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Research Article

Dikerogammarus villosus (Sowinski, 1894) in the River Odra estuary – another invader threatening Baltic Sea coastal lagoons

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Abstract

Dikerogammarus villosus is a pontogammarid species that has rapidly extended its range in Europe starting from the Ponto-Caspian basin. In the 1990s it moved from the Hungarian to Austrian section of the River Danube, and then (after the opening of the Main-Danube canal) invaded German inland waterways. Using the canals joining the different river systems, the species has reached the River Odra. There it quickly spread both up- and downstream, reaching for the first time the Baltic Sea coastal waters (the Szczecin Lagoon) by 2002, extending the list of alien species that can be found in the Baltic. Based on samples taken in 2002-2004, *D. villosus* occurrence in the Szczecin Lagoon and adjacent coastal waters were identified. A mass occurrence of the species was found in some places already in 2002. Owing to the fact that an important (both for open sea and inland traffic) shipping route crosses the lagoon, populated by the new species, it is very probable that the area can act as a stepping stone in dispersal of *D. villosus* to other oligohaline Baltic Sea coastal waters.

Key words: *Dikerogammarus villosus,* Szczecin Lagoon, introduced species; coastal lagoons; colonization

Introduction

Baltic coastal waters harbour at present all of the already established non-indigenous species that have made their way into the Baltic; in the coastal zone, those species are abundant and dominant (Nikolayev 1974; Leppäkoski and Olenin 2001; Leppäkoski et al. 2002). Baltic estuaries and coastal lagoons seem to offer particularly favourable conditions for those species (Olenin and Leppäkoski 1999; Orlova et al. 1999; Ezhova et al. 2005; Schories and Selig 2006). Therefore, the biological diversity in those areas is greatly affected by the presence of non-indigenous species; their distribution has been extended due to human mediation and has been termed xenodiversity (Leppäkoski and Olenin 2000). The River Odra (Oder) estuary, with the Szczecin Lagoon in its central part, is one of the xenodiversity centres in the Baltic (Gruszka 1999; Leppäkoski et al. 2002). As the major harbours in the area are meeting points for seaways and inland waterways, the estuary has been invaded by both brackish and freshwater immigrant species which became permanent, and in some cases dominant, components of the biota, particularly in the macrozoobenthos (Masłowski 1992; Osadczuk and Wawrzyniak-Wydrowska 1998; Gruszka 1999; Rödiger 2004). Wide tolerance to changes in, e.g., salinity, has made it possible for some benthic species such as *Dreissena polymorpha* (Pallas, 1771), *Potamopyrgus antipodarum* (Grey, 1843), *Chelicorophium curvispinum* (G. O. Sars, 1895), and *Cordylophora caspia* (Pallas, 1771) to broaden their range and to settle in estuarine areas of central and western Europe, including Baltic coastal waters (Nikolayev 1951; Jażdżewski 1980; Eno et al. 1997; Leppäkoski and Olenin 2000). By the beginning of the 20th century, those species managed to colonise the Szczecin Lagoon (see Gruszka 1999).

Recently, however, more newly immigrated malacostracans, mostly of Ponto-Caspian origin, have spread spectacularly over Europe, often invading estuarine areas, including those in the

Baltic Sea (Olenin and Leppäkoski 1999; Nehring 2000; Jażdżewski and Konopacka 2002; Zettler 2002; Arbačiauskas 2005; Grabowski et al. 2005; Jażdżewski et al. 2005; Berezina 2007; Grabowski et al. 2007a). The spread has been facilitated by connections of river basins via man-made canals and by intentional introductions (Jażdżewski 1980; Tittizer 1996; Bij de Vaate et al. 2002). Among those newcomers, gammarid amphipods are the dominant group so far with the following 8 species reported from the Baltic coastal waters: *Chaetogammarus ischnus* (Stebbing, 1899), *C. warpachowskyi* (G.O. Sars, 1894), *Dikerogammarus haemobaphes* (Eichwald, 1841), *D. villosus* (Sowinski, 1894), *Gammarus tigrinus* Sexton, 1939, *Gmelinoides fasciatus* (Stebbing, 1899), *Obesogammarus crassus* (G.O. Sars, 1894), and *Pontogammarus robustoides* (G.O. Sars, 1894).

So far *D. villosus*, a species belonging to the Pontogammaridae (a family originating from the Ponto-Caspian region), has been recorded only from the Szczecin Lagoon. The species has rapidly extended its range in Europe: migrating upstream the Danube, it spread from its native Black Sea basin (Carauşu et al. 1955; Mordukhai-Boltovskoi 1979; Nesemann et al. 1995) to the Slovak-Hungarian and then, in the 1980s and early 1990s, to the Austrian and German sections of the Danube (Csanyi 1994; Nesemann et al. 1995). The species may co-occur with two other congeners: *D. bispinosus* Martynov, 1925 (Müller et al. 2002; Kley and Maier 2006) and *D. haemobaphes* (Jażdżewski and Konopacka 1988; Kley and Maier 2006; this paper). *D. bispinosus* was earlier regarded as a subspecies of *D. villosus* (e.g. Carauşu et al. 1955; Mordukhai-Boltovskoi et al. 1969), but now, after Barnard and Barnard (1983), is referred to as a separate species (e.g. Jażdżewski and Konopacka 1988), the status being supported by the findings of genetic studies carried out by Müller and Schramm (2001) and Müller et al. (2002). According to these authors, the species reached the upper Danube (the Austrian waters) by 1998, and is expected to extend its range into the North Sea basin, as was earlier the case with (a) *D. haemobaphes* in 1993, in two successive waves of invasion (Schleuter et al. 1994; Schöll et al. 1995; Leuchs and Schleuter 1996) and (b) *D. villosus* in 1994 (Bij de Vaate and Klink 1995; Schöll et al. 1995). The expansion of those two species was possible due to the opening of the Main-Danube canal in 1992. Having invaded the River Rhein system, *D. villosus* could have displaced *D. haemobaphes* in Germany (Van der Velde et al. 2000, Kley and Maier 2006) and moved farther to colonise Swiss, French, and Dutch inland waterways (Devin et al. 2001; Bij de Vaate et al. 2002; Josens et al. 2005; Wittenberg 2006). The species moved eastwards by using canals joining different river systems in northern Germany (Grabow et al. 1998; Zettler 1999; Rudolph 2002), and reached the River Odra/Oder in the Baltic Sea basin between 1998 and 1999 (Müller et al. 2001; Jażdżewski and Konopacka 2002; Müller and Hertel 2004). Once in the Odra, it quickly spread both up- and downstream to reach the river's estuarine system. Thus, by appearing in the brackish Szczecin Lagoon by 2002, it made its first entry into the Baltic Sea coastal waters.

As described by Gruszka et al. (2003), samples collected in 2001 and 2002 showed the species to occur, in 2002, in the downstream reaches of the Odra south of Szczecin and in the southern part of the lagoon itself. Referring to their unpublished data, Jażdżewski et al. (2005), too, mentioned finding few individuals of *D. villosus* in samples collected from the lagoon in 2004, and thus confirmed the presence of the new invader in the Odra estuary.

In this paper, we discuss the distribution of *D. villosus* in the Szczecin Lagoon and its adjacent areas (Lake Dąbie and the terminal downstream section of the Odra) to summarise the first records of the species in Baltic coastal waters.

Study area

As described by Majewski (1980) and other authors (e.g., Robakiewicz 1993; Osadczuk and Wawrzyniak-Wydrowska 1998), the Szczecin Lagoon (German: Stettiner Haff or Oderhaff; Polish: Zalew Szczeciński) is a shallow (3.8 m mean depth), 910 km^2 area that forms the core part of the River Odra (Oder) estuary (Figure 1).

The lagoon is influenced both by the riverine discharge from the Odra and smaller rivers (e.g., the Peene and the Uecker) and by inflows of Baltic waters from the Pomeranian Bay; as a result, its salinity is about 1-2 PSU (Majewski 1980; Landsberg-Uczciwek 2004). The bottom in the nearshore zone and in the Odra mouth is sandy, mud being the prevalent sediment type of the central part. Shores are covered by littoral vegetation, dominated mainly by phytocoenoses of *Phragmitetum australis* (Gams 1927) Schmale 1939 (Majewski 1980). The lagoon is geo-

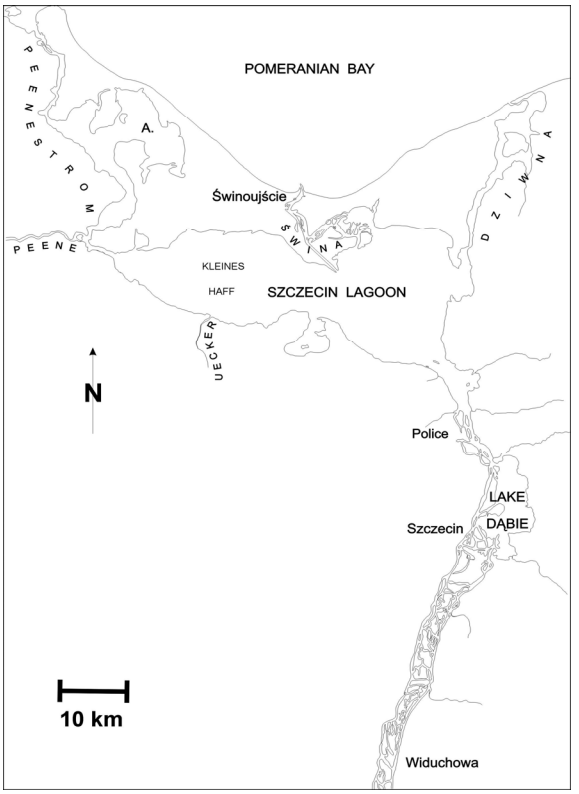

Figure 1. The Szczecin Lagoon and adjacent waters (A.: Achterwasser).

graphically divided into a smaller part to the west, belonging to Germany (Kleines Haff), and a larger, eastern part belonging to Poland (Wielki Zalew). This study was carried out in the Odra mouth (including the deltaic, freshwater Lake Dąbie) and in the Polish part of the lagoon.

Materials and methods

The sites supporting *Dikerogammarus villosus* in the Polish part of the Szczecin Lagoon and in the Odra downstream reaches up to the city of Szczecin were identified based on qualitative samples collected in 2002-2004. Figure 2 and Annex 1 show the sites sampled in particular years. The samples were obtained with various techniques used to collect benthic crustaceans, including a dredge (with 1 mm mesh), a Van Veen grab (0.7 mm sieve was used to extract the fauna), and a hand sieve (2 mm). In 2002, amphipods were also picked directly from stones retrieved from the shallow bottom and placed on a sheet of linen. Information on sampling techniques used at sites where *D. villosus* was found is given in Annex 1. The sampled animals were fixed in 10 % formalin. Amphipod collections from a total of 40 sites were checked for the presence of *D. villosus*.

Results

Annex 1 summarises the data produced by analysing samples of amphipods collected from the Odra north of Szczecin and from shallow waters in the Polish part of the Szczecin Lagoon. Three samples collected in 2002 (Figure 2) revealed the presence of *Dikerogammarus villosus* in the studied section of the river (location 1) and in the southern area of the lagoon in the vicinity of the Odra mouth (locations 2 and 3). In 2003, the species was found in the northern part of the lagoon on a shallow sandy bottom covered with stones, within *Dreissena* clumps at the foot of the cliff shore south of the Island of Wolin off Lubin (location 4); and at two other sites (locations 5 and 6) situated along the southern shores of the lagoon (Figure 2). The 2004 survey confirmed the results obtained in the preceding years (Figure 2) to show the presence of the invader both south of the lagoon, i.e., in the eastern part of Lake Dąbie (locations 10 and 11), in the Odra off Police (location 7), and in the Odra mouth area north of Police (locations 8 and 9). The species was found also to be present in the southern part of the lagoon at the Polish-German border (location 14) as well as in its northernmost part - in Lake Wicko and south of the Island of Wolin cliff in Lubin (locations 12 and 13).

The species was found to be accompanied by other alien amphipods that had earlier invaded the River Odra estuary (Annex 1). These are (in the order of the species' appearance): *Chelicorophium curvispinum*, *Gammarus tigrinus*, *Pontogammarus robustoides*, *Obesogammarus crassus*, and *D. haemobaphes*. Additionally, another alien amphipod, *Chaetogammarus ischnus*, rare in River Odra, was for the first time found in the Odra estuary, at a location invaded by *D. villosus* (Annex 1). No native gammarid amphipods were present in the samples containing *D. villosus*. *D. villosus* was not found in rivers Świna and Dziwna (sampled in 2002 and 2004), the watercourses connecting the Szczecin Lagoon with the Baltic Sea (the Pomeranian Bay).

Discussion

Having invaded the River Odra estuary at the end of the 20th century, the alien gammarid amphipods *Gammarus tigrinus*, *Pontogammarus robustoides*, and *Obesogammarus crassus* became permanent and often dominant components of the Szczecin Lagoon macrozoobenthos (Gruszka 1999; Konopacka 2003; Rödiger 2004; Jażdżewski et al. 2005; Wawrzyniak-Wydrowska and Gruszka 2005). The native *Gammarus pulex* (L., 1758), reported from the area until the 1970s (see Jażdżewski and Konopacka 1995), retreated from the Lagoon, probably - as suggested earlier by Gruszka (1999) - due to an increase in salinity recorded in the area in the 1980s (Landsberg-Uczciwek 2001; Radziejewska and Chabior 2004). However, according to Konopacka (2003), a possibility that the elimination of the native gammarids was facilitated by the presence of the two newcomers (notably *G. tigrinus* and *P. robustoides*) cannot be ruled out. Schmid (1999) related the low abundance of *G. pulex* in the Lower Odra to the presence of *G. tigrinus*. The species native to the Baltic, mainly *G. duebeni* Liljeborg, 1852 and *G. zaddachi* Sexton, 1912, can be found in areas affected by inflows of the Baltic waters in the northern part of the Szczecin Lagoon and in the straits connecting the Lagoon with the Pomeranian Bay (Gruszka 1999; Gruszka, unpublished data; Jażdżewski et al. 2005).

D. villosus and *D. haemobaphes* are two other newcomers that have appeared in the Odra estuary almost at the same time. The arrival of both species must have been quite recent, i.e., at the very beginning of the 21st century. As *D. villosus* was present in the samples collected in summer 2002, it can be inferred that this species reached the Lagoon as early as in 2001. About one year earlier, the two *Dikerogammarus* species, having successfully spread throughout Europe, were found in the downstream waters of the Odra: *D. haemobaphes* arrived from the east, while *D. villosus* came from the west (Müller et al. 2001; Bij de Vaate et al. 2002; Jażdżewski and Konopacka 2002; Gruszka et al. 2003; Grabowski et al. 2007a). Once in the downstream Odra, *D. villosus* very soon gained dominance over *D. haemobaphes* which, only a year earlier, was more abundant than its relative that had come from the west (Müller and Hertel 2004). In addition, *D. villosus* achieved dominance over other alien gammarid amphipods (*G. tigrinus* and *P. robustoides*) which had earlier spread upstream in the Odra (Müller et al. 2001; Müller and Hertel 2004). Further quantitative research should reveal whether these scenarios will be repeated in the Szczecin Lagoon.

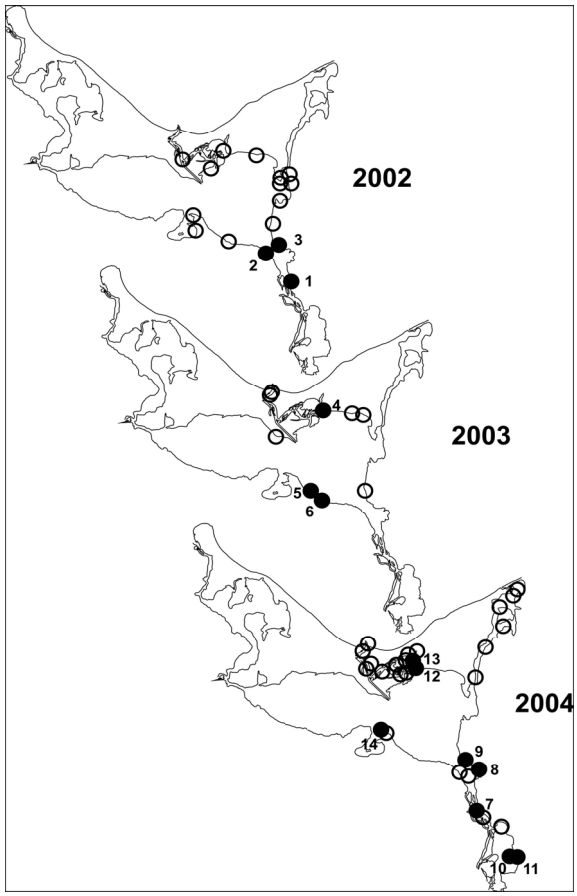

Figure 2. Location of sampling sites in the Szczecin Lagoon and adjacent waters sampled in 2002-2004. Empty frames show sites where *D. villosus* was not found, sites supporting *D. villosus* are marked with numbers corresponding to those given in Table 1: 1-3 (for 2002), 4-6 (for 2003), and 7-14 (for 2004). Details are provided in Annex 1.

The competitive potential of *D. villosus* was described in a number of studies: the larger *D. villosus* (the species can grow up to 3 cm; Nesemann et al. 1995) displaced *D. haemobaphes* at most locations in the upper Danube and in the Rhine system, thus stopping its further dispersal in southern Germany (Weinzierl et al. 1996; Haas et al. 2002; Kley and Maier 2006). It was shown to outcompete both native and alien gammarids in the Rhine and its deltaic system (Haas et al. 2002; Van der Velde et al. 2002; van Riel et al. 2007). Regarding the competition with *D. haemobaphes*, Kley and Maier (2006) suggest

that *D. villosus* acts as a more effective predator. It is also known that, owing to its predatory behaviour, *D. villosus* is able to eliminate other gammarids, both native (*Gammarus duebeni*, *G. pulex*) and alien (*G. tigrinus*), by preying on them (Dick and Platvoet 2000; Haas et al. 2002; MacNeil and Platvoet 2005; van Riel et al. 2006). Large adult *D. villosus* are capable of attacking other invertebrates, e.g. *Asellus aquaticus*, *Chelicorophium curvispinum*, and some insects. As shown by stable isotope studies, the large predatory adults occupy the trophic level identical to that of some fish (Dick et al. 2002; van Riel et al. 2006). However, *D. villosus* is an omnivore (van Riel et al. 2006) capable of feeding also on microalgae (Platvoet et al. 2006). A broad diet spectrum or omnivory is only one of a set of attributes of successful aquatic invaders, as described by Ricciardi and Rasmussen (1998) and by Van der Velde et al. (2000). Other attributes include a short life span and a short generation time, a rapid growth with an early sexual maturity, a larger size than that of most relatives, a high reproductive capacity, a high genetic variability, a wide environmental tolerance, gregariousness, and an ability to disperse rapidly in association with human activities (e.g. shipping). *D. villosus* was shown to possess a high reproductive capacity, manifested in the very high fecundity; comparatively small eggs; small juveniles compared to adult body length, which implies rapid growth; early maturity; a short generation time; and multiple reproduction (three generations per year) (Devin et al. 2004; Kley and Maier 2006; Grabowski et al. 2007b; Pöckl 2007). Comparison of these life history traits among different (both native and invasive) amphipod species made by Grabowski et al. (2007b) indicates *D. villosus* as belonging to the group of species with high competitive potential.

Devin et al. (2004) pointed to the female-biased sex-ratio as another characteristic that can favour successful establishment of the species in new regions. Nesemann et al. (1995) and Reinhold and Tittizer (1997) clearly demonstrated the role of ships in spreading the gammarid along inland waterways. Bruijs et al. (2001) and Wijnhoven et al. (2003) showed that *D. villosus* is an eurytopic species with a wide range of tolerance to temperature and salinity, a trait that renders the species capable of colonising the eutrophic Baltic Sea coastal lagoons. These lagoons are well prepared to receive a new invader that prefers hard substrates formed by clumps of the earlier Ponto-Caspian invader, *Dreissena polymorpha*, similarly to the situation in the Rhine (Haas et al. 2002). Another Baltic coastal water body, the Vistula Lagoon, will probably be soon colonised by *D. villosus* as the species has already entered the River Vistula basin: it was reported from River Bug in 2003 (Konopacka 2004). When this happens, the probability of the species' spreading into other coastal waters of the Baltic will increase significantly. This in turn will augment the risk of the species' invading the Great Lakes of North America (Ricciardi and Rasmussen 1998; Bruijs et al. 2001).

Conclusions

Dikerogammarus villosus, a potential new invader, reached the Szczecin Lagoon by 2002 and become another constituent of the amphipod assemblages in some shallow bottom locations covered by stones and/or *Dreissena polymorpha*. Monitoring of the adjacent waters should show whether *D. villosus* is in future capable of colonising the lagoon and adapting to varying salinity, typical of the Świna and the northernmost section of the Dziwna. Because the Szczecin Lagoon is intersected by a shipping route important both for ocean-going and for coastal and inland ship traffic, it is very probable that the area may play a role of a stepping stone in the species' dispersal into other oligohaline coastal waters of the Baltic Sea.

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Annex 1. Records of *Dikerogammarus villosus* in the Polish part of the Szczecin Lagoon and adjacent waters in 2002-2004 with sampling techniques indicated (D, dredg;, G, grab; H, hand siev; S, picking from stones onto a sheet of linen).

Year	No.	Geographic coordinates		Record date	Depth (m)	No. of *D. villosus* individuals collected	Other amphipod species found in the location	Habitat description (sampling technique)
		Latitude, N	Longitude, E					
2002	1.	53° 33.25'	14° 37.06'	4.07.2002	0.5	> 1000	*C. ischnus, D. haemobaphes, O. crassus, P. robustoides*	stones on sandy bottom, bulrushes and reeds (S, H)
	2.	53° 39.40'	14° 31.64'	11.07.2002	0.5	> 100	*G. tigrinus, D. haemobaphes, O. crassus, P. robustoides, C. curvispinum*	stones on sandy bottom, roots of trees (S)
	3.	53° 40.30'	14° 32.05'	3.10.2002	1	1	*P. robustoides, G. tigrinus, O. crassus*	sandy bottom (D)
2003	4.	53° 51.78'	14° 26,49'	2.07.2003	0.7	25	*G. tigrinus, O. crassus, P. robustoides, C. curvispinum*	sandy bottom with pebbles/stones, clumps of *Dreissena polymorpha* (G)
	5.	53° 42.25'	14° 21.45'	2.10.2003	0.5	10	*G. tigrinus, O. crassus, P. robustoides, C. curvispinum*	reeds (G)
	6.	53° 40.67'	14° 25.11'	2.10.2003	0.5	13	*G. tigrinus, O. crassus, P. robustoides*	reeds (G)
2004	7.	53° 33.40'	14° 35.75'	27.03.2004	2.5	3	*G. tigrinus, D. haemobaphes*	sandy bottom with pebbles/stones, clumps of *Dreissena polymorpha* (D)
	8.	53° 38.95'	14° 36.44'	2.08.2004	1.5	8	*G. tigrinus, D. haemobaphes*	bulrushes, sticking, organic sediment, covered with shells and sand (G)
	9.	53° 39.95'	14° 34.50'	6.08.2004	0.5	14	*D. haemobaphes, P. robustoides, C. curvispinum*	clump of *D. polymorpha* on the shell of *Anodonta* from sandy bottom (H)
	10.	53° 27.73'	14° 42.33'	2.09.2004	2	6	*D. haemobaphes*	clumps of *D. polymorpha*, sponges (G)
	11.	53° 27.73'	14° 42.41'	2.09.2004	1.5	16	*D. haemobaphes, O. crassus, P. robustoides*	gravel, densely packed sand, peebles, *D. polymorpha* (G)
	12.	53° 53.37'	14° 25.35'	2.7.2004	0.5	9	*G. tigrinus*	sandy-gravelly bottom with stones (G)
	13.	53° 52.26'	14° 25.37'	25.10.2004	1.5	1	*G. tigrinus, O. crassus*	sand, bulrushes (G)
	14.	53° 44.39'	14° 17.59'	8.7.2004	0.7	3	*G. tigrinus*	dense reed belt (G)