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Invasion of Lake Ontario by the Ponto–Caspian predatory cladoceran *Cercopagis pengoi*

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Abstract: *Cercopagis pengoi*, a waterflea native to the Ponto–Caspian region, was discovered during 1998 in Lake Ontario. Individuals were found throughout the lake during summer snagged on sportfishing lines. The population included parthenogenetic (92%) and sexual (2%) females and males (6%). *Cercopagis* has a very long caudal appendage that is more than five times the body length and terminates in a distinctive loop. Females and males from Lake Ontario were significantly smaller than individuals from the Neva Estuary, Baltic Sea. In Eurasia, C. *pengoi* occurs in relatively warm fresh and brackish waters (0–14‰) at population densities usually <3000 individuals·m^{-3}; mean and maximum population densities in Lake Ontario were 170 and 322 individuals·m^{-3}, respectively. The presence of females with resting eggs indicates that *Cercopagis* will likely establish in Lake Ontario. As with other recently introduced invertebrates, *Cercopagis* likely was transported to the Great Lakes in ballast water from eastern Europe. The rapid influx of Ponto–Caspian species into the Great Lakes warrants further study including identification of source populations, mechanisms of dispersal, impacts on recipient ecosystems, and efficacy of ballast water exchange programs.

Résumé : On a détecté en 1998 dans le lac Ontario la présence de *Cercopagis pengoi*, une puce d'eau indigène de la région ponto–caspienne. On a trouvé des individus partout dans le lac durant l'été, fixés à des lignes à pêche. La population comprenait des femelles qui se reproduisaient par parthénogenèse (92%) et par reproduction sexuée (2%) ainsi que des mâles (6%). *Cercopagis* a un très long appendice caudal (longueur plus de cinq fois supérieure à celle du corps) qui se termine en une boucle distinctive. Les femelles et les mâles du lac Ontario étaient significativement plus petits que les sujets de l'estuaire de la Neva, dans la mer Baltique. En Eurasie, on trouve *C. pengoi* en eau douce ou saumâtre (salinité de 0 à 14‰) relativement chaude et à des densités habituellement inférieures à 3 000 individus·m^{-3}; les densités de population moyenne et maximale dans le lac Ontario étaient de 170 et 322 individus·m^{-3}, respectivement. La présence de femelles avec des oeufs durables indique que *Cercopagis* s'établira probablement dans le lac Ontario. Comme dans le cas d'autres invertébrés récemment introduits, *Cercopagis* a probablement été transporté dans les Grands Lacs dans des eaux de lest provenant d'Europe de l'Est. Vu l'influx rapide d'espèces ponto–caspiennes dans les Grands Lacs, on devra entreprendre de nouvelles études, ayant trait notamment à l'identification des populations sources, aux mécanismes de dispersion, aux impacts sur les écosystèmes récepteurs et à l'efficacité des programmes de changement de lest liquide.

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Introduction

The introduction of nonindigenous species to new habitats is one of the most significant mechanisms by which humans are altering the planet. Transfer of ballast water between international ports has seriously affected the composition of aquatic communities worldwide (e.g., Cohen and Carlton 1998). Mills et al. (1993) reported 55 nonindigenous invertebrates and fishes in the Laurentian Great Lakes, of which a majority are native to Eurasia (55%). A number of Ponto–Caspian (Caspian Lake, Black and Azov seas) taxa have established in the Great Lakes in recent years, including *Dreissena polymorpha*, *Dreissena bugensis*, *Echinogammarus ischnus*, *Neogobius melanostomus*, and *Proterorhinus marmoratus* (Ricciardi and Rasmussen 1998). Ponto–Caspian waterbodies are highly speciose relative to

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the Great Lakes and may pose a significant invasion risk (see Dumont 1998). Invasions from this region could occur through direct transfer or via secondary introductions from invaded habitats elsewhere in Europe (Ricciardi and Rasmussen 1998; MacIsaac 1999). For example, the amphipod *E. ischnus* invaded the Great Lakes only after it established in the lower River Rhine.

In this study, we describe the first record of the Ponto–Caspian waterflea *Cercopagis pengoi* in Lake Ontario. We assess reproductive and morphological characteristics of individuals recovered from Lake Ontario and contrast these patterns with individuals from the Neva Estuary, Baltic Sea. Finally, we review the distribution and ecology of *Cercopagis* in eastern Europe.

Materials and methods

Plankton samples were collected on 27 August 1998 from western Lake Ontario using bottom to surface hauls (≤27 m) of a 0.5-m-diameter, 253-μm-mesh plankton net. Eight samples were collected ≤5 km offshore between Oakville and Grimbsy, Ontario, and preserved in buffered, sugar–formalin or in 70% ethanol. Bottom to surface (10 m) samples were also collected during July 1997 from Neva Estuary, Baltic Sea, using a 20-cm-diameter, 150-μm-mesh plankton net and preserved in 4% formalin. Morphological and reproductive characteristics of formalin-preserved *Cercopagis* from Lake Ontario and Neva Estuary were assessed using a dissecting microscope (6–50×). Images were outputted via a videocamera and framegrabber to image analysis software on a personal computer. Total body (tip of head to base of caudal appendage), brood chamber, and caudal appendage lengths were measured on individuals with three spine pairs on the caudal appendage. Individual segments of the caudal appendage were measured and summed. Size differences between North American and European populations were assessed using *t*-tests with Systat 7.0 after data were $\ln(x + 1)$ transformed.

Results and discussion

Cercopagis pengoi (Ostroumov) belongs to the family Cercopagidae (Crustacea: Onychopoda), which comprises the genera *Bythotrephes* and *Cercopagis* (Mordukhai-Boltovskoi and Rivier 1987). Cercopagids have a well-developed abdomen, a long caudal appendage, and reduced carapace valves that present as a dorsal brood pouch in females (Rivier 1998). The head contains a single, compound eye. Animals possess four pairs of segmented, thoracic limbs that are modified for grasping. The genus *Cercopagis* was established by Sars in 1897 based on animals from the Azov Sea and Caspian Lake (Sovinskii 1904). Owing to similarities in the caudal appendage, animals were originally identified by Pengo and Grimm as marine representatives of *Bythotrephes* (Sovinskii 1904). *Cercopagis* shares many other morphological features with the genus *Bythotrephes*, which is considered ancestral to the family Cercopagidae (Rivier 1998). Parthenogenetic and sexual female *C. pengoi* possess a caudal appendage that is more than five times the body length and includes a distinctive terminal loop (Fig. 1). Three pairs of spines are widely spaced on the caudal appendage. Length of the first spine exceeds the diameter of the caudal appendage at its base. The brood chamber has a distinctly pointed apex. Distinctive "forms" of the species occur in Caspian Lake (*Cercopagis pengoi gracillima*) and in Aral Lake (*Cercopagis pengoi aralensis*) (Rivier 1998).

Cercopagis pengoi is native to Caspian and Aral lakes, the Don Estuary, and the Azov Sea and to coastal lakes and the Dniester and Dnieper–Bug estuaries of the Black Sea (Fig. 2) (Mordukhai-Boltovskoi 1968). The species has been introduced elsewhere in the Ponto–Caspian region and to gulfs of the Baltic Sea (Tseeb 1964; Scherbak 1989). The latter invasion was first observed in 1992 in the Gulf of Riga and likely resulted from discharge of ballast water (Ojaveer and Lumberg 1995; Panov et al. 1996). *Cercopagis* distribution now extends to the Gulf of Finland, Aland Sea, and Baltic Sea proper.

Cercopagis was first observed in Lake Ontario by sport fishers who experienced difficulty retrieving fishing lines fouled by individuals snagged by their caudal appendage. Reports of fouling commenced 31 July 1998 and continued intermittently over the following month in all regions of the lake. *Cercopagis* was observed in water between 17.4 and 23.9°C. Fouling of fishing lines near Hamilton, Ontario, declined after upwelling reduced overnight surface temperature from 19.5 to 11.0°C (week of 24 August). *Cercopagis* also fouled Ontario Ministry of Natural Resources gill nets set in the north-central region of the lake, near Brighton and Wellington, Ontario, during the first week of August. However, *Cercopagis* was not reported near Wellington the following week, after a shift in prevailing winds had caused an upwelling event and a reduction (9.3°C) in surface water temperature. In Caspian Lake, C. *pengoi* appears at 17°C, achieves maximum abundance at 20–25°C, and disappears in autumn at between 16 and 13°C (Mordukhai-Boltovskoi and Rivier 1987). In the Baltic Sea, maximum abundance (300–2000 individuals·m^{-3}) occurs during summer (16–20°C), although individuals are also found in October (12.7–8°C) (Ojaveer and Lumberg 1995; Panov et al. 1996; V. Panov, unpublished data). In cooling reservoirs of Ukrainian nuclear power plants, huge populations (>100 000 individuals·m^{-3}) were observed at 24–30°C (S. Afanasiev, personal communication). Mordukhai-Boltovskoi and Rivier (1987) reported that Caspian populations declined above 30°C.

The life stage(s) involved in the invasion of Lake Ontario is not known, although introduction of either planktonic individuals or resting eggs could effect successful colonization. In the absence of plausible alternative dispersal mechanisms, it is almost certain that *Cercopagis* was introduced into North America via discharge of contaminated ballast water. *Cercopagis pengoi* or its resting eggs may survive transit in ballast tanks even if the tanks have been flushed with saline water, owing to the species' salinity tolerance. *Cercopagis pengoi* inhabits the Dnieper River reservoirs and Dnieper–Bug tidal estuary (0.1–4‰) and fresh and brackish waters of the Azov Sea (<10‰), Caspian Lake (<14‰), and Lake Drevno, Bulgaria (5–14‰) (Mordukhai-Boltovskoi 1968; Scherbak 1989; Mordukhai-Boltovskoi and Rivier 1987). In the Baltic Sea, *Cercopagis* occurs in the Gulf of Finland (0.5–6‰), the Aland Sea (5–6‰), and the sea proper (6–8‰).

Density of *Cercopagis* in Lake Ontario on 27 August 1998 averaged 170 individuals·m^{-3} (SD = 110, maximum = 322, n = 8). Density may have been highest in subsurface

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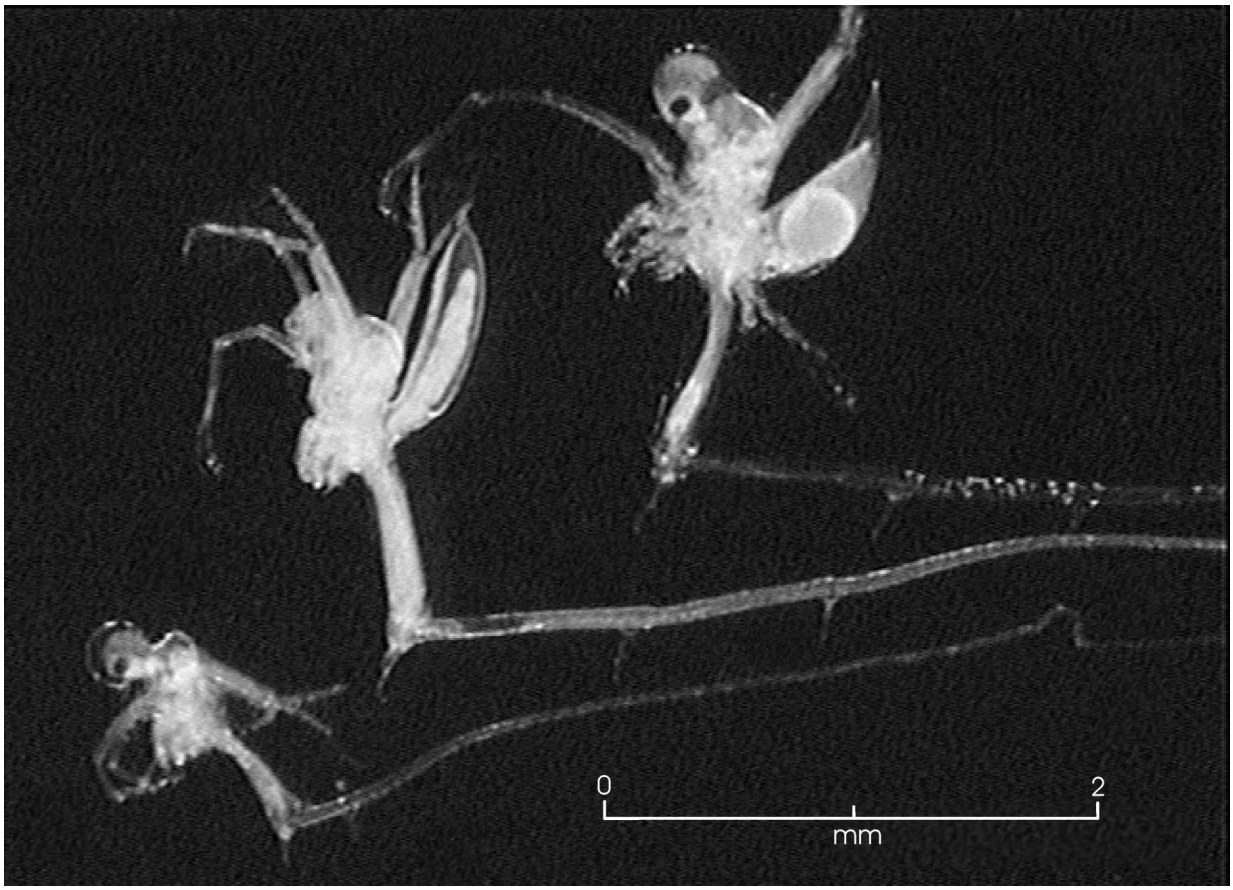
Fig. 1. *Cercopagis pengoi* in Lake Ontario: sexual female with resting egg (top), parthenogenetic female with embryo (centre), and male (bottom). The caudal appendage of the females is truncated, although a distal loop is present in the complete appendage of the male. Individual body lengths 1.77, 1.48, and 1.12 mm, respectively; caudal appendage lengths 8.93, 7.71, and 3.80 mm, respectively.



waters, as fouling of gill nets set between the surface and 27.5 m depth was greatest at 17.5 m. *Cercopagis* resides in surface waters in the Baltic Sea (10–12 m) (V. Panov, unpublished data) and Caspian Lake (0–50 m), although it also migrates vertically in deeper sections (≤ 100 m) of the latter basin (Mordukhai-Boltovskoi 1968; Mordukhai-Boltovskoi and Rivier 1971). Nocturnal migrations may limit planktivory while facilitating feeding on zooplankton. *Cercopagis pengoi* is consumed by a variety of planktivorous fishes in European water bodies (Ojaveer and Lumberg 1995; Rivier 1998). The importance of fish predation in affecting distribution and population density is not clear, although planktivory appeared to limit *Cercopagis* abundance in Tsimlyansk Reservoir, Russia (Glamazda 1971).

Cercopagis from Lake Ontario were much smaller than individuals from the Baltic Sea, possibly reflecting higher predation intensity. For example, body length of sexual (1.55 mm, $n = 6$) and parthenogenetic (1.36 mm, $n = 41$) females from Lake Ontario was significantly (*t* tests, $P < 0.03$) less than that of individuals from the Baltic Sea (1.81 mm, $n = 4$; 1.83 mm, $n = 34$). Although fecundity can be difficult to ascertain, parthenogenetic females from the Baltic Sea had larger brood chambers (1.47 versus 1.01 mm; *t*-test, $P < 0.001$) and appeared to carry more eggs than Lake Ontario animals. Parthenogenetic females from Lake Ontario produced a maximum of eight resolvable embryos, while gametogenic females produced a maximum of two resting eggs. Mean caudal appendage lengths (±SD) of sexual and parthenogenetic females from Lake Ontario were 8.49 (0.62) and 7.50 (1.35), respectively. Body size of *Cercopagis* males from Lake Ontario (1.17 mm, $n = 7$) was also significantly ($t = 2.72$, df = 6.9, $P = 0.03$) smaller than that of animals from the Baltic Sea (1.49 mm, $n = 2$).

Cercopagis preys on zooplankton by tearing the integument and ingesting its contents (Mordukhai-Boltovskoi 1968). Rivier (1998) inferred that *Cercopagis* consumes nauplii, copepodites, and adult calanoid copepods (*Eurytemora grimmi*), although feeding rate data are lacking. Considering the much larger populations of *Cercopagis* than *Bythotrephes* in Lake Ontario, the similarities between *Cercopagis* and *Bythotrephes* morphology, and observed effects of *Bythotrephes* on zooplanktn communities (Yan and Pawson 1997), *Cercopagis* may be expected to have a greater impact on small-bodied zooplankton and foodweb dynamics in Lake Ontario. Suppression by *Cercopagis* of small zooplankton abundance could adversely affect planktivorous fish. Studies on the Baltic Sea indicate that *Bythotrephes* abundance also is suppressed in the presence of *Cercopagis* (V. Panov, unpublished data).

Insufficient evidence exists to determine whether *Cercopagis* will be an energetic link or sink in Lake Ontario. Clarification of this issue is vital in order to predict impacts in

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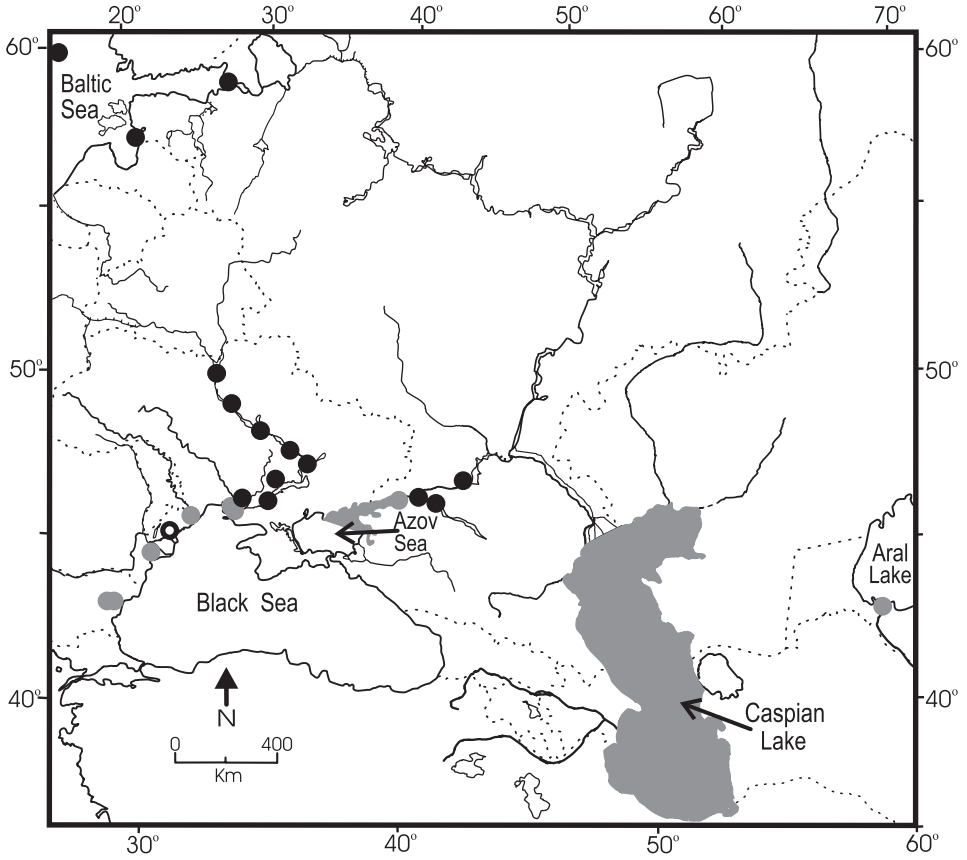
Fig. 2. Distribution of *C. pengoi* in Eurasia. The species is native to Caspian and Aral lakes and to the Black Sea and Azov Sea basins (shaded circles) but has been introduced into reservoirs and canals on the Dnieper, Don, and Manych rivers and into the Baltic Sea (solid circles). The origin of the population in Lake Katlabukh (Danube Delta) has not been resolved (open circle).



other lakes. If *Cercopagis* establishes in Lake Ontario, as appears likely, many other lakes in the Great Lakes basin may be vulnerable to invasion. Asexual reproduction and production of resting eggs and a "sticky" caudal appendage promote rapid population growth, viability during unfavourable periods, and rapid dispersal. *Cercopagis* could be dispersed to new basins via ballast water transfer, fishing gear, bait buckets, and trailered boats, in plumage or digestive tracts of waterfowl or fish, or on contaminated plankton nets. Precautions must be exercised until dispersal modes and community impacts of this invader are established.

Recent invasions by Ponto–Caspian taxa have dramatically altered Great Lakes ecosystems. Additional invasions from this region may be anticipated unless species sources and dispersal mechanisms are identified and countered. Recent invasions by *Cercopagis* and *Echinogammarus* into the Great Lakes warrant further study on the efficacy of ballast water exchange programs, as both of these species likely colonized after implementation of the ballast water control strategy. The most likely source of North American *Cercopagis* is the Black Sea, adjacent to the ports of Kherson or Nikolayev, or the Baltic Sea. Large populations of *Cercopagis* have been reported near these Black Sea ports, while the Baltic Sea has been identified as the source of *Bythotrephes*, another exotic cladoceran in the Great Lakes (D. Berg, D. Garton, H. MacIsaac, and V. Panov, unpublished data). Genetic analyses may help resolve the source of *Cercopagis* in the Great Lakes.

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