions and changes in energy transfer pathways of the ecosystem, would be expected to take place in Lake Ontario than in the Baltic Sea.

In 1998, there were clear differences in zooplankton community composition between sites in the eastern basin at which *C. pengoi* was found and sites in the western basin where it was not. *Bosmina longirostris* accounted for between 19 and 60% of the

non-nauplii crustaceans at the latter sites, while at sites supporting *C. pengoi* it accounted for between 0.2 and 3%. The dominant daphnid in the lake, *Daphnia retrocurva*, showed the opposite trend, being on average nearly twice as abundant at sites with *C. pengoi*. Other differences were noted between the two basins, such as a distinct decrease in cyclopoid copepodites in the east, and a shift in rotifer dominance from *Polyarthra vulgaris* in the west to *Ascomorpha ovalis* in the east (Barbiero *et al.* in press). It is unclear whether these differences in 1998 were due to impacts of *C. pengoi* on the zooplankton community. Populations of most zooplankton species have been shown to develop in the east and subsequently move west (Patalas 1969), so differences in distribution could have been due to differences in population timing.

In the Gulf of Riga (Baltic Sea), after the invasion of *C. pengoi*, the abundance level of its potential prey—*Bosmina coregoni maritima*—has been significantly lower than during the pre-invasion period. Densities of other native, small-sized cladocerans (*Evadne nordmanni* and *Pleopsis polyphemoides*) or nauplii of copepods did not exhibit any notable changes after the invasion (Ojaveer *et al.* 2000). Information on the feeding habits of *C. pengoi* would be necessary to relate the above documented changes in zooplankton community composition to predation by *C. pengoi*, but unfortunately such information is not available as yet. Therefore, at this point it can only be stated that similar changes have occurred in the zooplankton communities of recently invaded ecosystems, specifically decreases in *Bosmina* abundance, and hypothesized that these changes may be the result of direct predation.

Long-term stomach content investigations of the most abundant planktivorous fish (herring, *Clupea harengus membras*, smelt, *Osmerus eperlanus,* and three-spined stickleback, *Gasterosteus aculeatus*) in the Gulf of Riga revealed that the mean share of *C. pengoi* in fish stomachs did not exceed 7% (Ojaveer *et al.* 2000). However, being an energetically profitable prey item due to its relatively large size, the cladoceran can periodically make up a substantial portion (up to 100%) of fish diet (Ojaveer and Lumberg 1995). Other results from the Baltic Sea, for instance that *C. pengoi* is not a preferred food either for juvenile or adult fish, and that utilization of *C. pengoi* is dependent upon a species-specific threshold size of fish, are in agreement with those of *Bythotrephes* in the Great Lakes (Ojaveer *et al.* 2000, Barnhisel and Harvey 1995). These studies suggest that (a) existing knowledge on similar

species (*Bythotrephes*) can probably be extrapolated for *Cercopagis*, and (b) fish stock structure and abundance is of crucial importance for explaining spatio-temporal patterns of *C. pengoi* population dynamics in invaded ecosystems.

Parthenogenetic females appear initially in the pelagic zooplankton community in spring, after hatching from over-wintered resting eggs, and are the dominant form throughout the growing season (MacIsaac *et al.* 1999). Sexual females, which produce resting eggs, typically appear in late summer after the appearance of males. Thus, their high productivity is very important for the survival of the *Cercopagis* population over the winter and for providing a sufficient seed population for the next spring.

The significantly larger body size of ovigerous sexual females in the first year of introduction (1998), compared to that in 1999, was accompanied by elevated fecundity of *C. pengoi*. In 1998, they usually (over 60%) carried 2-egg broods while in 1999 only 4.9% had 2 eggs. Obviously, the elevated fecundity of gamogenetic females in 1998 facilitated an expansion of the distribution of the species to all areas of the lake and supported increases in abundance. However, the larger body size of parthenogenetic females did not result in elevated clutch size (Grigirovich *et al.* 2000).

The common pattern of diurnal vertical migration of zooplankton is to ascend to the surface waters at dusk and descend back to cold water layers at dawn. The two most commonly cited hypotheses on the adaptive value of vertical migration of zooplankton are the demographic and predation hypotheses (Lampert 1989). The demographic hypothesis assumes that growth is retarded at low temperatures which results in greater body size of migrating plankters, and consequently elevated fecundity (McLaren 1974). The predation hypothesis assumes that by avoiding the illuminated surface waters layers during the day, zooplankton reduce the risk of visual predation (Zaret and Suffern 1976). Since food is often more abundant in the surface waters, predator avoidance usually involves a trade-off between predation and food availability. In addition, increased temperatures in the surface water can increase productivity (Lampert 1989), therefore, vertical migration may be a compromise between several factors (Vuorinen 1987). The data from this study suggest that *C. pengoi* does not exhibit any clear pattern of vertical migration in the offshore region of Lake Ontario at the depth intervals examined. Most of the individuals stayed in the epilimnion, and to some extent within

the metalimnion. The results from this study on the vertical distribution pattern of the species agree with those obtained in the Gulf of Finland (Baltic Sea). Krylov *et al.* (1999) have found higher *C. pengoi* densities in the warmer upper 10 m layer at both inshore and offshore stations, with the exception of one station located in the central Gulf of Finland where the highest densities were recorded at 25 to 33 m depth. However, overall densities were very low at this station ($\leq 10/m^3$). Thus, in general, the risk of exposure to potential predators in the upper illuminated warm water environment may be compensated for by elevated productivity of this warm-water preferring species, and may not be great enough to warrant an energy-consuming diurnal migration through the thermocline to cooler water. In addition, *C. pengoi* might be less vulnerable to predation than native zooplankton species because of its long tail spine.

The low abundance of body carcasses (dead individuals) in deeper water layers probably points to the fact that energy transfer to higher trophic levels, stored in the *C. pengoi* population, takes place mostly in the upper water layers and a negligible proportion ($< 3\%$) sinks to deeper layers, below 40 m. However, part of *C. pengoi* production is transported to deeper waters in the Baltic Sea by being predated by older smelt and herring that inhabit the colder water layers. This is probably due to an insufficient amount of preferred food items (large calanoid copepods and mysids) in deeper water layers that forces these fish to perform upward vertical migrations to search for prey in the surface waters (Ojaveer *et al.* 2000). The closely related invasive cladoceran *Bythotrephes cederstroemi* has similarly been identified in small numbers in stomachs of hypolimnetic deepwater sculpins, probably having been ingested as dead animals due to their relatively high sinking rate as explained by Evans (1988), but possibly also due to active swimming by fish (Coulas *et al.* 1998).

Significantly higher abundances and biomass of the warm-water preferring *C. pengoi* were found in open deep water than in shallower, near-coastal areas in Lake Ontario. In contrast to most of the stations in open parts of the lake and in the eastern basin (mean surface temperature 21.0°C), several near-coastal sampling sites in the northern and western part were characterized by lower temperatures (below 20°C, min. = 15.5°C) and less pronounced thermal stratification. This probably points to recent wind-induced water movements, such as upwelling events. Therefore, the driving forces behind the spatial variability in the distribution of *C. pengoi* observed are proba-

bly dynamic and complex, including both abiotic (stability and thermal conditions of the upper water column) and biotic (predator abundance and prey availability) components.

Based on the current field data, a larger impact on the Lake Ontario ecosystem due to *C. pengoi* is probably to be expected in the open part of the basin, where more favorable conditions allow the development of larger standing stocks. In the Baltic Sea (Gulf of Riga), in contrast, the highest population densities were recorded in shallower and relatively closed areas and *Cercopagis* abundance was the lowest in open areas and in stations situating in the region of currents (Ojaveer *et al.* 1999).

REFERENCES

Barbiero, R.P., Little, R.E., and Tuchman, M.L. Results from the USEPA's biological open water surveillance program of the Laurentian Great Lakes: III. Zooplankton. *J. Great Lakes Res.* (in press).

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

Campbell, L., and Chow-Fraser, P. 1995. Differential effects of chemical preservatives and freezing on the length and dry weight of *Daphnia* and *Diaptomus* in an oligotrophic lake. *Arch. Hydrobiol.* 134:255–169.

Carlton, J.T. 1999. The scale and ecological consequences of biological invasions in the world's oceans. In *Invasive Species and Biodiversity Management*, ed. T. Sadlund, pp. 195–212. Dordrecht, The Netherlands: Kluwer Academic Publishers.

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

Evans, M.S. 1988. *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. *J. Great Lakes Res.* 14:234–240.

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 Caspian Lake. *Arch. Hydrobiol.* 149:23–50.

Haney, J.F., and Hall, D.J. 1973. Sugar coated *Daphnia*: a preservation technique for Cladocera. *Limnol. Oceanogr.* 18:331–333.

Kapiris, K., Miliou, H., and Moraitou-Apostolopouloum M. 1997. Effects of formaldehyde preservation on biometrical characters, biomass and biochemical composition of *Acartia clausi* (Copepoda, Calanoida). *Helgol. Meeresunters.* 51:95–106.

Ketelaars, H.A.M., Lambregts-van de Clundert, F.E., Carpentier, C.J., Wagenvoort, A.J., and Hoogenboezem, W. 1999. Ecological effects of the mass occurrence of the Ponto-Caspian invader, *Hemimysis anomala* G. O. Sars. 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Netherlands, with notes on its autecology and new records. *Hydrobiologia* 394: 233–248.

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.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* 3:21–27.

Lehman, J.T. 1991. Causes and consequences of cladoceran dynamics in lake Michigan: implications of species invasion by *Bythotrephes*. *J. Great Lakes Res.* 17:437–445.

———, and Caceres, C.E. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Limnol. Oceanogr.* 38: 879–891.

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

Makarewicz, J.C., Grigorovich. I.A., Mills, E., Damaske, E., Cristescu, M.E., Pearsall, W., LaVoie, M.J., Keats, R., Rudstam, L., Hebert, P., Halbritter, H., Kelly, T., Matkovich, C., and MacIsaac, H.J. 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in Lake Ontario. *J. Great Lakes Res.* 27(1):19–32.

McLaren, I.A. 1974. Demographic strategy of verical migration by a marine copepod. *Am. Nat.* 108:91–102.

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 the establishment of *Bytotrephes cederstroemi*. *Can. J. Fish. Aquat. Sci.* 49:2009–2019.

———, 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.* 19:1–54.

Mordukhai-Boltovski, F.D., and Rivier, I.K. 1987. *Predatory cladocerans Podonidae, Polyphemidae, Cercopagidae and Leptodoridae in the world fauna*. Leningrad: Nauka (in Russian).

Nalepa, T.F., Fahnenstiel, G.L., and Johengen, T.H. 1999. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality: A case study in Saginaw Bay, Lake Huron. In *Non-indigenous freshwater organisms. Vectors, biology and impacts*, eds. R. Claudi and J. H. Leach, pp. 255–271. Washington, D.C.: Lewis Publishers.

Niermann, U., Bingel, F., Gorban, A., Gordina, A.D., Gücü, A.C., Kideys, A.E., Konsulov, A., Radu, G., Subbotin, A.A., and Zaika, V.E. 1994. Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991–1992. *ICES J. Mar. Sci.* 52:395–406.

Ojaveer, E., Lumberg, A., and Ojaveer, H. 1998. Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES J. Mar. Sci.* 55:748–755.

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

———, Lankov, A., Eero, M., Kotta, J., Kotta, I., and Lumberg, A. 1999. Changes in the ecosytem of the Gulf of Riga from the 1970s to the 1990s. *ICES J. Mar. Sci.* 56 Suppl.:33–40.

———, Simm, M., Lankov, A., and Lumberg, A. 2000. Consequences of invasion of a predatory cladoceran. ICES C.M.2000/U:16.

Patalas, K. 1969. Composition and horizontal distribution of crustacean plankton in Lake Ontario. *J. Fish. Res. Board Can.* 26:2135–3146.

Ricciardi, A., and Rasmussen, J.B. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Can. J. Fish. Aquat. Sci.* 55:1759–1765.

Rutherford, E.S., Rose, K.A., Mills, E.L., Forney, J.L., Mayer, C.M., and Rudstam, L.G. 1999. Individual-based model simulations of a zebra mussel (*Dreissena polymorpha*) induced energy shunt of walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) populations in Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* 56:2148–2160.

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.

Uitto, A., Gorokhova, E., and Valipakka, P. 1999. Distribution of the non-indigenous *Cercopagis pengoi* in the coastal waters of the eastern Gulf of Finland. *ICES J. Mar. Sci.* 56 Suppl.:49–57.

Vuorinen, I. 1987. Vertical migration of *Eurytemora* (Crustacean:Copepoda): A compromise between the risks of predation and decreased fecundity. *J. Plankton Res*. 9:1037–1046.

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.* 37:409–425.

Zaret, T., and Suffern, J.S. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* 21:804–813.

Zmudzinski, L. 1999. *Cercopagis pengoi* (Cladocera) conquered the southern Baltic Sea. *Baltic Coastal Zone* 2:95–96.