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The role of abiotic and biotic factors in interspecific competition of Polish crayfish – comprehensive literature review

by

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Abstract

Invasive species are those that have been transferred by humans out of their natural range. Native crayfish species in Polish waters include: *Astacus astacus* and *Pontastacus leptodactylus*, whereas invasive species are: *Pacifastacus leniusculus*, *Faxonius limosus*, *Procambarus clarkii* and *Procambarus virginalis*. The objective of this study was to determine how abiotic and biotic environmental factors contribute to interspecific competition of Polish crayfish based on the available literature. Abiotic factors affecting the interspecific competition include tolerance to extreme pH values, calcium ion content, temperature, oxygenation, water salinity, preferred substrate and the type of water bodies. Biotic factors are, inter alia, pathogens, food base, plant cover and interactions in the prey–predator system, as well as interactions between crayfish species. The most important abiotic factors are water temperature and oxygenation, while the most important biotic factor is the crayfish plague – a deadly disease for native species. Each invasive species has a different set of traits and adaptations that enable a successful invasion. However, a successful invasion of a given species is not determined by one, but many adaptations that coexist.

Key words: invasive species, native species, agonistic interactions, negative impact

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Introduction

According to the European Union, Regulation No. 1143/2014, a species, subspecies or lower taxa introduced beyond their distribution range should be considered alien taxa. Furthermore, the aforementioned regulation (No. 1143/2014) distinguishes an invasive alien species as one whose introduction and/or spread threatens the biodiversity of native fauna and flora and can cause damage to the economy or adversely affect human health. Invasive alien species may include those that are currently in the process of expansion, as well as those whose populations and range are stable, and even those with declining populations, but still harming nature and/or the economy (Najberek & Solarz 2016). Species of unknown or speculative origin are referred to as cryptogenic. They belong to little-studied taxonomic groups and are often described taxonomically by different names in each new area (Carlton 2009). According to Jaroszewicz (2011), the tendency to spread and colonize new territories is inscribed in the life strategy of each organism, and biological invasion is a phenomenon consisting in the rapid spread of a species (colonization, breeding, further spread, duration and negative impact on fauna and flora) in an area outside its natural occurrence. Currently, species ranges are changing rapidly due to i.a. human activity, and invasive species are expanding their geographic range limits, as demonstrated by comparing current data (GDOS 2018) with e.g. "Atlas of Crayfish in Europe" (Souty-Grosset et al. 2006).

Crayfish belong to the largest and longest-living crustaceans inhabiting freshwater ecosystems (Kozák et al. 2015). In Poland, one can observe both native species of crayfish (noble crayfish and narrow-clawed crayfish) and invasive species (signal crayfish, spiny-cheek crayfish, red swamp crayfish, marbled crayfish). There are five native species of crayfish in Europe (Souty-Grosset et al. 2006): *Astacus astacus* (Linnaeus 1758), *Pontastacus leptodactylus* (Eschscholtz 1823), *Pontastacus pachypus* (Rathke 1837), *Austropotamobius pallipes* (Lereboullet 1858) and *Austropotamobius torrentium* (Schrank 1803), and five invasive species (EU Regulation 1143/2014): *Faxonius limosus* (*Orconectes limosus*) (Rafinesque 1817), *Faxonius virilis* (*Orconectes virilis*) (Hagen 1870), *Pacifastacus leniusculus* (Dana 1852), *Procambarus clarkii* (Girard 1852), *Procambarus virginalis* (Lyko 2017).

A. astacus (noble crayfish) belongs to the Astacidae family (Table 1). Until the end of the 19th century, it was a common species and very abundant throughout the country, after which it began to decline quickly, especially in the northern, western and central parts of the country (Śmietana et al. 2004). It is currently partially protected. According to Strużyński (2007), the species was found in small watercourses, lakes and large lowland rivers, but due to anthropopressure such as pollution, drainage, intensification of agriculture, overfishing and pathogens, its current occurrence in Poland is local – mostly in the south-eastern part (Kouba et al. 2014).

P. leptodactylus (narrow-clawed crayfish) belongs to the Astacidae family (Table 1). It is not native to the entire European continent, as it occurs mainly in the waters of Southeastern Europe and the Middle East (Ponto-Caspian region; Koksal 1988). The wide range of this species results from the creation of numerous navigable routes as well as the intentional introduction that initiated the dominance of narrow-clawed crayfish in waters of Central Europe from the 18th century, which is now found in surface waters throughout Europe except Scandinavia (Strużyński 2007). Narrow-clawed crayfish and noble crayfish are very sensitive to pathogenic diseases which, together with overfishing and environmental pollution, effectively reduce the population of these species (Svoboda 2015).

P. leniusculus (signal crayfish) also belongs to the Astacidae family and comes from the western part of the United States (Strużyński 2007). It was brought to Europe in 1969 (Sweden), while the first attempt to introduce the signal crayfish into Polish waters

Table 1

Body parameters and life expectancy of crayfish

Species	Total length (mm)	Maximum mass (g)	Maximum age (years)	References
A. astacus	200–250	> 200	25	Collins et al. 1983; Strużyński 2007
A. leptodactylus	150–200	150	20–25	Trouilhé 2006; Strużyński 2007
P. lenisculus	200	> 200	20	Mastyński & Andrzejewski 2005; Strużyński 2007
F. limosus	122 (female); 111 (male)	*	5	Kulmatycki 1936; Pieplow 1938
P. clarkii	150	> 200	*	Paglianti & Gherardi 2004; Loureiro et al. 2015
P. virginalis	103	> 30.1	*	Vogt et al. 2015

* – no data

took place in 1972, followed by the Inland Fisheries Institute between 1972 and 1983 (Jażdżewski & Konopacka 1995; Fig. 1A). Although the reasons for the introduction of this species outside its natural range are complex, the main one is the drastic decline in the population of native species, caused by progressive eutrophication of waters, pathogens and displacement by invasive crayfish (Krzywosz et al. 1995). The life cycles of signal crayfish and native species are similar, moreover, the new species has several beneficial breeding characteristics, including faster weight gain and maturity compared to the native crayfish (Krzywosz et al. 1995; Table 1). Signal crayfish are currently recorded mainly in northern Poland (Holdich et al. 2009; Dobrzycka-Krahel et al. 2017; Fig. 1A).

F. limosus (spiny-cheek crayfish) belongs to the Cambaridae family. It naturally lives in freshwater bodies of the United States (Holdich & Black 2007). This species was introduced into European waters at the turn of the 19th and 20th century, with the first successful introduction in a reservoir located in the Myśla River system in 1890 (Fig. 1B). The reason for its introduction in Europe was a significant reduction in the number of European crayfish associated with overfishing and pathogens (Grabowski 2011). In Europe, the spiny-cheek crayfish was initially successfully used as bait and fish food, which led to the introduction of this species in other countries (Holdich & Black 2007). In Poland, it is a common species in the Oder and Vistula river basins, as well as in water bodies of Pomerania and Masuria (Jaszczołt & Szaniawska 2011 after others); it does not occur in south-eastern Poland (Souty-Grosset et al. 2006), except one place (Fig. 1). The species is smaller than the native species (Table 1).

P. clarkii (red swamp crayfish) belongs to the Cambaridae family. The natural habitats of this species are bodies of water in North America between San Antonio and El Paso del Norte, where it is found in both lotic and lentic waters (Strużyński 2007). It was first discovered as an invasive species in 1997 around Baden-Baden, Germany. It is fished and bred on a large scale for consumption in the Southeastern United

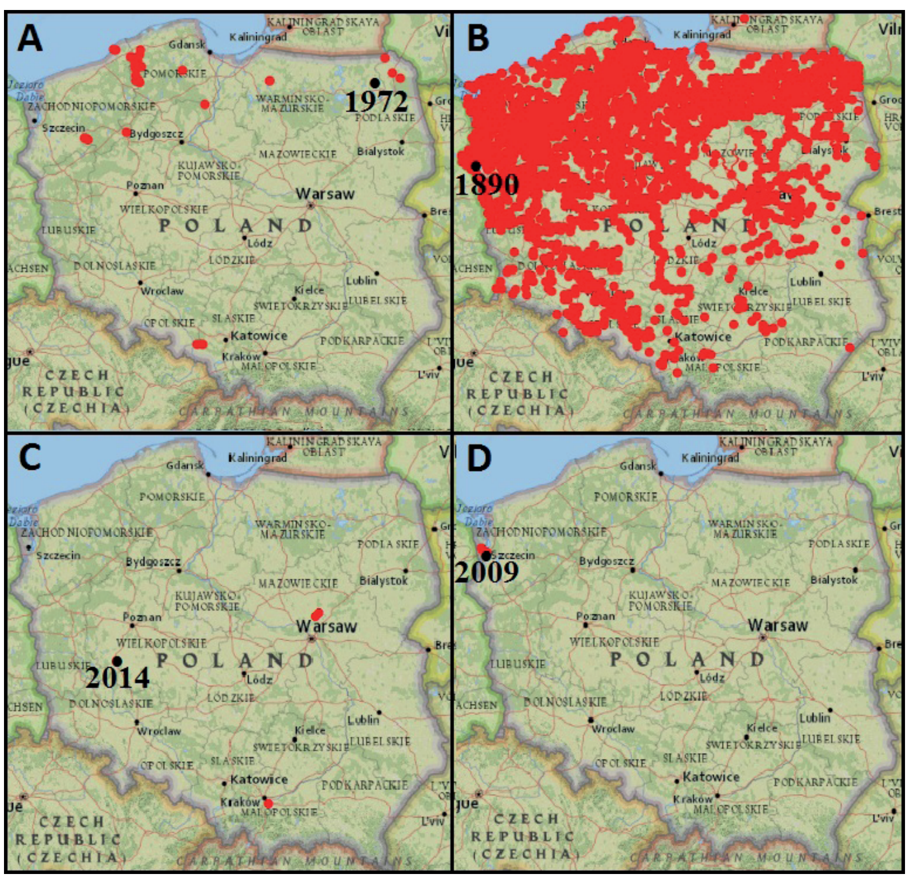

Figure 1

First observation (black dots) and distribution (red dots) of invasive crayfish in Poland in January 2020; A – *P. leniusculus* (signal crayfish), B – *F. limosus* (spiny-cheek crayfish), C – *P. clarkii* (red swamp crayfish), D – *P. virginalis* (marbled crayfish) (http://geoserwis.gdos.gov.pl/)

States and Europe (Grabowski 2011; Table 1), and is also important in recreational and commercial fishing (Holdich 2002). In Polish waters, it was first found in the Samica River in 2014 (Fig. 1C; GDOS 2018), and in a small pond by the Vistula River near Kraków and Warsaw in 2018, where it most likely escaped from breeding or was deliberately released by aquarists (Maciaszek et al. 2019).

P. virginalis (marbled crayfish) belongs to the Cambaridae family. The first reports on parthenogenetic reproduction of this species come from 1995 from Germany, where such a way of reproduction was observed in an aquarium in one unidentified crayfish individual, which, due to its color, was called marbled crayfish (Martin et al. 2010). No naturally occurring marbled crayfish had been found anywhere before (Souty-Grosset et al. 2006); they were observed in Germany after 1995 as an invasive species (Chucholl et al. 2012). Molecular studies have shown that this species is most closely related to slough crayfish *Procambarus fallax* (Hagen 1870) and on this basis it was concluded that the marbled crayfish is a parthenogenetic form of slough crayfish (Martin et al. 2010; Vogt et al. 2015). Individuals of this species reproduce through females laying unfertilized eggs from which genetically identical females develop (Błaszak 2011; Table 1). Males of marbled crayfish were not found in laboratory populations or natural populations (Seitz et al. 2005), which confirms that the only form of reproduction is parthenogenesis through female specimens. According to the General Directorate for Environmental Protection in Warsaw (2018), the marbled crayfish was first recorded in the natural environment in 2009, and since 2018 the species has been observed in isolated populations. Unfortunately, it is not known how large these populations are (Fig. 1D).

The objective of the study was to show the role played by abiotic and biotic environmental factors in the interspecific competition between native and invasive crayfish occurring in Poland and to compare the rank of these factors. The knowledge presented in this study will provide a better insight into the issue and may prove beneficial to other countries where a similar set of species occurs.

Abiotic environmental factors

pH

The pH of the environment affects the pH of the body, and thus the proper course of physiological reactions and processes, including resorption or deposition of alkaligenous calcium, which is necessary, among others, for proper molting, muscle and nervous system processes (Edwards et al. 2015). In general, pH above 7 is considered optimal for crayfish (Strużyński 2007; Table 2). Noble crayfish are most sensitive to adverse environmental conditions (Pârvulescu et al. 2011). The species with the widest range of tolerance is the marbled crayfish, which can occur in waters with both acidic and clearly alkaline reaction (Table 2).

Content of calcium ions

Crustaceans are among the animals with the highest Ca requirements due to their calcified exoskeletons and regular molt cycles (Edwards et al. 2015). The content of calcium ions in water is not a constant value and changes throughout the day, mainly due to changing CO_2 concentration, which is a consequence of respiratory processes of aquatic vegetation (Strużyński 2007). The range of 20–60 mg l^{-1} is considered optimal for native species of crayfish (Strużyński 2007). Narrow-clawed crayfish were bred with the greatest efficiency in water containing 68 mg l^{-1} Ca^{2+} (Strużyński & Niemiec 2001). Stable populations of narrow-clawed crayfish, signal crayfish, and spiny-cheek crayfish were observed in tanks with Ca^{2+} content of 37 mg l^{-1} (Krzywosz & Krzywosz 2002). The highest survival rate in laboratory studies on the growth of red swamp crayfish was observed at 45.5 mg l^{-1} Ca^{2+}, while the fastest weight gain and the

Table 2

Optimum pH and tolerance range of crayfish

Species	pH		
	Optimum	Range	References
A. astacus	7.8–8.0	4–11	Pârvulescu et al. 2011; Kozák et al. 2015 after Svobodová et al. 1987
P. leptodactylus	7–9	6.8–7.8	Mazlum et al. 2010; Kozák et al. 2015 after Svobodová et al. 1987
P. leniusculus	7.8–8.0	7.2–9.1	Hesni et al. 2008; Dobrzycka-Krahel et al. 2017
F. limosus	*	6.7–9.1	Kozák et al. 2005; Ďuriš et al. 2006
P. clarkii	*	6.5–8.6	Smart et al. 2002; Scalici et al. 2009
P. virginalis	7.5–8.0	*	Velisek et al. 2014

* – no data

most frequent molting were observed at 65.5 mg l^{-1} Ca^{2+} (Yue et al. 2009). Stable populations of marbled crayfish, on the other hand, were recorded in waters with a concentration of 31.6 mg l^{-1} Ca^{2+} (Veselý et al. 2017).

Water temperature and oxygenation

Oxygen deficiency can result in large-scale mortality. The most temperature-tolerant species is narrow-clawed crayfish (Table 3), which is physiologically well-adapted to life in stagnant waters, characterized by periodic increases in temperature.

To ensure adequate breeding conditions for commercially important crayfish, the oxygen concentration should be maintained at a minimum of 6 mg l^{-1} (Broussard & Engineer 1984; Table 4). In the case of spiny-cheek crayfish, the physicochemical parameters mentioned above are of little importance, which means that this species can be found in unclassified waters. In the case of red swamp crayfish, a temperature of 33°C is lethal to adults, while a temperature below 13°C causes growth inhibition (Arrignion et al. 1990; Strużyński 2007 after Suprunovich 1988). When the water temperature drops below 10°C, the development of embryos in eggs is inhibited (Loureiro et al. 2015). Narrow-clawed crayfish is a species that tolerates the lowest water oxygenation of 2 mg l^{-1}, but only in a short period of time (Kozák et al. 2015 after Sládeček 1988; Table 4). Marbled crayfish is a thermophilic species whose reproduction is inhibited when temperature drops to 15°C (Seitz et al. 2005; Pârvulescu et al. 2017). No data are available on the optimal water oxygen content and the range of tolerance for signal crayfish.

Water salinity

Salinity is an important abiotic factor affecting key life processes of animals such as feeding, growth, and reproduction, which determines their long-term survival, distribution and success in ecosystems (Veselý et al. 2017). Few crustacean species have successfully adapted to life in higher water salinity, which makes them all the more interesting in studies involving patterns of ontogeny of osmoregulation in crustaceans (Susanto & Charmantier 1999). Species are generally divided into euryhaline and stenohaline organisms, which reflects their ability to adapt to a wide or narrow range of salinity (Veselý et al. 2017). The red swamp crayfish is the species with the highest tolerance to high salinity (Table 5); only four out of 96 individuals grown for 54 days died during the experiment (Bissattini et al. 2015). In the case of marbled crayfish, intolerance to salinity can significantly reduce its ability to occupy new habitats. For this species, 100% mortality was observed at a salinity of 7 PSU (no data on lower salinity), while no higher mortality was observed in the absence of salinity (Veselý et al. 2017; Table 5).

Table 3

Optimum water temperature and tolerance range of crayfish

Species	Temperature (°C)		
	Optimum	Range	References
A. astacus	20.0	1.0–28.0	Strużyński 2007; Reynolds & Souty-Grosset 2011
P. leptodactylus	17.0–21.0	4–32.0	Karimpour et al. 2011; Reynolds & Souty-Grosset 2011; Kozák et al. 2015 after Svobodová et al. 1987
P. leniusculus	13.0–23.0	1.0–33.0	Holdich 2002; Reynolds & Souty-Grosset 2011
F. limosus	c. 20.0	from 10.0	Pieplow 1938; Dubé & Portelance 1992; Kozák et al. 2015
P. clarkii	21.0–29.0	to 34.0–35.0	Arrignion et al. 1990; Holdich 2002; Reynolds & Souty-Grosset 2011
P. virginalis	18.0–25.0	*	Seitz et al. 2005; Pârvulescu et al. 2017

* – no data

Table 4

Optimum water oxygen content and tolerance range of crayfish

Species	Oxygen content (mg l^{-1})		
	Optimum	Range	References
A. astacus	8.0–9.0	from 3.2	Mastyński & Andrzejewski 2005; Reynolds & Souty-Grosset 2011
P. leptodactylus	8.0–9.0	from 2.0	Mastyński & Andrzejewski 2005; Kozák et al. 2015 after Sládeček 1988
F. limosus	*	from 4.7	Babović et al. 2011
P. clarkii	*	from 3.0	Souty-Grosset et al. 2006
P. virginalis	*	from 2.9	Lőkkös et al. 2016

* – no data

Table 5

Maximum water salinity tolerance in adult individuals

Species	Water salinity (PSU)	
	Range	References
A. astacus	to 14.0	Rasmussen & Bjerregaard 1995
P. leptodactylus	to 20.8	Susanto & Charmantier 1999; Kozák et al. 2009
P. leniusculus	to 21.0	Rutledge & Pritchard 1981; Holdich et al. 1997
F. limosus	to 7.0	Jaszczołt & Szaniawska 2011
P. clarkii	to 35.0	Bissattini et al. 2015; Dörr 2020
P. virginalis	to 0.0	Veselý et al. 2017

* – no data

Preferred substrate and type of water body

Noble crayfish is widely regarded as an indicator of clean waters. The species prefers well-oxygenated flowing waters, but is also found in retention and post-mining reservoirs near rivers and streams (Strużyński et al. 2001). Narrow-clawed crayfish are characteristic of lentic waters. Narrow-clawed crayfish and spiny-cheek crayfish are less demanding in terms of substrate. Due to their very light body structure, these two species are adapted to life on a loamy, muddy, slightly muddy or sandy bottom (Haertel-Borer et al. 2005; Strużyński 2007). The situation is quite different in the case of noble crayfish and signal crayfish, whose structure, body mass and biology are similar. These two species prefer sandy and gravel substrates, as well as those consisting of small stones in which they do not sink (Engdahl et al. 2013). Spiny-cheek crayfish is an eurybiotic species that can be found in various types of both lentic and lotic waters, but prefers warm, slow-flowing and still waters, with rich aquatic vegetation and a muddy bottom (Kozák et al. 2015). Populations of this species inhabiting different types of reservoirs do not show significant differences in their development or growth (Ďuriš et al. 2006; Holdich & Black 2007). Red swamp crayfish shows similar substrate preferences as narrow-clawed crayfish and spiny-cheek crayfish. The species occurs in large numbers on loamy and muddy bottoms, where it can successfully dig burrows and tunnels, while avoiding gravel and stony substrates (Hanshew & Garcia 2012). It prefers lentic waters, while in watercourses it occupies places with the slowest current, giving way to noble and signal crayfishes (Bernardo et al. 2011). Marbled crayfish is a very flexible species in terms of environmental conditions. It is found in both lotic and lentic waters with a muddy bottom (Lőkkös et al. 2016), mainly in lakes, canals, streams, shallow ditches, rivers, ponds and around ports (Chucholl et al. 2012).

Biotic environmental factors

Crayfish disease

The disease with the greatest impact on crayfish populations in Poland is the crayfish plague caused by oomycetes (Oomycota) *Aphanomyces astaci* (Schikora 1906). This disease was brought into Europe from North America in the 19th century (Grabowski 2011). American crayfishes (spiny-cheek crayfish, signal crayfish, red swamp crayfish) and marbled crayfish show high resistance to the crayfish plague (and at the same time are its vectors), in contrast to native species, in which the disease causes high mortality (Unestam 1969, Svärdson 1992). However, if alien species are exposed to stress or impaired immunity as a result of molting, infection with other pathogens or an adverse environment, they may also die (Schrimpf et al. 2013).

The life cycle of *A. astaci* includes three basic forms: mycelium in host tissues and infectious units found in water, i.e. zoospores and cysts (Svoboda 2015). Mycelium hyphae, growing above the host epithelium, form the so-called primary spores, which shortly after being released from hyphae tips encapsulate and form a clump of tightly adherent primary cysts (Strużyński 2007). After a period of dormancy, the primary cysts release biflagellate zoospores that are able to move actively and demonstrate host chemotaxis (Rantamäki et al. 1992). The chemotaxis response is slow but facilitates the spread of oomycetes (Cerenius & Söderhäll 1992). Zoospores can survive from several days to a week in water and bottom sediments (Unestam 1973). If they encounter a host during this time, they lose cilia and form a secondary cyst that can release further zoospores or germinate, forming a form capable of penetrating the outer lipid membrane of the crayfish epithelium owing to the released enzymes with high lipid degradation capacity (Rantamäki et al. 1991). When zoospore production is inhibited, the spread of the disease stops (Cerrenius & Söderhäll 1992).

A. astaci is represented by five genetic groups that occur in different crayfish species. Group A (genotype As) is present only in native species, group B (PsI) and group C (PsII) are associated with *P. leniusculus*, group D (Pc) – with *P. clarki*, and group E (Or) – with *F. limosus* (Kozubíková et al. 2011). Groups B and C were isolated from signal crayfish, however, group C has only been found in signal crayfish originating from Canada and has not yet been reported from Europe (Ungureanu et al. 2020). In addition, differences in virulence of strains were demonstrated. Group B caused rapid and total mortality of *A. astacus* in laboratory experiments, while group A was generally less pathogenic (Becking et al. 2015). Although European crayfish are generally very susceptible and usually die within a few days after infection, the evidenced-based evolutionary adaptation of the host and pathogen appears to be the cause of the survival of some *A. astacus* populations co-occurring with invasive species, e.g. *F. limosus* and *P. leptodactylus*, observed in some places (Panteleit et al. 2018). Furthermore, not all invasive species populations (and individuals in infected populations) must be infected with *A. astaci* (Pârvulescu et al. 2012; Schrimpf et al. 2013), which can prevent native species from being infected.

Crayfish plague has been decimating European crayfish populations for over 150 years, which is why *A. astaci* from Oomycota is considered as one of the 100 most invasive species in the world (DAISE 2019). Crayfish plague is transmitted by natural diffusion, along with the water current, through infected individuals: people (fishing and fishing gear), fish and other animals, including crustaceans, e.g. alien species of shrimps (Unestam 1973; Strużyński 2007; Mrugała et al. 2019). *A. astaci* attacks only the soft parts of the epithelial tissue of the crayfish body, as well as cerebral and abdominal ganglia that are part of the nervous system (Nybelin 1936; Kocyłowski & Miączyński 1960). Behavioral changes are also observed, involving increased daily activity, moving along the river banks, going ashore, as well as difficulties in moving and assuming the dorsal position (Kocyłowski & Miączyński 1960). Infection with *A. astaci* is fatal even at temperatures close to 0°C (Unestam 1973). The "cotton" mycelium between all segments of the body (Fig. 2A), especially the legs (Fig. 2B), can be observed in individuals of the noble crayfish that died of *A. astaci*; it can also cover the eyeballs (Fig. 2C), forming a layer containing numerous balls with invasive forms (Fig. 2D; Svoboda 2015).

Thelohaniasis, or porcelain disease, is a serious disease that affects a number of decapod crustaceans,

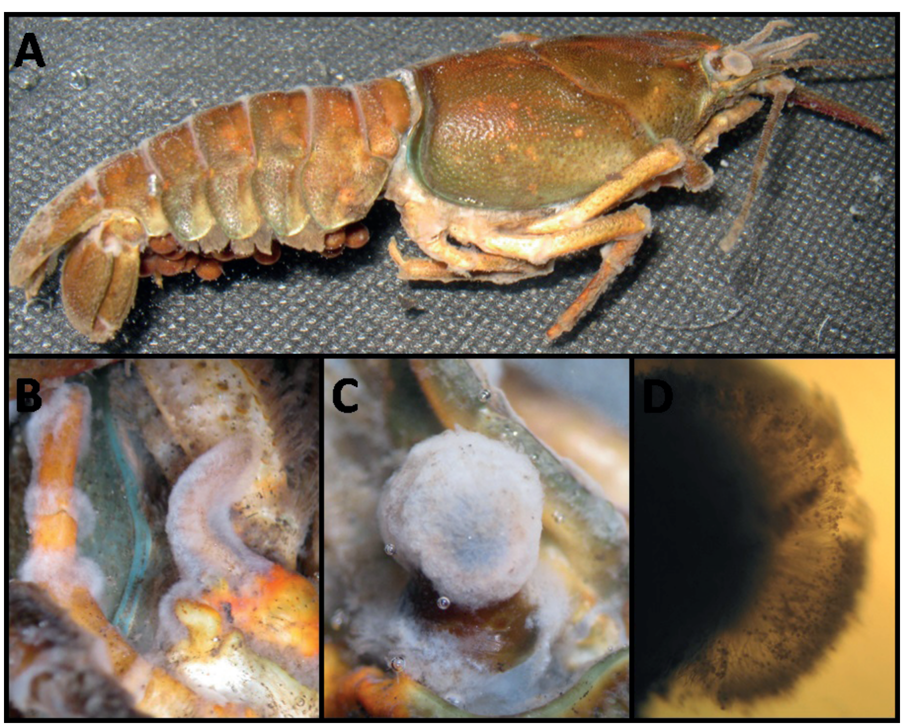

Figure 2

Symptoms of the plague on dead noble crayfish (after Jiří Svoboda) including freshwater crayfish. It is caused by the microsporidian parasite *Thelohania contejeani* (Sprague & Couch 1971) and was originally described in Europe by Henneguy and Thelohan in 1892 as a causative agent of a disease that caused large losses in crayfish populations. In Poland, *T. contejeani* infects mainly noble crayfish (Voronin 1971). The disease has also been reported in several crayfish species from different countries (McGriff & Modin 1983). *T. contejeani* reproduces inside crayfish muscle cells, using them to form spores (Imhoff et al. 2009). The host muscle tissue is continuously infected by successive spore stages, ultimately leading to muscle damage and subsequent death (Strużyński 2007). In the late stage of the disease, the inner side of the abdominal area becomes transparent and white due to the huge amount of white spores released into the muscle tissue (Unestam 1973). In addition to muscles, cysts can also be found in abdominal, limb and various gastric muscles, in the eyestalk, in supraoesophageal ganglion cells, around the gills, hepatopancreas, and haemolymph (Cossins 1973; Cossins & Bowler 1974). Signal crayfish can also be vectors of this disease without showing symptoms of the disease (Imhoff et al. 2009).

Food base

The food base is not specific for any crayfish species, but merely regulated by its availability (Smart et al. 2002; Strużyński 2007). Therefore, each population of crayfish of the same species can feed on a different diet, while being omnivorous at the same time (Gutiérrez-Yurrita et al. 1999; Englund & Krupa 2000). It is believed that the type of food consumed by crayfish is a seasonal feature (Pieplow 1938). Crayfish also show cannibalistic tendencies toward smaller individuals, even those closely related, especially when population density is too high and there is not enough food in the environment (Celada et al. 1993; Loureiro et al. 2015). In early spring and late autumn, a wide variety of food of animal origin is the most popular choice. These may include mollusks, aquatic insect larvae, annelids, nematodes, flatworms, tadpoles, fry, other crustaceans, as well as weakened or recently dead vertebrates, such as fish and amphibians (Loureiro et al. 2015), and thus they also fulfil an extremely important sanitary function. At the peak of the growing season, however, crayfish switch to plant food, mainly vascular vegetation, including American waterweed (*Elodea canadensis* Michaux 1803), hornwort (*Ceratophyllum demersum* Linnaeus 1753), water-lily (*Nuphar* sp.) (Strużyński 2007), as well as shining pondweed (*Potamogeton lucens* Linnaeus 1753), water violet (*Hottonia palustris* Linnaeus 1753), and plants of the watermilfoil genus (*Myriophyllum* sp. Linnaeus 1753) (Goszczyński & Jutrowska 1996). They also eat algae of the *Chara* genus and moss *Fontinalis* sp. (Tondryk 2001).

Plants

The plant cover has several important functions. In addition to its protective function for young individuals who successfully find shelter there during their growth or molting, the vegetation itself serves as a food base, and at the same time as home to invertebrates, which are also part of the crayfish diet (Strużyński 2007). While both native and invasive crayfish (in particular signal crayfish and red swamp crayfish) exert a negative impact on macrophytes, the invasive crayfish tend to have slightly smaller effects (Twardochleb et al. 2013). The negative impact on macrophytes results from the fact that they are consumed, cut and pulled out or unearthed by crayfish individuals. All species of crayfish are most likely to be found near or among dense fields of American waterweed (*E. canadensis*), hornwort (*C. demersum*) and *Chara* sp., whose presence indicates a high content of calcium in water necessary for the proper growth and development of crayfish (Strużyński 2007).

Prey–predator interactions

All species of crayfish are a very important element of the food web as a food base for other animals. Crayfish in headwater streams are exposed to predation from two sources: fish and terrestrial predators including wading birds and mammals (Englund & Krupa 2000). Wels catfish *Silurus glanis* (Linnaeus 1758), European eel *Anguilla anguilla* (Linnaeus 1758), common perch *Perca fluviatilis* (Linnaeus 1758), brown bullhead *Ameiurus nebulosus* (Lesueur 1819) and trout (Salmonidae) cause the most serious depletion in crayfish populations, and the dominance of these species often leads to the disappearance of crayfish populations (Strużyński 2007). Fish predation affects the distribution of different size classes of crayfish in stream pools along the depth gradient, which is an evolutionary response to predator pressure. Fish prey mainly on small crayfish in deep water, and a comparison of the crayfish distribution in pools with and without fish indicates that small crayfish respond to this threat by increasing their use of shallow areas (Englund & Krupa 2000). In order to protect themselves from predators and other crayfish, most crayfish species dig burrows and corridors deep into the banks of watercourses and the shores of reservoirs, which can cause the slopes to collapse and small trees to sink into the water (Gardere 1992). A particular intensification of common perch preying occurs during the period when native crayfish become independent, when common perch individuals wait for juvenile crayfish near burrows or other hideouts, where they stay with a female, and catch them immediately after leaving the shelter (Strużyński 2007). Terrestrial predators feeding on crayfish include: birds, for example: grey heron *Ardea cinerea* (Linnaeus 1758), great egret *Ardea alba* (Linnaeus 1758), purple heron *Ardea purpurea* (Linnaeus 1766) and Eurasian bittern *Botaurus stellaris* (Linnaeus 1758), as well as mammals, especially the American mink *Neovison vison* (Schreber 1777) and the Eurasian otter *Lutra lutra* (Linnaeus 1758) (Englund & Krupa 2000; Strużyński 2007; Loureiro et al. 2015).

Particularly noteworthy is the red swamp crayfish, which has shown high behavioral flexibility in response to the presence of a potential predator. This species proved to use a wider range of information about the increased predation risk than native species, responding more strongly to heterospecific alarm cues (Hazlett et al. 2003). Provided that the prompt detection of alarm substances alerts an animal to the presence of a predator and thus increases the likelihood of avoiding it, this ability can contribute to the success of the species in new environments where new predators may be present; for example, the red swamp crayfish showed that it is capable of learning and remembering associations between different predation risk cues (Gherardi 2006). When trained to associate a new cue [i.e. goldfish *Carassius auratus auratus* (Linnaeus 1758)] with predation risk following pairing with a conspecific alarm scent, individuals of the invasive species remembered that association longer than native species (Acquistapace et al. 2003). However, alarm substances were found to stimulate feeding-related activities in red swamp crayfish bred in aquaculture ponds (Daniels et al. 2004). This phenomenon suggests that these crayfish, when reared in an environment with reduced predation risks, can respond differently to cues that in more risky habitats inform about the danger and further emphasizes the extreme flexibility of the behavior of this species (Gherardi 2006).

Crayfish interactions

All crayfish species exhibit cannibalistic tendencies toward their own species' representatives (Loureiro et al. 2015).

There is evidence to suggest that highly invasive crayfish tend to exhibit stronger interspecific aggression toward natives species, thus limiting access to critical resources for competitors (Linzmaier et al. 2018 after others).

The competition between spiny-cheek and marbled crayfish deserves special attention. In agonistic encounters, marbled crayfish were on average more aggressive than spiny-cheek crayfish, even against larger opponents (Linzmaier et al. 2018), which shows that in direct clashes this species can actively displace spiny-cheek crayfish from their habitats.

Red swamp crayfish and signal crayfish can coexist in one river, but due to their different habitat preferences they generally occupy different habitats (Bernardo et al. 2011). In this case, the dominance of one of these species is determined by water temperature, which prevents red swamp crayfish from becoming dominant.

According to Söderbäck (1991), laboratory tests on noble crayfish and signal crayfish show that the latter wins direct clashes with native species, showing more frequent strikes, threats and chases. This applies to both juvenile and adult forms. This shows that the signal crayfish can be a more aggressive and dominant species compared to the noble crayfish. The same is true for signal crayfish and narrow-clawed crayfish. Signal crayfish are more aggressive, more often initiate skirmishes and other interactions, and much more often win fights with narrow-clawed crayfish, effectively repelling them in laboratory conditions (Hudina et al. 2016).

Discussion

The red swamp crayfish is tolerant of environments with the lowest pH, which is why it can occur in acidified, unclassified waters and eutrophic reservoirs, as opposed to the noble crayfish, which is an indicator of clean waters (Strużyński 2007; Scalici et al. 2009). Therefore, in the case of deteriorating Polish surface water, the red swamp crayfish will have an advantage over the native species as it will be able to function successfully in conditions unfavorable to other species.

With regard to the content of calcium ions dissolved in water, no clear difference is observed between the species. Therefore, it should not be considered as a factor of greater importance in the interspecific competition of crayfish.

Water temperature and oxygenation are closely related. Thus, species with a wide temperature tolerance range are the same as those resistant to deficiencies of oxygen dissolved in water, which in the face of progressive global warming and warmer seasons gives them a clear advantage over native species that can die as a result of overheating and hypoxia. The highest tolerance to high temperature and low oxygenation is shown by red swamp crayfish (Holdich 2002; Reynolds & Souty-Grosset 2011), while it is worth noting that marbled crayfish is able to survive in reservoirs with an ice cover under which the temperature is 4°C, which enables them to survive winter in Poland (Lőkkös et al. 2016).

Both native and invasive crayfish species, with the exception of marbled crayfish (Veselý et al. 2017), show some tolerance to water salinity. The species with the highest tolerance to water salinity is the red swamp crayfish, which theoretically, similarly to spiny-cheek and signal crayfish, could successfully colonize the waters of the Baltic Sea if not for its thermal limitations.

Noble crayfish and signal crayfish show different preferences for the substrate compared to other species mentioned in this work, which means that their ecological niches do not overlap. Among invasive crayfish, the marbled crayfish is the most flexible in terms of substrate and current selection (Chucholl et al. 2012), hence it can be found in any types of water bodies.

Crayfish plague caused by *A. astaci* is one of the most important factors affecting the interspecific competition of crayfish. Invasive species are rather resistant to the plague, enabling them to colonize deserted ecological niches due to the dying of noble crayfish and narrow-clawed crayfish, which are quicker to give way to invasive species (Svoboda 2015).

All the above-mentioned crayfish species are omnivorous – they can feed on macrophytes and algae, actively prey on zoobenthos or feed on carrion (Englund & Krupa 2000; Loureiro et al. 2015). The type of food consumed by crayfish species is not specific, but depends on its availability (Strużyński 2007). Therefore, it is not a factor significantly affecting competition between crayfish species in Poland.

The vegetation cover has the same ecological function for all the listed crayfish species. However, the invasive crayfish are more likely to destroy and reduce macrophytes present in the environment (Twardochleb et al. 2013), which can lead to a decline in biodiversity in surface waters.

When interacting with predators, the red swamp crayfish shows the most useful adaptations. This species demonstrates a faster and stronger defense response in the presence of a predator than other crayfish species (Hazlett et al. 2003). Red swamp crayfish remember kairomones, which in the event of a re-encounter with a predator will trigger a faster defensive response giving a better chance of survival (Gherardi 2006).

Resistance to the crayfish plague alone gives invasive species a huge advantage over susceptible species, because the former can easily occupy free ecological niches or actively displace weakened and dying native crayfish populations.

In their study, Schrimpf et al. (2013) investigated what contributes to the long-term coexistence of spiny-cheek and noble crayfish in several reservoirs of Central Europe. The authors showed that out of three scenarios, i.e. noble crayfish resistance, reduced pathogenicity of *A. astaci* or absence of the pathogen in the environment, the third scenario significantly contributes to maintaining the balance between these two crayfish species. This means that they can coexist, as can noble crayfish and narrow-clawed crayfish, which coexist for many years and decades, without dominating each other (Kozák et al. 2015).

However, resistance to the crayfish plague alone does not guarantee the invasive success. Only the combination with other factors gives an advantage over other invasive species. Due to its high flexibility and resistance to changing and adverse environmental conditions, the spiny-cheek crayfish effectively complements the niches previously occupied by native crayfish, which give way due to the resulting interspecific pressure and lethal crayfish plague (Holdich & Black 2007). All these factors mean that the spiny-cheek crayfish may in the future become the dominant decapod species in European waters, even though it has no economic significance (Strużyński 2007). Marbled crayfish are as resistant as spiny-cheek crayfish. They can reproduce by parthenogenesis, which gives them a huge advantage over all other species of crayfish, because it does not require the presence of a second individual of the opposite sex to reproduce (Martin et al. 2010). In addition, this species can reproduce several times a year, provided the water temperature does not fall below 15°C (Pârvulescu et al. 2017), which means that with the current climate warming, the range of this species extends to areas of normally lower water temperature.

Conclusions

Not one, but many parallel adaptations determine the invasion success of the species in question. It can therefore be concluded that the more characteristics a given species has, the greater its coverage for the functions of an ecological niche, whether through outnumbering other species or using an unoccupied niche. However, this does not have to be a prerequisite, as one adaptation is possible, which in itself gives a huge advantage over other species.

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