

Invasion biology of Ponto-Caspian onychopod cladocerans (Crustacea: Cladocera: Onychopoda)

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Abstract We review the patterns of recent range expansions and the biology of the invasive Ponto-Caspian predatory onychopod cladocerans: *Cercopagis pengoi*, *Evadne anonyx*, *Podonevadne trigona*, *Cornigerius maeoticus* and *Cornigerius bicornis*. Recent invasions of *C. pengoi*, *E. anonyx* and *C. maeoticus* into the Baltic Sea can be attributed to the climate change, facilitating invasibility of the eastern Baltic Sea coastal ecosystems by the warm water Ponto-Caspian species and intensive shipping activities via the Volga-Baltic waterway (European “northern invasion corridor”). All three species can be considered to be established in pelagic communities of the eastern Gulf of Finland. Only one onychopod species, *C. pengoi* has invaded the North American Great Lakes via an existing invasion corridor between the eastern Baltic and the Great Lakes. Invasive onychopods may

possess adaptive life cycles, switching to early gamogenetic reproduction which enables their establishment in recipient ecosystems and further dispersal. Analysis of temperature and salinity ranges of the Ponto-Caspian onychopod species in native and invaded habitats, indicates that they are potentially able to form populations in a wide range of inland and coastal water ecosystems in temperate zones. Ponto-Caspian onychopods can be considered as “high risk” invasive species, in terms of their potential for range expansion and impact on recipient ecosystems.

Keywords Invasive crustaceans · Onychopoda · Ponto-Caspian species · Invasion history · Risk assessment

Introduction

The Ponto-Caspian region (the Black, Azov seas and the Caspian Lake, including their basins) is serving as an important donor for invasive aquatic alien species worldwide, specifically for European and North American inland waters, with shipping-related activities as a main vector of both inter- and intracontinental dispersal (Mordukhai-Boltovskoi, 1964a; Panov et al., 1999; Ricciardi & MacIsaac, 2000; Reid & Orlova, 2002; Vanderploeg et al., 2002; Ketelaars, 2004; Galil et al., 2007). Within Europe, inland and coastal waters in the Baltic Sea

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and North Sea basins are the main recipient areas for invasions of Ponto-Caspian species (Jazdzewski, 1980; Bij de Vaate et al., 2002; Jazdzewski & Konopacka, 2002; Ketelaars, 2004; Galil et al., 2007). At present, 22 fish and aquatic invertebrate species of Ponto-Caspian origin are successfully established in the Baltic Sea basin, comprising almost a third of all established non-indigenous aquatic species in the Baltic (Olenin et al., 2006). In the Laurentian Great Lakes during the last two decades, 8 Ponto-Caspian species have successfully established themselves, causing significant ecological impacts (Vanderploeg et al., 2002; Grigorovich et al., 2003a). Invasion success of Ponto-Caspian species in inland and coastal waters outside their native range can be attributed primarily to the euryhalinity of the Ponto-Caspian biota (Mordukhai-Boltovskoi, 1964b; Dumont, 1998, 2000).

Intensive shipping activities in the Ponto-Caspian region itself have also resulted in a number of biological invasions in the Black, Azov seas and the Caspian, with severe economic and ecological consequences for their ecosystems (Shiganova et al., 2001; Grigorovich et al., 2002; Grigorovich et al., 2003b; Dumont et al., 2004). As a consequence, the Ponto-Caspian region may serve as a secondary donor for these invasive species via existing corridors, specifically to the Baltic and North seas.

Dispersal patterns of Ponto-Caspian species had been recently reviewed by Bij de Vaate et al. (2002) and Ketelaars (2004). These reviews have further developed the concept of inland European waterways as intracontinental invasion corridors from the Ponto-Caspian region to inland and coastal waters in the Baltic and North sea basins, an idea which was initially suggested for the Volga-Baltic inland waterway (Panov et al., 1999). These reviews, however, have focused on benthic macroinvertebrate organisms and comparatively low attention has been given to the invasive planktonic Ponto-Caspian predatory “cladocerans” (Crustacea: Branchiopoda: Onychopoda), which include 5 onychopod species found in the Black, Azov seas and the Caspian Lake, namely *Cercopagis pengoi* (Ostroumov, 1891), *Evadne anonyx* Sars, 1897, *Podonevadne trigona* (Sars, 1897), *Cornigerius maeoticus* (Pengo, 1879) and *Cornigerius bicornis* (Zernov, 1901) (Mordukhai-Boltovskoi, 1964b; 1979). These species possess

euryhalinity due to their evolution and, consequently, they are well adapted to invade new environments, specifically *C. pengoi*, *P. trigona* and *C. maeoticus*, which were found spreading outside their native range already in the mid 20th century following the construction of reservoirs in the Dniepr, Don and Volga rivers (Mordukhai-Boltovskoi, 1979; Dumont, 2000). Moreover, Dumont (2000) considered the origin of all known onychopod species monophyletic; all 33 onychopod species were found to have originated in the Ponto-Caspian basin, with two freshwater and seven marine species possessing either a world-wide, or wide distribution in the northern hemisphere as a result of natural range expansion from the Ponto-Caspian area. Genetic studies of onychopods have revealed that diversification of this group has occurred over the past 10–20 million years and that disruptive selection by predators is considered as the main driving force in shaping the body plane diversity of onychopods (Cristescu & Hebert, 2002).

This group of obviously invasive species, however, has attracted serious attention of invasion biologists comparatively recently, after human-mediated spread of the “freshwater Palearctic” *Bythotrephes longimanus* Leydig 1860 from eastern Europe to North America and the “euryhaline Ponto-Caspian” *C. pengoi* to the Baltic Sea and North American Great Lakes (see reviews by Krylov et al., 2004 and Panov et al., 2004).

In the present paper, we have summarized available information on invasion histories and biology of Ponto-Caspian onychopods, which have expanded their native ranges in geographic Europe comparatively recently as a result of human-mediated invasions. This background information is essential for developing approaches to risk assessment of further spread and determining the ecological impacts of these invasive species.

Invasion history of Ponto-Caspian onychopods

Cercopagis pengoi

Cercopagis pengoi (Ostroumov, 1891) (Superorder Cladocera: order Onychopoda: family Cercopagidae) is native to the Sea of Azov, Caspian and Aral lakes (*C. pengoi* disappeared from the

latter after an increase in salinity of the lake along with most other onychopods—see Rivier (1998)), certain river estuaries of the Black Sea (Danube, Dnieper and Bug rivers) and the Gebenjinskoe Lake in Bulgaria (Rivier, 1998). Between 1960–1975, after construction of the dams on the Don and Dnieper rivers in the Black Sea basin, *C. pengoi* invaded the freshwater reservoirs of Kakhovka, Zaporozhsk, Kremenchug, Tsyml'yansk and Veselovsk (Krylov et al., 1999). Most recently, in 2000–2005, *C. pengoi* was recorded in zooplankton samples from the Volga River reservoirs; Volgograd, Saratov and Kuibyshev (Eugene A. Bychek unpubl.) (Fig. 1).

In 1992, *C. pengoi* was first found outside the Ponto-Caspian basin in the Baltic Sea area (Gulf of Riga and Gulf of Finland), possibly as a result of the discharge of ballast water (Ojaveer & Lumberg, 1995; Ojaveer et al., 2000). After these first records, *C. pengoi* was found in the Neva River estuary in 1995, already at high densities and has since become a common zooplankton species in the eastern Gulf of Finland (Panov, 1996; Avinsky, 1997; Krylov et al., 1999; Panov et al., 1999; Uitto et al., 1999). In 1997, *C. pengoi* was reported from the central Baltic Sea and Swedish coastal waters (Gorokhova et al., 2000) and in 1999, it had spread to the Gulf of Bothnia, Gulf of Gdansk and the lagoons of the southern Baltic Sea (Bielecka et al., 2000; Leppäkoski

et al., 2002; Krylov et al., 2004) (Fig. 1). In the Gulf of Finland, in areas of mass development of *C. pengoi* (hundreds and thousands of ind. m³), fishing nets are often clogged by this species which results in severe economic losses for the local coastal fishery (Panov et al., 1999).

In summer 1998, *C. pengoi* was found outside Eurasia for the first time, where it was recorded snagged on sport fishing lines and in zooplankton samples in Lake Ontario in North America (MacIsaac et al., 1999; Barbiero & Tuchman, 2000). Most likely, this is a result of secondary introduction by ships ballast water from the eastern Baltic via an existing invasion corridor, identified in case of *Bythotrephes longimanus* invasion by Berg et al. (2002). A recent genetic study by Cristescu et al. (2001) demonstrated that the population of *C. pengoi* in the North American Great Lakes is most likely to have originated from the Baltic Sea source population, namely the Neva Estuary (eastern Gulf of Finland). From Lake Ontario, *C. pengoi* has spread in only a few years to Lake Michigan, western Lake Erie and some adjacent inland lakes (Charlebois et al., 2001; Therriault et al., 2002).

Cornigerius maeoticus and *Cornigerius bicornis*

Cornigerius maeoticus (Pengo, 1879) (Superorder Cladocera: order Onychopoda: family Podonidae) is native to the Sea of Azov, lower reaches of the Danube, Dniepr and Bug rivers and the Caspian Lake (Rivier, 1998). Rivier (1998) has also found by studying valve morphology in *C. maeoticus*, that there are two subspecies, *C. maeoticus maeoticus* (Pengo, 1879), inhabiting the Ponto-Azov area and *C. maeoticus hircus* (Sars, 1902), which is characteristic for the Caspian Lake. However, genetic evidence for the separation of Ponto-Caspian onychopods by subspecies is lacking (Cristescu & Hebert, 2002) and in present paper we have not considered the subspecies of *C. maeoticus* (see also case study of *Podonevadne trigona*).

As in the case of *Cercopagis pengoi*, the expansion of *C. maeoticus* (subspecies *C. m. maeoticus* sensu Rivier (1998)) outside its native range, started after the creation of the reservoirs

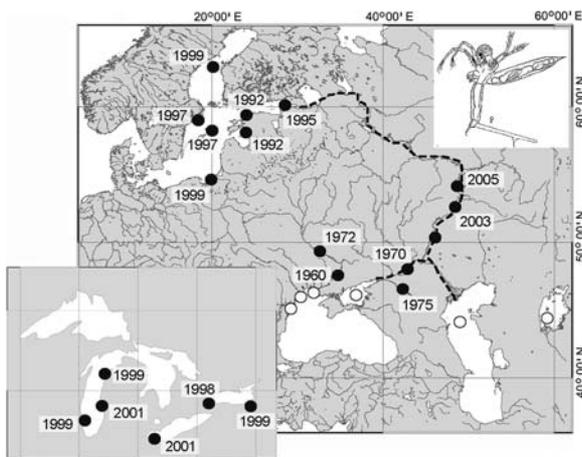


Fig. 1 Distribution of *Cercopagis pengoi* in the native range (open cycles) and sites of first records of its range expansion (filled cycles). Dashed line indicate the “northern invasion corridor”

on the Don, Dnieper, and Volga rivers, with *C. maeoticus* appearing in the Kakhovka (1959), Tsimlyansk (1961), Zaporozhsk (1965) and Kremenchug (1969) reservoirs (Rodionova et al., 2005). In the 1970s, this species was first recorded in the Volga River basin (Volgograd Reservoir) and in the remaining Dnieper River reservoirs (the Kiev, Kanev, Dneprodzerzhinsk and Kakhovka). In the mid 1990s, it was found in the Saratov and Kuibyshev reservoirs of the Volga River (Eugene A. Bychek unpubl.). In 2003, *C. maeoticus* was first recorded outside the Ponto-Caspian basin in the eastern Baltic Sea (Rodionova et al., 2005) (Fig. 2).

The congeneric species with a known invasion history, *C. bicornis* (Zernov, 1901) is mainly found in spring in the Sea of Azov and Caspian Lake and has expanded its native distribution range to Tsimlyansk Reservoir and the Dniepr canals (Rivier, 1998).

Podonevadne trigona

Podonevadne trigona (Sars, 1897) (Superorder Cladocera: order Onychopoda: family Podonidae) is native to the Caspian Lake, Sea of Azov and the lagoons of the Dniestr, Dniepr and Bug rivers (Rivier, 1998). As for *Cornigerius maeoticus*, Rivier (1998) distinguishes by valve mor-

phology two subspecies of *P. trigona*, with subspecies *P. trigona trigona* (Sars, 1897) found in the Caspian Lake. The other subspecies, *P. trigona ovum* (Zernov, 1901) is characteristic for the Ponto-Azov basin and after construction of reservoirs in the Dniepr and Don rivers, it invaded Kakhovka (1959), further reservoirs of the Dniepr River and Don river basin and the Tsimlyansk reservoir (1966) (Rivier, 1998) (Fig. 3).

Evadne anonyx

Evadne anonyx Sars, 1897 (Superorder Cladocera: order Onychopoda: family Podonidae) is native to the Caspian and Aral lakes (currently it is not present in the Aral due to increased salinity) and possibly the Ponto-Azov basin (Mordukhai-Boltovskoi, 1966; Rivier, 1998). Unlike other invasive onychopods, *E. anonyx* has no recent invasion history in the Ponto-Caspian basin. However, in 2000 it was first recorded outside its native range in the eastern Gulf of Finland, Baltic Sea and currently, this species can be considered to be well established in the easternmost Baltic (Rodionova & Panov, 2006) (Fig. 4). This case study can be considered as an example of long-distance intracontinental transfer of alien species by ballast water directly from the Caspian Lake to the eastern Baltic Sea. Genetic

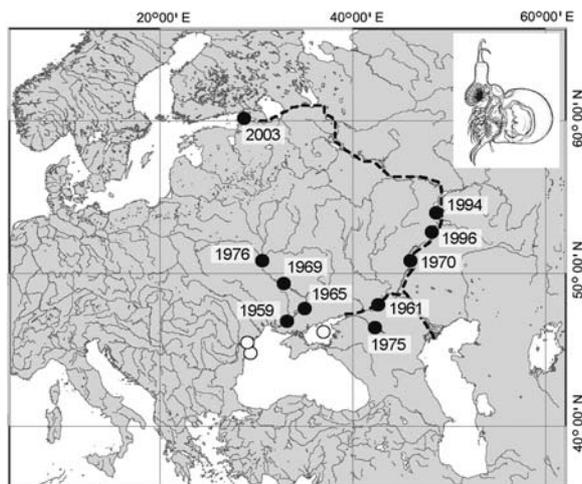


Fig. 2 Distribution of *Cornigerius maeoticus* in the native range (open cycles) and sites of first records of its range expansion (filled cycles). Dashed line indicate the “northern invasion corridor”

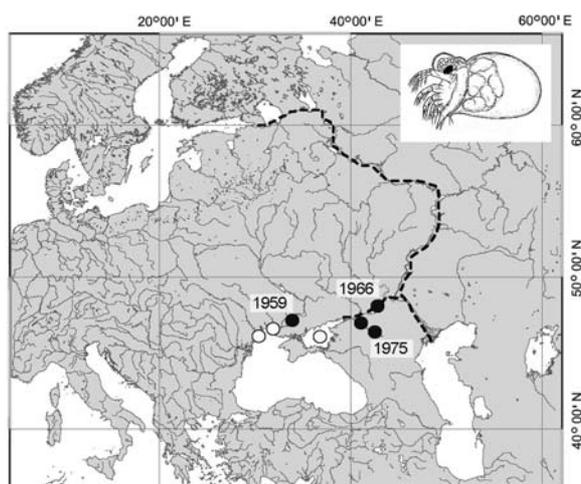


Fig. 3 Distribution of *Podonevadne trigona* in the native range (open cycles) and sites of first records of its range expansion (filled cycles). Dashed line indicate the “northern invasion corridor”

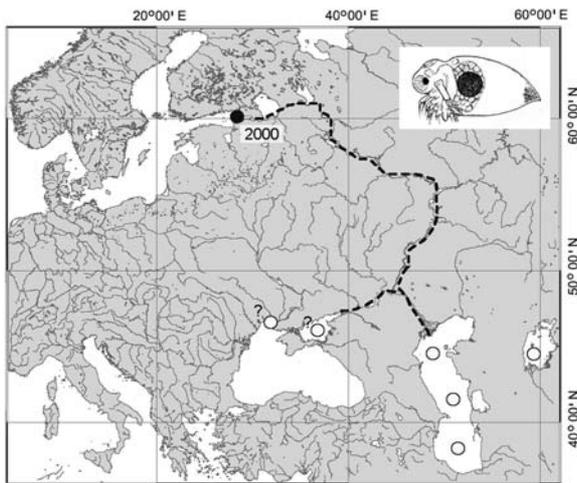


Fig. 4 Distribution of *Evadne anonyx* in the native range (open cycles) and sites of first records of its range expansion (filled cycles). Dashed line indicate the “northern invasion corridor”

studies, however, of *E. anonyx* in recipient and potential donor areas are needed to validate this hypothesis.

General patterns of biology of the invasive onychopods

Comprehensive reviews of the biology of the Ponto-Caspian onychopods are available elsewhere (Mordukhai-Boltovskoi, 1966; Rivier, 1998). Also, a comprehensive comparative study of *C. pengoi* variability in body dimensions and population demography in the Caspian, Lake Ontario and the Baltic Sea has been recently published by Grigorovich et al. (2000). In the present paper, we review patterns of biology of this group, which are essential for understanding the comparatively broad native range of these species, their invasion success in recipient ecosystems and for risk assessment purposes (predictions of future introductions of invasive species and their possible ecosystem impacts). Selected biological traits of Ponto-Caspian invasive onychopods are given in Table 1.

Temperature and salinity tolerance

Ponto-Caspian invasive onychopods are usually considered as “thermophilic” species, reaching

their maximal abundance in the middle of summer at temperatures above 15°C and typically disappearing in months with temperatures below 10°C (Mordukhai-Boltovskoi, 1966; Rivier, 1998; Krylov et al., 1999). However, this “thermophily” is relative and may not be the limiting factor for potential species distribution in a latitudinal direction, as all invasive Ponto-Caspian onychopods, like most Cladocera, are able to survive unfavorable cold water conditions in winter as resting eggs in bottom sediments.

Most Ponto-Caspian onychopods have a relatively high salinity tolerance and can be considered as “euryhaline” species. *Cercopagis pengoi*, *Podonevadne trigona* and *Cornigerius maeoticus* may live in freshwater and in water with a salinity up to 13‰ (Rivier, 1998). Salinity tolerance of *Evadne anonyx* was considered much narrower, from 9 to 13.5‰ in the native distribution range (Rivier, 1998), but *E. anonyx* has been recently found in the Neva Estuary (easternmost Baltic Sea) at salinities between 1–3‰ (Rodionova & Panov, 2006), which indicates the wider salinity tolerance of this species. In contrast with other invasive onychopoda, it is likely that *E. anonyx* is unable to survive pure freshwater conditions, which is a potential reason for the absence of an invasion history for this species in reservoirs of Ponto-Caspian rivers.

Analysis of temperature and salinity tolerances of these invasive onychopod species, therefore, indicates that they are potentially able to form populations in a wide range of inland and coastal water ecosystems in temperate regions.

Life cycle and reproduction patterns

Like most Cladocera, invasive Ponto-Caspian onychopods possess an heterogonic reproductive cycle and are able to undergo parthenogenetic and amphigonic (sexual, or gamogenetic) reproduction. As a general feature of most Cladocera, onychopods hatch from resting eggs, that survive the winter in bottom sediments, in late spring-early summer. For the rest of the summer, they typically reproduce parthenogenetically and then switch to sexual reproduction in the fall to produce resting “winter” eggs (Rivier, 1998; Rivier, 2004). Mordukhai-Boltovskoi (1966) first

Table 1 Selected biological traits of invasive Ponto-Caspian onychopods: fe-p = instar III parthenogenetic females, fe-g = instar III gamogenetic females, male = instar III males, numbers in parenthesis indicate range

Species	Lifestage	Length, mm	Height, mm	Fecundity, Eggs ind ⁻¹	Temperature range, °C	Salinity range, ‰	Reference
<i>Cercopagis pengoi</i>	fe-p	1.73		13		Freshwater—13	Rivier, 1998;
Caspian population							Grigorovich et al., 2000
Baltic Sea population	fe-p	2.41 (2.19–2.53)		5.9 (1–15)	8–24	0.6–3.0	Rodionova & Panov, unpubl.
	fe-g	2.40 (2.24–2.56)		1.4 (1–2)			
	Male	2.14 (1.85–2.50)					
Great Lakes population	fe-p	1.45		2–13		Freshwater	Grigorovich et al., 2000;
	fe-g	1.58		1–2			Makarevich et al., 2001;
	Male	1.37					Ojaveer et al., 2001
Volga River population	fe-p	1.68–1.83			19.1–23.3	Freshwater	Bychek, unpubl.
<i>Cornigerius macoticus</i>	fe-p	0.5–0.8	0.6–0.9			Freshwater—13	Rivier, 1998
Ponto-Azov population	Male	0.6	0.65				
Baltic Sea population	fe-p	1.09		7.7 (5–10)	11–21	0.7–1.7	Rodionova & Panov, unpubl.
Volga River population	fe-p	0.53–0.91			16.2–23.3	Freshwater	Bychek, unpubl.
	Male	0.5					
<i>Cornigerius bicomis</i>	fe-p	0.6–0.7				Freshwater—13	Rivier, 1998
Ponto-Azov population							
<i>Evadne anonyx</i>	fe-p		2.0–2.1			9–13.5	Rivier, 1998
Caspian population	Male		1.2–1.4		10–25		
Baltic Sea population	fe-p	0.66	1.1	3.9 (1–6)	11–24	1–3	Rodionova & Panov, 2006
	fe-g	0.65	1.1	1.7 (1–2)			
	Male	0.49	0.79				
<i>Podonevadne trigona</i>	fe-p	0.4–0.5			11–16	Freshwater—13	Rivier, 1998
Ponto-Azov population							

noted that gamogenetic reproduction, with the development of resting “latent” eggs, is often found in onychopod species that are widely distributed beyond the Caspian—in the Aral Sea and Pontoazov basins, namely in *Cercopagis pengoi*, *Cornigerius maeoticus*, *Evadne anonyx* and *Podonevadne trigona*. In addition, in the same species males and winter eggs are more numerous in the shallow freezing waters of Azov Sea and lagoons than in the deep Caspian (Mordukhai-Boltovskoi, 1966).

Invading population of *C. pengoi* in the Neva Estuary (easternmost Baltic Sea) showed a remarkable reproductive strategy, producing a large number of resting eggs during the summer months in 1996 (Panov et al., 1996; Krylov & Panov, 1998), followed by a gradual decline in gamogenetic reproduction by 2000. This strategy is the likely result of selective fish predation on more visible sexual females with resting eggs (Panov et al., 2004). Prolonged summer gamogenetic reproduction was also found in *E. anonyx* which has become recently established in the eastern Gulf of Finland (Rodionova & Panov, 2006).

It has been suggested that a large pool of resting eggs from *C. pengoi* in the Neva Estuary has enabled this species to achieve rapid population growth in recipient ecosystems and to pose an increased risk of dispersal by ships’ ballast water (Panov et al., 1996; Krylov & Panov, 1998; Panov et al., 1999). Indeed, this pattern of reproductive strategy has facilitated the secondary invasion of *C. pengoi* from the eastern Baltic to the North American Great Lakes, which occurred just a few years after the establishment of this species in the eastern Baltic. Populations of *C. pengoi* in Lake Ontario in the first years after invasion, also possessed an unusual midsummer period of sexual reproduction (Grigorovich et al., 2000; Makarewicz et al., 2001), which was characteristic for the source population in the eastern Baltic Sea (Neva Estuary) (Panov et al., 2004).

Feeding and predatory impacts

Onychopoda are generally considered as active predators; they capture prey (mainly small planktonic crustaceans) with the first pair of thoracic

legs (thoracopods I), retain it using their other three pairs of thoracic legs (thoracopods II–IV), crush the cuticle by using their mandibles and suck out the body contents (Rivier, 1998). Experimental studies on the feeding biology of Ponto-Caspian onychopods are generally lacking (but see Witt & Caceres, 2004). Analysis of their gut contents and direct observations indicate that these species may consume plankton invertebrates, including rotifers, copepods and cladocerans, and algae (Rivier, 1998).

Field observations of long-term and seasonal changes in zooplankton communities invaded by *Cercopagis pengoi*, showed changes in the abundance of some native species, which can be attributed to the direct predation by *C. pengoi*. In the Baltic Sea, *C. pengoi* was found to affect the population size of the previously abundant *Bosmina coregoni maritima* (Ojaveer et al., 2000) and may potentially affect other groups of zooplankton (Uitto et al., 1999; Telesh & Ojaveer, 2002).

In Lake Ontario, *C. pengoi* is already playing an important role in the zooplankton (Ojaveer et al., 2001; Makarewicz et al., 2001, 2003) and may suppress some native zooplankton species, including rotifers, juvenile copepods and small cladocerans, namely *Bosmina longirostris* (Benoit et al., 2002; Laxson et al., 2003).

Biotic interactions with other predators

Information is scarce on the biotic interactions of Ponto-Caspian onychopoda with other predators in their native and extended range, but it is essential for the estimation of biological resistance of already invaded and potential recipient ecosystems.

In their native range in the Caspian Lake, onychopods are an important part of the diet of many commercial planktivorous fish (Rivier, 1998). Recently, the abundance of native zooplankton species in the middle and south Caspian has significantly declined, due to the predatory impact of the accidentally introduced Atlantic ctenophore *Mnemiopsis leidyi* (Shiganova et al., 2001; Shiganova et al., 2004).

In the recipient ecosystems, the Ponto-Caspian invasive onychopods can also be controlled to

some extent by the native and/or introduced predators, specifically by fish. In the Baltic Sea, *Cercopagis pengoi* is actively consumed by the Baltic herring *Clupea harengus membras* (Ojaveer et al., 2000; Antsulevich & Välipakka, 2000). Gorokhova et al. (2004) found that gamogenetic females of *C. pengoi* carrying dark visible resting eggs are more vulnerable to fish predation (Baltic herring and sprat *Sprattus sprattus*). These data on the selective predation of zooplanktivorous fish on gamogenetic females may support our initial hypothesis on the role of invader-selective fish predation in the rapid evolution of the life cycle of invading species (Panov et al., 2004).

Results from a study of Lake Ontario fish (alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax*), indicate that *C. pengoi* are effectively consumed by adult alewife. However, *C. pengoi* were not found in the stomachs of juvenile fish, with which this invasive onychopod species may compete for smaller zooplankton (Bushnoe et al., 2003). The latter study also showed that *C. pengoi* may reach high abundances in the invaded ecosystem even under conditions of heavy predation by local fish populations.

Among invertebrate predators, the invasive onychopod species *Bythotrephes longimanus* seems to be the most effective predator of the Ponto-Caspian *C. pengoi* both in the Baltic Sea and the North American Great Lakes. At an intensively studied location in the Neva Estuary, *C. pengoi* coexists with native populations of *B. longimanus* (source population of *B. longimanus* for North American Great Lakes—see Berg et al. (2002), with a strong localised negative relationship between these two predatory cladocerans. The larger predator, *B. longimanus* effectively controlling the smaller *C. pengoi* (Panov et al., 2004). The ability of *B. longimanus* to control *C. pengoi* in North American Great Lakes, has also been recently demonstrated in an experimental study of predator-prey relationships between these two species by Witt & Cáceres (2004). The high abundance of *B. longimanus* in Lake Erie (Barbiero & Tuchman, 2000) may, therefore, be considered a likely “ecosystem biotic resistance” factor for the development of abundant populations of *C. pen-*

goi in this lake. At present, the latter onychopod species is the most abundant in Lake Ontario, where *B. longimanus* is rare compared with all the North American Great Lakes. However, the biotic interactions of *C. pengoi*, as well as of other invasive onychopod species, requires further study.

Qualitative risk assessment

The first predictions of range expansion of Ponto-Caspian species were produced in one of the early works by Mordukhai-Boltovskoi (1964b). This was the first attempt of “qualitative” risk assessment for the Ponto-Caspian invasive species, based on information relating to their biological patterns, invasion histories and potential pathways of introduction. However, Ponto-Caspian onychopods were not considered in this paper.

The first qualitative risk assessments for Ponto-Caspian invasive onychopods were conducted in the late 1990s, after the invasion of *Cercopagis pengoi* into the Baltic Sea and North American Great Lakes. Panov et al. (1999) predicted the invasion into the Neva Estuary (eastern Baltic) of two common onychopod species, *Cornigerius maeoticus* and *Podonevadne trigona* which had known invasion histories in the Ponto-Caspian basin via the Volga-Baltic invasion corridor (European “northern invasion corridor”). Indeed, in 2003 *C. maeoticus* was first recorded in the Neva Estuary (Rodionova et al., 2005), but the second new onychopod invader after *C. pengoi* in the Baltic was *Evadne anonyx*, which was first recorded in the zooplankton of the Neva Estuary in 2000 (Rodionova & Panov, 2006). The latter species was not previously considered as a high risk species, because *E. anonyx*, before its invasion in the eastern Baltic, had no invasion history and was not considered to be able to develop sustainable populations at salinities below 9‰ (Rivier, 1998). In the eastern Gulf of Finland, *E. anonyx* successfully established itself in areas with low water salinities as low as 1–3‰ (Rodionova & Panov, 2006). The unexpected invasion of *E. anonyx* into the eastern Baltic Sea may indicate that the most common Ponto-Caspian onychopods (*P. trigona*, *P. camptonyx*, *P. angusta*,

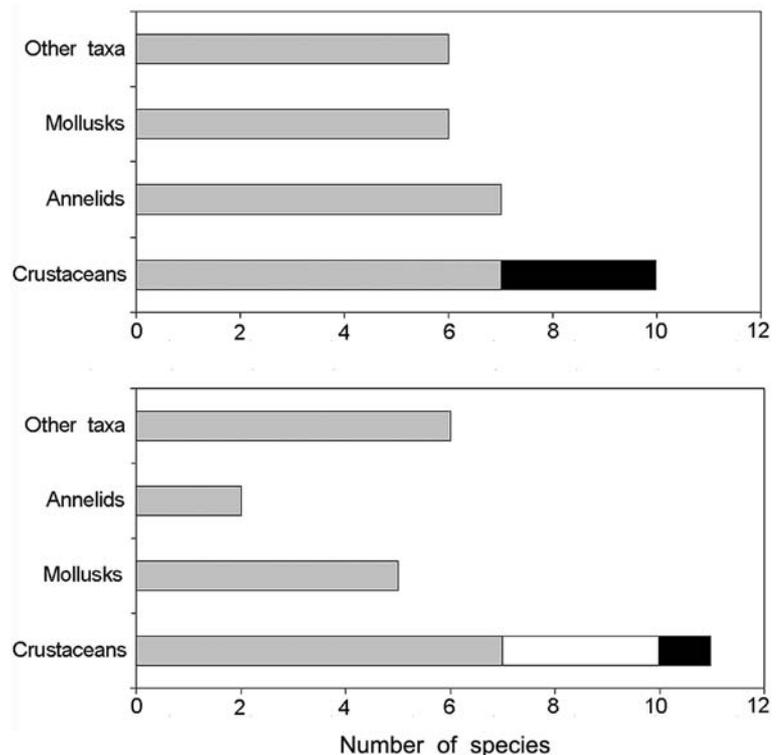
Polyphemus exiguous, *Evadne prolongata*) may pose some risk of long-distance intracontinental transfer if appropriate pathways of introduction are available (shipping along the Volga-Baltic inland waterway). In general, the Ponto-Caspian onychopods pose the highest risk for the Baltic Sea, as all the alien cladocerans established in the eastern Baltic belong to this group (Fig. 5), and the rapid and successful establishment of three onychopod species has occurred in this region during last 15 years.

It is important to note, that during the last two decades invasion rates of Ponto-Caspian species in the eastern Gulf of Finland (the upper part of the Volga-Baltic waterway) have increased drastically, with at least 50% of the established Ponto-Caspian species invading the gulf since 1986. In addition, during the last 50 years the rates of successfully established alien species in the eastern Gulf of Finland were 5-fold higher for Ponto-Caspian species than for species from other origins. The most recent Ponto-Caspian invaders to the Gulf of Finland, onychopod crustaceans *C. pengoi*, *E. anonyx* and *C. maeoticus*, were

introduced to the gulf with the ballast water of ships via the northern invasion corridor during 1990–2000. This was a period of significant decline in shipping intensity via the Volga-Baltic inland waterway caused by an economic crisis and a switch to the market economy in Russia. This invasion phenomenon can, therefore, attributed to the environmental changes in the recipient ecosystem and its increasing invasibility to the warm water Ponto-Caspian species.

Grigorovich et al. (2003a) also suggested that only two invasive Ponto-Caspian onychopods were risk species for the North American Great Lakes, *C. maeoticus* and *P. trigona*. These species had an invasion history in the Ponto-Caspian basin and were initially considered as risk species for the eastern Baltic, donor area of invasive onychopods *Bythotrephes longimanus* and *Cercopagis pengoi* for the Great Lakes (Panov et al., 1999). Currently only one Ponto-Caspian onychopod species has invaded the Great Lakes (Fig. 5), but considering the existence of the defined invasion corridor between the eastern Baltic and the Great Lakes, introduction of other

Fig. 5 Taxonomic composition of alien invertebrate species introduced with ballast water to the Baltic Sea (top) and North American Great Lakes (bottom). Open bars indicate cladocerans, black filled bars—onychopods. Data used: Grigorovich et al., 2003a, Olenin et al., 2006



Ponto-Caspian onychopods to North America is possible. *C. maeoticus* poses the highest risk to the Great Lakes and *E. anonyx* is a risk species for the estuaries of the North American east coast (Rodionova & Panov, 2006).

It is important to note that the invasion of *C. pengoi* to the Laurentian Great Lakes took place after the implementation of the ballast water management options for ships entering the Great Lakes, namely the exchange of ballast water in the open ocean, which is currently considered as an effective measure to decrease the risk of transfer of freshwater organisms by ships. However, as it has been recently shown, that the resting eggs of freshwater invertebrates may hatch from the ballast water sediments which have previously experienced the influence of salt water (Bailey et al., 2003, 2004, 2005). Thus, Ponto-Caspian invasive onychopods producing large numbers of resting eggs, pose a very high risk of introduction with ballast waters, even with regular ballast water management procedures (specifically in the case of the prolonged seasonal gamogenetic reproduction of *C. pengoi* and, to a lesser extent, in *E. anonyx* in the recipient ecosystems), which might be ineffective in the case of aquatic invertebrates which produce resting eggs that accumulate in the sediments of ballast tanks (MacIsaac et al., 1999; Bailey et al., 2005).

The ability of *C. pengoi* to effectively colonize known recipient ecosystems in Europe and North America, despite a severe negative relationship with *B. longimanus* and strong selective fish predation, indicates that “biological resistance” to invasion by Ponto-Caspian onychopods can be important only on a localised and temporal basis. Thus, at present these species can be considered as “high risk”, in terms of their potential for range expansion and impact on recipient ecosystems. The application of more accurate quantitative risk assessments for this group requires further study, including experimental studies of salinity tolerance and inoculation rates of the resting stages from ships ballast water and other human-mediated vectors.

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