

**Benthic non-indigenous
species among indigenous
species and their habitat
preferences in Puck Bay
(southern Baltic Sea)***

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Abstract

To date 11 non-indigenous benthic taxa have been reported in Puck Bay (southern Baltic Sea). Five of the 34 taxa forming the soft bottom communities are regarded as non-indigenous to this area. They are *Marenzelleria* spp., *Mya arenaria*, *Potamopyrgus antipodarum*, *Gammarus tigrinus* and *Amphibalanus improvisus*. Non-indigenous species comprised up to 33% of the total number of identified macrofaunal taxa (mean 17%). The average proportion of aliens was 6% (max 46%) in the total abundance of macrofauna, and 10% (max 65%) in the biomass. A significant positive relationship was found between the numbers of native and non-indigenous taxa. The number of native taxa was significantly higher on a sea bed covered with vascular plants than on an unvegetated one, but no such relationship was found for their abundance. No significant differences were

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found in the number and abundance of non-indigenous species between sea beds devoid of vegetation and those covered with vascular plants, *Chara* spp. or mats of filamentous algae. *G. tigrinus* preferred a sea bed with vegetation, whereas *Marenzelleria* spp. decidedly preferred one without vegetation.

1. Introduction

In the Baltic Sea, as in other European seas, benthic invertebrates make up the largest proportion of non-indigenous species (Streftaris et al. 2005). Some 45 non-indigenous benthic species have so far been recorded in the Baltic (Baltic Sea Alien Species Database 2010, Woźniczka et al. 2011, Rudinskaya & Gusev 2012). Some of these species, like *Mya arenaria* Linnaeus, 1758 and *Amphibalanus improvisus* (Darwin, 1854) were introduced into the Baltic more than one hundred years ago and have become a permanent feature of the sea's macrofauna. But around half of the non-native species that have established populations were introduced after 1950 and within a short time gave rise to significant changes in the composition and structure of the Baltic macrofauna. The genus *Marenzelleria* (represented by three species: *Marenzelleria arctia* (Chamberlin, 1920), *Marenzelleria neglecta* Sikorski & Bick, 2004 and *Marenzelleria viridis* (Verrill, 1873)) is a good example (Sikorski & Bick 2004, Orlova et al. 2006, Blank et al. 2008, Maximov 2011). Since the end of the 1980s several new species have been observed for the first time in the southern part of the Baltic Sea, like *Gammarus tigrinus* Sexton, 1939 and *Palaemon elegans* Rathke, 1837 (Gruszka 2002, Janas et al. 2004a, Wawrzyniak-Wydrowska & Gruszka 2005). The invasion of these two species and the retreat of native species in the coastal water bodies of the southern Baltic has been documented in gammarids (Jażdżewski et al. 2004, Szaniawska et al. 2005, Surowiec & Dobrzycka-Krahel 2008) and palaemonids (Grabowski 2006).

The areas most likely to be colonised by new species are coastal lagoons and river mouths, where the broad diversity of habitats and low salinity allow the co-existence of species of both freshwater and marine origin (Paavola et al. 2005, Zaiko et al. 2007). One such area is Puck Bay, where eleven non-indigenous benthic species have settled. The studies carried out so far on the benthic communities of Puck Bay, dealing with species composition, density and biomass, have covered solely the non-indigenous species already present in these waters for several decades (e.g. Legeżyńska & Wiktor 1981, Wenne & Wiktor 1982, Kotwicki et al. 1993). An exception is the paper by Kotwicki (1997), which supplies information on the density and biomass of *Marenzelleria* spp. Species of benthic fauna new to this area have usually been treated in separate articles (Szaniawska et al. 2003, Janas

et al. 2004a, Janas & Wysocki 2005), or at most they have been compared to other species from the same family (e.g. Jazdzewski et al. 2005, Spicer & Janas 2006, Szaniawska et al. 2005, Grabowski 2006, Packaln et al. 2008). There are no papers, however, on the present-day occurrence of alien species forming benthic communities with other species, or on their proportions in the abundance of the entire macrozoobenthos. Such data are also scarce with respect to the whole Baltic Sea (Ezhova et al. 2005, Daunys & Zettler 2006). Moreover, only fragmentary data are available on the preferred habitats of non-indigenous species and on the relationships between native and non-native species (Zaiko et al. 2007).

The objective of this research was therefore to seek answers to the following questions:

1. What is the species composition, distribution and percentage share of non-indigenous species in the total number, abundance and biomass of benthic species in Puck Bay?
2. Does a dependence exist between the richness and abundance of indigenous and non-indigenous taxa?
3. Which habitats are preferred by non-indigenous species?

Alien species are considered to be one of the most serious threats to coastal ecosystems (Gray 1997). Information on distribution, abundance, biomass and habitat preferences are of crucial importance in developing permanent monitoring programmes for alien species or designing a suitable mechanism for managing coastal ecosystems. Although this investigation was rather site-specific, detailed studies allowed us to discover a general relationship between the richness of non-indigenous and indigenous species as well as the types of habitat preferred by particular non-indigenous species living in or in the process of colonising the Baltic Sea and other coastal areas.

2. Material and methods

2.1. Study area

The study was conducted in the shallow, inner part of Puck Bay, southern Baltic Sea. It is the westernmost part of the Gulf of Gdańsk. The inner Puck Bay covers an area of 0.34 km², and is bounded to the north by the Hel Peninsula and from the rest of the Gulf of Gdańsk by the periodically submerged Seagull Sandbar. The mean depth is 3.2 m, and the greatest natural depth is 9.2 m (Jama Kuźnicka). Almost the entire sea bed is covered by fine-grained sand. The underwater meadows that used to cover almost the whole bottom of the bay are now restricted to a few small areas. Here we find *Potamogeton* spp., *Ruppia maritima* Linnaeus, 1753,

Zannichellia palustris Linnaeus, 1753, as well as the rare *Zostera marina* Linnaeus, 1753 and the valuable meadows of *Chara* spp.

The temperature is subject to considerable seasonal variation, from -0.4°C to over 20°C ; in contrast, the salinity is relatively stable at c. 7 PSU (Nowacki 1993). During this study the temperature ranged from 16.5 to 25.5°C , and the salinity from 6.8 to 7.4 PSU with lower values only near the mouths of rivers (min. 5.2 PSU).

2.2. Sampling and data analysis

Samples of macrozoobenthos were collected in summer (July–August) 2007 from 61 sampling sites, with a depth range of 0.4–7.4 m. 3–5 replicate samples were collected at each station with a 225 cm^2 Ekman grab. The samples were passed through a 1 mm mesh sieve, and the plant and animal material remaining on the sieve were preserved in 4% formalin for further analysis in the laboratory. A total of 243 grab samples were collected and used in analyses.

To determine the species composition and distribution of the fast-moving non-indigenous crustaceans that could not be collected with the grab, additional samples were collected: in the littoral zone down to 1 m depth with a hand net (4 stations), at depths from 0.4 to 1.8 m with a modified 0.2×0.2 m Kautsky frame operated by a diver (42 stations at the same locations as the Ekman grab sampling points) and at depths from 3 to 5.5 m with a drag net from the r/v ‘Oceanograf 2’ (2 stations). To determine the species composition and distribution of the non-indigenous amphipods of the family Talitridae, samples were collected on the beach on the bay side of the Hel Peninsula (3 stations). All the organisms and their accompanying vegetation were preserved in 4% formalin. These observations served only to provide information on the distribution of other alien species and were not used in the analyses.

The animal organisms were identified to species level, or to the lowest possible taxonomic unit. *Marenzelleria*, oligochaetes, chironomid larvae, other insect larvae and bryozoans were not identified as to species. Species were categorised as non-indigenous to the Puck Bay area on the basis of the available literature (Spicer & Janas 2006, Baltic Sea Alien Species Database 2010).

The species composition of each grab sample was determined and the abundance and biomass of each taxon per 1 m^2 was calculated. Abundance data for indigenous and non-indigenous species were obtained by summing the data for the individual taxa. Identification of Gammaridae species was only possible with animals longer than 4 mm; it was therefore impossible

to separate the young individuals of native and non-indigenous gammarids. Thus, the juvenile gammarids were excluded from the analyses.

Maps showing the distribution, abundance and biomass of taxa were generated on the basis of averaged grab data from each station using the ArcGis 9.3 ESRI program. Some of the GIS layers used to draw the maps come from the GIS Centre of the University of Gdańsk. The other analyses used data from single grab samples. The relationships between the numbers and abundance of alien taxa and the numbers of native taxa were analysed by means of Cramer's V test. The abundance of non-native taxa in the samples (divided into 4 classes) was classified as follows: class 1 – 0–10 indiv. m⁻², class 2 – 11–100 indiv. m⁻², class 3 – 101–1000 indiv. m⁻² and class 4 – 1001–10 000 indiv. m⁻².

Depending on the presence or absence of plants as well as their dominance in the biomass, each macrozoobenthos sample was allocated to one of the four following classes, corresponding to one of the habitat types typical of this region: **No vegetation** – unvegetated soft bottom at depths from 0.7 to 7.4 m (113 samples); (2) **Vascular plants** – soft bottom with vascular plants (*Z. marina*, *Potamogeton* spp., *R. maritima*, *Z. palustris*) at depths from 0.4 to 5.3 m (75 samples); (3) **Chara** – soft bottom with the green alga *Chara* spp. at depths from 0.4 to 3.3 m (43 samples); (4) **Algal mats** – soft bottom covered by mats of filamentous algae, mainly brown algae, at depths from 0.7 to 5.5 m (12 samples). The frequency of each non-indigenous species in the whole study area and in particular habitat types was calculated. Data normality was assessed using the Shapiro-Wilk test. Since the data distributions were skewed, medians were used to approximate typical values. The significance of the differences obtained was evaluated with the non-parametric Mann-Whitney U-test at different levels. Differences were considered significant if *P* values (significance level) were less than 0.05. The analyses were performed with the STATISTICA 8 PL program (StatSoft, Poland).

3. Results

A total of 34 taxa were found on the soft bottom of Puck Bay, five of which – polychaetes of the genus *Marenzelleria*, two molluscs (*M. arenaria*, *Potamopyrgus antipodarum*) and two crustaceans (*G. tigrinus* and *A. improvisus*) – are species regarded as not indigenous to this region (Figure 1, Table 1 (see page 615)). In addition, using other research tools, two other species of crustacean were found: the prawn *P. elegans* and the dwarf crab *Rhithropanopeus harrisi* (Gould, 1841). The two species occurred both in the littoral zone on a sea bed covered with vascular plants (the crab was also present together with *Chara* spp.) and on a vegetation-free bottom

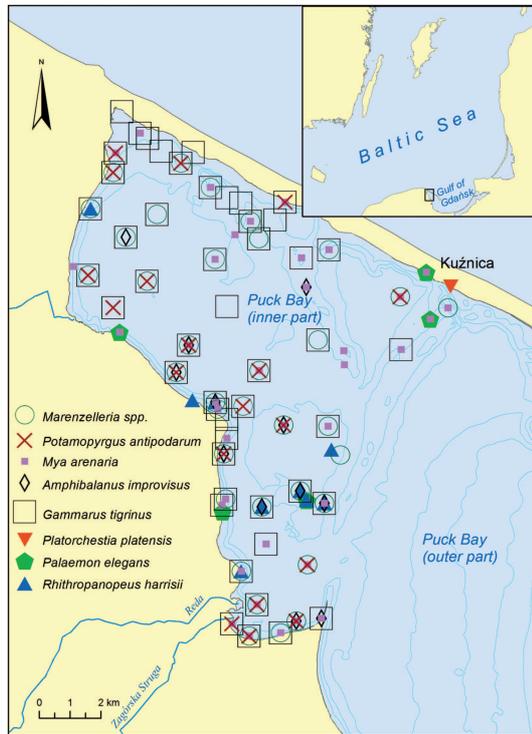


Figure 1. Distribution of eight non-indigenous taxa in Puck Bay

at a depth of 5.5 m. *P. elegans* was found at five stations and *R. harrisii* at nine. In addition, *Platorchestia platensis* (Krøyer, 1845) was present at one station on a beach reinforced by a stony embankment near Kuźnica (Figure 1).

The most important indigenous taxa forming benthic communities in Puck Bay both in terms of abundance and biomass were *Cerastoderma glaucum* (Bruguière, 1789), *Hydrobia ulvae* (Pennant, 1777), *Hydrobia ventrosa* (Montagu, 1803), *Hediste diversicolor* (Müller, 1776) and chironomid larvae.

The total number of taxa on the soft bottom varied from locality to locality, from three in a post-dredging pit in the northern part of Puck Bay (depth 6.9 m) to 26 in the southern part of the bay on a bottom overgrown with vascular plants (depth 1.5 m) (Figure 2). At least one non-native species was present at all but two stations. The maximum number of alien taxa – five – was found at only one station; at most stations (34%) three alien taxa were present. At all the stations where non-indigenous species were present they made up from 6 to 33% of all the taxa recorded at a station (mean = 17%).

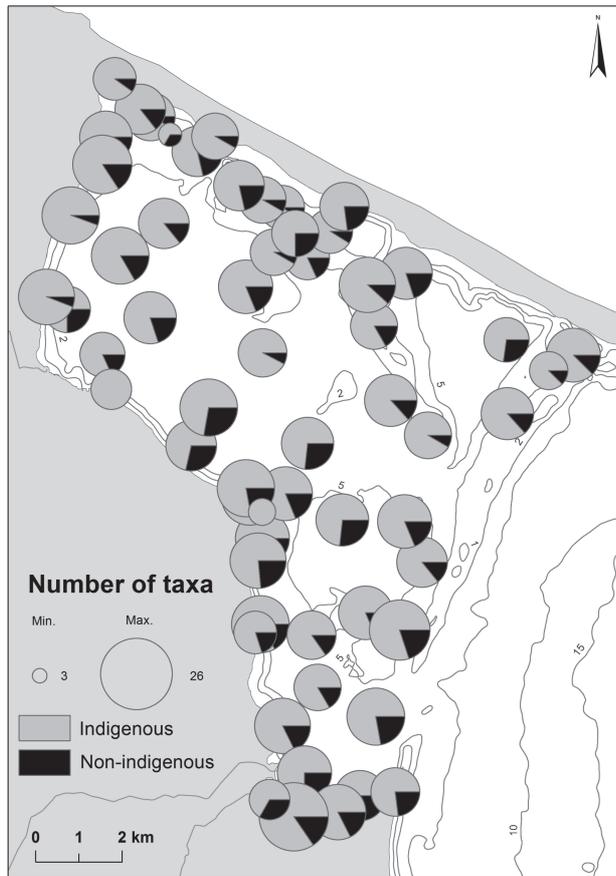


Figure 2. Numerical distribution of native and non-indigenous taxa in Puck Bay

The abundance of macrofauna at the various stations ranged from 2033 indiv. m^{-2} in the post-dredging pit to 34 152 indiv. m^{-2} off the Hel Peninsula at 1.4 m depth (Figure 3). The percentage of alien species in the total abundance varied from 0 to 46% (mean 6%). The proportions of these species in the abundance were largest in small, sheltered bays. The proportion of alien species in the total macrofaunal biomass reached 65% (mean 10%) (Figure 4). The percentage of Gammaridae juveniles in the total macrofaunal abundance was below 8.6% (mean 0.5%), but in the total biomass was no greater than 1%.

There was a significant positive correlation between the number of indigenous and non-indigenous taxa in the samples (Cramer $V = 0.36$, $P = 0.0001$) (Figure 5a). In samples containing no more than two indigenous taxa, there was one alien species at most. The largest numbers of alien

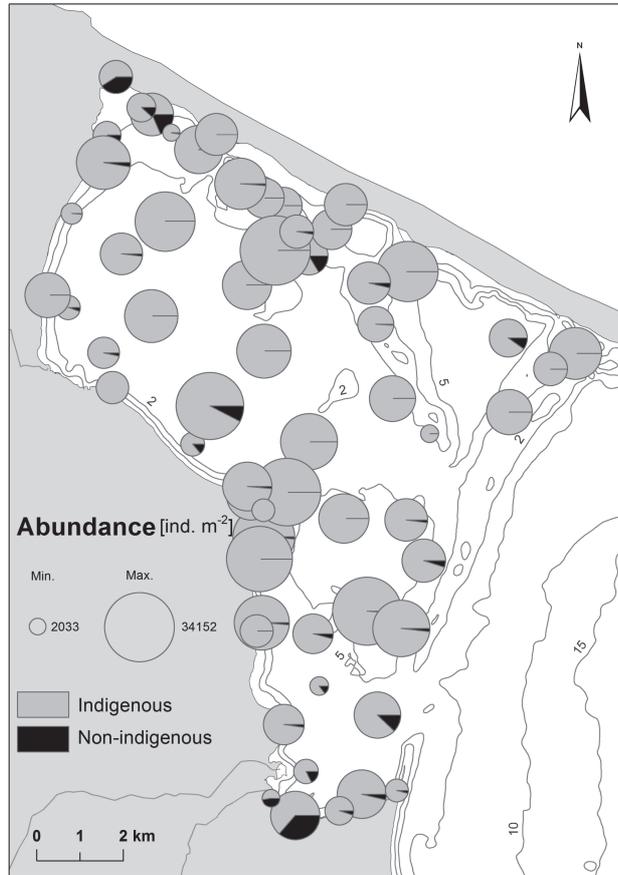


Figure 3. Proportions of non-indigenous species in the total abundance of macrofauna in Puck Bay

species (max 4) were found in samples where numbers of native taxa were also high (from 8 to 17).

There was a weak positive correlation between the number of indigenous taxa and the abundance of non-indigenous species inhabiting the same area (Cramer $V = 0.29$, $P = 0.057$) (Figure 5b). The abundance of non-indigenous species (> 7000 indiv. m^{-2}) was greatest in localities with the highest number of native species (16–17).

Analysis of the number of indigenous and non-indigenous taxa with respect to habitat revealed a significantly higher number of the former on a bottom dominated by vascular plants than on a vegetation-free bottom; likewise, the former were present in significantly greater numbers on a bottom covered by both vascular plants and *Chara* spp. than on one

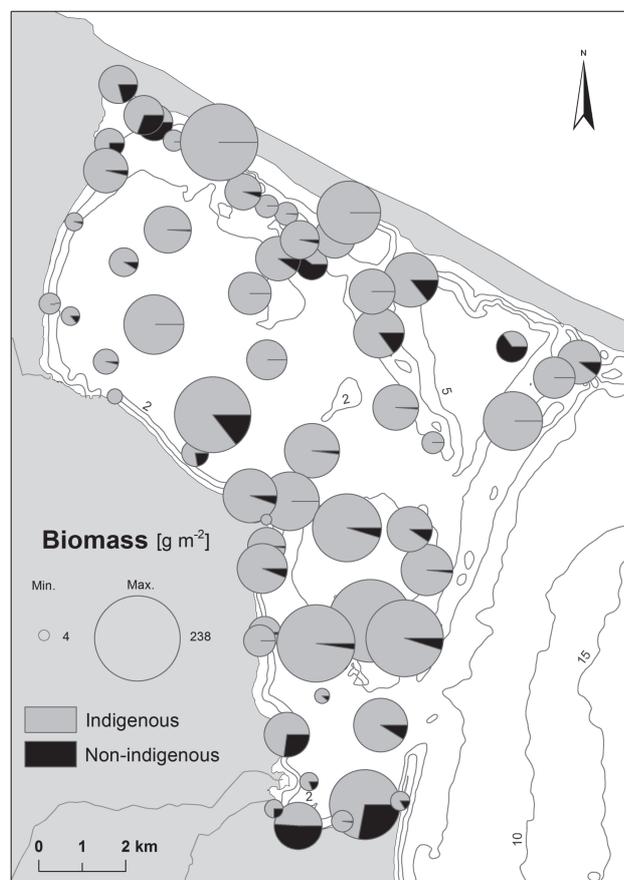


Figure 4. Proportions of non-indigenous species in the total biomass of macrofauna in Puck Bay

covered by a mat of filamentous algae (in both cases, $P < 0.05$) (Figure 6a). The number of indigenous taxa on a vegetated bottom varied from 2 to 17, whereas it did not exceed 15 on an unvegetated one and 11 on one with filamentous algae. No significant differences were found in the numbers of non-indigenous taxa between these habitats ($P > 0.05$); neither were there any significant differences in the abundance of macrofauna, both native and alien, between the various habitat types (Figure 6b). The median abundance of native species for the whole study area was 11 553 indiv. m^{-2} , whereas that for alien species was 178 indiv. m^{-2} .

The species occurring most commonly on the bottom of Puck Bay was *G. tigrinus* (frequency = 44%); the frequencies of two other non-indigenous taxa – *Marenzelleria* spp. and *M. arenaria* – were very similar (37 and 36%

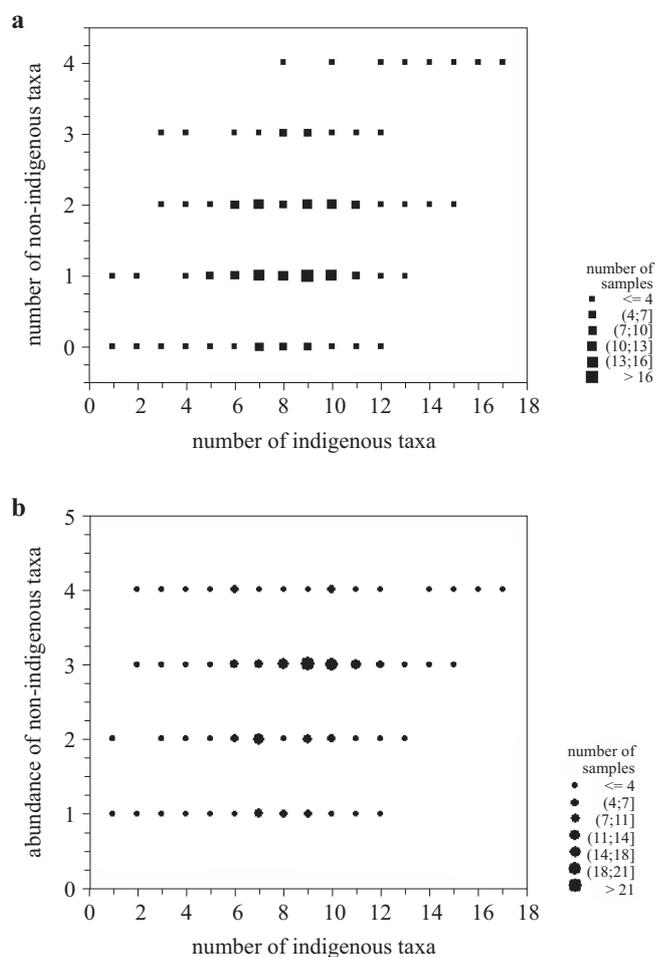


Figure 5. Dependence of a) the number of non-indigenous benthic taxa and b) the abundance of non-indigenous taxa on the number of native taxa in the various samples ($n = 243$). The abundance of non-native taxa in the samples in 4 classes: class 1 – 0–10 indiv. m^{-2} , class 2 – 11–100 indiv. m^{-2} , class 3 – 101–1000 indiv. m^{-2} and class 4 – 1001–10000 indiv. m^{-2}

respectively). The frequency of *P. antipodarum* in the study area was 19%, but that of *A. improvisus* was only 7%.

The amphipod *G. tigrinus* was present on the sandy unvegetated bottom (frequency of occurrence = 36%) but was far more common on sea beds overgrown with plants (> 50%) (Figure 7). Its abundance on a sea bed covered with vascular plants or *Chara* spp. was also greater and differed significantly from that on a soft unvegetated sea bed ($P < 0.05$) (Figure 8a). The median abundance on a sea bed covered with vascular plants

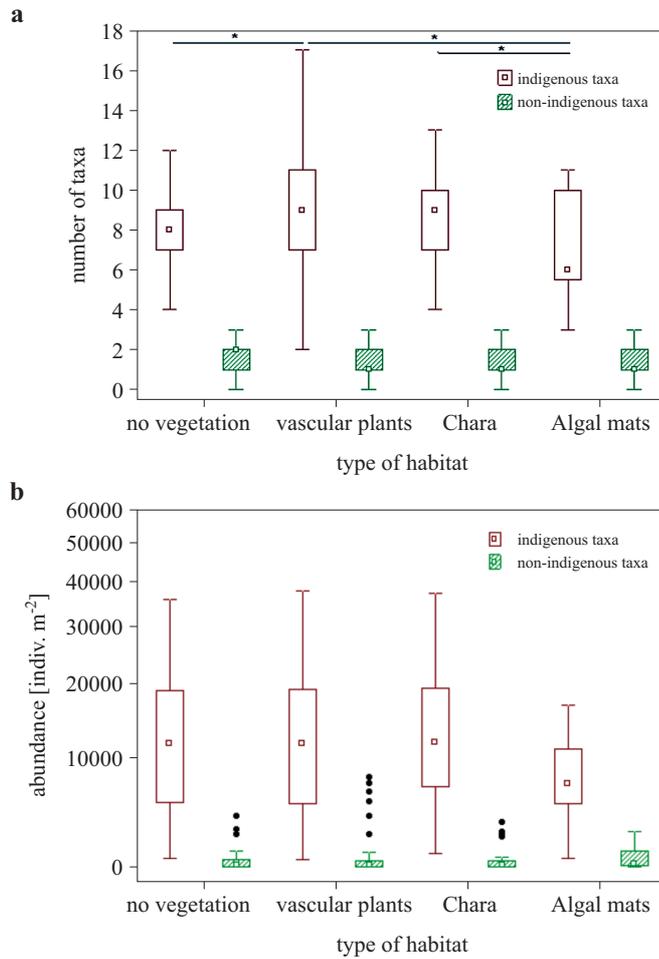


Figure 6. a) Number of taxa and b) abundance (logarithmic scale) of native and non-indigenous taxa in different habitats. Small square – median, box – interquartile range, whiskers – non-outlier range, dots – extremes. The horizontal line indicates a significant difference at $*P < 0.05$

or *Chara* spp. was 44 indiv. m⁻², and the greatest abundance on such a vegetated sea bed was 6399 indiv. m⁻².

In contrast, the polychaete *Marenzelleria* spp. displayed a clear preference for an unvegetated sandy bottom (frequency of occurrence = 51%). On a sea bed covered with algal mats the frequency of this species was 42%, but in localities covered by both vascular plants and *Chara* spp. it did not exceed 25% (Figure 7). The abundance of *Marenzelleria* spp. on a soft bottom was significantly greater than on bottoms with vascular plants or *Chara* spp. ($P < 0.01$). The median abundance in the first of these habitat

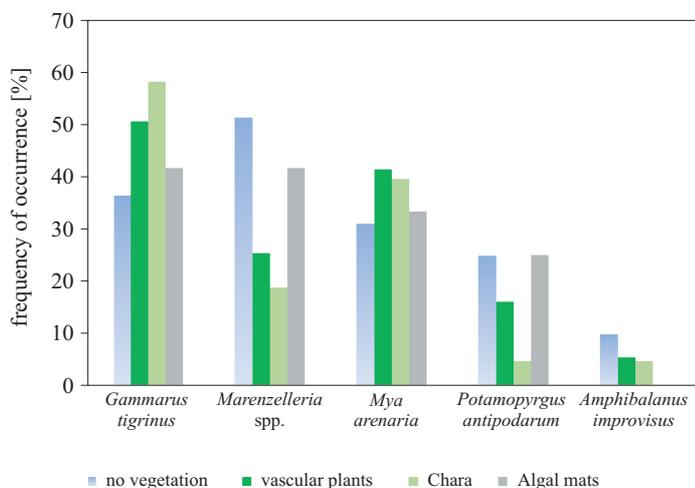


Figure 7. Frequency of occurrence of alien taxa depending on the type of habitat in Puck Bay ($n = 243$)

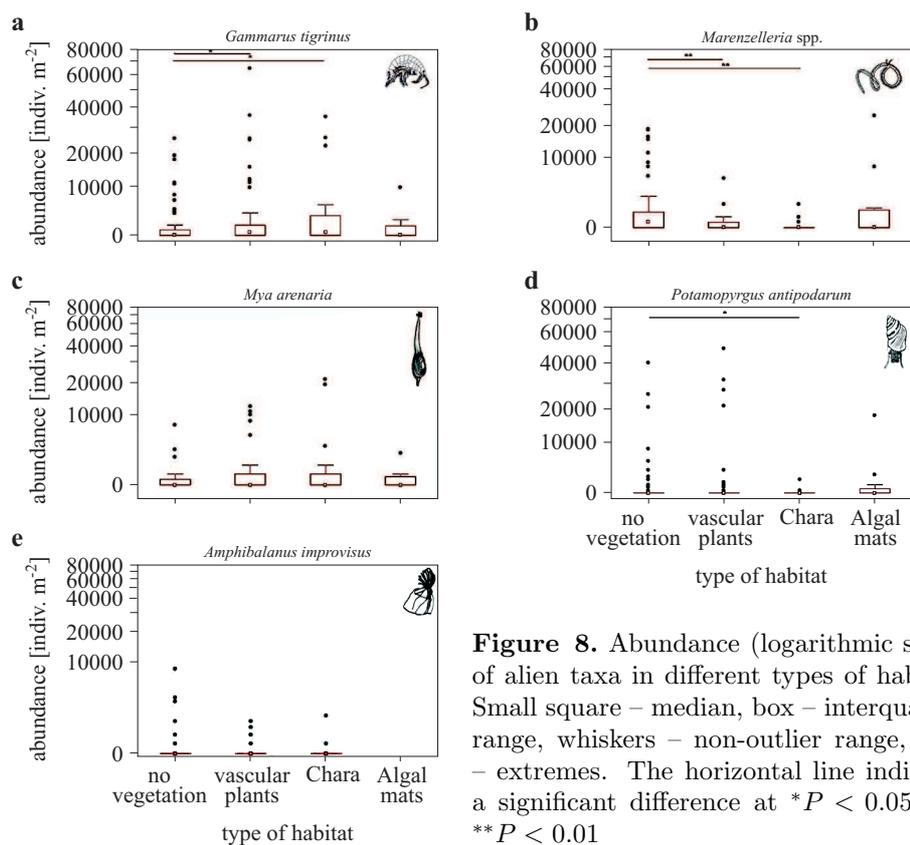


Figure 8. Abundance (logarithmic scale) of alien taxa in different types of habitat. Small square – median, box – interquartile range, whiskers – non-outlier range, dots – extremes. The horizontal line indicates a significant difference at * $P < 0.05$ and ** $P < 0.01$

Table 1. Macrofauna taxa in various parts of the Gulf of Gdańsk in the period 2002–2012. ‘+’ present, ‘-’ absent, **non-indigenous species in bold**

Taxa/region and depth depth [m]	Inner Puck Bay	Gulf of Gdańsk (excluding the inner Puck Bay)			
		0–9	10–29	30–60	> 60
Hydrozoa					
<i>Gonothyrea loveni</i> (Allman, 1859)	-	+ ⁷	-	-	-
<i>Cordylophora caspia</i> (Pallas, 1771)	+ ¹⁴	+ ⁷	-	-	-
Turbellaria nd.	-	+ ¹	-	-	-
Nemertea					
<i>Cyanophthalma obscura</i> (Schultze, 1851)	+	+ ¹	-	-	-
Polychaeta					
<i>Bylgides sarsi</i> (Kinberg in Malmgren, 1866)	-	-	+ ¹	+ ¹	+ ¹
<i>Hediste diversicolor</i> (O. F. Müller, 1776)	+	+ ¹	+ ¹	+ ¹	+ ¹
<i>Pygospio elegans</i> Claparède, 1863	+	+ ¹	+ ¹	+ ¹	+ ¹
<i>Streblospio shrubsolii</i> (Buchanan, 1890)	+	+ ¹	+ ¹	-	-
<i>Marenzelleria</i> spp. Mesnil, 1896	+	+ ¹	+ ¹	+ ¹	+ ¹
<i>Fabricia sabella</i> (Ehrenberg, 1836)	-	+ ¹⁰	-	-	-
<i>Manayunkia aestuarina</i> (Bourne, 1883)	-	+ ¹	-	-	-
Oligochaeta	+	+ ¹	+ ¹	+ ¹	+ ¹
Gastropoda					
<i>Hydrobia ventrosa</i> (Montagu, 1803)	+	+ ¹	+ ¹	+ ¹	-
<i>Hydrobia ulvae</i> (Pennant, 1777)	+	+ ¹	+ ¹	+ ¹	-
<i>Potamopyrgus antipodarum</i> (J. E. Gray, 1843)	+	+ ¹	+ ¹	-	-
<i>Theodoxus fluviatilis</i> (Linnaeus, 1758)	+	+ ¹	+ ¹	-	-
<i>Radix balthica</i> (Linnaeus, 1758)	+	+ ¹	-	-	-
<i>Limapontia capitata</i> (O. F. Müller, 1774)	+ ¹³	+ ¹³	-	-	-
<i>Tenellia adspersa</i> (Nordmann, 1845)	+ ¹³	+ ¹³	-	-	-
Bivalvia					
<i>Mytilus edulis</i> Linnaeus, 1758	+	+ ¹	+ ¹	+ ¹	-
<i>Cerastoderma glaucum</i> (Bruguère, 1789)	+	+ ¹	+ ¹	-	-
<i>Macoma balthica</i> Linnaeus, 1758	+	+ ¹	+ ¹	+ ¹	+ ¹
<i>Mya arenaria</i> Linnaeus, 1758	+	+ ¹	+ ¹	+ ¹	-
<i>Dreissena polymorpha</i> (Pallas, 1771)	-	+ ¹⁶	-	-	-
<i>Mytilopsis leucophaeata</i> (Conrad, 1831)	-	+ ¹²	-	-	-
Crustacea					
<i>Amphibalanus improvisus</i> (Darwin, 1854)	+	+ ¹	+ ¹	+ ¹	-
<i>Diastylis rathkei</i> (Krøyer, 1841)	-	-	+ ¹	+ ¹	-
<i>Heterotanais oerstedii</i> (Krøyer, 1842)	+	+ ¹	-	-	-
<i>Cyathura carinata</i> (Krøyer, 1847)	+	+ ¹	-	-	-
<i>Idotea chelipes</i> (Pallas, 1766)	+	+ ¹	-	-	-
<i>Idotea balthica</i> (Pallas, 1772)	+	+ ¹	-	-	-
<i>Idotea granulosa</i> Rathke, 1843	+	+ ¹	-	-	-
<i>Jaera</i> spp. Leach, 1814	+ ¹	+ ¹	-	-	-
<i>Lekanesphaera hookeri</i> (Leach, 1814)	+	+ ¹	+ ¹	-	-

Table 1. (*continued*)

Taxa/region and depth depth [m]	Inner Puck Bay	Gulf of Gdańsk (excluding the inner Puck Bay)			
		0–9	10–29	30–60	> 60
<i>Lekanesphaera rugicauda</i> (Leach, 1814)	+	–	–	–	–
<i>Asellus aquaticus</i> (Linnaeus, 1758)	+ ¹	+ ¹⁶	–	–	–
<i>Eurydice pulchra</i> Leach, 1815	–	+ ¹	–	–	–
<i>Saduria entomon</i> (Linnaeus, 1758)	–	–	+ ¹	+ ¹	+ ¹
<i>Gammarus duebeni</i> Lilljeborg, 1852	+ ⁴	+ ¹	–	–	–
<i>Gammarus zaddachi</i> Sexton, 1912	+	+ ¹⁰	+ ¹	+ ¹	–
<i>Gammarus salinus</i> Spooner, 1947	+ ⁴	+ ¹⁰	–	+ ¹	–
<i>Gammarus oceanicus</i> Segerstråle, 1947	+	+ ¹	+ ¹	+ ¹	–
<i>Gammarus tigrinus</i> Sexton, 1939	+	+ ⁴	+ ¹	–	–
<i>Pontogammarus robustoides</i> (G. O. Sars, 1894)	–	+ ¹¹	–	–	–
<i>Obesogammarus crassus</i> (G. O. Sars, 1894)	–	+ ¹¹	–	–	–
<i>Dikerogammarus haemobaphes</i> (Eichwald, 1841)	–	+ ¹¹	–	–	–
<i>Dikerogammarus villosus</i> (Sowinsky, 1894)	–	+ ¹¹	–	–	–
<i>Bathyporeia pilosa</i> Lindström, 1855	+	+ ¹	+ ¹	–	–
<i>Monoporeia affinis</i> (Lindström, 1855)	–	–	+ ¹	+ ¹	+ ¹
<i>Pontoporeia femorata</i> Krøyer, 1842	–	–	+ ¹	+ ¹	+ ¹
<i>Talitrus saltator</i> (Montagu, 1808)	–	+ ⁸	–	–	–
<i>Talorchestia deshayesii</i> (Audouin, 1826)	+ ¹	+ ⁸	–	–	–
<i>Platorchestia platensis</i> (Krøyer, 1845)	+ ¹	+ ⁸	–	–	–
<i>Orchestia cavimana</i> Heller, 1865	+ ^{5*}	–(+ ^{1**})	–	–	–
<i>Corophium multisetosum</i> Stock, 1952	+	+ ¹	–	–	–
<i>Corophium volutator</i> (Pallas, 1766)	+	+ ¹	+ ¹	+ ¹	+ ¹
<i>Apocorophium lacustre</i> (Vanhöfen, 1911)	–	+ ¹⁰	–	–	–
<i>Crassikorophium crassicorne</i> (Bruzelius, 1859)	–	+ ⁹	–	–	–
<i>Caprella mutica</i> Schurin, 1935	–	+ ^{10*}	–	–	–
<i>Leptocheirus pilosus</i> Zaddach, 1844	+	+ ¹⁰	–	–	–
<i>Neomysis integer</i> (Leach, 1814)	+	+ ¹	–	–	–
<i>Mysis mixta</i> Lilljeborg, 1852	+ ¹	–	–	–	–
<i>Praunus flexuosus</i> (Müller, 1776)	+	+	–	–	–
<i>Hemimysis anomala</i> Sars, 1907	+ ³	+ ³	–	–	–
<i>Crangon crangon</i> (Linnaeus, 1758)	+ ¹	+ ¹	+ ¹	–	–
<i>Palaemon adspersus</i> Rathke, 1837	+ ¹	+ ¹	–	–	–
<i>Palaemon elegans</i> Rathke, 1837	+ ¹	+ ¹	–	–	–
<i>Palaemonetes varians</i> (Leach, 1814)	+ ⁶	–(+ ^{1**})	–	–	–
<i>Rhithropanopeus harrisi</i> (Gould, 1841)	+	+ ¹	+ ¹⁵	–	–
<i>Eriocheir sinensis</i> H. Milne Edwards, 1854	+ ²	+ ²	–	–	–
<i>Carcinus maenas</i> (Linnaeus, 1758)	–	+ ¹	–	–	–
<i>Orconectes limosus</i> (Raffinesque, 1817)	–	+ ¹	–	–	–
Insecta nd.	+	+ ¹	–	–	–
Lepidoptera nd.	+ ¹	+ ¹	–	–	–
Chironomidae nd.	+	+ ¹	–	–	–

Table 1. (*continued*)

Taxa/region and depth depth [m]	Inner Puck Bay	Gulf of Gdańsk (excluding the inner Puck Bay)			
		0–9	10–29	30–60	> 60
Bryozoa					
<i>Einhornia crustulenta</i> (Pallas, 1766)	+	+ ¹	+ ¹	+ ¹	–
Priapulida					
<i>Halicryptus spinulosus</i> von Siebold, 1849	–	–	+ ¹	+ ¹	+ ¹
Number of indigenous taxa	43	46	23	18	10
Number of non-indigenous taxa	11	21	6	3	1

Present study ‘+’ without any abbreviations, (1) authors’ own unpublished data, (2) Normant et al. 2002, (3) Janas & Wysocki 2005, (4) Szaniawska et al. 2005, (5) Spicer & Janas 2006, (6) Grabowski 2006, (7) Dziubińska & Janas 2007, (8) Kotwicki et al. 2009, (9) Kruk-Dowgiałło et al. 2009, (10) Grzelak & Kukliński 2010, (11) Dobrzycka-Krahel & Rzemyskowska 2010, (12) Dziubińska 2011a, (13) Dziubińska 2011b, (14) Barańska pers. comm., (15) Hegele-Drywa pers. comm., (16) Smoła 2012.

* one individual, ** abundant in the Martwa Wisła.

types was 44 indiv. m⁻². The respective maximum abundances on bottoms covered with algal mats, a soft sea bed, on a bottom covered with vascular plants and on one covered with *Chara* spp. were 2444 indiv. m⁻², 1866 indiv. m⁻², 578 indiv. m⁻² and 222 indiv. m⁻² (Figure 8b).

The frequency of occurrence of *M. arenaria* ranged from 31% on a soft unvegetated bottom to 41% on a vegetated one (Figure 7). No significant differences were found between the abundances of this mollusc in the habitats investigated ($P > 0.05$) (Figure 8c).

The frequency of the mud snail *P. antipodarum* on a soft unvegetated bottom and on one covered with algal mats was 25%, whereas on a vegetated one it was no greater than 16% (Figure 7). The difference in the abundances of *P. antipodarum* was greater and statistically significant ($P < 0.05$) only between a bottom without plant cover and one overgrown with *Chara* spp. (Figure 8d).

The barnacle *A. improvisus* was present in all the habitat types examined except on bottoms covered with algal mats. Its frequency in the other habitats was less than 10% (Figure 7). No significant differences were found between the abundances of this species in the various habitats (Figure 8e).

4. Discussion

Eight non-indigenous taxa were found in the benthic communities of Puck Bay. In addition, the mysid shrimp *Hemimysis anomala* Sars, 1907

(Janas & Wysocki 2005), the talitrid amphipod *Orchestia cavimana* Heller, 1865 (Spicer & Janas 2006), and the hydroid *Cordylophora capia* (Pallas, 1771) (Barańska pers. comm.) were reported earlier from this region. There are two further non-indigenous crustacean species that have not yet been recorded in Puck Bay: the crayfish *Orconectes limosus* (Raffinesque, 1817) and the crab *Carcinus maenas* (Linnaeus, 1758), whereas another crab *Eriocheir sinensis* Milne Edwards, 1854 was found in the Gulf of Gdańsk (including Puck Bay). These three species have been recorded only occasionally and so far have been unable to establish viable reproducing colonies in the southern Baltic. The bivalve *Mytilopsis leucophaeata* (Conrad, 1831), a gammarid species of Ponto-Caspian origin, recorded in one place in the Gulf of Gdańsk and present in large numbers in the Vistula Lagoon and at the Vistula mouth, and the bivalve *Rangia cuneata* (Sowerby I, 1832), found in the Vistula Lagoon, have not yet been found in Puck Bay (Surowiec & Dobrzycka-Kraheil 2008, Dobrzycka-Kraheil & Rzemkowska 2010, Dziubińska 2011a, Rudinskaya & Gusev 2012). The number of non-indigenous species in Puck Bay is similar to that found off the German Baltic coast (14) (Nehring 2002), but is somewhat lower than the number found off the coast of Lithuania (20) (Daunys & Zettler 2006, Zaiko et al. 2007), or in the Odra estuary (> 20) (Wawrzyniak-Wydrowska & Gruszka 2005).

The number of non-indigenous species in European waters is the largest near coasts, i.e. in estuaries, lagoons and harbours; this number decreases with distance from the shore, which is where species-rich benthic communities occur (Wolff 1999, Nehring 2002, Reise et al. 2006). Alien species make up a significant component of the soft bottom macrofauna assemblage in the inner part of Puck Bay, where they make up from 6 to 33% of the total number of taxa (mean 17%), on average 6% of the total abundance (max 46%) and 10% of the total biomass (max 65%). In the Vistula Lagoon alien species comprise nearly 27% of the total number of zoobenthos species (Ezhova et al. 2005). On the German North Sea coast most of the aliens occur in the brackish water zone of estuaries (making up 10% of the total macrofauna) (Nehring 2002). A far greater proportion of non-native species in the total macrofaunal biomass has been recorded in the Gulf of Finland (70–90% – Orlova et al. 2006 or even > 99% in the deepest part of the gulf – Maximov 2011) and in the Curonian Lagoon (> 90% – Zaiko et al. 2007).

In Puck Bay a positive relationship was found between the numbers of non-indigenous and indigenous taxa. Indeed, a similar, strong positive relationship has also been found between these two groups of animals if we take into account all available data on benthic fauna composition from

different parts of the Gulf of Gdańsk (where the correlation coefficient R is 0.92, $P < 0.05$) with a decreasing trend in numbers of both taxa with depth (Table 1). Again, a similar trend was found in the case of the macrofauna of the Curonian Lagoon (Zaiko et al. 2007), and earlier for terrestrial plants (e.g. Levine 2000, Pyšek et al. 2002, Sax 2002). This positive correlation between the diversity of native and non-native species is probably the result of environmental factors such as habitat heterogeneity, resource availability, which positively affect the diversity of native and alien species alike (Levine & D'Antonio 1999).

It has been suggested that the resistance of a community to the invasion and subsequent large-scale establishment of alien species is related to the existing species richness (Stachowicz et al. 1999, Levine & D'Antonio 1999). If this is the case, then associations consisting of a larger number of species should be able to counteract invasions of alien species by limiting their abundance or biomass. This applies, for example, to marine hard-substrate communities, where the available space occupied by native species might substantially reduce invasion success (Stachowicz et al. 1999). However, in the associations of the soft sandy bottom of Puck Bay, where competition for space is not so strong, the relationship between the number of native taxa and the abundance of alien ones was found to be a positive one. A similar positive dependence between community diversity and the abundance of *G. tigrinus* was demonstrated in the mesocosm experiment conducted in the northern Baltic Sea (Herkül et al. 2006).

The presence of phytobenthic species had a positive influence on the number of native species, but did not significantly affect their abundance. Many other studies have shown a significantly higher species diversity, and also abundance and biomass, in vegetated areas than on bare sediment (e.g. Pihl 1986, Boström & Bonsdorff 1997). The species dominating the macrofauna was the mollusc *C. glaucum*. Young animals less than 5 mm in size were present in very large numbers not only on vegetated sediment, but also in areas of bare sandy sediment and where the sea bed was covered with mats of filamentous algae. Alien species were present in all habitats, and their numbers in these habitats were similar. Although the abundances of alien species in the various habitat types were very similar, the percentages of particular alien species in the total abundance varied in accordance with their habitat preferences.

The American amphipod *G. tigrinus*, one of the latest newcomers to the southern Baltic, was the most widely distributed and most numerous alien species in the whole of the inner Puck Bay. *G. tigrinus* was first recorded in Puck Bay in 2001 (Gruszka 2002), and by 2007 its frequency of occurrence had reached 44%. In other areas frequencies of occurrence

have been much higher, e.g. 94% in the Szczecin Lagoon 3 years after it was described in 1991 (Wawrzyniak-Wydrowska & Gruszka 2005) and 79% in the Curonian Lagoon in 2004, when it was first described there (Daunys & Zettler 2006). It was most frequent in calm, vegetated waters near the shore, where its abundance reached 6399 indiv. m⁻². These calculations did not take juvenile individuals into account, although it is highly likely that most were of this species. At all the stations where juvenile gammarids occurred, adults were also present (with one exception these were always *G. tigrinus*). Only 0.4% of all the gammarids analysed were adults of the native species. If we assume, therefore, that at those stations where only adult individuals of *G. tigrinus* were found the juveniles were also of this species, the density of this alien species then rises to 6844 indiv. m⁻², and the percentage of alien species in the total macrofaunal assemblage reaches a maximum of 49%. Higher densities, even in excess of 10 000 indiv. m⁻², due to the presence of juveniles, were recorded in summer and autumn in the Szczecin Lagoon (Wawrzyniak-Wydrowska & Gruszka 2005).

Bare, soft sediment was more frequently and more numerous colonised by *Marenzelleria* spp. and *P. antipodarum*. The American spionid polychaetes *Marenzelleria* spp. were most numerous on soft sediment below 3 m depth and very much more so on sediment devoid of vegetation. In the Gulf of Riga the species prefers to live in shallow areas on sand or gravel substrates, but also in decently vegetated areas (Kotta et al. 2008). In the Curonian Lagoon this species occurs on almost all substrates, occurring in 13 of the 16 habitats analysed (Zaiko et al. 2007). In the Szczecin Lagoon *Marenzelleria* spp. was first described in 1985 (Bick & Burchardt 1989); now it is the dominant species on the soft sediment in many parts of the Baltic, including the bodden coasts of northern Germany (Schiewer 2008), the Vistula Lagoon (Ezhova & Spirido 2005) and the Gulf of Finland (Orlova et al. 2006). This species has been present in the Polish zone of the Baltic since 1988 (Gruszka 1991). It is found down to a depth of 75 m but abundances and biomasses have been high on soft sediment to depths of c. 20–25 m and even at 60 m (Warzocha et al. 2005). The greatest abundances recorded off river mouths in the Gulf of Gdańsk – up to 1500 indiv. m⁻² – are rather lower than those found in Puck Bay (max 2444 indiv. m⁻²).

The gastropod *P. antipodarum*, originating from New Zealand, first appeared in the central Baltic in 1926–30 (Jensen & Knudsen 2005). In Puck Bay it preferred a sandy bottom. In the 1990s this snail occurred at a depth of 37 m on a muddy bottom rich in organic matter together with two other snail species: *H. ulvae* and *H. ventrosa* (Janas et al. 2004b). In the Curonian Lagoon this gastropod was reported only from the sandy sediment of the littoral zone (Zaiko et al. 2007), but in the Bothnian Bay it

was present primarily in sheltered bays with muddy bottoms (Leppäkoski et al. 2002).

The mollusc *M. arenaria*, a component of the Baltic macrofauna for several hundred years, was present in all habitats, though somewhat more frequently and more numerous on vegetated bottoms. These animals were mainly small individuals no larger than 10 mm. Young *M. arenaria* develop on a variety of substrates; they were one of the components of the associations forming on settlement panels deployed in the Gulf of Gdańsk (Dziubińska & Janas 2007). The adult animals, which grow to a size of 53 mm, live buried in the sediments of Puck Bay, to depths even in excess of 10 cm.

The barnacle *A. improvisus* occurred on vascular plants and *Chara* spp., but being a fouling organism, it prefers a hard bottom and *Mytilus edulis* beds as a substrate for settling on.

The least propitious as regards colonisation, especially by native fauna, were bottom sediments covered with mats of filamentous algae. Seven of the native species and one non-indigenous species (*A. improvisus*) recorded in all the other habitats were not found here. The abundance of native species was also somewhat lower here than in the other habitats. Drifting algae turning up on a sandy bottom may induce increased species diversity of benthic fauna by enhancing habitat complexity; on the other hand, they may induce hypoxia or even anoxia events in the shallow sandy bottom (Norkko & Bonsdorff 1996, Norkko et al. 2000). The unstable habitat formed by algal mats is more suitable for opportunistic species, a group to which belong only a few native benthic species from the littoral zone but practically all the alien ones. Floating mats of filamentous green algae in the Curonian Lagoon were very numerous colonised by alien gammarids of Ponto-Caspian origin (Leppäkoski et al. 2002).

In summary, alien species in the Puck Lagoon, like the native ones, prefer regions with favourable environmental conditions, e.g. a broad habitat diversity, an abundance of food and good oxygen conditions. This is in agreement with Levine (2000), who concluded that it is the most diverse communities that might be at the greatest risk of invasion, a situation that could have important implications for coastal ecosystem management. In the benthic associations of these habitats the greatest changes may occur as a result of the appearance of new species. In the case of Puck Bay such habitats are the vegetated and unvegetated areas of the sea bed lying just offshore. Other areas susceptible to the expansion of new species are hydroengineering structures, but these require separate study.

Some authors perceive alien species as additional elements of the biota, enhancing the diversity of continually changing ecosystems. This

is particularly so in the case of the geologically young Baltic Sea (Bonsdorff 2006). New species enrich communities with new functions: for instance, specimens belonging to the genus *Marenzelleria* are able to bioturbate sediment deeper than most native species (Zettler et al. 1994, Olenin & Leppäkoski 1999), positively affecting the biogeochemical processes in the sediment (Norkko et al. 2012). Although there is still little information on the subject, alien species must by now be new components of the trophic web, having become prey items for several fish species like perch *Perca fluviatilis*, eel *Anguilla anguilla*, eelpout *Zoarces viviparus*, cod *Gadus morhua* and the non-indigenous round goby *Neogobius melanostomus* (Winkler & Debus 1996, Kelleher et al. 1998, MacNeil et al. 1999, Gruszka & Więcaszek 2004). Other authors have applied the term 'biological pollution' to non-indigenous benthic species, thus comparing living creatures to chemical contaminants (Olenin et al. 2007). Alien species are a major threat to both the structure and functioning of communities or even whole ecosystems, and benthic communities are the most seriously affected (Streftaris et al. 2005). Experimental studies on the polychaete *M. viridis* have demonstrated its adverse influence on certain native species (Kotta et al. 2001, Kotta & Ólafsson 2003), although field observations have not confirmed this so far (Orlova et al. 2006). Likewise, the appearance of the amphipod *G. tigrinus* has caused a reduction in the number of native species; in this case, both field studies (Jażdżewski et al. 2004, Szaniawska et al. 2005, Grabowski et al. 2006, Surowiec & Dobrzycka-Krahel 2008) and mesocosm experiments (Herkül et al. 2006, Orav-Kotta et al. 2009) provide evidence for this. The prevention of new introductions is therefore of the utmost importance, particularly in view of the fact that species introductions are irreversible and accumulate over time (Reise et al. 2006). Once a new species has turned up in the environment, it brings about changes in the ecosystem that can be both positive and negative. Nonetheless, every new species should be treated on its own merits and be accorded the respect due to all living organisms.

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