Helgol Mar Res (2006) 60: 121–126
DOI 10.1007/s10152-006-0030-y

ORIGINAL ARTICLE

Kristjan Herkül · Jonne Kotta · Ilmar Kotta

Distribution and population characteristics of the alien talitrid amphipod *Orchestia cavimana* in relation to environmental conditions in the Northeastern Baltic Sea

Received: 24 April 2005 / Accepted: 21 November 2005 / Published online: 1 February 2006

Abstract The talitrid amphipods were found for the first time in the Northeastern Baltic Sea in 1999. *Orchestia cavimana* inhabited damp wracks cast up on shore within a 200 m area of Saaremaa Island. In the following year, the species expanded its range to a few kilometres. In 2002, six additional locations of *O. cavimana* were found in Saaremaa Island and two locations in the Northwestern part of Estonia. Abundances and biomasses were highest in the first year of the invasion. In the following years, the values stabilized on remarkably lower levels. Population characteristics of the species varied significantly between locations. The average biomass and abundance were 9 g dw m^{-2} and 1975 ind m^{-2}, respectively. Wrack biomass and interaction between wrack biomass and exposure were the best predictors of the abundances and biomasses of *O. cavimana*. Humidity explained additional variability in biomasses. The size structure of the population of *O. cavimana* was mostly related to humidity and wrack biomass. The Southern coast of the Baltic Sea may be regarded as the initial donor region for the Estonian populations of *O. cavimana*. The vector of this invasion is most likely related to the natural dispersal of the drifting algae but human activities as a transport vector can not be excluded. The incredible speed of the invasion of *O. cavimana* and its high biomasses indicate that the species will very likely extend its distribution along the coast of the Northeastern Baltic Sea in the following years.

Communicated by K. Reise

K. Herkül · J. Kotta · I. Kotta
Estonian Marine Institute, University of Tartu,
Mäealuse 10a, 12618 Tallinn, Estonia

K. Herkül (✉)
Institute of Zoology and Hydrobiology,
University of Tartu, Vanemuise 46, 51014 Tartu, Estonia
E-mail: kristjan.herkyl@sea.ee
Tel.: +372-67-18935
Fax: +372-67-18900

Keywords *Orchestia cavimana* · Nonindigenous species · Amphipoda · Baltic Sea

Introduction

The dispersal of species to new areas has an impact on local ecosystems (Parker et al. 1999). New species entering ecosystems may dramatically change the species diversity, trophic structure, structure and dynamics of populations, nutrients availability and flow, and primary production of the local ecosystem (Carlton 1996). Successful invasive species may render previously stable systems unbalanced and unpredictable (Carlton and Geller 1993; Carlton 1996; Ruiz et al. 1999). Hence, biological invasions may represent severe threats to the integrity of natural communities, endangered species, and economy (Carlton and Geller 1993; Carlton 1999a, b).

Owing to its low number of species and extensive anthropogenic impact, the ecosystem of the Baltic Sea is considered vulnerable to biological invasions (Stachowicz et al. 1999; Levine and D'Antonio 1999; Leppäkoski and Olenin 2001). In recent decades, the number of nonindigenous species has increased exponentially and the ranges of existing exotics have expanded rapidly in the Baltic Sea area (Gruszka 1999; Leppäkoski and Olenin 2001). Among most recent newcomers, *Marenzelleria neglecta* (Sikorski and Bick sp. nov.) and *Cercopagis pengoi* (Ostroumov) have invaded practically all suitable biotopes in the Baltic Sea within a few years period (Kotta and Orav 2001; Zettler et al. 2002; Telesh and Ojaveer 2002). Well-established alien *Dreissena polymorpha* (Pallas) suddenly expanded its distribution area in the 1990 and 2000 (Kotta 2000b).

The Talitridae is the only family of amphipods which has truly terrestrial species, and although many are found close to the sea on the upper parts of the shore, some occur considerable distances inland (Lincoln 1979). It is a very large family that comprises five genera:

Talitrus Latreille, *Orchestia* Leach, *Talorchestia* Dana, *Talitroides* Bonnier, and *Brevitalitrus* Bousfield (Lincoln 1979). Talitrid amphipods are important members of the wrack fauna throughout the world (Persson 1999). *Orchestia* is a large cosmopolitan genus comprising more than 70 recognised species which are semiterrestrial, typically living amongst intertidal stones and algae, although some are found inland, and may occur several 100 m above sea-level (Lincoln 1979).

In the Baltic Sea, five species of talitrid amphipods have been found. Two of these, *Talorchestia deshayesii* Audouin and *Talitrus saltator* (Montagu), live on sandy beaches whereas *Platorchestia platensis* (Krøyer), *Orchestia gammarellus* (Pallas), and *O. cavimana* Heller are found in wrack beds on harder substrata, such as rocks, stones, gravel, and shore meadows (Persson 1999; Kotta 2000a). *O. gammarellus* has the widest distribution in the Baltic, and has been reported from the central parts of the Baltic proper (Persson 1999). Prior to 1999, there were no talitrid amphipod species found further North.

The talitrid amphipod *O. cavimana* has a relatively wide distribution area inhabiting Mediterranean, Black Sea, Red Sea, Atlantic coast of North Africa and of Europe up to the Southern North Sea (Lincoln 1979). In the Baltic Sea, the species has been previously found only in a few Southern coastal sites in Poland and Germany (Žmudziński 1974; Järvekülg 1979). The Ponto-Caspian region, but likely Asia, is suggested as its origin (Kinzelbach 1965, 1972; Belgian Biodiversity Platform 2004, www.biodiversity.be/bbpf/forum/invasion/invspecies.html). To date, the information about arrival, invasion vector, range expansion, current distribution, and possible impact of the species is extremely limited. The aims of this paper are (1) to follow the establishment and range expansion of *O. cavimana* in the Baltic Sea, and (2) to relate the biomass distribution and size structure of the populations to habitat characteristics.

Materials and methods

Wrack fauna was sampled annually at 79 sites of the Estonian coastal sea during the last week of September or the first week of October 1998, 1999, 2002, and 2004 (Fig. 1). One sample was taken at each station except for a site in the Northern Saaremaa Island (first location of *O. cavimana* in Estonia) where three replicate samples were taken annually in 1998–2004. Sites were selected to cover maximum salinity range, different sediment, and wrack types. Shores which were overgrown with reeds were excluded. At every site, exposure (an estimate how much a site is exposed to open sea in degrees), steepness of coastal slope (a distance between shoreline and 5-m depth isoline), number, width and height of wrack belts, total coverage of wrack within a belt, dominant plant species, level of decomposition and humidity, type and granulometry of sediment particles were estimated. The sites were classified as dry, moist, and wet. Where talitrid amphipods were found, a biomass sample was taken using 20×20 cm metal frame. Typically, the algal belt was a few metres wide. Within the belt, the densities of *O. cavimana* varied little whereas the densities varied highly at the edges of the belt. Therefore, the samples were taken within well developed and not fragmented parts of wrack belt. The material inside the frame was quickly removed and packed into a plastic bag. Samples were kept deep-frozen until analysis in the laboratory.

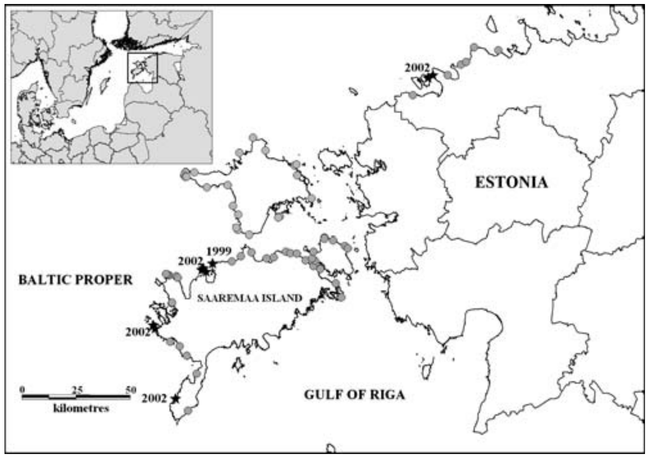

Fig. 1 Study area. *Filled circles* indicate the sampling sites of talitrid amphipods and stars the locations where *O. cavimana* were found. *Years* show the time of first record of *O. cavimana* in a site

Talitrid amphipods were picked up from the sample under a stereomicroscope. Animals were counted and divided into the following groups: adult males, adult females, and juveniles (see Lincoln 1979). The smallest males with visible sexual characteristics were 9-mm long. Thus, all animals below 9 mm were considered juveniles. The length of all individuals was measured by camera lucida using a stereomicroscope to the nearest 0.1 mm. Dry weight of individuals was measured to the nearest 0.1 mg after drying at 60°C for 48 h. Plants were separated by species and dry weight (60°C, 336 h) of each species was measured. For each plant species, the level of decomposition was estimated on three-stage scale: fresh, semi-decayed, and highly decayed. In some cases of very low amphipod densities, no animals were captured inside the quadrate. These samples were excluded from the statistical analyses.

For univariate analyses, the statistical programme "Statistica" was used (StatSoft Inc. 2004). We employed analysis of variance (ANOVA) to describe differences between sexes and environmental conditions in stations with and without *O. cavimana*, chi-square test to analyse sex ratio, and linear regression to analyze relationships between population characteristics of *O. cavimana* and habitat characteristics. Prior to the analyses, normality (Shapiro-Wilk W-test) and homoscedasticity (Bartlett's test) of the data was checked. Multivariate data analyses were performed using the package "PRIMER" (Clarke and Warwick 2001). Double square root transformed data were used for Bray-Curtis similarity matrices. BIOENV analysis was used to explain the importance of habitat characteristics in determining the abundance, biomass, and size structure of *O. cavimana*. ANOSIM permutation test was performed to examine differences in abundance, biomass, and size structure due to habitat characteristics.

Results

The investigated habitats were mainly exposed shores. The steepness of coastal slope varied highly. The distances between shoreline and 5-m depth isoline ranged from 75 m to about 12 km with an average at 1,518 m. Limestone sediments were predominant followed by granite boulders. The wrack coverage within a belt was on average 57%, varying between 5 and 100%. Altogether 19 plant species were identified in the wrack, *Fucus vesiculosus* L. had highest biomasses followed by *Zostera marina* L. and *Furcellaria lumbricalis* (Huds.) J. V. Lamour. The plant species were mainly fresh to semi-decayed, and the wrack beds were predominantly moist to wet.

Despite intensive field sampling in 1998, the talitrid amphipods were not found within the wrack fauna. *O. cavimana* was found for the first time on the coast of Northern Saaremaa Island in 1999 (Fig. 1). *O. cavimana* inhabited damp wrack cast up on shore. The species was restricted within 200 m shore area. The average abundance and biomass were 22,400 ind m^{-2} and 14 g dw m^{-2}, respectively. In 2000, the species expanded its range to a few kilometres but the average abundance and biomass decreased to 2,433 ind m^{-2} and 2 g dw m^{-2}, respectively.

In 2002, *O. cavimana* was found in nine areas (Fig. 1). In 2004, the distribution of *O. cavimana* had remained the same as in 2002. However, the abundance of the species had decreased considerably in the majority of stations. Only three locations had sufficiently high abundances for capturing animals into the sampling frame.

Orchestia cavimana inhabited very exposed shores except for a partly sheltered site on the western coast of Saaremaa Island. However, there was no statistically significant difference in exposure between the sites with and without *O. cavimana*. Similarly, there were no statistical differences in the sediment characteristics regardless of the presence of *O. cavimana*. In the presence of *O. cavimana*, the wrack coverage varied between 40 and 100% with an average at 73%, and the wrack biomass varied between 1,224 and 4,924 g dw m^{-2} with an average at 2,712 g dw m^{-2}. In the absence of *O. cavimana*, the average coverage and biomass were lower, 54% and 1,820 g dw m^{-2}, respectively. Altogether 14 algal species and four higher plants were found in the habitats of *O. cavimana*. The number of plant species in wrack varied between 3 and 13 with an average at nine. *F. vesiculosus* prevailed in the wrack in seven areas and *Polysiphonia fucoides* (Huds.) Grev. in the other two areas. *Pilayella littoralis* (L.), *Z. marina*, and *Ruppia maritima* L. were the second dominant plant species within the wrack.

The biomasses and abundances of *O. cavimana* ranged between 0.6–29.0 g dw m^{-2} and 50–6,275 ind m^{-2}, respectively. The average biomass was 9.1 g dw m^{-2} and the average abundance was 1,975 ind m^{-2}. The amphipod length varied between 3 and 20 mm with an average at 9.9 mm. The 9–10 mm size class formed nearly 40% of the population density and biomass. The amphipod dry weight varied between 0.0001 and 0.0201 g with an average at 0.005 g. Males had significantly greater average length than females (11.4 mm vs. 10.4 mm, one-way ANOVA, $P < 0.001$). The differences in the weights were not statistically significant (one-way ANOVA, $P = 0.22$). The average sex ratio was female-biased (1:0.83, chi-square test, $P < 0.05$).

BIOENV analysis suggested that wrack biomass, humidity, and interaction between wrack biomass and exposure were the best predictors of the abundances of *O. cavimana* whereas wrack biomass and interaction between wrack biomass and exposure explained the variability in biomasses. The size structure of the population of *O. cavimana* was mostly related to humidity and wrack biomass (Table 1).

The biomass of *O. cavimana* increased with the wrack biomass (Fig. 2). However, there was no significant relationship between the biomass of wrack and the abundance of *O. cavimana*. The abundance of *O. cavimana* correlated positively with the biomass of higher plants in the wrack (linear regression analysis, $r^2 = 0.52$, $P < 0.05$). The variability in juvenile dry weight correlated with average size of sediment particles (linear regression analysis, $r^2 = 0.83$, $P < 0.05$). The humidity of wrack was significantly related to the abundance of *O. cavimana*. The amphipod abundances were highest in moist, intermediate in wet, and lowest in dry wrack, respectively. However, only dry and moist wrack were significantly different in terms of amphipod abundances (233 ind m^{-2} vs. 4,000 ind m^{-2}, ANOSIM, $P = 0.042$).

Table 1 The combination of the best environmental variables that predicts abundance, biomass, and biomass size structure of *O. cavimana* in the study area

Similarity matrix	Significant environmental variables	Spearman ρ
Abundance	humidity of wrack wrack biomass wrack biomass × exposure	0.676
Biomass	wrack biomass wrack biomass × exposure	0.600
Abundance size structure	humidity of wrack wrack biomass	0.623
Biomass size structure	humidity of wrack wrack biomass	0.609

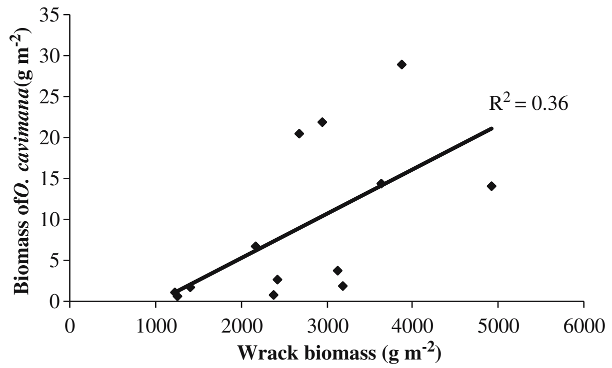

Fig. 2 Relationship between the biomass of wrack and the amphipod *O. cavimana* in the study area

In the station of the first record of *O. cavimana* (Northern coast of Saaremaa Island), the highest abundance and biomass of the talitrids were found in 1999. In the following years, the abundance and biomass have stabilized on remarkably lower levels with a slight increase in 2004 (Fig. 3).

Discussion

In the Northeastern Baltic Sea, *O. cavimana* inhabits damp wracks cast up on shore and the upper layer of sediment. The habitat corresponds to the previous records in the Baltic and other seas (Den Hartog 1965; Lincoln 1979; Żmudziński 1974; Curry et al. 1972). The amphipod reaches its maximum length (Lincoln 1979) in the Estonian coastal sea, suggesting that environmental conditions during summer are favourable in the area.

The studied environmental factors did not predict the presence of *O. cavimana* in a site. As the amphipod is a recent immigrant, it is likely that the species has not yet colonized all suitable habitats in the Northeastern Baltic Sea due to the stochastic nature of invasion process.

Population characteristics varied considerably between and within sites. Most of the variability was explained by quantity and quality of wrack. Quantity, composition, and other properties of wrack are important for aspects of foraging and habitat suitability (Backlund 1945; Persson 1999). In our study area, the biomass of *O. cavimana* was higher in areas of more intensive accumulation of wrack whereas the abundances increased only with the biomass of higher plants.

The type and granulometry of sediment are also important habitat qualities of *O. cavimana*. The variability in juvenile weight increased with the average size of sediment particles, indicating that juvenile amphipods are more associated with sediment than adults. Juveniles may require better protection in the exposed environments. Alternatively, they may actively search for more decayed plant debris that can be found in the upper layer of sediment.

Orchestia cavimana was found for the first time on the coasts of Northern Saaremaa Island, the Northeastern Baltic Sea in 1999 corresponding to the extension of its Baltic distribution of some 400 km. The species was observed only in a single site and the amphipod densities were very high. The exact time of the first inoculation of *O. cavimana* remains uncertain. Considering the high densities of the amphipod in 1999, it is likely that the species arrived on the Estonian shore either in late 1998 or early 1999. Alternatively, the species may have arrived even earlier providing that the amphipods had densities below detection limits. However, this seems very unlikely as the site has been regularly surveyed since 1994 (database of the Estonian Coastal Sea Monitoring Program, available at Estonian Marine Institute, Estonia).

In the following years, the amphipod abundances stabilized on remarkably lower levels. This is in agreement with earlier observations that in many cases invading species attain a peak of population density and then decline due to interactions between the invader and its resources or enemies (Carlton 1996; Williamson and Fitter 1996). In 2002, eight additional locations of *O. cavimana* were found in Saaremaa Island and Northwestern Estonia corresponding to the additional extension of its Baltic distribution of some 150 km. The distribution of *O. cavimana* remained the same in 2004, indicating that the amphipod can survive extremely severe winters (e.g. 2002/2003), and therefore the species has a potential for invading coastal areas further North. However, the densities were extremely low in 2004 at most stations. In Britain, a severe winter did not affect the populations of *O. cavimana* and the colonies of amphipod remained active beneath snow (Curry et al. 1972). The winter temperature, however, might become a regulating factor of the range expansion of *O. cavimana* in colder climate. In the Baltic Sea area, the high temperature in the wrack banks through autumn to spring is an ecological factor which positively influences the populations of the talitrid amphipod *O. gammarellus* (Backlund 1945).

The timing of the range expansion of *O. cavimana* may be connected with climate warming. Shorter period

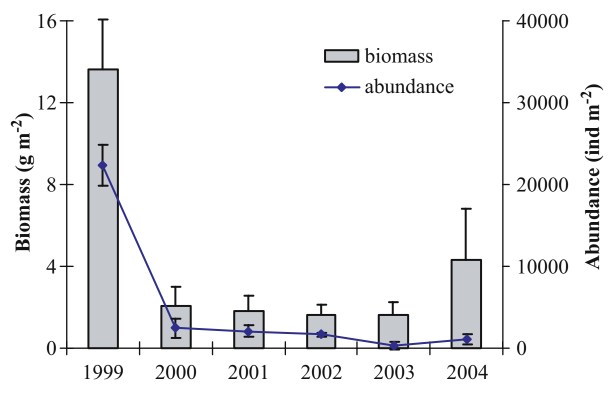

Fig. 3 Interannual variation in the abundance and biomass of *O. cavimana* (±SE) at the station of the first record of the species (Northern coast of Saaremaa Island)

of ice cover and strong storms in autumn and winter may favour the transport of wrack over large distances. As the climate warming in Northern Europe has been primarily expressed as warmer winters (Ottersen et al. 2001), it is likely that the hibernating conditions for the species have become more favourable.

The Southern coast of the Baltic Sea may be regarded as the initial donor region for the Estonian populations of *O. cavimana*. It remains unknown whether *O. cavimana* first colonized Northern coasts of Saaremaa Island and then dispersed to the other sites in the Northeastern Baltic Sea or if there have been several secondary introductions from the Southern Baltic Sea to the Northern Baltic Sea.

The vector of this invasion is unknown but most likely it is related to the natural dispersal of the drifting algae. However, as the Northern Saaremaa Island is an important recreational area, unintentional introduction cannot be excluded. Wildish (1970) showed that talitrid amphipods survived at least 14 days of submersion. In another experiment (Persson 2001), the mortality of submerged *O. gammarellus* and *P. platensis* was very low during first 2 weeks but some individuals of both species survived more than 3 months of submersion. The results suggest that long dispersal episodes are possible, even entirely submerged. Animals may survive even longer episodes of dispersion when attached to material drifting on the surface of water. In the Baltic Sea, dispersion probably takes place in late autumn when the water level is high and storms are frequent (Persson 2001).

Prior to 1999, the Northernmost distribution limit of the amphipod was located at the Southern coasts of the North and Baltic Seas (Žmudziński 1974; Lincoln 1979). To date, *O. cavimana* is found as North as in Estonia. The incredible speed of the invasion of *O. cavimana* and its high biomasses indicate that the species has formed permanent populations and will very likely extend its distribution on the coasts of Estonia in the following years.

Acknowledgements This study was financed by the Estonian Target Financing Programmes Nos. 0182578s03 and 0182579s03. Funding was also obtained through Estonian Science Foundation grant No. 6016 and US. Government Grant (SEN100-02-GR069). The authors acknowledge the support by the MARBEF Network of Excellence "Marine Biodiversity and Ecosystem Functioning", which is funded in the Community's Sixth Framework Programme (contract no. GOCE-CT-2003-505446). This publication is contribution number MPS-06007 of MarBEF. The opinions, findings, and conclusions or recommendations expressed herein are those of the authors and do not necessarily reflect those of the US. Government. The experiments comply with the current laws of the country in which they were performed.

References

Backlund HO (1945) Wrack fauna of Sweden and Finland: Ecology and chorology. Opuscula entomologica supplementum, Helsingfors OY Tilgmann AB, Lund

Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261:78–82

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78:97–106

Carlton JT (1999a) The scale and ecological consequences of biological invasions in the World's oceans. In: Standlund OT, Schei PJ, Viken A (eds) Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht, pp195–212

Carlton JT (1999b) A journal of biological invasions. Biol Invasions 1:1

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. 2nd edn. Plymouth Marine Laboratory, Plymouth

Curry A, Grayson RF, Milligan TD (1972) New British records of the semi-terrestrial amphipod *Orchestia cavimana*. Freshw Biol 2:55–56

Den Hartog C (1965) The amphipods of the deltaic region of the Rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. Neth J Sea Res 2:40–67

Gruszka P (1999) The River Odra estuary as a gateway for alien species immigration to the Baltic Sea basin. Acta Hydrochim Hydrobiol 27:374–382

Järvekülg A (1979) The bottom fauna of the Eastern Baltic Sea. Valgus, Tallinn

Kinzelbach R (1965) Ein Flochkrebs, *Orchestia cavimana* Heller, am Oberrhein. Beitr Naturk Forsch SüdwDtl 24:153–157

Kinzelbach R (1972) Zur Verbreitung und Ökologie des Süßwasser-Strandflohs *Orchestia cavimana* Heller 1865 (Crustacea; Amphipoda: Talitridae). Bonn Zool Beitr 23:267–282

Kotta J (2000a) First record of the Talitrid amphipod *Orchestia cavimana* in the Northern Baltic Sea. Proc Estonian Acad Sci Biol Ecol 49:221–224

Kotta J (2000b) Impact of eutrophication and biological invasions on the structure and functions of benthic macrofauna. Dissertationes Biologicae Universitatis Tartuensis, Tartu University Press, Estonia 63:1–160

Kotta J, Orav H (2001) Role of benthic macroalgae in regulating macrozoobenthic assemblages in the Väinameri (north-eastern Baltic Sea). Ann Zool Fenn 38:163–171

Leppäkoski E, Olenin S (2001) The meltdown of biogeographical pecularities of the Baltic Sea: the interaction of natural and man-made processes. Ambio 30:202–209

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Lincoln RJ (1979) British marine amphipoda: Gammaridea. British Museum (Natural History), London

Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH., Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Persson L-E (1999) Growth and reproduction in two brackish water populations of *Orchestia gammarellus* (Amphipoda: Talitridae) in the Baltic Sea. J Crust Biol 19:53–59

Persson L-E (2001) Dispersal of *Platorchestia platensis* (Kröyer) (Amphipoda: Talitridae) along Swedish coasts: a slow but successful process. Estuar Coast Shelf Sci 52:201–210

Ruiz GM, Fofonoff P, Hines AH (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnol Oceanogr 44:950–972

Stachovicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286:1577–1579

StatSoft Inc (2004) Electronic statistics textbook. Tulsa, OK. StatSoft. WEB: http://www.statsoft.com/textbook/stathome.html

Telesh IV, Ojaveer H (2002) The predatory water flea *Cercopagis pengoi* in the Baltic Sea: Invasion history, distribution and implications to ecosystem dynamics. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive aquatic species of Europe. Kluwer Academic Publishers, Dordrecht, pp 62–65

Wildish DJ (1970) Some factors affecting the distribution of *Orchestia* Leach in estuaries. J Exp Mar Biol Ecol 5:276–284
Williamson MH, Fitter A (1996) The characters of successful invaders. Biol Conserv 78:163–170
Zettler ML, Daunys D, Kotta J, Bick A (2002) History and success of an invasion into the Baltic Sea: the polychaete *Marenzelleria* cf. *viridis*, development and strategies. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive aquatic species of Europe—distribution, impacts and management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 66–75
Żmudziński L (1974) Świat zwierzęcy Bałtiku. Wydawnictwa Szkolne i Pedagogiczne, Warszawa