Alien invasive species in the north-eastern Baltic Sea:
population dynamics and ecological impacts

Henn Ojaveer and Jonne Kotta (eds)

Tallinn 2006

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Contents

1. Introduction

It is commonly accepted and agreed that invasion of alien species is one of the most serious and gradually increasing threats to aquatic ecosystems. This human-aided process has initiated significant, unpredictable and irreversible changes to both abiotic and biotic environment in a variety of waterbodies worldwide (e.g. Carlton, 1996a, 1999; Karatayev et al., 2002; Ojaveer et al., 2002; Vanderploeg et al., 2002) and may cause severe economic damage to humans.

Over one hundred different alien species have been recorded in the Baltic Sea while not all of them have been able to form self-sustaining populations. As a result of bioinvasions, both the biotic and abiotic environment of the Baltic Sea has been substantially changed (e.g. Olenin & Leppäkoski, 1999; Leppäkoski et al., 2002). However, as invasion of alien species is a continuous process (including also secondary spread within the sea) and in order to give deeper insight into the consequences of bioinvasions, we have carried out studies in several sub-basins of the NE Baltic Sea in the following three major directions: (1) Investigation of the distribution and population dynamics of the selected alien species incl. in relation to spatio-temporal dynamics of the key environmental parameters; (2) Description of the composition of biota in most important port areas as the high-risk areas in terms of biological invasions, and (3) Assessment of the ecological impact of selected invasive species on natural communities through a set of lab and field experiments.

The Editors

Fig. 1. Map of the NE Baltic Sea with major sub-basins, bays and ports studied.

2. Distribution and population dynamics of selected pelagic alien invertebrate species in Estonian marine waters

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SUMMARY

The predatory cladoceran *Cercopagis pengoi*, larvae of the cirriped *Balanus improvisus* and the polychaete *Marenzelleria neglecta* are common in the Estonian coastal sea. Their abundance tends to be higher in Pärnu Bay (NE Gulf of Riga) than in Narva and Tallinn bays (southern Gulf of Finland). The distribution area of the hydromedusa *Maeotias marginata*, on the contrary, is confined to a restricted area and only a few individuals were found during 2002–2005. The long-term abundance dynamics of the three most numerous species during 1992–2005 show high variability within and between the studied locations.

MATERIAL AND METHODS

Long-term dynamics of *Cercopagis pengoi* (Ostroumov) and larvae of *Balanus improvisus* Darwin and *Marenzelleria neglecta* (Sikorski and Bick sp. nov.), was studied in the Gulf of Riga (Pärnu Bay) and the Gulf of Finland (Tallinn and Narva bays) (Fig. 1). Zooplankton in Pärnu Bay was weekly sampled from May to October in 1970–2005. In the Gulf of Finland the sampling was done fortnightly from June to August and monthly in May, September and October. The sampling in Tallinn Bay was carried out in 1997–2005 and in Narva Bay in 1999–2005.

The samples were collected by vertical hauls through the whole water column with a Juday net (mouth surface area 0.1 m², mesh size 90 μm; altogether 1492 samples). Samples were preserved in 4% formaldehyde solution and analysed by the routine method (HELCOM, 1988).

In order to calculate the abundance of *C. pengoi*, all individuals in a sample were counted. In the analyses of seasonal dynamics and interannual changes of *C. pengoi*, all samples collected in the Gulf of Finland during May–October were used regardless of whether they contained *C. pengoi* or not. For analysing other species in the Gulf of Finland, the samples from shallow coastal stations in Tallinn and Narva bays were used.

For assessing the spatial distribution and population abundance of the hydromedusa *Maeotias marginata* Modeer, special surveys were carried out in the Väinameri Archipelago, the area of the first observation of the species (Väinölä & Oulasvirta, 2001). Two methods were used to collect the hydromedusae *M. marginata*: horizontal tow of a Hensen plankton net (net opening diameter 80 cm, towing speed 2–3 knots at

a depth of 1–3 m) and SCUBA diving. The sampling time covered late August to early September with the total number of sampling events of 57: Hensen net in 2002 and 2003, combined sampling with Hensen net and SCUBA diving in 2004 and SCUBA diving in 2005. The research area covered is presented in Fig. 2.1
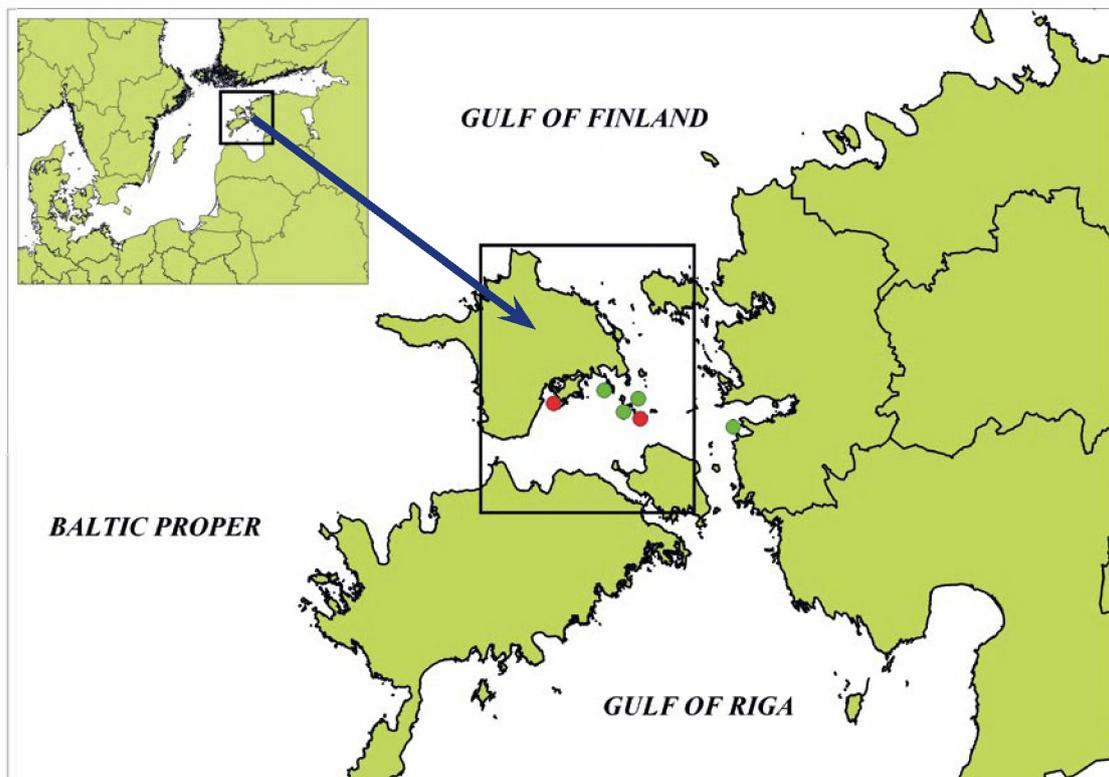
Fig. 2.1. Records of *Maeotias marginata* in the Väinameri area. The sampling area covered by the current study is shown by the black rectangle. Red dots indicate locations where the species was found. Green dots indicate findings by Väinölä and Oulasvirta (2001).

RESULTS AND DISCUSSION

The cirriped *B. improvisus* and the polychaete *M. neglecta* are benthic as adults and have pelagic larvae. The cladoceran *C. pengoi* spends the whole life cycle in the pelagic system except for benthic resting eggs. *M. marginata, M. neglecta* and *C. pengoi* are among the most recent newcomers in the Baltic Sea (Ojaveer & Lumberg, 1995; Bick & Zettler, 1997; Väinöla & Oulasvirta 2001) whereas the invasion of *B. improvisus* dates back to the late 19th century (Välikangas, 1926; Lindquist, 1959). *B. improvisus* and *M. neglecta* originate from North America and *C. pengoi* from the Ponto-Caspian area. *M. marginata* is considered as native to the Azov and Black seas, the mouths of the Don and Kuban rivers and the Danube estuary (Mills & Rees, 2000). The transfer of ballast water between international ports is suggested as a potential vector of these invasions (Leppäkoski & Olenin, 2001).

Nauplii of *B. improvisus* are generally abundantly present in the study area. The number of *B. improvisus* nauplii was gradually decreasing since the 1970s until the mid-1980s, after that the abundance has increased again (Kotta et al., 2006b). The maximum abundance was always recorded in summer, in June or July. The average abundance of nauplii (shown as mean ± SE, 10^3 ind. m^{-3}) calculated for the years 1997–2005 was significantly higher in Pärnu Bay (6.8 ± 1.7) than Narva and Tallinn bays (2.7 ± 0.9 and 1.4 ± 0.3, respectively). The multi-annual abundance dynamics exhibits high variability both within and between the bays studied (Fig. 2.2). However, a similar abundance dynamics pattern was recorded, for instance, for Pärnu and Narva bays during the last four years. Of the environmental variables studied, temperature in the near-bottom layer had the best match with the abundance of *B. improvisus* larvae in Pärnu Bay. Other variables (salinity, nutrient load, ice conditions) predicted less than 5% of the variability (Kotta et al., 2006b).

The cladoceran *C. pengoi* (Fig. 2.3) was first found in the Baltic Sea in 1992 (Ojaveer & Lumberg, 1995). For the period data are available for all the bays studied (1999–2005) it appears that the average abundance of the species was significantly lower in Tallinn Bay than in Pärnu and Narva bays (40 ± 12, 122 ± 30 and 88 ± 24 ind. m^{-3}, respectively). It should be mentioned here that Pärnu and Narva bays are relatively more sheltered than Tallinn Bay. Since the invasion, the density of *C. pengoi* gradually increased in Pärnu Bay until 2001 and then dropped to the level of the early 1990s.

The highest population abundance of *C. pengoi* was recorded in Narva Bay in 2002 with other notably high-abundance years of 1999 and 2005 (Fig. 2.2). It has been suggested and discussed by many authors that thermal stratification of the water column is an important variable for the dynamics of *C. pengoi* in the different invaded areas. It has also been suggested that the density of the cladoceran increases with rising temperature stratification, i.e. with decreasing wind stress (e.g., Uitto et al., 1999; Ojaveer et al., 2001; Kotta et al. 2006b).

Although the abundance of the small-sized cladoceran *Bosmina coregoni maritima* (P. E. Müller) exhibited considerable variability before the *C. pengoi* invasion into the Gulf of Riga, and was quite low in some years, post-invasion populations have been consistently and significantly lower than pre-invasion populations. Similarly, the abundances of other cladocerans – *Evadne nordmanni* Loven and *Pleopsis polyphemoides* (Leuckart) – were lower after the invasion of the predatory cladoceran compared to the pre-invasion period (Ojaveer et al., 2004). A shift in the timing of population development of *B. c. maritima* in the Gulf of Riga has also occurred; after the invasion populations have disappeared from the zooplankton community several weeks earlier than before the invasion. The initial development of copepod nauplii populations has shifted to earlier in the season since the invasion, while the initial seasonal decline of nauplii has coincided with the appearance of *C. pengoi* in the zooplankton. A second decline in the

abundance of copepod nauplii has tended to occur when the *B. c. maritima* population was nearly depleted (the second half of August) but *C. pengoi* was still rather abundant (Ojaveer et al., 2004). In the Gulf of Finland, at higher abundance of *C. pengoi* above the thermocline, the cladoceran *B. c. maritima* stayed below the thermocline (Põllumäe & Väljataga, 2004). This indicates direct predation of *C. pengoi* on *B. c. maritima*. As no diurnal vertical migration of *C. pengoi* has been recorded and the majority of the population is located in the upper water layer (e.g., Gorokhova et al., 2000), the deeper water layers may be considered as a refuge for prey species such as *B. c. maritima*.
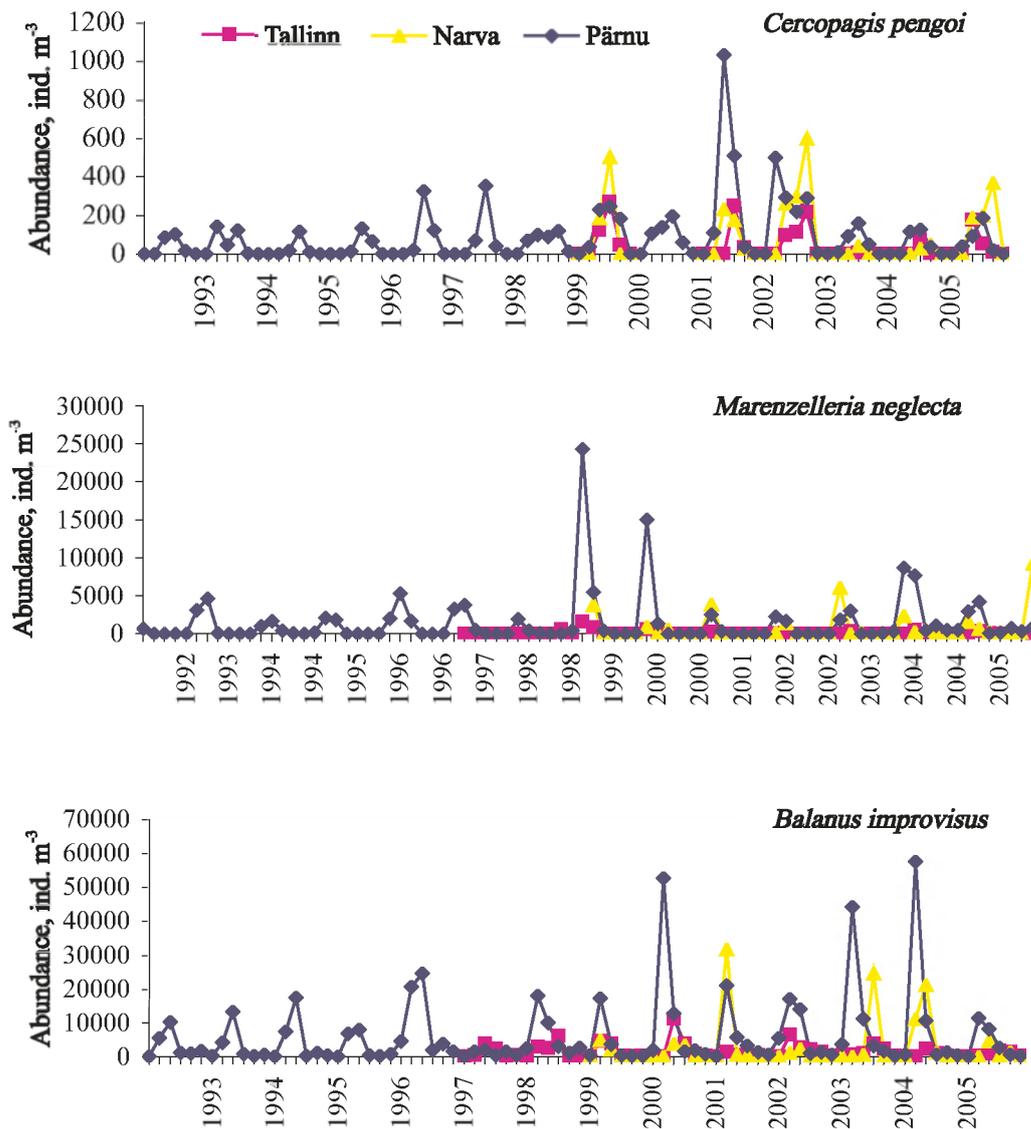
Fig. 2.2. Annual abundance dynamics (ind. m^{-3}) of the cirriped *Balanus improvisus* larvae, the cladoceran *Cercopagis pengoi* and the polychaete *Marenzelleria neglecta* larvae in three bays at the Estonian coast since the appearance of *C. pengoi* and *M. neglecta* larvae in Pärnu Bay (during 1992–2005).

Fig. 2.3. Parthenogenetic female cladoceran *Cercopagis pengoi*. The brood-pouch is full of embryos. Only the first part of the caudal appendage bearing three pairs of barbs is shown. *Photo by A. Põllumäe.*

The multi-annual abundance dynamics of the larvae of *M. neglecta* confirms high variability both within and between the bays with different sub-regional long-term dynamics patterns (Fig. 2.2). The average abundance of the larvae (mean ± SE, 10^3 ind. m^{-3}) in 1997–2005 was higher in Pärnu Bay than in Narva and Tallinn bays ($1.8 ± 0.6$, $0.8 ± 0.2$ and $0.1 ± 0.0$, respectively). Thus, the larval abundance of the species was substantially higher in the Gulf of Riga than in the Gulf of Finland. The studied abiotic environmental variables in Pärnu Bay (temperature, salinity, nutrient load, ice conditions) did not explain the interannual variability in the seasonal cycle of *M. neglecta* (Kotta et al., 2006b). Since the abundance of *M. neglecta* in the Gulf of Riga is higher by an order of magnitude, the abundance of larvae in Pärnu Bay depends upon the dispersal, i.e. the movement of water in the whole Gulf of Riga.

The hydromedusa *M. marginata* was first found in the Väinameri Archipelago in late summer 1999, where it was observed in four locations (Väinölä & Oulasvirta, 2001). All our sampling efforts during the past four years have resulted in four findings of the species in this area: two young caught in 2002 (with bell diameter of 1.5 mm and 3.0 mm) and two larger individuals detected in 2003 (bell diameter 15 mm and

30 mm) (Fig. 2.4). This confirms that the species is present in low abundance in the Väinameri Archipelago. Undoubtedly, substantially more information is needed on the species from the invaded area in order to conclude anything on the population size, food-web interactions and potential ecological impact on native communities (in case the abundance of the alien species increases in the future).

Fig. 2.4. Young (above) and adult (right) hydromedusae *Maeotias marginata* in Väinameri Archipelago. *Photos by A. Põllumäe.*

3. Invasion history and distribution of the key benthic alien invertebrate species in the Estonian coastal sea

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SUMMARY

The crustaceans *Gammarus tigrinus* and *Chelicorophium curvispinum* are among the most recent newcomers in the Estonian coastal sea. *G. tigrinus* was observed for the first time in the Estonian coastal sea in Kõiguste Bay, northern Gulf of Riga, in 2003. In 2004 the species was already abundant in the whole bay area comprising up to 100% of the gammarid abundance. In 2005 *G. tigrinus* was also found in the bays adjacent to Kõiguste Bay but also in Rame Bay located about 50 km eastwards from Kõiguste Bay. *Chelicorophium curvispinum* was observed for the first time in the Estonian coastal sea in the eastern Gulf of Finland in 2005. *C. curvispinum* was found between 1 and 4.9 m depth associated with a belt of the green alga *Cladophora glomerata*. Together with juvenile gammarids *C. curvispinum* was a prevailing invertebrate species in the samples.

MATERIAL AND METHODS

Data about different macrophytobenthos and macrozoobenthos assemblages were compiled from different mapping studies. A total of 4391 benthic samples were collected during 1972–2005. At depths less than 20 m the material for the mapping studies was collected by a SCUBA diver using a Tvärminne (Kangas, 1972), suction (Hiscock & Hoare, 1973) or PVC core sampler. Additionally, a van Veen or Ekman bottom grab was used through the whole studied depth range. Sediment samples were washed through a 0.25 mm mesh. In the laboratory animals were counted under a stereo dissecting microscope. The total dry weight of the animals in each sample was weighed to the nearest 0.5 mg and calculated for an area of 1 m^2.

RESULTS AND DISCUSSION

The crustaceans *Gammarus tigrinus* Sexton and *Chelicorophium curvispinum* Sars are among the most recent newcomers in the Estonian coastal sea. *G. tigrinus* originates from North America and *C. curvispinum* from the Ponto-Caspian area. The transfer of ballast water between international ports is suggested as a potential vector of all these invasions (e.g. Leppäkoski & Olenin, 2001).

G. tigrinus was observed for the first time in the Baltic Sea in 1975 (Bulnheim, 1976). However, it was not until 2003 that the first specimen of the invasive gammarid was found in the Estonian coastal sea (Fig. 3.1). A mesocosm experiment was performed

in the shallow area of Kõiguste Bay, northern Gulf of Riga in 2003. During this experiment we measured how susceptible the artificially assembled communities were to the addition of species from neighbouring areas. At the end of the experiment the invasive species *G. tigrinus* was observed in many mesocosms. The species was mainly associated with the communities that contained the cockle *Cerastoderma glaucum* Bruguiere. Densities ranged between 100 and 800 ind. m^{-2}. In 2003 the gammarid was not found in traditional benthos stations although the bay was intensively monitored throughout the ice-free season.

Fig. 3.1. *Gammarus tigrinus* from Kõiguste Bay. *Photo by J. Kotta.*

In 2003 there were no records of *G. tigrinus* from other parts of the Gulf of Riga including port areas in Riga and Pärnu. On the other hand, an important yacht harbour is located at the inner part of Kõiguste Bay. Thus, it is likely that the species was introduced to the northern part of the Gulf of Riga through yacht traffic and the donor region was likely the Curonian, Odra or Vistula Lagoon (Jazdzewski & Konopacka, 2002; Bochenek et al., 2004; Daunys & Zettler, in press).

In 2004 *G. tigrinus* was already found in the whole Kõiguste Bay area. The species had higher abundances and biomasses in spring and autumn than in summer. The gammarid abundances were usually estimated at 25 ind. m^{-2} and biomasses at 0.01 g m^{-2}. In the inner parts of the bay the abundances and biomasses exceeded 250 ind. m^{-2} and 1 g m^{-2}, respectively. These abundance and biomass values were comparable to native gammarid densities prior to the invasion of *G. tigrinus*. Though, if *G. tigrinus* was

mainly confined to the inner parts of Kõiguste Bay then the native gammarids had higher densities in more exposed parts of the bay.

Concurrently with the invasion of *G. tigrinus* the abundance and biomass of native species have significantly declined. Nowadays, the share of *G. tigrinus* among the native amphipods usually reaches 25% in the total gammarid abundances and biomass. In the inner part of Kõiguste Bay, however, the share of the invasive gammarid may exceed 75% both in abundance and biomass (Fig. 3.2–3.5). In 2005 *G. tigrinus* was also found in the bays adjacent to Kõiguste Bay but also in Rame and Kuressaare Bays located respectively about 50 km eastwards and westwards from Kõiguste Bay (Fig. 3.6).
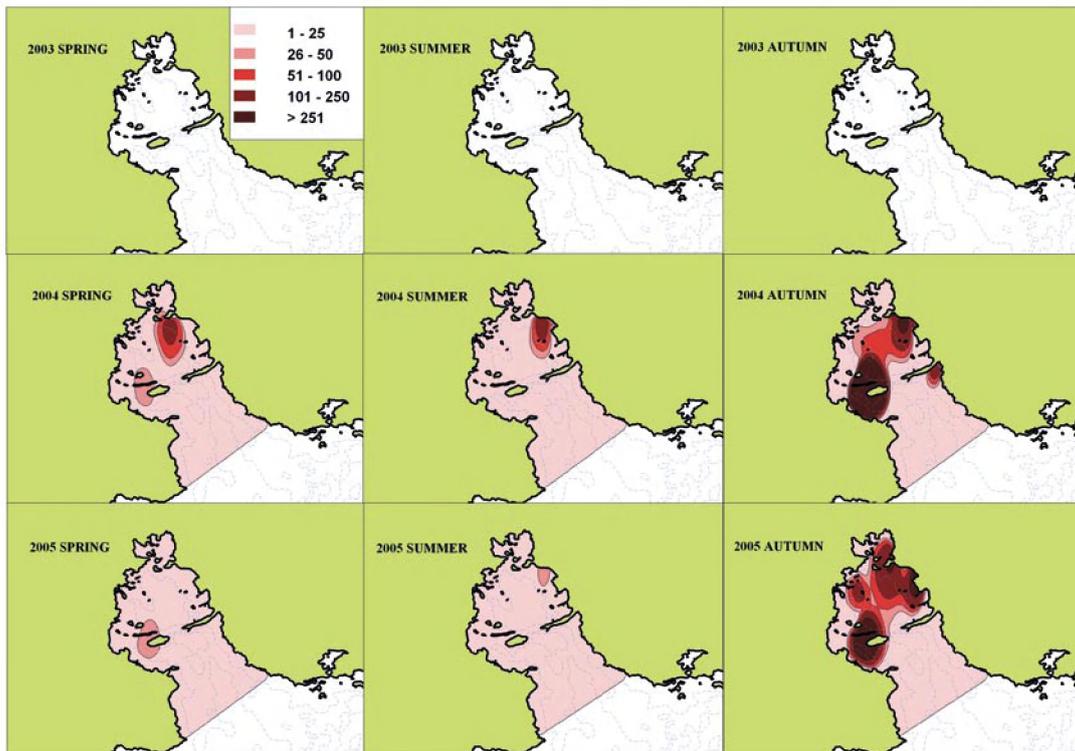
Fig. 3.2. Spatial distribution of abundance of *Gammarus tigrinus* (ind. m^{-2}) in Kõiguste in 2003–2005.
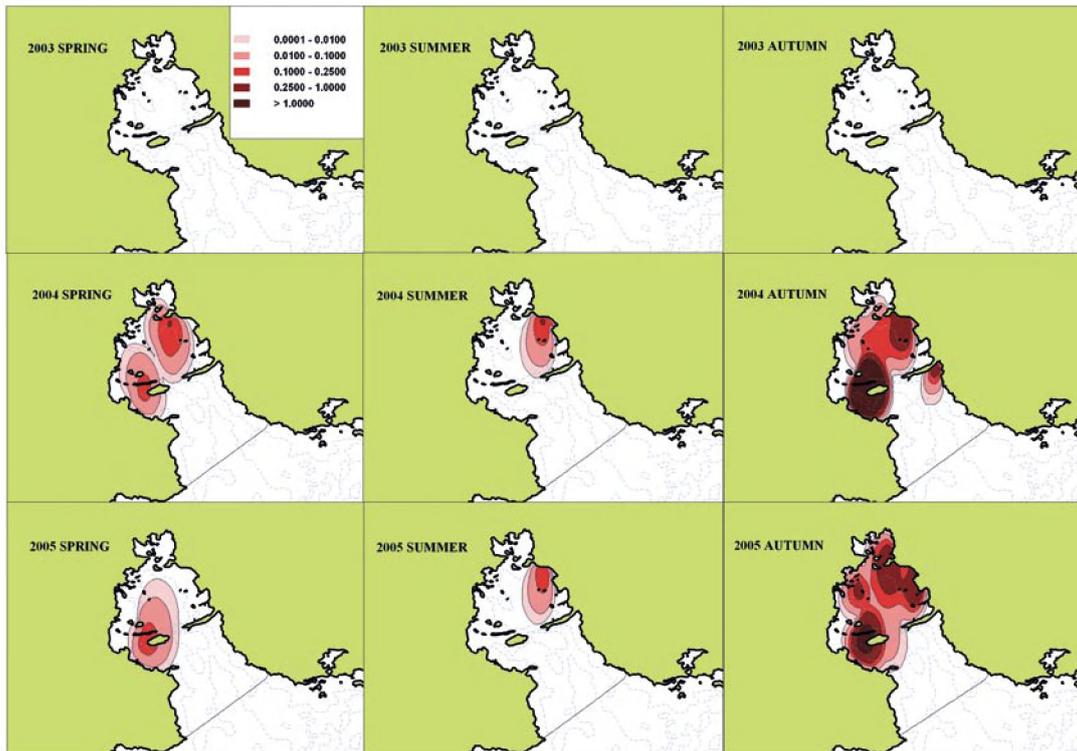
Fig. 3.3. Spatial distribution of biomass of *Gammarus tigrinus* (g dw. m^{-2}) in Kõiguste Bay in 2003–2005.
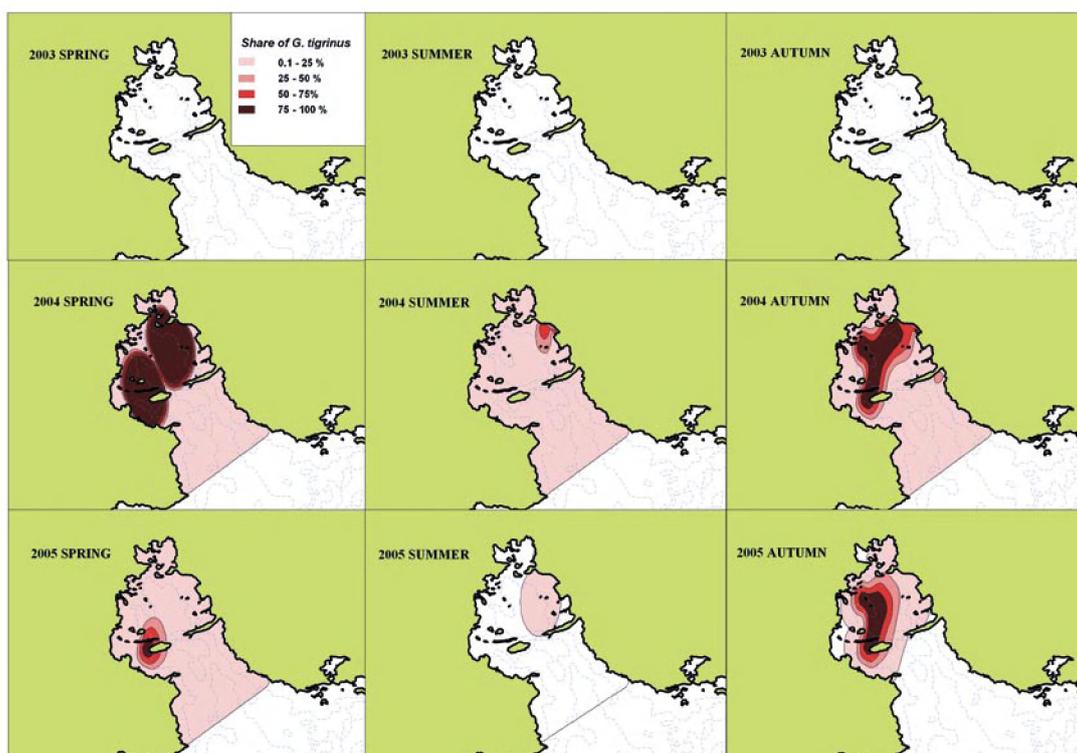
Fig. 3.4. Share of *Gammarus tigrinus* in the total gammarid abundance (%) in Kõiguste Bay in 2003–2005.
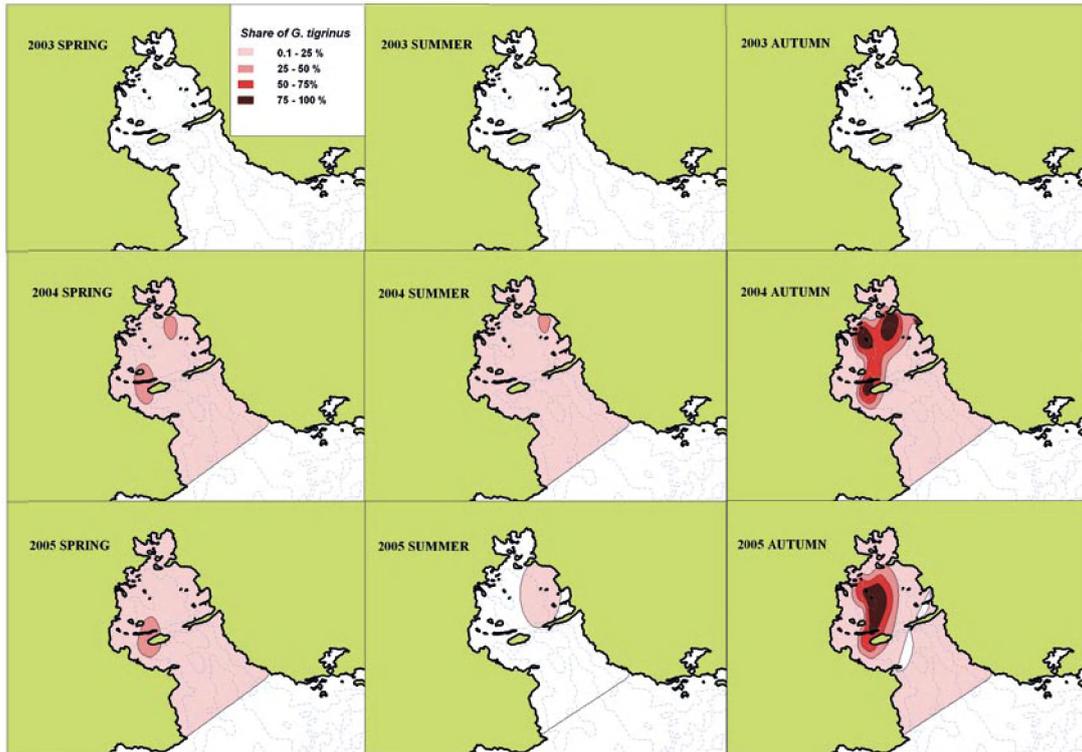
Fig. 3.5. Share of *Gammarus tigrinus* in the total gammarid biomass (%) in Kõiguste Bay in 2003–2005.

Fig. 3.6. Distribution of *Gammarus tigrinus* in the Estonian coastal sea in 2005.

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Similarly to *G. tigrinus*, *C. curvispinum* was found in the Baltic Sea area already in the 1920s (Nikolaev, 1963), but only recently the species expanded its distribution area (Gruszka, 1999; Jazdzewski & Konopacka, 2002; Leppäkoski et al., 2002). *C. curvispinum* was observed for the first time in the Estonian coastal sea in 2005 (Fig. 3.6). The invasive amphipod was found in connection with the traditional monitoring of phytobenthic communities in the Sillamäe area in the eastern Gulf of Finland. Thus, this is the northernmost documented location of *C. curvispinum* in the Baltic Sea. The Curonian Lagoon is the closest basin where the invasive amphipod is found (Leppäkoski et al., 2002). *C. curvispinum* was likely introduced to the Gulf of Finland either at the Sillamäe or Kunda port area by means of ship traffic.

C. curvispinum was found between 1 and 4.9 m depth associated with the belt of *Cladophora glomerata* (L.). The average density and biomass of the species ranged between 125–1425 ind. m^{-2} and 0.05–0.27 g m^{-2}, respectively The maximum densities were found at 3 m. Together with juvenile gammarids *C. curvispinum* was a prevailing invertebrate species in the samples.

Fig. 3.7. *Chelicorophium curvispinum* from the Sillamäe area. *Photo by J. Kotta.*

4. Chinese mitten crab *Eriocheir sinensis* in the north-eastern Baltic Sea

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SUMMARY

First records of the Chinese mitten crab *Eriocheir sinensis* in the Baltic Sea were made about eight decades ago. The present paper provides information on the seasonal and long-term population dynamics of *E. sinensis* based upon findings of the species in commercial gillnet fishing in the southern Gulf of Finland since 1991. The catch index was substantially higher in 2002–2005 than in the previous years. The highest catch indexes were observed in the periods of May–June and October–November. Questionnaire surveys on findings of *E. sinensis* in the various sub-basins of the NE Baltic Sea (southern Gulf of Finland, northern Gulf of Riga, Väinameri Arhipelago) revealed that the species is commonly found all over the studied coastal sea. As the reproduction of mitten crabs in the Baltic Sea is unlikely due to low salinities, it is assumed that the individuals caught have migrated into the area from the main European distributional area of the species in the south-eastern North Sea, a more than 1,500 km migration distance.

MATERIAL AND METHODS

Data were gathered by field sampling and by contacting commercial fishermen and relevant fisheries authorities.

Commercial gillnet fishing

The gillnet fishing (net height 1.5–1.8 m, mesh size a = 40–55 mm) was carried out in the shallow coastal area of Muuga Bay at the southern coast of the Gulf of Finland (Fig. 1) since spring 1991.

For each fishing operation that resulted in a catch of *Eriocheir sinensis* (Milne-Edwards), the catch-per-unit-effort (CPUE, number of crabs caught per hour fished and length of nets, in metres, employed) was calculated according to the formula:

$$CPUE = C * L^{-1} * D^{-1} \qquad (1)$$

where CPUE is the catch per unit effort, C is the number of crabs in a catch, L is the length of nets (in metres) and D is the duration of the catch (in hours).

In all years sampling was undertaken from March to December with relatively similar sampling intensity both in terms of the number of days fished and the number of nets

employed. The annual catch index was calculated according to the formula:

$$CI_a = \sum 10^3 * CPUE_i \qquad (2)$$

where CI_a is the annual catch index and $CPUE_i$ is the monthly total catch per unit effort.

The monthly catch index was calculated as:

$$CI_m = 10^6 * CPUE_I * MN^{-1} * MD^{-1} \qquad (3)$$

where CI_m is the monthly catch index, $CPUE_i$ is the monthly total catch per unit effort, MN is the monthly mean number of nets used and MD is the monthly mean number of days sampled.

Questionnaire surveys

Qualitative (presence/absence) data on the spatial distribution of the crab were obtained by telephone interviews with commercial fishermen and county fisheries authorities around the whole Estonian coast – southern Gulf of Finland, Väinameri Archipelago and northern Gulf of Riga (Fig. 1) – in early 2004. This information was amended with knowledge of fisheries scientists of the Estonian Marine Institute who carry out systematic experimental fish surveys in the Estonian coastal sea, and local commercial fishermen who continuously supply their information to scientists (so-called reference fishermen).

RESULTS AND DISCUSSION

The Chinese mitten crab (Fig. 4.1) has been found in the coastal areas of all major sub-basins of the north-eastern Baltic Sea: southern coast of Finland, northern part of the Gulf of Riga and coastal areas of the north-eastern Baltic Proper (Fig. 4.2). Although there are no solid quantitative records on the density of the crab, information from local fisheries authorities and fishermen indicates that the crab is likely more abundant in the eastern Baltic Proper compared to the eastern Gulf of Finland or the northern Gulf of Riga. In the region of Saaremaa Island (Fig. 4.2), the annual crab catch was around 100 individuals in recent years. The majority of the catch occurred in the western part of the island.

Fig. 4.1. Chinese mitten crab *Eriocheir sinensis*. Photo by *J. Kotta*.

The total number of crabs found in the long-term commercial gillnet fishing was low – 33 individuals. The highest catch (in numbers) was recorded in October 2002. On a monthly basis, a notably higher catch index occurred in spring (May–June) and autumn (October–November). Multi-annual dynamics of the crab catch index reveals substantially higher values for recent years (2002–2005) compared to all other years studied (1991–2001, Fig. 4.3). Both the seasonal and long-term dynamics of the species observed within the current study is generally in line with observations in neighbouring areas in the NE Baltic Sea (Ojaveer et al., submitted).

The Chinese mitten crab is omnivorous and feeds on a wide variety of benthic invertebrates (Gollasch, 1999). Prior to the invasion of *E. sinensis* such functional type was absent in the northeastern Baltic Sea. Concurrently with the increase in its density *E. sinensis* may pose a significant predation pressure on the native invertebrate communities. Nevertheless, as we lack quantitative abundance data and information on feeding habits and feeding rates of the crab, it is currently difficult to evaluate the impact of *E. sinensis* on benthic invertebrates. However, a direct positive impact of the increased crab abundance on (commercial) fish stocks is unlikely as there are no large predatory fishes in the northern Baltic Sea that are able to consume the crab. The crab density is probably too low at present to be able to exert measurable food-web mediated impacts, at least to the upper trophic levels.

Fig. 4.2. Spatial distribution (finding locations) of the Chinese mitten crab *Eriocheir sinensis* in the Estonian marine waters (dots). The location of the long-term gillnet monitoring station is indicated by an asterisk (updated from Kukk (ed.) 2005).

The only known record of the crab in an Estonian freshwater habitat dates back to April 2000 when one crab was found in artificial Mõdriku Lake situated ca 30 km from the sea and connected to the Gulf of Finland via a small river (Jõgi 2000). Thus, in Estonian waters, both the main distribution area and associated potential ecological impact of the species are currently restricted only to the brackish environment. In other Baltic Sea countries, the species has been found in several freshwater bodies, such as for instance Saimaa Lake District, Vuoksa River, Odra River, Lake Ladoga, Daugava River, Lake Vänern, Lake Mälaren (Ojaveer et al., submitted).

The whole Baltic Sea can be considered as a migration area for the species as the crab is unable to reproduce in low salinity conditions. The migration distance of the crab from the nearest reproduction ground (Elbe River estuary) via the Kiel Canal to the most distant finding location in Estonia (Narva Bay in the eastern Gulf of Finland) exceeds 1,500 km. This is about two times more than the recorded maximum upstream migration distance of the crab in the Elbe River.
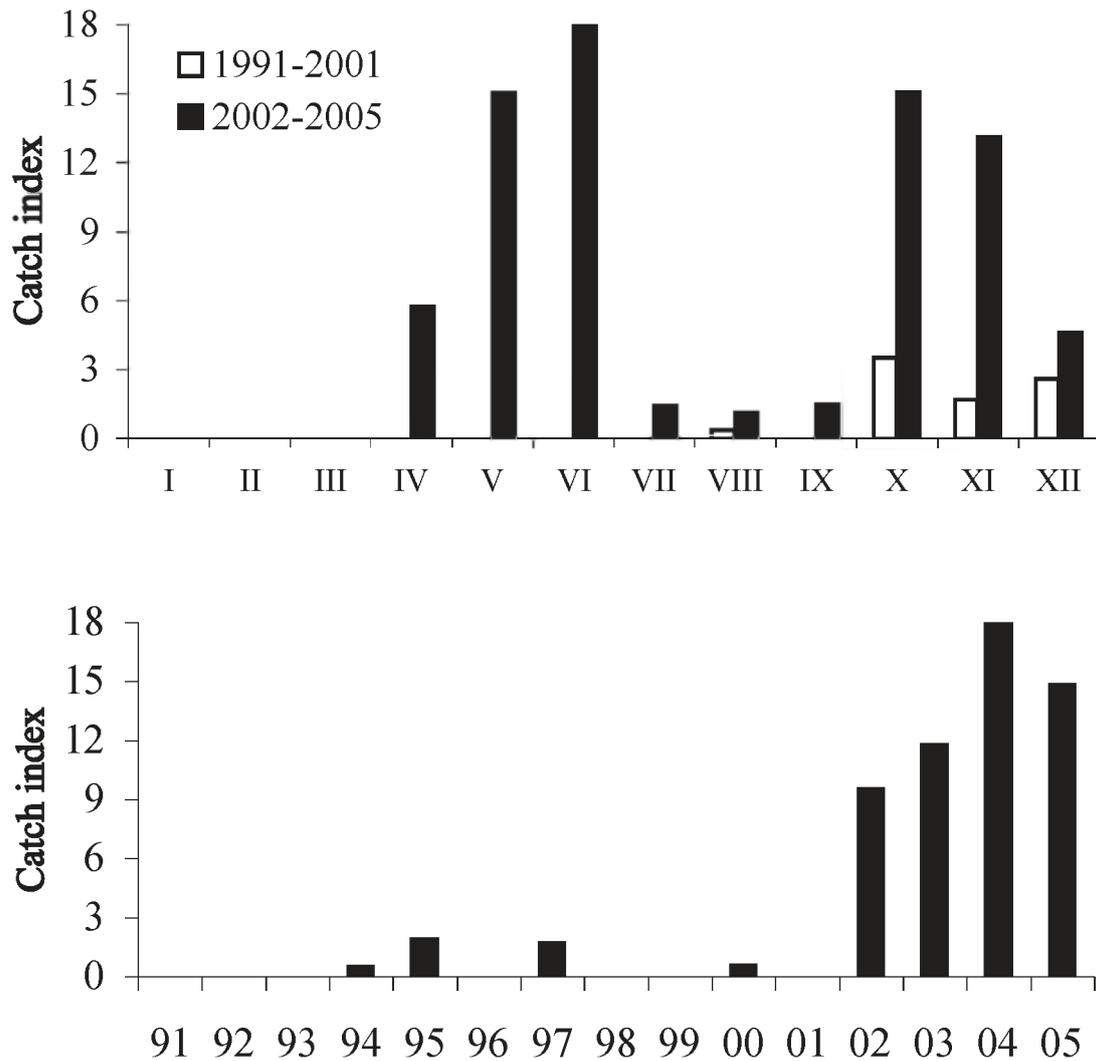
Fig. 4.3. Dynamics of monthly (upper panel) and annual (lower panel) catch index of the Chinese mitten crab *Eriocheir sinensis* in commercial gillnet fishing in the Gulf of Finland in March–December 1991–2005. Details on the calculation of catch indices are given in Material and Methods.

In the NE Gulf of Riga, males and females were represented in equal numbers (sex ratio 1:1) with the overall mean carapax width of 6.3 cm (±0.1 SE, range 5.9–7.4 cm, $n = 16$). This is in a line with Finnish and Russian data with one exception: the sex ratio between males and females was substantially different (2.4:1) in the Russian data set from the eastern Gulf of Finland (Ojaveer et al., submitted).

5. Invasion history and distribution of the semi-terrestrial invasive amphipod *Orchestia cavimana* in the Estonian coastal sea

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SUMMARY

The talitrid amphipod *Orchestia cavimana* was found for the first time in the north-eastern Baltic Sea in 1999. The talitrid amphipod inhabited damp wrack cast up on shore within a 200 m area in 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 north-western part of Estonia. Abundances and biomasses were the highest in the first year of invasion. In the following years the values stabilized on notably lower levels. 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.

MATERIAL 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. 5.1). One sample was taken in each station except for a site in northern Saaremaa Island (location of the first find of *Orchestia cavimana* Heller in Estonia) where three replicate samples were taken annually in 1998–2004. Sites were selected to cover a maximum salinity range, different sediments and wrack types. Shores that 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 (the 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. At the sites where talitrid amphipods were found, a biomass sample was taken using a 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 the 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.

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 used 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 analyse 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 were checked. Multivariate data analyses were performed using the package "PRIMER" (Clarke & 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 the abundance, biomass and size structure due to habitat characteristics.

RESULTS AND DISCUSSION

The Talitridae is the only family of amphipods that has truly terrestrial species, and although many are found close to the sea on the upper parts of the shore, some occur at considerable distances inland. It is a very large family, which 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 recognized species that are semiterrestrial, typically living amongst intertidal stones and algae, although some are found inland and may occur several hundred metres 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* 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 no talitrid amphipod species had been found further north.

The talitrid amphipod *Orchestia cavimana* has a relatively wide distribution area inhabiting the Mediterranean, Black Sea, Red Sea, Atlantic coasts of North Africa and 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 (Žmudzinski, 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 the arrival, invasion vector, range expansion, current distribution and possible impact of the species is extremely limited.

Orchestia cavimana was found for the first time on the northern coast of Saaremaa Island in 1999 (Fig. 5.1). *O. cavimana* inhabited damp wrack. The species was restricted within a 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 down to 2,433 ind m^{-2} and 2 g dw m^{-2}, respectively.

In 2002 *O. cavimana* was found in nine areas. 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.
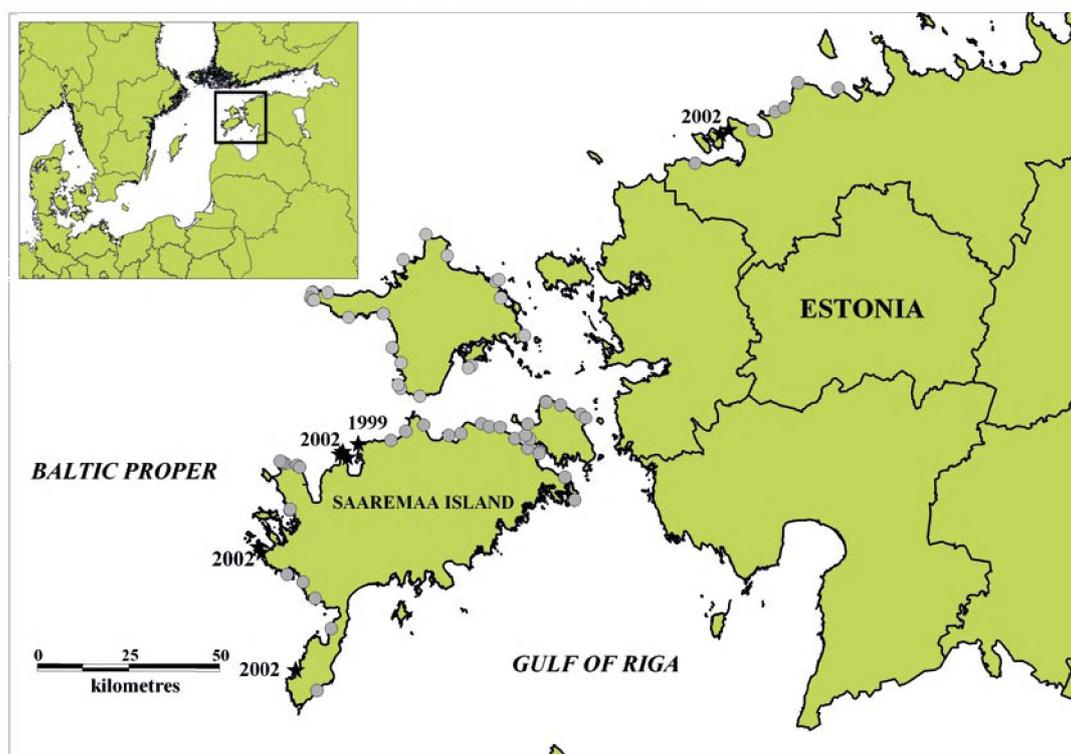

Figure 5.1. Study area. Filled circles indicate the sampling sites of talitrid amphipods and stars the locations where *Orchestia cavimana* was found. Years show the time of first record of *O. cavimana* in a site.

O. 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 of 73% and, the wrack biomass varied from 1,224 to 4,924 g dw m^{-2} with an average of 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 4 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 of 9. *Fucus vesiculosus* L. prevailed in the wrack in seven areas and *Polysiphonia fucoides* (Huds.) Grev. in the other two areas. *Pilayella littoralis* (L.), *Zostera marina* L. and *Ruppia maritima* L. were the second dominant plant species within the wrack.

The biomasses and abundances of *O. cavimana* ranged from 0.6 to 29.0 g dw m^{-2} and from 50 to 6275 ind m^{-2}, respectively. The average biomass was 9.1 g dw m^{-2} and the average abundance was 1975 ind m^{-2}. The amphipod length varied between 3 and 20 mm with an average of 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 of 0.005 g. Males had a significantly greater average length than females (11.4 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, $p < 0.05$).

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.

The biomass of *O. cavimana* increased with the wrack biomass (Fig. 5.2). 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 the 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 the highest in moist, intermediate in wet and the lowest in dry wrack.

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 stabilized on notably lower levels with a slight increase in 2004 (Fig. 5.3).
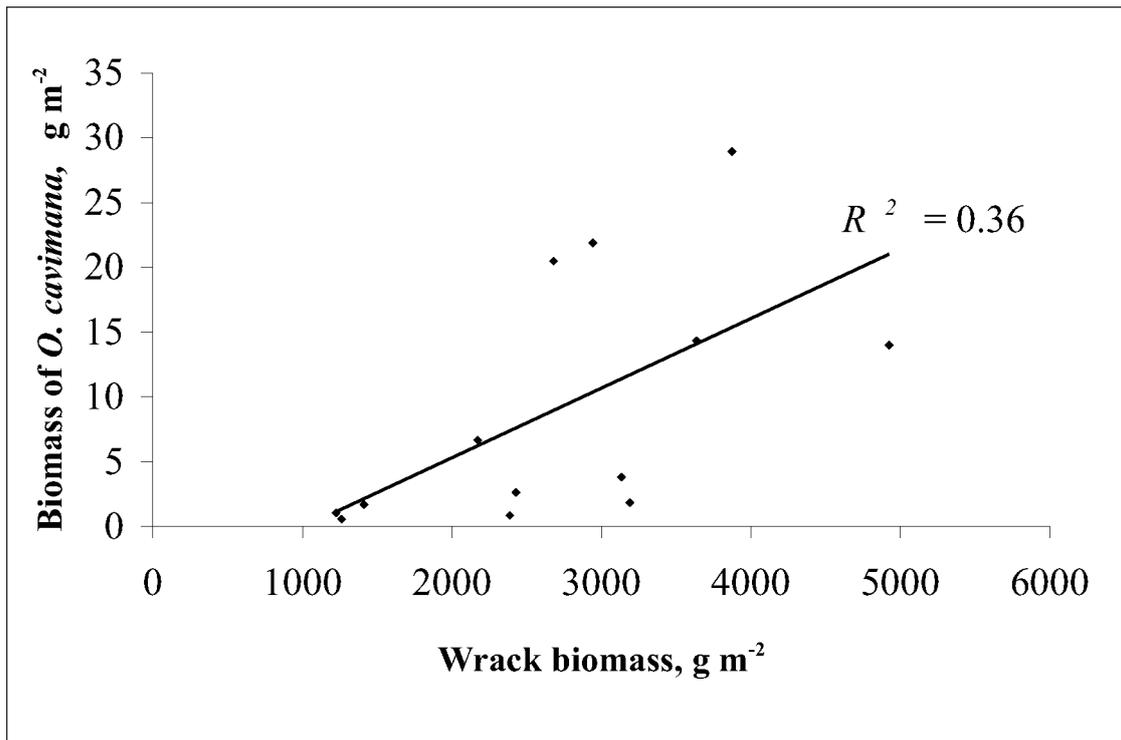
Figure 5.2. Relationship between the biomasses of wrack and the amphipod *Orchestia cavimana* in the study area.
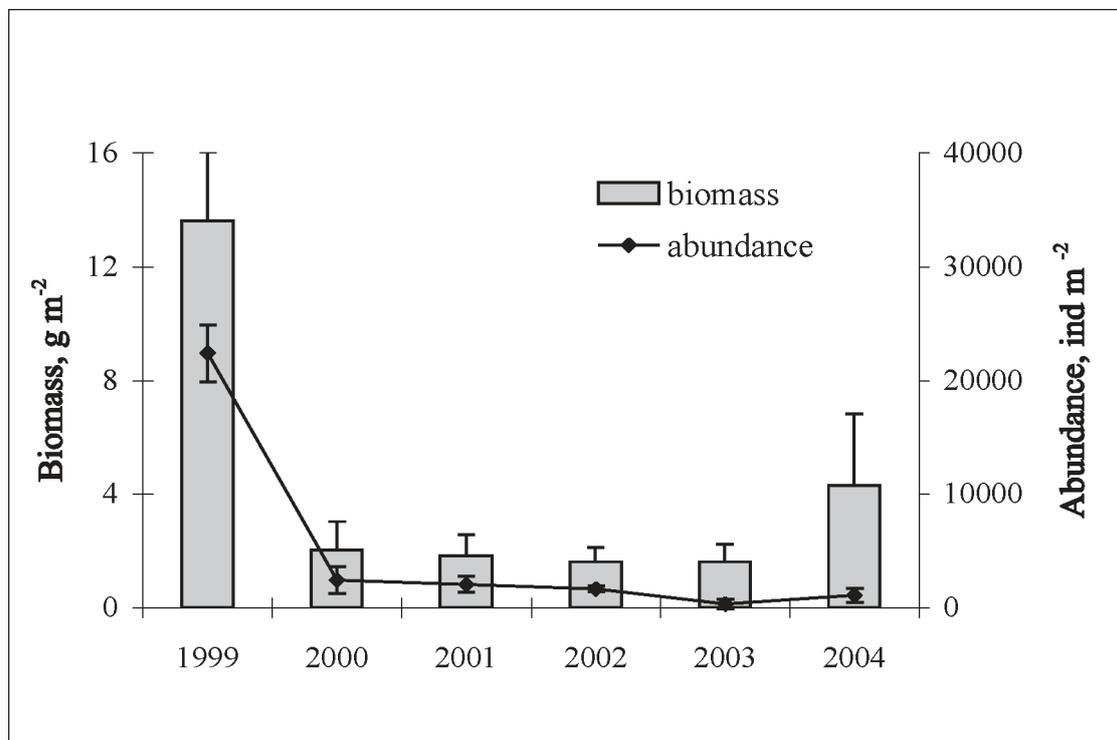

Figure 5.3. Interannual variation in the abundance and biomass of *Orchestia cavimana* (± SE) at the station of the first record of the species (northern coast of Saaremaa Island).

In the north-eastern Baltic Sea *O. cavimana* inhabits damp wracks and the upper layer of sediment. The habitat corresponds to the previous records in the Baltic and other seas (Den Hartog, 1965; Curry et al., 1972; Žmudzinski, 1974; Lincoln, 1979). 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 north-eastern Baltic Sea due to the stochastic nature of the invasion process.

Population characteristics varied considerably between and within sites. Most of the variability was explained by the quantity and quality of wrack. The quantity, composition and other properties of wrack are important for 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.

O. cavimana was found for the first time on the coasts of northern Saaremaa Island, the north-eastern Baltic Sea, in 1999. This corresponds 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 late 1998 or early 1999. Alternatively, the species may have arrived even earlier provided 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 the Estonian Marine Institute, University of Tartu).

In the following years the amphipod abundances stabilized on much 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, 1996b; Williamson & Fitter, 1996). In 2002 eight additional locations of *O. cavimana* were found in Saaremaa Island and north-western 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 the 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 climates. In the Baltic Sea area the high temperature in the wrack banks through autumn to spring is an ecological factor that positively influences the populations of the talitrid amphipod *Orchestia gammarellus* (Backlund, 1945).

The timing of the range expansion of *O. cavimana* may be connected with climate warming. A shorter period 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 north-eastern Baltic Sea or whether there were 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 drifting algae. However, as the northern coast of Saaremaa Island is an important recreational area, unintentional introduction cannot be excluded. Wildish (1970) showed that talitrid amphipods survive at least 14 days of submersion. In another experiment (Persson, 2001) the mortality of submerged *O. gammarellus* and *Platorchestia platensis* was very low during first two weeks but some individuals of both species survived more than three 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 our survey the northernmost findings of the invasive amphipod were reported from the southern coasts of the North and Baltic Seas (Žmudzinski, 1974; Lincoln, 1979). To date *O. cavimana* is found as far 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.

6. Invasion history and population structure of the alien gibel carp *Carassius gibelio* in Estonian marine waters

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SUMMARY

The gibel carp or Prussian carp *Carassius gibelio* originates from Asia. The fish was first introduced into fish ponds and small lakes of Estonia in 1948. In marine watres, the fish was first found in marine waters in 1985 in the Gulf of Riga and during the recent years the species became invasive. While in some shallow sheltered areas the species can reproduce and thrives well, in more open coastal areas only large adult specimens are caught. In some coastal areas gibel carp is the biomass dominant. Estonian coastal areas are inhabited by the bisexual form of the gibel carp while the fresh waters of the country, are mostly populated by the gynogenetic form.

MATERIAL AND METHODS

Data on the earliest appearance of gibel carp *Carassius gibelio* (Bloch) (Fig. 6.1) in different Estonian coastal waters was collected during the coastal fish monitoring surveys carried out according to the guidelines for the coastal fish monitoring (Thoresson, 1993) as well as using the network of appropriately trained commercial fishermen collaborating with the Estonian Marine Institute, University of Tartu. The fish was sampled using a series of monitoring gill nets (mesh sizes 17, 21, 25, 30, 33, 38, 42, 45, 50, 55, 60, 65 mm) on 10 September and 1 November 2002 in two close sites, Häädemeeste and Võiste (Fig. 6.2). The fishing locations of the monitoring programme and those of trained commercial fishermen are presented in Fig 6.2. The increasing abundance of the gibel carp is described using the commercial fisheries statistics from two counties: Saaremaa in the Gulf of Riga and Lääne-Virumaa in the Gulf of Finland. Sex of fish was determined visually by gonads.

RESULTS

First data on the occurence of the gibel carp in the Estonian marine waters originate from the Häädmeeste area, Gulf of Riga, when several specimens were found in 1985. In some areas, however, first specimens appeared only in 2002. The earliest appearance of the gibel carp in 11 coastal localities around the Estonian coast is presented in Fig. 6.2.

First specimens of gibel carp in the coastal waters of Saaremaa Island were registered in 1995. Until 1998 the commercial catch was very small, but it increased rapidly in 1999–2004, being 700, 1705, 3716, 6902, 5527 and 9151 kg, respectively. In the Gulf of Finland, the first specimens were recorded in 1997. Until 1999 only a few

Fig. 6.1. The gibel carp *Carassius gibelio*. Photo by M. Vetemaa.

specimens were caught, but then the number started to increase. In Lääne-Viru County the commercial catch in 2000–2004 was 40, 78, 105, 130 and 175 kg, respectively.

A sampling study carried out in autumn 2002 at Häädemeeste and Võiste revealed that the proportion of females was 59% (*n* = 340). Average CPUE at Häädemeeste and Võiste was 112 and 45 per used set of nets, respectively. The length distribution of fish at Häädemeeste and Võiste is presented in Fig 6.3. Based on the visual examination, males had normally developed gonads in both areas. At Häädemeeste the gibel carp made 56% and 85% of the total weight of fish caught by the used set of nets (10 September and 1 November, respectively), being thus clearly the dominant species in the sampled fish assemblages. At Võiste the gibel carp dominated also (51% of the fish biomass). However, small fishes such as sticklebacks (*Gasterosteus aculeatus* L. and *Pungitius pungitius* (L.)) and gobies (*Pomatoschistus* spp.) cannot be sampled by the typical coastal monitoring net sets. Thus, the share of the gibel carp in the total fish biomass is actually lower.

DISCUSSION

The gibel carp was introduced deliberately to Estonian artificial fish ponds in 1948. In 1949 the species was released into two lakes and during a few consecutive years fishermen transported it into many waterbodies over Estonia (Mikelsaar, 1984).

The gibel carp is rather similar to the crucian carp *Carassius carassius* (L.), which is not abundant in the Estonian coastal waters, but has always inhabited many shallow bays (like Matsalu Bay in Väinameri Archipelago). The similarity between the two species
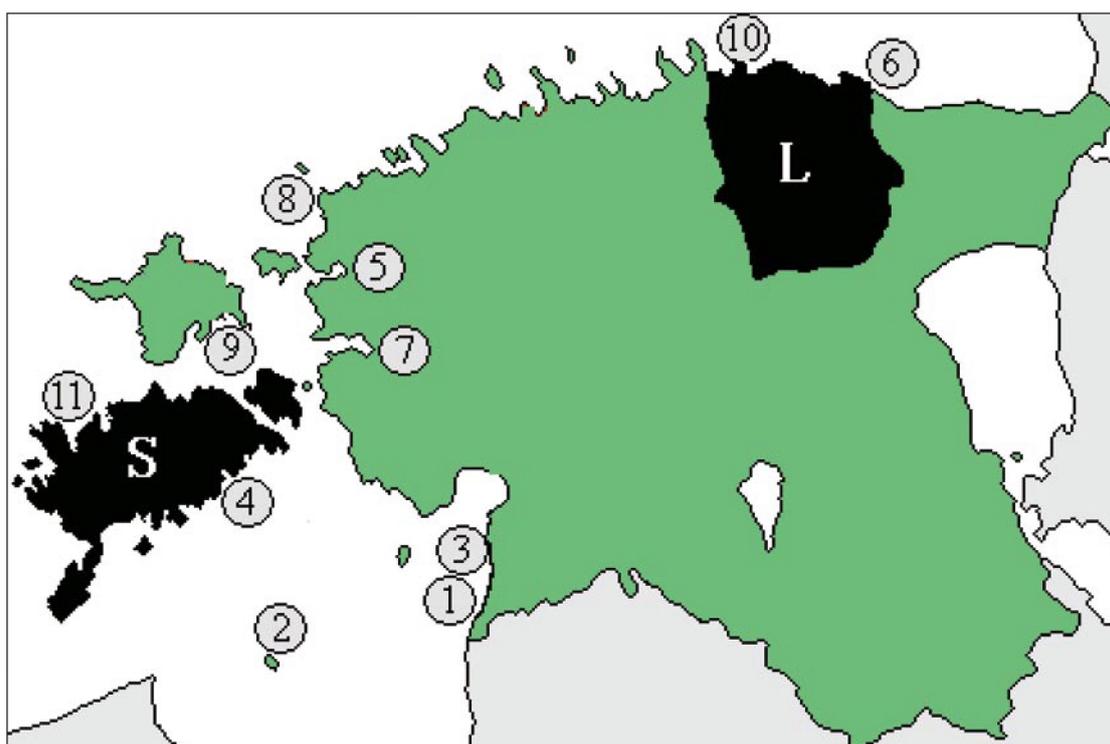
Fig. 6.2. First recorded catches of gibel carp *Carassius gibelio* in different Estonian coastal areas (CFM – coastal fish monitoring, F – data from trained fishermen). 1: Häädemeeste 1985 CFM; 2: Ruhnu 1988 F; 3: Võiste 1988 CFM; 4: south Saaremaa 1995 F; 5: Tagalaht 1997 CFM; 6: Mahu 1997 F; 7: Matsalu 1998 F; 8: Dirhami 1998 F; 9: Jausa 2000 CFM; 10: Käsmu 2000 F; 11: north Saaremaa 2002 F. S – Saare County, L – Lääne-Viru County.

is obviously a serious hindrance in very detailed mapping of the early distribution of the fish in the sea, since before the mass invasion started some fishermen probably registered them as crucian carp in their catch reports. In Pärnu Cunty (Gulf of Riga) it has been also registered (and sold on markets) as a common carp *Cyprinus carpio* L. In the present study only the first appearance data received from appropriately trained commercial fishermen were used.

During the last two decades the gibel carp has been registered in all main areas of the Estonian coastal sea. However, the existing distribution pattern suggests that the species is abundant only in densely vegetated shallow coastal areas like Häädemeeste, South Saaremaa bays, Jausa Tagalaht Bay (Fig. 6.2), whereas in more open coastal areas (deeper and colder water) usually only a few large adult specimens are caught (Saat & Taal, 2001; Saat & Kikas, 2002). In the present study the CPUE and the share in the total fish biomass was higher in shallower and densely vegetated Häädmeeste than at Võiste.

In some coastal areas of the southern Baltic Sea the gibel carp was common already a century ago (Bartel et al., 1996). In the Vistula Lagoon (Poland) this species was one

of the five most important species already during the period 1889–1920. Its abundance has not shown an increasing trend during the following research periods in 1933–1939, 1956 and at the end of the 1980s (Bartel et al., 1996). In the Curonian Lagoon the gibel carp was first registered in 1960, following the introduction into freshwater bodies of Lithuania in 1948–1957. In its way to the sea the species first appeared in the lower reaches of the River Nemunas, after that in the lagoon itself (Gaigalas, 2001). The species exists in the monitoring catches in the Curonian Lagoon but is not abundant; it inhabits shallow coastal areas, but not the open central area of the lagoon. The species has increased its abundance steadily during the last decade (Linas Lozys, personal communication). In Latvia the first specimens were caught in the Salacgriva area (only 40 km south from Häädemeeste where the fish was first found in Estonia), after which the species has been registered also in other coastal areas (Evalds Urtans, personal communication). While in the eastern coast of the Baltic Sea (Poland, Lithuania, Latvia, Estonia) the gibel carp is rather common, in the coastal areas of Sweden the species has not yet been registered (Inger Abrahamsson, personal communication).

The species appeared in the Estonian coastal sea only less than 20 years ago (more than 30 years after its appearance in many lakes and rivers). At the same time the fish has inhabited southern areas of the Baltic Sea like the Vistula River estuary already for a century (Bartel et al., 1996). So, the appearance in the Estonian coastal sea has been delayed by some factors. The species thrives in eutrophic waters with dense vegetation. The almost "explosive" distribution of the species during the late 1990s might be related to several unusually warm summers during the 1990s and low abundance of predatory fish. However, this needs to be proved in future studies.

There are two potential sources for the invasion of the species into the Estonian coastal sea. First, after the release in 1949 the species has inhabited many freshwater bodies and might have moved into the sea from rivers. Secondly, the species might have migrated into the Estonian coastal sea from the southern Baltic Sea where it existed already a century ago. Estonian coastal areas are inhabited by the bisexual form of the gibel carp while the fresh waters of the country are mostly populated by the gynogenetic form (Mikelsaar, 1984). This hints to the second immigration possibility, because in the southern Baltic Sea also both sexes exist (Linas Lozys, personal communication). However, further genetic studies are needed to solve this question.

In conclusion, the gibel carp has recently become a common species almost everywhere along the Estonian coast. There are no data that this invasion has caused serious damage to the coastal ecosystem or is causing substantial fishery losses due to the competition with native species. However, as in some coastal areas the species is already the biomass dominant, it is most likely affecting the native food webs.
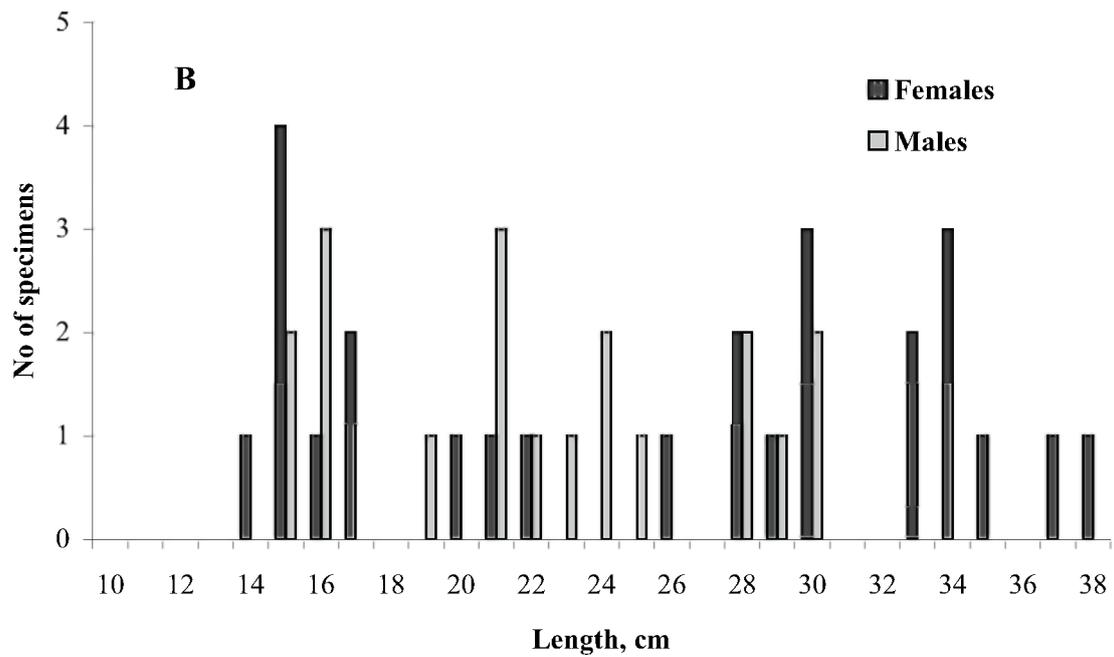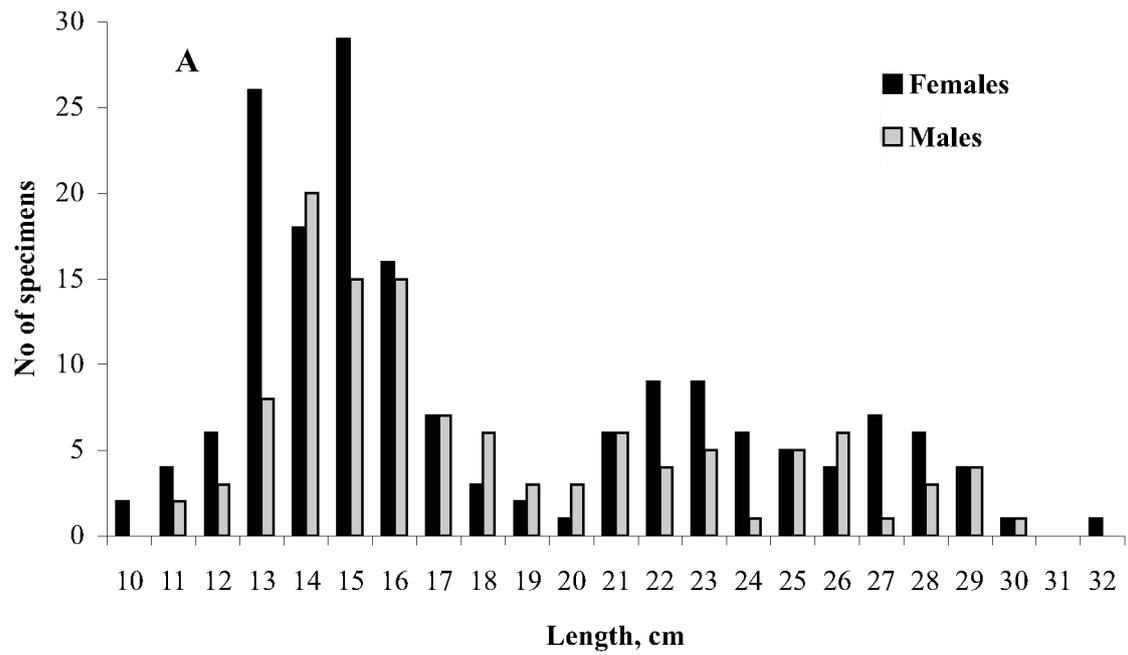
Fig. 6.3. The length distribution of the gibel carp *Carassius gibelio* at Häädemeeste (A, *n* = 290) and Võiste (B, *n* = 45), Gulf of Riga.

7. Port biological sampling as a tool for monitoring invasive species in high-risk areas of bioinvasions

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SUMMARY

Pelagic and benthic invertebrate communities were studied in Muuga harbour – one of the largest terminals in the Baltic Sea. The most common and abundant zooplankton species in Muuga harbour and in the adjacent sea areas were the same whereas the species composition differed between these areas with additional freshwater species being present in the harbour. Benthic invertebrate communities were very different in Muuga harbour and the adjacent sea areas. Within the port area the bottom deposits were unstable due to dredging activities and ship induced bottom turbulence. The number of native benthic invertebrate species was high but the number of invasive species was low in the harbour as compared to the adjacent sea areas.

MATERIAL AND METHODS

The composition of zooplankton and zoobenthos was investigated in the Estonian largest port area - Muuga harbour (Port of Tallinn, Gulf of Finland; Fig. 1). Samples were taken during the ice-free seasons, generally twice per month. In each occasion three predefined sites were visited (Fig. 7.1). In total 90 zooplankton samples were collected during the years 2002–2005 and 30 zoobenthos samples were collected in 2004–2005. Zooplankton sampling was performed directly from port terminals with a large Juday net (mesh size 90 μm). The samples were preserved until laboratory analysis in 4% formaldehyde solution. Samples were analysed semiquantitatively; the whole sample was analysed to identify all species. Total zooplankton biomass was estimated roughly according to the settling volume. All samples were stored for detailed analyses in the future, if necessary. Macrozoobenthos samples were colleced with an Ekman bottom grab. The sediment samples were washed through a 0.25 mm mesh. In the laboratory the animals were counted under a stereo dissecting microscope. The total dry weight of the animals in each sample was determined to the nearest 0.5 mg and calculated for an area of 1 m^2.

RESULTS

The most frequent and abundant zooplankton species in Muuga harbour and in the adjacent area (Muuga Bay) are similar: the copepods *Acartia bifilosa* (Giesbrecht) and *Eurytemora affinis* (Poppe) and the rotifer *Synchaeta baltica* Ehrenberg. The full list of mesozooplankton species in Muuga harbour is given in Table 7.1. There were two

biomass peaks during a season in the harbour area. The maximal zooplankton biomass was found in July, very high numbers occurred also in spring (Fig. 7.2). Samples from late summer prove that in years with favourable conditions for *Cercopagis pengoi*, it can occur in high concentrations also in enclosed port areas.

Four zooplankton species were present in the harbour area that had not been encountered in the national monitoring station in Muuga Bay during the last decade: *Chydorus sphaericus* (O. F. Müller), *Diaphanosoma brachyurum* (Lievin), *Asplanchna* sp. and *Argulus foliaceus* L. The first three are typical freshwater species and appear sometimes in the littoral zone of the Baltic Sea. The fish louse *A. foliaceus* is rarely encountered in zooplankton samples; however, this species is very common in the littoral zone.

The full list of macrozoobenthic species in Muuga harbour is given in Table 7.2. Benthic invertebrate communities are very different in Muuga harbour and the adjacent sea areas. Within the port dredging activities are regularly carried out. Besides, bottom deposits are very mobile owing to ship induced bottom turbulence. Sediments are covered with finer deposits rich in organic matter. Consequently, the species diversity and densities are highly variable. When the level of physical disturbance was high the communities contained no or only a few macrobenthic species such as the native amphipod *Corophium volutator* (Pallas) and the invasive cirriped *Balanus improvisus* Darwin. *Macoma balthica* (L.) may appear at the later stages of succession following the reduction of physical disturbance. When the level of physical disturbance was low benthic communities had relatively high diversity as the organic rich bottom deposits offered good dietary conditions for most deposit feeders. Besides the above-mentioned species Oligochaeta, *Hediste diversicolor* (O. F. Müller), *Hydrobia ulvae* (Pennant), *Mytilus edulis* L., *Cerastoderma glaucum* (Poiret), *Mya arenaria* L. and Chironomidae larvae occurred in these areas. Macrobenthic abundance and biomass varied between 250 and 3,000 ind. m^{-2} and 2 and 160 g m^{-2} in the Muuga Port area in 2004–2005.

Sea areas adjacent to Muuga Port were affected by large-scale dredging in 2003–2004. The bottom deposits of the area were covered with a few centimetre thick layer of artificial sediments. Macrobenthic diversity was low in 2004–2005. The following native invertebrate taxa were found: *H. diversicolor*, Oligochaeta, *H. ulvae*, *Hydrobia ventrosa* (Montagu), *M. balthica* and *C. volutator*. Among nonindigenous species only *Potamopyrgus antipodarum* was recorded. Since the commencement of dredging the abundance and biomass of macrozoobenthos increased manifold, reaching 3,600–5,100 ind. m^{-2} and 350 g m^{-2} by 2004. This increase was mainly due to the thriving of the bivalve *M. balthica*. In 2005 the abundances and biomasses were gradually declining, being estimated at 650–2,400 ind. m^{-2} and 50–150 g m^{-2}. However, the communities are still indicating the earlier disturbance of dredging.
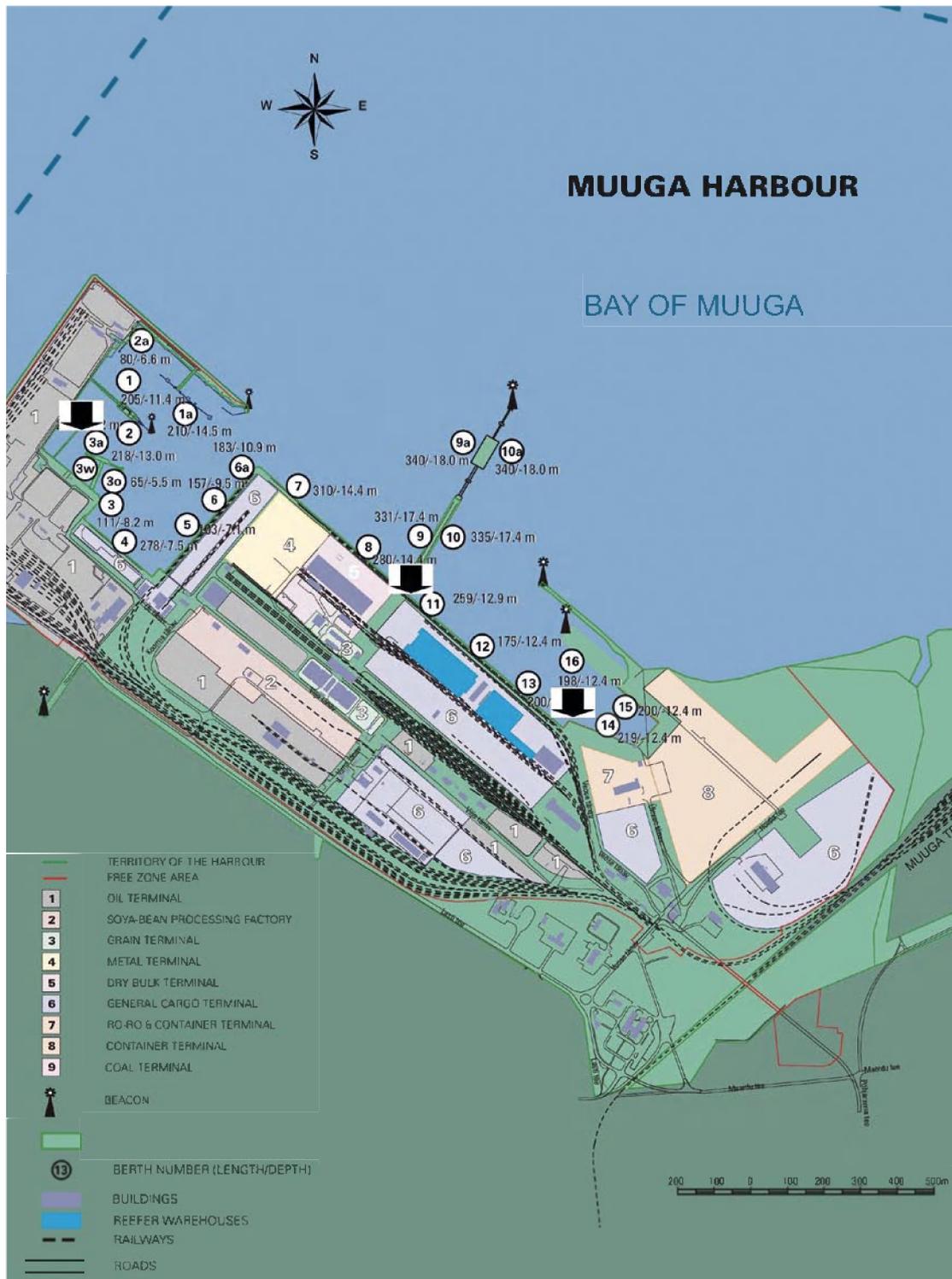
Fig. 7.1. Sampling sites in Muuga harbour (indicated by black arrows, from left to right): Site 1 – Ro-Ro and Container terminal; Site 2 – Grain terminal; Site 3 – Oil terminal. Source of the map: //www.portoftallinn.com/

Table 7.1. Mesozooplankton diversity in Muuga harbour during the ice-free season in 2002–2005. For location of sites see Fig. 1. Alien species are given in bold

	Site 1	Site 2	Site 3
COPEPODS			
Limnocalanus macrurus G. O. Sars	+	+	+
Acartia bifilosa (Giesbrecht)	+	+	+
Eurytemora affinis (Poppe)	+	+	+
Centropages hamatus (Lilljeborg)	+	-	+
Temora longicornis (O. F. Müller)	+	-	-
Pseudocalanus minutus elongates (Boeck)	+	+	+
Mesocyclops leuckarti (Claus)	+	+	+
Harpacticoida (Ectinosoma curticorne Boeck*)*	+	+	+
CLADOCERANS			
Bosmina coregoni maritima (P. E. Müller)	+	+	+
***Cercopagis pengoi* (Ostroumov)**	+	+	+
Chydorus sphaericus (O. F. Müller)	+	-	+
Daphnia sp.	-	+	-
Diaphanosoma brachyurum (Lievin)	-	-	+
Evade normanni Loven	+	+	+
Pleopsis polyphemoides (Leuckart)	+	+	+
Podon intermedius Lilljeborg	+	+	-
ROTIFERS			
Asplanchna sp.	+	+	-
Keratella cochlearis recurvispina (Gosse)	+	+	+
Keratella cruciformis eichwaldi (Thompson)	+	-	+
Keratella quadrata quadrata (O. F. Müller)	+	+	+
Synchaeta baltica Ehrenberg	+	+	+
Synchaeta monopus Plate	+	+	+
MEROPLANKTON			
Polychaeta larvae	+	+	+
Balanus improvisus* Darwin *larvae	+	+	+
Gastropoda larvae	+	+	+
Lamellibranchiata larvae	+	+	+
OTHERS			
Fritillaria borealis Lohmann	+	+	+
Argulus foliaceus L.	+	-	-
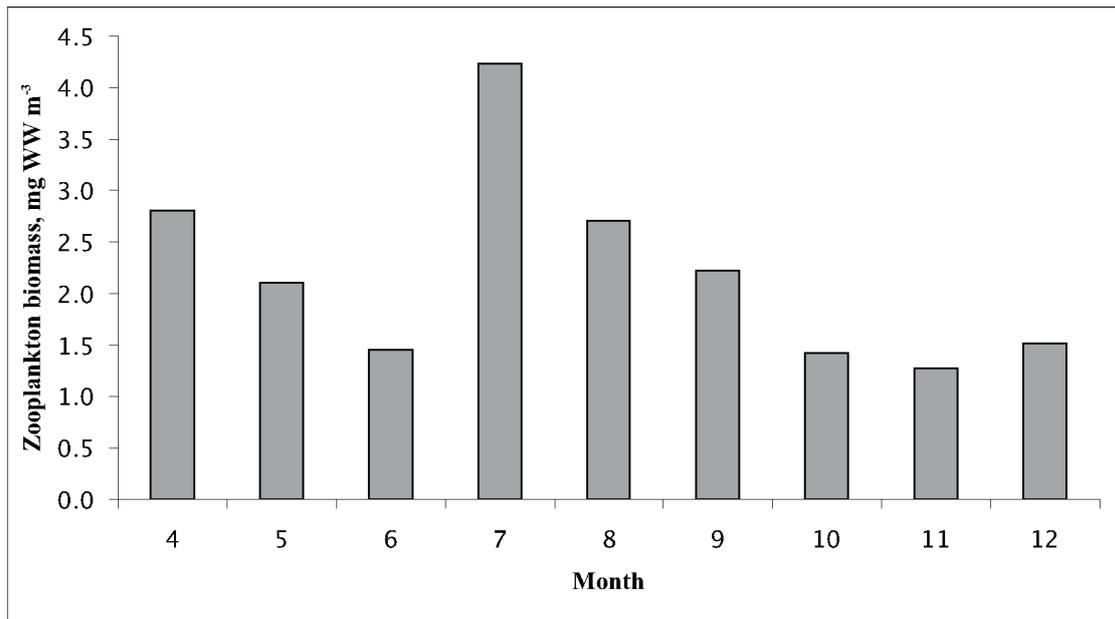
Fig. 7.2. Monthly average zooplankton biomass (mg wet weight m⁻³) in Muuga harbour in 2002–2005.

The round goby *Neogobius melanostomus* (Pallas) (Fig. 7.3), a demersal fish species of the Ponto-Caspian origin, was first found in the Baltic Sea in the Puck Bay (Poland) in the early 1990s (Skora & Stolarski, 1993). Since then the fish has colonized deeper waters and expanded its distribution area both to south and north (Sapota & Skora, 2005). In April 2002, one individual of the species (Tl 17.8 cm, Tw 84.7 g, male) was caught by commercial fishermen in the sea area adjacent to Pärnu port (Shpilev & Ojaveer, 2003). The recent contacts with leisure fishermen fishing in Muuga harbour suggest that the fish has further colonized northern-eastern parts of the Baltic Sea. According to fishermens reports from this area, *N. melanostomus* is a relatively common fish species in their catches (although not very abundant) and if caught, fishermen eat it with pleasure. Basic biological parametres of the two males caught in the Muuga harbour area on 6 October 2005 were: Tl = 17.3 cm, Tw = 95.9 g and Tl = 20.1 cm, Tw = 168.8 g (Ojaveer, 2006).

Table 7.2. Macrozoobenthos diversity in Muuga Harbour during the ice-free season in 2002–2005. For location of sites see Fig. 1. Alien species are shown in bold

	Site 1	Site 2	Site 3
CRUSTACEANS			
Neomysis integer (Leach)	+	-	-
Gammarus salinus Spooner	+	-	-
Corophium volutator (Pallas)	+	+	+
Balanus improvisus Darwin	+	+	+
Monoporeia affinis (Lindström)	-	+	-
Gammarus oceanicus Segerstråle	-	+	-
Jaera albifrons Leach	-	+	-
Crangon crangon (L.)	+	-	-
Saduria entomon (L.)	-	+	-
WORMS			
Oligochaeta	+	+	+
Hediste diversicolor (O. F. Müller)	+	+	+
Prostoma obscurum Schultze	+	+	+
Halicryptus spinulosus (v. Siebold)	-	+	-
BIVALVES			
Mytilus edulis L.	+	+	+
Macoma balthica (L.)	+	+	+
Cerastoderma glaucum (Poiret)	+	+	+
Hydrobia ulvae (Pennant)	+	+	+
Hydrobia ventrosa (Montagu)	-	+	+
Mya arenaria L.	+	+	+
Potamopyrgus antipodarum (J. E. Gray)	-	+	-
Theodoxus fluviatilis (L.)	+	-	-
INSECTS			
Chironomidae	+	+	+

Fig. 7.3. Two individuals of the round goby *Neogobius melanostomus* caught in Muuga
harbour in October 2005. *Photo by A. Põllumäe.*

8. Estimation of consumption rates of the predatory cladoceran *Cercopagis pengoi* in laboratory conditions

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SUMMARY

The predatory cladoceran *Cercopagis pengoi*, native to the Ponto-Caspian region, was first found in the Baltic Sea in the early 1990s. There are strong signals from field observations that the population abundance of a dominant native cladoceran *Bosmina coregoni maritima* is depressed and the seasonal abundance dynamics of copepod nauplii has changed after this invasion. Considering the very limited knowledge on feeding habits of *C. pengoi* (largely due to species-specific peculiarities), we conducted a set of laboratory feeding experiments with this species as a predator and several native more abundant mesozooplankton species as a prey. The goal of the current study was to identify potential prey items for *C. pengoi* in the lab conditions and to estimate the consumption rates of the species for various prey taxa at different prey mixtures and densities.

MATERIAL AND METHODS

Specimens of *Cercopagis pengoi* Ostroumov were collected with Juday net (mesh size 90 μm, mouth diameter 0.1 m²) from upper layers of Pärnu Bay (NE Gulf of Riga) and placed into 3 l containers. In order to reduce the stress, the collected material was quickly (within 1 hour) transported to the lab. In the lab, the animals were separated by means of a wide mouth pipette and placed singly into 1 l containers containing filtered seawater with aeration. Mostly large parthenogenetic females were used. It was carefully inspected that the selected individuals were free of attached detritus or other material and healthy, i.e., freely swimming during a 24-hour period. The young were born at night and these newly born first instar individuals were used in feeding experiments. However, some experiments were carried out with adult, third instar *C. pengoi* parthenogenetic females.

Mesozooplankton for prey were collected from Pärnu Bay simultaneously with *C. pengoi*, pipetted out of the water and placed into filtrated seawater in 2 l containers where they were kept in aerated conditions until feeding experiments.

Experiments were conducted in 1 l vessels at 20 ± 2 °C, allowing only diffuse overhead light. Each container was filled with 0.8 l filtrated seawater where 1 individual of *C. pengoi* was added. There was no aeration during the experiment. Healthy prey (15–50 per vessel) was added to containers. The prey density (ca 10 to 65 thousand individuals m⁻³) corresponded to that in the field conditions in Pärnu Bay. We visually controlled whether *C. pengoi* individuals were intact at the beginning of the experiments and several times during the experimental terms by observing their swimming behaviour. To prevent food

plankton sedimentation, we also mixed the vessels gently on these occasions. In addition, mesozooplankton swimming caused some turbulence in the flasks.

The duration of the experiments was usually $8 (\pm 4)$ hours. After the incubation period, experiments were terminated by addition of formalin to all vessels. The contents of experimental vessels were concentrated by reverse filtration (using 60 µm mesh) and observed using a dissecting microscope to assess predator and prey mortality, as well as the condition of the animals. Prey individuals found trapped within the water surface film were considered as live after the experimental period.

Altogether eight series of experiments, each in 25 replicates, were performed. The following prey was used: *Bosmina coregoni maritima* (P. E. Müller), *Balanus improvisus* Darwin larvae and nauplii and copepodids of *Eurytemora affinis* (Poppe) and *Acartia bifilosa* (Giesbrecht). Control experiments, without predators, were carried out exactly in the same manner as with *C. pengoi*. These were performed with all prey species separately.

Results of the predation experiments (the consumption rate of *C. pengoi*) are expressed as number of prey *C. pengoi*$^{-1}$ hour^{-1} consumed. Prey density in experiments is shown per litre (i.e., ind. l^{-1}).

RESULTS

The control experiments (without predator) showed that a prey species-specific approach should be implemented when interpreting the results. On average two individuals of copepod nauplii may have been lost during the experiment whereas for all the remaining diet items the mean potential loss was one. It appears that the share of successful experiments (including those where the predator actually died during the experiment) was relatively high, on average 75% (Table 8.1). The highest rate of unsuccessful experiments was in the case of copepodids (33%), the most successful experiments were those were *B. c. maritima* (80%) or copepod nauplii (82%) were used as prey.

Table 8.1. Number of feeding experiments of *C. pengoi* with various single and mixed diet items

Diet	Total experiments	Successful experiments
Balanus improvisus larvae	20	15
Bosmina coregoni maritima	10	8
Copepodids	61	41
Copepod nauplii	49	40
B. improvisus larvae + copepod nauplii	45	32
Copepod nauplii + copepodids	25	20
Total	210	156

The consumption rate of *C. pengoi* on *B. improvisus* larvae and *B. c. maritia* as single prey is rather similar with the highest value recorded for copepod nauplii and the lowest for copepodids (Table 8.2). The relation of consumption rates and prey densities was studied for *B. improvisus* larvae and copepod nauplii. It was obvious that a higher prey density resulted in an elevated consumption rate. This increase was most evident for copepod nauplii. When copepod nauplii and *Balanus* larvae were given at equal densities (19 prey l^{-1}), copepod nauplii were preferred: consumption rates were 0.42 ± 0.02 and 0.34 ± 0.04 *C. pengoi*$^{-1}$ hour^{-1} (mean $\pm$ SE), respectively (Fig. 8.1). When provided with mixed prey items at equal densities (19 prey l^{-1}) *C. pengoi* again consumed copepod nauplii at a higher rate than copepodids (0.51 ± 0.03 and 0.06 ± 0.03 *C. pengoi*$^{-1}$ hour^{-1}, respectively).

Experiments on the consumption of single prey by *C. pengoi* provided at two different density levels (above and below 30 prey l^{-1}) indicate that (1) the consumption rates do not differ for copepod nauplii and *B. c. maritima*, and (2) the more *B. improvisus* larvae are available, the more they are consumed (Fig. 8.2). Both *C. pengoi* juveniles and parthenogenetic adults consumed at similar rates *B. c. maritima* and copepod nauplii. A substantial difference was observed for *B. improvisus* larvae, who were utilized at a higher rate by adult than by juvenile *C. pengoi* (Fig. 8.3). The above suggests that copepod nauplii and *B. c. maritima*, if available, are the major prey for the *C. pengoi* population.

Table 8.2. Consumption rates of *Cercopagis pengoi* for various diet items

| Diet	Consumption rate (number of prey *C. pengoi*$^{-1}$ hour^{-1}; mean $\pm$ SE)
Balanus improvisus larvae	0.73 ± 0.04
Bosmina coregoni maritima	0.66 ± 0.06
Copepodids	0.40 ± 0.03
Copepod nauplii	0.94 ± 0.05
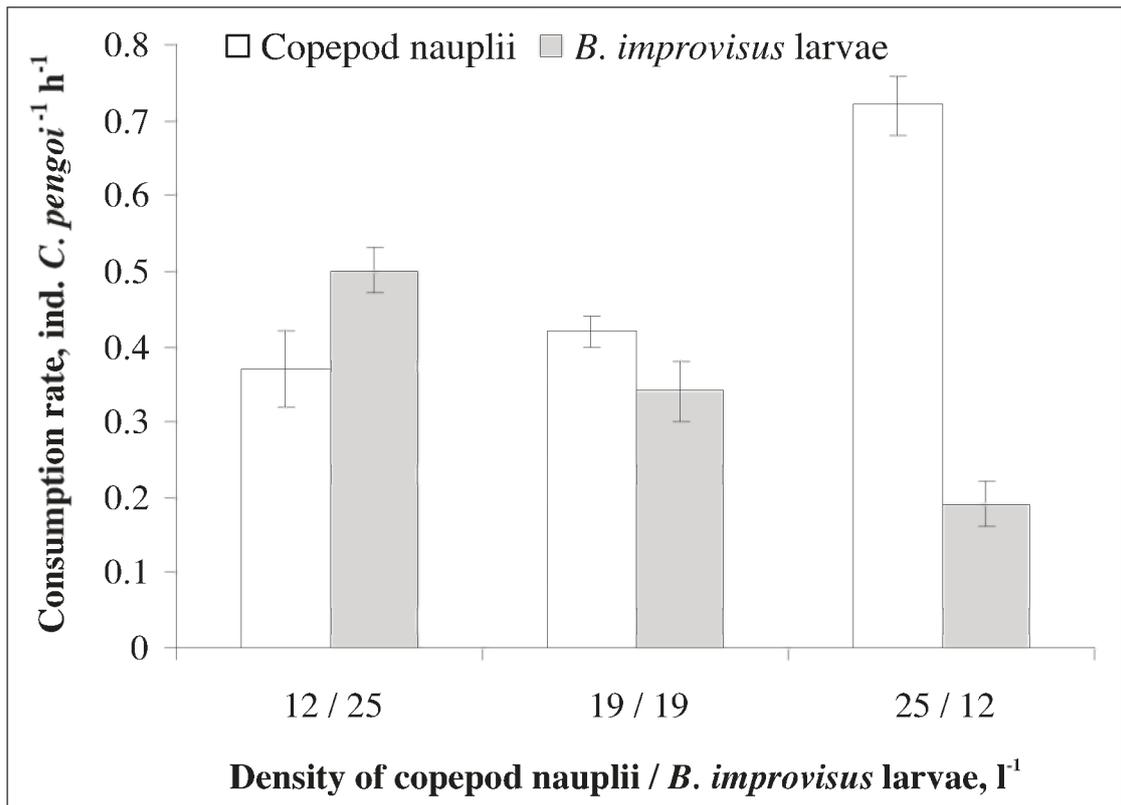
Fig. 8.1. Consumption rate of *Cercopagis pengoi* for Balanus improvisus larvae and copepod nauplii (*C. pengoi*[-1] hour[-1], mean ± SE) at three different mixed prey densities (l[-1]).
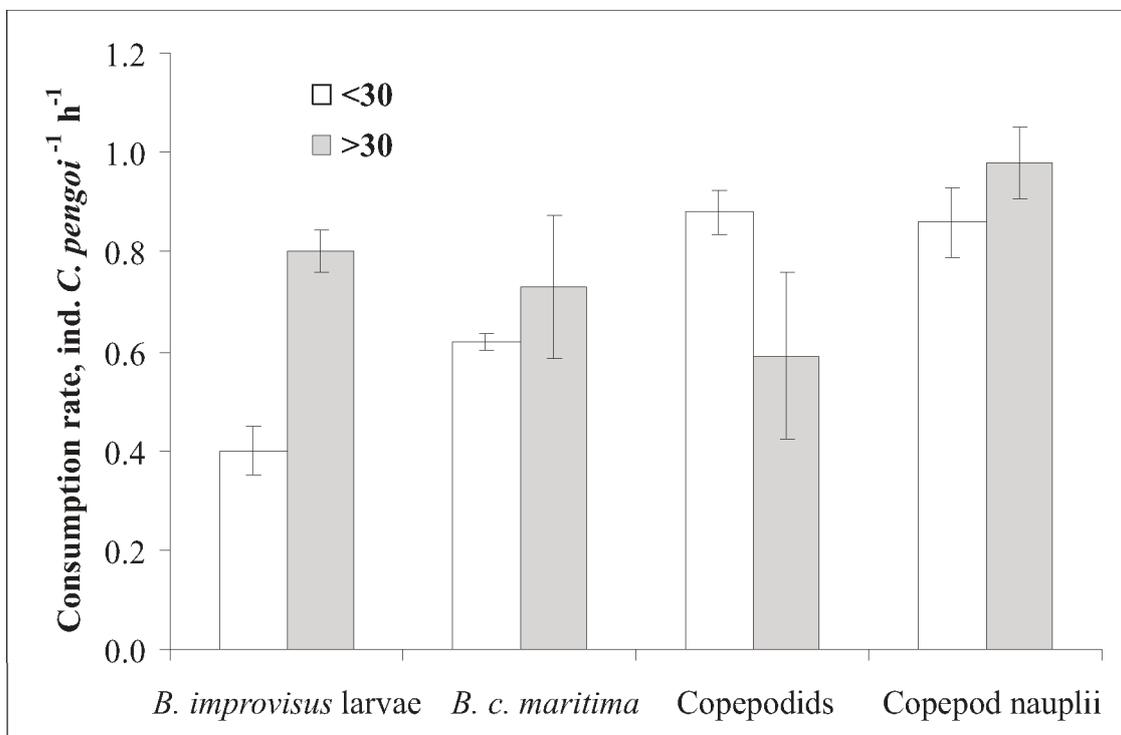
Fig. 8.2. Consumption rate of *Cercopagis pengoi* for various prey taxa (*C. pengoi*[-1] hour[-1], mean ± SE) at two different single prey densities (l[-1]).
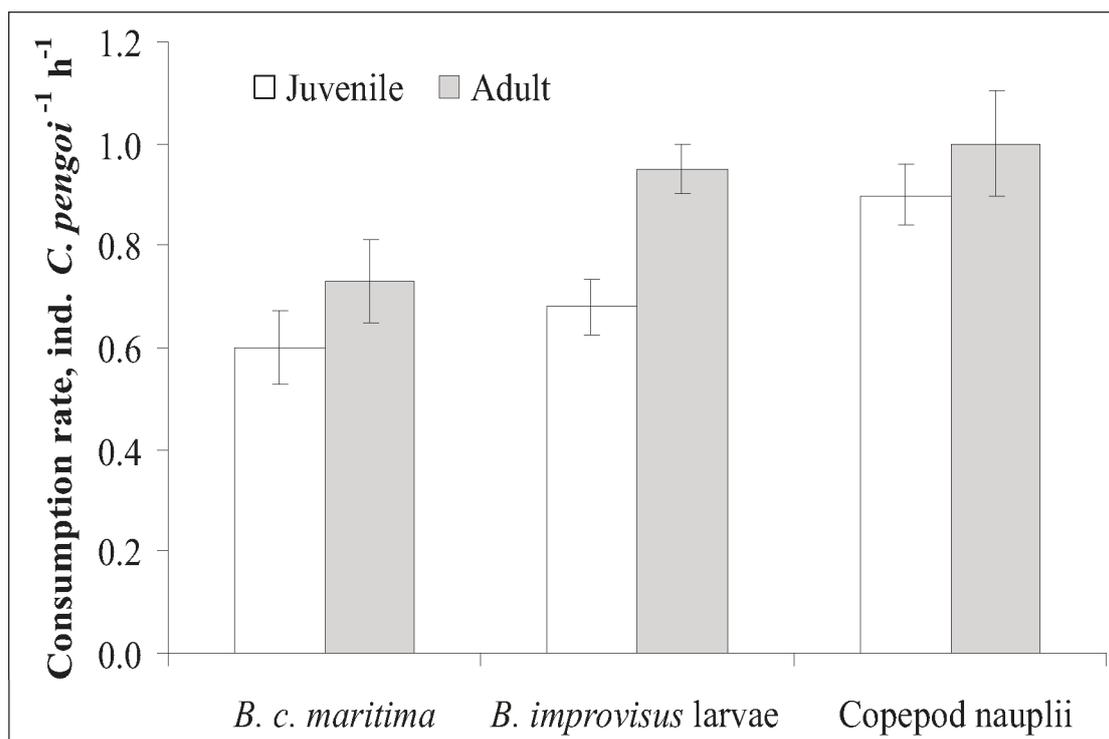
Fig. 8.3. Consumption rates of *Cercopagis pengoi* juveniles (stage I) and adults (parthenogenetic females) (*C. pengoi*⁻¹ hour⁻¹, mean ± SE) for different single prey items.

DISCUSSION

Cercopagis pengoi is extremely sensitive to handling and experimental manipulations and survive poorly in captivity (Gorokhova et al., 2005). Still, some short-term experiments have been carried out for studying the feeding habits of the species. For instance, Laxson et al. (2003) proved that *C. pengoi* preys on small-sized mesozooplankton species. Witt and Caceres (2004) estimated potential predator–prey interactions of two predatory cladocerans, *C. pengoi* and *Bythotrephes longimanus*, in lab conditions. However, most studies on the feeding of *C. pengoi* and potential impact of the species on plankton communities are based on field data by using a bioenergetic model (Telesh et al., 2001; Laxson et al., 2003; Thompson et al., 2005; Gorokhova et al., 2005). As data available on the feeding, energetics and physiology of *C. pengoi* are limited, knowledge on another predatory cladoceran – *Bythotrephes* – has been applied (e.g. Yurista & Schulz, 1995).

The prey taxa used in the current study dominate, except *B. c. maritima* in recent years, at various stages of mass development of the *C. pengoi* population. We faced severe difficulties in obtaining the necessary amount of *B. c. maritima* as the species has practically disappeared from the plankton community in the NE Gulf of Riga. According to Gorokhova (1998), the diet of *C. pengoi* contains 60% of copepods (nauplii and copepodids of *Acartia* spp., *E. affinis* and *T. longicornis*), 20% of rotifers (*Synchaeta* spp.) and 20% of cladocerans (*E. nordmannii*). The results of our current laboratory

experiments suggest that *C. pengoi* is able to consume these copepod (and most likley also cladoceran) species whereas the consumption rate is higher in the case of higher prey densitiy.

In their lab experiments Laxson et al. (2003) obtained similar consumption rates of *C. pengoi* for *Daphnia retrocurva* and *Bosmina longirostris*: 2.8 $C.\ pengoi^{-1}$ day^{-1}. Our results (when calculated to the same time interval) vary between 4.8 (copepodids) and 11.3 (copepod nauplii) $C.\ pengoi^{-1}$ day^{-1} and are thus notably higher than those obtained by Laxon et al (2003). However, the same authors also used bioenergetic modelling and obtained the following consumption rates: 2.1–4.7 for *D. retrocurva* and 7.1–7.5 $C.\ pengoi^{-1}$ day^{-1} for *B. longirostris*. Considering also differences in prey size, it is concluded here that these consumption rates are in good agreement with the results of the current study.

9. Potential impacts of key invasive benthic invertebrate species

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SUMMARY

The ecological impacts of the cirriped *Balanus improvisus* and the polychaete *Marenzelleria neglecta* were investigated in the north-eastern Baltic Sea. *B. improvisus* promoted the growth of the green alga *Enteromorpha intestinalis*. *M. neglecta* enhanced the content of sediment chlorophyll *a* and reduced the growth and survival of the polychaete *Hediste diversicolor* and the growth of the amphipod *Monoporeia affinis*.

MATERIAL AND METHODS

The effect of the suspension feeder *Balanus improvisus* Darwin on the growth of the green alga *Enteromorpha intestinalis* (L.) was studied in the Gulf of Finland in June–September 2002. We used 3 l buckets whose outsides were fully overgrown with small barnacles of 2 mm length. By cleaning the bucket, the density of barnacles was set at 0, 10, 20, 40, 70, 80 and 100%. Each density was replicated 3 times. Zero coverage represented control values. The buckets were filled with clean pebbles and covered with tightened mesh cloth to enable algal settlement without any space competition with barnacles, i.e. barnacles occurred only outside and on the top edge of the bucket. The buckets were randomly placed on the exposed seafloor at a depth of 0.5 m. At the end of the experiment the coverage and total dry weight of *B. improvisus* and *E. intestinalis* were determined.

Competitive interactions between the shallow water species *Macoma balthica* L., *Cerastoderma glaucum* Bruguière, *Hediste diversicolor* (O. F. Müller), the deep water amphipod *Monoporeia affinis* Lindström and the introduced polychaete *Marenzelleria neglecta* (Sikorski and Bick sp. nov.) were experimentally quantified in laboratory and a shallow water bay of the Gulf of Finland. Test organisms were added in densities consistent with their values in the field (replicated 3 times). At the end of the experiment the sediment in the mesocosms was sampled for chlorophyll *a* and phaeopigments (Strikland & Parsons, 1972). Living animals were counted and changes in the survival and growth of test organisms were estimated. Further details on the sampling, material processing and experimental design are presented in the following publications: Kotta, 2000b; Kotta et al., 2001; Kotta & Ólafsson, 2003; Kotta et al., 2004a; Orav-Kotta, 2004; Kotta et al., 2006a,b,c.

RESULTS AND DISCUSSION

The ecology and impact of marine invaders are little known. We rely on field data and a few papers linking experimental and field observations (Parker et al., 1999). For the Baltic Sea there exists some information on the impacts of benthic invasions (Kotta et al., 2001; Kotta & Møhlenberg, 2002; Kotta & Ólafsson, 2003) whereas data on pelagic species are rather rare (Leppäkoski & Olenin, 2001; Leppäkoski et al., 2002).

Our field experiments indicated that *B. improvisus* promoted the settlement success and growth of the green alga *E. intestinalis*. In the treatment without *B. improvisus* (control treatment) the algal coverage was below 5%. The coverage of *E. intestinalis* increased curvilinearly with the coverage and biomass of *B. improvisus*. The development of *E. intestinalis* was better explained by the coverage of the barnacles than their biomass (Fig. 9.1). No other macroalgal and attached invertebrate species were found on the buckets.

Field experiments showed that *B. improvisus* promoted the settlement success and further development of the filamentous algae in the study area. The mechanism behind this relationship is likely the increased nutrient availability in the benthic system through the biodeposition of suspension feeders (Reusch et al., 1994; Kautsky, 1995). As macroalgal coverage was low in the treatment without *B. improvisus*, nutrients rather than the space was limiting algal growth in the experiment. Rising nutrient load has been shown to compensate for the herbivore pressure on the early life stages of *E. intestinalis* (Lotze et al., 2000) as the spore germination and growth of the species may be reduced up to 99% by mesograzers (Lotze et al., 1999). Besides, the growth of an adult algal canopy is also favoured by small-scale nutrient enrichment (Lotze et al., 2000).

Prior to the invasion of *B. improvisus* there was no benthic suspension feeding mode in the northern Baltic Sea where salinity is below 5 psu and the climate is too cold for another non-indigenous suspension feeder *Dreissena polymorpha* (Pallas) (Leppäkoski & Olenin, 2001). Thus, the invasion of *B. improvisus* potentially increased the energy flows from the pelagic system to benthos and caused a shift from pelagic production to benthic production.

An in situ experiment, combining natural densities of native species and the introduced polychaete, showed that sediment chlorophyll *a* content in the treatment with *M. neglecta* was significantly higher than in all other treatments (one-way ANOVA, $p < 0.001$). *M. neglecta* was found to significantly reduce the survival of *H. diversicolor* (one-way ANOVA, $p = 0.024$) and the growth of *M. affinis* (one-way ANOVA, $p = 0.033$). The survival of *M. neglecta* was significantly reduced by the presence of *M. balthica* (one-way ANOVA, $p < 0.001$). Field data agreed with the experimental finding that *M. affinis* was not found even at moderate densities of *M. neglecta*. On the other hand, the negative effect of *M. balthica* on *M. neglecta* was observed in pristine conditions and

Fig. 9.1. Polynomial regressions between the densities of *Balanus improvisus* and *Enteromorpha intestinalis* on the mesocosms in the Gulf of Finland in 2002.

not in eutrophicated areas.

Competitive interactions between *M. neglecta* and native fauna may explain why the polychaete densities are low when the densities of *M. balthica* are high and why *M. affinis* has not recovered in the area with a high density of *M. neglecta*. Competitive superiority of *M. balthica* over *M. neglecta* is likely to be due to this species' efficient feeding modes and better tolerance of food shortages (e.g. Brafield & Newell, 1961; Ólafsson, 1986; Kotta et al., 2004a). Because *M. balthica* is one of the most common species in the soft bottom sediments (Segerstråle, 1957; Hällfors et al., 1981), competitive interactions between *M. neglecta* and *M. balthica* appear to be a key factor limiting the further expansion of *M. neglecta* in the study area.

Higher sediment chlorophyll *a* content in the treatments with *M. neglecta* indicates higher biodeposition and/or bioturbating activity of the polychaete as compared to the native fauna. According to Pelegri and Blackburn (1995), polychaetes significantly accelerate nitrogen remineralization and transformation processes within the sediment. As *M. neglecta* burrows much deeper and more actively than the native polychaetes, the amount of reworked sediments, i.e. the availability of nutrients to microalgal growth, is higher in the presence of *M. neglecta.*

To conclude, all studied alien species are potentially able to affect biodiversity and modify organic matter and energy transfer pathways compared to the pre-invasion time. Further studies should quantify the changes in the energy flow through the food-web as a result of alien species and assess the realized potential of competition between alien invertebrates and native species for the same food and habitat resource.

10. The predatory cladoceran *Cercopagis pengoi* in fish diet: observations from field

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SUMMARY

After the invasion of the predatory cladoceran *Cercopagis pengoi* to the Gulf of Riga the pelagic and bentho-pelagic food-web has changed. *C. pengoi* has taken a position between the mesozooplankton and planktivorous fish. The species is a valuable additional food resource but may also cause additional food competition with young and pelagic fish. The main predator of *C. pengoi* in the Gulf of Riga is herring *Clupea harengus membras*. In addition, the share of this cladoceran is significant in the diet of two species of sticklebacks *Gasterosteus aculeatus* and *Pungitius pungitius*, young smelt *Osmerus eperlanus* and in some cases also bleak *Alburnus alburnus*. In summer all the listed fishes consume *C. pengoi* more actively. For instance, *C. pengoi* may make up to 60% of the diet of large herring. Our calculations suggest that in most cases, fish tend to avoid *C. pengoi*. However, adult herring and three-spined stickleback show some preference to this invader during the warmest time when the abundance of the prey is the highest.

MATERIAL AND METHODS

In 1994-1998 the materials for stomach examinations was collected during monthly daytime experimental bottom trawl surveys in the Gulf of Riga in 1994–1998 during May–September (for details see Ojaveer et al., 2004). In 1999–2004 fish were caught by a pelagic commercial trawl in the whole open part of the Gulf of Riga (depth over 20 m) in at least 12 stations during daytime in July. From each catch 20 individuals were taken and stored in 4% formaldehyde solution. Stomach analyses were performed according to Melnichuk (1980). The total length and weigh of the fish were measured. The wet weight of the whole stomach content was datermined. Larger food organisms (Mysidae, Amphipoda, fish) were weighed and counted separately. The remaining part (zooplankton) was diluted in water and counted in the Bogorov chamber like an ordinary plankton sample.

Zooplankton samples were collected with a Juday net (vertical hauls, mouth area 0.1 m², 90 μm mesh size) after the trawling event from the bottom to the surface in the years 1994–1998 and 2001–2004. Samples were preserved in 4% formaldehyde solution and analysed applying routine methods. The total volume of a sample was examined for *Cercopagis pengoi* (Ostroumov) whereas for other zooplankton taxa a subsample was

examined. For calculating feeding preferences the Ivlev electivity index was used (Ivlev, 1977). In 1994–1998 a total of 2080 herring *Clupea harengus membras* L., 1117 smelt *Osmerus eperlanus* (L.), 769 three-spined stickleback *Gasterosteus aculeatus* L., 80 nine-spined stickleback *Pungitius pungitius* (L.) and 30 bleak *Alburnus alburnus* (L.), and in 1999–2004 2363 herring, 177 smelt and 1208 three-spined stickleback were analysed.

RESULTS AND DISCUSSION

Invasion of the Ponto-Caspian cladoceran *Cercopagis pengoi* into the NE part of the Gulf of Riga was reported in 1992 (Ojaveer & Lumberg, 1995). Prior to the appearance of *C. pengoi*, the most abundant pelagic fish species fed mainly on copepods dominated by *Eurytemora affinis* (Poppe), *Acartia* spp. and *Limnocalanus grimaldii* (De Guerne). Among the food objects were also the cladocerans *Bosmina coregoni maritima* (P. E. Müller), *Pleopsis polyphemoides* (Leuckart) and *Evadne nordmannii* Loven. During that period the proportion of *E. affinis* amounted to 64% (Jakobson, 1970; Kostrichkina, 1970; Shestakov, 1970; Trauberga, 1979; Lankov, 1986, 1988). In the mid-1990s, the diet of herring in the Gulf of Riga still consisted mostly copepods (*E. affinis* and *Acartia* spp.). The share of cladocerans in herring diet in summer exceeded 25%, for the three-spined stickleback and smelt the respective value was 16–17% (Ojaveer et al., 1997).

Large cladocerans with big eyes, particularly females with resting eggs, are an attractive prey for pelagic fish. However, our results show that when consuming large cladocerans that have relatively long caudal appendage, the body length of the fish serves as a limiting factor. The minimum size of different fishes having preyed upon *C. pengoi* varies with fish species. The nine-spined stickleback starts feeding on this cladoceran when it has attained the total length of 3.4 cm, the three-spined stickleback and herring at a length of 4.1 cm, the bleak at a length of 6.2 cm and the smelt at a length of 7.3 cm. As an exception, herring larvae of the length of 2.2 cm contained *C. pengoi* in their intestines.

The main predator of *C. pengoi* in the Gulf of Riga is the most abundant pelagic fish – herring. In the years of 1994–1998, the share of this cladoceran in herring stomachs reached over 20% wwt in a few length groups and over 10% for several length groups. The proportion of *C. pengoi* in the diet of other fishes was several times lower (Fig. 10.1). These values represent means for the whole main feeding period (May–September) of these fish.

However, in the warmest season, when *C. pengoi* is abundant in plankton, herring consumes a much higher proportion of this alien prey. For example, in herring length groups of 15–17 cm, the share of *C. pengoi* may reach over 60% whereas larger length groups consume a notably higher proportion of *C. pengoi* than smaller individuals. In the summer pelagic environment, other fish consume *C. pengoi* also at considerably
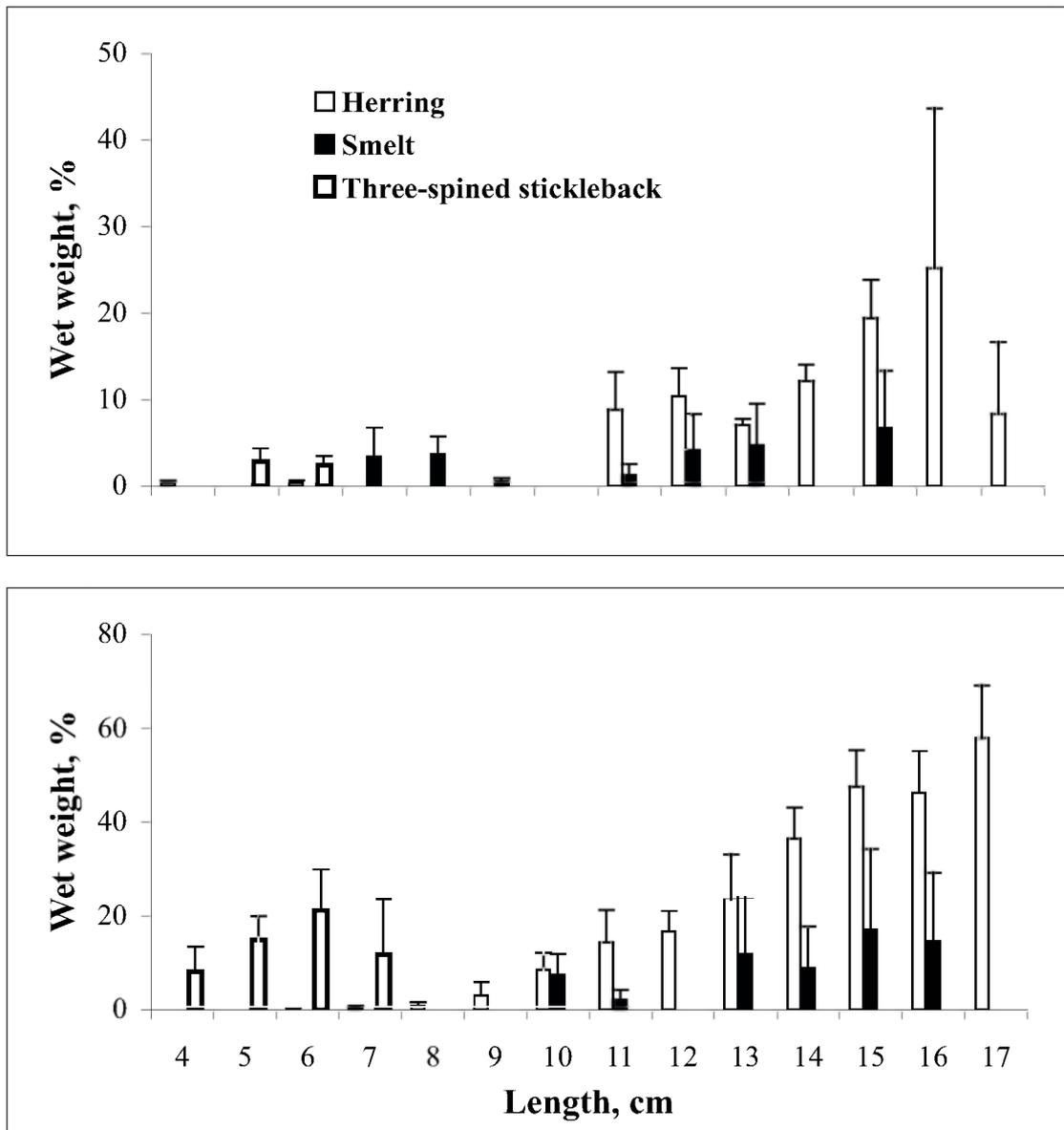
Fig. 10.1. Contribution (wet weight %, mean ± SE) of *Cercopagis pengoi* in the diet of herring *Clupea harengus membras*, smelt *Osmerus eperlanus* and three-spined stickleback *Gasterosteus aculeatus* in the Gulf of Riga during the main feeding period (May–September) in 1994–1998 (upper panel) and in the open part in July in 1999–2004 (lower panel).

higher rates than during the whole feeding period (Fig. 10.1). In addition, some other fish species that mostly inhabit the near-coastal areas (nine-spined stickleback and bleak) can also consume large portions of *C. pengoi*, up to 100%.

Earlier investigations in feeding preferences of major pelagic fishes in the northern Baltic Sea have shown noticeable preference of female copepods with eggs and cladocerans with developed embryos (Hansson et al., 1990; Flinkman et al., 1992). During the period of most intense planktivory in August in the Northern Baltic Proper
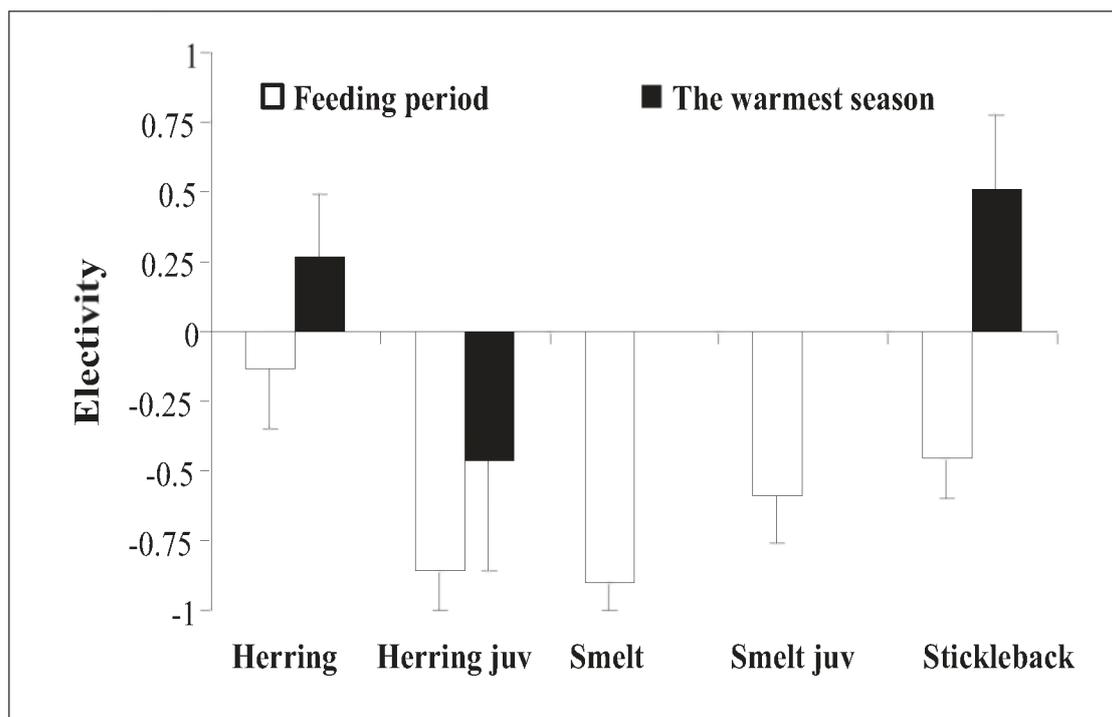
Fig. 10.2. Electivity index (mean ±SE) of fishes for *Cercopagis pengoi* in the Gulf of Riga during the main feeding period in the NE part of the basin in 1994–1998 and over the whole basin during the warmest season in 2001–2004.

the preferred prey in this area is mature *Temora longicornis* (O. F. Müller), egg- or embryo-carrying *Eurytemora affinis*, *Pseudocalanus elongatus* (Boeck), *Pleopsis polyphemoides* and *Evadne nordmannii* (Flinkman, 1999). A small avoidance and/or neutrality is against embryo-carrying *B. c. maritima*. The copepod *Acartia* spp. is one of the most avoided prey (Flinkman, 1999). In the mid 1990s, the most preferred prey species were *E. affinis*, *B. c. maritima* and *P. polyphemoides* whereas *Acartia* spp. was avoided in the Gulf of Riga (Ojaveer et al., 1997).

Results of the current study suggest that most fish tend to avoid the alien *C. pengoi* in most cases. This is evidenced by negative electivity index (Fig. 10.2). The avoidance is the most prominent in the case of juvenile herring and adult smelt. Most likely, juvenile herring is too small to catch this cladoceran and adult smelt is rather a demersal than a planktonic feeder.

However, as noted above, *C. pengoi* was exceptionally found in a single case even in the stomach of a herring larva. A positive electivity index of adult herring and three-spined stickleback was recorded in the warmest season in samples from the pelagic trawl (0.27 and 0.51, respectively) whereas juvenile herring firmly stayed on the negative side of the scale (–0.46).

Thus, the carnivorous *C. pengoi* has taken the position between the mesozooplankton and planktivorous fishes (see also Simm et al., 2006, this volume). Fish predation on *C. pengoi* was species-specific and size-dependent. When *C. pengoi*

occurred abundantly in the plankton its share in the diet of fish was substantial. The species should be considered as a valuable additional food resource for the period when prey of suitable size and energy value is lacking as there is evidence that large herring and smelt consume this species very actively. In addition, consumption of *C. pengoi* by smelt enhances energy transfer from the surface waters to the cold deeper water layers. At the same time, invasion of this predatory cladoceran has also increased food competition in the pelagic and bentho-pelagic ecosystem between several invertebrates and fish and invertebrates (Kotta et al., 2004b; Ojaveer et al., 2004).

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