

Impacts

ECOLOGICAL IMPACT OF PONTO-CASPIAN INVADERS IN THE BALTIC SEA, EUROPEAN INLAND WATERS AND THE GREAT LAKES: AN INTER-ECOSYSTEM COMPARISON

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Abstract

We review the ecological impacts of Ponto-Caspian invaders in the Baltic Sea, selected lakes and rivers in inland Europe, and the North American Great Lakes. Each of these regions has been invaded multiple times in recent decades by Ponto-Caspian invertebrates and fishes. In attempt to identify predictable patterns, we compared the magnitude and direction of the impacts of these invaders on ecosystem components (phytoplankton, zooplankton, benthos and fish) and processes within each region. Most introductions appear to have increased local species richness rather than replace native species. Their impact on functional (rather than taxonomic) diversity, however, is of ecological importance. Ponto-Caspian organisms have become dominant members of various trophic levels (herbivores, detritivores and consumers) in benthic and pelagic food webs. They have apparently caused large-scale ecosystem impacts in the Great Lakes, whereas their role in Baltic Sea ecosystem is less pronounced, more spatially limited and, in part, camouflaged by other long-term ecological changes such as eutrophication. In all three regions, Ponto-Caspian invaders have altered multiple abiotic and biotic components and energy flow of ecosystems. Owing to the paucity of studies using pre- and post-invasion datasets, we cannot yet produce robust predictions for most of these invaders.

1 Introduction

During the past 200 years, biological invasions associated with human activities have resulted in largescale mixing of previously isolated biotas. Species endemic to Ponto-Caspian basins (Black, Caspian and Azov seas and the adjacent rivers emptying into these seas) have become established in inland Europe, the Baltic Sea and, most recently, the North American Great Lakes. In Europe, the Caspian and Ponto-Azovian fauna have spread in different manners and at different geological periods to Turkey, the Aral ba-

sin, the Euphrates river, European river systems, and the Adriatic Sea (Bacescu 1966). This expansion was facilitated by two major activities. Firstly, the construction of numerous canals and reservoirs on Ponto-Caspian rivers allowed organisms to disperse to Central and West European river systems through previously disconnected waterways by active migration, attachment to hulls and barge traffic, or transport in ship ballast tanks (Jazdzewski 1980). Secondly, Ponto-Caspian crustaceans were transplanted as food to stimulate fish production in European lakes and reservoirs during the 20th century; within an immense former USSR program of transplantations of Peracarida, beginning about 1950, more than 30 amphipod species from the "Caspian complex" were used for acclimatization purposes (Gasiunas 1964). Consequently, a biased selection of over 40 Ponto-Caspian species have expanded their ranges from the southeast European source pool into central and western Europe (Jazdzewski 1980; Kinzelbach 1995; Olenin & Leppäkoski 1999). The colonization of European ports by these species led to their immigration to North America by transoceanic shipping. Most nonindigenous species discovered in the Great Lakes since the mid-1980s are Ponto-Caspian endemics and more are expected to arrive in the future (Ricciardi & MacIsaac 2000).

There are many documented examples of invasions altering aquatic communities and ecosystems (e.g., Van den Brink et al. 1993a; Strayer et al. 1999). One approach to develop useful predictions about their impacts is to compare the effects of multiple, spatially independent invasions of a given species (e.g. Grosholz & Ruiz 1996; Ricciardi et al. 1997, 1998). This empirical approach tests whether a species has similar, predictable impacts in different regions. Here we apply this approach to a group of Ponto-Caspian species invading inland Europe, the Baltic Sea, and the North American Great Lakes, these areas representing a model in which three previously isolated biotas have become exposed to each other through human-mediated introduction of species.

2 Similarities and differences between regions

The three basins compared in this review exhibit many of striking similarities, but also evident differences (Table 1). They are isolated from the ocean by physical and ecological barriers. Geologically and biologically, they are young formations, and natural changes are still taking place when their ecosystems are subjected to maturation processes (Leppäkoski & Mihnea 1996). Similar threats to the aquatic environment are present in these areas, e.g., increasing urbanisation, pollution and eutrophication due to heavy industries, intense agriculture and aquaculture, overexploitation of fish stocks, and abundant sea traffic and port activities.

3 Invasive species of Ponto-Caspian origin in the three areas compared

Ponto-Caspian species contribute significantly to animal life in most of West European rivers (Table 2). Tittizer (1996) listed 31 nonindigenous invertebrate species from German rivers, among them 11 species of Ponto-Caspian origin. Amongst macroinvertebrate species in German rivers, their number has been estimated at 6-14%, with the rivers Rhine, Neckar and Odra being the most invaded (> 12%); in lowland rivers and canals close to the North Sea coast their prevalence increases to 20-30% (oligochaetes and chironomid larvae excluded; Tittizer 1996). Among the 29 nonindigenous fish species recorded in the rivers Elbe and Rhine, there are five species originating from the

Black Sea basin via the river Danube (Lelek 1996). Bacescu (1966) reported 16 Caspian invertebrate species from the Danube, 1,000 km from the Black Sea coast, some of which are recent invaders in the West European rivers and/or the Baltic Sea (e.g., the flatworm *Palaeodendrocoelum romanodanubialis*, polychaete *Hypania invalida*, amphipods *Pontogammarus obesus*, *Corophium curvispinum* and mysid *Limnomysis benedeni*) whereas some other species (mysids *Paramysis lacustris* and *P. intermedia*) were restricted to the lower 200 km part of the river.

Table 1. Basic characteristics for the Black Sea (together with its tributaries, the core donor area for invasive Ponto-Caspian species), the Baltic Sea, and the Laurentian Great Lakes. Data for Baltic and Black Seas from Leppäkoski & Mihnea (1996), those for the Great Lakes from Beeton (1965), Vollenweider et al. (1974) and Charlton (1991).

	Black Sea	Baltic Sea	Great Lakes
Latitude (°N)	41-46	54-66	41-49
Surface area, km ²	423,500	412,600	244,160
Drainage area, km ²	2,405,000	1,729,000	521,830
Age ^a , yr	9,000	7,500	< 10,000
Salinity ^b , PSU			surface:
- surface	17-18	6-7	L. Ontario, 0.20
- bottom	22	10-13	L. Erie, 0.17
Primary production ^b , g C m ⁻² yr ⁻¹	150-200	140-160	L. Superior, < 90 L. Huron, 100 L. Michigan, 130 L. Ontario, 180 L. Erie, 160-310 L. Erie (central): from 5 (1960s) to > 8 (1990s)
Changes in water transparency in the 1900s, m	from > 18 to > 8	from > 9 to > 6	

a) for the Black and Baltic Seas, last penetration of salty waters, b) central parts, offshore waters.

In the Baltic Sea, 22 species of Ponto-Caspian origin have been recorded; of them over 12 have been able to establish permanently (Baltic Sea Alien Species Database 2001). Their proportion diminishes westward: *Dreissena polymorpha* is the only species belonging to this group in Danish coastal waters (Knudsen 1989), only *Cordylophora caspia* has been reported from the North Sea coast of Germany, and *D. polymorpha*, *C. caspia*, and *Lithoglyphus naticoides* have been reported from brackish waters of the Netherlands (Reise et al. 1999).

In the Great Lakes, 15 Ponto-Caspian species are known to have been established, 13 of these having invaded during the past two decades; in fact, most of the animals that have invaded the Great Lakes since 1985 are Ponto-Caspian in origin (Ricciardi & MacIsaac 2000; Ricciardi 2001). Of the species listed in the Table 2, better-studied invaders such as *D. polymorpha*, *Echinogammarus ischnus*, *Hemimysis anomala*, *Cercopagis pengoi*, *C. caspia*, *C. curvispinum*, and *Neogobius melanostomus* were selected for further analysis.

4 Effects on abiotic and biotic environment

Nonindigenous Ponto-Caspian species have affected both abiotic environment and biotic components in the recipient areas studied. In this impact evaluation, available relevant literature on the selected exotic species has been used.

Table 2. Species of Ponto-Caspian origin recorded in European inland waters, the Baltic Sea and the Great Lakes and the date when first observed (? – undocumented).

Taxon	Inland Europe	First record	Baltic Sea	First record	Great Lakes	First record	Reference
Hydrozoa							
<i>Cordylophora caspia</i>	?	?	Curonian and Vistula Lagoons	1800s	Lake Erie	1956	Davis 1957, BMB WG NEMO 2001
<i>Maeotias marginata</i>			Väinameri	1999			Väinölä & Oulasvirta 2001
Turbellaria							
<i>Dendrocoelum romanodanubiale</i>	River Main	?					Schleuter & Schleuter 1998
Oligochaeta							
<i>Paranais frici</i>			Neva Bay	1995			BMB WG NEMO 2001
<i>Potamothenis heuschleri</i>			Neva Bay	1995			BMB WG NEMO 2001
<i>P. vejdvskyi</i>			Neva Estuary	1995			BMB WG NEMO 2001
Polychaeta							
<i>Hypania invalida</i>	Danube, Rhine Rivers	?					Tittizer 1996
Crustacea, Cladocera							
<i>Cercopagis pengoi</i>	Reservoirs and canals on Dniepr and Don Rivers		Gulf of Riga	1992	Lake Ontario	1998	Mordukhai-Boltovskoi & Rivier 1987; MacIsaac et al. 1999; BMB WG NEMO 2001
Crustacea, Amphipoda							
<i>Corophium curvispinum</i>	Vistula, Odra, Elbe, Severn, Lower Rhine Rivers	1913 1923 <1935 1987	Curonian, Vistula and Szczecin lagoons	1920s (possibly in the 1850s)			Van den Brink et al. 1989; BMB WG NEMO 2001
<i>C. mucronatum</i>					Lake St Clair	1997	Grigirovich & MacIsaac 1999
<i>Echinogammarus ischnus</i>	Vistula, Ems, Rhine Rivers	1928 <1978 1989	Curonian Lagoon	1962	Detroit River	1995	Gasiunas 1964; Van den Brink et al. 1993b; Witt et al. 1997; BMB WG NEMO 2001
<i>Chaetogammarus warpachowskyi</i>	Main and Rhine Rivers, Lithuanian Lakes	1960s	Curonian lagoon	1962			Gasiunas 1964; Jazdzewski 1980
<i>Obesogammarus crassus</i>	Lithuanian Lakes	1960s	Curonian lagoon	1962			Gasiunas 1964; Jazdzewski 1980
<i>Pontogammarus robustoides</i>	Lithuanian Lakes	1960	Curonian lagoon	1962			Gasiunas 1964; Jazdzewski 1980
<i>Dikerogammarus villosus</i>	Danube, Main, Rhine Rivers	1994 1995					Bij de Vaate & Klink 1995; Tittizer 1996; Giesen 1998; Jazdzewski 1980; Lvova et al. 1996; Tittizer 1996; Giesen 1998;
<i>D. haemobaphes</i>	Danube, Main, Rhine, Moscow Rivers	1993 1994					
Crustacea, Mysidacea							
<i>Hemimysis anomala</i>	Lithuanian Lakes, Main River	1960s 1997	Curonian lagoon	1962			Gasiunas 1964; Schleuter & Schleuter 1998; Ketelaars et al. 1999

Taxon	Inland Europe	First record	Baltic Sea	First record	Great Lakes	First record	Reference
<i>Limnomysis benedeni</i>	Danube River Lithuanian Lakes	? 1960s	Curonian lagoon	1962			Gasiunas 1964; Wittman 1995
<i>Paramysis lacustris</i>	Lithuanian Lakes	1960s	Curonian lagoon	1962			Gasiunas 1964
Crustacea, Isopoda <i>Jaera istri</i>	Danube, Main, Rhine Rivers	1995					Tittizer 1996
Bivalvia <i>Dreissena polymorpha</i>	Elbe, Rhine Seine, Loire, Odra Rivers	<1828 <1860	Curonian and Vistula lagoons	<1824	Lake St Clair	1988	Hebert et al. 1989; BMB WG NEMO 2001
<i>D. bugensis</i>	Volga River	Late 1980s			Lake Ontario	1989	Mills et al. 1993; Orlova et al. 2000
Mollusca, Gastro- poda <i>Lithoglyphus naticoides</i>	Rhine River	1800s	Curonian and Vistula Lagoons	1800s			Tittizer 1996
Pisces <i>Neogobius melanostomus</i>	Moscow River	mid 1980s	Gulf of Gdansk	1990	St. Clair River (Lake Huron outflow)	1990	Sokolov et al. 1989; Jude et al. 1992; Skora & Stolarski 1993;
<i>Proterorhinus marmoratus</i>					St. Clair River (Lake Huron outflow)	1990	Jude et al. 1992
<i>A. stellatus</i>	?	?	Gulf of Finland, Gulf of Bothnia	1999			S. Anatsky, pers. comm.
<i>Hucho hucho</i>	Rhine, Elbe Rhine Rivers	1957- 1960					Lelek 1996
<i>Huso huso</i>	Rhine River	?	Gulf of Riga	1962			Lelek 1996; BMB WG NEMO 2001
<i>Abramis sapa</i>	Rhine River	?					Lelek 1996
<i>Umbra krameri</i>	Rhine River	?					Lelek 1996

4.1 ABIOTIC COMPONENTS

Among the Ponto-Caspian invaders, it is *D. polymorpha* that has been primarily responsible for water transparency alterations. Even if populations of zebra mussels store huge amounts of organic matter, energy and calcium carbonate, their filtration ability is likely to be the most important impact at the ecosystem level. Water transparency in Lake St. Clair and western Lake Erie doubled within a few years after zebra mussel invasion (Holland 1993; Griffiths 1993). Also, turbidity declined by 60% within four years of invasion in Saginaw Bay (Skubinna et al. 1995). In Europe, water transparency increased after the invasion of *D. polymorpha* from 2 to 4 m in the Lake Lukomskoe, Belarus (Lyakhnovich et al. 1983) and in Lake Como, Italy (Binelli et al. 1997; Table 3). The clearing capacity of zebra mussel populations in the Dutch lakes IJsselmeer and Markermeer was sufficient to filter both lakes at least once or twice a month, the filtration rate being regulated by the content of suspended matter: the filtration rate shows an inverse exponential relationship with the total dry matter content of the water (Reeders et al. 1989). In Mikolajskie lake (Poland), *D. polymorpha* became the main filter-feeding species. A zebra mussel population, estimated at 236 tons, was able to filter 53,

Unionidae 0.9, and Sphaeriidae 600,000 m³ of water during the 6 months season. The estimated quantity of seston filtered by *D. polymorpha* was 160 tons, whereas unionids filtered 2.5 tons and sphaerids about 2 tons dry weight, respectively (Stanczykowska 1975). Here consumption of seston amounts to almost 9% of pelagic primary production, while faeces reach 13% of the annual sedimentation of tripton (Stanczykowska et al. 1975). In the Szczecin Lagoon (Polish coast), the *D. polymorpha* population was estimated to consume 53 tons of seston h⁻¹ (Stanczykowska 1977). Similar effects were caused by *C. curvispinum*, whose colonization lower River Rhine coincided with a decrease in total suspended matter due to increase in overall filtration capacity of the benthic community (Van den Brink et al. 1993a).

Invasions have altered the cycling of nutrients in some of study basins. Multifold increases in concentrations of total phosphorus, ammonia, nitrate and nitrite in the surface waters of Lake Erie were observed following invasion by *Dreissena* spp. (Strayer 1999; Makarewicz et al. 2000). Mellina et al. (1995) showed by mass balance modelling and lab experiments that zebra mussels have uncoupled the phosphorus-chlorophyll relationship in Lake Erie and Lake St. Clair. Total phosphorus, phosphate and nitrate values decreased after the invasion of *D. polymorpha* in Lake Como, Italy (Binelli et al. 1997). *Dreissena* beds, similarly to those formed by *Mytilus edulis* in marine habitats, release huge amounts of inorganic nutrients into the water column directly or via the microorganisms and meiofauna that process the feces and pseudofeces.

Zebra mussels are a primary food source for waterfowl in the lower Great Lakes and transfer organochlorine contaminants to these predators (Mazak et al. 1997). Because zebra mussels have relatively high contaminant concentrations in their tissues (Brieger & Hunter 1993), and because round gobies (*Neogobius melanostomus*) feed predominantly on zebra mussels in the Great Lakes (Ray & Corkum 1997), they may transfer PCBs and other organic contaminants to their predators and further lead to increased exposure of humans to contaminants (Strayer 1999). However, this hypothesis, originally proposed by Jude et al. (1995), has not been tested. Nevertheless, zebra mussels are altering pathways and environmental fate of contaminants in Lake Erie. They also increase sedimentation of PCB's and cadmium by up to 10-fold (Dobson & Mackie 1998). *D. polymorpha* is likely altering bioaccumulation pathways of heavy metals and organic contaminants in the Rhine-Meuse basin via waterfowl (e.g. *Aythya farina* and *A. fuligula*) which prey on the mussels (Hendriks et al. 1998). Similar studies are lacking in the Baltic Sea.

Shell deposits of *Dreissena* have changed former soft bottoms (sand or silt) into shell gravel, and create patches of hard substrate for sessile species on sites in the coastal lagoons of the Baltic Sea (Olenin & Leppäkoski 1999) and in the Great Lakes (Garton et al. 1998). The amphipod *C. curvispinum* builds networks of mud tubes on firm substrata; it has transformed hard substrata in the lower Rhine River by fixing up to 4 cm of mud on stones (Van den Brink et al. 1993a). *C. caspia* forms dense "bushes" - colonies on submerged trees, hydrotechnical constructions, piers, etc., and traps particulate material on its stolons, and creates microhabitats for several associated species in, e.g., the Curonian Lagoon (Olenin & Leppäkoski 1999).

4.2 BIOTIC COMPONENTS

Most invasions by Ponto-Caspian species have not resulted in native species loss to date, and so they have generally increased local species richness (alpha diversity) in European inland waters (Jazdzewski 1980; Kinzelbach 1995) and in the Great Lakes (e.g., Stewart et al. 1998a,b). However, several native species in the Great Lakes and inland Europe have declined locally following invasion (see below). A more subtle long-term consequence of invasions is the increasing homogenization of aquatic ecosystems (e.g., Rahel 2000). Ponto-Caspian species have become dominant members of several food webs in inland Europe (Kinzelbach 1995), the Baltic Sea (Olenin & Leppäkoski 1999), and the Great Lakes (Stewart et al. 1998a; MacIsaac et al. 1999; Johannsson et al. 2000). Thus, variation in species composition between regions (beta diversity) has been reduced. Very little attention has been devoted to assessing impact of species of Ponto-Caspian origin on native biota and renewable resources in aquatic ecosystems, with the exception of *D. polymorpha* in European inland waters and in the Great Lakes. Even these assessments have been based on a retrospective rather than predictive approach. Ecosystems have assimilated nonindigenous Ponto-Caspian species to a certain extent; in fact, most Ponto-Caspian species appear to be ecologically benign in their new areas of occurrence. There are examples, however, of large-scale effects on structural and functional diversity with prominent food-web impacts in the most heavily affected recipient areas for the most successful and aggressive invaders in the three basins considered in this review.

4.2.1 Bacterioplankton

Selective removal of large bacteria ($< 0.9\mu\text{m}$) by *D. polymorpha* was observed at eutrophic stations in Saginaw Bay, Lake Huron. However, *D. polymorpha* favoured, probably indirectly, the development of heterotrophs by nutrient excretion at the oligotrophic environment (Cotner et al. 1995). *D. polymorpha* also appears to have caused 'blooms' of *Microcystis aeruginosa* in Lake Erie and Saginaw bay owing to selective grazing (Vanderploeg et al. 1996).

4.2.2 Phytoplankton and primary production

Zebra mussels have caused dramatic declines (30-90%) in phytoplankton biomass in western Lake Erie and Saginaw Bay (Lake Huron): chlorophyll *a* concentrations fell by approximately 60% in both of these habitats after the establishment of dense mussel beds (reviewed by MacIsaac 1996; Strayer 1999). Planktonic diatom populations in western Lake Erie declined by almost 90% within a few years following mussel invasion (Holland 1993). In Europe a few observations are available. Significant reduction in chl *a* values (from 18-13.3 $\mu\text{g l}^{-1}$ to 8.6 $\mu\text{g l}^{-1}$), possibly as a result of *H. anomala* predation on algae were recorded in Biesbosch reservoir, the Netherlands (Ketelaars et al. 1999). Chl *a* values also decreased after the invasion of *D. polymorpha* in Lake Como, Italy (Binelli et al. 1997) and *H. anomala* to Biesbosch reservoir, the Netherlands (Ketelaars et al. 1999). In the Baltic Sea, such direct observations are lacking. However, Kotta et al. (1998) suggested that at sites of high abundances of *D. polymorpha* limitation of phytoplankton production may occur in the Gulf of Riga.

4.2.3 Benthic algae

Biomass of benthic algae has increased and composition has changed (from dominance by diatoms to filamentous green algae) in Saginaw Bay, presumably as a result of increased light penetration caused by zebra mussel filtration (Lowe & Pilsbury 1995; Strayer 1999).

4.2.4 Zooplankton

Dramatic effects on zooplankton were evident after the invasion of *Hemimysis* invasion to Biesbosch reservoir, the Netherlands: *Daphnia* spp., *Bosmina* spp., Ostracoda and Rotifera declined sharply in abundance. This was explained by predation by *H. anomala* (Ketelaars et al. 1999). Similarly, significantly lower population abundances of a small-bodied cladoceran *Bosmina* sp., a probable prey of *C. pengoi*, were recorded after invasion of this predatory cladoceran to the Gulf of Riga (Ojaveer et al. 2000). Considerable spatial differences were recorded in the zooplankton community of the Lake Ontario in the first year of invasion of the predatory *C. pengoi*: in the eastern part where *C. pengoi* was present, the cladoceran community was dominated by *Daphnia retrocurva* whereas in the western part where *C. pengoi* was absent, *Bosmina longirostris* prevailed. However, besides invertebrate predation, these differences could also be due to differences in population timing (Barbiero et al. 2000). No predation rate data exist to directly determine the impact of *Cercopagis* invasion on zooplankton or phytoplankton in the Great Lakes. However, based on the relative sizes of *Cercopagis* and *Bythotrephes*, and on *Bythotrephes* apparent selectivity for small zooplankton prey, it may be expected that *Cercopagis* will impact primarily small crustaceans and/or rotifers (Grigorovich et al. 1998).

The disappearance of the invertebrate predators *Leptodora kindtii* and *Bythotrephes longimanus* after invasion of *Hemimysis anomala* to Biesbosch reservoir, the Netherlands, appears to be linked to competition for food with this mysid species (Ketelaars et al. 1999). Small zooplankton (e.g. rotifers and copepods) declined by 74% in western Lake Erie at the same time that zebra mussel populations increased to densities up to 300,000 ind m⁻² (MacIsaac et al. 1995). Declines in zooplankton are related to both ingestion by zebra mussels and the loss of phytoplankton stocks because of zebra mussel filtration. *Dreissena veligers* now contribute 10% to 25% of zooplanktonic production in Lake Erie (Johannsson et al. 2000). A similar decline was observed in the Hudson River (Atlantic coast of North America). After zebra mussels became abundant in the river in 1992, phytoplankton biomass was reduced by 80-90% and zooplankton biomass by more than 70% (Pace et al. 1998). The invasion of *D. polymorpha* in Lake Lukomskoe similarly caused a significant decrease in total abundance of filter-feeding zooplankton (Karataev & Burlakova 1995).

4.2.5 Zoobenthos

Benthic communities in Lake St. Clair and western Lake Erie have increased in species richness following zebra mussel invasion (Griffiths 1993; Stewart et al. 1998a), at least initially, although one study showed that diversity on rocky substrata in Lake Ontario returned to pre-invasion levels after several years (Haynes et al. 1999). The diversity of native mussel (unionid) communities has declined rapidly following zebra mussel invasion in the Great Lakes and St. Lawrence River (Schloesser & Nalepa 1994; Ricciardi et

al. 1996, 1998). This is attributable primarily to the effects of fouling on native mussels but also to food competition, reducing food concentrations to levels too low to fuel the unionid and sphaeriid populations; in fact, the zebra mussel has had effects on all major taxa of freshwater molluscs in North America (Strayer 1999). Similar high mortalities have rarely been reported from European lakes invaded by zebra mussels; distinct unfavourable effects of overgrowth with *Dreissena* on the body growth and body weight of Unionidae were not observed in the lakes of northern Poland (Lewandowski 1976). Ricciardi et al. (1998) offered three reasons for the difference in documented impacts of *Dreissena* on native mussels in both regions: (i) very few European studies have examined changes in mussel communities following invasion; (ii) densities and infestation levels of *Dreissena* on native mussels are at least 10-fold lower in Europe compared with North America; and (iii) central European freshwater unionid mussel fauna (1 species *Margaritifera*, ca 10 species Unionidae (e.g. Haas 1969)) is depauperate compared with the North American fauna (~300 spp. described) and has had evolutionary experience with *Dreissena*, whose distribution expanded into northern and central Europe prior to the last glaciation before retreating to Ponto-Caspian basins. Thus, European species may have already experienced selection pressures to adapt to fouling by *Dreissena*.

Densities of macroinvertebrates on rocky substrata increased 2-8 fold following the development of zebra mussel densities of 1,500-4,000 ind m⁻² in the upper St. Lawrence River. Field experiments using artificial substrata and manipulated zebra mussel densities demonstrated that the change in abundance was due to mussel colonization through enhancing populations of deposit-feeding organisms (primarily amphipods), small gastropods, and predatory invertebrates (leeches, flatworms, water mites), and by displacing net-spinning caddis flies (Ricciardi et al. 1997). The associated fauna in zebra mussel aggregations is stimulated, in part, by feces of the mussels. A population of *D. polymorpha* at 2,200 ind m⁻² has been estimated to produce feces 3,520 mg-dw 24 h m⁻² (Stanczykowska 1975). Madenjian's (1995) model for western Lake Erie predicts that 50,000 ind m⁻² in the basin produce 1.4 megatons of pseudofeces (from ingesting 6.4 megatons of phytoplankton) over six months. Deposit-feeders, especially amphipods and chironomid larvae, have also increased in response to zebra mussel colonization in Lake St Clair and Lake Erie (Griffiths 1993; Stewart et al. 1998a). Following zebra mussel invasion, fresh shell-free benthic biomass increased by a factor of 50 in western Lake Erie, by a factor of 7 in the central Lake Erie, and by a factor of 40 in eastern Lake Erie; dreissenid mussels themselves account for over 95% of the benthic biomass (Johannsson et al. 2000). Huge interannual variations in density and biomass are characteristic of *D. polymorpha* populations. In the Mikolajskie lake, its biomass varied within 0-1,800 g shell-free wwt m⁻² within a couple of years (Stanczykowska 1975).

D. polymorpha was the dominant species in Polish dimictic lakes and in the least fertile (100-300 µg-P l⁻¹) polymictic lakes where it accounted for 40-70% of mollusc abundance (Stanczykowska 1984). In the Baltic Sea, distribution areas of *D. polymorpha* and the native filter-feeder *M. trossulus* normally do not overlap. However, in some areas in the eastern Gulf of Riga these species co-occur (J. Kotta, pers. comm.).

In many cases the invasive species represent a new function (e.g., feeding strategy) or an entirely new trophic level and will, thus, restructure the community into which they

were introduced. Non-native nektonic species (e.g., mysids and amphipods) swim actively and spend part of their time in the water column, and may also dwell within or on the bottom. They form dense populations in the Curonian Lagoon, and serve as important links in energy transfer between pelagic and benthic subsystems. *D. polymorpha* is known to have caused increases in local density and diversity of other benthic invertebrates in lakes and rivers (see above) and coastal lagoons (Olenin & Leppäkoski 1999). The mussels also offer refuge from large predators for associated species. Predator-avoidance behaviour of the snail *Physella heterostropha*, in combination with the structurally complex habitat provided by *Dreissena* beds, can reduce predation of fish on the snails (Stewart et al. 1999). Likewise, the amphipod *E. ischnus* may be displacing native *Gammarus fasciatus* in Lake Erie (Dermott et al. 1998), in part owing to use of *Dreissena* refuges from fish predation by the former species (H. MacIsaac, pers. comm.).

Reduction in macroinvertebrate species richness and substantial decrease in abundance of several macrozoobenthic taxa (Chironomidae, *Hydropsyche contubernalis*, *Asellus aquaticus*, *Gammarus tigrinus*, *Potamopyrgus antipodarum* and *D. polymorpha*.) was observed concomitantly with the enormous abundance increase of *C. curvispinum* in the Lower Rhine. The proposed mechanism is competition for food (Van den Brink et al. 1993a; Strayer 1999) and the transformation of substrate with muddy encrustations that prevent settlement of zebra mussel larvae and other fauna that prefer bare hard substrates (Rajagopal et al. 1999; Van der Velde et al. 1999). Dick & Platvoet (2000) showed that *Dikerogammarus villosus* is rapidly eliminating a native European amphipod *Gammarus duebeni* and an introduced amphipod *G. tigrinus* from parts of the Netherlands (particularly the Markermeer and the IJsselmeer). Microcosm experiments demonstrate that predation by *D. villosus* on both species occurs over a range of water conductivities. Both newly-moulted and intermoult animals are preyed upon. Recently, Kelleher et al. (1999) proved that invasions of exotic amphipods have had positive impact in the lower Rhine River by restoring predator-prey relationships, since the breakdown in its trophic structure in 1986. The same study demonstrated that *C. curvispinum*, together with other invasive crustaceans, play a significant role in energy mediation and trophic interactions in the lower Rhine River ecosystem.

4.2.6 Fish and birds

Populations of native benthic fishes, mottled sculpins *Cottus bairdi* and longperch *Percina caprodes*, in the St. Clair River declined sharply after the arrival of the round goby *Neogobius melanostomus*, apparently due to competition for food and space (Jude et al. 1995). Round gobies can penetrate interstitial spaces in coarse sediments to obtain food, and therefore may become predators of lake trout eggs; they have been shown to prey on lake trout eggs in the laboratory (Chotkowski & Marsden 1999). In the Gulf of Gdansk (Baltic Sea), competition for food and displacement of several native demersal fishes (e.g., flatfishes, eelpout *Zoarces viviparus*, and black goby *Gobius niger*) by invading *N. melanostomus* has been suggested to take place (Skora & Stolarski 1993, K.E. Skora & J. Rzeznik, pers. comm.). In addition, the same authors claimed that high abundances of the round goby may cause relaxation of predation pressure on several native fish in the Baltic Sea (e.g., sandeel *Ammodytes tobianus* and sprat *Sprattus sprat-*

tus) by being more favourable food for most abundant piscivores than the above-named species.

Increased water transparency following zebra mussel invasion has promoted prolific growth of macrophytes in Lake St. Clair (MacIsaac 1996) and Saginaw Bay, Lake Huron (Skubinna et al. 1995). In Lake St. Clair, this provoked a shift in fish communities: walleye *Stizostedion vitreum*, which are adapted to turbid conditions, were replaced by fish that are favoured by weed beds (northern pike *Esox lucius*, muskellunge *E. masquinongy*, and bass *Micropterus* spp.) (MacIsaac 1996). In addition to the habitat change, *Dreissena* can control walleye abundance through the food-web: according to individual-based model prediction, shunting of energy from pelagic to benthic pathways by *Dreissena* results in elimination of walleye high-recruitment years in Oneida Lake that led to 30% reduction in adult walleye abundance (Rutherford et al. 1999). In Europe, adult individuals of *D. polymorpha* are directly incorporated into the food-web by being eaten by several species of fish (whitefish, eel, carp, bream, white bream, orfe, sturgeon and flounder), by crayfish *Orconectes limosus* (native to North America), and by waterfowl such as coot *Fulica atra*, tufted duck *Aythya fulicula*, common pochard *A. ferina*, mallard *Anas platyrhynchos*, gadwall *A. strepera*, red-crested pochard *Netta rufina*, eider *Somateria mollissima*, goldeneye *Bucephala clangula*, goosander *Mergus merganser*, merganser *M. serrator*, moorhen *Gallinula chloropus*, gulls *Larus* spp., sheld-duck *Tadorna tadorna*, and dabchick *Podiceps ruficollis* (Stanczykowska 1977).

By consuming *C. pengoi*, the diet composition of Baltic herring *Clupea harengus membras*, smelt *Osmerus eperlanus*, three-spined stickleback *Gasterosteus aculeatus*, and nine-spined stickleback *Pungitius pungitius* has changed after invasion of the cladoceran. The introduction of *C. pengoi* to the Baltic Sea may prove beneficial to fisheries production if it enhances utilization and transfer of mesozooplankton biomass (e.g., *Bosmina*) to planktivorous fishes (Ojaveer et al. 2000). Exotic amphipods are the most important prey taxa for dominant benthivorous fish in the lower Rhine River. Although their importance for fish has been constant over the last decade (Kelleher et al. 1999), significant changes in diet composition of certain fish species (perch and eel) and dietary overlap between them has occurred. These changes appear to be due to alterations in food supply caused by invasion of the amphipod *C. curvispinum* (Kelleher et al. 1998). Yellow perch *Perca flavescens* kept in enclosures with and without zebra mussels in an experimental pond (using fish and sediment from Lake St. Clair) showed differences in diet and growth rate (Thayer et al. 1997): growth rates of adult perch were higher in the presence of zebra mussels, presumably because of increased densities of invertebrate prey.

5 Comparative analysis of ecosystem impacts

When comparing the ecological changes caused by invasive species, we should distinguish between types and scales of impact. The types of impact are the same or very similar in all three regions compared. Invasive Ponto-Caspian species modify abiotic and biotic conditions for other species, they alter the pathways of energy transfer and influence cycling of contaminants within new ecosystems, thus, acting as habitat and ecosystem engineers (Jones et al. 1994; Stewart et al. 1998b, 1999; Olenin & Leppäkoski 1999; Table 3).

The magnitude and geographical dimension of the ecological impacts of Ponto-Caspian invasions in most cases are quite different between the inland European freshwater bodies, Baltic Sea and Great Lakes. The most prominent and larger-scale changes, both in the pelagic and benthic ecosystems, have recently taken place in the Great Lakes (Table 4). This is mainly due to the invasion of the zebra mussel, which has had multiple ecosystem impacts both in habitat modifications and at all trophic level. Another invader, *C. pengoi* was discovered in the Great Lakes only in 1998 and has not been present long enough for its impact to be measured.

Ecological impacts of the Ponto-Caspian species in European inland waters are locally substantial but certainly less pronounced at the regional scale. The Baltic Sea, the only brackish-water habitat amongst the studied water-bodies, has seemingly suffered by Ponto-Caspian species invasions the least with the highest impact to benthic communities; the impact of *C. pengoi* on the pelagic subsystem remains to be assessed in more detail. The fact that the Baltic Sea has suffered relatively the least could partly be due to geographic location of the basin: it is situated in a zone of colder climate than the remaining regions studied. This fact may be important for development of populations of Ponto-Caspian species originating from considerably warmer climatic conditions.

In addition, it should be stressed that although ecological effects of similar Ponto-Caspian species were generally unidirectional in the three areas compared, different species were often responsible for major ecosystem changes in these three geographically remote regions. Due to large differences in invasion histories of the same species in the three regions, quite often the ecological effects are not directly comparable either because of lack of relevant studies in the past or of different population abundance (and consequently, magnitude of impact) of each species in different systems.

Table 3. Examples of habitat engineering and ecosystem changes caused by Ponto-Caspian invasive species in the Baltic Sea, inland European freshwater bodies and North American Great Lakes (criteria largely adopted from Stewart et al. 1998b, 1999; Olenin & Leppäkoski 1999). [1) modifies rocky bottom or sediment substrate, 2) provides refuges from predators and currents, 3) traps and accumulates POM in interstitial microhabitats, 4) increases water clarity (= lowers concentrations of POM and suspended solids), 5) affects macrophyte canopy, 6) redirects energy from pelagic to benthic subsystems or *vice versa*, 7) provides additional prey to planktivorous and/or benthivorous fish, 8) provides food for waterfowl, 9) excludes competing species, 10) increases soluble (bioavailable) nutrients (N, P), 11) influences cycling of organic and/or metal contaminants, 12) ? – undocumented].

Species/function	1	2	3	4	5	6	7	8	9	10	11
<i>C. caspia</i>	x	x	x								
<i>C. pengoi</i>							x				
<i>P. robustoides</i>						X	x				
<i>E. ischnus</i>	x					x	x		x		x?
<i>C. curvispinum</i>	x	x	x	x	x	x	x		x		x?
<i>H. anomala</i>						x	x				
<i>D. polymorpha</i>	x	x	x	x	x	x	x	x	x	x	x
<i>N. melanostomus</i>						x	x	x	x		x

Another very important difference is the effort expended to quantify effects of exotic species in the three regions. Experimental studies on invasive Ponto-Caspian species are very recent (performed mainly during the 1990s) in all three areas compared in this

review, but most advanced in North America. Therefore, even though the effects of introduced species appear to be strongest in the Great Lakes, it is possible that this reflects, in part, effort devoted to the topic. Available evidence indicates that all three regions have been moderately to strongly altered by invasions over very short periods of time.

Several ecosystem processes (e.g., nutrient and contaminant cycling, energy flow), involving multiple trophic levels, are affected. In general, the largest community changes were recorded for zooplankton and zoobenthos. However, effects on diversity have not been well studied for the majority of these invasions; although most invasions appear to add to local (alpha) diversity, in some cases diversity declines have occurred at this scale. As the same small pool of common dominant species become established (e.g., *N. melanostomus*, *D. polymorpha*, *C. pengoi*) in different areas, we can expect variation in diversity across regions (i.e. beta diversity) to decline. Some evidence suggests that these co-evolved invaders may be facilitating each other's population growth and spread (Ricciardi 2001). Therefore, we can predict that further ecosystem disruption is likely as more Ponto-Caspian invaders expand their ranges into these regions.

Table 4. Documented effects of Ponto-Caspian invasions on affected ecosystems in inland Europe, Baltic Sea, and the North American Great Lakes. Effect strength is indicated as strong (***), moderate (**), or weak/none (*), ? – undocumented.

	Inland Europe	Baltic Sea	Great Lakes
<i>Abiotic components</i>			
Transparency	***	*	***
Nutrient cycling	**	**	**
Contaminant cycling	*?	?	**
Benthic substrate	***	**	***
<i>Biotic components</i>			
Phytoplankton	**	?	***
Zooplankton	***	**	***
Fish	?	*	**
Zoobenthos	***	***	***
Periphyton	*	?	**
Macrophytes	?	?	**

Based on generally similar patterns of ecological effects of Ponto-Caspian invaders in the different regions studied and previous evidence from inland Europe, future introductions by *C. curvispinum* and *H. anomala* to the Great Lakes ecosystems could be predicted to cause significant impacts; these should include, amongst others, severe changes in the increase in filtration capacity of these ecosystems and further transformations in phytoplankton, zooplankton and zoobenthos communities, including probable declines in zebra mussel densities (see Van den Brink et al. 1993a; Kelleher et al. 1998; Ketelaars et al. 1999).

Our review revealed substantial gaps in the knowledge of the ecological effects of Ponto-Caspian invaders in the various invaded regions. We lack basic impact studies on important ecosystem processes and/or trophic levels (e.g., changes in native species richness, phytoplankton/primary productivity, contaminant cycling, fisheries), even for the most abundant and well-recognized invasive species. Moreover, only a few studies

examine the cascading effects of invasions in aquatic food webs. However, this knowledge is of high priority importance for proper ecosystem management. The scarcity of predictive information demands that systematic and well-coordinated research be initiated to provide better scientific advice for the management of aquatic invaders, but aquatic ecosystem especially.