

Geological and evolutionary underpinnings for the success of Ponto-Caspian species invasions in the Baltic Sea and North American Great Lakes

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Abstract: Between 1985 and 2000, ~70% of new species that invaded the North American Great Lakes were endemic to the Ponto-Caspian (Caspian, Azov, and Black seas) basins of eastern Europe. Sixteen Ponto-Caspian species were also established in the Baltic Sea as of 2000. Many Ponto-Caspian endemic species are characterized by wide environmental tolerances and high phenotypic variability. Ponto-Caspian fauna evolved over millions of years in a series of large lakes and seas with widely varying salinities and water levels and alternating periods of isolation and open connections between the Caspian Sea and Black Sea depressions and between these basins and the Mediterranean Basin and the World Ocean. These conditions probably resulted in selection of Ponto-Caspian endemic species for the broad environmental tolerances and euryhalinity many exhibit. Both the Baltic Sea and the Great Lakes are geologically young and present much lower levels of endemism. The high tolerance of Ponto-Caspian fauna to varying environmental conditions, their ability to survive exposure to a range of salinities, and the similarity in environmental conditions available in the Baltic Sea and Great Lakes probably contribute to the invasion success of these species. Human activities have dramatically increased the opportunities for transport and introduction and have played a catalytic role.

Résumé : Entre 1985 et 2000, environ 70 % des espèces qui ont envahi pour la première fois les Grands-Lacs d'Amérique du Nord étaient endémiques aux bassins versants de la région pontocaspienne de l'Europe de l'Est, soit ceux de la mer Caspienne, de la mer d'Azov et de la mer Noire. En 2000, 16 espèces pontocaspiennes s'étaient déjà établies dans la Baltique. Plusieurs des espèces pontocaspiennes endémiques se caractérisent par leur grande tolérance aux conditions de l'environnement et par leur variabilité phénotypique élevée. La faune de la région pontocaspienne a évolué sur une période de millions d'années dans une série de grands lacs et de mers à salinités et niveaux d'eau extrêmement variables; il y a eu aussi des alternances de périodes d'isolement et de contact entre les bassins des mers Caspienne et Noire et entre ces bassins et la Méditerranée et l'océan global. Ces conditions ont sans doute exercé une sélection sur les espèces endémiques pontocaspiennes qui explique la grande tolérance aux conditions du milieu et le caractère euryhalin que montrent plusieurs d'entre elles. La Baltique et les Grands-Lacs sont deux régions géologiquement jeunes qui contiennent beaucoup moins d'espèces endémiques. La forte tolérance de la faune pontocaspienne aux conditions variables de l'environnement, sa capacité de survivre à de salinités variables et la ressemblance des conditions du milieu dans la Baltique et les Grands-Lacs contribuent au succès de l'invasion de ces espèces. L'activité humaine a multiplié de façon spectaculaire les occasions de transport et d'introduction et a ainsi servi de catalyseur.

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Introduction

Analysis of the global distribution of nonindigenous species found in an invaded ecosystem may reveal particular

geographic regions that are significant donors for species introductions to that ecosystem. Analyses of the characteristics and evolution of target-donor ecosystems may provide further insight into the success of such multiple invasions.

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Fig. 1. The North American Great Lakes.

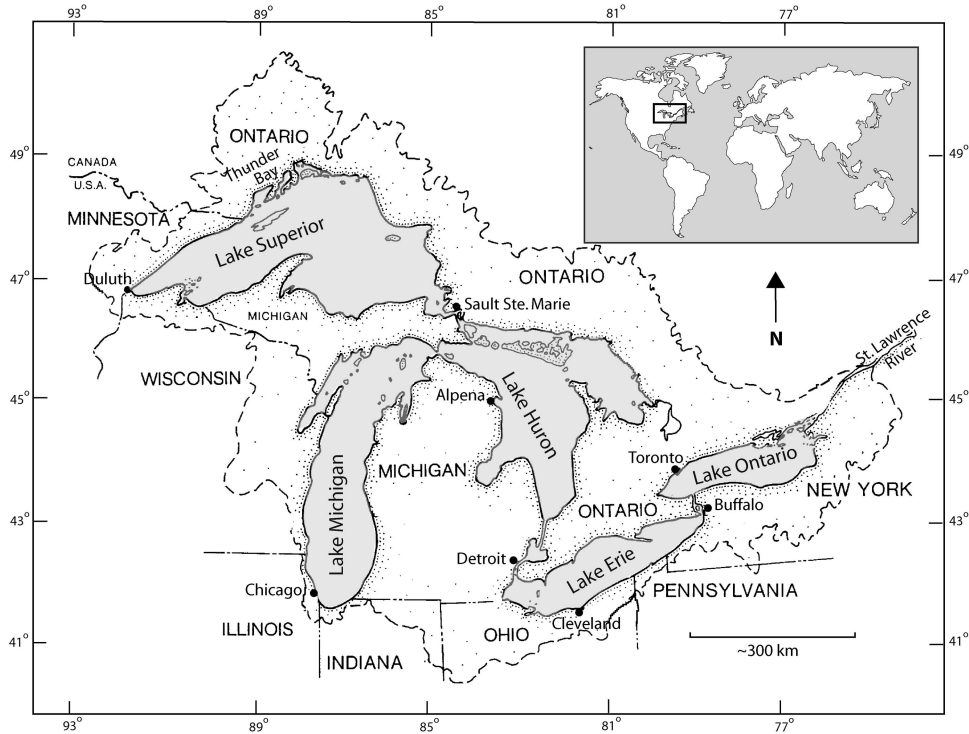
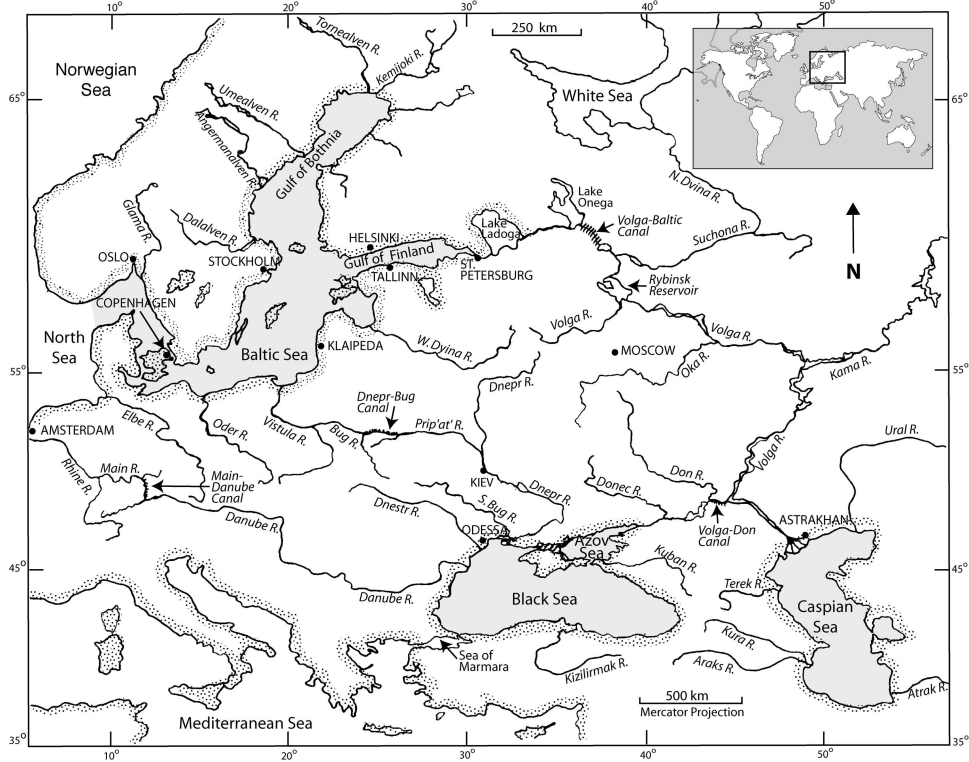


Fig. 2. The Baltic, Black, Azov, and Caspian seas and the river and canal networks that interconnect them.



Eight of the 15 new nonindigenous species identified in the North American Great Lakes (Fig. 1; hereafter referred to as the “Great Lakes”) between 1985 and 2001 were native to fresh and brackish waters of the Black, Azov, and Caspian seas (Fig. 2), also known as the Ponto-Caspian basins

(Ricciardi and MacIsaac 2000; Ricciardi 2001). These basins also appear to be the source of significant invasions to the Baltic Sea (Fig. 2), where 16 Ponto-Caspian species are considered as established (Leppäkoski and Olenin 2001). As a result, components of Ponto-Caspian food webs are being

reproduced in the Great Lakes (Ricciardi and MacIsaac 2000; Ricciardi 2001) and in lagoons and estuaries of the Baltic Sea (Leppäkoski and Olenin 2001). Ponto-Caspian species have substantially altered habitat characteristics, native biodiversity, ecosystem productivity, and water quality in both systems (Ricciardi and MacIsaac 2000; Ojaveer et al. 2002). Thus, these three geographically separate and distinct water basins have become increasingly linked biologically. To understand the success of Ponto-Caspian species in the modern Baltic Sea and Great Lakes, we examine and compare the three basins and their geologic history and faunal evolution. We discuss our findings in the context of three invasion model frameworks.

Invasion model frameworks

Three model frameworks for understanding species invasions can be found in the literature. The historical model considers that combinations of life history characteristics, such as ability to alternate between parthenogenesis and gamogenesis, presence of resting eggs and (or) free-living stages in the life cycle, broad feeding niches, and broad physiological capabilities, predisposes some species for greater invasion success than others (Lodge 1993; Ricciardi and MacIsaac 2000). During early stages of an introduction, the "Allee effect" (i.e., reduction in population growth rate because mates are difficult to find or because a critical number of individuals must be exceeded for sexual reproduction to occur (Begon et al. 1986)) may prevent dioecious species from becoming established. A strategy that allows parthenogenetic reproduction through the warm season, resulting in accumulation of high numbers of individuals in the inoculated population, followed by gamogenetic reproduction, for example, would clearly be advantageous (e.g., Cercopagids). The presence of free-living stages (e.g., Dreissenids) facilitates both long-distance human-mediated transfer and fast colonization of target ecosystems. However, the importance of factors such as feeding specialization and physiological adaptability have either been poorly quantified or yielded conflicting results (McMahon, 2002).

The vulnerability model identifies attributes that are thought to render ecosystems more vulnerable to invasions (Lodge 1993), such as native species diversity, degree of habitat disturbance, and environmental and climatic matches between donor and recipient areas. However, some studies have demonstrated that invasive species establishment may be positively related to native species diversity (Stohlgren et al. 1999).

The propagule model is based on propagule pressure (the frequency and load of propagules of a potential invader supplied to an ecosystem (Williamson 1996)). Closely allied with the propagule pressure model is the establishment of "invasion corridors" (a pathway that facilitates long-distance dispersal of species to particular regions (Ricciardi and MacIsaac 2000)) between source and destination areas, such as the Volga River system connecting the Caspian and Black seas and the Baltic Sea. If a repetitive invasion vector, such as ships carrying and discharging ballast water, is also associated with an invasion corridor, then the magnitude and intensity of inoculations will be much higher, resulting in much greater propagule pressure in the destination area. Invasion corridors also promote "invasion meltdown"

(Ricciardi 2001) in the destination area by moving a large number of propagules from one particular donor area to the destination area, leading to the development of co-evolved food webs. We show that elements of all three invasion model frameworks can be found in the success of Ponto-Caspian species in both the Baltic Sea and Great Lakes.

The Ponto-Caspian basins: Black Sea, Sea of Azov, and Caspian Sea

Physical characteristics

We provide general physical and environmental characteristics for the Ponto-Caspian basins, as well as for the Baltic Sea and the Great Lakes (Table 1).

Black Sea

The Black Sea (~41–46°N) is located in southeast Europe in a semi-arid climate zone. It connects in the north to the Sea of Azov and in the southwest to the Mediterranean Sea via the Sea of Marmara, the Bosphorus Strait, and the Dardanelles. The waters of the Black Sea basin deeper than ~150 m are anoxic and contain H₂S. A permanent halocline is maintained by colder low-salinity surface water averaging 17.5–19 ppt overlying warmer deep waters with a salinity averaging 22 ppt. Low near-surface salinity is maintained by the influx of freshwater from rivers (Fig. 2) and decreases to <13 ppt near the mouths of the Danube and Dneestr rivers. To the northeast, the outflowing water from the Sea of Azov reduces the salinity to 16–17 ppt (Zenkevich 1963; Stanners and Bourdeau 1995).

Sea of Azov

The Sea of Azov, a relatively small, shallow, and slightly brackish continental water body, can be considered a gulf of the Black Sea (Zenkevich 1963) or an extended estuary of the Don River (Bronfman 1995). The climate around the basin is continental temperate and the mean annual water temperature is about 11.5°C. Ice forms along the northern coasts during winter. The Taganrog Gulf is a large, shallow embayment in the northeast that comprises ~15% of the total area of the Sea. Salinity in the Sea of Azov varies from <1 ppt at the eastern end of the Taganrog Gulf, owing to river inflow, to ~13 ppt near the opening to the Black Sea (Bronfman 1995). In 1952, the Taganrog Gulf, and thus the Sea of Azov and the Black Sea, were connected to the Caspian Basin via the Volga–Don Canal (Fig. 2).

Caspian Sea

The Caspian Sea spans ~36–47°N and has arid to semi-arid continental and Mediterranean climatic zones. Unlike both previously described seas, it can be considered a large brackish-water lake and is physiographically divided into three parts: northern (47–44°N), middle (44–40.5°N), and southern (40.5–36.5°N). Three major rivers, the Volga, the Ural, and the Terek, empty into the northern Caspian, whereas the Kura and several smaller rivers enter the middle and southern Caspian. The eastern side of the basin is characterized by a lack of permanent rivers and streams (Stanners and Bourdeau 1995).

The surface water temperature of the Caspian Sea ranges from 24 to 27°C during the summer and from 9°C in the south to 0°C in the north, where sea ice forms, during win-

Table 1. Physical characteristics of the Ponto-Caspian basins,^a the Baltic Sea,^b and the Great Lakes.^c

	Black Sea	Sea of Azov	Caspian Sea	Baltic Sea	Great Lakes
Maximum dimensions (km)					
~East–West	1149	340	E–W varies, 204–566	E–W varies, 120–440 not including the Gulf of Finland	Superior: 563 E–W × 257 N–S
~North–South	611	135	1200	N–S: 1340	Michigan: 190 E–W × 494 N–S Huron: 245 E–W × 332 N–S Erie: 388 E–W × 92 N–S Ontario: 311 E–W × 85 N–S
Maximum depth (m)	2245	12	North: 20 Middle: 788 South: 1025	459	Superior: 406 Michigan: 282 Huron: 229 Erie: 64 Ontario: 244
Mean depth (m)	1240	7	North: 6 Middle: 176 South: 325	55	Superior: 147 Michigan: 85 Huron: 59 Erie: 19 Ontario: 86
Surface area (km ²)	4.6×10^5	3.8×10^4	4.4×10^5	4.1×10^5	Superior: 8.2×10^4 Michigan: 5.8×10^4 Huron: 6.0×10^4 Erie: 2.6×10^4 Ontario: 1.9×10^4 Total: 2.4×10^5
Volume (km ³)	5.3×10^5	324	7.7×10^4	2.1×10^4	Superior: 1.2×10^4 Michigan: 4.9×10^3 Huron: 3.5×10^3 Erie: 0.5×10^3 Ontario: 1.6×10^3 Total: 2.3×10^4
Catchment area (km ²)	1.9×10^6	5.7×10^5	1.4×10^6	1.8×10^6	Superior: 1.3×10^5 Michigan: 1.2×10^5 Huron: 1.3×10^5 Erie: 7.8×10^4 Ontario: 6.4×10^4 Total: 7.7×10^5
Mean runoff (km ³ ·year ⁻¹)	270	39	324 (176–431)	~472	Superior: 44 Michigan: 32 Huron: 44 Erie: 22 Ontario: 28 Total: 170
Salinity range (ppt)	<13–22	<1–12	North <1–11 Middle/South 12–13	Surface, east of Kattegat: 1–8 Bottom, east of Kattegat: 8–15 in south; <8 in north	Basinwide: <0.2 (total dis- solved solids)
Surface water temperature range (°C)	<0–25	<0–31	0–27	0–20	Superior: 0.0 – 19.9 Michigan: –0.05–5.1 Huron: 0.05–22.7 Erie: 0.04–26.9 Ontario: 0.2–25.8

^aSee Zenkevich (1963), Bronfman (1995), Kaplin (1995), Mandych et al. (1995), Stanners and Bourdeau (1995), and Dumont (1998).

^bSee Grasshoff (1975) and Stanners and Bourdeau (1995).

^cSee Government of Canada and U.S. Environmental Protection Agency (1995), U.S. Army Corps of Engineers and Great Lakes Commission (1999), and the Great Lakes Surface Environmental Analysis (2001), available from NOAA – Great Lakes Environmental Research Laboratory, Ann Arbor, Mich. (<http://coastwatch.glerl.noaa.gov/statistic/>).

ter. The northern Caspian Sea is characterized by strong salinity gradients from <1 ppt and slightly oligohaline conditions to the north in the avandelta and mouth areas of the Volga River to 11–12 ppt along its transitional mixing zone

with the middle Caspian. The size and position of the mixing zone varies with the volume of Volga River outflow and sometimes covers almost the whole area of the northern Caspian Sea (Katunin 1986).

The water level of the Caspian Sea has been characterized by strong periodic fluctuations of up to 6 m over the last 2500 years and >200 m on a geologic time scale (Dumont 1998). Two major changes in water level occurred during the 20th century. The level decreased from -26 m to -29 m relative to sea level between 1930 and 1977, but has risen to its present position of about -27.5 m relative to sea level since 1978. There is no clear agreement on an exact cause for the modern water level oscillations, but climatic changes and human activities are strongly suspect (Kaplin 1995; Stanners and Bourdeau 1995).

All three Ponto-Caspian basins are closed or semiclosed, characterized by large catchment areas exceeding the surface areas of the basins 5–6 times. Significant changes in water quality and in ecosystem structure and function attributed to cultural eutrophication and resultant changes in trophic status are the most commonly shared anthropogenic impacts among all three basins during the latter half of the 20th century (Stanners and Bourdeau 1995; Zaitzev and Mamaev 1997). The Caspian Sea has the highest rate of eutrophication, whereas the Sea of Azov is the most eutrophied. The deep waters of the middle and southern Caspian Sea basins have become anoxic, resulting in a partial to complete loss of benthic fauna in these areas (Stanners and Bourdeau 1995).

Geologic and faunal evolution of the Ponto-Caspian basins

The origins of the water bodies occupying the modern Ponto-Caspian basins are linked by their geologic past. We provide a synopsis of the geologic and biologic evolution important to understanding the invasive success of modern Ponto-Caspian fauna (Tables 2–4). The following discussion draws from the literature cited (Tables 2–4) and particularly from the detailed descriptions provided by Mordukhai-Boltovskoi (1960), Zenkevich (1963), and Dumont (1998).

Synchronous evolution

During the early Mesozoic Era, ~200 million years ago (mya), the Tethys Sea linked the basins of the Atlantic and Pacific oceans via southern Europe and central Asia, forming the World Ocean. Collision of continental masses during the mid-Tertiary Period isolated the Tethys Sea from the rest of the World Ocean. Following isolation of the Tethys Sea, the geologic and biologic evolution of the Ponto-Caspian basins was synchronous until the late Miocene Epoch (Table 2). By the middle Miocene Epoch (~15 mya), the formation of the Alps, Carpathians, Balkan, and Caucasus mountains divided the remnant Tethys Sea into a number of isolated water bodies. One of them, the Sarmatian Sea, included the Caspian and Euxinian (Black Sea) depressions (that would later become the modern Ponto-Caspian basins), and the Pannonian depression, situated to the west of two preceding depressions. The Early-Sarmatian Sea was characterized by less-than-oceanic salinity owing to freshwater inflow and was inhabited by typically marine fauna (Neveeskaya 1971). Part of the Early-Sarmatian Sea later separated to become the brackish-water Pannon Lake, which lost its connection to adjacent marine areas ~12 mya after emergence of the Carpathian Mountain chain. At its maximum size 9.5 mya, the lake's area was about 250 000 km² (Geary et al. 2000). Increasing freshwater input to the remaining part of the Sarmatian Sea resulted in successively

lower salinities in the Mid- and Late-Sarmatian Sea, and much of the marine fauna endemic to the Tethys Sea became extinct.

The Sarmatian Sea evolved into the Maeotic Sea, which may have been even less saline, resulting in further displacement of marine species by brackish-water fauna. However, a new short-lived transgression during this time period once again linked it to the ocean, the salinity increased, and marine species returned.

The Pontic Lake–Sea formed during the late Miocene Epoch and is considered to be the last stage of synchronous evolution of the Ponto-Caspian basins. The depressions that became the modern basins of the Black and Caspian seas were still interconnected through the present-day northern Caucasus but had also reconnected to the Pannonian depression. The Early-Pontic Lake–Sea contained fauna of mixed origin, including immigrants from the Pannon Lake. These fauna flourished through Pontian time and were the precursors of the modern “autochthonous” Caspian fauna (Mordukhai-Boltovskoi 1960). At the end of the middle Miocene Epoch, the Pannon Lake separated again (Starobogatov 1994) and existed as an enclosed basin with a high level of endemism in molluscan fauna until the Pliocene Epoch when it disappeared (Geary et al. 2000).

At the end of the Miocene Epoch, the Earth's crust rose in the northern Caucasus, gradually splitting the large Pontic Lake–Sea into two smaller disconnected brackish-water basins, the Late-Pontic Lake–Sea in the Euxinian depression (Table 3a) and the Babadjan Lake–Sea, which was restricted to the southern Caspian depression (Table 3b). Since then, the Caspian Sea and the Black Sea – Sea of Azov basins have evolved separately, although temporary links between them were formed from time to time.

Post-Miocene evolution of the Euxinian depression

During the late Pliocene Epoch, the Euxinian depression (Table 3a) went through several transformations. The Kimmearian and Kujal'nik lake–seas were characterized by a gradual decrease in salinity and successive changes of endemic brackish-water fauna. With the beginning of the Pleistocene Epoch and the Ice Age, the size of the Euxinian water body shrank and the salinity and species composition continued to change, as did the outline of the sea. The next three phases (Gurian Lake–Sea, Chauda Lake–Sea, and Ancient Euxinian Sea) contained brackish water and, based on fossil mollusk assemblages, possessed endemic fauna identified as “Ponto-Caspian”. Typical marine forms were absent in these basins (Neveeskaya 1971).

After the late Mindel (Elsterian) Glaciation (0.5–0.4 mya), the Chauda Lake–Sea filled with meltwaters and evolved into the nearly fresh Ancient Euxinian Sea, the outline of which closely resembled the modern Black and Azov seas. It was connected to the Caspian depression through the Kumo–Manych depression to the northeast and to the Sea of Marmara through the Bosphorus Strait to the southwest. However, the Sea of Marmara was isolated from the Mediterranean at the time, so no saline water or fauna of an oceanic nature entered the Ponto-Caspian basins during this period. The Ancient Euxinian Sea evolved into the Uzunlar Sea during the Riss–Würm Interglacial Period (0.15–0.1 mya) when the Euxinian depression became connected to the Medi-

Table 2. Ponto-Caspian basin evolution: phase 1, synchronous development.^a

Geologic Epoch	Name of water body	Time (mya)	Salinity (ppt)	Main geologic events	Main events in faunal evolution	
Caspian, Euxinian (Black Sea), and Pannonian depressions are connected						
Miocene (22–5 mya)	Early-Sarmatian Sea	15–12.5	~20		Decrease of marine faunal diversity, development of Sarmatian brackish-water fauna	
	Mid-Sarmatian Sea	12.5–10	17–20	Separation from Pannonian basin	Displacement of marine fauna by endemic Sarmatian fauna	
	Caspian and Euxinian depressions are separated from Pannonian depression					
	Late-Sarmatian Sea	10–8.3	6–17		Flourishing of Sarmatian fauna	
	Maeotic Sea	8.3–6.4	6–15	Transgression and reconnection with World Ocean	Further displacement of marine fauna and successive new invasions of marine fauna through short-lived connections; further flourishing of Sarmatian lineages. Development of brackish-water endemic fauna in Pannonian basin	
	Early- and Mid-Pontic lake-seas	6.4–5.8	12–15	Tectonic sagging, transgression and reconnection with Pannonian basin	Immigration of endemic Pannonian fauna (precursors of modern autochthonous Caspian fauna) into the united basins and gradual displacement of marine and Sarmatian lineages	

Note: mya = millions of years ago.

^aAfter Andrusov (1918), Arkhangel'sky and Strakhov (1938), Mordukhai-Boltovskoi (1960), Zenkevich (1963), Neveeskaya (1971), Starobogatov (1994), Kaplin (1995), Mandych et al. (1995), Dumont (1998), and Molostovsky and Guzhikov (1999).

terranean basin. This marked the beginning of the Mediterranean phase (Table 4a) in the evolution of the Black Sea.

By 90 thousand years ago (kya), the Karangat Sea formed as the salinity increased, and marine flora and fauna once again entered the basin. The higher salinity forced brackish-water fauna and Pontic-type fauna into lower salinity areas of bays and limans (river estuaries) around the periphery of the Karangat Sea. This may also have been when the modern Sea of Azov first formed (Bronfman 1995). Late in this period, the Karangat Sea was replaced by the Girkan Sea, and a reconnection with the Caspian depression allowed a faunal exchange between the two areas.

The NeoEuxinian Lake coincided with the Würm Glaciation, and connection with the ocean was again broken, salinity was again reduced, and oceanic flora and fauna disappeared. The Ponto-Caspian endemic fauna that survived in the bays and limans of the Karangat Sea returned to the open part of the basin. Starting ~9 kya, the basin entered its current phase, and the precursor to the modern Black Sea was formed. Following the last period of glaciation, the water level in the Black Sea rose more slowly than that of the World Ocean as glacial meltwaters were released across the northern hemisphere. A connection to the Mediterranean Sea was once again established through the Bosphorus and Dardanelles about 7.5 kya (Ryan et al. 1997), and by ~6 kya, the Black Sea became sufficiently saline to support a large number of Mediterranean species. Today about 75% of the Black Sea fauna are Mediterranean settlers ("Mediterranean immigrants") and the Ponto-Caspian endemic species have again retreated to the low-salinity bays and limans.

Post-Miocene evolution of the Caspian depression

The Babadjan Lake-Sea (Table 3b) occupied only the southern Caspian depression and was situated in an arid cli-

mate with decreased freshwater input, resulting in a gradual increase in salinity and decrease in size owing to either strong evaporation under the arid climate (Starobogatov 1994) or tectonic sagging (Kaplin 1995). The Babadjan Lake-Sea was eventually replaced by the Balakhan Lake, which also occupied only the most southern part of the Caspian depression.

After the Balakhan Lake, the brackish-water Ackchagyl Lake-Sea developed in the Caspian depression and became connected with the Kujal'nic Lake-Sea in the Euxinian depression (Table 3a) through the Kuma-Manych depression. This evolutionary stage was characterized by development of fauna with some marine elements but with no similarity to those of the Maeotic or Pontic stages or to the fauna in the Kujal'nic basin, and their origin is still under discussion (Mordukhai-Boltovskoi 1960; Zenkevich 1963; Starobogatov 1994). The successive lake-sea stages (Apsheon, Baku, Khazar, and Khvalyn) that followed the Ackchagyl Lake-Sea were also brackish water bodies and experienced large oscillations in water level at various times. Typical autochthonous Caspian fauna are found in the palaeontological records starting with the Apsheon stage of the Caspian depression. The appearance of this fauna was probably due to immigration (invasion) of Pontic endemics to the Caspian depression from the Euxinian depression via the Kumo-Manych connection during the first or both major Pliocene-Pleistocene transgressions (Table 3b) and their subsequent evolution in the Caspian depression.

The formation of the Khvalyn Lake-Sea about 90 kya (Table 4b) marked the beginning of the Mediterranean phase in the Caspian depression. Repetitive connections with the Euxinian depression resulted in immigration of at least nine Mediterranean invertebrate species and three Mediterranean fish species from the Euxinian depression ((Mordukhai-

Table 3. Ponto-Caspian basin evolution: phase 2, separation—Euxinian and Caspian depressions.^a

Geologic Epoch	Name of water body	Time (mya)	Salinity (ppt)	Main geologic events	Main events in faunal evolution	
(a) Euxinian depression						
Late Miocene (5.8–5 mya)	Late-Pontic Lake–Sea	5.8–5	10–15	Separation of both basins	Development of “Pontian” fauna with many lineages related to modern autochthonous Caspian fauna	
↓	Pliocene (5–2 mya)	Kimmerian Lake–Sea Kujal’nik Lake–Sea	5–2.6 2.6–1.7	5–12 5–12		Flourishing of Pontian lineages Flourishing of Pontian lineages. Migration of Pontian fauna to the Apsheron basin via Kumo–Manych connection
	↓	Pleistocene (2–0.09 mya)	Gurian Lake–Sea	1.7–0.9	5–8	Co-existence of Pontian lineages and modern autochthonous Caspian lineages
Chauda Lake–Sea		0.9–0.4	5–8	Isolation from Mediterranean Basin	Exchange with neighboring Baku basin, immigration of freshwater fauna, development of brackish water lineages ancestral to modern estuarine liman relicts	
Ancient Euxinian Sea		0.4–0.25	5–8	Reconnection with Mediterranean Basin via Sea of Marmara	Immigration of Mediterranean fauna, development of endemic lineages	
Uzunlar Sea		0.25–0.09	5–12	Transition to the Mediterranean Phase, salinization of the basin	Expansion of Mediterranean fauna, restriction of endemic and Caspian autochthonous fauna to freshest areas	
(b) Caspian depression						
Late Miocene (5.8–5 mya)	Babadjan Lake–Sea	5.8–5.2	15–30	Separation of both basins; climate aridization	Brackish and freshwater lineages extinguished by gradual salinization of the basin	
↓	Balakhan Lake	5.2–2.5	Differing opinions: 300 or fresh?	Single lake in southern basin	Three versions: hypersaline fauna, freshwater fauna, or absence of macroorganisms	
	Pliocene (5–2 mya)	Ackchagyl Lake–Sea	2.5–2	5–12	First transgression (~ 50 m above sea level), connection with Euxinian basin, followed by regression	Origin of fauna is under discussion
↓	Pleistocene (2–0.09 mya)	Apsheron Lake–Sea	2–0.7	5–12	Second major transgression	Appearance of modern “autochthonous” Caspian lineages; their migration to the Gurian basin
	Early- and Late-Baku lake–seas	0.7–0.35	5–12	Turkyan regression caused by Mindel glaciation, followed by transgression	Development of modern autochthonous Caspian lineages. Faunal exchange between Baku and Chauda basins	
	Early-Khazar Lake–Sea	0.35–0.25	5–12	Interglaciation and water level transgression up to 20 m above sea level, followed by regression	Reconnection and faunal exchange between basins, immigration of Mediterranean fauna from Euxinian basin	
	Late-Khazar Lake–Sea	0.25–0.09	5–12	Transgression followed by regression to 50 m below sea level during Riss Glaciation	Modern lineages of autochthonous fauna predominate, limited dispersal of Mediterranean species	

Note: mya = millions of years ago.

^aAfter Andrusov (1918), Arkhangel’sky and Strakhov (1938), Mordukhai-Boltovskoi (1960), Zenkevich (1963), Nevesskaya (1971), Starobogatov (1994), Kaplin (1995), Mandych et al. (1995), Dumont (1998), and Molostovsky and Guzhikov (1999).

Boltovskoi 1960; Zenkevich 1963). The modern Caspian Sea came into existence about 9 kya as the last glaciers receded from the area. The climate and hydrologic regime in the region since then have favored a slight increase in the salinity, reaching about 13 ppt in the southern part of the basin.

Origin of modern Ponto-Caspian fauna

The wide fluctuations in salinity and alternating connections and isolation over millions of years between the Caspian and Euxinian depressions and between the Ponto-Caspian region, the Mediterranean basin (World Ocean), and

Table 4. Ponto-Caspian basin evolution: Mediterranean phase—Euxinian and Caspian depressions.^a

Geologic Epoch	Name of water body	Time (mya)	Salinity (ppt)	Main geologic events	Main events in faunal evolution
(a) Euxinian depression					
Late Pleistocene (0.09–0.01 mya)	Karangat and Girkan seas	0.09–0.04	15–20	1st Mediterranean phase, interglaciation and transgression	Invasion of Caspian fauna to Euxinian depression during Girkan stage. Establishment of Mediterranean fauna
	Surozhsky and then NovoEuxinian Lake	0.04–0.009	0–5	Tectonic sagging and cutoff of exchange with Mediterranean Sea, decrease of salinity	Dispersal of Caspian fauna immigrated from Late Khvalyn Lake–Sea. Mediterranean fauna extinguished
↓					
Holocene (0.01 mya to present)					
	Ancient Black Sea	0.009–0.007	Increases	Secondary sagging of Aegean area and intrusion of saline Mediterranean waters to the basin	Immigration and establishment of Mediterranean fauna, autochthonous Caspian fauna depressed and restricted to freshest areas
	Modern Black and Azov seas	0.007–present	<1–22		Formation of modern fauna, continued addition of Mediterranean–Atlantic fauna
(b) Caspian depression					
Late Pleistocene (0.09–0.01 mya)	Early-Khvalyn Lake–Sea	0.09–0.04	3–8	Largest transgression during Quaternary period: 46–48 m above sea level; reconnection with Euxinian Basin	Invasion by Mediterranean fauna from Girkan Sea, establishment of euryhaline Mediterranean species
	Late-Khvalyn Lake–Sea	0.04–0.009	3–8	Enotayev regression: 64 m below sea level; followed by transgression up to 10 m above sea level. Several regressive, transgressive and stable water level stages	Repetitive invasions and establishment of euryhaline Mediterranean species. Immigration of glacial opportunists
↓					
Holocene (0.01 mya to present)					
	Novocaspian Basin and modern Caspian Sea	0.009–present	<1–13	Four major water level fluctuations with maximum lake level 20 m below sea level	Formation of modern fauna
↓					

Note: mya = millions of years ago.

^aAfter Arkhangel'sky and Strakhov (1938), Mordukhai-Boltovskoi (1960), Zenkevich (1963), Starobogatov (1994), Bronfman (1995), Kaplin (1995), Mandych et al. (1995), and Dumont (1998).

the Pannonian depression dramatically influenced the evolution and adaptation of Ponto-Caspian fauna, resulting in their selection for euryhalinity. Species richness (Fig. 3a) has subsequently decreased as faunal composition has become heterogeneous (Figs. 3b, 3c).

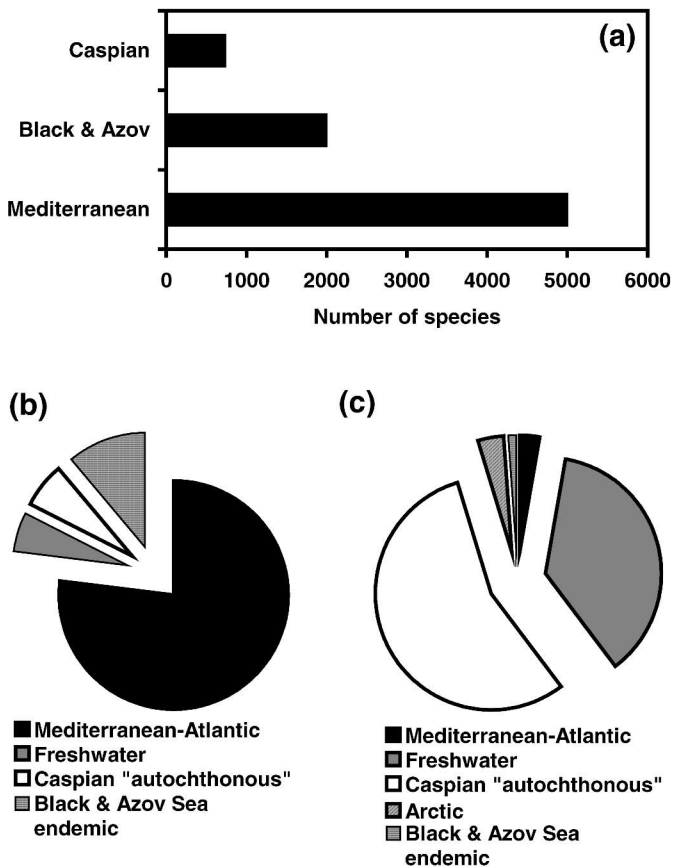
Among endemic Ponto-Caspian groups, the autochthonous Caspian species are primary contributors to species diversity of the Caspian Sea (Fig. 3c) and play a significant role in the diversity of the Sea of Azov and estuaries of Ponto-Caspian rivers. They include species whose ancestors lived in the Tethys Sea and brackish-water Sarmatian and Pontic seas. The marine ancestry of these species contributes to their success as invasive organisms. For example, the zebra mussel, *Dreissena polymorpha*, despite being a freshwater organism, has a free-living planktonic (veliger) stage like that of marine bivalves. This characteristic has allowed it to expand its range to other continents via the ballast water of transoceanic ships.

A special “liman-Caspian” group can be distinguished from among the endemic fauna of the Black Sea and its estuaries (Zhuravel 1969; Starobogatov 1994). This group is com-

posed of relict species that may have evolved in estuaries of the semi-enclosed late Miocene and Pliocene basins that occupied the Euxinian depression, although Mordukhai-Boltovskoi (1960) suggests a more recent origin during the Pleistocene Epoch. *Dreissena bugensis* is the best-known representative of this fauna, occurring since Chauda time (Starobogatov 1994). Some of these species are closely similar to the autochthonous Caspian fauna that inhabited the Caspian depression, whereas others can be traced to lineages originating in the Pannonian basin (e.g., *D. bugensis*). Until recently, the dispersal of these liman-Caspian relicts was restricted to watersheds of the South Bug River, Dnepr–Bug liman, and the Ingulets River estuary. From there they have been intentionally introduced or spread via shipping and other vectors to the Dnepr and Volga rivers and the Baltic Sea (Zhuravel 1969).

Because of the geologic history of the Ponto-Caspian basins, many Ponto-Caspian endemic species surviving to modern times are characterized by a high tolerance for, or physiological adaptation to, salinity fluctuations (e.g., Beliaev and Birshtein 1940; Karpevich 1955; Romanova 1970) and therefore can

Fig. 3. Comparison of invertebrate species numbers in the Caspian, Black and Azov, and Mediterranean seas (without Protozoa, Rotatoria, Gastrotricha, Kinorhyncha) (Birshtein et al. 1968; Vodianskii 1972; Orlova 2000): (a) number of species in each sea during the 1960s, (b) contribution of different faunal groups to species diversity of the Black and Azov seas during the 1950s–1960s, and (c) contribution of different faunal groups to species diversity of the Caspian Sea.



establish and reproduce in oligohaline and fully fresh waters. This feature has permitted more than 60 invertebrate Ponto-Caspian species, including coelenterates, mollusks, crustaceans, and polychaetes, to penetrate freshwater areas upstream of Ponto-Caspian basin estuaries (Mordukhai-Boltovskoi 1979).

The contemporary Black and Azov seas are now populated mostly by Mediterranean–Atlantic fauna (Table 4a, Fig. 3b), including at least 1790 metazoan species in the Black Sea and 200 in the Sea of Azov (Vodianskii 1972; Gomoiu 1975). The number of Mediterranean species has been increasing since the 1960s in both seas. The process of modern “mediterraneanisation” of the Black and Azov basins is caused by both direct human activities and decrease of freshwater input (Vodianskii 1972). During the 20th century, at least 21 metazoan invertebrates native to the Atlantic Ocean and Mediterranean Sea were introduced and became established in the Caspian basin through intentional stocking, construction of seaways (e.g., the Volga–Don Canal), and shipping (Zenkevich 1963; Karpevich 1975; Orlova 2000). In addition, species endemic to the Black Sea, including the liman-Caspian group, additional North Atlantic species, and invertebrates of Indo-Pacific origin, contribute about 40% of

the nonindigenous invertebrates in the modern Caspian Sea (Grigorovich et al. 2002).

A group of freshwater opportunistic immigrants represents another component of the Ponto-Caspian fauna. Freshwater species, including rotifers, non-onychopod cladocerans, copepods, oligochaetes, mollusks, chironomids, and cyprinid and percid fishes, inhabit the northern basin of the Caspian Sea as well as estuaries and fresher areas of the Black and Azov seas. This group likely colonized the basins in the Ponto-Caspian region during phases of low salinity and were subsequently selected for euryhalinity (Zenkevich 1963).

A group of Arctic glacial relicts (~23 invertebrate species, at least two fish species, and the Caspian seal (*Phoca caspica*)) are present in the Caspian Basin (Mordukhai-Boltovskoi 1960) and likely entered from the north during or just after the last glacial (Würm Glaciation) period in Europe through a system of intermediate ice-dammed waters or via the massive Siberian Proglacial Lake (Romanova 1970). These (mainly) crustacean species, which show little or no speciation, now inhabit the deep, cold waters of the Caspian Sea to an upper temperature limit of ~10°C (Romanova 1970). One fish species from this group of Arctic relicts, the salmon *Salmo trutta labrax*, inhabits the Black and Azov seas as well.

The Baltic Sea

Physical characteristics

The Baltic Sea is a platform basin in northern Europe connected with the Atlantic Ocean via the North Sea through the Danish Straits (Fig. 2, Table 1). It can be considered an estuarine-type water body where the salinity regime is driven by the balance between saltwater inflow from the North Sea and freshwater inflow from contributing rivers. There is a positive freshwater balance owing to a combination of large catchment area (over four times the water surface area) and numerous large rivers draining into the basin (Stanners and Bourdeau 1995).

The bottom topography is characterized by a series of basins, the largest of which is the Baltic Proper, occupying the southern half of the Baltic Sea. Two major gulfs extend eastward off the Baltic Proper, the Gulf of Riga and the Gulf of Finland. The northern half of the Baltic Sea includes the Gulf of Bothnia, composed of the Bothnian Sea (south) and Bothnian Bay (north). Because of the complicated bathymetry, water exchange with the saline North Sea produces permanent salinity stratification in the Baltic Sea at ~60 m and a resultant oxygen-deficient stagnant layer below the halocline throughout the Baltic Proper.

Surface salinity is highest in the southwest where the Baltic Proper transitions to the Kattegat, a narrow, shallow channel that connects the Baltic Proper with the North Sea. The salinity gradient through the Kattegat acts as a barrier, isolating the brackish and low-salinity surface waters of the Baltic Sea from the Atlantic Ocean. A sharp thermocline develops in the upper water column of the Baltic during the summer, and surface water temperatures range from 12 to 19°C. Water temperature in the deeper waters is generally 5–6°C with some colder patches. Ice forms during the winter and covers a significant part of the Baltic, especially Bothnian Bay, which can be ice-covered for up to 6 months each year. Dur-

ing the latter half of the 20th century, the Baltic Sea was affected by an overall decrease in water quality, with severe eutrophication now found in all areas (Gudelis 1989; Stanners and Bordeau 1995).

Geologic evolution

The modern Baltic Sea is a geologically young postglacial water body. The Baltic Sea depression was covered with ice during the last glacial advance of the Pleistocene and filled with freshwater in the late Quaternary period after recession of the ice cover, starting ~13 kya. During the early postglacial period, the Baltic depression contained a system of glacial lakes (Blazhchishin 1998), which coalesced into a single large lake, South Baltic Proglacial Lake, by ~12.7 kya (Kvasov 1975). This lake was followed by four successive periods of fresh- and brackish-water transgressions and regressions starting about 10 kya that were driven by interactions between rising sea levels and isostatic rebound in the Baltic region. Oscillations in water level, changes in temperature, and salinity variations from freshwater to mesohaline conditions (18 ppt) in the main basin were common and resulted in frequent changes in the dominant biological assemblages. The latter are reflected in the names given to these four periods of Baltic Sea history (Grasshoff 1975): Yoldia Sea, ~10–9.5 kya, cold, fresh to brackish water, characterized by arctic species such as *Yoldia arctica*; Ancylus Lake, ~9.5–7.0 kya, fresh water initially, becoming warmer and brackish (8–12 ppt) by the end of this period, named for *Ancylus fluvialis*, a freshwater gastropod; Littorina Sea, ~7.0–4.0 kya, warm with brackish salinity ranging from 8 to 18 ppt, named for *Littorina littorea*, a brackish water snail; Post-Littorina Sea, ~4 kya to present, sometimes referred to as Mya Sea after *Mya arenaria*, a brackish water mussel that appeared during this period. The various saltwater and freshwater transgressions and regressions were not synchronous throughout the entire Baltic basin, resulting in differences of as much as 1000 years in the dates ascribed to the beginning and end of each period, depending on location.

There are few data on fauna of the early postglacial lakes, but available evidence suggests that the aquatic environment in these basins was fresh and that the basins had no significant connection with the ocean. Sediments deposited during this period consist mainly of inorganic material, suggesting low biological abundance and productivity, and also reveal evidence for periodic intrusions of marine water, but none that resulted in salinity increases sufficient to support development of marine or brackish-water biota. Marine and brackish glacial relicts as well as Atlantic marine species first appeared during the Yoldia Sea phase. The Ancylus Lake was characterized by freshwater fauna, with marine and brackish-water biota surviving only in refuges. The sedimentary record shows that biological productivity was 10-fold higher during the Ancylus Lake period than during the Yoldia Sea phase, suggesting high quantitative development of biota in the ecosystem (Gudelis 1989; Blazhchishin 1998).

The Littorina Sea marked the onset of brackish-water conditions that have persisted to the modern Baltic Sea. The fauna of the Littorina Sea was of mixed origin and contained all previous groups: freshwater, Atlantic, and glacial relict species. The productivity of the Littorina Sea was even

higher than that of Ancylus Lake, as evidenced by the sedimentary record for this time period (Gudelis 1989).

Origin of modern Baltic Sea fauna

The evolution of what might be considered “endemic” Baltic fauna occurred over the last 4000 years in conditions close to those found in the modern Baltic, i.e., presence of a salinity gradient and stratification of the basin. The resulting “native” communities are simply organized with relatively low diversity and with strong dominance of several species belonging to deposit feeders, seston feeders, and predators. For example, *Macoma* + *Pontoporeia* (*Monoporeia*) + *Halicriptus* comprise one of the main communities in soft bottom areas of the Baltic Proper, whereas communities with *Mytilus* dominate on hard bottom areas. Dominant “native” species in saline areas are often glacial relicts or Atlantic species that entered during periods when the basin was connected with the ocean, with resultant saltwater transgressions. In more diluted areas, freshwater species together with glacial relicts such as *Monoporeia affinis* dominate. In shallow and freshwater habitats, these communities are composed of typical freshwater species (Fig. 4).

Much of the present-day biological diversity in the Baltic Sea reflects the relatively recent establishment of non-indigenous species introduced intentionally or unintentionally via human activities. Olenin and Leppäkoski (2000) reported at least 97 established nonindigenous species and noted that the availability of habitats in the Baltic ranging from fresh through brackish to saline supports foreign species with widely differing environmental tolerances. At least 16 of the established nonindigenous species are endemic to the Ponto-Caspian basins and play important roles in Baltic estuarine and lagoonal ecosystems (Leppäkoski et al. 2002).

The Great Lakes

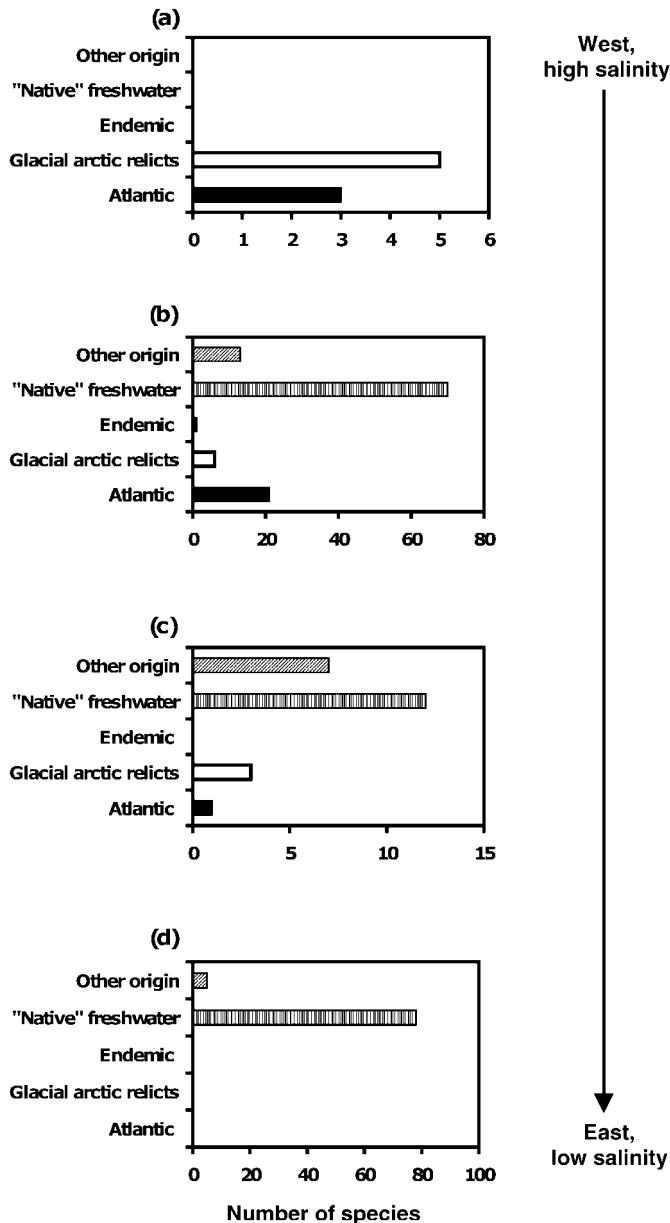
Physical characteristics

Like the Baltic Sea, the Great Lakes are geologically young and were formed by glaciation at the end of the Pleistocene Epoch. The Great Lakes system (Fig. 1) consists of five interconnected large lakes (Superior, Michigan, Huron, Erie, and Ontario) and their connecting channels, including Lake St. Clair, which lies between Lakes Huron and Erie. The Great Lakes basin is landlocked but connects to the Atlantic Ocean by the 1550-km St. Lawrence River (Seaway), which flows from the eastern end of Lake Ontario to the Gulf of St. Lawrence (U.S. Army Corps of Engineers and Great Lakes Commission 1999).

Except where specifically cited, the following discussion draws on data, statistics, and summaries from Government of Canada and U.S. Environmental Protection Agency (1995), Beeton et al. (1999), and U.S. Army Corps of Engineers and Great Lakes Commission (1999).

The Great Lakes system is the largest surface freshwater reservoir in the world. Physical characteristics (Table 1) vary across the basin because of its overall size and the varying types of bedrock underlying each lake. The northern end of the basin lies in a subarctic climate zone, whereas the rest of the basin is situated in a humid continental temperate zone. Ice forms on all of the Great Lakes to a greater or lesser degree during most winters.

Fig. 4. Contribution of different faunal groups to species diversity of the macrozoobenthos in the Baltic Sea: (a) Baltic Proper, Asko area (M.I. Orlova, personal communication, May 1994 data); (b) Gulf of Riga littoral zone (Kotta et al. 1998); (c) St. Petersburg area (eastern Gulf of Finland) outside Neva Bay, 1997–1998 (Alimov and Panov (1997) and Alimov et al. (1998)); (d) in Neva Bay, 1997–1998 (Alimov and Panov (1997) and Alimov et al. (1998)).



All of the Great Lakes are situated above sea level, with water surface elevations ranging from ~183 m above mean sea level on Lake Superior to ~74 m on Lake Ontario. A distinctive characteristic of the Great Lakes is the variation of water levels daily, seasonally, and on longer time periods. None of the rivers flowing into the basin is large enough to individually have a significant affect on water levels. Changes in water levels are mainly determined by the balance between over-lake precipitation plus land runoff (including groundwater) and transpiration plus evaporation plus

outflow. The most significant outflow is through the St Lawrence River, ~224 km³·year⁻¹. The amount of water lost equals that gained on long-term average, but water levels across the basin vary by 0.1–0.6 m seasonally to annually and by 1.8–2 m on an irregular decadal or longer cycle.

The water quality in bays and harbors and some large open-lake areas of the Great Lakes became severely degraded during the 20th century as a result of cultural eutrophication and toxic chemicals from human activities, much like what has occurred in the Ponto-Caspian basins and the Baltic Sea. However, in 1972, the United States and Canada established a binational Great Lakes Water Quality Agreement that set goals for nutrient and toxic chemical load reductions and established outright bans on some of the most detrimental chemicals (e.g., dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs)). By the 1990s, a significant improvement in water quality was apparent, toxic chemical accumulation in fish had decreased, and the trophic status of each lake had improved. Lakes Superior, Michigan, and Huron are classified as oligotrophic except for inner Green Bay on Lake Michigan and inner Saginaw Bay on Lake Huron, which remain eutrophic. Lake Erie has recovered to the extent that the eastern and central basins are classified as oligotrophic to mesotrophic and the western basin is generally considered mesotrophic. Similarly, Lake Ontario is characterized as oligo-mesotrophic to mesotrophic (International Joint Commission 1989).

Geologic evolution

The glacial history of the Great Lakes basin and the resultant formation of the Great Lakes are well documented. The following discussion is based on Teller (1987) and the recent summary by Larson and Schaetzl (2001).

Part of the Great Lakes Basin, particularly Lake Superior and part of Lake Huron, lies at the southern edge of the Canadian Shield, a large mass of hard Precambrian metamorphic and igneous rocks. Abutting the southern edge of the Shield are geologically younger and softer sedimentary rocks, such as limestone, shale, sandstone, halite, and gypsum, of Paleozoic age (230–600 mya). Because of their differing resistances to erosion, these strata are most responsible for the location and existence of the basins that became the modern Great Lakes.

During the Pleistocene Epoch, extensive glaciation of North America episodically covered and then retreated from all or part of the Great Lakes basin. Although evidence suggests that continental glaciation covered all or part of the basin at least six times over the last 800 000 years, the terrestrial record is incomplete due to erosion by each successive ice sheet. Only the last advance, the Wisconsin Glaciation (Laurentide Ice Sheet), is well documented.

Differential resistance to erosion of the Paleozoic strata underlying the area determined drainage patterns that developed during the pre-Wisconsin glacial and interglacial periods. As the Laurentide Ice Sheet advanced through the region to its maximum southern extent (21–18 kya), it broadened and deepened the preglacial drainage network of valleys and depressions to form the precursors to the five modern Great Lakes basins. As the ice sheet retreated (starting ~18 kya), these deeply scoured basins became the foci for accumulation of glacial meltwater, which ponded in a series of proglacial

lakes that initially drained south to the Mississippi River and Gulf of Mexico. Proglacial lakes gradually extended northward and eastward as the ice sheet continued its retreat.

Isostatic rebound played a major role in determining the outlets and water levels of the Laurentide proglacial lakes and continues to impact the modern Great Lakes today. Drainage from the early proglacial lakes fluctuated between outflow to the south and outflow through eastern outlets into the flooded Lake Ontario basin – St. Lawrence Valley and south into the Champlain–Hudson River Valley system to the Atlantic Ocean. By about 10 kya, outflow was entirely to the east through the St. Lawrence River to the Atlantic Ocean, and by 9.5 kya, the general outline of the modern Great Lakes had formed.

There is no evidence that saltwater or brackish water was present in any of the postglacial Great Lakes basins. By 12 kya, a large proglacial lake formed covering the present Lake Ontario basin and a portion of the St. Lawrence Valley as far east as Quebec. Shortly after 12 kya, the glacial margin blocking the St. Lawrence Valley at Quebec retreated far enough north to open the valley all the way to the Atlantic Ocean. Although saltwater flowed into the St. Lawrence Valley to form the Champlain Sea, a marine embayment that extended as far west as Ottawa, there is no evidence that it extended into the Lake Ontario basin. Thus, the history of evolution of the modern Great Lakes is not only short, but also exclusively freshwater.

Origin of modern Great Lakes fauna

The Great Lakes do not have the species diversity and endemism typically found in ancient lakes, such as the African rift lakes or Lake Baikal, but they do provide a diversity of habitats and spatial heterogeneity that has contributed to the stability of the invertebrate population (Beeton et al. 1999). Many species are cosmopolitan, but there is also a high level of endemism in some taxa, such as coregonid fish (A. Ricciardi, McGill University, Montreal, Québec, personal communication). Diatoms are a major component of the plankton in each lake, as are blue-green and green algae and phytoflagellates. Among the latter, different species are found in some of the Great Lakes but not in others. A high level of species diversity and endemism are also characteristics of freshwater unionid mussels in North America. Diverse and stable unionid assemblages were also characteristic of the Great Lakes, but native populations in the lakes were decimated by the zebra mussel invasion that started in the late 1980s (Ricciardi et al. 1998).

As the Laurentide Ice Sheet advanced across northeastern and central North America, freshwater fauna in its path either didn't survive or were pushed ahead in ice-dammed waters in front of the advancing glacier and survived in refugia south of the ice margin (Carter et al. 1980). During glacial retreat, these species dispersed via the northwardly expanding proglacial lakes that preceded the modern Great Lakes. A small number of organisms have been identified as glacial opportunists (or glacial relicts), *Mysis relicta* Loven, *Diporeia* spp., *Limnocalanus macrurus* Sars, *Senecella calanoides* Juday, and possibly *Diaptomus sicilis* and *D. ashlandi*. They are believed to have arrived in the mid-continent region via ice-dammed waters pushed ahead of the advancing Laurentide Ice Sheet and probably originated in

brackish areas of the Arctic Ocean. They form a distinctive deepwater community in the modern lakes and generally dominate the benthic community in abundance and biomass (Carter et al. 1980; Beeton et al. 1999).

Before human settlement and related human activities, the Great Lakes, with the exception of Lake Ontario, were protected from natural invasions of aquatic species via the St. Lawrence River by the imposing physical barrier of Niagara Falls between Lakes Erie and Ontario. The first recorded entry of a nonindigenous species (sea lamprey) occurred by canal in the early 1800s, and the number of successful introductions has more or less paralleled the growth of human activities in the region since then. Mills et al. (1993) documented 139 established nonindigenous species in the Great Lakes and analyzed both pathways and source regions. Ricciardi (2001) updated the total to 162. Eurasian endemics dominate the nonindigenous inventory with 94 of 162 identified species. The next largest identified source region was the North American Atlantic watershed with 19 species. Ponto-Caspian species comprise about 50% of invasions (8 of 15 new species) identified between 1985 and 2000, and ~73% of the new invasions (8 of 11 new species) attributed to ballast tank transport by transoceanic vessels during the same time period (Ricciardi and MacIsaac 2000; Ricciardi 2001)

Discussion

The success of Ponto-Caspian species invasions in both the Baltic Sea and the Great Lakes contains elements of each of the invasion-theory frameworks described previously (see Introduction). Many Ponto-Caspian species evolved and survived through millions of years of changing environmental conditions, resulting in euryhalinity and wide adaptive capabilities that may have selected them for high invasion success (historic model). The Baltic Sea and Great Lakes exhibit much lower species diversity than the Ponto-Caspian basins, both are “disturbed” ecosystems, and all three are climatically compatible (vulnerability model). Interconnection of river systems across Europe via canals established readily available direct invasion corridors between the Ponto-Caspian basins and the Baltic Sea, and economic globalization during the last two decades of the 20th century increased the frequency of ship traffic, and thus ballast water discharge, between all three regions (propagule model).

The success of Ponto-Caspian species in the Great Lakes is paradoxical. There is relatively little direct vessel traffic between the Black Sea and the Great Lakes, and thus direct vectors between the two systems are few in number (R.I. Colautti, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, unpublished data). This suggests a low frequency of direct propagule delivery. The time required to transit the Mediterranean Sea and Atlantic Ocean adds an additional barrier. Further, there is no salinity gradient in the Great Lakes, so all successful invaders must be freshwater tolerant.

The same invasion corridors that connect the Ponto-Caspian basins to the Baltic Sea may serve indirectly to provide species to the Great Lakes through secondary invasions via ballast water originating from the Baltic Sea. The St. Lawrence Seaway provides direct access to the Great Lakes for ships

carrying ballast water, and most transoceanic vessel traffic entering the Great Lakes originates from northern European ports (Mills et al. 1993; R.I. Colautti, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, unpublished data). From 1959, when the St. Lawrence Seaway opened, through 2000, 36 of 50 non-indigenous aquatic species established in the Great Lakes during that time period are attributed to ballast tank transport and discharge of ballast water (Mills et al. 1993; Ricciardi 2001). Establishment of invasion corridors linking the Great Lakes with European ports and the Baltic Sea, the spread of Ponto-Caspian species through European river and canal systems to European ports, and the euryhaline adaptation of many Ponto-Caspian species appear to be major factors in the recent Ponto-Caspian introductions (MacIsaac and Grigorovich 1999; Ricciardi and MacIsaac 2000). Although chemical conditions in the Great Lakes differ significantly from those in the open Black, Azov, and Caspian seas, most Ponto-Caspian species that have invaded the Great Lakes are endemic to coastal waters of these basins or to estuaries of Ponto-Caspian rivers. Consequently, the chemical characteristics of areas occupied by Ponto-Caspian species in their native habitats and in the Great Lakes may be much more similar than seems apparent. Ricciardi (2001) has also raised the possibility of facilitation or invasional meltdown associated with the Ponto-Caspian invaders in the Great Lakes.

Consequently, the surge of Ponto-Caspian species in the Great Lakes that started in the mid-1980s may have resulted from two complementary factors: (i) establishment of corridors that enhanced the transfer of propagules between the Ponto-Caspian basins, the Baltic Sea, and the Great Lakes and (ii) the establishment of facilitative interactions between invaders from the same endemic region. The voluntary (1989, Canada) and mandatory (1993, U.S.A.) open-ocean ballast exchange implemented for ships entering the Great Lakes may also be acting as an additional filter that favors the survival of euryhaline Ponto-Caspian species over other potential invaders because of incomplete exchange resulting in brackish conditions.

Summary

The long and complex geologic evolution of the Ponto-Caspian basins involved periodic connections to and isolation from the World Ocean, succession from interbasin connections to separation and isolation, and then reconnection (Black Sea) to the ocean (Mediterranean Sea) in more recent geologic time. These events resulted in the evolution of diverse modern faunal assemblages of mixed origins consisting of endemic (autochthonous) Ponto-Caspian species, Mediterranean–Atlantic immigrants, and arctic Pleistocene glacial relicts, with characteristics of freshwater, brackish water, and marine taxa represented. In particular, the autochthonous Ponto-Caspian species, a diverse group of endemic euryhaline fauna that evolved from ancestral marine immigrants in the ancient Ponto-Caspian basins, are characterized by wide adaptive capacities and constitute a significant portion of the invasive species currently spreading to regions in northern Europe and to the Great Lakes.

In contrast to Ponto-Caspian basin evolution are the histories of the Baltic Sea and Great Lakes. Both the Baltic Sea and Great Lakes ecosystems are less than 12 000 years old. The biota of the geologically young Baltic Sea are also of mixed origin and contain immigrant species from the Atlantic Ocean as well as some arctic glacial relicts. However, unlike Ponto-Caspian fauna, Baltic Sea fauna are characterized by low diversity and continuing immigration of marine Atlantic elements. The biota of the Great Lakes is similar to that in other large glacial lakes in North America, Europe, and Asia (e.g., Lakes Ladoga and Onega) but differs from these systems by the relatively high species diversity found in some faunal groups. Glacial relict species also constitute an important component of benthic and planktonic communities in the Great Lakes.

The Ponto-Caspian basins, the Baltic Sea, and the Great Lakes are geographically remote and, until recently, were separated by physical barriers that prevented species migrations between them. Human activities and modification of river systems associated with facilitation of ship-borne trading routes established direct and indirect interconnections that have become invasion corridors. The evolution of the Ponto-Caspian basins was significantly longer and more complex than that of either the Baltic Sea or the Great Lakes, resulting in euryhaline faunal groups with wide adaptive capacities. Thus, many of the coastal and estuarine Ponto-Caspian species have been evolutionarily selected for survival in habitats found in the Baltic Sea (fresh-to-brackish) and Great Lakes (fresh).

Several factors appear to play a significant role in this invasion story: (i) the presence of the autochthonous and liman-Caspian fauna with ancestral marine origins, but which evolved through one or more significant phases of lacustrine conditions resulting in euryhalinity and broad adaptive capabilities; (ii) the availability and human enhancement of invasion corridors between ecosystems with suitable environmental conditions and habitats favorable for the invading species; and (iii) facilitation of invasions through invasional meltdown. The modern invasion corridors established by transoceanic vessels are capable of dispersing species across broad geographic barriers to different biogeographic realms in much the same way that the formation of large proglacial lakes led to the dispersal of species among systems and basins that later became physically isolated from each other.

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