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Research article

Implications of water ionic composition for invasion of euryhaline species in inland waters – an experimental study with *Cercopagis pengoi* from the Northern Baltic Sea

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Abstract

Osmoregulation efficiency greatly determines the settling of aquatic invasive species in a new environment. The successful establishment of invasive cladoceran *Cercopagis pengoi* in the North American Great Lakes raises the question about a possible invasion of this species from the Baltic Sea to freshwater bodies like the Finnish Lake District using canals and rivers as invasion corridors. However, major ion concentrations (Na^+, Ca^{2+}, Mg^{2+}, Cl^-, SO_4^{2-}) in Finnish and in many other North European fresh waters are much lower than those in the Great Lakes. In our study we compared the survival of nonacclimated *C. pengoi* in waters collected from the Baltic Sea and Lake Saimaa as well as in experimentally ion-enriched Lake Saimaa water, which resembles the ion characteristics of the waters of the Great Lakes colonized by *C. pengoi*. In short-term experiments (24 and 56 h), the survival of *C. pengoi* was poor in Lake Saimaa water compared with Baltic Sea or enriched Lake Saimaa water. LT_{50} was lowest in Lake Saimaa water (9.51 h), followed by Baltic Sea water (18.4 h) and enriched Lake Saimaa water (20.5 h). Furthermore, single ion additions improved survival in Lake Saimaa water. According to this preliminary study, imminent invasion of *C. pengoi* to freshwater systems with low concentrations of major ions appears unlikely. However, the impact of adaptation on the survival and dispersion of *C. pengoi* remains open.

Key words: *Cercopagis pengoi*, osmoregulation, Baltic Sea, Finnish Lake District, Great Lakes

Introduction

Cercopagis pengoi is a predatory cladoceran species of Ponto-Caspian origin. In the Baltic Sea, this species was detected for the first time in 1992 (Ojaveer and Lumberg 1995). As an opportunistic invader, the spread of *C. pengoi* has been fast, and today this species inhabits most areas of the Baltic Sea (Gorokhova et al. 2000, Litvinchuk and Telesh 2006, Olszewska 2006, Panov et al. 2007). According to the genetic studies of Cristescu et al. (2001), the invasion corridor to the North American Great Lakes runs via the Baltic Sea.

The effects of *C. pengoi* on the zooplankton community structure have been observed as decreased abundance of small herbivorous zooplankton species in the Baltic Sea and in the Great Lakes, especially when the biomass of *C. pengoi* is high (e.g. Laxson et al. 2003, Ojaveer et al. 2004, Litvinchuk and Telesh 2006). *C. pengoi* preys on small zooplankton species as well as on juvenile copepods (Rivier 1998). *C. pengoi* is an important prey for fish, especially for Baltic herring (e.g. Antsulevich and Välipakka 2000), while simultaneously appearing to compete with fish for food sources (Gorokhova et al. 2005).

The establishment of *C. pengoi* in the Great Lakes and its adaptability to various environmental conditions have raised the question about the risk of invasion of this species to the Finnish Lake District. This large freshwater system (area ca. 10,460 km^2) is connected to the Baltic Sea via the Saimaa Canal, allowing cargo ships entry to the inland ports. Moreover, pleasure boats use the Saimaa Canal as a passage between the Baltic Sea and Finnish lakes. In Sweden, several inland lakes, including Lake Vänern, Europe's third largest lake, and Lake Mälaren, are also connected to the Baltic Sea (Figure 1). In a risk assessment by Pienimäki and Leppäkoski (2004), which was based on literature references, the authors listed 29 nonindigenous species with the potential for introduction and establishment in Finnish lakes, six of these with a high probability, including *C. pengoi*.

Environmental conditions together with species-specific physiological characteristics set natural barriers for dispersal and invasion of nonindigenous species. Limited osmoregulation capacity is one of the barriers hindering transfer between marine and freshwater environments. *C. pengoi* is an euryhaline organism capable of hyperosmotic regulation in brackish and fresh waters (Aladin 1982, Aladin and Potts 1995). Although *C. pengoi* inhabits fresh waters of several Laurentian Great Lakes, the concentrations of major ions in these lake waters differ greatly from those found in the Finnish Lake District and in several other Scandinavian lakes. Water in these lakes is predominantly very "soft", with low ion concentrations (Table 1). Lake Superior also has low ion concentrations and fewer established nonindigenous species than Lake Ontario. According to Grigorovich et al. (2003), one reason for its lower invasibility might be the low calcium concentration in this lake.

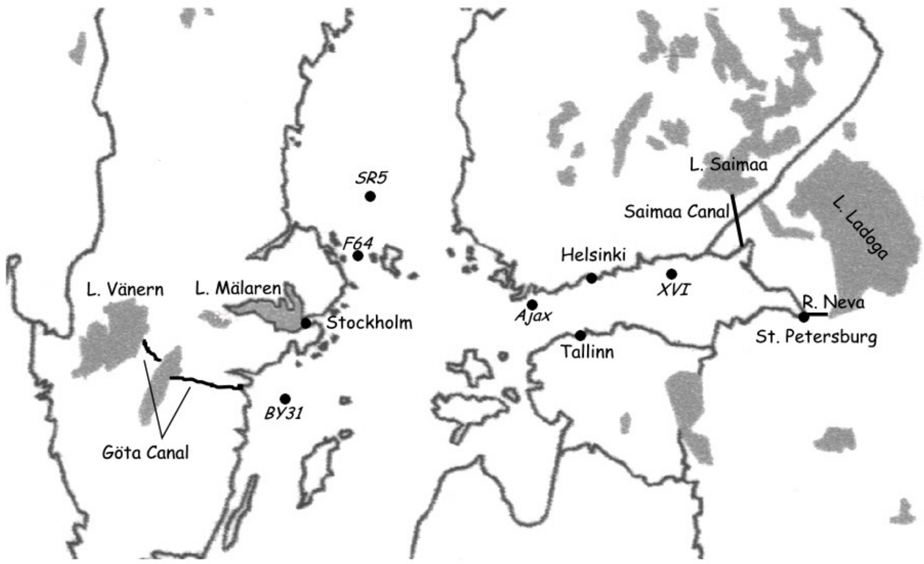

Figure 1. Study area and description of selected freshwater waterways around the Northern Baltic Sea

Table 1. Concentrations of major ions (mg l^{-1}) in selected water bodies. Values are taken from the Atlas of the UN Global Environment Monitoring System - Water Programme, Tables 5 and 7. Osmolarity was calculated by adding the molar concentrations of all major ions present. The equivalent value is equal to the molarity multiplied by the valence of the ion. Values from our study are indicated by asterisks. Water bodies with established *C. pengoi* populations are indicated in boldface

	Mg^{2+}	Ca^{2+}	Na^{+} mg l^{-1}	K^{+}	SO_4^{2-}	Cl^{-}	Osmolarity mOsm l^{-1}	Equivalent mEq l^{-1}
***Baltic Sea**	240	98	1800	67	410	3000	181.2	197.8
*Lake Saimaa	1.3	5.2	4.4	1.3	9.5	3.0	0.591	0.846
*Enriched Lake Saimaa water	6.8	17.0	16.0	1.3	34.0	17.0	2.26	3.31
River Neva	2.5	9.8	3.0	1.5	9.6	6.8	0.807	1.25
Lake Ladoga	2.5	9.8	3.0	1.5	6.8	9.6	0.857	1.26
Lake Vänern	1.4	8.0	6.6	1.2	17.5	6.8	0.948	1.39
Lake Superior	2.8	12.4	1.1	0.6	3.2	1.9	0.574	1.04
Lake Huron	6.7	28.1	3.2	0.8	17.2	6.3	1.49	2.47
Lake Michigan	10.0	32.0	3.4	0.9	15.5	6.2	1.72	3.09
Lake Erie	8.3	37.4	11.5	1.2	25.7	24.5	2.76	4.30
Lake Ontario	8.1	40.3	12.6	1.4	29.4	27.5	3.00	4.62
River Dniepr	7.5	22.5	8.0	3.0	35.8	15.2	2.09	3.33
River Volga	9.9	50.2	17.9	1.6	62.1	18.9	3.66	5.96
Caspian Sea	756	381	3096	67	3000	5280	356.9	428.6

Although research on osmoregulatory capacity of cladocerans has been carried out in both freshwater and marine environments (Aladin 1982, Aladin 1991 and references therein, Aladin and Potts 1995), the roles of ion composition and concentrations in the survival of *C. pengoi* in fresh waters remain unclear. We therefore decided to collect more information by comparing the survival of *C. pengoi* in different ionic environments, namely in the natural waters of the Baltic Sea (BSW) and Lake Saimaa (LSW) and in ion-enriched Lake Saimaa water (ELSW) adjusted to correspond to the major ion characteristics of the Great Lakes colonized by *C. pengoi*. The aims of this study were thus to examine the role of water chemistry underlying the establishment of nonindigenous species, and the risk of *C. pengoi* invasion in the Finnish Lake District and in other soft freshwater environments.

Methods

Sampling of material

Sampling was conducted by vertical hauls (50 – 0 m) using a 200 µm WP-2 net equipped with a closed cod end at sampling stations XV1, AJAX, BY31, F64, and SR5 in the northern Baltic Sea in August 2005 (Figure 1). Animals were separated under a microscope from pooled samples of 3 to 6 hauls, put into small vials containing filtered BSW, and kept at 15°C in a temperature-controlled room for 12 h before the experiments. Parthenogenic females, mainly instars II-III (80-100%) with a few instar I individuals (0-20%), were selected for the experiments.

Salinity and temperature were measured by CTD-casts (Conductivity-Temperature-Density sonde, Seabird, SBE 911), according to accredited methods used at the Finnish Institute of Marine Research. Salinity of LSW was measured with a salinometer (Autosal Model 8400), with a detection limit of 0.2. Salinity values are expressed according to Practical Salinity Scale (psu), which is a dimensionless unit.

Surface water (1 m) from LSW was collected at station 28 situated in open, southern Lake Saimaa (67.8938°N, 35.8060°E), with a bottom depth of 20 m.

Experimental conditions

Before the experiments, natural waters were filtered through a glass microfiber filter (Whatman GF/C). Waters used in the experiments were prepared as follows:

1) Surface water (1 m) from Lake Saimaa (= LSW).
2) Surface water (1 m) from the Baltic Sea (= BSW).
3) Filtered LSW was enriched with different combinations of $MgCl_2$, $MgSO_4$, $CaSO_4$, $CaCl_2$, NaCl, $NaHCO_3$, or with all salts mentioned above (= ELSW). The addition of ions was based on the concentrations found in Lake Ontario. Potassium was excluded because the ion concentration did not differ markedly between Lake Saimaa and Lake Ontario (Table 1).

Ion concentrations in experimental media were analyzed in an accredited water laboratory, Saimaan Vesiensuojeluyhdistys, according to SFS-EN-ISO 10301 (Cl^- and SO_4^{-2}) and SFS-EN-ISO 14911 (Na^+, K^+, Ca^{2+}, and Mg^{2+}) standards. The measured ion concentrations are listed in Table 2.

Table 2. Ion concentrations (mg l^{-1}) of waters used in the experiments. Osmolarity and equivalent values are calculated as described in Table 1

Water/ added salt	Mg^{2+}	Ca^{2+}	Na^+	K^+	SO_4^{-2}	Cl^-	Osmolarity mOsm l^{-1}	Equivalent mEq l^{-1}
BSW	240	98	1800	67	410	3000	181.2	197.7
LSW	1.3	5.2	4.4	1.3	9.5	3.0	0.591	0.846
ELSW	6.8	17.0	16.0	1.3	34.0	17.0	2.26	3.08
$CaSO_4$	1.3	25.0	4.4	1.3	33.0	3.0	1.36	2.38
$CaCl_2$	1.3	23.0	4.4	1.3	9.5	16.0	1.44	2.16
$MgCl_2$	8.4	5.2	5.2	1.3	9.5	21.0	1.43	2.00
$MgSO_4$	8.5	5.2	4.4	1.3	32.0	3.0	1.12	1.93
NaCl	1.3	5.2	14.0	1.3	9.5	16.0	1.37	1.66
$NaHCO_3$	1.3	5.2	15.0	1.3	9.5	3.0	1.05	1.33

Before the experiments, the viability of animals was checked under a microscope before transferring them one by one into 15 ml glass vials. The same handling procedure was applied in all experiments. No previous acclimation to the test medium was used. Each vial contained one or two animals depending on their availability. The vials were kept at a temperature of 15°C for 24 or 56 h (station F64 only) in dim light conditions. Animals were not fed during the experiment. Mortality was determined as in Kivivuori and Lahdes (1996) for *Daphnia magna*. The viability of the animals was checked every 2 or 4 h by gently agitating the tube for 15 s. The criterion for death was met when thoracopod movement ceased. Animals were followed throughout the experiments, and time of death was recorded at the check-point when limb movement did not appear. The number of replicate experiments and the animals used in the experiments are shown in Table 4A-C.

Statistics

The time (in hours) at which 50% of the animals had died (LT50), with 95% confidence limits, was calculated with PROBIT analysis according to Finney (1971) using a computer program from the Swedish National Environmental Agency. The significance of differences in mortality between treatments and stations was tested with One Way Analysis of Variance (ANOVA). Comparisons between two treatments were calculated with a parametric t-test for normally distributed groups and a nonparametric Mann-Whitney Rank Sum Test for nonnormally distributed groups. In statistical treatments, the computer program SigmaStat for Windows (2.0) was used. The level of significance was set at 5% ($P < 0.05$).

Results

Salinity of the surface water at the sampling stations varied between 4.1 and 5.7, and temperature between 16.4°C and 18.3°C (Table 3). The salinity of LSW was < 0.2 and the pH 7.2. In the Baltic Sea, pH of the surface water varies between 8.3 and 8.5 (Data Register of the Finnish Institute of Marine Research).

Table 3. Water depth, salinity, and temperature of the surface water at sampling stations

Station	Depth (m)	Salinity (psu)	Temperature (°C)
St. 28	20	< 0.2	19.3
XV1	64	4.06	18.3
AJAX	60	5.43	17.1
BY31	446	5.75	16.4
F64	285	5.54	16.4
SR5	126	5.57	16.4

In the northern parts of the Baltic Sea, the maximum biomass of *C. pengoi* is reached when seawater temperature is at its highest, usually in late July – August, or even in September (e.g. Krylov et al. 1999, Ojaveer et al. 2004). In 2005, however, warm weather already in June (water temperature 16°C in mid-June) probably caused an earlier occurrence of the cladocerans. During the sampling occasions in mid-August numerous dead animals were found. The population may have already been in the declining phase, and the physiological condition of the animals was sub-optimal, except at station F64 in the Åland Sea. The good condition of *C. pengoi* at station F64 allowed the duration of the experiment to be prolonged to 56 h, the other experiments being 24 h each. After the first shock phase caused by the acute transfer of animals to the test medium, a plateau in mortality rate was reached. Survival of *C. pengoi* decreased drastically after 18-h and 45-h exposures in the 24-h and 56-h experiments, respectively (Figures 2 and 3).

Statistical analysis revealed no significant difference between survival rates measured at sampling stations XV1, AJAX, BY31, and SR5 in exposures to LSW ($P = 0.083$, $n = 4$), BSW ($P = 0.228$, $n = 3$), or ELSW ($P = 0.154$, $n = 3$). Results were therefore pooled for subsequent statistical analyses. Due to the different exposure time, data from F64 were treated separately.

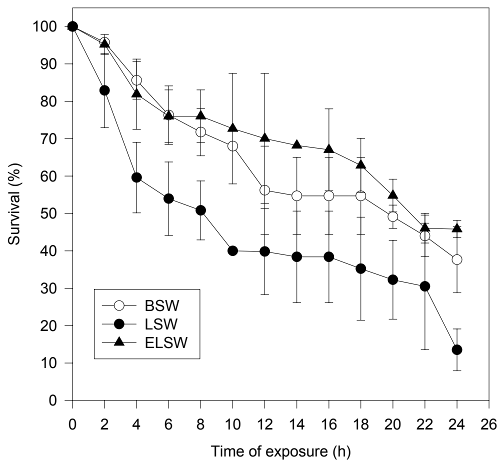

Figure 2. Survival (%) of *Cercopagis pengoi* exposed to BSW, LSW, and ELSW for 24 h. Values are mean ± SE for three replicates for BSW and ELSW and four replicates for LSW based on pooled data collected at sampling stations XV1, AJAX, BY31, and SR5 (see Table 4A)

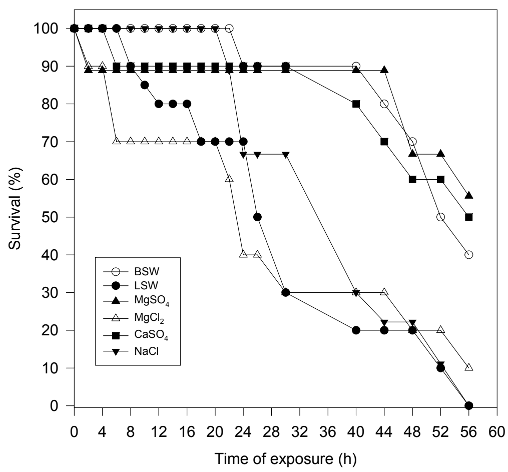

Figure 3. Survival of *Cercopagis pengoi* exposed to different ionic conditions for 56 h at station F64 in the Åland Sea (see Table 4C)

The time (in hours) in which 50% of the animals had died, LT_{50}, calculated for the pooled data was shortest in LSW (9.51 h), followed by BSW (18.4 h) and ELSW (20.5 h) (Table 4A). Analysis of the data showed that there was a significant difference in mortality between LSW and ELSW ($P = <0.001$***, $df = 70$) and a less significant difference between LSW and BSW (P

= 0.008**, df = 72). By contrast, no significant difference was observed between ELSW and BSW (P = 0.408, df = 58).

Table 4. LT_{50} (24 h) and 95% lower and upper confidence limits calculated from A) pooled data of the sampling stations XV1, AJAX, BY31, and SR5, B) data of sampling station BY31, and
C) LT50 (56 h) and 95% lower and upper confidence limits calculated from data of sampling station F64
(NE – number of experiments, NA – number of animals)

A)

Exposure medium	LT_{50} (h)	Lower (h)	Upper (h)	NE	NA
LSW	9.51	3.39	11.36	4	85
BSW	18.40	17.17	19.89	3	82
ELSW	20.51	18.39	23.51	3	49

B)

Enrich-ment of LSW	LT_{50} (h)	Lower (h)	Upper (h)	NE	NA
LSW	5.68	-1.08	9.50	1	22
$NaHCO_3$	13.70	11.76	15.89	1	22
$CaCl_2$	15.68	10.45	27.64	1	18
$MgSO_4$	16.42	10.45	27.64	1	20
ELSW	21.83	18.12	28.36	1	22
BSW	22.32	19.06	28.18	1	20

C)

Enrich-ment of LSW	LT_{50} (h)	Lower (h)	Upper (h)	NE	NA
$MgCl_2$	26.27	21.39	31.75	1	10
LSW	28.26	24.85	32.15	1	10
NaCl	33.80	30.54	37.58	1	10
BSW	54.06	48.42	64.12	1	10
$CaSO_4$	61.28	49.54	89.38	1	10
$MgSO_4$	74.82	54.52	162.80	1	10

At two stations, BY31 and F64, higher availability of the animals allowed experiments with different ion combinations. At station BY31 (Table 4B), survival time increased as follows: LSW < $NaHCO_3$-enriched LSW < $CaCl_2$-enriched LSW < $MgSO_4$-enriched LSW < ELSW < BSW. Table 4C shows the corresponding values for the 56-h experiment at station F64. The shortest survival times arose with exposures to $MgCl_2$-enriched LSW and LSW (26.3 and 28.3 h) and the longest with $CaSO_4$- and $MgSO_4$-enriched LSW (61.3 and 74.8 h), respectively. The survival time in BSW was 54.1 h.

Analyses presented in Tables 5 and 6 for experiments performed at stations BY 31 and F64 show significant differences in mortality between LSW, BSW, and ELSW treatments as well as in LSW-enriched with solely $MgSO_4$, $CaSO_4$, or $CaCl_2$. Enrichments with $NaHCO_3$, $MgCl_2$, or NaCl were less effective in improving viability (Figure 3).

Discussion

The common assumption that invasive species have broad physiological tolerance of has rarely been tested (Lee and Petersen 2003). *Cercopagis pengoi* colonizes various freshwater and brackish water environments, but the characteristics of the osmoregulative capacity of this species in soft fresh water are unknown. This study is a first attempt to examine the effects of limiting ions, their concentrations, and their combinations on the survival of *C. pengoi* in fresh water. Similar studies have been performed with the invasive zebra mussel, *Dreissena polymorpha*, where the effects of several chemical parameters on successful establishment of this species were tested (e.g. Dietz et al. 1994, Hincks and Mackie 1997). Negative growth and high mortality at calcium levels below 8.5 mg l^{-1} and maximum growth at levels of 32 mg l^{-1} were observed. These conditions occur in the Baltic Sea but not in the soft waters of Finnish lakes (Table 1, Mannio et al. 1998).

The significance of salinity in the distribution of aquatic animals is well known (e.g. Willmer et al. 2000). In fact, salinity together with temperature are the most powerful physico-chemical determinants of survival in aquatic invertebrates. The basis for this lies in the structural and functional characteristics of biological membranes and their adaptability to changes in the environment (Hazel and Williams 1990). MacIsaac et al. (2001) hypothesized about the role of salinity in the recent invasions of nonindigenous species in the Great Lakes. Although the salinity of Lake Ontario slightly increased in the 1900s, changes in salinity alone cannot account for the increasing rate of invasions by Ponto-Caspian invaders in the Great Lakes.

Table 5. Statistical analyses of survival time after different treatments at station BY 31. Statistical significance is indicated as *** = P<0.001, ** = P<0.01, * = P<0.05, or ns = not significant. For numbers of animals, see Table 4B

	BSW	$MgSO_4$	$CaCl_2$	$NaHCO_3$	ELSW
LSW					
P	< 0.001***	0.013*	0.016*	0.086 ns	0.002**
df	18	18	18	18	18
BSW					
P	-	0.038*	0.022*	0.077 ns	0.543 ns
df	-	18	18	18	18

Table 6. Statistical analyses of survival time after different treatments at station F64. Statistical significance is indicated as *** = P<0.001, ** = P<0.01, * = P<0.05, or ns = not significant. For numbers of animals, see Table 4C

	BSW	$MgSO_4$	$CaSO_4$	$MgCl_2$	NaCl
LSW					
P	0.007**	0.074 ns	0.050*	0.516 ns	0.289 ns
df	34	34	34	34	34
BSW					
P		0.074 ns	0.106 ns	<0.001***	0.070ns
df		34	34	34	34

While lakes and rivers are generally classified as freshwater environments (salinity < 0.5 psu), substantial differences exist in chemical properties between freshwater systems. In Table 1, the major ion concentrations in selected water bodies are compared (UNEP/GEMS/Water). Conversions of weight units to milliosmoles and milliequivalents were done in order to be comparable with the units typically used in physiology and in the evaluation of water quality. Waters of Lake Saimaa, Lake Superior, Lake Ladoga, and Lake Vänern have clearly lower ion concentrations than Lake Ontario, Lake Erie, or Lake Michigan. Interestingly, the last three lakes have an established *C. pengoi* population, while no observations of this invader species have yet been made in first-mentioned lakes (NOBANIS Database, USGS/NAS Database). In some reservoirs of the River Dniepr, where *C. pengoi* does appear (MacIsaac et al. 1999), ion concentrations are approximately the same as in Lake Ontario (Table 1).

When comparing the establishment of *C. pengoi* in European and North American fresh waters with the corresponding ion concentrations of these waters (Table 1), this species appears in water bodies where the concentrations of ions are greater than 1.5 mOsm l^{-1} or 3 mEq l^{-1}. Not only the major ion concentrations but also overall chemical composition is important, which further complicates the evaluation of invasion success. For example, *C. pengoi* does not at present appear in Lake Huron, in contrast to the neighboring Lakes Michigan and Erie, where ion concentrations are only slightly higher (see Table 1). Moreover, in our experiments, survival was not always correlated with medium concentration (Table 2, Figure 3). Correlation was better in 24-h (BY31) than 56-h (F64) experiments.

Calcium and magnesium ions combined with sulfate ions seem to improve the survival of *C. pengoi* more than when combined with chloride ions. This may be related to the behavior of potassium, sodium, chloride, and magnesium ions in extra- and intracellular solutes and in the functioning of membrane pumps and channels. In living tissues, Na^+ and Cl^- concentrations are higher and Mg^{2+} concentrations lower in extracellular than intracellular compartments. The roles of ion concentrations, limiting ions, and the ratios of mono- and divalent ions in *Cercopagis* physiology warrant further research. Possible synergetic effects of other factors, such as pH, trace metals, and content of organic matter, might also have an impact on survival.

The relevance of methods used in exposure tests has been discussed by Lahdes (2002) in connection with the measurement of temperature tolerance of crustaceans. In general, acute transfer to new conditions results in higher mortality rates than gradual transfer. The same conclusions apply to other tolerance tests, including salinity tolerance, as well. Acute transfer in our study is justified because it simulates conditions in which ballast water containing organisms is discharged into new environmental conditions. It should be noted, however, that in the long-term, after the first shock phase, differences in mortality values obtained by these methods approach each other, as shown by Lee and Petersen (2003) in the copepod *Eurytemora affinis*. Use of short-term exposure tests without previous acclimation in preliminary studies thus gives an estimation of the adaptability behavior of an organism, which was the one of the aims in our study. Gradual physiological adjustment to an environmental change (acclimation in laboratory conditions, acclimatization in natural conditions) is a phenotypic response, which is nonheritable (Willmer et al. 2000). Acclimation studies allow us to only discover the physiological plasticity determined by the genotype. Comprehensive understanding of the role of adaptation is essential in predicting permanent establishment of an invasive species in a new environment. To verify adaptive changes in osmoregulation capacity, series of long-term experiments on reproduction, development (including resting eggs), and physiological functions in different ionic conditions are needed, similarly to those conducted in evaluation of salinity tolerance in ciliate *Paramecium* (Smurov and Fokin 2001), homarid lobsters (Charmantier et al. 2001), and resting eggs (Bailey et al. 2003), or in evaluation of temperature tolerance polygons in fish (Cossins and Bowler 1987 and references herein). Especially the role of diapause in osmoregulative adaptation of invaders needs more attention (Panov and Caceres 2007).

In conclusion, while the survival of *C. pengoi* was very poor in our short-term laboratory experiments, a certain risk remains that this species will be introduced to soft freshwater systems like Lake Saimaa. Adequate concentrations of calcium, magnesium, potassium, and sodium salts are needed to ensure the survival of *C. pengoi* in fresh waters. Accordingly, the composition and concentrations of ions in lake waters may form a barrier against further spread of *C. pengoi* to freshwater habitats. More studies are needed to determine critical concentrations of ions and their combinations as well as the adaptive ability essential for successful establishment of this species in different freshwater ecosystems.

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