Tolerance of *Paramysis lacustris* and *Limnomysis benedeni* (Crustacea, Mysida) to sudden salinity changes: implications for ballast water treatment*

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Abstract

In order to draw implications for ballast water management, we tested the tolerance of two Ponto-Caspian mysid species *Paramysis lacustris* and *Limnomysis benedeni* to sudden salinity changes. The naturally stenohaline *P. lacustris* was more susceptible to higher salinities; its mortality rate at 19 PSU was 60%, whereas exposure to 23 PSU was 100% lethal. The euryhaline *L. benedeni* survived in salinities of up to 19 PSU, but experienced 100% mortality at 34 PSU. The return of both mysid species to fresh water after the 24 h exposure to higher salinities did not

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prevent further mortality. Considering the rather high short-term salinity tolerance of both species, a salinity of at least 30 PSU should be used as an appropriate biocide.

1. Introduction

The brackish water fauna of the Ponto-Caspian region (the Black Sea, the Caspian Sea, the Sea of Azov) has come to the attention of the scientific community as major invaders of aquatic ecosystems in Europe and North America (Leppäkoski & Olenin 2001, Vaate et al. 2002, Vanderploeg et al. 2002). In particular, crustaceans and molluscs from the Ponto-Caspian basin have turned out to be successful invaders (Devin et al. 2004), and their broad salinity tolerance has been suggested as an important factor enabling their spread (Reid & Orlova 2002). Indeed, salinity is one of the first abiotic factors that non-indigenous organisms encounter in new ecosystems, especially when transported by ballast waters. Most of the world's coastal ports are brackish water habitats (0.5 to 18 PSU), and transfer of organisms among ports constitutes a major source of invasions (Paavola et al. 2005). Replacing ballast waters in open ocean waters, or 200 nautical miles (370.4 km) from the shore has therefore been suggested as an efficient means of ballast water treatment (IMO 1997). In the brackish Baltic Sea, ballast waters should be replaced before a vessel enters the sea (Gollasch 2002), as even in its central part the surface water salinity is only 7–8 PSU (Stigebrandt 2001). Such strict management is particularly important in the Baltic Sea in view of the catastrophic increase of non-indigenous species in this enclosed ecosystem (Leppäkoski et al. 2002). Furthermore, given the intensity of shipping between the Baltic and other world ports, e.g. in the North American Great Lakes, the Baltic Sea is likely to be a stepping stone for further invasions (Cristescu et al. 2001, Panov et al. 2002, Szaniawska et al. 2003).

Introductions of Ponto-Caspian crustaceans into the Baltic Sea dates back to at least the 1960s, when a number of Ponto-Caspian mysid and amphipod species were transplanted into eastern European waters for fish food enrichment purposes (Ioffe 1973). Three taxa of mysid crustaceans, *Limnomysis benedeni*, *Paramysis lacustris* and *Hemimysis anomala*, were introduced to Lithuania; the former two soon established dense populations in the brackish Curonian Lagoon (Fig. 1) (Gasiunas 1972, Arbaciauskas 2002). Furthermore, *L. benedeni* and *H. anomala* have recently expanded their distributions along the Baltic Sea coasts and European rivers, occasionally reaching very high densities in their new habitats (Leppäkoski 1984, Wittmann 1995, Schleuter et al. 1998, Kelleher et al. 1999, Ketelaars et al. 1999, Wittmann et al. 1999, Weidema 2000,

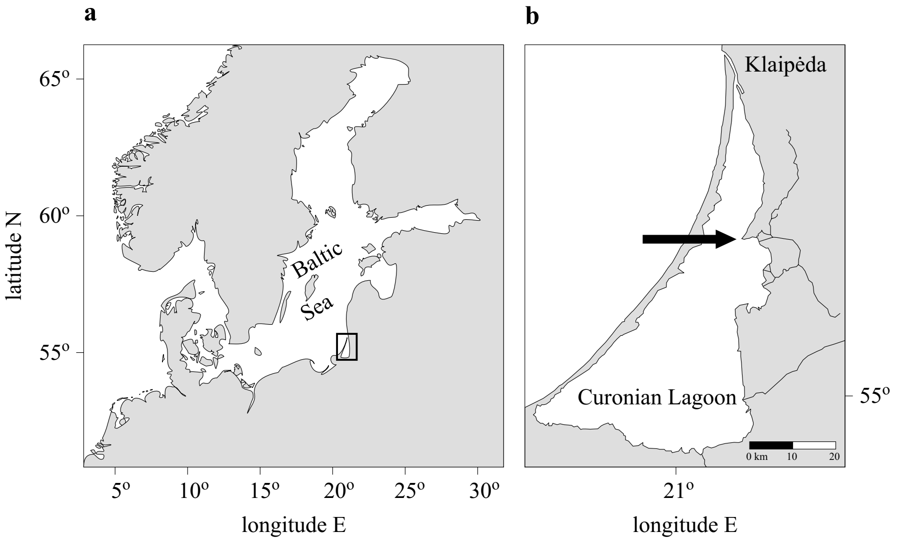

Fig. 1. Map of the Baltic Sea indicating the Curonian Lagoon (a). Collection site of *Paramysis lacustris* and *Limnomysis benedeni* in the Curonian Lagoon (b)

Wittmann & Ariani 2000, Zettler 2002). The third species, *P. lacustris*, has not yet been recorded in any new sites.

The aim of this study was to assess the short-term (24 h) tolerance of two Ponto-Caspian mysid taxa – *L. benedeni* and *P. lacustris* – to sudden salinity changes. These two species are nowadays widespread in the Curonian Lagoon and in the vicinity of the port of Klaipėda, and frequently occur in salinities of up to 7 PSU (Lazauskiene et al. 1995). *Paramysis sp.* have been found in ballast waters (Gollasch et al. 2002) and *L. benedeni* has been recorded on ship hulls (Wittmann et al. 1999), which demonstrates their potential for further invasions. In their natural habitats of the northern Ponto-Caspian region *L. benedeni* is one of the most euryhaline taxa and is found in salinities of 0–14 PSU, whereas *P. lacustris* is stenohaline and typically occurs in 0–3 PSU (Komarova 1991, Daneliya 2002). These species thus provide a good model system for testing the limits of salinity tolerance of brackish water species with different natural salinity preferences, which could be applicable to other brackish-water Ponto-Caspian taxa as well.

2. Material and methods

The experimental work was carried out in September–October 2004. Experiments were first conducted with *P. lacustris,* and after one week, with *L. benedeni.* Separate collections were made for each experiment. Mysids were collected in the central part of the Curonian Lagoon, where the water is nearly fresh and salinity fluctuations are negligible. The collected mysids were transported to the laboratory, gently inspected and sexed under a stereomicroscope and placed in experimental vessels. Each experimental vessel contained 3 litres of ambient water from the collection site and ten mysid specimens. After a 24 h adaptation period, dead specimens (mysids not responding to mechanical touch) were replaced with living ones that had been acclimatised in the same conditions. Survival after an instantaneous salinity increase was tested for six different salinity concentrations: 7, 11, 15, 19, 23 and 34 PSU; the 34 PSU concentration was used only for the euryhaline *L. benedeni*. For the sudden salinity increase, the ambient water in the vessels was replaced by water of different salinity concentrations, and three replicates were used for each sex and salinity value + control (Fig. 2). Water of different salinity concentrations was made by mixing the ambient water with artificial sea salt (Bio Marine Ltd); the salinity was checked with a conductometer. At the end of the 24 h exposure to higher salinities, the mysids were counted, their viability assessed as above (response to touch), and the water in the vessels replaced with an equivalent amount of filtered ambient (fresh) water. In order to make a proper statistical comparison prior to the salinity decrease experimental step, the number of specimens in each vessel was reduced to six. If fewer than six specimens survived the salinity increase step in at least one replicate of each sex/salinity value, the treatment was discarded from the salinity decrease step. After 24 h exposure to fresh water, the mysids were counted, their viability assessed, and the experiment was terminated. Throughout the experiment the mysids were kept at a constant temperature (18°C), at a constant oxygen concentration (9 mg dm^{-3}) and in darkness; they were not fed.

Statistical analysis of the two experimental steps, i.e. salinity increase and salinity decrease, was conducted separately and the number of surviving individuals was compared among treatments. Normality and homogeneity of variance of the data were tested using Bartlett's test (using the significance value $\alpha = 0.05$) (Sokal & Rohlf 1995). Since the test showed significant deviations from homoscedasticity ($p = 0.00$), the data was transformed by dividing the original counts of surviving individuals in each treatment by the standard deviation of survival counts in each salinity group, e.g. standard deviation of survival of both species and both sexes from 7 (11, 15, etc.) PSU. Analysis of variance (ANOVA) was conducted on the transformed data to assess the effects of salinity, species and sex on survival. Interaction among the factors was tested for the salinity increase step; such an assessment was not possible for the salinity decrease step owing to strong mortality during the first step (see results). Difference in survival was tested using

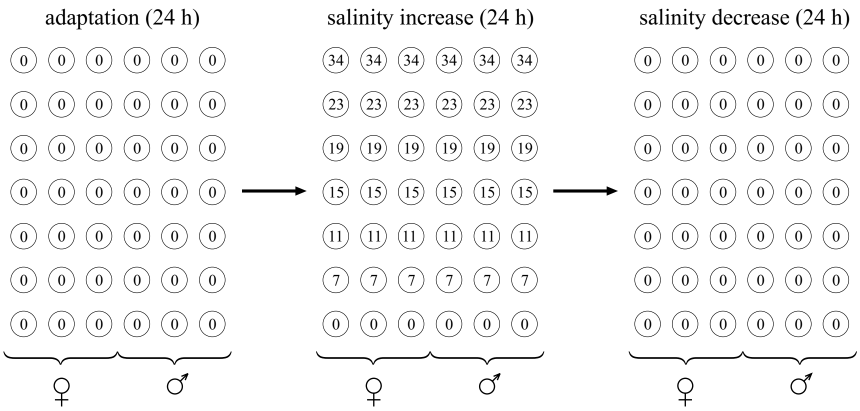

Fig. 2. Scheme of the experimental design, identical for both species (for details see methods). Circles represent experimental vessels and the numbers in the circles show applied salinity values [PSU]. The 34 PSU salinity treatment was used only for *Limnomysis benedeni*

Tukey's honest significance difference (HSD) test (Quinn & Keough 2002) and in pair-wise comparisons (Student's *t*-test) of sexes of the same species or between species at the same salinity value.

3. Results

Mortality rates of the mysids in the control treatments were small (one specimen on average), which showed that handling of the mysids during the experiment did not greatly affect survival (Fig. 3a). Both salinity and species factors had a significant effect on survival in ANOVA ($p < 0.05$), but the overall effect of sex was not significant ($p = 0.45$) (Table 1). No significant interaction among the three factors was seen for the salinity increase step ($p = 0.34$) (Table 1). *P. lacustris* was more susceptible to increases in salinity than *L. benedeni*, and survival rates differed ($p < 0.05$) between the two species for salinity increases to 15, 19, 23 PSU (Fig. 3a). Considerable mortality of *P. lacustris* (20%) was evident already at 15 PSU, 60% mortality was reached at 19 PSU and 100% mortality at 23 PSU. At 19 PSU, survival of male and female *P. lacustris* was different, even if no overall effect of sex on the survival was indicated by ANOVA. Only c. 10% of *P. lacustris* males survived the salinity increase to 19 PSU, whereas female survival was c. 70% ($p < 0.00$). For *L. benedeni,* 10% mortality was observed at 19 PSU, 30% at 23 PSU, while transfer to the 34 PSU water caused 100% mortality. No difference in survival was observed between the sexes of *L. benedeni* in any treatment ($p > 0.1$ in *t*-tests for each salinity value).

Table 1. Effects of salinity, species and sex on survival of *Paramysis lacustris* and *Limnomysis benedeni* after an instantaneous salinity increase (24 h exposure) and a subsequent decrease (24 h exposure); results of the multifactor analysis of variance

Factors	Salinity increase			Salinity decrease		
	df	*F*	*p*	*df*	*F*	*p*
salinity(A)	5	3298.29	0.000	5	737.16	0.0000
species (B)	1	39.94	0.000	1	5.80	0.0196
sex (C)	1	0.55	0.461	1	0.59	0.4454
interaction						
A × B	5	1.13	0.358			
A × C	5	1.88	0.114			
B × C	1	1.08	0.303			
A × B × C	5	1.17	0.338			
residual	48			52		
Total	71			59		

df – degrees of freedom, *p* – significance value, *F* – *F* ratio.

Returning the mysids to fresh water in the second experimental step did not stop the mortality caused by the sudden salinity increases; the linear correlation between the salinity experienced in the first experimental step and survival during the second step was -0.83 ($p = 0.00$). Thus 20% of *P. lacustris* females from the 19 PSU treatment survived the 24 h desalination step, and in *L. benedeni* the same was seen after the 23 PSU treatment (Fig. 3b).

4. Discussion

As expected, *L. benedeni* is more tolerant to sudden salinity changes than *P. lacustris*. A mortality rate of 20% or more during the 24 h exposure was observed already at 15 PSU in *P. lacustris*, but only at 23 PSU in *L. benedeni*. The critical salinity values of short-term survival determined in experimental conditions are typically considerably higher than the upper limits of salinity in the natural distribution areas (Khlebovich 1974, Karpevitch 1975, but see Kefford et al. 2004 for a different opinion). For instance, for Onychopoda crustaceans *Evadne anonyx* and *Podonevadne trigodna* this difference was about 5 PSU (Aladin 1995), for isopod crustaceans *Asellus aquaticus* it was 7 PSU and for bivalves *Dreissena polymorpha* 3 PSU (Khlebovich 1974).

In the case of the Ponto-Caspian mysids, the mortality of *P. lacustris* in experimental conditions was higher at 15 PSU, although in its natural

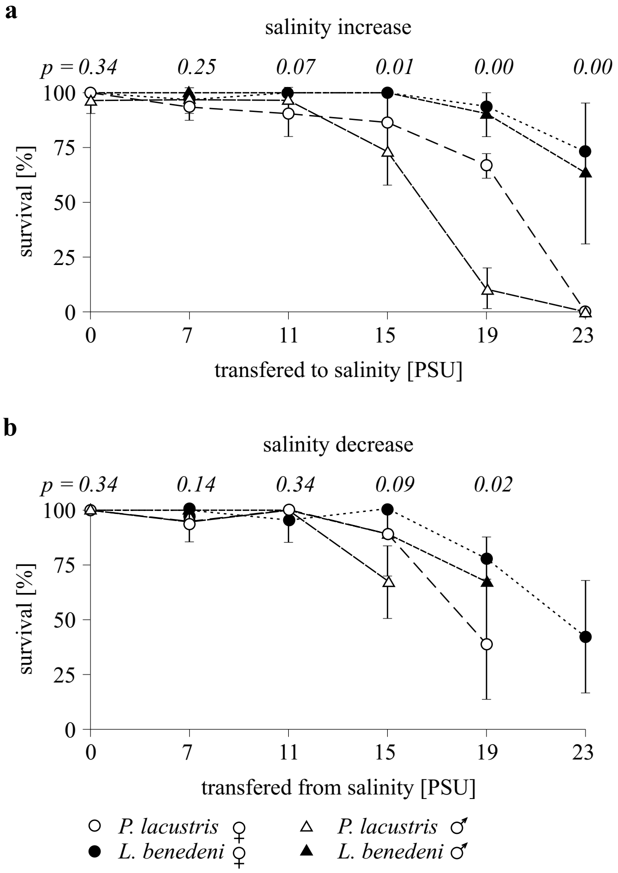

Fig. 3. Survival rates of *Paramysis lacustris* and *Limnomysis benedeni* specimens after instantaneously raised salinities (a) and the subsequent exposure to fresh water conditions (b). Error bars represent one standard deviation ($n = 3$). Significance values p apply to the difference between the species

habitats the species is typically confined to salinities of less than 3 PSU (Daneliya 2002). For *L. benedeni* the corresponding critical salinity during the experiment was 19–23 PSU, whereas it is known to occur naturally in waters of 0–14 PSU (Komarova 1991, Daneliya 2002). Even in the Curonian Lagoon, the upper salinity limits of *P. lacustris* seem to be higher than in its native Ponto-Caspian distribution area; constant and viable populations are known from areas where salinity conditions often reach 5–6 PSU (Lazauskiene et al. 1995). The data suggest that factors other than salinity may also be important in delimiting species distributions, e.g. competition with other numerous brackish water mysid species in Ponto-Caspian estuaries; but this is not the case in the Curonian Lagoon. One of the immediate competitors of *P. lacustris* in Ponto-Caspian areas could be its sister species *P. sowinskii*, a species that has only recently been discovered and split from *P. lacustris* (Daneliya 2002). The two species are closely related morphologically, but have different ecological preferences; the upper limit of salinity in natural habitats of *P. sowinskii* is c. 5–6 PSU (Daneliya 2002). The identification of cryptic species within what was earlier considered to be *P. lacustris* in fact invalidates earlier experimental data on salinity tolerance in *P. lacustris* (e.g. Karpevitch 1955, 1958), as the experiments might have involved mixed material from both species. The conclusion drawn from earlier experiments aiming to test short- (several hours) and long-term (37 days) survival in various salinity conditions was that the maximum salinity levels that could be tolerated without moulting and juvenile growth being disturbed were 7.5 PSU for *P. lacustris* (sensu lato) (Karpevitch 1955, 1958) and 11 PSU for *L. benedeni* (Băcescu 1940 in Komarova 1991). The latter value is somewhat surprising, as *L. benedeni* is found at higher salinities even in natural Ponto-Caspian populations (Komarova 1991). Generally, the experimental conditions and criteria used to evaluate species viability have not been explicitly described in these experiments and proper comparisons with the newly obtained results are difficult. With regard to the cryptic *P. sowinskii* species, it is also possible that it was introduced to Lithuania together with *P. lacustris*. Stocks for introductions were taken from the Dniepr and Simferopol reservoirs (Arbaciauskas 2002), where the two species are likely to occur sympatrically (Daneliya 2002). Yet inspection of samples from the Kaunas reservoir and from the Curonian Lagoon (collected in 2004 and including part of the material used for this study) did not reveal any specimens of *P. sowinskii* (M. Daneliya personal communication).

The critical salinity values obtained for the two mysid species in our study can now be compared with those for other brackish water taxa. For instance, the 23 PSU that caused 100% mortality of *P. lacustris* in our study is close to the lethal 25 PSU value in the Ponto-Caspian amphipod *Dikerogammarus villosus* (Bruijs et al. 2001). In natural habitats *D. villosus* is found in a salinity range of 0–5 PSU (Mordukhai-Boltovskoi et al. 1969), a range similar to that of *P. lacustris*. The optimal salinity range for the cladoceran *Cercopagis pengoi* is 2–10 PSU, even though occasional specimens are recorded in 13 PSU (Mordukhai-Boltovskoi & Rivier 1987). Finally, our findings that *P. lacustris* females tolerated salinity shock better than males are congruent with results from other species, e.g. *Boeckella hamata, Acartia tonsa* or *Eurytemora affinis* copepods (Cervetto et al. 1999, Hall & Burns 2001). As females of these species are typically larger than males, e.g. in *P. lacustris* females are 10–16 mm and males are 7–9 mm (Komarova 1991), they also have a smaller surface-to-volume ratio, which is believed to enhance female osmoregulation (Hall & Burns 2001). However, we did not record any obvious difference in survival between the two sexes of *L. benedeni*, even though males of this species are smaller than females.

The return of the mysids to fresh water salinity conditions did not stop the mortality. On the one hand, the shock of salinity increase might have been responsible for the inability of the species to recover even after a relatively short (24 h) exposure. On the other hand, the sudden salinity decrease could itself have been an additional mortality factor, but our experiments were not designed to test this. The practical implications of the observations suggest that even a short-term exposure to oceanic salinity levels is likely to cause a very high mortality of brackish water organisms, and could be an efficient way of preventing invasions of mysids, amphipods and other taxa that have no salinity-resistant resting eggs. However, considering the rather high short-term salinity tolerance of both stenohaline and euryhaline mysid species, exposure to a high salinity will act as an appropriate biocide only when the salt concentration is at least 30 PSU. In the case of the Baltic Sea this means that surface water salinities in the central part of the sea (7–8 PSU) are not sufficient.

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