Oceanological and Hydrobiological Studies
Vol. XXXIV, Supplement 1

Institute of Oceanography (175-193) University of Gdańsk
2005

Research Article

NATIVE AND ALIEN MALACOSTRACAN CRUSTACEA ALONG THE POLISH BALTIC SEA COAST IN THE TWENTIETH CENTURY

KRZYSZTOF JAŻDŻEWSKI*, ALICJA KONOPACKA,
MICHAŁ GRABOWSKI

Department of Invertebrate Zoology & Hydrobiology
University of Lodz, ul. Banacha 12/16
90-237 Lodz, Poland

e-mail: kryjaz@biol.uni.lodz.pl

Key words: alien species, invasive Crustacea, brackish waters, faunal changes

Abstract

A total of 56 species of malacostracan Crustacea have been recorded along the Polish coast of the Baltic. This includes 12 species of Isopoda, one each of Tanaidacea and Cumacea, six of Mysidacea, 28 of Amphipoda, and eight of Decapoda. While the majority of these species are native ones, 11 alien species account for nearly 20% of the total malacostracan fauna. These species are *Hemimysis anomala* (a mysid), *Chelicorophium curvispinum*, *Chaetogammarus ischnus*, *Gammarus tigrinus*, *Dikerogammarus haemobaphes*, *D. villosus*, *Pontogammarus robustoides*, *Obesogammarus crassus* (amphipods), as well as *Orconectes limosus*, *Rhithropanopeus harrisii* and *Eriocheir sinensis* (decapods). Seven species – one mysid and six amphipods – are of Ponto-Caspian origin, and three species come from American waters (one amphipod and two decapod species). One of the decapods, the Chinese mitten crab, is of Asian origin. This paper presents the history of the discovery of particular taxa in Polish Baltic offshore waters and emphasizes the fact that the main wave of the invasion of alien malacostracan species began within the past few decades. The faunistic changes that have occurred in the gammarid

assemblage structure in recent decades along the Polish Baltic coast, especially in its lagoons, are also presented.

INTRODUCTION

Malacostracan crustaceans play an important role in the littoral and sublittoral zones of marine and brackish waters. At the same time, as comparatively large invertebrates, they were positively identified rather early which means that monitoring their occurrence and changes in distribution was and is relatively reliable.

Malacostracans are also richly represented in the ecological group of genuine brackish water species (Remane 1958). In the oligo- and mesohaline waters of the Baltic proper, they constitute a significant proportion of the macroinvertebrate fauna. The share of non-indigenous species in this animal group has rapidly increased in the last decade (Leppäkoski and Olenin 2000a, Leppäkoski *et al*. 2002a,b). This recent increase of xenodiversity clearly threatens the native biogeographical peculiarity of the originally boreal Baltic Sea (Olenin and Leppäkoski 1999, Leppäkoski and Olenin. 2000b). Therefore, it is necessary to monitor the fauna of Baltic waters, and this must be based on sound taxonomic knowledge of this group.

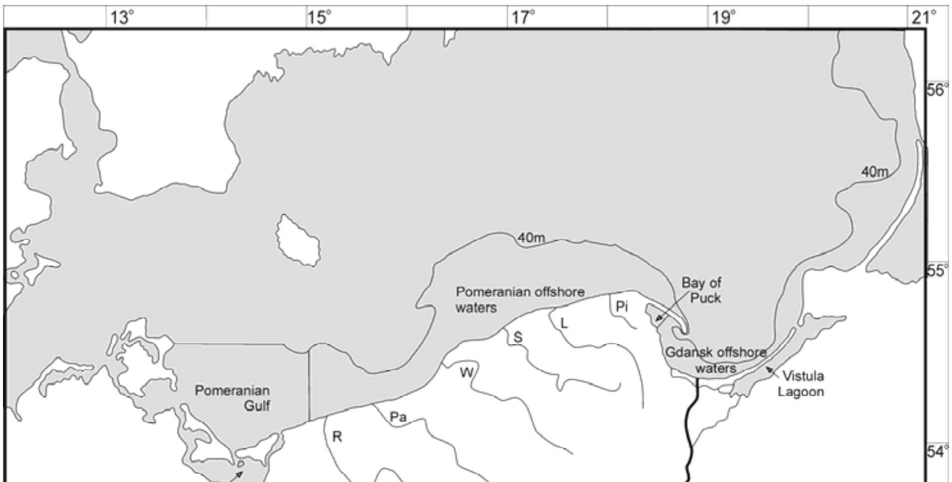

Fig. 1. Southern Baltic – division according to Jażdżewski and Konopacka (1995) R – Rega, Pa – Pasłęka, W – Wieprza, S – Słupia, L – Łupawa, Pi – Piaśnica.

The aim of the present study was to inventory the malacostracan fauna along the Polish Baltic coast paying special attention to recent faunal changes.

In order to use the fundamental Polish source, *Catalogus faunae Poloniae*, edited by the Museum and Institute of Zoology, Polish Academy of Sciences, the southern Baltic Sea was divided into 13 regions. Six of them are offshore regions (Fig. 1) limited to the north by the 40 m isobath. From west to east these regions are the Szczecin Lagoon, the Pomeranian Gulf, Pomeranian offshore waters, the Bay of Puck (Puck Lagoon), the Gulf of Gdańsk coastal waters, and the Vistula Lagoon. State borders divide the Szczecin and Vistula lagoons into the Polish and German and Russian parts, respectively. The estuaries of numerous small and medium-sized rivers are located along the 300-km long Pomeranian coastline; the larger six of these are illustrated in Fig. 1. These estuaries often contain small fisheries harbors and are rich in artificial secondary hard bottoms that offer suitable conditions for algal growth and sheltered habitats where malacostracan crustaceans can usually be collected in number. The monitoring stations for this study were often located in such places. Salinity is the primary feature that determines hydrobiont distribution, and the salinity ranges in particular regions are presented in Table 1.

Table 1

Salinity of the Polish Baltic waters.

Region	Salinity (PSU)
Pomeranian Gulf	7-9
Szczecin Lagoon	0.5-1.5
Pomeranian offshore waters	7-8
Bay of Puck	6-7
Gulf of Gdańsk coastal waters	6-7
Vistula Lagoon (Polish part)	1-5
Estuaries	2-5

MATERIAL AND METHODS

This paper is based on a detailed survey of ample and reliable faunistic literature (see Jażdżewski and Konopacka, 1995) and on the authors' own materials collected along the Polish Baltic Sea coast in the 1960s and in 2000-2005. Additional material from the Szczecin Lagoon, collected in the 2000-2004 period, was kindly provided by Prof. Norbert Wolnomiejski (Sea Fisheries Institute, Świnoujście). The most recent monitoring provided researchers with very rich material; however, it is limited to the shallowest parts of the Baltic littoral and mainly to the phytal zone and secondary hard bottoms.

Table 2

Malacostracan Crustacea in offshore Polish Baltic waters – first discovery and species characteristics.

Author (date)	Species	First record in Poland	Distribution	Salinity preferences
Zaddach (1844)	*Calliopius laeviusculus* (Krøyer, 1838)	GOW	SB	M
	Leptocheirus pilosus Zaddach, 1844	GOW	MB	B
	Melita palmata (Montagu, 1804)	GOW	MB	M
	Mysis relicta Loven, 1862	GOW	SB	B
	Jaera albifrons Leach, 1814, *sensu lato*	GOW	BR	M
	Idotea balthica (Pallas, 1772)	GOW	MB	M
	Talitrus saltator (Montagu, 1808)	GOW	MB	T
Möbius (1873)	*Corophium volutator* (Pallas, 1766)	GOW	BR	M
	Neomysis integer (Leach, 1814)	POW	BR	B
	Praunus flexuosus (O.F.Müller, 1776)	GOW	BR	M
	Crangon crangon (L., 1758)	GOW	MB	M
	Saduria entomon (L., 1758)	BOP	AB	B
	Pontoporeia femorata Krøyer, 1842	GOW	AB	M
	Diastylis rathkii (Krøyer, 1841)	POW	SB	M
Zaddach (1879)	*Bathyporeia pilosa* Lindstroem, 1855	GOW	BR	M
	Palaemon adspersus Rathke, 1837	GOW	MB	M
Seligo (1899)	*Sphaeroma rugicauda* Leach, 1814	GOW, POW	LB	B
	Heterotanais oerstedi (Krøyer, 1842)	GOW, POW	MB	B
	Talorchestia deshayesii (Audouin, 1826)	POW	MB	T
Enderlein (1908)	*Cyathura carinata* (Krøyer, 1848)	BOP	MB	B
Vanhöffen (1911)	*Apocorophium lacustre* (Vanhöffen, 1911)	VL	BR	B
Sexton (1913)	*Gammarus locusta* (L., 1758)	GOW	BR	M
Sexton (1913)	*Gammarus zaddachi* Sexton, 1912	GOW	BR	B
Dahl (1916)	*Idotea chelipes* (Pallas, 1766)	BOP, VL	MB	B
Demel (1925)	*Eurydice pulchra* Leach, 1815	POW	LB	M
Herold (1925a)	*Asellus aquaticus* (L., 1758)	SL	BR	F
Herold (1925b)	*Orchestia cavimana* Heller, 1865	SL	MB	T
Schellenberg (1925)	*Chelicorophium curvispinum* (G.O. Sars, 1895)	SL	PC	F
Demel (1926)	*Mysis mixta* Liljeborg, 1852	GOW	AB	M
Hagmeier (1926)	*Monoporeia affinis* (Lindström, 1855)	GOW	SB	B
Demel (1928)	*Carcinus maenas* (L., 1758)	GOW	BR	M
Haeckel (1930)	*Eriocheir sinensis* Milne Edwards, 1854	SL	EA	B
Neuhaus (1933)	*Gammarus duebeni* Liljeborg, 1852	SL	SB	B
Schellenberg (1942)	*Chaetogammarus ischnus* (Stebbing, 1899)	GOW	PC	F
Birshtein (1952)	*Rhithropanopeus harrisii* Gould, 1841	VL	NA	B
Mańkowski (1955)	*Praunus inermis* (Rathke, 1843)	POW	SB	M
Micherdziński (1959)	*Gammarus oceanicus* Segestråle, 1947	GOW	AB	M
	Gammarus salinus Spooner, 1947	GOW	BR	B
Ławiński & Szudarski (1960)	*Palaemonetes varians* (Leach, 1814)	GOW	MB	B
Żmudziński (1962)	*Ampithoe rubricata* (Montagu, 1808)	GOW	SB	M
	Crassicorophium crassicorne (Bruzelius, 1859)	GOW	SB	M
Jażdżewski (1963)	*Sphaeroma hookeri* Leach, 1814	BOP	MB	B
Sywula (1964)	*Idotea granulosa* Rathke, 1843	POW	MB	M
Gruner (1965)	*Jaera albifrons syei* Bocquet, 1950	POW	BR	B
	Jaera ischiosetosa Forsman, 1949	GOW	BR	M
Jażdżewski (1966)	*Jaera praehirsuta* Forsman, 1949	BOP	BR	M
Demel (1967)	*Orconectes limosus* (Rafinesque, 1817)	GOW	NA	F
Jażdżewski (1967)	*Corophium multisetosum* Stock, 1952	GOW	BR	B
Jażdżewski (1970)	*Gammarus inaequicauda* Stock, 1966	BOP	BR	M
Jażdżewski (1975)	*Chaetogammarus stoerensis* (Reid, 1938)	POW	BR	M
Gruszka (1995)	*Gammarus tigrinus* Sexton, 1939	SL	NA	B
Gruszka (1999)	*Pontogammarus robustoides* (G.O. Sars, 1894)	SL	PC	B
Jażdżewski & Konopacka (2000)	*Dikerogammarus haemobaphes* (Eichwald, 1841)	VL	PC	F
Konopacka & Jażdżewski (2002)	*Obesogammarus crassus* (G.O. Sars, 1894)	VL	PC	B
Gruszka et al. (2003)	*Hemimysis anomala* G.O. Sars, 1907	SL	PC	B
Janas, Zarzycki, Kozik (2004)	*Palaemon elegans* Rathke, 1837	GOW	MB	M
Konopacka (2004 unpublished)	*Dikerogammarus villosus* (Sovinskij, 1894)	SL	PC	F

Region: BOP – Bay of Puck, GOW – Gdańsk offshore waters, POW – Pomeranian offshore waters, SL – Szczecin Lagoon, VL – Vistula Lagoon

Distribution: AB – Arctic-Boreal, SB – Subarctic-Boreal, BR – Boreal, LB – Lusitanian-Boreal, MB – Mediterranean-Boreal, PC – Ponto-Caspian, NA – North-American, EA – East-Asiatic

Salinity preferences: M – marine euryhaline, B – brackishwater, F – freshwater euryhaline

These habitats are especially suitable for the many amphipod, isopod, and decapod taxa that comprise the bulk of the Baltic malacostracan fauna. Samples from the 2004 survey were collected using a hand net or dredge and, to ensure that samples were rich in specimens and comparable, every one was the result of a 45-minute sampling effort by two people. The material from net hauls was picked out on the spot by another two people and fixed in 96% ethanol. The rest of the sample was preserved in a 4% formalin solution and was sorted later in the laboratory. The samples usually consisted of hundreds of specimens, which permitted estimating the proportions among the various taxa, especially in the case of gammaridean amphipods, the group that dominated the vagile macrozoobenthos in the littoral zone.

RESULTS AND DISCUSSION

History of faunistic surveys

The biota of the Baltic Sea have been studied for a relatively long time; basic knowledge of southern Baltic fauna dates to the second half of the nineteenth and the early twentieth centuries. It is significant to remember that, at the time, the northern part of Poland was under German administration. Thus, the first fundamental data come from papers by the German scientists Zaddach, Möbius, and Seligo. Original records of various malacostracan crustaceans in Polish Baltic waters are scattered and were published mostly in Latin, German, and Polish. The respective volume of *Catalogus faunae Poloniae* concerning this animal group was published in Polish (Jażdżewski and Konopacka 1995) with a short summary in English (Jażdżewski and Konopacka 1993). This volume is a compilation of the literature up to 1992. Therefore, the authors decided to present in this paper a brief survey of the very first records of various species in Polish Baltic waters (Table 2) accompanied by their zoogeographical and ecological characteristics.

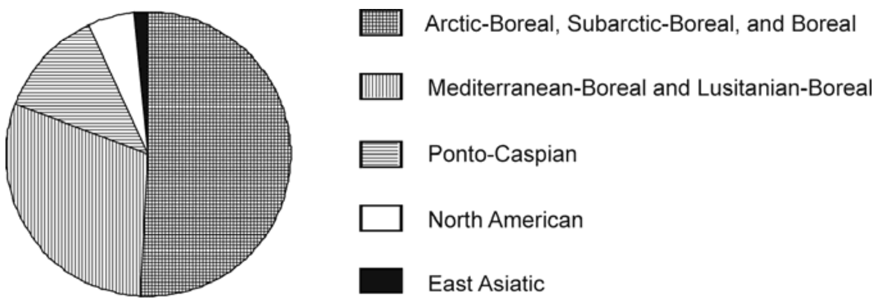

Fig. 2. Proportion of various zoogeographical elements in the malacostracan fauna of the Polish Baltic coast.

Biogeographical and ecological remarks

A total of 56 malacostracan crustaceans have been recorded in the six Polish offshore regions mentioned above, among them one tanaid, one cumacean, six mysid, eight decapod, 28 amphipod, and 12 isopod species.

The Baltic fauna of Crustacea Malacostraca is dominated by boreal and Arctic (Subarctic)-boreal elements (Fig. 2). Nearly 30% of the malacostracans have Mediterranean-boreal or Lusitanian-boreal distribution and often the limits of their thermic preferences lie just within Polish offshore waters (*Sphaeroma* spp., *Cyathura carinata*, *Eurydice pulchra*, and *Palaemonetes varians*). The authors maintain that all taxa occurring in both the Baltic and North seas should be recognized as native species regardless of when they were first noted Baltic. Many species occur at the limits of their natural distributions, which is related to their thermic and/or salinity tolerance ranges. For instance, this is the case with *Carcinus maenas*, *Palaemon elegans*, *Gammarus inaequicauda*, and *Chaetogammarus stoerensis*, species whose eastern range limits in the Baltic are presently usually situated in Polish coastal waters. However, the distribution range of some Atlantic species can broaden very rapidly and take on the characteristics of an invasion; this is the case with *P. elegans*, which has already been noted in the Gulf of Finland (Kekkonen 2003, Lavikainen and Laine 2004)

Nearly 20%, or 11 of the 56 malacostracan crustaceans ever recorded along the Polish Baltic coast, are aliens. Of them, there are seven amphipods, three decapods, and one mysid. They mainly originate from the Ponto-Caspian basin (*Chaetogammarus ischnus*, *Pontogammarus robustoides*, *Dikerogammarus haemobaphes*, *D. villosus*, *Obesogammarus crassus*, *Chelicorophium curvispinum*, *Hemimysis anomala*) and North American coastal waters (*Orconectes limosus*, *Rhithropanopeus harrisi*, *Gammarus tigrinus*), while one species (*Eriocheir sinensis*) is of Asian origin. The history of their arrival has been almost fully established. The two alien crabs, *Eriocheir* and *Rhithropanopeus*, were probably transported directly from Asia in vessel ballast waters. All of the other species entered Baltic coastal waters from its drainage areas where they had been intentionally introduced, or they migrated to the area using man-made canals that joined formerly separated drainage basins.

The salinity preferences of all the Malacostraca Crustacea inhabiting the Baltic Sea are relatively well known (Fig. 3). They can be divided into three main categories: (i) euryhaline marine species (*Gammarus oceanicus*, *Carcinus maenas, Mysis mixta*); (ii) genuine brackish water species (both *Sphaeroma* species, *Idotea chelipes*, *Gammarus zaddachi*, *Gammarus duebeni*, *Obesogammarus crassus*, *Pontogammarus robustoides*, *Rhithropanopeus harrisi*); (iii) euryhaline freshwater species (*Asellus aquaticus*, *Orconectes limosus*, *Dikerogammarus* species, *Chaetogammarus ischnus, Chelicorophium* *curvispinum*). The last category is a minor admixture, whereas the marine euryhaline and genuine brackish water crustaceans dominate and are represented by similar proportions of some 45% in the total number of recorded malacostracan species.

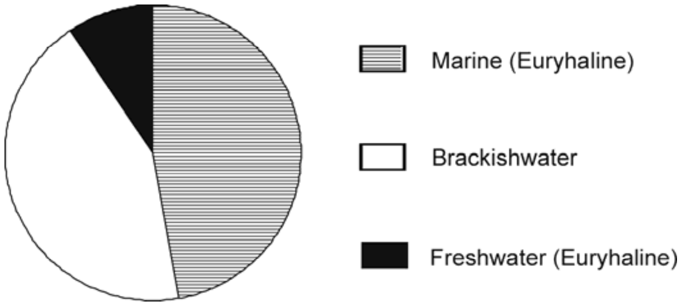

Fig. 3. Proportion of species with three basic salinity preferences in the malacostracan fauna of the Polish Baltic coast.

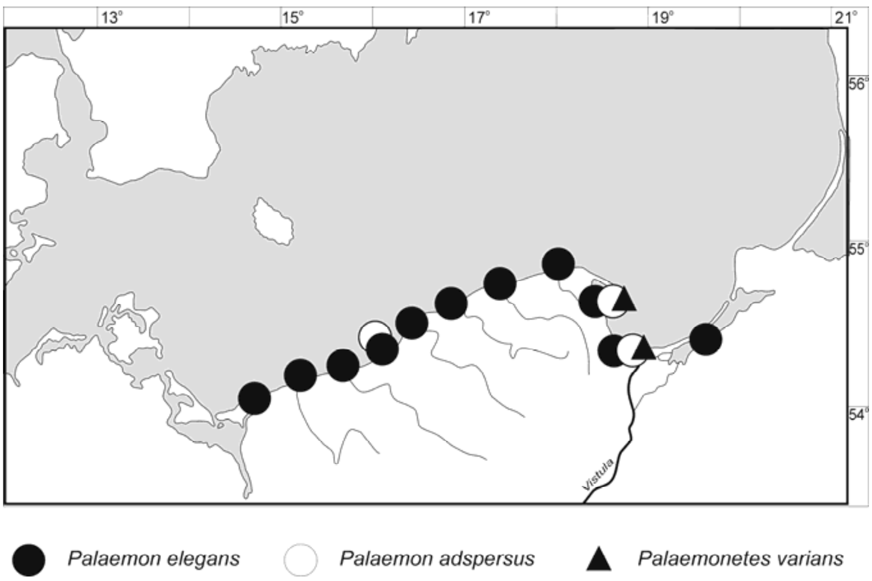

Fig. 4. Distribution of palaemonid shrimps along the Polish Baltic coast from the 2004 survey.

Recent faunistic changes

Some of the results from the 2004-2005 survey are worthy of comment in light of the historical data.

1) *Palaemon elegans*, a species recently recorded in the Gulf of Gdańsk by Janas *et al*. (2004), appeared to be the most common palaemonid shrimp in Polish offshore waters (Fig 4). This species is new to Polish fauna, and yet it occurs most often as the only palaemonid species along the Pomeranian coast. In the Bay of Puck, it is commonly accompanied by *P. adspersus*, and in the Vistula deltaic system both species occur along with *Palaemonetes varians*. However, in the Vistula Lagoon, *P. elegans* was the only shrimp species noted.

2) Of the three species of *Idotea* occurring along Polish Baltic shores, *I. chelipes* and *I. granulosa* are common, while in open Baltic localities, *I. granulosa* dominated *I. chelipes*, which was more numerous at sheltered stations (Fig. 5). This information corresponds well with the observations by Sywula (1964).

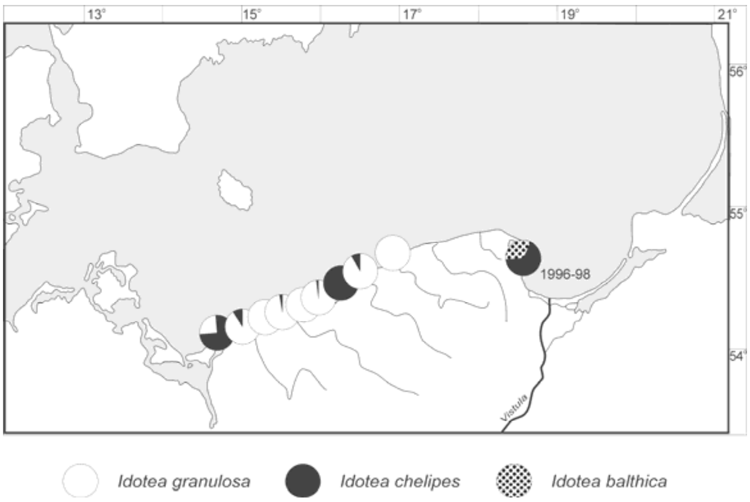

Fig. 5. Distribution of *Idotea* species in Polish Baltic waters from the 2004 survey (Bay of Puck – 1996-1998).

3) Of rare species that had only been noted sporadically to date along the Polish coast (Jażdżewski 1976), *Calliopius laeviusculus* and *Chaetogammarus stoerensis* were still present in the 2004 survey, although only single individuals were noted (*C. laeviusculus* – a total of 19 individuals in Niechorze, Dźwirzyno, and Ustronie Morskie; *C. stoerensis* – three individuals in Kołobrzeg).

4) As in previous surveys, four corophiid species, *Apocorophium lacustre*, *Chelicorophium curvispinum*, *Corophium volutator* and *C. multisetosum*, occur patchily along the length of the Polish coast.

5) The *Jaera albifrons* group was only rarely noted in recently collected materials, and among some 3,000 malacostracans examined, only single *Jaera* individuals were found.

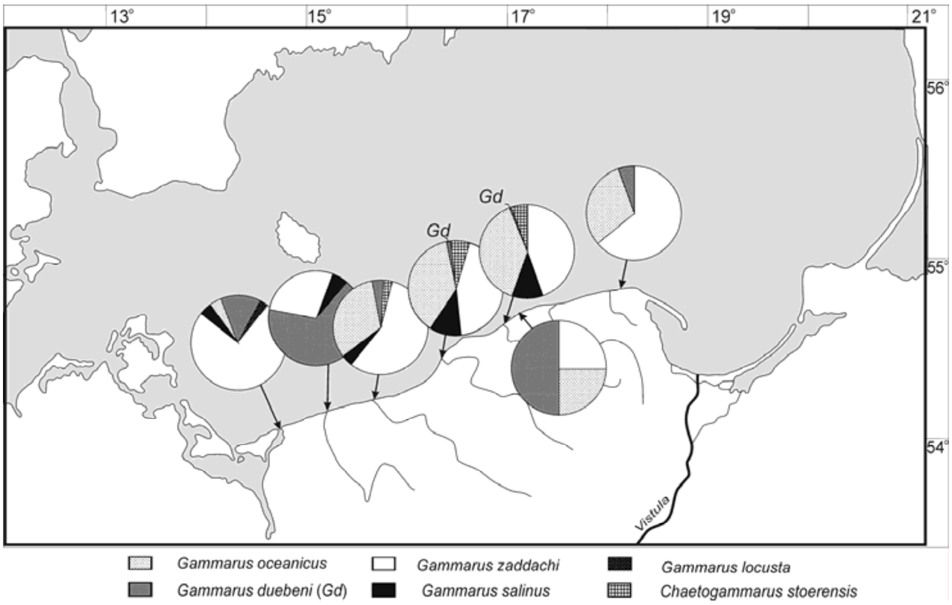

Fig. 6. Composition of gammarid assemblages along the Polish Baltic coast in 1969.

In the materials collected several decades ago and recently, the most abundant were gammarid amphipods. In 1969 (Jażdżewski 1975 and unpublished data), only native gammarids were recorded (Fig. 6), with *Gammarus zaddachi* as the most frequent dominant species. In some samples taken at more sheltered stations, this species yielded to *G. duebeni*, whereas *G. oceanicus* had an important share in many samples. The least common and least abundant species were *Gammarus locusta* and *Chaetogammarus stoerensis*.

The 2004 survey revealed a new situation. Although *G. zaddachi* remained the dominant species in Baltic offshore waters, and *G. duebeni* and *G. oceanicus* still occurred in significant proportions, the share of the new alien species *Gammarus tigrinus* became significant at some river mouths (Fig. 7).

Drastic changes were observed in all of the Polish lagoons (Szczecin, Bay of Puck and Vistula). Other non-native species appeared that seriously outnumbered the native species (Gruszka 1995, 1999, 2002, Jażdżewski *et al.* 2002, Konopacka and Jażdżewski 2002, Konopacka 2003, Szaniawska *et al.*

2003 and present survey). In the first and the last basins these aliens are *Gammarus tigrinus*, *Pontogammarus robustoides*, and *Obesogammarus crassus*; they are accompanied by *Dikerogammarus haemobaphes* at the least saline stations. This phenomenon of the replacement of native gammarid species by aliens in oligohaline Baltic brackish waters exhibits a dynamic, increasing tendency.

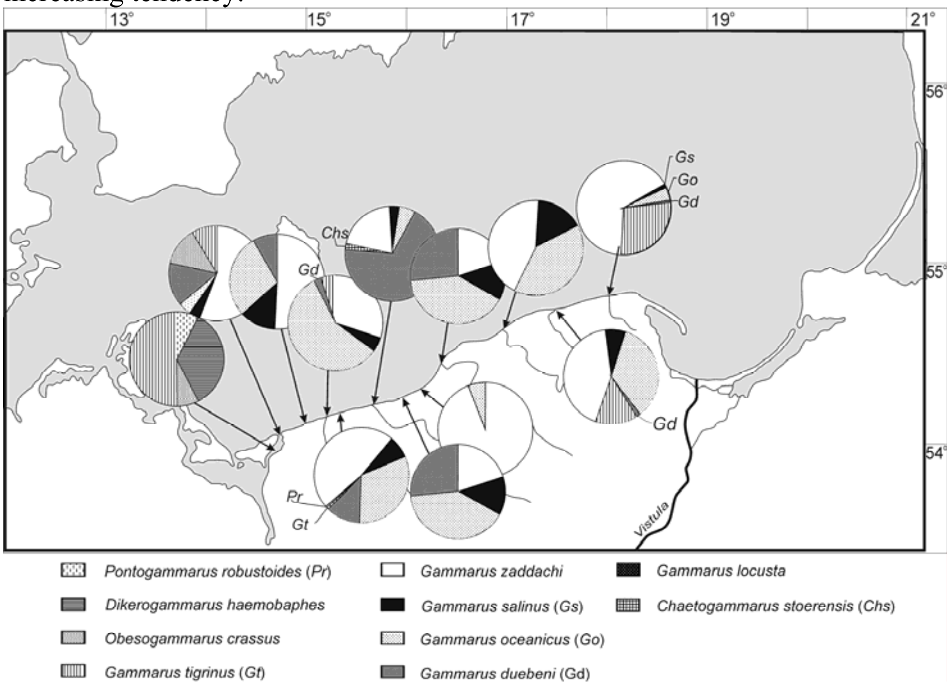

Fig. 7. Composition of gammarid assemblages along the Polish Baltic coast in 2004.

Figure 8 presents the former and current gammarid fauna composition in the lagoons. The older data from the Szczecin Lagoon are merely qualitative and are based on very modest information, and it is only known that *G. zaddachi* and *G. duebeni* were noted in this basin in the early twentieth century (Stephensen 1929, Neuhaus 1933, Micherdziński 1959, Jażdżewski 1975). In the 1980s, Gruszka (1995, 1999) reported the first sighting of the American *Gammarus tigrinus* and then the Ponto-Caspian *Pontogammarus robustoides* in the Szczecin Lagoon. Another Ponto-Caspian gammarid, *Dikerogammarus haemobaphes*, was observed in the lower Oder River at the entrance to this lagoon by Müller *et al.* (2001). Another representative of Pontogammaridae, *Obesogammarus crassus*, has also been recorded in this lagoon (Konopacka 2003). Based on the richer samples from Dr. Wolnomiejski and on the authors' own materials, four alien species completely dominate the gammarid communities of this basin, and the single individuals of *Dikerogammarus villosus*, noted earlier in the lower Oder River (Müller *et al*. 2001), also appeared in the Szczecin Lagoon. No native gammarid specimens were recorded in this material comprised of 1,000 individuals.

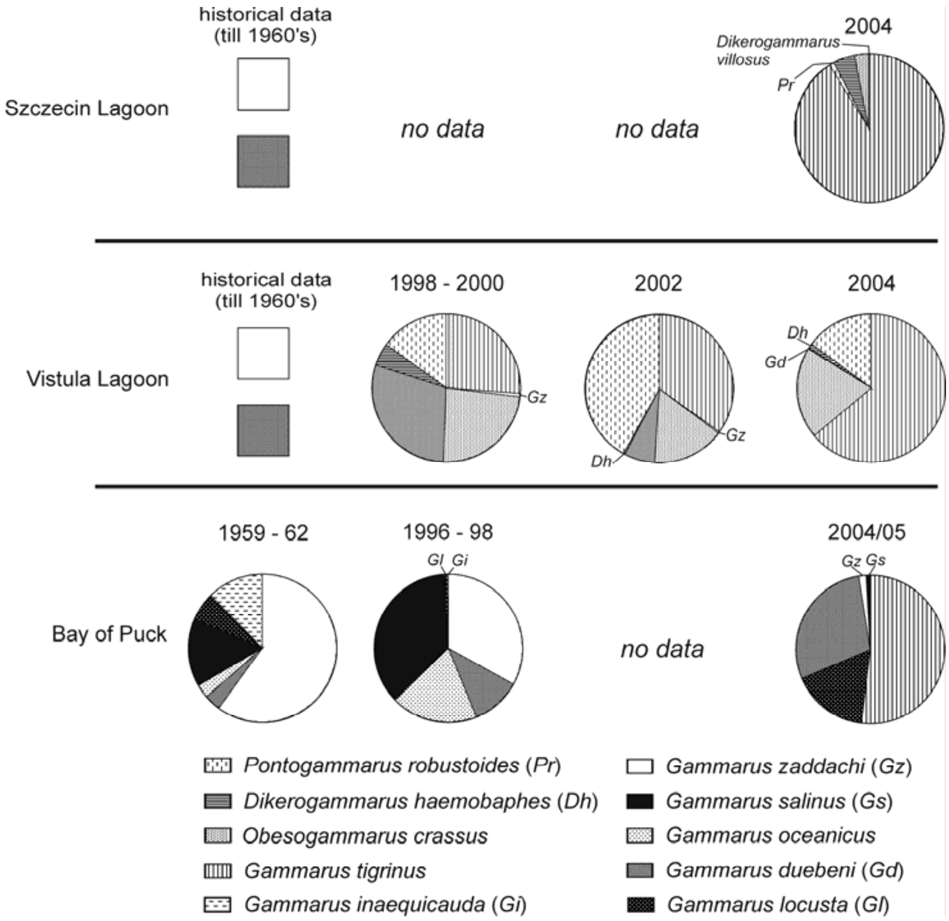

Fig. 8. Changes in the composition of gammarid assemblages in the Szczecin Lagoon, Vistula Lagoon, and Bay of Puck in recent decades (1996-1998 data from Jęczmień & Szaniawska 2003, and unpublished data).

Quite a similar situation was observed in the Vistula Lagoon, where faunistic studies during the twentieth century, especially those conducted at its end, were much more detailed. From the time the first native species were recorded (*G. zaddachi* by Vanhoffen (1917) and *G. duebeni* by Schellenberg (1942)) until the end of the twentieth century, only these two gammarid species were noted (Żmudziński 1957, Jażdżewski 1975, Cywińska and Różańska 1978, Jażdżewski *et al*. 2004). However, in the late 1990s, alien gammarid species were discovered in the Polish part of the lagoon (Jażdżewski and Konopacka 2000, Konopacka and Jażdżewski 2002, Jażdżewski *et al*. 2002, 2004). The scenario of these changes can be described rather precisely. Due to the increasing eutrophication of Vistula Lagoon waters (Różańska and Więcławski 1978), *Gammarus duebeni*, the native species best adapted to pollution and oxygen depletion, began to successively dominate the other native, *G. zaddachi*. Both species were present until the end of the 1990s (Fig. 8), when the aliens arrived. Initially, the Ponto-Caspian taxa (*Pontogammarus robustoides* and/or *Obesogammarus crassus*) took the dominant position with *G. duebeni* still comprising an important share of the gammarid fauna with an increasing proportion of *G. tigrinus*, especially in the northern part of the lagoon. The 2004 sampling revealed that *G. tigrinus* had become the nearly decisive dominant and had also outcompeted the pontogammarids in many places.

The Bay of Puck, a much more open basin, was thoroughly studied in the late 1950s and early 1960s (Jażdżewski 1971, 1973), and then again repeatedly in the late 1970s (Wiktor *et al*. 1980). The dominants were consistently *G. zaddachi*, *G. salinus*, and *G. oceanicus*, with a diminishing share of *G. locusta* and *G. inaequicauda* and an increasing proportion of *G. duebeni* (Fig. 8). This change is also evidence of the increasing eutrophication of the bay. In 2001, Gruszka (2002) discovered *G. tigrinus* in the Bay of Puck and soon this species became a dominant in the shallow waters of the northern part of the bay, along the Hel Peninsula. A small contribution of native species was noted in the southern part (Szaniawska *et al*. 2003). The authors' 2004 and 2005 samples from the entire Bay of Puck (a total of over 600 individuals) confirmed the preceding information (Fig. 8). Four native species - *G. duebeni*, *G. locusta*, *G. zaddachi*, and *G. salinus*, still occurred in the samples that were dominated by *G. tigrinus*.

All of the data indicate that in sheltered Baltic waters – especially lagoons – *G. tigrinus* has recently become the most successful alien invader. The main reasons for success appear to be the unusual ability of this species to withstand pollution and its extreme euryhalinity (Bousfield 1973, Bulnheim 1984, Pinkster *et al*. 1992). The severe eutrophication of all Polish Baltic lagoons is a well-documented phenomenon (Różańska and Więcławski 1978, Wołowicz *et al*. 1993, Garbacik-Wesołowska *et al*. 1998, Poleszczuk and Sitek 1998).

It can be concluded that the changes that have occurred in the malacostracan fauna in Polish Baltic coastal waters during the last century are indeed serious. Moreover, their acceleration in the last decade is obvious and well documented. The most spectacular changes are the rapid expansion in the range of *Palaemon elegans* in the southern Baltic and the drastic change in the composition of gammarid fauna, especially in sheltered localities and shallow, eutrophic lagoons. It is here that alien species (the North American *G. tigrinus* and at least three Ponto-Caspian species - *D. haemobaphes*, *P. robustoides*, and *O. crassus*) have outcompeted native gammarids and occur in various proportions in different parts of these lagoons depending on salinity. Native gammarids still dominate in open, non-sheltered Baltic waters. However, species that are less resistant to pollution, like *G. inaequicauda*, *G. salinus*, and *G. locusta*, now occur in low or very low proportions and seem to be endangered; they were, however, recently recorded in offshore waters near the Sambian peninsula (Rudinskaya 2002, Gusev and Urbanovich 2004), and in an early spring survey in 2005, *G. locusta* was comparatively abundant in the sample from the central part of the Bay of Puck.

Why are such serious changes occurring in the composition of malacostracan fauna along the Polish Baltic coast? One of them is undoubtedly the intentional introduction of alien crustaceans in neighboring regions, *e.g.*, *Gammarus tigrinus* in German waters in the 1950s, and *Obesogammarus crassus* and *Pontogammarus robustoides* in Lithuania in the 1960s (see Jażdżewski and Konopacka 2000, Arbaciauskas, in press, this volume). All of these species are euryhaline, brackish water animals that prefer oligohaline conditions, and this is probably why they have spread efficiently in the Baltic. Another reason is the breaking of natural biogeographic barriers through the construction of artificial canals that connect previously isolated river systems, and pollution that has resulted in increased salinity in large European rivers (Bij de Vaate *et al*. 2002). Possibly, this has enabled the oligohaline *Dikerogammarus hameobaphes* to invade both the Vistula and Oder systems and to enter their deltaic systems. Some introductions stem from global sea transport (*Rhithropanopeus harrisi*, *Eriocheir sinensis*) (Rodriguez and Suarez 2001). Another important factor is the natural colonization of Baltic coastal waters by Atlantic species (possibly aided by human transport), as is probably the case with *Palaemon elegans*. It is important to remember that all of the species discussed are euryoecious with nonspecific food preferences and they protect their juveniles. All these features support invasion success. On the other hand, the Baltic is a unique system that is very young on the geological time-scale where natural succession has not yet reached the level of "dynamic equilibrium".

ACKNOWLEDGEMENTS

Many thanks are due to Ewa Janowska and Karolina Bącela for their invaluable help and dedication in the field and laboratory. We would also like to acknowledge all those who contributed to our efforts during fieldwork: Anna Jażdżewska, Joanna Grabowska, Piotr Janowski, Radomir Jaskuła, and Krzysztof Pabis. Some of the material analyzed was collected and kindly provided by Prof. Norbert Wolnomiejski (Sea Fisheries Institute, Świnoujście). This research was partially financed by the Polish State Committee for Scientific Research (KBN), grant no 2 P04G 076 026 p01.

REFERENCES

Bij De Vaate A., Jażdżewski K., Ketelaars H.A.M., Gollasch S., Van Der Velde G., 2002, *Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe*, Can. J. Fish. Aquat. Sci., 59, 1159-1174

Birshtejn J. A., 1952, *Istorija odnogo kraba*, Priroda 9, p. 118

Bousfield E. L., 1973, *Shallow-water gammaridean Amphipoda of New England*, Ithaca, N. Y., 312 pp.

Bulnheim H-P., 1984, *Physiological responses of various Gammarus species to environmental stress*, Limnologica (Berlin), 15, 461-467

Cywińska A., Różańska Z., 1978, *Zoobentos zalewu Wiślanego*, Stud. i Mat. Oceanolog., 21, Biologia Morza, 4, 145-160

Dahl F., 1916, *Die Asseln oder Isopoden Deutschlands*, Jena, 90 pp.

Demel K., 1925, *Spis zwierząt bezkręgowych Bałtyku naszego*, Arch. Ryb. Pol., 1, 1-6

Demel K., 1926, *Contribution á la connaissance de la faune benthique dans les eaux polonaises de la Baltique*. Bull. Int. Acad. Pol., Cl. Math. Nat., B, Cracovie, 1925, 967-977

Demel K., 1928, *Krab raczyniec* (Carcinus maenas) *w polskich wodach Bałtyku*, Wszechświat, II, 1(34), 12, p. 122

Demel K., 1967, *Nasz Bałtyk*, [in:] *Przyroda Polska*, Warszawa, 156 pp.

Enderlein G., 1908, *Biologisch-faunistische Moor- und Dünen Studien. Ein Beitrag zur Kenntnis biosynöcischer Regionen in Westpreussen,* Ber. Westpr. Bot.-Zool. Ver., 30, 54-238

Garbacik-Wesołowska A., Poleszczuk G., Sitek S., Olszewski P., 1998, *Water in port basins of Świnoujście: general characteristics and comparison of chemical composition of near-bottom and interstitial water from surface sediments,* Proceedings of Polish-German Symposium, Świnoujście, 19-20

November 1996, *The problems of management of fishery resources in the Polish and German waters of the Szczecin Lagoon and Pomeranian Bay,* 7-30

Gruner H. E., 1965, *Krebstiere oder Crustacea*. V. *Isopoda*, [in:] *Die Tierwelt Deutschlands*, 51, 1, Jena, 149 pp.

Gruszka P., 1995, Gammarus tigrinus *Sexton, 1939 (Crustacea: Amphipoda) - nowy dla fauny Polski gatunek w estuarium Odry*, [in:] I Konf. *Przyrodnicze aspekty badania wód estuarium Odry i wód jeziornych województwa szczecińskiego*, Mat. Konf. No. 7, Uniw. Szczecin, p. 44

Gruszka P., 1999, *The River Odra estuary as a gateway for alien species immigration to the Baltic Sea basin*, Acta hydrochim. hydrobiol., 27, 374-382

Gruszka P., 2002, Gammarus tigrinus *(Sexton, 1939) (Crustacea, Amphipoda) - a new species in the Puck Bay (southern Baltic)*, [in:] Abstracts 4th European Crustacean Conference, 22-26 July 2002, Univ.Lodz., Poland, 40-41

Gruszka P., Wawrzyniak-Wydrowska B., Żurawska J., 2003, *Alien crustacean species in the river Odra estuary (Baltic Sea)*, [in:] Baltic Sea Science Congress 2003, Helsinki, Abstracts, p.130

Gusev A., Urbanovich O. A., 2004, *Vidovoj sostav i ekologicheskajakharakteristika makrozoobentosa v Kaliningradskoj zone Baltijskogo morja v sentjabre 2001 goda,* Tr. Atlant. N-IIRKhO, Promyslovo-biologicheskie issledovanija Atlantniro v 2002-2003 godakh, Kaliningrad, 2, Ekologija gidrobiontov, 4-19

Haeckel W., 1930, *Die chinesiche Wollhandkrabbe* (Eriocheir sinensis *Miln.-Ed.*) *ein Irrgast in Ostdeutschland, ein Tier der Fauna Nordwestdeutschlands*, Ber. Westpr. Bot.-Zool. Ver., 52, 91-98

Hagmeier A., 1926, *Die Arbeiten mit dem Petersenschen Bodengreifer auf der Ostseefahrt April 1925*, Ber. Deutsch. Wiss. Komm. Meeresf., Berlin, N.F., 2, 4, 92-95

Herold W., 1925a, *Die Asseln Pommerns und der Pommerschen Küstengewässer*, Abh. Ber. Pomm. Nat. Ges. Stettin, 5, 21-32

Herold W., 1925b, *Der Amphipode Orchestia cavimana Heller in Pommern*, Abh.Ber. Pomm. Nat. Ges. Stettin, 6, 109-110

Janas U., Zarzycki T., Kozik P., 2004, Palaemon elegans - *a new component of the Gulf of Gdańsk macrofauna*, Oceanologia, 46 (1), 143-146

Jażdżewski K., 1963, Sphaeroma hookeri *Leach (Crustacea, Isopoda) a new species in the fauna of the Polish Baltic Sea coast*, Bull. Soc. Sci. Lett., Łódź, XIII, 12, 1-9

Jażdżewski K.,. 1966, Jaera albifrons praehirsuta *Forsman w Zatoce Puckiej*, Przegl. Zool., 10 (3), 290-292

Jażdżewski K, 1967, *Notatki faunistyczne z Górek Wschodnich*, Przegl. Zool., 11, 282-285

Jażdżewski K., 1970, Gammarus inaequicauda *Stock in the Baltic Sea*, Crustaceana, 19 (2), 216-217

Jażdżewski K., 1971, *Ekologia pancerzowców* (*Malacostraca*) *Zatoki Puckiej*, Acta Biol. et Med., Soc. Sci. Gedan., 16, 9-77

Jażdżewski K., 1973, *Ecology of gammarids in the Bay of Puck*, Oikos, Suppl., 15, 121-126

Jażdżewski K., 1975, *Morfologia, taksonomia i występowanie w Polsce kiełży z rodzajów* Gammarus Fabr. *i* Chaetogammarus Mart. *(Crustacea, Amphipoda)*, Acta Univ. Lodz., Lodz, 185 pp.

Jażdżewski K., Konopacka A., 1993, *Survey and distribution of Crustacea Malacostraca in Poland*, Crustaceana, 65 (2), 176-191

Jażdżewski K., Konopacka A., 1995, *Pancerzowce prócz równonogów lądowych (Malacostraca excl. Oniscoidea)*, Katalog fauny Polski, 1 (13), Warszawa, 165 pp.

Jażdżewski K., Konopacka A., 2000, *Immigration history and present distribution of alien crustaceans in Polish waters,* [in:] *The biodiversity crisis and Crustacea,* Proc. 4th Intern. Crustacean Congress, von Vaupel Klein J.C., Schram F.R. (eds.), vol. 2, Brill, Leiden, Crust. Iss., 12, 55-64

Jażdżewski K., Konopacka A., Grabowski M., 2002, *Four Ponto-Caspian and one American gammarid species (Crustacea, Amphipoda) invading Polish waters*, Contr. Zool., 71 (4), 115-122

Jażdżewski K., Konopacka A., Grabowski M., 2004, *Recent drastic changes in the gammarid fauna (Crustacea, Amphipoda) of the Vistula River deltaic system in Poland caused by alien invaders*, Div. Distrib., 10, 81-87

Jęczmień W., Szaniawska A., 2000, *Changes in species composition of the genus* Gammarus Fabr. *in Puck Bay*, Oceanologia, 42 (1), 71-87

Kekkonen T., 2003, *Suomelle uusi katkarapulaji löytyi Hangon Tvärminnestä* [on line] http://www2.fimr.fi/en/itamerikanta/bsds/1124.html

Konopacka A., 2003, *Further step to the west* - Obesogammarus crassus *(G. O. Sars, 1894) (Crustacea, Amphipoda) already in Szczecin Lagoon,* Lauterbornia, 48, 67-72

Konopacka A., Jażdżewski K., 2002, Obesogammarus crassus *(G.O. Sars, 1894) - one more Ponto-Caspian gammarid species in Polish waters,* Fragm. Faun., 45, 19-26

Lavikainen T. and Laine A.O., 2004, *First record of the invasive prawn* Palaemon elegans *in the brackish northern Baltic Sea*. Mem. Soc. Faun. Flor. Fenn., 80, 14-16

Leppäkoski E., Olenin S., 2000a, *Non-native species and rates of spread: lessons from the brackish Baltic Sea,* Biol. Inv., 2, 151-163

Leppäkoski E., Olenin S., 2000b, *Xenodiversity of the European Brackish Water Seas: the North American Contribution,* [in:] *Marine Bioinvasions*, Proceedings of the First National Conference, January 24-27, 1999, Pederson J. [ed.], Massachusetts Institute of Technology, 107-119

Leppäkoski E., Gollasch S., Gruszka P., Ojaver H., Olenin S., Panov V., 2002a, *The Baltic - a sea of invaders,* Can. J. Fish. Aquat. Sci., 59, 1175-1188

Leppäkoski E., Olenin S., Gollasch S., 2002b, *The Baltic Sea - a field laboratory for invasion biology,* [in:] *Invasive Aquatic Species of Europe. Distribution, Impacts and Management,* Leppäkoski E., Gollasch S., Olenin S. [eds.], Kluwer Academic Publishers, 253-259

Ławiński L., Szudarski M., 1960, *Nowy przybysz w naszej hydrofaunie,* Przegl. Zool., 4, 121-123

Mańkowski W., 1955, *Badania planktonowe na południowym Bałtyku w roku 1951*. Pr. Morsk. Inst. Ryb., 8, 197-233

Micherdzinski W., 1959, *Kiełże rodzaju* Gammarus Fabr. *(Amphipoda) w wodach Polski*, Acta Zool. Cracov., 4, 527-637

Möbius K., 1873, A. *Die wirbellosen Thiere der Ostsee*, Jber. Comm. Wiss. Untersuch. Deutsch. Meere (für das Jahr 1871), 1, 97-144

Müller O., Zettler M.L., Gruszka P., 2001, *Verbreitung und Status von* Dikerogammarus villosus *(Sovinski, 1894) (Crustacea: Amphipoda) in der mittleren und unteren Strom-Oder und den angrenzenden Wasserstraßen*, Lauterbornia, 41, 105-112

Neuhaus E., 1933, *Studien über das Stettiner Haff und seine Nebengewässer. I. Untersuchungen über die algemeinen hydrographischen und biologischen Verhältnisse*, Z. Fischerei, 31, 427-489

Olenin S., Leppäkoski E., 1999, *Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons*, [in:] *Biological, Physical and Geochemical Features of Enclosed and semi-enclosed Marine systems,* Blomqvist E. M., Bonsdorff E., Essink K. [eds.], Hydrobiologia, 393, 233-243

Pinkster S., Scheepmaker M., Platvoet D., Broodbakker N., 1992, *Drastic changes in the amphipod fauna (Crustacea) of Dutch inland waters during the last 25 years*, Bijdr. Dierk., 61, 193-204

Poleszczuk G., Sitek S., 1998, *Water quality status of lake Wicko Małe subsequent to the start up of the biological treatment plant in Międzyzdroje,* Proceedings of Polish-German Symposium, Świnoujście, 19-20 November 1996, *The problems of management of fishery resources in the Polish and German waters of the Szczecin Lagoon and Pomeranian Bay,* 43-52

Remane A., 1958, *Ökologie des Brackwassers*, Die Binnengewässer, Stuttgart, 22, 1-216

Rodrigez G., Suarez H., 2001, *Anthropogenic dispersal of decapod crustaceans in aquatic environments*, Interciencia, 26 (7), 282-288

Różańska Z., Więcławski F., 1978, *Badania czynników środowiskowych Zalewu Wiślanego w warunkach antropopresji*, Stud. i Mat. Oceanolog., 21, Biologia Morza, 4, 9-36

Rudinskaya L. V., 2002, *Makrozoobentos v rajonie Sambijsko-Kurshskogo plato Baltijskogo morja*, Tr. Atlant. N-IIRKhO, Promyslovo-biologicheskie issledovanija Atlantniro v 2000-2001 godakh, Kaliningrad, 2, 58-69

Schellenberg A., 1925, *Ausländische vertreter unserer Krebsfauna*, Ost. Naturwart, 4, 185-190

Schellenberg A., 1942, *Krebstiere oder Crustacea*, IV: *Flohkrebse oder Amphipoda*, [in:] *Die Tierwelt Deutschlands*, 40, Jena, 252 pp.

Seligo A., 1899, *Westpreussiche Krebsthiere*, Schr. Naturf. Ges. Danzig, N. F., 10, 1, 60-63

Sexton E.W., 1913, *On a collection of* Gammarus *from the Königsberg Museum*. Schr. Phys.-Ökon. Ges. Königsberg , 54, 90-94

Stephensen K., 1929, *Amphipoda*, Tierwelt der Nord und Ostsee, 10 (f), 188 pp.

Sywula T., 1964, *A study on the taxonomy, ecology and the geographical distribution of species of genus* Idotea Fabricius (*Isopoda, Crustacea*) *in Polish Baltic.* II. *Ecological and zoogeographical part*. Bull. Soc. Amis. Sci. Poznań, D, Poznań Livr. 4, An. 1963, 173-199

Szaniawska A., Łapucki T., Normant M., 2003, *The invasive amphipod* Gammarus tigrinus *Sexton, 1939, in Puck Bay*, Oceanologia, 45 (3), 507-510

Vanhöffen E., 1911, *Beitrage zur Kenntnis der Brackwasserfauna im Frischen Haff*, SB. Ges. Naturf. Fr. Berlin, 1911, 399-405

Vanhöffen E., 1917, *Die niedere Tierwelt des Frischen Haffs*, SB. Ges. Naturf. Fr. Berlin, 1917, 113-147

Wiktor K., Skóra K., Wołowicz M., Węsławski M., 1980, *Zasoby skorupiaków przydennych w przybrzeżnych wodach Zatoki Gdańskiej*, Zeszyty Nauk. UG - Oceanografia, 7, 135-160

Wołowicz M., Kotwicki S., Geringer d'Odenberg M., 1993, 8. 15. *Wieloletnie zmiany biocenozy Zatoki Puckiej w rejonie ujścia oczyszczalni ścieków w Swarzewie*, [w:] *Zatoka Pucka*, Korzeniewski K. (ed.), Inst. Oceanogr. UG, 510-519

Zaddach E. G., 1844, *Synopseos Crustaceorum Prussicorum prodromus*, Dissertatio zoologica quam script ex auctoritate amplissimi philosophorum ordinis in Academia Albertina pro facultate docendi adipiscenda, Regimonti, 39 pp.

Zaddach E. G., 1879, *Die Meeres-Fauna an der preussischen Küste*, Schr. Phys.-Ökon. Ges. Königsberg, 19, 9-39

Żmudziński L., 1957, *Zoobentos Zalewu Wiślanego*, Pr. Morsk. Inst. Ryb., 9, 453-500

Żmudziński L., 1962, *Nowe gatunki obunogów (Amphipoda) Zatoki Gdańskiej*, Przyr. Pol. Zach., 4 (1960), 101-107