



History of aquatic invertebrate invasions in the Caspian Sea

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Abstract

Incorporation of the fossil record and molecular markers into studies of biological invasions provides new historical perspectives on the incidence of natural and human-mediated invasions of nonindigenous species (NIS). Palaeontological, phylogeographic, and molecular evidence suggests that the natural, multiple colonizations of the Caspian basin via transient connections with the Black Sea and other basins played an important role in shaping the diversity of Caspian fauna. Geographically isolated, conspecific Ponto-Caspian lineages that currently inhabit fragmented habitats in the Ponto-Caspian region show limited genetic divergence, implying geologically recent episodes of gene flow between populations during the Pliocene to Pleistocene. Several molluscan lineages in the Caspian Sea may have descended from Lake Pannon stock before the Late Miocene isolation of the Caspian depression, about 5.8 million years ago. Anthropogenic activities during the 20th century were responsible for a 1800-fold increase in the rate of establishment of new aquatic species in the Caspian Sea compared to the preceding two million years of natural colonization. The observed success of NIS invasions during the 20th century was due primarily to human-mediated transport mechanisms, which were dominated by shipping activities (44%). Human-mediated species transfer has been strongly asymmetrical, toward the Volga Delta and Caspian Sea from or through Black and Azov Seas. Global and regional trade, particularly that mediated by commercial ships, provides dispersal opportunities for nonindigenous invertebrates, indicating that future invasions in the Caspian Sea are anticipated.

Introduction

The enclosed Caspian Sea is the world's largest brackish waterbody, comprising nearly 40% of the earth's continental surface water (Mordukhai-Boltovskoi 1960; Dumont 1998). One of the remarkable aspects of its fauna is the high level of endemism (Dumont 2000). Among the 950 extant aquatic metazoan species recorded, 424 taxa are endemic or shared partly with the Black–Azov and Aral Seas (Mordukhai-Boltovskoi 1964, 1979; Kasymov 1987). Several groups of crustaceans (e.g. Mysidacea, Cumacea, Amphipoda, and Onychopoda) and molluscs (e.g. Cardiidae and Pyrgulidae) have produced species flocks (Mordukhai-Boltovskoi 1960, 1979). At least 159 species have ranges that encompass naturally

isolated habitats in the Caspian Sea, freshened areas, inlets, and estuaries of the Black and Azov Seas, and lower reaches of rivers draining into the Black, Azov, and Caspian Seas basins (hereafter, Ponto-Caspian region) (Mordukhai-Boltovskoi 1960). There is little understanding of the origin of these discontinuous distributions, despite well-known distributional patterns for some species (Mordukhai-Boltovskoi 1960; Dumont 2000; Richter et al. 2001).

Since the Late Miocene isolation of the Caspian depression, its fauna has been regarded as a 'relict' of the preceding Sarmatian Sea, which existed from 14.5 to 8.3 million years ago (mya) during the Miocene (Sovinskii 1904; Dumont 1998, 2000; Richter et al. 2001). However, fossil deposits strongly indicate morphological discontinuities among biotas of

successive phases of the Caspian Sea from the Miocene through to the Pliocene (Mordukhai-Boltovskoi 1960; Zenkevich 1963). In their concept of species, Mordukhai-Boltovskoi (1960) and Zenkevich (1963) assumed that morphologically recognized species in the fossil record differed in their genetic makeup. The fossil record also indicates that the Early Pliocene marked the earliest appearance of true Caspian lineages, which subsequently disappeared for at least three million years, before reappearing in the Late Pliocene (Mordukhai-Boltovskoi 1960).

Mordukhai-Boltovskoi (1960) suggested that several Ponto-Caspian molluscan species descended from lineages that originated in Lake Pannon, a Miocene–Pliocene enclosed basin that existed in central Europe from 12 to 4 mya. Spectacular adaptive radiation in several molluscan groups produced nearly 100% endemism in Lake Pannon, which Geary et al. (2000) attributed to the lake's antiquity and physical stability (e.g. salinity of 5‰). Conversely, the Caspian basin experienced dramatic salinity fluctuations and phases of transgressions and regressions during the Tertiary and Quaternary (Mordukhai-Boltovskoi 1960; Zenkevich 1963). Several Pannonian lineages (e.g. *Dreissena*, *Cardiidae*) likely penetrated into the Caspian depression after the re-union of Lake Pannon with the Pontic basin (Mordukhai-Boltovskoi 1960).

The advent of genetic techniques now provides an opportunity for estimation of the relative timing of the divergence of extant lineages under the assumption of a molecular clock (e.g. Cristescu et al. 2001). Among the most useful techniques that are now employed to explore past gene flow events are allozyme and DNA sequence analyses (e.g. Berg and Garton 1994; Stepien et al. 1999; Cristescu et al. 2001; Berg et al. 2002). Cristescu et al. (2001) established that the Ponto-Caspian onychopod *Cercopagis pengoi* lineage split during the Pleistocene, 0.8 mya, forming two divergent mitochondrial (mt) DNA lineages in the Caspian and Black–Azov basins. This finding supports Mordukhai-Boltovskoi's (1960) hypothesis of geologically recent (i.e. Late Pliocene and Pleistocene) episodes of faunal migration between the Caspian and Black Sea basins.

Attempts to compare the extent of palaeobiological (i.e. Late Pliocene–Holocene) invasions with modern human-mediated introductions in the Caspian Sea have been constrained by incomplete historical information of faunal compositions (e.g. Rass 1978; Nikolaev 1979). The primary focus of this study is to appraise

the accelerating rate of human-mediated invasions as compared to natural historical levels. We combine fossil, molecular, and phylogeographic evidence to estimate the extent of invasions resulting from natural mechanisms of dispersal during the last two million years (i.e. Late Pliocene–Holocene), as well as those mediated by anthropogenic activities during the 20th century. Coupling fossil records with knowledge of physical history of the Caspian depression allows us to explore dispersal vectors and resulting distributional patterns for species throughout geologic time.

Historic context of faunal turnovers in the Caspian depression

The great age of the Caspian Sea once led biologists to postulate that the modern Ponto-Caspian fauna is the remnant of the ancient Sarmatian Sea (Table 1, Figure 1A). A veliger-like, planktonic larval stage in development of Ponto-Caspian bivalves is the only known evidence that can be interpreted to reflect their marine origin (Orlova 2000). Nevertheless, the earliest appearance of Ponto-Caspian lineages in the Caspian basin is recorded in fossil deposits of the Early Pliocene (about 5 mya) age (Mordukhai-Boltovskoi 1960). Several Ponto-Caspian hydrobiid and rissoid gastropod species were recognized from older deposits of Miocene (Sarmatian and Maeotic) age (V.V. Anistratenko, Institute of Zoology, Kiev, Ukraine, pers. comm.; Figures 1A, B). However, authorities disagree with respect to the species-level classification of these morphologically cryptic molluscan groups. In most fossil groups there exist no true Ponto-Caspian taxa even at the genus level. Found in Sarmatian clay, six gammarid amphipod species, belonging to the genera *Praegmelina*, *Andrussowia*, and *Gammarus*, are morphologically divergent from modern Ponto-Caspian taxa (Derzhavin 1951; Mordukhai-Boltovskoi 1960). Furthermore, fossil molluscs from Lake Pannon exhibit greater affinities to modern Ponto-Caspian species than to fossil Sarmatian species. *Dreissena* spp. are among the lineages that originated in Lake Pannon, then spread to the Pontic Sea, and later evolved into Ponto-Caspian lineages (Geary et al. 2000). Among the 900 molluscan species described from Lake Pannon, several lineages of dreissenids, cardiids, and melanopsids have long fossil records extending back to the Miocene (Geary et al. 2000). Situated in close geographic proximity

Table 1. Summary of faunal turnovers related to geologic events in the Caspian Sea and adjacent waters based on geologic-stratigraphical studies of deposits.

Geologic epoch (mya)	Time (mya)	Link?		Main events related to Caspian depression and its fauna
		Caspian depression	Black Sea depression	
Miocene 23–5.3	14.5–12.5		Early Sarmatian (20–30%)	Caspian, Black Sea and Pannonian depressions united in Sarmatian Sea; Tethys and Sarmatian lineages
	12.5–10.0		Middle Sarmatian (17–20%)	Lake Pannon (5–12%) separated from Sarmatian Sea
	10.0–8.3		Late Sarmatian (6–17%)	freshening; extinction of marine lineages; evolution of endemic brackish-water lineages
	8.3–6.4		Maeotic (6–15%)	Transient link with Mediterranean Sea (30–40%); expansion and extirpation of Mediterranean lineages
	6.4–5.8		Pontic (10–15%)*	Transgression and reconnection with Lake Pannon (5%)*; freshening; diversification of Pontic lineages
Pliocene 5.3–1.8	5.8–5.2		Late Pontic (10–15%)*	Basins separated; extirpation of Ponto-Caspian lineages; evolution of Babadjanian brackish-water lineages
	5.2–3.4		Balakhian (0.1% or 300‰?)	Extinction of Babadjanian species; expansion of freshwater species; diversification of Pontic lineages in Cimmerian Sea
	3.4–2.0		Akhagayl (5–12%)*	Evolution of Akhagaylian brackish-water lineages; major Akhagaylian transgression; link with Kuyalnik Sea
	2.0–0.7		Apsheron (5–12%)*	Major Apsheronian transgression; transient link with Kuyalnik and Gurian Seas; expansion of Ponto-Caspian species
	0.7–0.35		Baku (5–10%)*	Turkyan regression during Mindel glaciation; transgression and link with Chauda Sea, faunal interchange
Pleistocene 1.8–0.01	0.35–0.25		Early Khazar (5–12%)*	Interglacial; transgression and link with Ancient Euxinian Sea, faunal interchange; transient link between Black Sea and Mediterranean basin (30–40%), intrusion of Mediterranean species
	0.25–0.06		Late Khazar (5–12%)*	Transgression; regression during Riss glaciation; salination of Uzunlar Sea, expansion of Mediterranean species
	0.06–0.019		Early Khvalyn (8–12%)*	Major transgression and reconnection with Girkan Sea, re-colonization of Girkan basin by Ponto-Caspian species; disconnection of Girkan basin from Mediterranean Sea
	0.019–0.009		Late Khvalyn (3–13%)*	Transgressive-regressive stages; expansion of Ponto-Caspian species in Surozhsk and New Euxinian Seas; intrusion of Mediterranean species in Late Khvalyn Sea
	0.009–present		New Caspian (<1–13%)* modern Caspian (<1–13%)*	Reconnection of Ancient Black Sea with Mediterranean Sea (30–40%) and transition to second Mediterranean phase, colonization by Mediterranean species
Holocene 0.010–present			Modern Black Sea (<13–22%)* Modern Azov Seas (<1–12%)*	Human-mediated invasions by nonindigenous species from around world

Summarized from Derzhavin 1951; Mordukhai-Boltovskoi 1960; Zenkevich 1963; Chepalyga 1985; Geary et al. 2000.

Presence of Ponto-Caspian lineages are indicated by *, except for sole occurrence of *Dreissena* spp. indicated by †. Salinity is shown in parentheses. Caspian and Black Sea depressions were united until Late Miocene, about 5.8 mya. Subsequent transient reconnections between concurring basins in Caspian and Black Sea depressions are indicated with arrows.

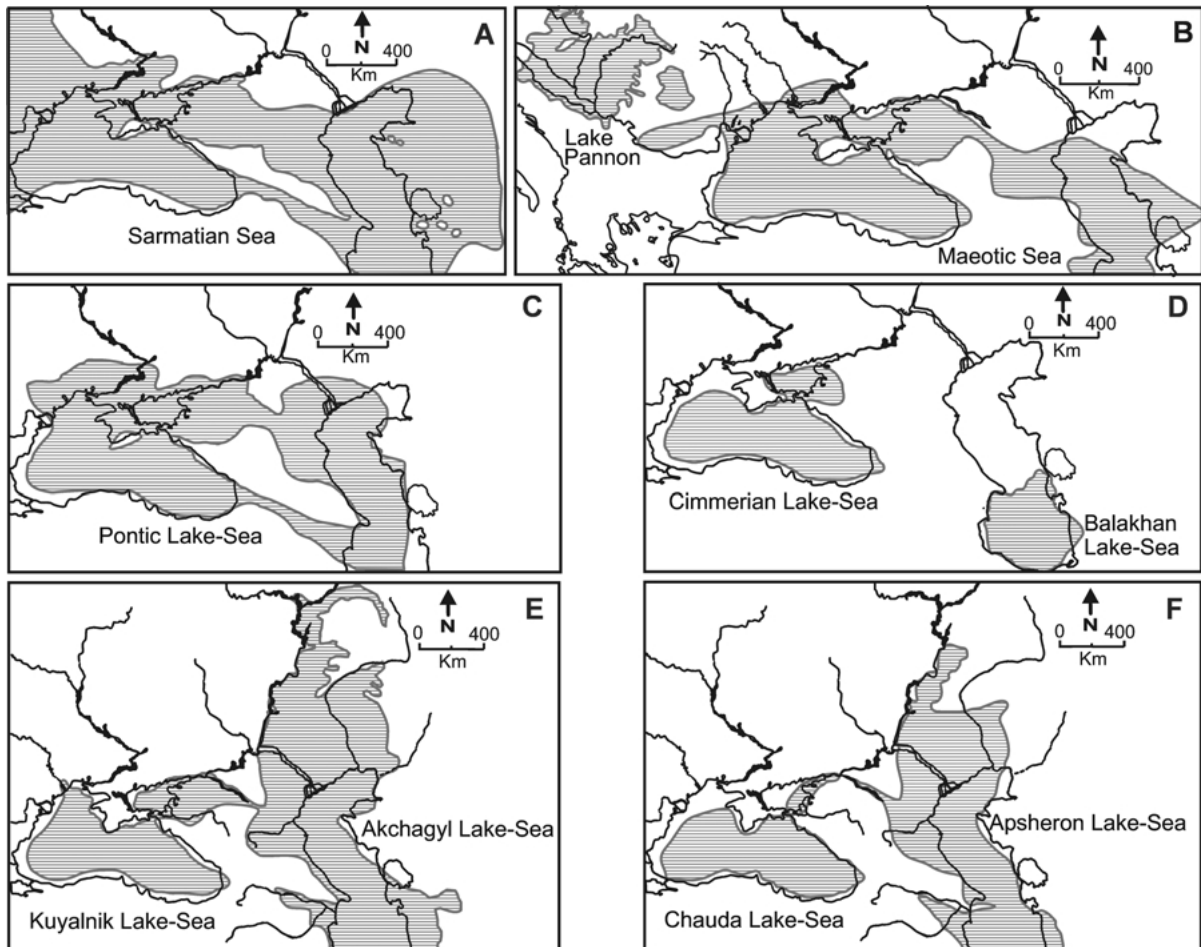


Figure 1. Map of the Ponto-Caspian region showing successive geologic basins in Caspian and Black Sea depressions (shaded) and modern boundaries of Caspian, Black and Azov Seas: Sarmatian Sea (A), Maeotic Sea (B), Pontic Lake-Sea (C), Balakhan and Cimmerian basins (D), Akchagyl and Kuyalnik (E), Apsheron and Chauda basins (F). Modified from Zenkevich (1963). See Table 1 for geologic time scale.

to the Pontic Sea depression, Lake Pannon became united with the former basin during the Late Miocene (Figures 1B, C, Table 1). The newly established sea-way facilitated mass eastward migration of Pannonian fauna to the Pontic Sea (Zenkevich 1963). This major colonization pulse is marked in the fossil record of Pliocene (Pontic) age by the appearance of dreissenids and cardiids, including Ponto-Caspian lineages of *Didacna*, *Monodacna*, *Dreissena rostriformis*, and *D. polymorpha* (see Zenkevich 1963 for additional taxa).

After the Pliocene elevation of the Caucasus Mountains, the Caspian and Black Sea depressions became separated (Figures 1C, D). This isolation had a devastating impact on the Pliocene Caspian Sea biota, resulting in mass extinction of Ponto-Caspian taxa with

a prior history in the basin (Mordukhai-Boltovskoi 1960; Zenkevich 1963). Detailed analyses of stratigraphical ranges of fossil invertebrates suggest that the aquatic fauna of the Caspian basin was neither ecologically nor genetically continuous during the Pliocene to Pleistocene (Table 1). Ponto-Caspian lineages had disappeared from deposits of Babadjanian, Balakhanian, and Akchagylian age (Figures 1D, E). These extinctions are not an artifact of an incomplete Pliocene–Pleistocene fossil record in the Caspian Sea, since the fossil record of the same age is rich and continuous in sediments underlying the Black Sea (Mordukhai-Boltovskoi 1960). We interpret the 3.8 million years' absence of Ponto-Caspian species in the Pliocene–Pleistocene Caspian deposits as evidence of their extirpation.

The opening of transient connections between the Caspian and Black Sea depressions during the Pliocene and Pleistocene played an important role in shaping the biotic composition of the Caspian Sea (Table 1). These connections facilitated several successive migrations of faunal components between these basins (Mordukhai-Boltovskoi 1960; Zenkevich 1963). For example, during the major Akchagylian transgression, a connection temporarily re-established between the Akchagyl and Kuyalnik Seas through the Manych depression (Figure 1E). This probably facilitated the recolonization of at least two species – *Dreissena rostriformis* and *D. polymorpha* – that once lived in the Caspian depression (Mordukhai-Boltovskoi 1960).

Beginning in the Late Pliocene (about 2.0 mya), Ponto-Caspian lineages first appeared in great numbers in the sedimentary layers and have produced a continuous fossil record that extends to the present (see Mordukhai-Boltovskoi 1960 and Zenkevich 1963 for a list of species). Many taxa previously confined to the Black Sea depression during Kuyalnik and Chaudinian phases expanded their distributions to the Apsheron Sea via the Kuma–Manych depression (Figure 1F). This flow of immigrants from western basins probably proceeded into subsequent phases of the Caspian basin including the Baku and Khazar Seas (Table 1).

Succession of glacial and interglacial cycles occurred throughout the Russian plain during the Pleistocene (about 1.6 mya to 10,000 years ago), resulting in drastic salinity fluctuations and phases of transgressions and regressions of the Caspian basin (Zenkevich 1963; Chepalyga 1985; Dumont 1998). Either during the Pleistocene or immediately following, at least 24 Arctic invertebrate taxa penetrated the Caspian basin with glacial meltwater (Orlova 2000). In the Holocene, a transient link was re-established across the Caucasus region, enabling invasion of more than 10 Atlantic–Mediterranean invertebrate species into the Caspian Sea (Rass 1978; Orlova 2000). Radiocarbon dating of *Cerastoderma* (Mollusca) shells indicates that this intrusion occurred during the Middle Holocene (Chepalyga 1985), but Derzhavin (1951) and Rass (1978) suggested that their appearance was related to an earlier link during the Late Khvalyn transgression (Table 1). Holocene Atlantic–Mediterranean invaders are represented by the bivalves *Cerastoderma lamarcki* and *C. umbonatum*, polychaete *Fabricia sabella*, bryozoan *Bowerbankia imbricata*, copepod *Calanipeda aquae-dulcis*, and several platyhelminth species (Mordukhai-Boltovskoi 1960; Kasymov 1982;

Chepalyga 1985; Chepalyga and Tarasov 1997). Atlantic–Mediterranean platyhelminthes lost their native hosts and switched to native Caspian clupeid and acipenserid fishes, implying that the Atlantic–Mediterranean faunal component was likely more speciose during the Holocene than at present (Mordukhai-Boltovskoi 1960). Chepalyga and Tarasov (1997) suggested that some of these invaders were transported with ancient reed boats sailing the Kuma–Manych waterway. However, no historical evidence has been presented to confirm the existence of this entry vector.

Studies of recent sedimentary layers in the Caspian Sea revealed modern invasion pulses, which coincide with stocking efforts during the early 20th century and with the opening of the Volga–Don Canal in 1952 (Chepalyga and Tarasov 1997; Figure 2). Hence, coupling the fossil record with knowledge of physical history of the Caspian Sea provides insights into colonization events and faunal turnovers over geologic time, although precise timing of these events is rarely possible to determine using only palaeontological and geologic evidence. Consequently, critical evaluation of invasion histories, in light of molecular clock data, is essential for our understanding of biological invasions.

Pliocene–Holocene invasions

Although Ponto-Caspian lineages are known from Late Miocene Caspian deposits (see Table 1), we interpret their subsequent absence over the following 3.8 million years as true evidence of their extirpation. We therefore consider Pliocene–Holocene invaders to be those that were unknown in Babadjanian, Balakhanian, and Akchagylian stages (i.e. about 5.8–2 mya). Thus, these species may have subsequently immigrated into the Caspian depression from the Black Sea depression and other adjacent areas or are derived from taxa that did. We assume, after Mordukhai-Boltovskoi (1960), that post-Pliocene diversification in the Caspian fauna has been limited and largely occurred at the subspecies level. Recent evidence from three mt DNA sequences supports this hypothesis (Cristescu and Hebert 2002). However, a few Ponto-Caspian onychopod lineages including *Cornigerius* and *Podonevadne* have had a more prolonged episode of speciation from the Miocene to Pleistocene (Cristescu and Hebert 2002). Using palaeontological, ecological, and molecular evidence, we assembled a total of 456 extant

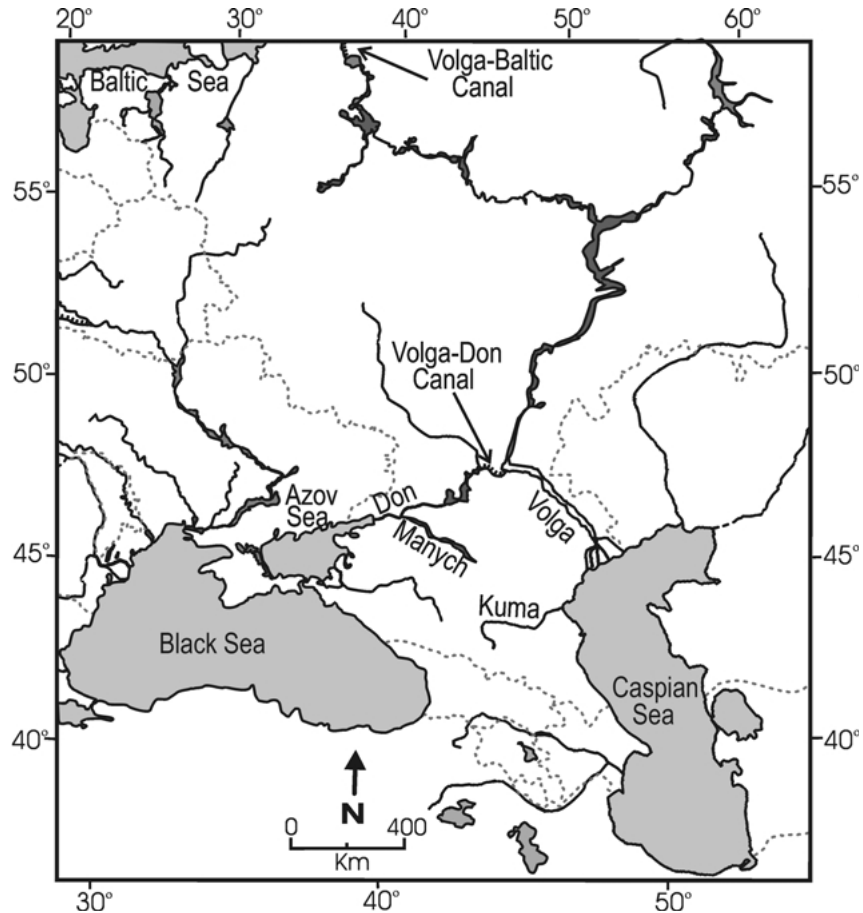


Figure 2. Map showing location of the modern Caspian, Black and Azov Seas and the Volga–Don Canal.

Table 2. Estimates of invertebrate species invasions to the Caspian basin during the last two million years (Late Pliocene–Holocene up to the early 1900s) via natural mechanisms.

Geologic epoch	Time (mya)	Source region	Number of species
Late Pliocene–Pleistocene	2.0–0.8	Black Sea basin	422
Pleistocene	1.8–0.01	Arctic basin	24
Holocene (up to the 1900s)	0.01–present	Azov–Black Sea basin	10

Summarized from Derzhavin 1951; Mordukhai-Boltovskoi 1960, 1979; Chepalyga 1985; M.E.A. Cristescu, unpub. data.

invertebrate species (Table 2) that naturally colonized the Caspian basin between the Late Pliocene and Holocene or are descended from Pliocene–Holocene non-Caspian ancestors; this approach is similar to that employed by Vermeij (1991). The bulk (92.5%) of these palaeobiological invasions is

represented by Ponto-Caspian lineages that were classified by Mordukhai-Boltovskoi (1960, 1979). *Dreissena rostriformis* and *D. polymorpha* were not considered because they were present in older Akchagylian sediments (Zenkevich 1963). Arctic and Atlantic–Mediterranean lineages collectively represent 7.5% of invasions between the Late Pleistocene to Holocene, until the early 1900s (Table 2).

Mordukhai-Boltovskoi (1960) synthesized the long-term history of Ponto-Caspian lineages, in which periods of faunal isolations and species extinctions were intermingled with species invasions (see summary in Table 1). The precise timing of these faunal turnovers is poorly chronicled in the fossil record, except for some molluscan taxa (Mordukhai-Boltovskoi 1960). However, application of molecular clocks now provides a powerful tool for dating important historical processes shaping populations in isolated habitats such as past fragmentation and gene flow events.

The estimated number of Ponto-Caspian species involved in the Late Pliocene–Pleistocene colonization of the Caspian basin should be considered provisional because present species-level systematics remains controversial and species richness appears to be overestimated for several taxa (e.g. Mordukhai-Boltovskoi 1979; Grigorovich et al. 2000). For example, two morphologically distinctive members of the subgenera *Cercopagis* and *Apagis* (i.e. *Cercopagis* (*Cercopagis*) *pengoi* and *C. (Apagis) ossiani*) were characterized by the same haplotype for NADH dehydrogenase subunit 5 (ND5) mt gene in Lake Ontario, while allopatric European populations of *C. pengoi* consisted of up to five haplotypes (Makarewicz et al. 2001). These results suggest that *C. ossiani* and *C. pengoi* represent a single species, while the status of three other species of the subgenus *Apagis* await taxonomic re-assessment. Additional grounds for the inclusion of Ponto-Caspian taxa not chronicled in the fossil record were: (1) both non-molluscan and molluscan invertebrates often possess similar physiological tolerances, environmental preferences, and ‘intrinsic invasive features’ that could contribute equally to extinction or invasion; (2) many species are represented by divergent mtDNA conspecific lineages forming Caspian Sea and Black–Azov Sea clades that are morphologically almost indistinguishable (e.g. Cristescu et al. 2001; Cristescu and Hebert 2002).

Cercopagis lineages inhabiting the Caspian and Azov–Black Sea basins shared a common ancestry some 0.8 mya (Cristescu et al. 2001). Each surveyed population has experienced bottleneck events in the past as evidenced by limited genetic diversity at cytochrome *c* oxidase subunit 1 (COI) and ND5 loci (Cristescu et al. 2001). Arguably, Black Sea lineages of *Cercopagis pengoi* are characterized by higher genetic diversity than their Caspian counterparts, supporting Mordukhai-Boltovskoi’s (1960) hypothesis that the former basin is the most likely source of the lineages in the Caspian basin. However, the basins currently support differing mtDNA lineages, suggesting the possibility that genetic drift has arisen from the founder effect.

By coupling mtDNA sequence diversity at COI, the ribosomal small and large subunits (12S and 16S) with the arthropod mt clock, Cristescu and Hebert (2002) estimated that generic and subgeneric differentiation within Onychopoda occurred over 10–20 mya. Although this estimate may be speculative due to problems with molecular clock cal-

ibration, it is congruent with the rate of genetic change estimated for Ponto-Caspian amphipod crustaceans (M.E.A. Cristescu, University of Guelph, Ontario, pers. comm.). Thus, the overall correspondence among taxa provides evidence for the antiquity of Ponto-Caspian lineages at genus and species levels (Richter et al. 2001; Cristescu and Hebert 2002).

There is some evidence that reduced gene flow with habitat isolation may produce intraspecific mtDNA divergence (e.g. Cristescu et al. 2001). However, available mtDNA sequence data on intraspecific populations residing in the Caspian and Azov–Black basins are limited to several crustacean species, including *Cercopagis pengoi*, *Cornigerius maoticus*, *Podonevadne trigona*, *Pontogammarus maoticus*, and *P. crassus* (M.E.A. Cristescu, pers. comm.). Surveys of mtDNA in these populations revealed limited genetic divergence at COI, rarely exceeding 2%, indicating that episodes of gene flow occurred between these lineages during the Pleistocene (Cristescu et al. 2001; M.E.A. Cristescu, pers. comm.). Thus, studies of mtDNA divergence provide new insights into the incidence of natural dispersal events that are poorly chronicled in the fossil record.

20th-century introductions of nonindigenous invertebrate species

Invasions occurred naturally in the Caspian Sea as a result of geological and climatic events throughout geologic time, while during historic time humans became the major vector for aquatic introductions (i.e. human-mediated invasions after Carlton 1996) in the Caspian region and throughout the world (Karpevich 1975; Ruiz et al. 1997; Cohen and Carlton 1998; Orlova 2000).

Our survey encompasses introduced nonindigenous species (NIS) that were absent from the Caspian Sea and Volga River delta prior to the 1900s, but which successfully colonized and naturalized in this region beyond their historic geographical ranges. Based on literature and field observations, we identified a total of 36 invertebrate NIS that were introduced through human-mediated vectors and became self-sustaining during the 20th century (Table 3).

Our ability to evaluate the extent of 20th-century invasions in the Caspian Sea is limited by the paucity of published information. Therefore, the number of recognized NIS appears underestimated and conservative compared to that recorded in other marine and estuarine

Table 3. Nonindigenous aquatic invertebrate species established in the Caspian Sea during the 20th century.

Taxonomic group	Species name	Year(s)	Native region	Entry vector	References
Mollusca	<i>Mytilaster lineatus</i>	1917–1919	Mediterranean	A	Bogachev 1928
Nematoda	Nematoda (NS) ¹	1917–1919?	Mediterranean	A	Chepalyga and Tarasov 1997
Crustacea	<i>Palaemon elegans</i>	1930–1934	Atlantic–Mediterranean	A	Zenkevich 1963
	<i>Palaemon adspersus</i>	1931–1934	Atlantic–Mediterranean	A	Zenkevich 1963
Crustacea	<i>Ergasilus</i> sp. (NS) ²	1930–1934	Mediterranean–Pontic?	A	Mikhailov 1958
Trematoda	<i>Haploporus longicolum</i> ²	1930–1934	Mediterranean–Pontic	A	Mikhailov 1958
	<i>Haplospalanchnus pachysoma</i> ²	1930–1934	Mediterranean–Pontic	A	Mikhailov 1958
	<i>Saccocoelium obesum</i> ²	1930–1934	Mediterranean–Pontic	A	Mikhailov 1958
	<i>Ancyrocephalus vanbenedenii</i> ²	1930–1934	Mediterranean–Pontic	A	Zablotskii 1966
	<i>Wlassenkotrema longicollum</i> ²	1930–1934	Mediterranean–Pontic	A	Zablotskii 1966
Polychaeta	<i>Nereis diversicolor</i>	1939–1940	Atlantic–Mediterranean	D	Hartman 1960
Mollusca	<i>Abra ovata</i>	1939–1940s	Atlantic–Mediterranean	D	Karpevich 1968
Crustacea	<i>Corophium volutator</i> f. <i>orientalis</i> (as <i>Corophium anodon</i>)	<1951	Atlantic–Mediterranean	?	Derzhavin 1951; Romanova 1975
	<i>Balanus improvisus</i>	1955	Pacific–Atlantic	S	Derzhavin 1956
	<i>Balanus eburneus</i>	1956	Atlantic	S	Zevina 1965
Coelenterata	<i>Blackfordia virginica</i>	1956	Pontic–West Atlantic	S	Logvinenko 1959
Crustacea	<i>Pleopis polyphemoides</i>	1957	Atlantic–Mediterranean	S	Mordukhai-Boltovskoi 1962
Bryozoa	<i>Electra crustulenta</i>	1958	Mediterranean	S	Abrikosov 1959
	<i>Conopeum seurati</i>	1958	Mediterranean	S	Zevina and Kuznetsova 1965
Crustacea	<i>Rhithropanopeus harrisi</i>	1958	West Atlantic	S	Nebolsina 1959
Mollusca	<i>Hypanis colorata</i>	1959	Pontic	M	Saenkova 1960
Coelenterata	<i>Moerisia maeotica</i>	1959	Pontic?	S	Mordukhai-Boltovskoi 1979
	<i>Bougainvillia megas</i>	1960	Pontic	S	Zevina 1965
Polychaeta	<i>Ficopomatus enigmaticus</i>	1961	Atlantic	S	Zevina 1965
Kamptozoa	<i>Barentsia benedeni</i>	1962	East Atlantic–Pacific	S	Zevina and Kuznetsova 1965
Crustacea	<i>Iphigenella shablensis</i>	<1969	Pontic	M?	Mordukhai-Boltovskoi et al. 1969
Mollusca	<i>Lithoglyphus naticoides</i>	1971	European	M	Pirogov 1972
Trematoda	<i>Apophallus muehlingi</i>	1971	European	M	Biserova 1990
	<i>Rossicotrema donicum</i>	1971	European	M	Biserova 1996
	<i>Nicola scriabini</i>	1971	European	M	Biserova 1996
Crustacea	<i>Acartia tonsa</i> (as <i>Acartia clausi</i>)	1981	Atlantic–Indian	S	Kurashova and Abdullaeva 1984
	<i>Podon intermedius</i>	1985	Atlantic–Mediterranean	S	Kurashova et al. 1992
Mollusca	<i>Tenellia adspersa</i>	1989	Atlantic–Mediterranean	S	Antsulevich and Starobogatov 1990
Crustacea	<i>Gammarus aequicauda</i>	<1994	Mediterranean	S	Piatkova and Tarasov 1996
Mollusca	<i>Dreissena bugensis</i>	1994	Pontic	S	Arakelova et al. 2000
Ctenophora	<i>Mnemiopsis leidyi</i>	<1999	West Atlantic	S	Ivanov et al. 2000

Year indicates time of first sighting or published record for inadvertently introduced species, and time interval for stocked target or contaminant species. Hosts of parasites: 1 – *Mytilaster lineatus*; 2 – *Mugil saliens*; 3 – *Lithoglyphus naticoides*. Keys to vectors of introduction: A – accidental releases; D – deliberate stocking; S – shipping activities; M – multiple vectors; ? – unknown or uncertain. NS – species identity not provided.

habitats of the world (see Ruiz et al. 1997, 2000). To test this possibility (i.e. that NIS introductions occurred but were not recognized), we sampled a series of shallow-water habitats in the Volga Delta and Caspian Sea in search of nonindigenous amphipod species. We selected the Amphipoda because they are the best-studied invertebrate group in the Caspian Sea, with 74 resident species recognized prior to commencement of maritime shipping via the Volga–Don seaway (Mordukhai-Boltovskoi 1960, 1979; Birshtein and Romanova 1968). During August 2000, samples were collected in the Volga Delta channels and littoral

zone of the northern and central Caspian Sea, where several crustacean and molluscan NIS are known to occur. A dip net (250-mm mesh) was used for sweeping through vegetation, rocks, and bottom sediments. Using current taxonomic keys (Mordukhai-Boltovskoi et al. 1969; Grigorovich 1989), we identified two introduced amphipod species, *Iphigenella shablensis* and *Gammarus aequicauda* (= *Gammarus locusta*) that were previously reported, but were not recognized as established in the Caspian basin (see Piatkova and Tarasov 1996 for more details). However, our field survey revealed that both species are locally abundant

(at densities >100 individuals m^{-2}), with *I. shablensis* occurring principally in the Volga Delta and northern Caspian and *G. aequicauda* in the central Caspian adjacent to the Apsheron peninsula. Populations of both *I. shablensis* and *G. aequicauda* included ovigerous females and juveniles, indicating that both species were reproducing and likely established.

Owing to uncertainties in systematics of groups with poorly distinguishable morphological features, the occurrence and sequence of NIS arrival are poorly documented for nematodes, polychaetes, and copepods (e.g. Chepalyga and Tarasov 1997). For example, the polychaete *Nereis diversicolor* was deliberately stocked in the Caspian Sea during 1939–1941, but was misidentified and treated as *Nereis succinea* for two decades (Hartman 1960). It is still not clear whether *N. succinea* is established in the Caspian Sea (e.g. Karpevich 1968, 1975). Likewise, the non-indigenous calanoid copepod *Acartia tonsa* has been erroneously reported as *A. clausi* (Kurashova and Abdullaeva 1984; N.V. Shadrin, Institute for Biology of Southern Seas, Sevastopol, Ukraine, pers. comm.). Detailed morphological analyses of calanoid copepods have revealed that the former species represents an Atlantic–Mediterranean introduction (in both the Caspian and Black Seas), while *A. clausi* is a Black Sea resident (N.V. Shadrin, pers. comm.).

During arrival and establishment phases, NIS are difficult to detect due to small population sizes. Several, or arguably most, introductions in the Caspian Sea were discovered only after populations had reached high abundances (e.g. the bivalve *Mytilaster lineatus*). For example, massive efforts were made to introduce the Atlantic–Mediterranean bivalve *Abra ovata* (= *A. segmentum*) between 1947 and 1948 (Chepalyga and Tarasov 1997). However, recent analyses of Caspian sedimentary deposits revealed that the species was inadvertently introduced and became established earlier, with stocked *Nereis*, between 1939 and 1941 (Chepalyga and Tarasov 1997). However, owing to a small population size, *A. ovata* remained undetected until 1955 (Karpevich 1968).

We are aware of three cyprinid fish species native to eastern Asia, grass carp *Ctenopharyngodon idella*, silver carp *Hypophthalmichthys molitrix*, and bighead carp *Aristichthys nobilis* that were stocked and became self-sustaining in many regions of Eurasia, including the Volga Delta and north Caspian Sea (Karpevich 1975; Ivanov 2000). One additional nontarget fish, snake-head *Ophiocephalus argus* was also introduced as a result of these stocking efforts (Zaitsev and Öztürk

2001). Globally these fishes are vectors for numerous parasitic helminthes (Karpevich 1975; Grigorovich et al. 2002). Because no record of parasites exists from the Caspian basin, it is possible that the estimate of the NIS fraction shall increase as additional data become available.

Nonindigenous species that have been successfully introduced to the Volga River delta and Caspian Sea during the 20th century include 58.3% of NIS native to the Atlantic–Mediterranean region (i.e. Lusitanian region of Atlantic Ocean, Mediterranean and Black Seas), 19.4% derived from the North Atlantic region (i.e. Atlantic coasts of Europe or North America), and 11.1% introduced from the Pontic region (i.e. inlets, coastal, and estuarine regions of northern Black Sea). Boreal European–Siberian region, Atlantic, Pacific, and Indian Oceans collectively account for the remaining 11.2% of NIS.

Nonindigenous invertebrates were introduced to the Caspian Sea through a variety of mechanisms, the importance of which varied over time (Figure 3A). Most of these introductions occurred after 1952, when the Caspian Sea was opened to maritime navigation through the Volga–Don Canal. Since that time, shipping has become the largest transport vector, accounting for 44.4% of all introductions to the Caspian Sea. Most sessile marine invaders arrived on ships' hulls during the late 1950s and early 1960s, whereas transportation in ballast tanks of cargo ships was likely the largest single entry mode for free-living invertebrates since the 1980s (Figure 3A, Table 3). During the 1970s, the combination of multiple and often interacting entry vectors (i.e. canal and commercial shipping traffic) facilitated entry of the gastropod *Lithoglyphus naticoides* and at least three parasitic trematode species carried with their gastropod host (Table 3). Thus, over a 40-year period since 1952, vectors related to shipping shifted from those associated with hull fouling to those associated with ballast water discharge (Grigorovich et al. 2002). Other NIS gained entry as nontarget species with aquaculture (27.8%) or through combinations of two or more entry mechanisms that acted jointly (19.4%). Two species (*Nereis diversicolor* and *Abra ovata*) were stocked deliberately. Introductions of invertebrates for commercial purpose started in 1897, although initial efforts to stock the Black Sea oyster *Ostrea edulis* and blue mussel *Mytilus galloprovincialis* were unsuccessful (Karpevich 1975).

Introductions of *Mytilaster lineatus*, *Abra ovata*, and *Lithoglyphus naticoides* are interesting because their fossil shells have been found in Caspian deposits

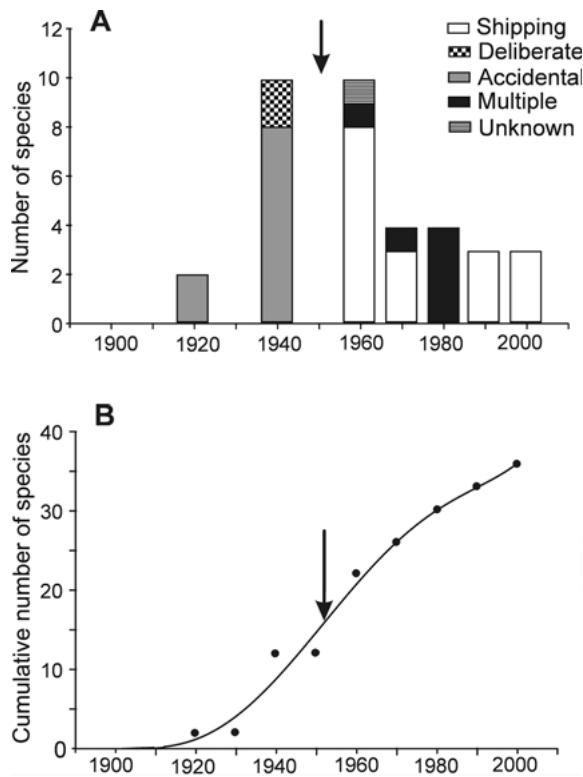


Figure 3. Time trends in introductions of nonindigenous aquatic invertebrates established in the Ponto-Caspian region, sorted by entry mechanism (A). Opening of the Volga–Don Canal (1952) is indicated by arrows. Cumulative number of nonindigenous invertebrate species established in the Caspian Sea and Volga River delta over the 20th century (B). Trends in nonindigenous invertebrate introductions are best described by polynomial function ($R^2 = 0.986$).

from earlier geologic epochs (Pirogov 1972; Orlova 2000). Consequently, the successful naturalization of these species appears to have resulted from multiple inoculations that occurred over an extended period of time.

Invasion trends in the Caspian Sea

Species invasions over the last two million years have challenged the biological integrity of the Caspian Sea. Long-term fluctuations in sea level and climate have breached natural barriers to dispersal for species from several donor regions, notably Lake Pannon, the Black Sea basin, and the Arctic Ocean. During the 20th century, several invertebrate invasions in the Volga Delta and adjacent northern Caspian Sea likely resulted from natural passive dispersal through wind or waterfowl. Examples include the anomopod

cladoceran *Daphnia lumholtzi*, which is indigenous to Australia, southern Asia, and Africa, and the bryozoan *Lophopodella carteri*, which is native to southern Asia, Indonesia, and Africa (Benhing 1928; Abrikosov and Kosova 1963). However, during the 20th century (Figure 3B), human-mediated invasions have occurred with increasing frequency and now constitute the dominant mechanism of the Caspian Sea fauna change (Logvinenko 1965; Ivanov et al. 2000). Recent human-mediated invasions are attributable largely to the creation of ‘invasion corridors’ (i.e. primary transportation vectors and dispersal pathways) linking the Caspian Sea with the Azov and Black Seas (Ricciardi and MacIsaac 2000; MacIsaac et al. 2001). Since the opening of the Volga–Don Canal in 1952, shipping traffic has become the largest vector for transfer of NIS to the Caspian Sea (Figure 3A). Among the 36 NIS recorded in the Caspian Sea and Volga Delta after 1952, 23 taxa possess a suite of characteristics amenable to transportation on ship hulls or in ballast tanks (Zevina 1965; Zevina and Kuznetsova 1965; Gollasch and Leppäkoski 1999).

A recent series of invasions by *Mnemiopsis leidyi* and other marine invertebrates indicates that ballast water transport has become the largest vector for NIS transfer to the Caspian Sea. Three factors that mediate the rate of marine invasions are: (1) an increase in vector size (e.g. more ballast water due to more or larger ships); (2) an increase in NIS inoculation owing to faster ships; and (3) an improvement in vector quality (e.g. ballast water is not contaminated with pollutants) (Carlton 1996). Future NIS introductions are expected to continue as long as expanding regional and global trade provides enhanced dispersal opportunities for aquatic organisms (Gollasch and Leppäkoski 1999; Ivanov 2000).

Based on combined molecular, palaeontological, and ecological data, we recognize 456 invertebrate species that have, since the Late Pliocene, naturally colonized the Caspian basin or are descended from the these taxa. Thus, over the past two million years, the long-term average rate of species invasions is approximately 0.02 species per 100 years. In contrast, the rate of human-mediated establishment is 36 species over the past 100 years. Therefore, the incidence of human-mediated species introductions in the Caspian Sea corresponds to an 1800-fold increase in rate of invasion compared to the background, natural level. Although natural dispersal vectors may account for some recent invasions, human-mediated transfer is dominant, due

primarily to shipping activities (Carlton 1996). Hebert and Cristescu (2002) estimated that human-mediated dispersal of cladocerans might exceed the natural rate in the Laurentian Great Lakes by up to 50,000-fold.

During the last two million years, the Caspian basin has been a target and donor region during several episodes of faunal interchange via natural connections that were temporarily established with the Black Sea basin and the Arctic Ocean. Species and possibly higher-level clades have dispersed to the Caspian Sea and naturalized. Interestingly, this faunal interchange has become strongly asymmetrical since the Holocene. Numerous NIS have been transferred to the Caspian Sea from the Black–Azov basins and from other regions around the world (Tables 2 and 3), yet no invertebrates have dispersed in the opposite direction (e.g. Nikolaev 1979).

Currently, over 30 Ponto-Caspian metazoan species reside in the Volga, Ural and other southward flowing rivers that empty into the Caspian Sea (Mordukhai-Boltovskoi 1960, 1979). Geographical patterns of these distributions are consistent with pathways provided by the rivers, which flow in north-south directions. Arguably, natural barriers (i.e. strong currents, salinity, and ion content) historically served to limit the dispersal by Ponto-Caspian invertebrates in these potential ‘invasion corridors’ (Mordukhai-Boltovskoi 1960). Many of these distributional patterns have been interpreted as the result of dispersal events, principally those mediated by humans during the last century (Dumont 1998, 2000; Orlova 2000). However, recent morphological and molecular evidence provides little support for this hypothesis. For example, at least two invading onychopod cladocerans endemic to the Black–Azov basin, *Podonevadne trigona ovum* and *Cornigerius maeoticus maeoticus*, were identified for the first time from the Volgograd reservoirs during the 1990s (I.K. Rivier, Institute for Inner Water Biology, Borok, Russia, pers. comm.), while the occurrence of phenotypically-divergent, conspecific forms endemic to the Caspian Sea (i.e. *P. trigona trigona* and *C. maeoticus hircus*) have not been confirmed in this reservoir (I.K. Rivier, pers. comm.). Likewise, molecular markers have revealed that the Black–Azov basin, not the Caspian Sea, was the source of invasion of the Volgograd Reservoir by *Cercopagis pengoi* (M.E.A. Cristescu, pers. comm.).

Application of fossil and molecular evidence into the study of historical invasions provides insights on

the accelerating rate of species invasion in the Caspian Sea that has been mediated by anthropogenic activities. However, additional fossil and molecular data will be required to provide finer resolution of the invasion history of this basin and the role of human activities in shaping the current Caspian fauna.

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