The Characteristics and Potential Ecological Effects of the Exotic Crustacean Zooplankter *Cercopagis pengoi* (Cladocera: Cercopagidae), a Recent Invader of Lake Erie[1]

DOUGLAS D. KANE, ERIN M. HAAS, AND DAVID A. CULVER[2], Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, OH 43210

ABSTRACT. The invasive zooplankter *Cercopagis pengoi* was recorded for the first time in Lake Erie during August 2001 following previous colonization of Lakes Ontario and Michigan. *Cercopagis pengoi* (Cladocera: Cercopagidae) is from the Ponto-Caspian region of Eurasia, as is a previous cercopagid invader, *Bythotrephes longimanus*. *Cercopagis* tolerates a wide range of salinities and temperatures, has many life history traits characteristic of a successful invader, and has previously invaded the Baltic Sea. *Cercopagis* may affect native zooplankton populations and fish populations through both predation and competition, although the extent of these interactions is not yet known. More research regarding basic life history traits and ecology of *Cercopagis* is needed to assess the role it will play in Lake Erie.

OHIO J SCI 103 (4):79–83, 2003

INTRODUCTION

Nonindigenous species have invaded the Great Lakes at an accelerating pace since the 1800s. The Great Lakes is home to at least 139 nonindigenous fishes, invertebrates, fish disease pathogens, plants, and algae (Mills and others 1994). Recently researchers have been paying closer attention to the biogeography of these invaders. Seventy percent of the invading species that have been discovered since 1985 are native to the waters of the Ponto-Caspian region (Black, Caspian, and Azov Seas) (Ricciardi and MacIsaac 2000). Organisms from this region have had negative effects on the Great Lakes, causing extinctions of native species, alterations to habitat, and disruptions of foodwebs (Ricciardi and MacIsaac 2000). This suite of Ponto-Caspian invaders has succeeded due to its broad range of environmental tolerances, its taxonomic diversity, and its increased colonization of European ports (Ricciardi and MacIsaac 2000).

Crustaceans previously composed only 4% of the invaders to the Great Lakes (Mills and others 1994). Recently, however, the Great Lakes have been invaded by a number of crustacean species, including an amphipod, *Echinogammarus ischnus* (Witt and others 1997), and the cladocerans *Bythotrephes longimanus* (Bur and others 1986; Lange and Cap 1986), *Cercopagis pengoi* (MacIsaac and others 1999), and *Daphnia lumholtzi* (Muzinic 2000). Three of these species are of Ponto-Caspian origin (*E. ischnus*, *B. longimanus*, and *C. pengoi*). Ricciardi and Rasmussen (1998) predicted that other amphipods (*Corophium* spp.) and mysids may be the next crustacean invaders from the Ponto-Caspian area to invade the Great Lakes. The increase of Ponto-Caspian invaders, especially since the introduction of *Dreissena polymorpha* and *Dreissena bugensis* into the Great Lakes, may be a case of what Simberloff and Von Holle (1999) call "invasional meltdown." In this process the presence of one or more non-native species facilitates the invasion of other species that share a common geographic and evolutionary history with the initial invader(s).

Samples from August and September 2001 from the western basin of Lake Erie contained *Cercopagis pengoi* (Therriault and others 2002), and *C. pengoi* has been previously found in Lake Ontario (MacIsaac and others 1999) and Lake Michigan (Charlebois and others 2001). *Cercopagis pengoi* biofouls fishermen's lines (MacIsaac and others 1999) and may have a number of negative impacts on the biota of Lake Erie. The characteristics of *Cercopagis* and its possible ecological effects are discussed in this paper.

MATERIALS AND METHODS

Zooplankton samples were collected by the Ohio Department of Natural Resources (ODNR) as part of the Ohio State University's Lake Erie Plankton Abundance Study (LEPAS). This ongoing study (1995-present) seeks to monitor long-term trends in lower trophic level interactions that affect the recruitment of fish species in Lake Erie. The discovery of *Cercopagis pengoi* was not an intended goal for LEPAS, rather it was a byproduct of a rigorous spatial and temporal sampling regimen that allowed us to detect this new invader. Sampling was conducted approximately once every two weeks from 30 April 2001 to 2 October 2001 at eight stations in the western basin of Lake Erie. A total of 79 zooplankton samples was collected from western Lake Erie and analyzed during 2001. An additional 28 samples from central Lake Erie and 61 samples from eastern Lake Erie were collected and analyzed the same way, but contained no *Cercopagis*. Zooplankton sampling and enumeration methodology is outlined below and followed the methodology used by previous researchers (Frost and Culver 2001).

Vertical tow samples were collected using a front-weighted zooplankton net (0.5-m diameter, 64-μm mesh) fitted with a General Oceanics 2030R model flow meter and 500-ml jar. The net was lowered with the

[1]Manuscript received 29 November 2001 and in revised form 27 March 2002 (#01-34).
[2]Corresponding author: culver.3@osu.edu

open end pointing downward until the 2.0 kg weight fastened to the front bridle by a 1.0-m line hit bottom. The net was then retrieved, allowing the water column to be sampled both as the net was lowered and as it was pulled up, while avoiding collecting mud from the bottom. Samples were then concentrated and preserved with a 4% sugar formaldehyde solution (Haney and Hall 1973).

In the laboratory, each sample was diluted to a known volume, typically from 500 ml to 3000 ml unless the sample contained an extremely small or large amount of zooplankton, requiring lower or larger dilution volumes. After dilution, all zooplankton in at least two subsamples of 5-10 ml were identified and counted. Samples were processed using a Wild M5A dissecting microscope fitted with a calibrated ocular micrometer so body measurements could be obtained to the nearest 0.05 mm. Cladocerans and copepods were identified to species while rotifers were identified to genus. Additional subsamples were analyzed until at least 100 individuals of the most common taxon were recorded. *Cercopagis* was initially discovered in one subsample from station 27. After *C. pengoi* was discovered in this subsample, all 2001 samples (N = 21) from station 27 and 29 were examined in their entirety for the presence of *C. pengoi* and another cercopagid, *Bythotrephes longimanus.* Zooplankton data on taxa other than *C. pengoi* will be reported elsewhere.

Cercopagis pengoi individuals were measured from the top of the head to the base of the caudal process, which can be over five times the length of the body (Makarewicz and others 2001). Biomass was calculated from length measurements using Grigorovich and others' (2000) equation: $\log W = 0.375 + 2.442 \log L$, where W is dry body mass (µg) and L is length (mm). The volume of water (L) sampled was calculated using the number of flowmeter revolutions multiplied by the net constant (5.2765 L/revolution). Densities and biomass of individuals, as well as average biomass, were then calculated.

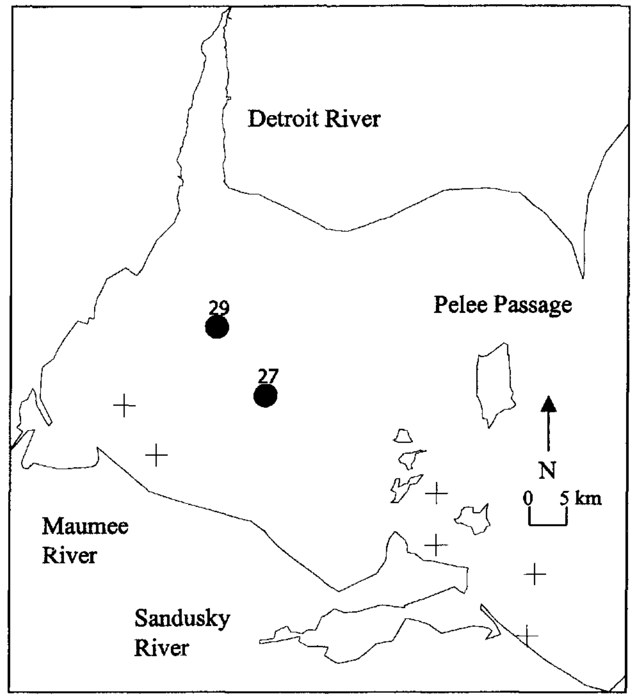

FIGURE 1. Sites sampled in the western basin of Lake Erie during 2001. Filled-in circles denote sites whose samples contained *Cercopagis pengoi*, sampled sites that did not contain *C. pengoi* are denoted by crosses. Site 27 is located at 41" 46.32' N, 83" 3.17' W; Site 29 is located at 41" 51.59' N, 83" 8.07' W.

RESULTS

Samples containing *C. pengoi* were collected at two sites in the western basin of Lake Erie, south of the Detroit River during 2001 (Fig. 1). This area is near where other researchers reported sampling *Cercopagis pengoi* in late August 2001 (MacIsaac, pers. comm.). Average length of the body (less the tail) at the two sites was 1.0 mm ± 0.07 (mean ± standard error), while the average weight of individuals at the sites was 2.4 ± 0.36 µg. Only seven individuals were collected and both densities and biomasses were extremely low (Table 1). For both sites combined, densities were 1.0 ± 0.7/m^3. Average biomass was also very low at 3.0 ± 0.2 µg/m^3.

Average body length of individuals found in this study was somewhat less than values for parthenogenetic females found in Lake Ontario (0.99 mm vs 1.36 mm) (MacIsaac and others 1999). Median densities of *C. pengoi* in Lake Ontario (295/m^3) (Ojaveer and others 2001) greatly exceeded our mean of 1.0/m^3. Likewise, median dry-weight biomass in Lake Ontario (13,400 µg DW/m^3) (Ojaveer and others 2001) exceeded our average biomass value of 3.0 µg/m^3. Because no *Bythotrephes* individuals were found on these sampling dates at these sites, data on *Leptodora kindti* from these samples are included for comparison of *Cercopagis* with another predatory cladoceran (Table 1). Average *Leptodora* total body length is almost twice that of *Cercopagis* excluding the tail. Further, average *Leptodora* biomass is almost three times that of *Cercopagis.* Finally, *Leptodora* average density is more than five hundred times the density obtained for *Cercopagis,* while the average biomass of *Leptodora* is greater than one thousand times the biomass obtained for *C. pengoi. Cercopagis* from the western basin of Lake Erie appear to be of small size, low density, and low biomass when compared to *C. pengoi* from Lake Ontario and *Leptodora* from the western basin of Lake Erie.

DISCUSSION

Cercopagis pengoi has successfully invaded Lakes Ontario and Michigan (MacIsaac and others 1999; Charlebois and others 2001), and now appears to be established in Lake Erie (Therriault and others 2002). Individuals found in the western basin of Lake Erie likely entered the lake via the Detroit River from the upper lakes. Therefore currents could have carried individual colonizers into this area from the Detroit River.

Now that *C. pengoi* is present in Lake Erie, it is important to study the extent to which it will become established and the impact it will have on the lake ecosystem. Characteristics of *C. pengoi,* as they relate to ten characteristics of successful invaders outlined be-

TABLE 1

Lengths, weights, densities, and biomasses of Cercopagis pengoi *sampled during August and September 2001 in the western basin of Lake Erie. Average length, average weight, density, and biomass of* Leptodora kindti *from the same dates are included for comparison. No individuals of* Bythotrephes longimanus *were found. See Fig. 1 for site identification.*

Site	Date	Number of Individuals	Average Length (mm)	Average Weight (µg)	Density (#/m³)	Biomass (µg/m³)
Cercopagis						
27	8 Aug	1	1.1	2.8	0.5	1.0
29	27 Aug	1	1.1	3.2	0.3	1.0
27	6 Sep	5	1.0	2.2	2.6	6.0
Average		2.3	1.1	2.7	1.1	2.7
Leptodora						
27	8 Aug	12	1.9	5.9	720	4,300
29	27 Aug	20	1.9	7.0	630	4,400
27	6 Sep	0	0.0	0.0	0	0
Average		16	1.9	6.5	675	4,350

low (Ricciardi and Rasmussen 1998), may provide some answers.

1. *Abundant and Widely Distributed in Original Range*

Cercopagis pengoi is native to a large area (>3.5 million km²) containing the Caspian and Aral Seas, the Don Estuary, and the Sea of Azov, and to coastal lakes and the Dneiper-Bug and Dniester estuaries of the Black Sea (MacIsaac and others 1999). Further, densities of *Cercopagis* between 0.1 and 8.0/L, and as high as 26/L, have been recorded in its native range (Makarewicz and others 2001).

2. *Wide Environmental Tolerance*

Cercopagis pengoi exhibits a wide environmental tolerance to a number of abiotic factors. It is euryhaline, occurring in waters with salinities ranging from 0.1 to 14% (MacIsaac and others 1999), including numerous sites in the Baltic Sea, such as the gulfs of Riga (Ojaveer and others 1998) and Finland (Krylov and others 1999). *Cercopagis pengoi* is also very eurythermic, persisting in waters as cold as 8° C and, at lower abundances, at temperatures as high as 30° C (MacIsaac and others 1999).

3. *Short Generation Time*

Although no current studies evaluating generation time in *C. pengoi* have been conducted, generation times in other cladocerans (for example, *Daphnia*) are short, especially at higher temperatures (Hall 1964; Edmondson and Litt 1982). Total developmental time at 21° C for the cercopagid *Bythotrephes*, from embryonic stage through instar III, has been measured as approximately 10 days (Lehman and Branstrator 1995). *C. pengoi* most likely has short generation times, based on those of other cladocerans and its rapid increases in abundance during the year. More research needs to be conducted with regards to *Cercopagis pengoi* population dynamics.

4. *Rapid Growth*

Although no current studies evaluate growth rates of *Cercopagis pengoi*, growth rates in *Daphnia* (Edmondson and Litt 1982) and *Bythotrephes* are rapid (Sprules and others 1990), especially at higher temperatures. Studies of the cercopagid *Bythotrephes* have found both high individual growth efficiencies (conversion of 25% of prey biomass into predator biomass) (Lehman and Branstrator 1995) and population growth rates (0.075/day at 8° C to 0.146/day at 15° C, assuming no juvenile or adult daily mortality) (Sprules and others 1990). Rapid growth would also be consistent with the large increases in *C. pengoi* observed at various times during the year.

5. *High Reproductive Capacity*

C. pengoi can reproduce both parthenogenetically and gametogenetically, depending on a number of environmental cues (Grigorovich and others 2000). Since parthenogenetic females are present at most times of the year and asexual reproduction is rapid relative to sexual reproduction, *C. pengoi*'s reproductive capacity should be high. The closely related *Bythotrephes* has an early age-at-first-reproduction (13 days), short egg development time (8 days), and a high intrinsic rate of increase (as high as 0.146/day, assuming no predation mortality) at 15° C (Sprules and others 1990). Decreased ages at first reproduction and egg development times were found for *Bythotrephes* as temperatures increased. At 8° C, age at first reproduction was 26 days, and egg development time was 16 days, as compared to 13 and 8 days, respectively, at 15° C (Sprules and others 1990). Increased temperature leads to shorter developmental times and higher reproductive rates in other cladocerans, such as *Daphnia* spp. (Edmondson and Litt 1982). Therefore, *C. pengoi*'s reproduction rate may be high during high water temperatures in the summer, due both to these factors and its tolerance of high temperatures.

6. *Early Sexual Maturity*

Although sexual maturity may only occur during times of abiotic or biotic stresses, *C. pengoi* can reproduce parthenogenetically at instars I, II, and III (Grigorovich and others 2000). Further, instar II sexual females have, in rare cases, been found to be fecund as well as instar III females (Grigorovich and others 2000); early sexual maturity is consistent with *C. pengoi* being a successful invader.

7. *Broad Diet (Opportunistic Feeding)*

Uitto and others (1999) have shown that *Cercopagis pengoi* in European lakes eats a broad range of prey foods including 60% copepods (nauplii and copepodites of the genera *Acartia, Eurytemora,* and *Temora*), 20% rotifers, and 20% podonids (*Evadne nordmanni*). These three groups vary considerably in size and trophic position, thus providing evidence of a broad diet.

8. *Gregariousness*

Cercopagis pengoi can achieve densities up to 26,000/m^3 (Makarewicz and others 2001). Studies have shown that abundances are usually highest in the epilimnion in both Lake Ontario (Ojaveer and others 2001) and the Gulf of Finland (Krylov and others 1999). Further, in order for sexual reproduction to occur, males and females must overlap spatially and temporally. All of these reasons indicate that *C. pengoi* is, to some extent, gregarious. This gregariousness may increase invasion potential by providing for greater abundances of initial colonizers.

9. *Possessing Natural Mechanisms of Rapid Dispersal*

Cercopagis pengoi resting eggs have been found to pass undamaged through fish digestive systems (Ansulevich and Valipakka 2000). Thus, migratory fish and even waterfowl could provide rapid dispersal of *C. pengoi.* Further, since *C. pengoi* is a planktonic organism, currents within lakes, between lakes, and in rivers may cause it to disperse rapidly.

10. *Commensal with Human Activity (for example, Ship Ballast Transport)*

Cercopagis pengoi was most likely introduced into the Great Lakes and Baltic Sea through ballast water (MacIsaac and others 1999; Cristescu and others 2001). Since *C. pengoi* is planktonic and produces resting eggs, either of these life stages could have been transported via shipping. Furthermore, it is possible that even if ships carrying the organisms flushed their ballast tanks with saline water, the euryhaline *C. pengoi* would have survived (MacIsaac and others 1999). Given the frequent passage of ships from both lakes Ontario and Michigan through lakes Huron, St. Clair, and Erie, it is surprising that *Cercopagis* did not become established in these lakes earlier than it did.

Potential Ecological Effects

Now that *C. pengoi* is widespread in the Great Lakes, it is important to determine whether it will become abundant in the western basin of Lake Erie and to study its possible ecological consequences for this ecosystem.

In order to determine whether *C. pengoi* will become abundant in western Lake Erie, a comparison with the unsuccessful establishment of the cercopagid *Bythotrephes longimanus* in western Lake Erie is necessary. There are a number of hypotheses as to why *Bythotrephes* has been an unsuccessful invader to western Lake Erie. Previous studies have found that *Bythotrephes'* abundance in western Lake Erie was negatively correlated with water temperature (Berg and Garton 1988) and it thus was absent from the western basin for much of the summer. Further, *Bythotrephes* abundance was also negatively correlated with *Leptodora* abundance. This negative correlation between *Bythotrephes* and *Leptodora* has also been found in Lake Michigan, and has been ascribed to either competition between the two species or predation by *Bythotrephes* on *Leptodora* (Branstrator 1995). Further, Garton and others (1990) found that *Bythotrephes* could not seasonally acclimate to temperature (measured by the interaction of season, temperature, and mortality) and that reduced fecundity, presence of sexual eggs, and greater presence of males were evidence that *Bythotrephes* had reached an environmental limit with respect to the high summer temperatures (23-25° C) of western Lake Erie. However, in a number of bodies of water in Europe *Cercopagis pengoi* has been shown to have its highest abundance (>100,000 individuals m^{-3}, in one case) in water temperatures between 20-30° C (MacIsaac and others 1999), temperatures that are similar or even higher than summer water temperatures found in western Lake Erie. Although *Bythotrephes* has failed to become abundant in western Lake Erie, the differing thermal tolerances of *Cercopagis* make its success more likely.

If *Cercopagis* does become established in the western basin, it may have a number of ecological effects. *C. pengoi* eats the calanoid copepod *Eurytemora* (Uitto and others 1999). *Eurytemora affinis* is present in Lake Erie and has been shown to be an important part of the diet of the rainbow smelt (*Osmerus mordax*) (Faber and Jermolajev 1966; Gopalan and others 1998), which is a commercially important introduced species in the Great Lakes. Because both *Cercopagis* and rainbow smelt consume *Eurytemora*, competition may occur between them. Young-of-year rainbow smelt are often caught in high numbers in the western portion of the central basin of Lake Erie (that is, 184 individuals caught per hour trawling (CPHT) in October monitoring by the Ohio Department of Natural Resources (1999), as compared to 1.1 and 2.3 CPHT for the zooplanktivorous alewife (*Alosa pseudoharengus*) and gizzard shad (*Dorosoma cepedianum*)). Further, *Cercopagis* is eaten by a broad range of fish families in Europe. In the Baltic Sea, for example, *C. pengoi* is important in the diets of herring (Clupeidae), sticklebacks (Gasterosteidae), bleak (Cyprinidae), and smelt (Osmeridae) (Ojaveer and others 1998). The authors found that *C. pengoi* made up 50% of herring food at some sites and almost 100% at others. Clupeids such as the alewife and gizzard shad occur in Lake Erie (ODNR 1999), and alewives have been shown to prey upon *Bythotrephes* in the Great Lakes (Branstrator and Lehman 1996), so clupeids should most likely consume *Cercopagis*, which has a similar morphology and ecology. Therefore, *C. pengoi* may provide a new source of food for these planktivores, as well as for rainbow smelt. Future research will determine to what extent competition with, and predation upon, *Cercopagis* will affect the fish of the Lake Erie ecosystem.

Native predaceous cladocerans (*Leptodora kindti*), and the herbivorous *Daphnia* spp. decreased contemporaneously with the invasion of *Bythotrephes* into Lake Michigan (Lehman and Caceres 1993). Others (for example, Dumitru and others 2001) have suggested that predation by *Bythotrephes* has influenced plankton dynamics, including the possibility that *Daphnia* abundance is controlled by *Bythotrephes* predation, rather than by the native yellow perch (*Perca flavescens*) (Hoffman and others 2001). Further, *Bythotrephes* has quickly become abundant in the diets of planktivorous fish, such as the lake herring (*Coregonus artedii*) (Coulas and others 1998). *Cercopagis* may have similar trophic consequences.

The environment and suite of organisms found in the western basin of Lake Erie appear to be amenable to the establishment of *Cercopagis pengoi*. However, further monitoring, lab and field experiments will be needed in order to determine whether *C. pengoi* will become established in the western basin of Lake Erie.

ACKNOWLEDGEMENTS. We thank the ODNR for their extensive sampling efforts. Nate Gargasz (Ohio State University) was invaluable in analyzing samples for the presence of *Cercopagis pengoi*. We would also like to thank Dr. David Jude, Center for Great Lakes and Aquatic Sciences – University of Michigan, for showing Doug Kane samples of *Cercopagis pengoi* from Lake Michigan. Finally, we would like to thank two anonymous reviewers who greatly improved the quality of this manuscript. This research was supported by grants from the Ohio Lake Erie Protection Fund (LEQI 01-05), and by the Federal Aid in Sport Fish Restoration Program (F-69-P-7, Fish Management in Ohio) administered jointly by the U. S. Fish and Wildlife Service and the Ohio Division of Wildlife.

LITERATURE CITED

Ansulevich A, Valipakka P. 2000. New important food object of the Baltic herring in the Gulf of Finland. Int Rev Hydrobiol 85(5-6):609-19.

Berg DJ, Garton DW. 1988. Seasonal abundance of the exotic predatory cladoceran, *Bythotrephes cederstroemi*, in western Lake Erie. J Great Lakes Res 14(4):479-88.

Branstrator DK. 1995. Ecological interactions between *Bythotrephes cederstroemi* and *Leptodora kindtii* and the implications for species replacement in Lake Michigan. J Great Lakes Res 21(4):670-9.

Branstrator DK, Lehman JT. 1996. Evidence for predation by young-of-year alewife and bloater chub on *Bythotrephes cederstroemi* in Lake Michigan. J Great Lakes Res 22(4):917-24.

Bur MT, Klarer DM, Krieger KA. 1986. 1st records of a European cladoceran, *Bythotrephes cederstroemi*, in Lakes Erie and Huron. J Great Lakes Res 12(2):144-6.

Charlebois PM, Raffenberg MJ, Dettmers JM. 2001. First occurrence of *Cercopagis pengoi* in Lake Michigan. J Great Lakes Res 27(2):258-61.

Coulas RA, MacIsaac HJ, Dunlop W. 1998. Selective predation on an introduced zooplankter (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. Freshwater Biology 40(2):343-55.

Cristescu MEA, Hebert PDN, Witt JDS, MacIsaac HJ, Grigorovich IA. 2001. An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. Limnol Oceanogr 46(2):234-9.

Dumitru C, Sprules WG, Yan ND. 2001. Impact of *Bythotrephes longimanus* on zooplankton assemblages of Harp Lake, Canada: an assessment based on predator consumption and prey production. Freshwater Biology 46(2):241-51.

Edmondson WT, Litt AH. 1982. *Daphnia* in Lake Washington. Limnol Oceanogr 27(2):272-93.

Faber DJ, Jermolajev EG. 1966. A new copepod genus in the plankton of the Great Lakes. Limnol Oceanogr 11(2):301-3.

Frost PC, Culver DA. 2001. Spatial and temporal variability of phytoplankton and zooplankton in western Lake Erie. J Freshwater Ecology 16(3):435-43.

Garton DW, Berg DJ, Fletcher RJ. 1990. Thermal tolerances of the predatory cladoceans *Bythotrephes cederstroemi* and *Leptodora kindti* relationship to seasonal abundance in western Lake Erie. Can J Fish Aquat Sci 47(4):731-8.

Gopalan G, Culver DA, Wu L, Trauben BK. 1998. The effect of recent ecosystem changes on the recruitment of young-of-year fish in western Lake Erie. Can J Fish Aqua Sci 55(12):2572-9.

Grigorovich IA, MacIsaac HJ, Rivier IK, Aladin NV, Panov VE. 2000. Comparative biology of the predatory cladoceran *Cercopagis pengoi* from Lake Ontario, Baltic Sea, and Caspian Sea. Arch Hydrobiol 149(1):23-50.

Hall DJ. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology 45(1):94-112.

Haney JF, Hall DJ. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnol Oceanogr 18(2):331-3.

Hoffman JC, Smith ME, Lehman JT. 2001. Perch or plankton: top-down control of *Daphnia* by yellow perch (*Perca flavescens*) or *Bythotrephes cederstroemi* in an inland lake? Freshwater Biology 46(6):759-75.

Krylov PI, Bychenkov DE, Panov VE, Rodionova NV, Telesh IV. 1999. Distribution and seasonal dynamics of the Ponto-Caspian invader *Cercopagis pengoi* (Crustacea, Cladocera) in the Neva Estuary (Gulf of Finland). Hydrobiologia 393:227-32.

Lange C, Cap R. 1986. *Bythotrephes cederstroemi* (Schodler) (Cercopagidae, Cladocera) – a new record for Lake Ontario. J Great Lakes Res 12(2):142-3.

Lehman JT, Branstrator DK. 1995. A model for growth, development, and diet selection by the invertebrate predator *Bythotrephes cederstroemi*. J Great Lakes Res 21(4):610-19.

Lehman JT, Caceres CE. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. Limnol Oceanogr 38(4):879-91.

MacIsaac HJ, Grigorovich IA, Hoyle JA, Yan ND, Panov VE. 1999. Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran *Cercopagis pengoi*. Can J Fish Aquat Sci 56(1):1-5.

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

Mills EL, Leach JH, Carlton JT, Secor CL. 1994. Exotic species and the integrity of the Great Lakes. Bioscience 44(10):666-76.

Muzinic CJ. 2000. First record of *Daphnia lumholtzi* Sars in the Great Lakes. J Great Lakes Res 26(3):352-4.

[ODNR] Ohio Department of Natural Resources, Ohio Division of Wildlife, Lake Erie Fisheries Unit. 1999. Ohio's Lake Erie Fisheries. 94 p.

Ojaveer H, Kuhns LA, Barbiero RP, Tuchman ML. 2001. Distribution and population characteristics of *Cercopagis pengoi* in Lake Ontario. J Great Lakes Res 27(1):19-32.

Ojaveer E, Lumberg A, Ojaveer H. 1998. Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). ICES J Marine Sci 55(4):748-55.

Ricciardi A, MacIsaac HJ. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends in Ecology and Evolution 15(2):62-5.

Ricciardi A, Rasmussen JB. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can J Fish Aquat Sci 55(7):1759-65.

Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1(1):21-32.

Sprules WG, Riessen HP, Jin EH. 1990. Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. J Great Lakes Res 16(3):346-51.

Therriault TW, Grigorovich IA, Kane DD, Haas EM, Culver DA, MacIsaac HJ. 2002. Range expansion of the exotic zooplankter *Cercopagis pengoi* (Ostroumov) into western Lake Erie and Muskegon Lake. J Great Lakes Res 28(4):698-701.

Uitto A, Gorokhova E, Valipakka P. 1999. Distribution of the non-indigenous *Cercopagis pengoi* in the coastal waters of the eastern Gulf of Finland. ICES J Marine Sci 56(Supplement):49-57.

Witt JDS, Hebert PDN, Morton WB. 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. Can J Fish Aquat Sci 54(2):264-8.