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Spiny-cheek crayfish *Orconectes limosus* (Rafinesque, 1817) on its way to the open coastal waters of the Baltic Sea

by

Anna Szaniawska,
Aldona Dobrzycka-Krahel*,
Joanna Jaszczołt

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Department of Experimental Ecology of Marine Organisms, Institute of Oceanography, Faculty of Oceanography and Geography, University of Gdańsk, Al. M. Piłsudskiego 46, 81-378 Gdynia, Poland

* Corresponding author: *oceadk@ug.edu.pl*

Abstract

The aim of this work was to assess the adaptive capabilities of the spiny-cheek crayfish *Orconectes limosus* (Rafinesque, 1817) in the open coastal waters of the Baltic Sea. The results could help to predict the likely further expansion of this species and its colonization of brackish waters. The following aspects were discussed in the paper: the occurrence of the species in the Polish coastal zone of the Baltic Sea, the plasticity demonstrated in the body size of individual crayfishes, food preferences, hemolymph osmolality and reproduction in waters of different salinities, which enable the species to colonize brackish waters. In the Vistula Lagoon (salinity 2-3 PSU), where the population of *O. limosus* is stable, the length of individuals ranged from 77 to 118 mm. These crayfish mostly fed on fodder; the second and the third food preferences were crayfish abdominal muscle and green algae. *O. limosus* is a hyper-regulator in freshwaters and at low salinities (up to 13 PSU), and a hyporegulator at higher salinities (14, 21, 28, 35 PSU). Laboratory studies showed that the embryonic development of *O. limosus* at salinities of 3 and 7 PSU was normal and a high level of reproductive success was achieved. Salinity of 3 PSU is more favorable for the development of juveniles than 7 PSU. It seems to be just a matter of time before this crayfish starts to form populations in the brackish, coastal waters of the Baltic Sea.

Key words: *Orconectes limosus*, distribution, food preferences, osmoregulation, reproduction

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Introduction

The Baltic Sea, inhabited by a small number of species and subject to strong human pressure, is susceptible to colonization by new species. As each new species can affect the functioning of marine communities, the importance of each newcomer has to be analyzed individually (Arbačiauskas 2005). It is often the case that interactions between alien and native species are not different from relationships between native species in their natural communities (Reise et al. 2006). Species that colonized the Baltic in the past have become an integral part of this ecosystem.

The spiny-cheek crayfish *Orconectes limosus* (Rafinesque, 1817) is native to eastern North America (Burič et al. 2006) and is the first crustacean introduced into Polish waters (Jażdżewski 1970; Jażdżewski & Konopacka 1993). In 1890, Max von dem Borne introduced around 100 individuals of this species to ponds in Barnówko near Dębno Lubuskie (West Pomerania Province, Poland) (Lehman & Quiel 1962; Leńkowa 1962). This non-native crayfish has spread very rapidly and now occurs in inland waters in more than 20 European countries (Lodge et al. 2000). The number of known populations of this species in invaded regions has increased and its further expansion is still being observed (Kouba et al. 2014). In 1900-1939, about 20 new localities of this crayfish were found in the area of present-day northern Poland, and between 1950 and 1990, the species was recorded in several other regions. By 2010, the species occurred in several hundred localities in lakes and rivers of northern Poland (Śmietana 2013). After 100 years, it was found that the spiny-cheek crayfish was primarily responsible for the disappearance of native crayfish (*Astacus astacus* (Linnaeus, 1758) and *Pontastacus leptodactylus* (Eschscholtz, 1823)) (Mastyński 1999). The pet trade of freshwater crayfish including *O. limosus* (e.g. in Germany and the Czech Republic) has grown rapidly in recent decades and become an important pathway for the introduction of new non-native species to Europe (Chucholl 2013; Patoka et al. 2014; 2015). Alien species are the subject of many studies (Carlton 2009; Pyšek & Richardson 2010), but understanding of biological invasions still requires further research.

In the Baltic Sea, the spiny-cheek crayfish has been reported from the Curonian Lagoon (Burba 2008). The species was present in the Polish coastal waters already in the 1950s (Wiktor 1955).

The species occurs in other Baltic countries such as Latvia (Briede 2011), Germany (Groβ et al. 2008; Martin et al. 2008), the Kaliningrad Oblast, i.e. the part of Russia adjacent to Poland (Burba 2010).

Salinity is a crucial limiting factor for many organisms (Remane 1971; Bonsdorff & Person 1999; Cognetti & Maltagliati 2000). The low salinity of the Baltic waters supports the "natural minimum of species". With such a small number of species, many ecological niches and habitats are open to newly arrived species (Nehring 2001). In the Baltic, about 70% of alien species occur in the 0-10 PSU salinity zone (Paavola et al. 2005). For many freshwater invertebrates, the salinity barrier separating fresh waters from sea waters is insurmountable. It is important to determine why the spiny-cheek crayfish is present in the Polish coastal zone and to examine whether and how this crayfish can adapt to waters of low salinity. Osmoregulation is a crucial mechanism for overcoming this barrier. At salinity of 8 PSU, the ion ratios characteristic of sea waters are constant, whereas the ion ratios in fresh waters are very variable. While the body fluids of most marine invertebrates have the same osmotic pressure as sea water, their composition and the concentrations of their constituents are different. The body fluids of freshwater invertebrates have a higher osmotic concentration than the surrounding water (hyperosmotic animals) (Lockwood 1977). Osmoregulation involves the movement of ions against the concentration gradient and therefore requires an energy input. Presumably, the energy cost incurred by freshwater organisms when adapting to brackish water conditions is lower than in fresh water. Hence, the osmotic concentration of the body fluids in *O. limosus* in brackish waters is expected to be very similar to the osmotic concentration of the external environment. Moreover, having moved from fresh to sea waters, the spiny-cheek crayfish would have to reproduce and the new generation would have to develop in the new environment to form a population.

Despite its negative influence on the environment, the spiny-cheek crayfish is an attractive pray for many fish, aquatic invertebrates, birds and mammals. It is thus a significant link in the food web (Stańczykowska 1986). Being an omnivore, this crayfish also plays a crucial role in the structure of aquatic ecosystems (Śmietana 2013). Knowing the energy values of male and female spiny-cheek crayfish, one can assess its role in the food web of a given water body and its suitability for consumption on the one hand, and determine how it utilizes the energy contained in its food on the other (Normant et al. 2002), hence when assessing the importance of the spiny-cheek crayfish, one should not take into consideration only its adverse effect on the environment, e.g. on native crayfish species. The introduction of this North American crayfish to Polish waters and breeding it in open water bodies led to unforeseen ecological consequences.

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As the species is able to overcome ecological barriers, it continuously extends its distribution range. It is important to define parameters enabling the species to colonize the brackish waters in the coastal zone of the Baltic Sea. Consequently, the objectives of this work were as follows: to confirm the occurrence of *O. limosus* in the Polish coastal zone of the Baltic, to show the measured size of individual crayfishes and to assess food preferences of *O. limosus* under laboratory conditions, to determine the osmoregulatory ability of the species and to examine the possibilities of reproduction and the development of young spiny-cheek crayfish in brackish waters.

Further research on adaptive capabilities of the species in new conditions, especially in waters of low salinity, are required in the context of the colonization of new water bodies by *O. limosus*, including lakes and watercourses near the coast, as well as coastal brackish waters. Can the freshwater spiny-cheek crayfish colonize low-salinity sea waters, reproduce in these conditions and create a population there?

The presence of freshwater species in the coastal zones of the seas and saline waters of different water reservoirs is described in the literature. This paper shows data about abilities of freshwater crayfish to survive and thrive in saline waters.

Distribution

The first information on the occurrence of *O. limosus* in the Polish brackish lagoons, coastal lakes (S = 1-2 PSU) and river mouths comes from the 1930s (Wiktor 1955; Gajewski & Terlecki 1956; Żmudziński 1961). Jażdżewski & Konopacka (1993) also reported the spiny-cheek crayfish from the coastal zone of the Baltic Sea, although the authors did not provide the exact locality. Gruszka (1999) reported *O. limosus* from the Oder Estuary. The next data come from April 2002, when dead specimens were found in the Baltic coastal waters between Karwia and Jastrzębia Góra (S = 8-10 PSU) (author's own observations) and in the Baltic coastal zone near Władysławowo (S = 8 PSU) (K. Skóra, pers. comm.). Further information comes from September 2006, when this crayfish was recorded in the estuary of the Czarna Woda River into the Baltic (S = 8-10 PSU). In August and September 2010, the crayfish was found at the Vistula estuary (S = 2-3 PSU), and in the same year – in the area of Góra Szwedów (S = 8-9 PSU). Śmietana (2013) recorded the presence of spiny-cheek crayfish near Darłowo, at the estuary of the Wieprza River (S = 10 PSU) and at Ustka (S = 10 PSU). The species was reported from the Szczecin Lagoon (S = 4 PSU), Pomeranian Bay (S = 7 PSU) and the Gulf of Gdańsk (S = 7.5 PSU) (Jaszczołt

Figure 1

Records of spiny-cheek crayfish in the Polish coastal zone of the Baltic Sea in 2002-2014 based on the literature data and personal communications (for details see text)

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& Szaniawska 2011). In 2011, specimens were found on the beach at Świnoujście (www.iswinoujscie.pl) and in 2014, on the beach at Ustronie Morskie (K. Skóra pers. comm.) (Fig. 1). At all these localities in the Baltic coastal waters, only single specimens of spiny-cheek crayfish were found; some of them were encrusted with *Amphibalanus improvisus* (Darwin, 1854) – a marine crustacean. This indicates that the crayfish must have spent some considerable time in sea water.

Adult males and females, berried females and juveniles have been found in the Vistula Lagoon, which proves that the species has an established population there.

The Baltic Sea is inhabited by a small number of decapod crustaceans. At the same time, it is exposed to colonization by alien species due to strong human impact (Reise et al. 2006). When conquering new water areas, a distance from the shoreline is crucial (Gruszka 1999; Paavola et al. 2005; Zaiko et al. 2007; Leppäkoski et al. 2009; Preisler et al. 2009). Non-native species have mainly colonized coastal and estuarine zones in the Baltic (Olenin & Leppäkoski 1999; Zaiko et al. 2010), including the Curonian and Vistula Lagoons, the Neva and Oder estuaries, and the Bay of Mecklenburg. In addition to providing suitable ecological niches, these regions are channels along which non-native species can reach the open sea, thereby enabling them to expand their range to as yet uncolonized areas of the coastal zone (Leppäkoski & Olenin 2000). The ratio of alien to native species is 1:40 in oceanic waters, 1:20 in open-sea waters and 1:5 in estuaries and lagoons (Reise et al. 1999; Wolff 2000; Nehring 2006).

In 1890, the spiny-cheek crayfish was introduced for the first time in Europe, to ponds near Barnówko (Lehman & Quiel 1962) (then in Germany, now in Poland). Sometime later, the species escaped into the Oder River. Following the second introduction in the early 20th century, the crayfish was found in the Vistula (Kulmatycki 1935). Afterward, the species expanded its range at a rate of about 10 km per year (Gajewski & Terlecki 1956). In 1900, there were only four localities of this crayfish in Pomerania, while by 1939 the number increased to 23. The species spread rapidly in the second half of the 20th century: in the 1970s, there were 102 localities in Pomerania and by the beginning of the 21st century – more than 800 (Śmietana 2013).

The spiny-cheek crayfish inhabits almost all types of freshwater bodies in Central Europe, and its range covers more than 20 countries (Pöckl et al. 2006; Holdich et al. 2009; Kouba et al. 2014) and is constantly expanding (Pârvulescu et al. 2009; Burba 2010). By the 1960s, the species had already colonized fresh waters in three-quarters of the area of Poland (Leńkowa 1962). At the beginning of the 21st century, only a small area in the south-east of the country remained uncolonized (Krzywosz 2004). It occurs both in large rivers (the Vistula, the Oder) and in fire-fighting reservoirs in large cities (Strużyński & Śmietana 1998). It has displaced native crayfish *A. astacus* and *P. leptodactylus* from all water bodies in which it occurs (Mastyński & Andrzejewski 2005). In the early 21st century, its numbers have decreased in many water bodies throughout Poland (Krzywosz 2004; Krzywosz et al. 2014). It is believed that *O. limosus* may have been ousted by another American species, the signal crayfish *Pacifastacus leniusculus* (Dana, 1852) (Krzywosz 2004; Krzywosz et al. 2014; Heese 2013). Since 2002, its range has begun to include the coastal waters of the Baltic Sea. It is more common in estuaries and lagoons where water salinity is > 2 PSU. It prefers warm, calm waters (Bohl 1999). The coastal zone of the Baltic Sea, which covers permanently or temporarily saline waters in rivers, canals or lakes (Cieśliński 2010), provides conditions necessary for the survival of the species. These are high-risk areas, referred to as hot spots (Underwood et al. 2000).

Plasticity of *O. limosus*

The successful expansion of the spiny-cheek crayfish can be attributed to its considerable physiological plasticity and the fact that the species is eurytopic. The species shows many characteristics facilitating its fast dispersal and ability to establish new populations (Krzywosz 2004).

Size of individuals

The overall length of the animals (TL) was measured over the maximally extended abdomen from the tip of the rostrum to the rear edge of the telson (Kossakowski 1962; Ďuriš et al. 2016; Buřič et al. 2010). The spiny-cheek crayfish occurring in brackish and fresh waters differ in size. The maximum size (121 mm in length) was recorded by Chybowski (2000). The crayfish characterized by large maximum total lengths (118 mm in length) was recorded in the Vistula Lagoon (Skrzecz & Szaniawska 2005) where the salinity is 2-3 PSU. Crayfish occurring in lakes of Warmia had maximum lengths of 110 mm (Kossakowski 1966), those from lakes in the East Suwałki Lake District had maximum lengths of 107 mm, and those from the Masurian lakes were 95 mm long at most (Krzywosz et al. 2014). The maximum total length of the crayfish caught in lakes of Western Pomerania was 105 mm (Śmietana 2013) (Table 1). However, the differences in the maximum size do not always imply the differences

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Table 1

Maximum total lengths of spiny-cheek crayfish in Polish and other waters

Locality	Maximum length (mm)	Author
Vistula Lagoon (Poland)	118.0	Author's own study
Lakes in Pomerania (Poland)	109.5	Śmietana 2013
Lakes in Western Pomerania (Poland)	100.2	Śmietana 2008
Lakes in Warmia (Poland)	110.0	Kossakowski 1966
Lake Pobłędzie (northern Poland)	107.0	Krzywosz et al. 2006
Poland	121	Chybowski 2000
lentic waters (Czech Republic)	116.5	Ďuriš et al. 2006
Central lakes (Germany)	107.0	Lieder 1959, after Śmietana 2013
North-eastern lakes (Germany)	110.0	Pieplow 1938
Delaware River (USA)	110.0	Holdich & Black 2007
Lakes in New England (USA)	109.0	Momot 1984

in the mean size. We do not have statistically confirmed differences between the maximum size of individuals from various water bodies. It is not possible to compare the impact of fresh and marine waters on the *O. limosus* body condition based on the maximum TL.

O. limosus is one of the smallest crayfish in Europe. In European waters, its body is no longer than 90-100 mm (Hamr 2002), although Leńkowa (1962) reported the maximum length of 120 mm. According to Krzywosz et al. (2014), the mean length of spiny-cheek crayfish caught in Polish lakes during the last 10 years (up to 2014) was 93 mm. Before that period, the value was 7 mm smaller and amounted to 86 mm (Krzywosz et al. 2014). In the Vistula Lagoon, males and females have roughly the same body dimensions and the range of particular parameters, however, females have broader abdomens (23.6 ± 2 mm) than males (20.3 ± 2 mm) (Skrzecz & Szaniawska 2005). In the Vistula Lagoon, the largest individuals reach the length of 118 mm at salinity 2-3 PSU. The Vistula Lagoon and the northern part of the Curonian Lagoon are brackish water bodies, in which this species has a stable population (Burba 2008; Kruk 2011). The occurrence of larger crayfish in the Vistula Lagoon and in the Curonian Lagoon may be due to water salinity that reduces the osmotic concentration gradient between the animal's body fluids and its living environment. Another reason why these crayfish achieve larger sizes in newly colonized waters could be the lack of natural enemies. Krzywosz et al. (2014) believe that the larger sizes of crayfish are due to the superior food resources available. It is often believed that large individuals are characteristic of small populations living in recently colonized water bodies. This may well be the case in the parts of the Vistula Lagoon covered by our study.

The claws play a crucial role in the aggressive and defensive behavior of crayfish, in intra- and interspecific competitive mechanisms, in confrontations with individuals of the same or another species (Gherardi & Cioni 2004). The spiny-cheek crayfish has smaller claws than native crayfish or the signal crayfish. Individuals with larger claws may have greater chances of survival in confrontations with animals less generously endowed (Martin & Moore 2008).

Food preferences

In the experiments (Staszak & Szaniawska 2006), crayfish were acclimated for 7 days to laboratory conditions (T = 12°C, fresh water, S = 100% aeration, not fed). Each of the 21 animals was kept separately in a tank (21 × 20 × 20 cm). The water in all tanks was aerated. The crayfish were supplied with shelters made of PVC. Each crayfish was supplied with one of the following brackish waters' food types: animal-based (cod or crayfish abdominal muscle), plant-based (green algae, *Enteromorpha* spp.) or granulate fodder. Prior to feeding, the wet weight of the animals was measured. In order to calculate the amount of food consumed, all uneaten food was removed from the experimental units after 24 h, weighed and dried at T = 55°C to obtain the dry weight. Food consumption rates (C = J ind.$^{-1}$ h^{-1} d.w.) were calculated using the formula given by Klekowski & Fischer (1993). The favorite food of spiny-cheek crayfish was fodder (mean consumption rate was C2 = 308.27 J ind.$^{-1}$ h^{-1} d.w., T = 12°C). Crayfish abdominal muscle was the second most favored food (C2 = 228.70 J ind.$^{-1}$ h^{-1} d.w.), and plant food was third (C2 = 43.77 J ind.$^{-1}$ h^{-1} d.w.). The least preferred food was cod (C2 = 15.02 J ind.$^{-1}$ h^{-1} d.w.) (Fig. 2). Within the 80-112 mm length range of individuals, no significant differences were found between the crayfish size and the food consumption rate (Staszak & Szaniawska 2006), using statistical analysis: Mann-Whitney U test for $p < 0.05$.

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Food resources are an important factor determining whether new areas can be colonized and how widespread could be a species in a given water body. Like other crayfish species, *O. limosus* is an omnivore that feeds on a wide range of foods, including macrophytes, algae, detritus and macroinvertebrates (Vojkovska et al. 2014). Being omnivorous throughout their life cycle, crayfish may prefer different types of food at different stages of their life, with juveniles feeding mainly on animal plankton and later on benthic invertebrates, while adults consuming mostly plants and detritus (Goddard 1988; Usio 2000). In large densities, the crayfish can resort to cannibalism (Goddard 1988). Under laboratory conditions, its preferred food was fodder (REP 497 Export, Aller Aqua), which is rich in proteins (53%) and lipids (14%), and has a high energy value (20.8 J mg^{-1} d.w.) (Staszak & Szaniawska 2006). Fodder is used to feed many species that are bred for consumption by humans, and its composition is selected in such a way as to encourage animals to eat it and to ensure the largest possible biomass growth. Another preferred food was crayfish abdominal muscle, because it has a similar biochemical composition as the crayfish and is readily assimilable. It is rich in lipids (13% of d.w.) (Goddard 1988) and protein (80% of d.w.) (Holdich & Lowery 1988). The algae offered as food have the lowest energy value (10.1 J mg^{-1} d.w.) (Haroon & Szaniawska 1995), and their consumption was relatively low. The size and dimensions of the offered food may also affect the food preferences. For example, the dietary preferences of *Procambarus mexicanus* (Erichson, 1846) were largely dependent on the ability to handle plant material rather than the plant chemistry itself (Hernández-Muňoz et al. 1999). Food preferences also depend on the age of individuals, season and time of the day (Whitledge & Rabeni 1996). Temperature is crucial for feeding of poikilothermic animals, although it was found that at 12 and 18°C there were only small, statistically insignificant differences in the amount of food ingested at the higher water temperature (Staszak & Szaniawska 2006).

The fact that fodder was the preferred food in the laboratory indicates that artificial food products are most suitable for breeding these animals. Even though in natural conditions cannibalism is not frequent, the abdominal muscle of *O. limosus* was often consumed under breeding conditions (our own observations).

Osmoregulation

Osmotic concentrations were determined microcryoscopically, based on the method used in many studies of osmoregulation (Dobrzycka & Szaniawska 1995; Dobrzycka-Krahel & Szaniawska 2005; 2007). A stereoscopic microscope (NIKON SMZ800) with a polarizing (C-POL) accessory was used to observe the melting of hemolymph crystals. In the experiments (Michałowska et al. 2002), the osmolality of hemolymph increased with salinity. There was a significant increase in the osmolality of hemolymph, from 333.5 ± 82.2 mOsm kg^{-1} at 0 PSU to 879.5 ± 32.6 mOsm kg^{-1} at 35 PSU. *O. limosus* is a hyper-regulator at 0 and 7 PSU and a hyporegulator at higher salinities > 13 PSU. The transition from hyper- to hyporegulation was found to occur at 385.0 mOsm kg^{-1} (ca 13 PSU). The osmotic concentration was 333.53 ± 82.20 mOsm kg^{-1} at 0 PSU, 340.08 ± 16.39 mOsm kg^{-1} at 7 PSU, 409.33 ± 50.49 mOsm kg^{-1} at 14 PSU, 503.86 ± 6.49 mOsm kg^{-1} at 21 PSU, 601.389 ± 42.783 mOsm kg^{-1} at 28 PSU and 879.5 ± 32.57 mOsm kg^{-1} at 35 PSU (Fig. 3) (Michałowska et al. 2002).

Crayfish can adapt to a wide range of environmental factors (McMahon 1986). At the end of the Mesozoic era, they became independent of the marine environment (Hobbs 1988), becoming adapted to life in fresh waters, although some species preserved the ability to survive in brackish waters (Mantel & Farmer

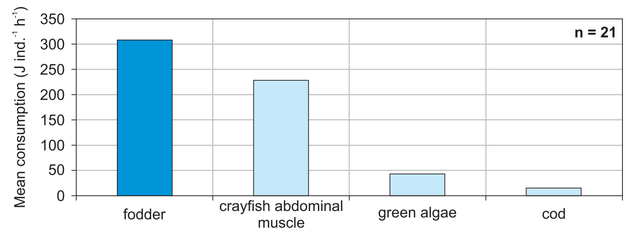

Figure 2

Food preferences of *Orconectes limosus* in experimental conditions based on four selected food sources (based on Staszak & Szaniawska 2006)

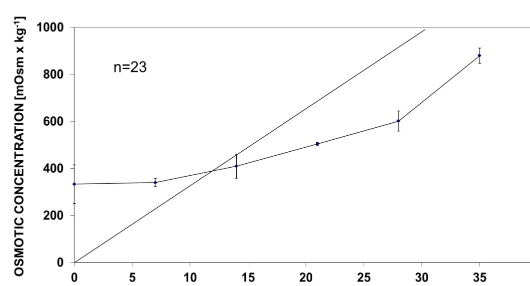

Figure 3

Osmotic concentrations of *Orconectes limosus* at different salinities (based on Michałowska et al. 2002)

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1983). Andrews (1967) studied seasonal changes in the hemolymph composition of *O. limosus* from fresh waters with respect to temperature, sex and individual body size. Other studies were performed to investigate the effect of water salinity on osmotic body fluid concentrations in other crayfish species: *Austropotamobius pallipes* (Lereboullet, 1858), *P. leptodactylus*, *P. leniusculus* (Holdich et al. 1997, Kerley & Pritchard 1967, Wheatley & McMahon 1982). They showed that all these species are capable of osmoregulation over a wide range of salinity, just as *O. limosus*. The present study has shown that both fresh and saline waters are not osmotic barriers for *O. limosus*.

Reproduction and growth

In the experiments (Jaszczołt & Szaniawska 2011), the animals were kept in aquaria (0.34 m^2, V = 117 dm^3) with 10 cm long PCV tubes as shelters. The salinity was 3 ± 0.5 PSU and 7 ± 0.5 PSU (T = ca 16°C, Sat > 80%, measured with a WTW Ecoline LF 170 TetraCon 700 probe) and pH was 6.7-8.2 (measured with a WTW ph 197 Sen Tix 97 T probe). The water was filtered, aerated, and illuminated with a low intensity of light until the crayfish larvae hatched, after which a 12/12h photoperiod was applied. The animals were acclimated to the experimental salinity in steps of 1 PSU and 1.5 PSU every other day, starting from an initial salinity of 2 PSU. A recirculating system was used. Natural water with salinity of 7 PSU was pumped into aquaria directly from Puck Bay, while water with salinity of 3 PSU was prepared by diluting the 7 PSU water with tap water. Ten females with pleopodal eggs were kept at each salinity. The young crayfish were separated from their mothers after gaining independence and were individually weighed to the nearest mg one month after hatching. To assess the crayfish growth rate, 50 juveniles (10 groups of specimens from 5 females) from 3 PSU water and the same number from 7 PSU water were used. The growth rate was assessed as the mean increase in carapace length at molt. The young crayfish were weighed to the nearest 1 mg, and their total length (TL) and carapace length (CL) were measured to the nearest 0.5 mm on the basis of photographs, using the Corel Draw 11 program. The increase in carapace length of juvenile specimens was classified into four groups: < 1.0, < 1.5-2.0 >, < 2.5-3.0 > and < 3.5-4.0 > mm. The growth examination lasted 3 months. The young crayfish were fed twice a day with artificial fodder.

No loss or death of eggs were recorded in ovigerous females taken from the environment and kept at salinities of 3 and 7 PSU. Neither of the two salinities influenced the development of eggs or juvenile stages. Berried females survived the exposure to salinities of 3 and 7 PSU, while incubating their eggs and their mortality occurred only after molting. Eggs hatched into stage 1 juvenile, and all molted into stage 2 juvenile. The total number of crayfish hatchlings from 10 females was 1100 at 3 PSU and 827 at 7 PSU. The total mortality of stage 2 juvenile was 1.6% at 3 PSU and 2.5% at 7 PSU. The reduction in the number of juveniles was approximately 50% five weeks after hatching at both salinities.

One month after hatching, the young crayfish varied in length from 9.0 to 13.5 mm at 3 PSU and from 10.0 to 15.0 mm at 7 PSU. The carapace length ranged from 4.5 to 7.0 mm at 3 PSU and from 5.0 to 7.5 mm at 7 PSU. The wet weight was 18-59 mg at 3 PSU and 20-67 mg at 7 PSU. The growth (CL) was 0.5 mm greater in the crayfish at 7 PSU than at 3 PSU (Fig. 4).

During the experiment, 77 molts (among 50 tested crayfish) occurred in 3 PSU and 44 molts (among other 50 tested crayfish) in 7 PSU. Differences in the growth between 7 and 3 PSU were statistically significant ($p < 0.05$), tested with the Mann-Whitney U test.

Increases in carapace length in the class of length < 1.0 mm represented the highest percentage, 58.4% at 3 PSU and 34.1% at 7 PSU, respectively. It was similar in the class < 1.5-2.0 > mm in the same salinities – ca 32%. At salinity of 7 PSU in the classes < 2.5-3.0 > and < 3.5-4.0 > mm, it was 25% and 6.8%, respectively, and was greater than at 3 PSU (9.1% and 1.3%, respectively) (Fig. 5).

The results showed that the embryonic development, hatching and the development of juveniles were normal at both salinities (3 and 7 PSU), and the body size of individuals was greater at 7 than at 3 PSU.

The spiny-cheek crayfish is capable of reproducing at the age of 1 + and the body length of 5-6 cm (Crome 1955). Mating usually takes place in autumn (Van den Brink et al. 1988; Holdich et al. 2006). Sometimes it takes place in spring (Strużyński 2000). Females do not extrude their eggs after the autumn mating season, waiting for the spring season. After the mating season, crayfish are hidden during daytime and generally less active (Buřič et al. 2009). The female carries from 250 to 400 eggs, and about 100 of them produce hatchlings (Leńkowa 1962; Jaszczołt 2013). According to Holdich et al. (2006), *O. limosus* can produce over 400 eggs. It is positively correlated with the body size and ranges between 31 and 555 eggs (Pieplow 1938; Kozák et al. 2006). Linear relationships between the female size and ovarian fecundity, pleopodal fecundity and production of juveniles at the 3rd fecundity stage is observed (Kozák 2009). The production of eggs by invasive females significantly increases at the active

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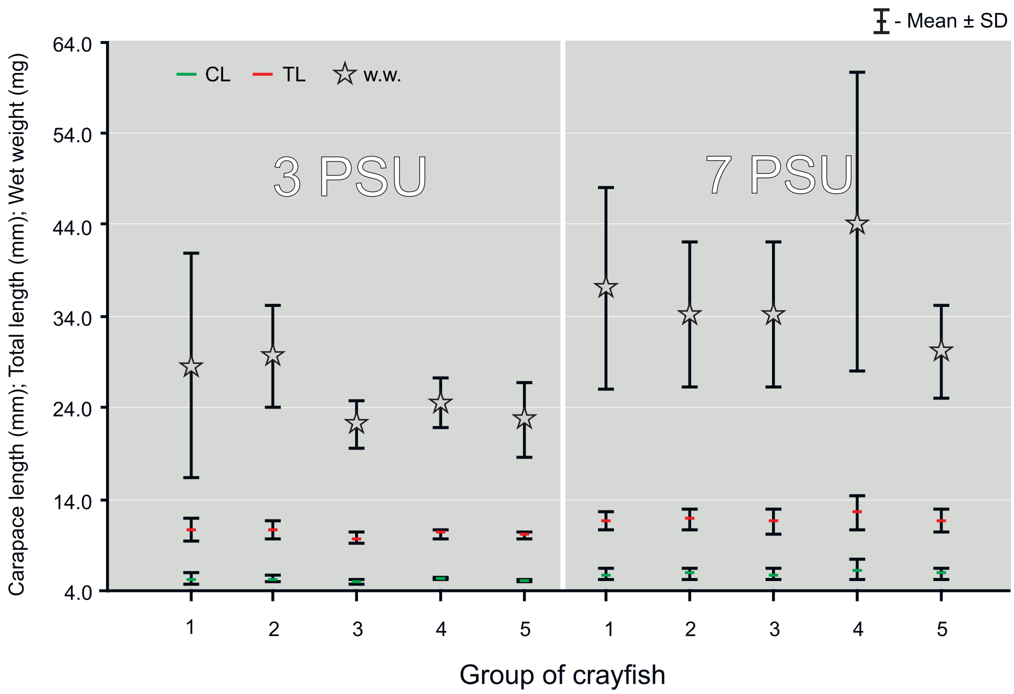

Figure 4

Carapace length (CL), total body length (TL) and wet weight (w.w.) for five groups of juvenile (one-month old) crayfish from 3 PSU and 7 PSU (based on Jaszczołt & Szaniawska 2011)

front of invasion. Invasive crayfish that carries the deadly crayfish plaque can reduce the population of indigenous crayfish. Invasive females can use the available resources to enhance their fecundity. *O. limosus* females closer to the invasion front produce significantly more eggs that are smaller in size (Pârvulescu et al. 2015). Laboratory studies performed in waters with salinities of 3 and 7 PSU indicate that the reproductive success of *O. limosus* at these salinities can be much more than 100 young (Jaszczołt & Szaniawska 2011). Unlike fresh water, saline

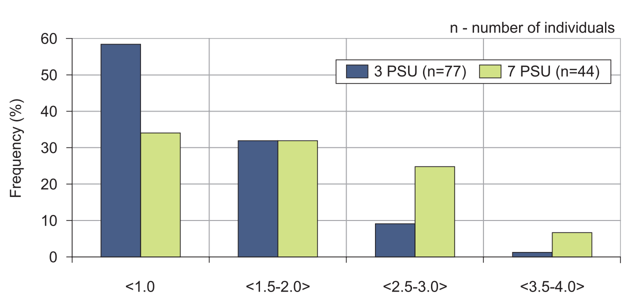

Figure 5

Frequencies of increase in carapace length of juvenile crayfish at salinities of 3 PSU and 7 PSU in the different length classes (based on Jaszczołt & Szaniawska 2011)

water has an antiseptic effect, which can contribute to the survival of a greater number of offspring in brackish waters. In the latter, the reproductive success is often reduced by various kinds of fungi that attack the eggs developing beneath the female's abdomen. It is not unlikely that crayfish in brackish waters are less exposed to pathogens, but it is also possible that others factors will appear, which can affect the overall condition of adults and/or developing eggs. The egg incubation period in *O. limosus* is 5-6 weeks (Krzywosz et al. 2014). According to Kozák et al. (2006), incubation of eggs lasts only 45 days, which gives a substantial advantage over the European native crayfish, whose incubation period is much longer (ca 8 months), as it sustains fewer losses during the embryonic development (Skurdal & Taugbøl 2002). During the mating season, the movement did not correlate with the water temperature and crayfish were active during daylight hours. The effect of water temperature on the movement was observed during the non-reproductive period (Buřič et al. 2009).

O. limosus success is due to its ability to reproduce by facultative parthenogenesis, in two mating seasons (autumn and spring). Females successfully reproduce using a long-term sperm storage. *O. limosus* spreads owing to its reproductive plasticity (Buřič et al. 2013).

Water salinity is one of the more important factors

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affecting the occurrence of aquatic species in newly colonized waters. Adults of the crustaceans *Eriocheir sinensis* H. Milne Edwards, 1853 and *Carcinus maenas* (Linnaeus, 1758) occur in the coastal waters of the Baltic Sea, but the low salinity (< 20 PSU) prevents them from reproducing (Anger 1990; Anger et al. 1998; Panning 1952).

The salinities of 3 and 7 PSU are often quoted as being critical for many aquatic species. Kinne (1971) states that eggs, embryos and reproducing adults are particularly sensitive to salinities of 5-8 PSU. The fact that 100% of the reproducing females survived and that no eggs were deformed or died at 3 and 7 PSU indicates that *O. limosus* is capable of adapting to low salinities. At these salinities, early juvenile stages of the spiny-cheek crayfish molted into the next juvenile form. Holdich et al. (1997) reproduced *P. leptodactylus* and *P. leniusculus* at 7 PSU. The first juvenile stage developed into the second stage, but this survived for only two weeks. At higher salinities (14 and 21 PSU), the majority of eggs lost their color and their development ceased. The crayfish that did hatch died shortly thereafter. These results show that compared to the native European crayfish and to the North American signal crayfish, *O. limosus* is able to better adapt to life in brackish waters, already in the early developmental stage.

This study has demonstrated that at salinities of 3 and 7 PSU, ovigerous females can survive, embryos develop normally, the species has better reproductive success than that described in the literature, and juveniles undergo successive molts in a regular way. These results provide a broad insight into considerable adaptive capabilities of *O. limosus* in brackish waters, already in the early stage of ontogenesis. They may indicate that *O. limosus* can reproduce in brackish waters with salinity of up to 7 PSU or probably even higher. Wherever the salinity does not exceed 3-5 PSU, effective reproduction is possible and juveniles are able to develop. As an omnivorous species in a new environment, the search for food should not be a factor preventing its further expansion. The body size is another important feature testifying to an animal's condition and adaptation to an environment (Guan & Wiles 1999). In the context of the reproduction rate of the spiny-cheek crayfish in fresh and brackish waters with salinity of 3 and 7 PSU, it is quite clear that young crayfish achieve the largest sizes at salinity of 7 PSU ($y = 0.3893 \times 2.55$), somewhat smaller at 3 PSU ($y = 0.1862 \times 2.95$) (Jaszczołt & Szaniawska 2011) and the smallest ones in fresh waters ($y = 0.0346 \times 3.20$, $R^2 = 0.999$) (Orzechowski 1984). In the case of *Procambarus clarkii* (Girard, 1852), salinity of up to 12 PSU stimulates the growth (Sharstein & Charfin 1979). On the other hand, Loyacano (1968) states that salinities of 10 and 20 PSU reduce the growth of individuals of this species; likewise, salinities from 5 to 18 PSU also reduce the growth of *P. leniusculus*. Salinities above 6 PSU inhibits and salinities below this level stimulate the growth of *Cherax destructor* Clark, 1936 (Mills & Geddes 1980). Presumably, the evolutionary history and the course of osmoregulation will govern the growth rates of different crayfish species in brackish waters (Mills & Geddes 1980).

In adults, the change in salinity to 3 and 7 PSU increases the rate of waste matter excretion and significantly decreases the metabolic efficiency for food consumed at these salinities. On the other hand, there is no change in the rate at which food is consumed (Jaszczołt 2013). This study has shown that salinities of up to 7 PSU do not reduce the occurrence of this species.

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