



## Establishment of the zebra mussel, *Dreissena polymorpha* (Pallas), in the Neva Estuary (Gulf of Finland, Baltic Sea): distribution, population structure and possible impact on local unionid bivalves

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### Abstract

The zebra mussel, *Dreissena polymorpha* (Pallas), has invaded the Neva Estuary (eastern Gulf of Finland) by mid 1980s. In order to assess the current status of the zebra mussel population in the area, the distribution, density and size-frequency structure of *D. polymorpha* were studied in the littoral zone of the Resort District of St. Petersburg in 1998, 2000 and 2001. The results indicate that the species is now established in the inner Neva Estuary. Recruitment of the local *D. polymorpha* population was not regular and occurred only in years with warm summers, while during comparatively cold summers the recruitment was limited or absent (in 1997 and 2000). Even this sporadic and limited recruitment maintained relatively high densities and biomasses of the local *D. polymorpha* population (as high as  $2229 \pm 801$  ind.  $m^{-2}$  and  $2025 \pm 196$  g  $m^{-2}$ ). We consider low availability of accessible substrates and limited recruitment as two possible reasons for the low impact of the zebra mussel on local unionid mussels in the Neva Estuary compared to other recipient ecosystems.

### Introduction

During the last two centuries approximately 100 alien species have been recorded in the Baltic Sea, most of which were introduced unintentionally by ship ballast water or hull fouling, or by spreading from primary sites of their deliberate releases into adjacent freshwater bodies (Leppäkoski & Olenin, 2000). The zebra mussel *Dreissena polymorpha* Pallas is one of the first alien species of Ponto-Caspian origin to have invaded the Baltic Sea basin in the beginning of the 19th century as a result of construction of canals in Europe. It was firstly found in the south-eastern Baltic lagoons and estuaries as early as in 1825 (Nowak, 1971; Starobogatov & Andreeva, 1994).

*Dreissena polymorpha* evolved in estuaries of the relatively warm Paratethys seas and lakes (Starobogatov, 1994). Zebra mussels cannot survive freezing (Karatayev et al., 1998). According to Bij de Vaate (1991), *D. polymorpha* growth starts at 6 °C. Water temperature above 12 °C is required for *D. poly-*

*morpha* gamete maturation, spawning and larval production (Garton & Haag, 1993; Kharchenko, 1995; Mackie & Schloesser, 1996; Nichols, 1996). Some authors have suggested that this relatively warm water Ponto-Caspian species is unable to establish populations above 60°N in latitude because of unfavourable temperature conditions (Starobogatov & Andreeva, 1994; Kharchenko, 1995). For more than 150 years, the distribution of the zebra mussel in the Baltic Sea was limited to latitudes below 60°N, and it was not documented in the eastern Gulf of Finland until the 1980s, despite available pathways (waterways from Ponto-Caspian seas to Northwest of Russia) and mechanisms of introduction (shipping). A recent range expansion of *D. polymorpha* in the North of Europe occurred in the 1980s–1990s, when the range of this species has expanded to Irish estuaries of in the North Atlantic (Minchin, 2000), and to relatively cool areas along the northern side of the eastern Gulf of Finland, including the Neva Estuary, the easternmost part of the Baltic Sea (Antzulevich & Lebardin, 1990; Välipakka

et al., 1996; Valovirta & Porkka, 1996; Orlova et al., 1999; Panov et al., 1999).

*Dreissena polymorpha* is considered an invasive organism, directly or indirectly affecting all levels of aquatic ecosystems (MacIsaac, 1996; Karataev et al., 1997). One of the most negative direct impacts of the zebra mussel in many lakes and rivers is on the diversity of native bivalve mussels, such as unionids (Lewandowsky, 1976; Nalepa et al., 1996; Ricciardi et al., 1998; Burlakova et al., 2000). In some recipient ecosystems, unionids and their shells are often among the most accessible and abundant substrates for settlement of zebra mussel juveniles. Heavy overgrowth of unionid valves by *D. polymorpha* impairs the filter-feeding and movement abilities of the unionids, impedes their growth, and also causes significant deformation of valves, and in some cases leads to extinction of local populations (Schloesser et al., 1996; Karatayev et al., 1997; Ricciardi et al., 1998; Burlakova et al., 2000).

The aim of this study was to assess the current state of the *D. polymorpha* population in the Neva Estuary, including its distribution, density and biomass dynamics in the Resort District of St. Petersburg (inner Neva Estuary) at the northern margin of the zebra mussel range in the Baltic Sea. We also examined whether the zebra mussels infest the local unionids as strongly as they do in other recipient ecosystems. We have focused specifically on the study of age-size structure of *D. polymorpha* settlements, in order to assess whether or not this invasive species has successfully established in the estuary.

## Materials and methods

### Area description

The Neva Estuary consists of the freshwater area Neva Bay and brackish water parts separated from the Bay by a storm-surge barrier since the early 1980s (Fig. 1). The Neva Bay receives water from the Neva River, the major tributary to the Baltic Sea and a connecting waterway between Lake Ladoga and the Gulf of Finland. The principal area for our investigations was located in the north-eastern part of the Neva Estuary, and covered around 17 km of the shoreline of the Resort District of St. Petersburg (60°09.32' N–60°11.37' N; 29°38.34' E–29°54.89' E; Fig. 1).

As a result of heavy eutrophication, intensive development of the filamentous green alga *Cladophora*

*glomerata* (L.) Kutz. in the littoral zone is a characteristic feature of the sampling sites (Orlova et al., 1999). High levels of exposure to wave action are also characteristic of the area throughout the vegetation season (from May to October). Heavy storm casts including different bottom organisms are the evidence of disturbance of the environment in the littoral and sublittoral zones by wind and wave actions. The contents of these storm casts depend strongly on wind direction, duration of the storms and water level fluctuations ( $\pm 0.5$  m). Ice cover is usually present in the area from December to mid April. The thickness of the ice cover in the eastern Gulf of Finland reaches 0.7–0.8 m during cold winters (Davidan & Savtchouk, 1997). Ice abrasion and freezing along with water level oscillations may have a significant impact on littoral zone communities at depths less than 1.5 m during the winter and spring seasons.

### Sampling

Quantitative samples of *D. polymorpha* were collected by SCUBA diving along one transect in June 1998 (transect 7; Fig. 1), and along 4 transects in July 2000 and 2001 (transects 7, 11, 13, 15; Fig. 1). Along each transect, samples were taken at standard depths of 0.5, 1.5, 3.0 and 5.0 m with 25 × 25 cm metal frames in three replicates. Sampling along transect 7 was repeated 3 times in the year 2000 (in May, July and September) in order to estimate seasonal variations in size structure of the population, and growth rate of shell length. Environmental variables measured during sampling of *D. polymorpha* included surface and bottom water temperature and conductivity, and oxygen content of the water. Temperature and oxygen content were measured with a WTW Ox 330 oxygen meter. Water conductivity was measured with a Dist WP4 conductivity meter, and then converted to salinity measurements in puss (practical salinity units). SCUBA divers visually estimated the projective cover of bottom by hard substrates at each sampling site.

Quantitative samples were transported alive in plastic bags to the laboratory, where all zebra mussels were detached from substrates, counted and weighed to the nearest 0.01 mg (wet weight with shell). Density (ind. m<sup>-2</sup>) and biomass (g m<sup>-2</sup>) of the zebra mussels were expressed as mean  $\pm$  standard deviation (SD). Data were <sup>10</sup>log-transformed (Log(*x*) + 1) and analysed using a one-way ANOVA implemented with STATISTICA Version 5.0 to estimate the distribution

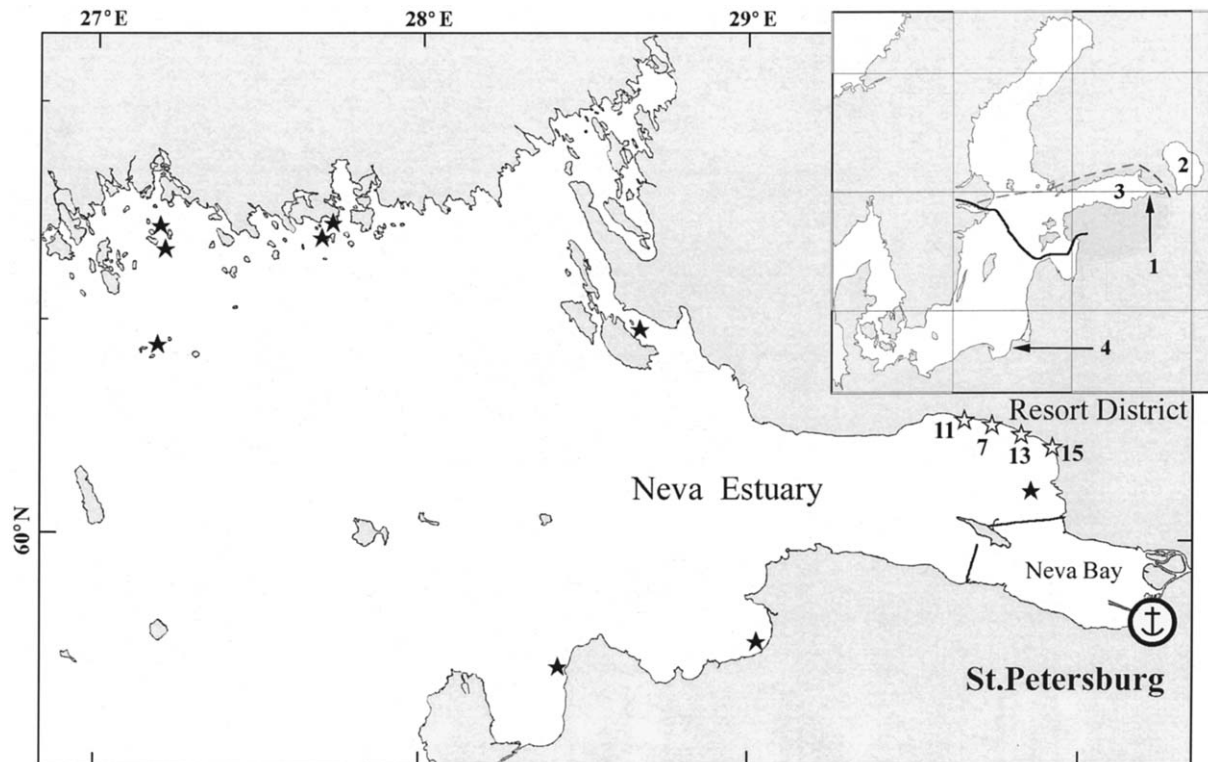


Figure 1. Distribution of *D. polymorpha* in the Neva Estuary and adjacent areas of the eastern Gulf of Finland. Open asterisks with numbers indicate sampling transects in the studied area. Filled asterisks indicate previous records of *D. polymorpha* (after Antzulevich & Lebardin, 1990; Antzulevich & Chivilev, 1992; Valovirta & Porkka, 1996; N. Kovaltchouk, pers. comm.). Areas indicated in the inserted map of the Baltic Sea: 1 = Neva estuary, 2 = Lake Ladoga, 3 = Gulf of Finland, 4 = Vistula Lagoon with contributing Pregel River, the solid line indicates the northern boundary for the *D. polymorpha* range in the Baltic Sea according to Leppäkoski (1984), the dashed line indicates the present northern boundary for the species.

and inter-annual variation of *D. polymorpha* density and biomass.

Shell length (maximum ammonal-posterior dimension) of each *D. polymorpha* individual taken from the quantitative sample was measured to the nearest 0.1 mm using callipers. Using these measurements, the mussels were divided into 1 mm size classes. Size-frequency distribution histograms were used to estimate the size structure of the *D. polymorpha* population. In the year 2000, the size-frequency distribution histograms were effective for visual discrimination of three age-size cohorts [over-wintered (1+), middle-aged (probably 2–3+) and the oldest ages (probably 4–6+)], which were then used to assess the seasonal variation in size structure and growth rate of the shell length. Growth rate of the shell length was calculated as the increase of mean shell length in each of three discernible cohorts and expressed in mm per month.

All collected unionids, both from quantitative sampling and additional ones from qualitative collec-

tions, were weighed (wet weight with shell, with the same accuracy as *D. polymorpha*) and the number and biomass of attached zebra mussels were determined. We estimated the extent of unionids infestation by zebra mussels as percent (%) of unionids with *D. polymorpha*. The number of *D. polymorpha* individuals per unionid mollusc (host), biomass of *D. polymorpha* per host and ratio between body mass of host and biomass of overgrowing *Dreissena* served as an estimate of the intensity of unionids' infestation by zebra mussels. Calculated values were compared to values taken from literature.

## Results

### *Environmental factors*

During the sampling in May 2000, the average water temperature was 8.7 °C at all stations, both in the

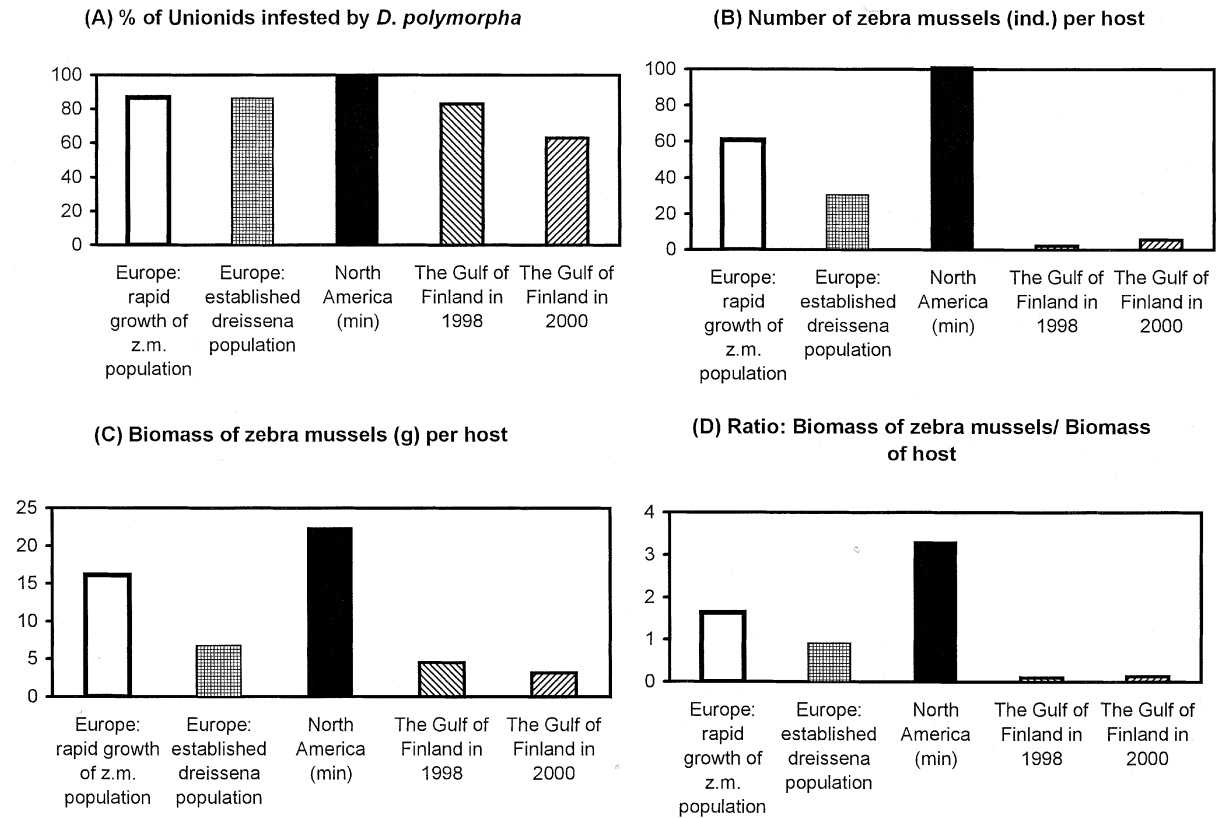


Figure 2. Comparative extent (A) and intensity (B, C, D) of infestation of unionids by *D. polymorpha* in the Neva Estuary and in other recipient areas in Europe and North America, based on our observations in 1998 and 2000 and the review by Karatayev et al. (1997). Only minimal values (Lake Vineyard) were taken for North America.

surface and bottom layers. In July 2000, water temperature ranged from 18.6 to 21 °C in the surface water and from 17.4 to 18.1 °C at the bottom. In September 2000, water temperature had decreased to 12–14 °C. In July 2001, surface water temperature ranged from 21.8 to 25.5 °C, and the upper bottom temperature ranged from 21.5 to 23.6 °C along transects, with the highest temperatures at the most shallow sampling sites. The deep-water areas of the Neva Estuary and eastern Gulf of Finland (depths >15 m) are stratified during summer and sometimes vertical temperature gradients, with a temperature decline of 2.5 °C per m of depth profile, occur (Panov et al., 1999). Oxygen saturation during daytime at depths from 1.5 to 5.0 m always exceeded 90% for the whole period of observations. Salinity measured from May to September in 1998–2001 ranged from freshwater (<0.4 psu) to brackish water (around 2 psu).

#### Colonization of hard substrates and infestation of unionids by *D. polymorpha*

Hard substrates were available at all depths along transect 7, with the projective cover ranging from 23 to 60%. In transects 13 and 15, hard substrates were present at the depths from 0.5 to 3.0 m, ranging from 57 to 100%. At transect 11, hard substrates were present only at the depths 0.5 and 1.5 m (62 and 75%, respectively).

In 9 frames (100 × 100 cm), collected on 29 June 1998 at depths 1.5, 3 and 5 m along transect 7, the substrate consisted of stones and debris (91%) and, to a lesser extent, of live molluscs, both zebra mussels (5%) and native unionids (4%). Substrates of all types and sizes were colonized by *D. polymorpha*. 87% of the total number of zebra mussels had settled on stones and debris, while 11% were found attached to large individuals of the same species and only 2% were found on unionids. These results indicate that shells of unionid mussels were not a preferred type of substrate

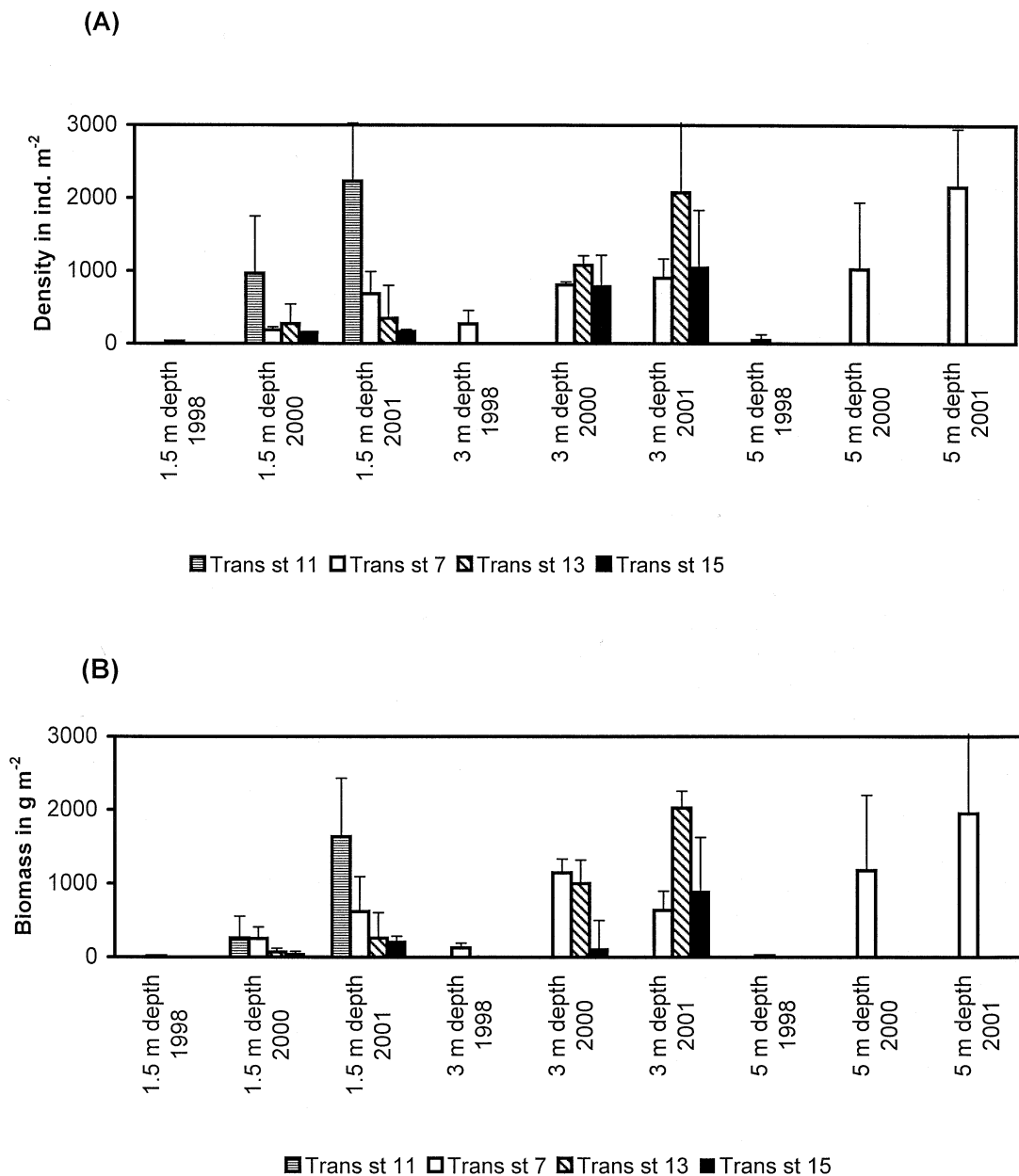


Figure 3. Quantitative characteristics of the *D. polymorpha* population from the Neva Estuary along four transects in June 1998, July 2000 and July 2001.

for zebra mussels than shells of larger conspecific individuals. In 1998 and 2000, around 60-70% of all collected unionids were colonized by *D. polymorpha*, as observed in other recipient aquatic ecosystems in Europe (Fig. 2A). However, the intensity of infestation was much lower than found in other water bodies (Fig. 2B, C, D).

#### *Spatial and temporal variations of D. polymorpha abundance and biomass*

Variations in density and biomass of *D. polymorpha* were related to the locations and depths of the transects (Fig. 3, Table 1). No permanent settlements of *D. polymorpha* were found at sites less than 1–1.5 m deep where ice abrasion, freezing and water level oscillation

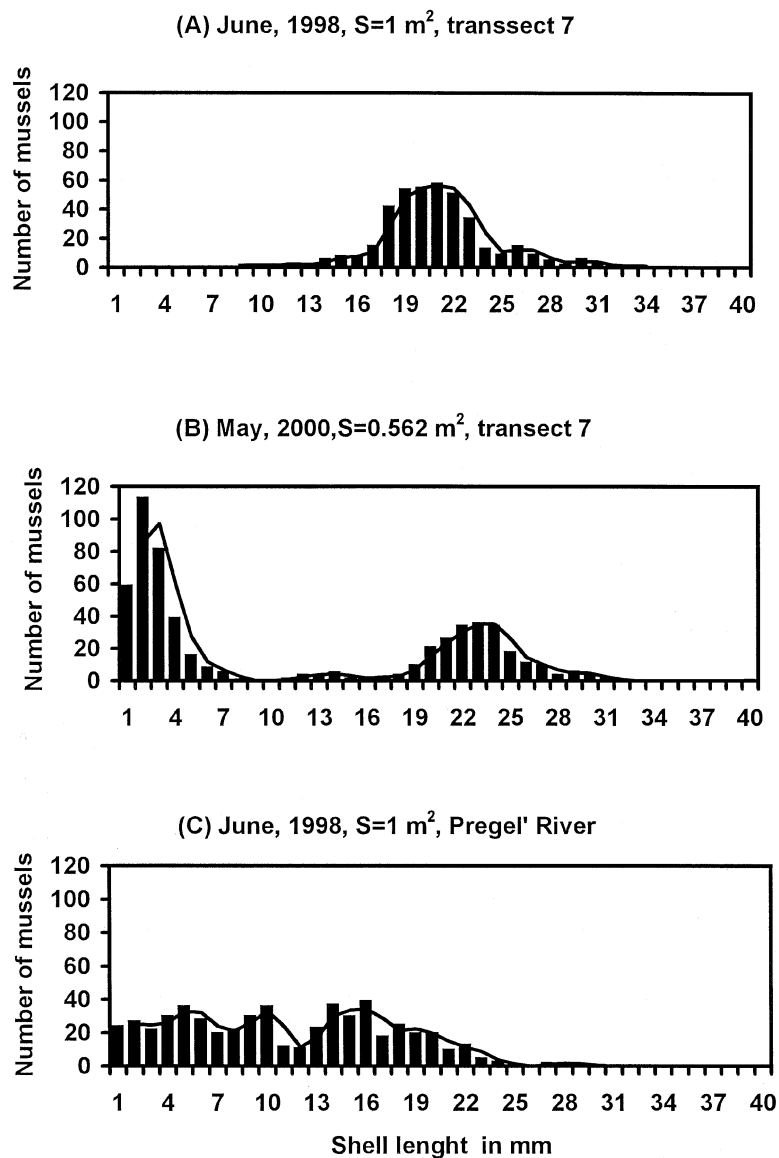


Figure 4. Size structure of the *D. polymorpha* population from the Neva Estuary, eastern Gulf of Finland (A, B) and of the *D. polymorpha* population from the Pregel River, Vistula Lagoon (C).

may affect the living assemblages. High abundance and biomass of the species in the study sites were usually found at depths of 3 to 5 m in the central transects 7 and 13, except for transect 11 where high abundance of zebra mussels was found at a depth of 1.5 m (Fig. 3). Variations in density and biomass of *D. polymorpha* between July 2000 and July 2001 were not statistically significant (Fig. 3, Table 1). However, both were significantly larger in 2000 and 2001 (2229 ind. m<sup>-2</sup> and 2025 g m<sup>-2</sup>) relative to 1998, when mean values did not exceed 125 ind. m<sup>-2</sup> and 269 g m<sup>-2</sup>.

#### *Size structure of the D. polymorpha population and growth of shell length*

In June 1998, young molluscs were not found in the local *D. polymorpha* population (Fig. 4A). However, a large cohort of over-wintered young mussels settled in autumn of the previous year was found in May 2000 (Fig. 4B). We used samples from the Pregel River (Vistula lagoon), collected in June 1998 (area 4 in the inserted map of the Baltic Sea in Fig. 1) for comparative analyses of size structure of two Baltic Sea

Table 1. One-way ANOVA results for *D. polymorpha* density and biomass variation. Data from samples collected in July 2000 and July 2001 along transects 11, 7, 13 and 15 at water depths 1.5–5 m were used. \* = Data from samples collected in June 1998, July 2000 and July 2001 along transect 7 only, df = degrees of freedom.

Variable	Density			Biomass		
	df	F-value	p-value	df	F-value	p-value
<i>Spatial variation:</i>						
Transect localization	3.68	6.579	<0.001	3.68	8.994	<0.000
Depth	2.69	17.554	<0.000	2.69	12.443	<0.000
<i>Temporal variation:</i>						
Year	1.70	0.248	<0.620	1.70	0.794	<0.376
Year*	2.24	30.691	<0.000	2.24	1.134	<0.000

populations of the zebra mussel. The size structure of the Pregel River population (Fig. 4C) was regular with the presence of all size classes. This age-size frequency pattern reflects the regular annual recruitment in Pregel River population of *D. polymorpha*, in contrast to the Neva Estuary population.

In the Neva Estuary the youngest cohort (shell length 1–8 mm), found in May 2000, persisted through the whole season as well as two older cohorts (Fig. 5). Limited recruitment in the *D. polymorpha* population was observed during summer 2000, which resulted in the appearance of only few 0+ individuals of zebra mussels in our samples in September (Fig. 5, lower chart). The analysis of the population size structure in July 2001 at depths of 1.5 m along the study area has revealed the presence of this cohort at all localities (Fig. 6). The highest abundance of these one-year old mussels was found in transect 11 (Fig. 6A), which was the sampling site furthest away from the freshwater Neva Bay (Fig. 1). The same was observed for the two-year old cohort. At 1.5 m of depth, the total density and biomass of the zebra mussels in the outer part of the estuary (transect 11) was higher than in the inner part (transects 13 and 15) (Fig. 3).

Seasonal changes in the size structure of *D. polymorpha* in 2000 allowed the estimation of growth rates in three cohorts. Individuals of the 1+ cohort were the fastest growing. Mean shell length in this cohort increased from 3 mm on 17 May to 8 mm on 9 July, and had reached 13 mm by 12 September 2000 (Fig. 5). The monthly rate of linear growth in this cohort averaged 2.5 mm month<sup>-1</sup> throughout the time of observation. The largest, probably 4–6-years old individuals with shell length of 17–31 mm in May, had the lowest monthly rate of linear growth, averaging 1 mm

month<sup>-1</sup> from May to September. The middle-aged cohort was represented by few individuals of likely 2–3 years old zebra mussels, whose shell length varied at the beginning of observation from 11 to 19 mm. The monthly rate of growth for this cohort was estimated at less than 2 mm month<sup>-1</sup>.

## Discussion

Our sampling survey revealed dense permanent settlements of *D. polymorpha* at the majority of the studied sites along the coastal zone of the Neva Estuary. The establishment success of this species is evidently facilitated by relatively favourable environmental conditions in the coastal zone. Summer temperatures in the Neva Estuary coastal zone in 2000 and 2001 were sufficient for *D. polymorpha* growth and above the limiting temperatures for reproduction. Estimates of salinity in the Neva Estuary littoral zone in 1998–2001 corresponded to favourable conditions for the species (Strayer & Smith, 1993) and oxygen saturation of waters in the studied area was also sufficient for oxyphylic species as *D. polymorpha* (Karatayev et al., 1998). As a result, the density and biomass of the zebra mussel along the study area in the Neva Estuary was close to the values indicated for lower reaches and estuaries of other eastern European rivers at localities without perennial macrophyte vegetation (1000 ind. m<sup>-2</sup> and 185 g m<sup>-2</sup> in lower Danube River, and 1730 ind. m<sup>-2</sup> and 1240 g m<sup>-2</sup> in the South Bug Liman; Karatayev et al., 1998).

Availability of hard substrate for attachment of *D. polymorpha* is one of the major factors affecting its distribution (Karatayev et al., 1998). Hard

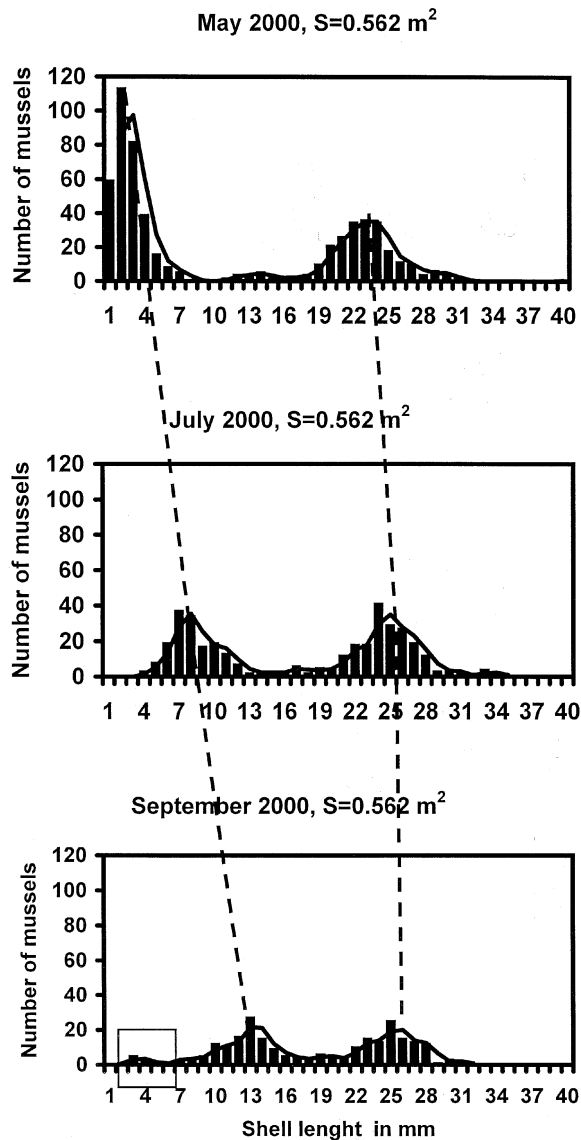


Figure 5. Size structure of the *D. polymorpha* population in transect 7 throughout the warm season of the year 2000. Black dashed lines indicate changes in mean size of two (youngest and oldest) cohorts. The quadrates below the picture indicate the new 0+ cohort, consisting of juveniles settled in late summer 2000. Each of the histograms is based on all nine quantitative samples collected at depths 1.5, 3 and 5 m.

substrates in the Neva Estuary were available for colonization by *D. polymorpha* at all locations studied. Probably, the availability of various suitable hard substrata for the settlement of the zebra mussel in the studied area of the Neva Estuary has resulted in a lower level of infestation of the local unionid mussels by *D. polymorpha*. Despite the fact that the number of infested unionids (60–70%) was as high as in other

European ecosystems (Fig. 2A), the intensity of infestation, characterised by all three estimated parameters (Figs 2B, C, D) was comparatively low. The low number and biomass of *D. polymorpha* per host is unlikely to cause any damage to shells and has no serious impact on the behaviour of unionids in the studied area, unlike the situation in Byelorussian lakes (Burlakova et al., 2000), North American Great Lakes (Nalepa et al., 1996; Schloesser et al., 1996; Karatayev et al., 1997) and Mississippi River (Ricciardi et al., 1998), where some species of Unionidae have become extinct after establishment of this invasive species. Insufficient recruitment of *D. polymorpha* in years with cold summers is probably another important reason of relatively low intensity of local unionids infestation by zebra mussels in the Neva Estuary.

The distribution of *D. polymorpha* toward the shoreline in the Neva Estuary coastal zone is probably limited by water level fluctuations and ice abrasion and freezing effects, like in other ecosystems in Europe (Karatayev et al., 1998). In late summer – early autumn, intensive developments of filamentous algae (*Cladophora glomerata*) may also be a limiting factor for the permanent settlement of zebra mussels. During this period, the biomass of filamentous algae in shallow locations (depths 0.5–1.0 m) may reach up to 500 g dry weight m<sup>-2</sup> (Orlova et al., 1999). Settlement of zebra mussel juveniles on such unstable substrate as filamentous algae would result in removal of settled juveniles from the population after algal detachment or die off. This effect might be also responsible for the lower density and lower biomass at shallow depths (1–1.5 m) in comparison to deeper locations.

Dispersal of *D. polymorpha* to the deeper, central part of the Neva Estuary is most likely limited by both a lack of hard substrate and low temperature of near-bottom waters, which is significantly below that required for growth and reproduction in *D. polymorpha*. The trend of increasing density and biomass of *D. polymorpha* toward the lower reaches of the estuary (from transect 15 to transect 11) may result from a prevailing passive drift of the zebra mussel larvae up west with the near shore current induced by Neva River water discharge, and their subsequent settlement downstream the parental population. As it was observed in the Volga River reservoirs (Kirpichenko, 1997) and in the Illinois and Hudson Rivers (Padilla et al., 2002), *D. polymorpha* larvae in flowing habitats, such as reservoirs and large rivers (and evidently estuaries of large rivers, e.g. the Neva River), can settle

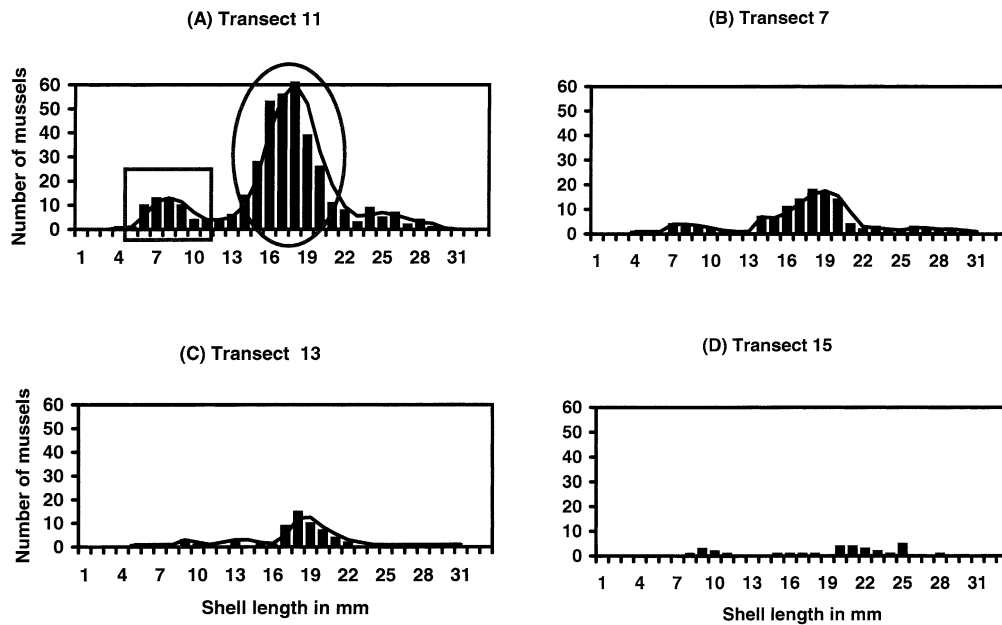


Figure 6. Size-frequency distribution of the *D. polymorpha* population in July 2001 at depths 1.5 m along four transects. Quadrates indicate the 1+ cohort (molluscs settled in 2000); circles indicate the 2+ cohort (molluscs settled in 1999).

far downstream from the locality where they were produced.

Temporal variations in density and biomass of *D. polymorpha* in the Neva Estuary are most likely due to the success of recruitment. The observed rapid increase of the zebra mussel density and biomass in 2000–2001 can be explained as a result of successful recruitment in summer 1999. The size structure of the Neva Estuary population, located at the northern margin of the species's range in the Baltic Sea, demonstrates a lack of breeding in summer 1997, or absence of sufficient passive drift of larvae from adjacent localities in the estuary, as shown by our survey in 1998. Valovirta & Porkka (1996) studied a population of *D. polymorpha*, located in Finnish waters along the north coast of the eastern Gulf of Finland and concluded that '... the species can reproduce in the north coast only in very favourable years'. The appearance of a new large cohort of over-wintering young individuals in the studied area (Neva Estuary) in May 2000, resulting from settlement during late summer-early autumn of the comparatively warm 1999 season, shows that successful recruitment of *D. polymorpha* is possible in locations north of latitude 60°N. During such successful seasons, occurring perhaps every 2–3 years, the population is able to restore its high level of density and biomass. In contrast, during periods with limited or absent recruitment, the abundance of zebra

mussels in the estuary may decline. Despite strong inter-annual fluctuations in density and size structure of the *D. polymorpha* population, the population has persisted in the Neva Estuary for at least 15 years (Antzulevich & Lebardin, 1990).

We suggest two main reasons for the observed irregular recruitment of *D. polymorpha* in the Neva Estuary. Firstly, temperature is obviously an important limiting factor for successful reproduction during cold summers according to temperature limits provided by literature. Secondly, the hydrological features of the studied area, which is highly dynamic in terms of currents and wind exposure, may be an important limiting factor for successful settlement and attachment of the mussel's juveniles, as suggested by the gradient in distribution of abundance of *D. polymorpha* (Figs 3, 6) along the coast at shallow water sites. The passive drift with near shore currents can remove a large part of zebra mussel larvae from the study sites even in warm years with successful reproduction. These larvae may settle along the shoreline westward. The population of *D. polymorpha* encountering even more hostile conditions along the south coast of Finland (Valovirta & Porkka, 1996) might have been established as a result of this passive drift of larvae, originating from the studied localities in the Neva Estuary. Other pools of larvae may settle in deeper parts of the Neva Estuary with unfavourable temperature conditions and lack of

suitable bottom substrates. The larvae also may drift to the parts of the Gulf of Finland with the water salinities exceeding 5.5 psu. According to Valovirta & Porkka (1996), 5.5 psu is the upper salinity limit of zebra mussel dispersal in the Gulf of Finland.

Despite that temperature of water in the studied areas of the Neva Estuary is not always optimal for recruitment, it is sufficient for the mussel growth. The rates of shell length growth in the studied population did not differ significantly from the estimates for other European populations (Walz, 1978).

The results of our field surveys in 1998–2001 indicate that the population of the invasive Ponto-Caspian mussel *D. polymorpha* in the Neva Estuary can be considered as established and permanent. Irregular recruitment is a particular characteristic of the Neva Estuary zebra mussel population. More research on metapopulation dynamics along the whole system of the Neva Estuary, including plankton larval stages and breeding strategy is required to discover the causes of these observations. The infestation of local bivalves by the zebra mussel in the Neva Estuary is less intensive than in other studies. This may be explained both by availability of other hard substrates for colonization by settling juveniles and by non-regular recruitment of the *D. polymorpha* population.

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