

Changes in genetic structure of North American *Bythotrephes* populations following invasion from Lake Ladoga, Russia

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SUMMARY

1. We used allozyme electrophoresis to compare *Bythotrephes longimanus* (Crustacea: Onychopoda: Cercopagididae) from recently founded North American populations with those from native European populations, and to examine changes in genetic structure of North American populations over time.
2. The genetic structure of North American populations in 1996 was similar to that of European populations, because of the disappearance of founder effects which distinguished North American from European populations in 1989.
3. The Lake Ladoga, Russia population was more closely related to North American populations than to other European populations, consistent with non-genetic evidence implicating Lake Ladoga as the source of North American populations.
4. Our results provide additional evidence of the presence of an invasion corridor that allows Urasian and Ponto-Caspian species to be introduced into North American freshwater ecosystems, and show that founder effects can erode over time following establishment of invasive species.

Keywords: exotic species, founder effect, genetic structure, Great Lakes invasion corridor

Introduction

The introduction of exotic species into novel environments is a major concern of scientists studying the effects of human activities on ecosystems (Vitousek *et al.*, 1997; Cohen & Carlton, 1998). The Laurentian Great Lakes have become home to a number of exotic organisms following the arrival of Europeans, with many of these species causing marked changes in the lakes' ecosystems (Mills *et al.*, 1993). The most

notorious invader is the sea lamprey [*Petromyzon marinus* (L)], which devastated native fish populations in the mid-20th century (Smith & Tibbles, 1980). Most recently, these ecosystems have experienced a spate of Eurasian species becoming established during the 1980s and 1990s. Prominent examples of recent introductions are fishes such as ruffe [*Gymnocephalus cernuus* (L)] and round goby (*Neogobius melanostomus* Pallas), zebra and quagga mussels (*Dreissena polymorpha* Pallas and *D. bugensis* Andrusov, respectively), and other benthic and planktonic invertebrates (reviewed in Mills *et al.*, 1993; MacIsaac, 1999). The mode of introduction of these exotic species is believed to be discharge of freshwater ballast transported

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from European waterways via ocean-going freighters (Sprules, Riessen & Jin, 1990; Mills *et al.*, 1993).

Bythotrephes sp., a Palearctic zooplankton, was first found in the Great Lakes in 1982 (Johannsson, Mills & O'Gorman, 1991). Initially identified as *B. cederstroemi* Schoedler, recent work has shown that this taxon is conspecific to *B. longimanus* Leydig (see discussion in Yan & Pawson, 1998 and MacIsaac *et al.* 2000). Lake Ladoga, Russia was implicated as a probable source of this exotic species because of its direct connection to the harbour of St Petersburg and the eastern Gulf of Finland via the Neva River, and because freighters bound for Great Lakes ports often take on ballast water at St Petersburg (Sprules *et al.*, 1990). At many times of the year, this ballast is fresh or oligohaline water because of the low salinity of the eastern Gulf of Finland, which is strongly influenced by the Neva River, a major tributary of the Baltic Sea. The zooplankton community in Neva Bay, a part of St Petersburg Harbour, is composed primarily of populations that originate in Lake Ladoga and are transported to the bay via the Neva River (Telesh, 1995). Thus, the potential exists for ship-mediated transcontinental transport of freshwater and euryhaline organisms between the Lake Ladoga-Neva estuary-Gulf of Finland system and the Laurentian Great Lakes.

Like most cladocerans, *B. longimanus* is a cyclic parthenogen. The primary mode of reproduction is clonal, interspersed with bouts of sexual reproduction under stressful environmental conditions, especially during late autumn (Hebert, 1987). As such, new populations can be established by the introduction of as few as one female individual. Large-lake populations of cladocerans are characterised by stable allele frequencies with genotypic arrays meeting Hardy-Weinberg expectation (HWE) because of regular episodes of sexual reproduction (reviewed in De Meester, 1996). A previous study of *Bythotrephes* found that populations from European lakes contained relatively low levels of intrapopulation genetic variation compared with other cladocerans, but that genotype frequencies met HWE (Berg & Garton, 1994). Interpopulation variation was low within drainage basins but high among basins in Finland and Germany. In contrast, 2–5 years old North American populations were characterised by genotype frequencies that were different from HWE as a result of heterozygote excesses at the phosphoglu-

comutase (PGM) locus and low levels of variation among populations (Weider, 1991; Berg & Garton, 1994).

Population genetic theory predicts that newly established populations will exhibit founder effects, including loss of genetic variation and/or alteration of genetic structure from passing through a bottleneck, if the founding population is small. Founder effects have been noted in a number of aquatic invertebrate taxa that show high levels of allele frequency divergence among populations (Boileau, Hebert & Schwartz, 1992; DeMelo & Hebert, 1994). Low levels of interpopulation genetic variation and heterozygote excesses found in North American populations of *B. longimanus* probably represent a founder effect due to the numerical dominance of some clonal groups (multiple locus genotypes) with a heterozygous genotype at the PGM locus.

We used allozyme electrophoresis to survey genetic variation in *B. longimanus* populations from the Laurentian Great Lakes and Lake Ladoga. Samples were collected in 1996, 9–12 years after invasion of the Great Lakes. We compared these results with an earlier (1989) allozyme survey of populations from the Great Lakes and other European lakes (Berg & Garton, 1994) to determine whether Lake Ladoga was the probable source of the North American populations, and to assess the stability of the unique genetic structure of the Great Lakes populations.

Methods

Bythotrephes longimanus were collected from Lakes Ladoga, Superior, Michigan, and the North Channel and main basin of Lake Huron from 28 July to 23 August 1996, using a 500- μ m mesh plankton net. Captured individuals were preserved in a 15% trehalose solution (Taylor, Finston & Hebert, 1994). Standard cellulose acetate electrophoresis techniques (Hebert & Beaton, 1989) were used to measure genetic variation at nuclear loci. Loci surveyed were alkaline phosphatase (ALP, EC 3.1.3.1), fumarase (FUM, 4.2.1.2), glutamate oxaloacetate transferase (GOT, 2.6.1.1), isocitrate dehydrogenase (IDH, 1.1.1.42), leucyl-alanine peptidase (PEP, 3.4.11), malate dehydrogenase (MDH, 1.1.1.37), malic enzyme (ME, 1.1.1.40), mannose phosphate isomerase (MPI, 5.3.1.8), (PGM 5.4.2.2), and phosphoglucose isomerase (PGI, 5.3.1.9) for all populations. Sample sizes

were 34–79 individuals per population. Data were analysed using Biosys-1 (Swofford & Selander, 1981) and Tools for Population Genetic Analysis (Miller, 1998). Polymorphic loci were defined as those in which the most common allele was present at a frequency ≤ 0.95 .

Results were compared with those from a previous study of *Bythotrephes* (Berg & Garton, 1994), in which sample sizes varied between 17 and 91 individuals per population for populations from the same Great Lakes sites sampled in this study plus additional sites in Lake Erie, south-eastern Finland (four lakes), Sweden (one lake), and Germany (two lakes). Two lakes in Finland contained sympatric *longimanus*-type and *cederstroemi*-type individuals; these were treated as separate populations consistent with our earlier study (Berg & Garton, 1994).

A cluster analysis of the 1996 data with European populations from 1989 was performed using UPGMA to create a dendrogram based on modified Rogers' genetic distance calculated for eight loci (FUM and GOT were not resolved in all European populations). Confidence in the nodes of the dendrogram was determined by bootstrapping 1000 replicates. Allele and genotype frequency differences among populations were tested using $R \times C$ contingency tables. In cases where expected values were too low to meet the assumptions of a chi-square distribution, we pooled rare alleles or genotypes. Deviations from HWE were tested using Fisher's Exact Test with a sequential Bonferroni adjustment of significance levels (Lessios, 1992). Genotypic distance (Hedrick, 1971) based on 10 loci was used to compare Great Lakes populations from 1989 and 1996, because 1989 populations did not have genotype frequencies that met HWE. A cluster analysis using genotypic distance based on the same 10 loci was performed for Lake Ladoga with all of the 1989 data. Differences in genotype frequencies, genetic and genotypic distances, and descriptive measures of genetic structure among years in the Great Lakes populations were tested using paired *t*-tests. Genotype frequencies and other proportional measurements were arcsin-transformed before analysis.

In order to determine whether changes in genotype frequencies between 1989 and 1996 might be explained by recombination alone, we assumed random mating of 1989 North American populations and calculated expected genotype frequencies. These

expected frequencies were then compared with the frequencies found in the 1996 North American populations using $R \times C$ contingency tables.

Results

Seven of the 10 loci sampled in 1996 had variation present. Two loci (PEP and PGM) were polymorphic, while rare alleles were found in single North American populations at five loci (FUM, IDH, MDH, ME, PGI; all at frequencies < 0.04). Clonal groups were identified based on genotypes at the PEP and PGM loci. The PGI locus was polymorphic in several 1989 European populations, while both the ALP and ME loci were polymorphic in one population.

The Lake Ladoga population was more similar to Great Lakes populations than to European populations (Fig. 1). Average genetic distance was significantly lower between the Great Lakes and Lake Ladoga populations (0.085 ± 0.013 SE.) than between Lake Ladoga and Finnish populations (0.202 ± 0.039) (Mann–Whitney test, $n = 10$, $P = 0.01$). All alleles present in Lake Ladoga were present in the Great

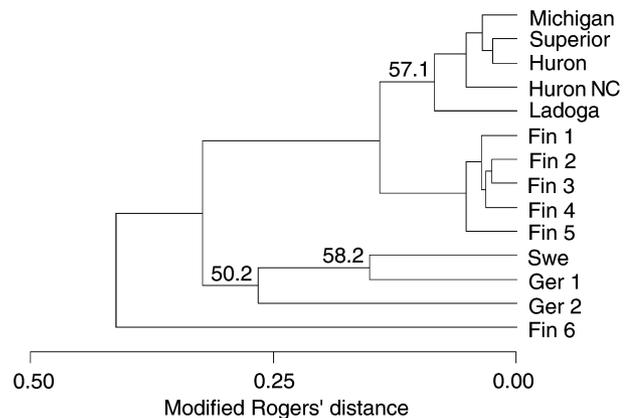


Fig. 1 Modified Rogers genetic distance among populations of *Bythotrephes* from North American (1996) and European lakes. Genetic distance was determined using eight allozyme loci per individual. The dendrogram was constructed using UPGMA. Numbers at nodes are the percentage of bootstrapped trees (out of 1000 total trees) supporting the node. All other nodes were supported by less than 50% of the trees (range = 10–45.3% of trees). Abbreviations for populations are 'Fin 1' and 'Fin 2' = Lake Päijänne, Finland, 'Fin 3' and 'Fin 4' = Lake Vuohijärvi, Finland, 'Fin 5' = Lake Kivijärvi, Finland, 'Fin 6' = Lake Kuolimo, Finland, 'Swe' = Lake Vänern, Sweden, 'Ger 1' = Stocksee, Germany, 'Ger 2' = Selenter See, Germany, 'Huron NC' = North Channel of Lake Huron. Swedish, German, and certain Finnish (2, 3, 5) populations are *longimanus*-type. All other populations are *cederstroemi*-type.

Lakes, while other European lakes contained alleles not found in the Great Lakes. The common MF heterozygote at the PGM locus in Great Lakes populations was also common in Lake Ladoga (Table 1). This genotype was found at very low frequency (0.02) in a single Finnish lake, while the F allele was completely absent from all five other Finnish populations. Nine clonal groups (the maximum number possible in a system with only two polymorphic loci and two alleles at each locus) were found in the Great Lakes, eight of which were also present in Lake Ladoga. No other clonal groups were found in Lake Ladoga. A large number of additional clonal groups were found in the other European lakes (Berg & Garton, 1994).

In 1996, neither allele nor genotype frequencies (Table 1) were significantly different among Great Lakes and Lake Ladoga populations at the PGM locus ($P > 0.4$ for both analyses). At the PEP locus, allele frequencies and genotype frequencies differed among populations, both when Lake Ladoga was included with the Great Lakes populations (Table 1, $P < 0.0001$) and when it was omitted ($P < 0.038$). Patterns for both of these loci were consistent with those from 1989 (Berg & Garton, 1994). Genotypic distances among Great Lakes populations were greater in 1996 than in 1989 ($t = 3.56$, $n = 6$ pairs, $P = 0.016$). This divergence was driven by changes in allele and genotype frequencies in some of the Great Lakes populations at the PGM and PEP loci (Table 1).

Great Lakes populations in 1996 were more similar in genetic structure to Lake Ladoga and other European lakes than were 1989 populations. In 1996, 100% of the tests for deviation from HWE were non-significant ($P = 0.05$ for experimentwise error rate).

In 1989, 40% of the tests for Great Lakes populations were significant, while only 12.5% of European populations showed significant deviation (Berg & Garton, 1994). These changes in genotype frequency arrays were caused by the disappearance of heterozygote excesses at the PGM locus from the 1996 Great Lakes populations ($t = 12.29$, $n = 4$ pairs, $P = 0.001$). Genotype frequencies at the PGM locus were not significantly different between Lake Ladoga and 1996 Great Lakes populations, but were significantly different between Lake Ladoga and 1989 Great Lakes populations ($P < 0.0001$). At the PEP locus, genotype frequencies were significantly different between years for Lake Superior and the Main Basin of Lake Huron ($P < 0.002$), but not for the other Great Lakes.

In contrast to the results shown in Fig. 1, the Lake Ladoga population clustered with populations from Finland when 1989 North American populations were used in the analysis. Again, this was mostly because European lakes did not have the extreme heterozygote excesses that characterised the North American populations during 1989. However, genotypic distances were lower between Lake Ladoga and 1989 North American populations (0.079 ± 0.005 , $n = 6$ pairs) than between Finnish lakes and 1989 North American populations (0.136 ± 0.007 , $n = 42$ pairs). Genotypic distances between Great Lakes populations and Lake Ladoga were smaller in 1996 than in 1989 ($t = 3.99$, $n = 4$ pairs, $P = 0.028$). Average values for descriptive measures of genetic structure were not significantly different between 1989 and 1996 populations from the Great Lakes (Tables 2, $t < 2.08$ for all tests, $n = 4$, $P > 0.1$), but this may be the result of a lack of statistical power because only four populations were measured in both 1989 and 1996.

Population	PGM					PEP			
	<i>n</i>	SM	MM	MF	FF	<i>n</i>	SS	SF	FF
Huron – Main Basin	55	0.000	0.400	0.382	0.218	57	0.719	0.193	0.088
Huron – North Channel	34	0.000	0.471	0.441	0.088	60	0.900	0.067	0.033
Michigan Superior	52	0.000	0.346	0.500	0.154	53	0.792	0.170	0.038
Ladoga	55	0.000	0.400	0.491	0.109	65	0.646	0.246	0.108
Great Lakes 1989	40	0.000	0.500	0.300	0.200	58	0.448	0.328	0.224
SE	69.3	0.000	0.133	0.719	0.148	69.0	0.931	0.058	0.011
Finland	(0.8)	(0.000)	(0.030)	(0.032)	(0.015)	(6.4)	(0.027)	(0.024)	(0.011)
SE	37.8	0.019	0.978	0.003	0.000	40.0	0.868	0.108	0.024
SE	(6.2)	(0.010)	(0.011)	(0.003)	(0.000)	(10.1)	(0.037)	(0.032)	(0.012)

Table 1 Genotype frequencies at polymorphic allozyme loci for populations of *Bythotrephes longimanus* from North American lakes and Lake Ladoga in 1996. *n* = sample size. 'Great Lakes 1989' entries are means for the same Great Lakes populations from summer 1989 (Berg & Garton, 1994). 'Finland' entries are means for six populations from Finnish lakes (Berg & Garton, 1994). SE are listed below means

Table 2 Descriptive measures of genetic variation in 1996 Great Lakes and Lake Ladoga populations of *Bythotrephes longimanus*. Numbers in parentheses are standard errors. Great Lakes 1989 data from Berg & Garton (1994)

Population	Mean sample size per locus	Mean number of alleles per locus	Polymorphic loci (%)	Mean heterozygosity	Number of clonal groups
Huron – Main Basin	59.2 (0.6)	1.2 (0.1)	20	0.05 (0.04)	9
Huron – North Channel	60.6 (3.0)	1.3 (0.2)	20	0.05 (0.04)	5
Michigan	54.5 (0.3)	1.4 (0.2)	20	0.07 (0.05)	8
Superior	72.0 (2.1)	1.4 (0.2)	20	0.08 (0.05)	9
Ladoga	73.0 (4.2)	1.2 (0.1)	20	0.06 (0.04)	8
Great Lakes Mean (1996)	61.6 (3.7)	1.3 (0.0)	20	0.06 (0.01)	7.8 (0.9)
Great Lakes Mean (1989)	56.2 (3.3)	1.3 (0.2)	18	0.07 (0.00)	5.8 (0.5)

Changes in genetic structure of North American populations between 1989 and 1996 were not a result of recombination alone. In three of eight comparisons (PEP and PGM in Lake Superior, PEP in the Main Basin of Lake Huron), 1996 genotype frequencies were significantly different from genotype frequencies predicted by random mating of 1989 populations. The fast allele at the PEP locus was present in Lake Superior in 1996, although it was not detected there in 1989.

Discussion

The genetic structure of North American populations of *B. longimanus* changed significantly from 1989 to 1996. Genotype frequencies for 1996 populations met HWE, consistent with results from Lake Ladoga and the European lakes sampled in 1989. Thus, the genetic structure of all Great Lakes populations of *Bythotrephes* has converged on that of long-established European populations. Our analyses assume that genotype frequencies of European populations of *B. longimanus* are stable over time. Previous work has demonstrated such stability in large-lake cladoceran populations (De Meester, 1996). The lack of such stability in North American populations is therefore particularly noteworthy.

The founder effect exhibited by Great Lakes populations in 1989 was especially obvious in the heterozygote excesses at the PGM locus (Berg & Garton, 1994); these heterozygote excesses disappeared by 1996. Because observed changes in genetic structure are caused by changes in frequencies of genotypes (rather than the appearance of new alleles), recombination during sexual reproduction is a potential explanation for these differences. However, our results show that recombination followed by random

mating does not completely explain changes in genetic structure from 1989 to 1996. In *Bythotrephes*, the rapid removal of founder effects that alter genetic structure is probably the result of both recombination and the continued influx of individuals from Lake Ladoga. The observation that North American populations from 1996 are more similar to the Lake Ladoga population than were North American populations from 1989 supports this hypothesis. Repeated colonisation of lakes has been invoked as a cause of differences in genetic structure between native and newly founded populations of other cladocerans (DeMelo & Hebert, 1994). Previous work has noted the persistence of founder effects among localised populations of pond-dwelling invertebrates, but such patterns were attributed to small numbers of founders and subsequent lack of gene flow among populations (Boileau *et al.*, 1992). In the case of North American *Bythotrephes*, it is possible that immigration from a source population has continued for over a decade and that the original founder effect has been eroded by incorporation of additional immigrants.

Our results are consistent with the hypothesis that *B. longimanus* populations within the Great Lakes arose from a single source, Lake Ladoga. We also provide further evidence of the existence of an invasion corridor that may allow other exotic species to be introduced from Eurasia into the Great Lakes (Ricciardi & MacIsaac, 2000; MacIsaac, Grigorovich, & Ricciardi, 2001). The Lake Ladoga-Neva estuary-Gulf of Finland corridor sits at the junction of an intra-continental shipping system that connects the Ponto-Caspian basin with the Baltic region, and a transoceanic route with ships travelling between the low salinity eastern Gulf of Finland and freshwater ports in the Laurentian Great Lakes. Lake Ladoga and the eastern Gulf of Finland have been invaded by

exotic species from the Ponto-Caspian basin and from more distant regions of Eurasia (Leppäkoski, 1993; Panov, Krylov, & Telesh, 1999). A large number of Ponto-Caspian endemics are currently established in the river/reservoir/canal system that connects the Baltic and Ponto-Caspian basins and many of these exotics are spreading northward (Table 3) (Panov *et al.*, 1999; MacIsaac *et al.* 2001). A large proportion of these Ponto-Caspian endemics is euryhaline, with populations established in fresh, brackish, and saline habitats within their native ecosystems. The potential exists for these species to become established in Lake Ladoga or the eastern Gulf of Finland and then move into St Petersburg harbour, where they can be incorporated into the ballast water of oceangoing freighters bound for the Laurentian Great Lakes.

Cercopagis pengoi (Ostroumov), a predatory cercopagid native to the Ponto-Caspian, illustrates the rapidity with which the invasion process may occur. It appeared in the Gulf of Finland in 1992, and is now common in the Neva estuary (Ojaveer & Lumberg, 1995; Krylov *et al.*, 1999). In 1998, *C. pengoi* was discovered in Lake Ontario at densities of up to 322 individuals \times m⁻³ (MacIsaac *et al.*, 1999). Analysis of mitochondrial DNA indicates that the Lake Ontario population is more closely related to the recently established Baltic Sea population than to Caspian Black Sea populations (Cristescu *et al.* 2001). These Ponto-Caspian species represent the current wave of invaders of North American freshwater ecosystems (Ricciardi & MacIsaac, 2000). The Lake Ladoga-Neva estuary-Gulf of Finland region appears to be serving as a 'stepping stone' that allows Ponto-Caspian freshwater and euryhaline species to move into

freshwater ecosystems on other continents (Ricciardi & MacIsaac, 2000).

Genetic analyses can track the movements of exotic species and identify routes of invasion. Using this approach, we have provided further evidence of the existence of an invasion corridor from the north-eastern Baltic to the Laurentian Great Lakes. This route has also been implicated in the dispersal of *C. pengoi* to the Great Lakes from south-eastern Europe (MacIsaac *et al.*, 1999; Cristescu *et al.* 2001). Without stringent regulation of ballast water discharge by freighters travelling between freshwater harbours, it is very likely that additional exotic species will be introduced into North America from Eurasia. Because many of these species are euryhaline, they may even be resistant to management practices such as midocean ballast water exchange. If so, transcontinental movement of ships carrying freshwater and euryhaline organisms in ballast will further contribute to the homogenisation of the world's aquatic fauna. In addition, these species may be transported as live individuals or as resting eggs in residual water and sediments in ships that officially declare 'No Ballast on Board' status when entering the Great Lakes. Thus, invasions may be expected to continue unless management strategies incorporate treatment of residual water in ballast tanks as part of ballast water treatment.

Analysis of the COI gene and minisatellite region DNA has revealed that *Bythotrephes* from Lake Ontario and a Fimish lake have identical sequences (Therriault *et al.* 2002). This provides further evidence that the eastern Baltic region is the source for North American *Bythotrephes*.

Species	Taxonomic group	Native region
<i>Cornigerius maeoticus</i> (Pengo)†	Cladoceran	Ponto-Caspian
<i>Podonevadne trigona</i> (Sars)†	Cladoceran	Ponto-Caspian
<i>Heterocope caspia</i> Sars†	Copepod	Ponto-Caspian
<i>Calanipeda aquaedulcis</i> Kritchagint	Copepod	Ponto-Caspian
<i>Corophium curvispinum</i> Sars†	Amphipod	Ponto-Caspian
<i>Dikerogammarus haemobaphes</i> (Eichwald)†	Amphipod	Ponto-Caspian
<i>Gmelinoides fasciatus</i> (Stebbing)*	Amphipod	Baikalian
<i>Hypania invalida</i> (Grube)†	Polychaete	Ponto-Caspian
<i>Archaeobdella esmonti</i> Grimm†	Leech	Ponto-Caspian
<i>Percottus glenii</i> Dybowski*	Bony fish	Russian Far East
<i>Neogobius kessleri</i> (Günther)†	Bony fish	Ponto-Caspian
<i>Clupeonella cultriventris caspia</i> Svetovidov†	Bony fish	Ponto-Caspian

*Present in Lake Ladoga-Neva estuary-Gulf of Finland.

†Present in reservoirs of the Volga River.

Table 3 Potential candidate species for introduction to the Laurentian Great Lakes via Lake Ladoga-Neva estuary-Gulf of Finland (Panov *et al.*, 1999)

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References

- Berg D.J. & Garton D.W. (1994) Genetic differentiation in North American and European populations of the cladoceran *Bythotrephes*. *Limnology and Oceanography*, **39**, 1503–1516.
- Boileau M.G., Hebert P.D.N. & Schwartz S.S. (1992) Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *Journal of Evolutionary Biology*, **5**, 25–39.
- Cohen A.N. & Carlton J.T. (1998) Accelerating invasion rate in a highly invaded estuary. *Science*, **279**, 555–558.
- Cristescu M., Hebert P.D.N., Witt J.D.S., MacIsaac H.J. & Grigorovich I.A. (2001) An invasion history for *Cercopagis pengoi* based on mitochondrial gene sequences. *Limnology and Oceanography*, **46**, 224–229.
- De Meester L. (1996) Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. *Ecoscience*, **3**, 385–399.
- DeMelo R. & Hebert P.D.N. (1994) Founder effects and geographical variation in the invading cladoceran *Bosmina (Eubosmina) coregoni* Baird 1857 in North America. *Heredity*, **73**, 490–499.
- Hebert P.D.N. (1987) Genotypic characteristics of the Cladocera. *Hydrobiologia*, **145**, 183–193.
- Hebert P.D.N. & Beaton M.J. (1989) *Methodologies for Allozyme Analysis Using Cellulose Acetate Electrophoresis*. Helena Laboratories, Beaumont, TX, USA.
- Hedrick P.W. (1971) A new approach to measuring genetic similarity. *Evolution*, **25**, 276–280.
- Johannsson O.E., Mills E.L. & O’Gorman R. (1991) Changes in the nearshore and offshore zooplankton communities in Lake Ontario – 1981–88. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1546–1557.
- Krylov P.I., Bychenkov D.E., Panov V.E., Rodionova N.V. & 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.
- Leppäkoski E. (1993) Non-indigenous species in the Baltic Sea. In: *Introduced Species in European Coastal Waters* (Eds C.F. Boudouresque, F. Briand & C. Nolan), pp. 67–75. EC Environment Programme and CIESM International Workshop, Monaco.
- Lessios H.A. (1992) Testing electrophoretic data for agreement with Hardy–Weinberg expectations. *Marine Biology*, **112**, 517–523.
- MacIsaac H.J. (1999) Biological invasions of Lake Erie: past, present and future. In: *State of Lake Erie (SOLE): Past, Present and Future* (Ed. M. Munawar), pp. 305–322. Backhuys, Leiden, The Netherlands.
- MacIsaac H.J., Grigorovich I.A., Hoyle J.A., Yan N.D. & Panov V.E. (1999) Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran *Cercopagis pengoi*. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1–5.
- MacIsaac H.J., Ketelaars H.A.M., Grigorovich I.A., Ramcharan C. & Yan N.D. (2000) Modeling *Bythotrephes longimanus* invasions in the Great Lakes basin based on its European distribution. *Archiv für Hydrobiologie*, **149**, 1–21.
- MacIsaac H.J., Grigorovich I.A. & Ricciardi A. (2001) Reassessment of species invasions theory: Lake Erie as an example. *Biological Invasions* (in press).
- Miller M. (1998) *Tools for Population Genetic Analysis (TFPGA)*. Northern Arizona University, Flagstaff, AZ, USA. <http://herb.bio.nau.edu/~miller/tfpga.htm>
- Mills E.L., Leach J.H., Carlton J.T. & Secor C.L. (1993) Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research*, **19**, 1–54.
- Ojaveer H. & Lumberg A. (1995) On the role of *Cercopagis (Cercopagis) pengoi* (Ostroumov) in Parnu Bay and the NE part of the Gulf of Riga ecosystem. *Proceedings of the Estonian Academy of Science and Ecology*, **5**, 20–25.
- Panov V.E., Krylov P.I. & Telesh I.V. (1999) The St. Petersburg harbour profile. *Initial Risk Assessment of Alien Species in Nordic Coastal Waters*, Vol. 8 (Eds S. Gollasch & E. Leppakoski), pp. 225–244. Nordic Council of Ministers, Copenhagen.
- Ricciardi A. & MacIsaac H.J. (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology and Evolution*, **15**, 62–65.
- Smith B.R. & Tibbles J.J. (1980) Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1780–1801.
- Sprules W.G., Riessen H.P. & Jin E.H. (1990) Dynamics of the *Bythotrephes* invasion of the St. Lawrence Great Lakes. *Journal of Great Lakes Research*, **16**, 346–351.

- Swofford D.L. & Selander R.B. (1981) *Biosys-1: A Computer Program for the Analysis of Allelic Variation in Genetics*. University of Illinois, Urbana, IL, USA.
- Taylor D.J., Finston T.L. & Hebert P.D.N. (1994) The 15% solution for preservation. *Trends in Ecology and Evolution*, **9**, 230.
- Telesh I.V. (1995) Rotifer assemblages in the Neva Bay, Russia: principles of formation, present state and perspectives. *Hydrobiologia*, **313**, 57–62.
- Therriault T.W., Grigorovich I.A., Gristescu M.E., Kete-laars H.A.M., Viljanen M., Heath D.D. & MacIsaac H.J. (2002) Taxonomic resolution of the genus *Bythotrephes* Leydig using molecular markers and re-evaluation of its global distribution, with notes on factors affecting dispersal, establishment and abundance. *Diversity and Distributions* (in press).
- Vitousek P.M., D'Antonio C.M., Loope L.L., Rejmánek M. & Westbrooks R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, **21**, 1–16.
- Weider L.J. (1991) Allozymic variation in *Bythotrephes cederstroemi*; a recent invader of the Great Lakes. *Journal of Great Lakes Research*, **17**, 141–143.
- Yan N.D. & Pawson T.W. (1998) Seasonal variation in the size and abundance of the invading *Bythotrephes*. Harp Lake, Ontario, Canada. *Hydrobiologia*, **361**, 157–168.

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