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CERCOPAGIS PENGROI AS AN INVASIVE SPECIES

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Abstract

The fishhook waterflea (*Cercopagis pengoi*) native to the Ponto-Caspian region, is an excellent example of an invasive species. Within one decade from its first appearance, *Cercopagis pengoi* has colonized nearly the entire Baltic Sea and most of the Great Lakes of North America. The species spread rapidly owing to its ecological and biological profile. The fishhook waterflea is an euryhaline organism marked by a predominance of parthenogenetic reproduction over sexual reproduction. This taxon quickly colonized inhabited ecosystems to create stable populations. The ecological and economic consequences of the species' appearance are noticeable, but they have not been fully investigated and require further analysis.

Key words: *Cercopagis pengoi*, invasive species, Baltic Sea, Great Lakes of North America

INTRODUCTION

Biological invasions are a widespread phenomenon in the world today. The emergence of alien species in new habitats has numerous consequences which are difficult to estimate. The results of studies into the existing invasions indicate that some of them give rise to serious ecological problems (changes in biodiversity, disrupted ecosystem balance) and economic losses (Occhipinti-Ambrogi and Savini 2003, Kołodziejak-Nieckuła 2005). One of invasive species is the fishhook waterflea (*Cercopagis pengoi*, Ostroumov 1891). Owing to its ecological and biological profile and, as reported by Karasiova et al. (2004), to the global warming, the fishhook waterflea colonized the Baltic Sea and the Great Lakes of North America in the 1990s. Its invasion generated substantial losses for the fishing industry and it had an adverse effect on the global economy. The ecological consequences of this invasion are less known because the species colonized new areas relatively recently, and its effect on ecosystems is difficult to estimate.

In most part, the multi-year research into the fishhook waterflea was conducted mainly in the north-eastern parts of the Baltic Sea and the Great Lakes of North America. In the Polish zone of the Baltic sea, *C. pengoi* has been investigated irregularly ever since it was first recorded there (Żmudziński 1998, Bielecka et al. 2000, Olszewska 2006). The species was studied more extensively in the Russian part of the Vistula Lagoon (Polunina 2005, Naumenko 2009). Hornatkiewicz-Żbik (1999) noted the presence of *C. pengoi* in the Vistula Lagoon, but did not report on the time and place of its occurrence or abundance.

The objective of the present study was to analyze the existing body of knowledge on the invasive species *C. pengoi*, its biological and ecological profile, its impact on inhabited ecosystems and the economy. In view of the absence of original research studies on the subject, this article justifies the need for follow-up research into the fishhook waterflea's invasion into the Polish section of the Vistula Lagoon.

TAXONOMY AND ORIGINS

The fishhook waterflea (*Cercopagis pengoi*) is a crustacean of the order Cladocera: Onchypoda, family Cercopagidae. According to Gorokhova et al. (2000), the name of the family has been corrected to Cercopagididae. It comprises 14 species in two groups: Bythotrephes, freshwater organisms (1 or 2 species), and *Cercopagis*, brackish water organisms (13 species), (Krylov et al. 1999, Jurasz et al. 2000). The genus *Cercopagis* has been further sub-divided into *Cercopagis* and *Apagis* which differ only with respect to the shape of the terminal part of the long caudal process. The subgenus of *Cercopagis* has a loop at the end of the caudal process which is not found in the organisms of the subgenus *Apagis* (Simm and Ojaveer 2006). The exact taxonomy of the genus is difficult to determine due to a high degree of polymorphism within species. The above contributed to problems in identifying the species of the genus *Cercopagis* which were found in the Baltic Sea and the Great Lakes. The organism termed as *C. pengoi* has a varied morphological structure that corresponds to the characteristic features of at least two species and two sub-species (Gorokhova et al. 2000). As demonstrated by Ojaveer et al. (2003) in the Gulf of Riga and Makarewicz et al. (2001) in the Great Lakes, the differences in appearance are manifested by two morphological forms of one species – *C. pengoi* – which appear at successive stages of development.

The family Cercopagididae originates in the Ponto-Caspian region. The majority of *Cercopagis* species are found exclusively in the Caspian Sea. Only two species, i.e. *C. (Cercopagis) neonilae* Sars 1902 and *C. (Cercopagis) pengoi* Ostroumov 1891, inhabit the Azov Sea, coastal freshwater bodies and estuaries of the Black Sea (Jurasz et al. 2000). The fishhook waterflea also inhabits selected river-mouths within the catchment area of the Black Sea, the rivers Danube, Dnieper and Bug, and the Bulgarian Lake Gebenjinskoe (Uitto et al. 1999, Bielecka et al. 2000, Panov et al. 2007). According to Rivier (1998), the species disappeared from its former native range in the Aral Sea due to salinification.

MORPHOLOGICAL CHARACTERISTICS

Cercopagis pengoi has a highly characteristic body structure comprising a small trunk and a long caudal process (Fig. 1). Body length ranges from 1.2 to 2.3 mm (females) and from 1.1 to 2.1 mm (males). The fishhook waterflea has no carapace or abdominal segmentation. The head is composed of a large eye and a second large pair of antennae. *Cercopagis pengoi* has four pairs of thoracic legs, and the first pair is 3-4 times longer than the remaining legs. As a characteristic feature of the species, the caudal process ending with a toothed loop is longer than the body (3 to 7 times), (Rivier 1998, Duriš et al. 2000).

The morphology of *C. pengoi* varies subject to location, development stage and sex. According to Grigorovich et al. (2000), parthenogenetic females reach the largest size at higher latitudes, suggesting that climatic conditions could affect body size. Juvenile organisms are usually smaller than adult forms. As reported by Antsulevich and Välipakka (2000), the body length of neonates ranges from 0.80 to 0.88 mm. Adult females are slightly larger than adult males.

C. pengoi adopts various morphological forms subject to its development stage. The spring neonates hatch from resting eggs, and they are characterized by a straight and relatively short caudal process with four tentacles directed forwards. The summer neonates have a relatively long caudal process with an S-shaped loop and tentacles that are straight or directed backwards (Ojaveer et al. 2003).

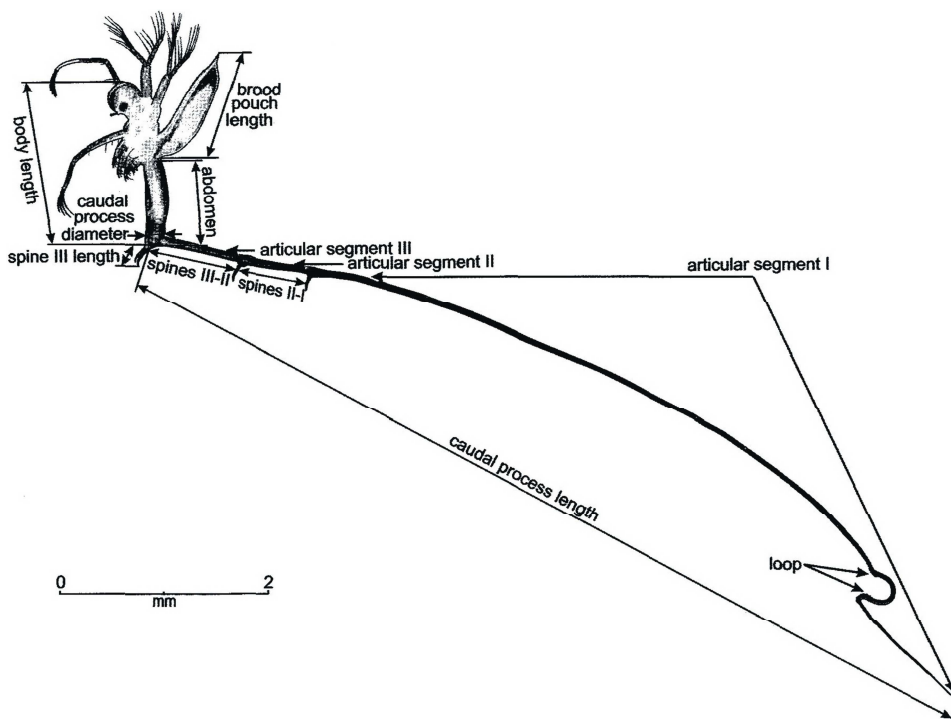


Fig. 1. Body structure of the *Cercopagis pengoi* (Grigorovich et al. 2000)

SPECIES BIOLOGY AND ECOLOGY

An in-depth knowledge of the biology and ecology of the fishhook waterflea is required to explain the relatively extensive natural range and the invasive success of the species. Such knowledge enables scientists to forecast possible introductions in the future and the species' effect on the colonized ecosystems (Panov et al. 2007). The main environmental factors that determine the distribution of zooplankton in brackish water bodies are salinity and temperature (Paturej 2005). *C. pengoi* demonstrates relatively high tolerance to the above factors (Table 1). It is an euryhaline

Table 1
Environmental characteristics (temperature °C and salinity ‰) of *C. pengoi* populations
(Gorokhova et al. 2000)

Species	Locality	Temperature		Salinity	
		range	optimal	range	optimal
<i>C. (C.) pengoi</i> , <i>C. (C.) pengoi gracillima</i>	Caspian Sea	13-30	20-25	<13.5	3-10
<i>C. spp</i>	Caspian Sea			2-13	9-10
<i>C. (C.) pengoi</i>	Azov Sea			<10	
<i>C. (C.) pengoi</i>	Black Sea			1-4	1-3
<i>C. (C.) pengoi</i> , <i>C. (C.) pengoi gracillima</i>	Caspian Sea	3-32	8-24	<15	4-10
<i>C. (C.) pengoi</i> , <i>C. (C.) pengoi gracillima</i>	Black and Azov seas	3-38	12-22	<13	5-8
<i>C. (C.) pengoi aralensis</i>	Aral Sea	4-36	11-26	<17	3-12
<i>C. (C.) pengoi</i>	Baltic Sea	8-20	16-20	0.5-6	
<i>C. (C.) pengoi</i>	Lake Ontario	17-24		<0.25	
<i>C. (C.) pengoi group</i>	Baltic Sea	12-26		3-7.5	

species capable of colonizing both freshwater and brackish water bodies with salinity up to 13‰ (River 1998), although the fishhook waterflea has also been reported from the Aral Sea at salinity levels of 15.92‰ (Aladin 1991). Owing to its euryhaline character, the species has a widespread geographic range. Temperature is also an important factor influencing the lifecycle of *C. pengoi*. Ponto-Caspian species are believed to be thermophilous organisms. The optimal temperature that contributes to their abundance is noted in the summer at above 15°C. Their populations dwindle when water temperature drops below 10°C (Rivier 1998). In the Baltic Sea, however, *C. pengoi* is observed at low densities at temperatures as low as 8°C (Krylov et al. 1999). The species was also noted at 30°C in the cooling water reservoirs of a nuclear plant in the Ukraine (MacIsaac et al. 1999).

In the Caspian Sea, *C. pengoi* is found mostly at a depth of 50-200 m (Gorokhova et al. 2000), while in new habitats, its presence is limited to upper, warmer layers at a depth of 5-30 m (Laxson et al. 2003, Karasiova et al. 2004). Daily, vertical migrations are reported only within the limits of the species' natural range (Mordukhai-

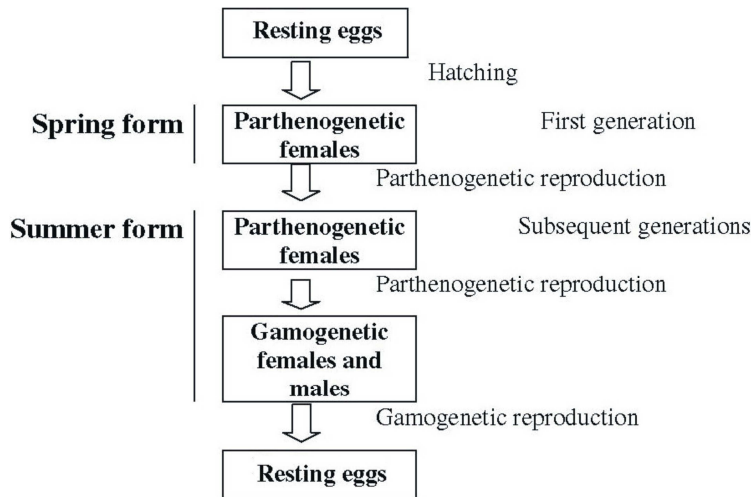


Fig. 2. Reproduction of *Cercopagis pengoi* (Simm and Ojaveer 2006)

Boltovskoi and Rivier 1971), and they have not been noted in the Baltic Sea or Lake Ontario (Krylov et al. 1999, Ojaveer et al. 2001).

C. pengoi populations are characterized by a similar sex structure regardless of geographic location. The species comprises generations of parthenogenetic females, gamogenetic females and males as well as juvenile forms. Parthenogenetic females are the predominant sexual form (Uitto et al. 1999, Grigorovich et al. 2000, Polunina 2005), accounting for 40-70% of the entire species population in the Gulf of Finland (Antsulevich and Välipakka 2000), and 92% in Lake Ontario (MacIsaac et al. 1999). The sexual development of the fishhook waterflea follows strategy *r* (Vanderploeg et al. 2002). Its lifecycle is similar to that of most cladocerans. The species is characterized by the alternation of sexual and parthenogenetic generations – heterogony (Panov et al. 2007), (Fig. 2). In general, the fecundity of females is higher in the Baltic Sea than in the Great Lakes and the Caspian Sea (Grigorovich et al. 2000). Parthenogenetic development may be one of the factors that contribute to the invasive success of the species as parthenogenesis supports rapid population growth within relatively short periods of time.

C. pengoi is an active predator which pursues its prey and captures it with the use of the first pair of thoracic legs (Mordukhai-Boltovskoi and Rivier 1971). In the northern parts of the Baltic Sea, its diet is composed mainly of copepods (60%), rotifers (20%) and cladocerans (20%), (Uitto et al. 1999). The data on the nutritional preferences of *C. pengoi* in the Great Lakes of North America remain scant.

INVASION HISTORY

The Ponto-Caspian region, the native range of *C. pengoi*, is a donor environment of various invasive species, especially for coastal and inland water bodies in Europe and North America. The above is due to the euryhaline character of the species

(Panov et al. 2007) as well as numerous geological and biological similarities between those regions, including isolation from oceans, young geological age and similar environmental threats posed by human activity (Ojaveer et al. 2002).

C. pengoi is the only species of the genus *Cercopagis* which spread outside its native range in the Ponto-Caspian region. The fishhook waterflea began to migrate to Eastern Europe in the 1960s and 1970s following the construction of dams on the Don and Dnieper rivers (Krylov et al. 1999, Grigorovich et al. 2000). *C. pengoi* was first noted outside the Ponto-Caspian region in the Baltic in the early 1990s. According to various authors (Bielecka et al. 2000, Panov et al. 2002, Litvinchuk and Telesh 2006, Simm and Ojaveer 2006), in 1992, this cladoceran appeared simultaneously in the Gulf of Riga and in the open waters of the Gulf of Finland. Żmudziński (1998), Uitto et al. (1999) and Antsulevich and Välipakka (2000) claim that the species was observed in the Gulf of Riga three years before it was first reported in the Gulf of Finland. These discrepancies are probably explained by the fact that *C. pengoi* populations disappeared from the Gulf of Finland in 1993 and 1994, and were reinstated to this water body in 1995 (Karasiova et al. 2004). An increase in the abundance of *C. pengoi* and the species' invasion into other regions of the Baltic Sea was reported in the following decade (Simm and Ojaveer 2006). In 1997, the fishhook waterflea was observed in the central part of the Baltic Sea (Gotland Basin) and in the coastal waters of Sweden (Gorokhova et al. 2000), and in 1999, it expanded further south (Gdańsk Bay) and north (Gulf of Bothnia), (Żmudziński 1998). In this period, the discussed cladoceran was also observed in the Vistula Lagoon connected to the Baltic Sea by the Pilawa Strait, both in its Russian (Polunina 2000) and Polish section (Hornatkiewicz-Żbik 1999). According to Olszewska (2006), *C. pengoi* was also found to inhabit shallow coastal waters of Poland, including the Bay of Pomerania and the Szczecin Lagoon, as well as in the area of Łeba and Żarnowiec.

In addition to the Baltic Sea, the fishhook waterflea also spread to the Great Lakes along the US and Canadian border. It was first noted in 1998 in Lake Ontario (MacIsaac et al. 1999). A year later, it was recorded in the nearby Finger Lakes in the state of New York and in Lake Michigan. In 2001, the species was found in Lake Erie and the Detroit River (Vanderploeg et al. 2002, Kane et al. 2003, Laxson et al. 2003).

The route of *C. pengoi*'s expansion to the Baltic Sea remains unexplained. Gorokhova et al. (2000) have proposed three possible vectors of the species' transport: biological factors (birds or fish transporting resting eggs in their digestive system), hydrological factors (current or wind) and human factors (accidental introduction via the water ballast of vessels, fishing equipment, river canals), with an indication that the last factor offers the most probable scenario. The majority of researchers (Pieni-mäki and Leppäkoski 2004, Panov et al. 2007) subscribe to this hypothesis and believe that the fishhook waterflea found its way to the Baltic Sea via resting eggs transported in the water ballast of vessels cruising between the Black Sea and the Baltic Sea. Jurasz et al. (2000) have suggested inland waters as a possible expansion route of the species. This theory is plausible because the river network of the Baltic Sea, the Black Sea and the North Sea was merged to form an interconnected system following the construction of numerous canals in the 18th to the 20th century. MacIsaac et al. (2001) proposed five routes of *C. pengoi*'s expansion to North America (Fig. 3). Regardless of the route, genetic studies have demonstrated that the Baltic

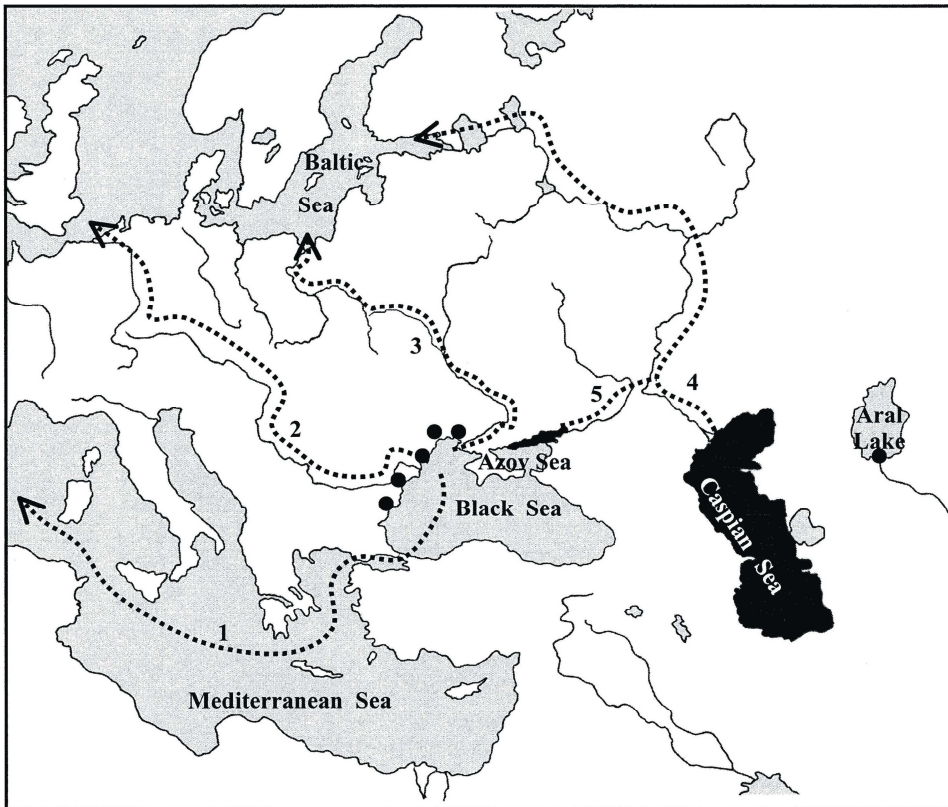


Fig. 3. Possible routes of *C. pengoi* invasion into the water bodies of North America: 1 – directly from the Black Sea or the Azov Sea, via the Mediterranean Sea to the Great Lakes; 2 – from the Black Sea or the Azov Sea, via the Danube, the canal connecting the Rhine, Main and Danube to the North Sea; 3 – from the Black Sea or the Azov Sea, via the Dnieper and the system of canals connecting the Pripyat and Bug rivers, to the Vistula or the Niemen and on to the Baltic Sea; 4 – from the Caspian Sea, via the Volga and its dam system, to the Volga-Baltic Waterway, the Neva, and on to the Baltic Sea; 5 – from the Black Sea or the Azov Sea, via the Don, the canal connecting Don with Volga, Volga with Neva, and on to the Baltic Sea (Cristescu et al. 2001, as cited by MacIsaac et al. 1999)

population of the fishhook waterflea originated from a small colonizing population in the Black Sea. The colonization of the Great Lakes, on the other hand, most probably resulted from the transfer of the species from the Baltic Sea via the water ballast of transatlantic vessels (MacIsaac et al. 1999, Cristescu et al. 2001).

THE SPECIES' EFFECT ON ECOSYSTEMS AND THE ECONOMY

C. pengoi invasions into the Baltic Sea and the Great Lakes of North America did not result in the loss of any native species and it even contributed to local species richness in the newly colonized areas (Ojaveer et al. 2002). The fishhook waterflea's

ecological effect on the colonized ecosystem has been poorly investigated. It is evaluated based on changes in local zooplankton structures after the invasion as well as an analysis of digesta samples collected from selected planktivorous species (Ojaveer et al. 2004).

Adverse effects of *C. pengoi* invasion were noted in the Gulf of Riga where the species deepened the population decline of a small native cladoceran, *Bosmina coregoni maritima*. According to Ojaveer et al. (2000), the above could be directly attributed to the predation pressure of *C. pengoi*. The authors based their conclusions on similar changes observed in the zooplankton structure colonized by another predatory cladoceran, *Bythotrephes cederstroemi* (which shows many similarities to *C. pengoi*). Changes in the zooplankton structure of Lake Ontario were also noted after an invasion of the fishhook waterflea. A clear drop was reported in the abundance of species such as *Daphnia retrocurva*, *Bosmina longirostris* and *Diacyclops thomasi* (Makarewicz et al. 2003). The elimination of small filtering organisms from the zooplankton community in line with the top-down strategy frees the phytoplankton from the predation pressure of zooplankton, and it could contribute to eutrophication (Uitto et al. 1999).

C. pengoi invasions also modify local trophic relations. The species could exert two types of effects on the food chain: it could compete with other planktivorous species that rely on the same sources of nutrition (e.g. herring, sprat, Mysidacea) or it could offer a dietary source for other organisms (Ojaveer et al. 2000, Vanderploeg et al. 2002). Owing to its large size, *C. pengoi* is preferred by large, planktivorous fish that rely on their vision to find prey. In the Baltic Sea, such fish include the herring (*Clupea harengus*), the sprat (*Sprattus sprattus*) and the three-spined stickleback (*Gasterosteus aculeatus*). Prior to the *C. pengoi* invasion, their diets were composed mainly of copepods of the order Calanoida (*Acartia* sp., *Eurytemora affinis* and *Temora longicornis*) and cladocerans (*Bosmina coregoni maritima* and *Pleopsis polyphemoides*). Upon its emergence, the fishhook waterflea had a 61% share of the herring's diet, a 70% share of the sprat's diet, and it was also observed in the diet of the three-spined stickleback (Gorokhova et al. 2004, Peltonen et al. 2004, Kotta et al. 2006). *C. pengoi* is also a source of nutrition for other predatory zooplankton species. According to the results of genetic research by Gorokhova (2006) and a study by Gorokhova and Lehtiniemi (2007), the fishhook waterflea is willingly consumed by the popular species native to the Baltic Sea – *Neomysis integer*, *Mysis mixta* and *Mysis relicta*.

The harmful effects of *C. pengoi* invasions are most severely felt by the fishing industry. The hook-shaped end of the caudal process enables this cladoceran to form dense clusters that freely float in water. Fishhook waterfleas are easily entangled on fishing nets, they clog and foul the nets and create serious problems for fishermen. The process of removing those organisms from fishing equipment is time-consuming and laborious. Nets have to be dried for minimum three days, and dried matter crumbling from the net may cause allergies (Hornatkiewicz-Żbik 1999, Kołodziejak-Nieckuła 2005). The fouling of fishing nets has serious economic repercussions. In 1996-2000, the fishing farm of Primorsb Ribak in the Gulf of Finland reported losses of USD 50,000 (Panov et al. 2002). Changes in the food web and energy flow at lower trophic levels caused by *C. pengoi* invasions could affect

fish production. The above could be a positive phenomenon, especially in periods of nutritional deficiency when the fishhook waterflea offers an additional source of food (Ojaveer et al. 2000), but it could also result in feeding competition. Owing to similarities in the diet of the analyzed cladoceran, fish fry and planktivorous fish (herring, sprat), massive *C. pengoi* invasions could limit the availability of food sources for fish (Pienimäki and Leppäkoski 2004).

CONCLUSIONS

C. pengoi scored a widespread invasive success in just 5-7 years since its introduction owing to the euryhaline character of the species and the predominance of parthenogenetic reproduction over sexual reproduction. The emergence of *C. pengoi* had a number of ecological consequences, including changes in the zooplankton structure and food webs. The species fouls fishing nets and causes serious losses for the economy, up to now this problem has not yet been thoroughly investigated and requires further analysis. Previous experience suggests that the fishhook waterflea could also invade neighboring water bodies. Its populations should be regularly monitored to identify the species' further expansion routes. The presence of *C. pengoi* in the Polish part of the Vistula Lagoon should be investigated in detail, as the existing data are scant and date back to the late 1990s (Hornatkiewicz-Żbik 1999). The studies carried out in 2007-2008 confirmed the presence of the fishhook waterflea in the Vistula Lagoon. The average abundance and biomass of *C. pengoi* reached 2 individuals/dm³ and 0.0068 mg/dm³, respectively, in July 2007, while an increase to 14 individuals/dm³ and 0.0605 mg/dm³ was reported in May 2008 (Paturej 2009). Based on the oral accounts from fishermen, the fishhook waterflea continues to spread in this water body, causing substantial problems for the fishing industry. For this reason, its distribution, densities, population structure and interactions with other species need to be investigated to determine the range of *C. pengoi* invasions and their effect on the ecosystem of the Vistula Lagoon.

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CERCOPAGIS PENGROI JAKO GATUNEK INWAZYJNY

Streszczenie

Wioślarka kaspijska, pochodząca z regionu pontokaspijskiego, jest doskonałym przykładem gatunku inwazyjnego. W ciągu zaledwie dekady, od momentu pojawienia się, skolonizowała prawie cały Bałtyk i większość z Wielkich Jezior Ameryki Północnej. Osiągnęła to dzięki swojej specyfice ekologicznej i biologicznej. Jest to gatunek charakteryzujący się dużą euryhalinowością i dominacją rozmnażania partenogenetycznego nad płciowym. Takson szybko zadomowił się w zasiedlonych ekosystemach i stworzył w nich trwałe populacje. Konsekwencje ekologiczne i ekonomiczne pojawienia się tego gatunku są zauważalne, ale do dziś nie są w pełni poznane i wymagają szerszych analiz.