PERSPECTIVE

Patterns and mechanisms of aquatic invertebrate introductions in the Ponto-Caspian region[1]

Igor A. Grigorovich, Hugh J. MacIsaac, Nikolai V. Shadrin, and Edward L. Mills

Abstract: The Black, Azov, and Caspian sea drainages (i.e., Ponto-Caspian region) have an extensive and long history of species introductions. Here we review patterns and mechanisms of introductions of aquatic invertebrate species into these ecosystems. Since the late 1800s, 136 free-living and 27 parasitic invertebrate species have been introduced outside their native ranges and have established reproducing populations in the Ponto-Caspian region. The bulk of these introductions are represented by crustaceans (53%), flatworms (15%), and molluscs (13%). Most of the introduced species are native to other areas within the Ponto-Caspian region (37%), with other sizable contributions from the Atlantic–Mediterranean (15%) and boreal European–Siberian (14%) geographic regions. Mechanisms of introductions were dominated by deliberate releases (29%) and shipping activities (22%), with the former occurring principally in freshwater habitats and the latter in marine and estuarine ones. Other introductions resulted from unintentional release (21%) and hydrotechnical development (14%), notably the construction of reservoirs and canals. Global and regional trade, particularly that mediated by commercial ships, provides dispersal opportunities for nonindigenous invertebrates to and within the Ponto-Caspian region, rapidly changing the composition of its endemic fauna.

Résumé : L'introduction d'espèces dans les bassins hydrographiques de la mer Noire, de la mer d'Azov et de la mer Caspienne (i.e., la région pontocaspienne) a une histoire longue et complexe. On trouvera ici une revue des patterns et des mécanismes des introductions d'espèces d'invertébrés aquatiques dans ces écosystèmes. Depuis la fin du 19^{e} siècle, 136 espèces d'invertébrés libres et 27 de parasites ont été introduites à l'extérieur de leur région d'origine et ont établi des populations qui se reproduisent dans la région pontocaspienne. La majorité de ces espèces est composée de crustacés (53 %), de vers plats (15 %) et de mollusques (13 %). La plupart des espèces introduites sont natives d'autres parties de la région pontocaspienne, mais il y a des contributions importantes provenant des régions géographiques atlantique/méditerranéenne (15 %) et européenne boréale/sibérienne (14 %). Les mécanismes principaux d'introduction sont les apports délibérés (29 %), surtout dans les habitats d'eau douce, et les activités de transport maritime (22 %) dans les habitats de mer et d'estuaires. D'autres introductions proviennent de relâchements involontaires (21 %) et de la construction d'ouvrages hydrotechniques (14 %), en particulier de réservoirs et de canaux. Les échanges internationaux et régionaux, surtout par l'intermédiaire des navires commerciaux, créent pour les espèces non indigènes des occasions de se disperser vers la région pontocaspienne et de s'y répandre, modifiant ainsi rapidement la composition de la faune endémique.

[Traduit par la Rédaction]

Introduction and history

The biotic integrity of the Black, Azov, and Caspian sea basins (hereafter, the Ponto-Caspian region) has been challenged by species invasions throughout geological history. During the Tertiary and Quaternary periods, for example, the geologic basins in this region experienced a dramatic sequence of glaciation cycles and phases of transgressions and regressions (e.g., Mordukhai-Boltovskoi 1960; Zenkevich 1963). Drastic fluctuations in salinity and sea levels dramatically altered the faunal composition in these basins (see Grigorovich et al. 2002 for summary of faunal turnovers).

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These geological events in the Ponto-Caspian region also affected genetic continuity between successive basins from the Miocene through to the Pleistocene epoch. The fauna of the Sarmatian Sea became extinct owing to an abrupt salinity decline following its seperation from the ocean. The resultant Maeotic Sea, recolonized by Mediterranean fauna, evolved into the Pontic Sea during the Late Miocene. The new, large brackish-water basin fostered evolution of the Ponto-Caspian lineages from various stocks acquired from the previous and neighbouring basins (Mordukhai-Boltovskoi 1960). Owing to the rise of mountains 5.8 to 5 million years before present (mybp), the Black Sea and Caspian Sea depressions became separated and the fauna in each basin evolved independently (Zenkevich 1963). However, transient connections between the basins during the Pliocene and Pleistocene promoted interbasin faunal migrations (see maps in Grigorovich et al. 2002). For example, during the Akchagylian transgression, a temporary connection was established through the Manych depression, facilitating faunal interchange (Zenkevich 1963). Massive immigration of the ancestral Ponto-Caspian lineages from the Kuyalnik and Chauda seas to the Apsheron Sea later occurred via this link (Mordukhai-Boltovskoi 1960; Zenkevich 1963). This flow of immigrants from western basins probably proceeded into the Baku and Early Khazar seas (Zenkevich 1963). Formation of the Bosphorus Strait resulted in the immigration of the Mediterranean fauna into the ancient Euxinian and succeeding Uzunlar and Karangat basins (Mordukhai-Boltovskoi 1960; Zenkevich 1963). During the Upper Pleistocene (~70 000 ybp), the link with the Mediterranean Sea was interrupted and the fauna of the "Caspian type" penetrated into the western Girkan basin through a temporary connection with the Early Khvalyn Sea (Mordukhai-Boltovskoi 1960; Zenkevich 1963). Recent immigration of Mediterranean species into the Black and Azov seas resulted from intermittent connections through the Dardanelles and Bosphorus straits beginning 9 to 7 thousand ybp, and continuing today (Zenkevich 1963).

Commercial development in the Ponto-Caspian region during the 20th century greatly facilitated the introduction of nonindigenous species (NIS) (e.g., Karpevich 1975*a*; Zaitsev and Mamaev 1997; see below). Construction of reservoirs and other man-made habitats in the drainage basins of eastern European rivers altered or eliminated geographic constraints to species distributions and set the stage for future biological invasions (Mordukhai-Boltovskoi and Galinskii 1974; Mordukhai-Boltovskoi and Dziuban 1976). These basins have also been subject to species stocking and biomanipulation programs, and are used intensively for commercial shipping.

Few studies, however, have attempted to consolidate data on human-mediated introductions of aquatic organisms in the Ponto-Caspian region (e.g., Karpevich 1975*a*; Zaitsev and Mamaev 1997). In this study, we assemble a comprehensive inventory of the introduced aquatic invertebrates in the Ponto-Caspian region since the late 1800s. Moreover, we synthesize the extent, timing, geographic origin, and dispersal mechanisms for introduced aquatic invertebrates to explore the patterns and processes of species introductions in the Ponto-Caspian region.

Survey methods

Survey area and organisms

Our study area encompasses the Black, Azov, and Caspian sea drainage basins, excluding the Danube River and the southern coastal areas of the Black and Caspian seas (see Fig. 1). We consider the freshwater, estuarine, and marine environments that intersect in the Ponto-Caspian region and are subject to invasion from adjacent areas.

Introduced species were defined to be those that successfully colonize and establish populations in regions outside of their historic or native geographic ranges. The categories "nonindigenous" and "indigenous" depend, of course, on the geographic scale under consideration (e.g., basin, region, or continent). Our survey focuses on all known and suspected species whose dispersal beyond their native geographic range has been mediated by human activities. We consider species not native to the Ponto-Caspian region, as well as indigenous ones that are introduced via anthropogenic activities to other, previously uncolonized sites within the region. We did not distinguish NIS whose introductions resulted from transfer across long geographic distances from those that represented local transfers from an adjacent area.

Species were classified according to their residence or invasion status. NIS status was characterized by the degree of certainty that a species was introduced to a particular area by anthropogenic activity. Thus, the status of each species was assigned to one of three categories: (*i*) "definite", for which there exists strong, direct evidence that a species was deliberately or unintentionally transferred outside of its native range by human activities; (*ii*) "probable", for which indirect evidence exists that the species' spread beyond its historic range was mediated by human activities, including habitat modification; and (*iii*) "possible" (i.e., cryptogenic), for those taxa for which no reliable historical data is available to discern whether they are indigenous or introduced (Carlton 1996).

Numerous aquatic species (e.g., *Cerastoderma lamarcki*), which are believed to have been dispersed in the Ponto-Caspian region using natural mechanisms, are beyond the scope of this study (see Zenkevich 1963 for examples). Navigation in the Black, Azov, and Caspian seas may have caused successful invasions during prehistoric times, although the routes and dispersal mechanisms for these invaders have yet to be resolved (Chepalyga and Tarasov 1997). Nevertheless, transient links may also have naturally facilitated faunal interchange between adjacent basins (e.g., Mordukhai-Boltovskoi 1960).

NIS database

We developed a comprehensive database containing records for 163 introduced aquatic invertebrate species gathered from various sources. In total, we were able to obtain nearly 700 records for these species, representing 95 water bodies in the Ponto-Caspian region. The majority of records were obtained from published literature. Additional data were collected from unpublished reports and dissertations, as well as from our field observations.

First appearance indicates the date of the first sighting or collection for inadvertently introduced species, and time of recorded release for stocked target or contaminant species.

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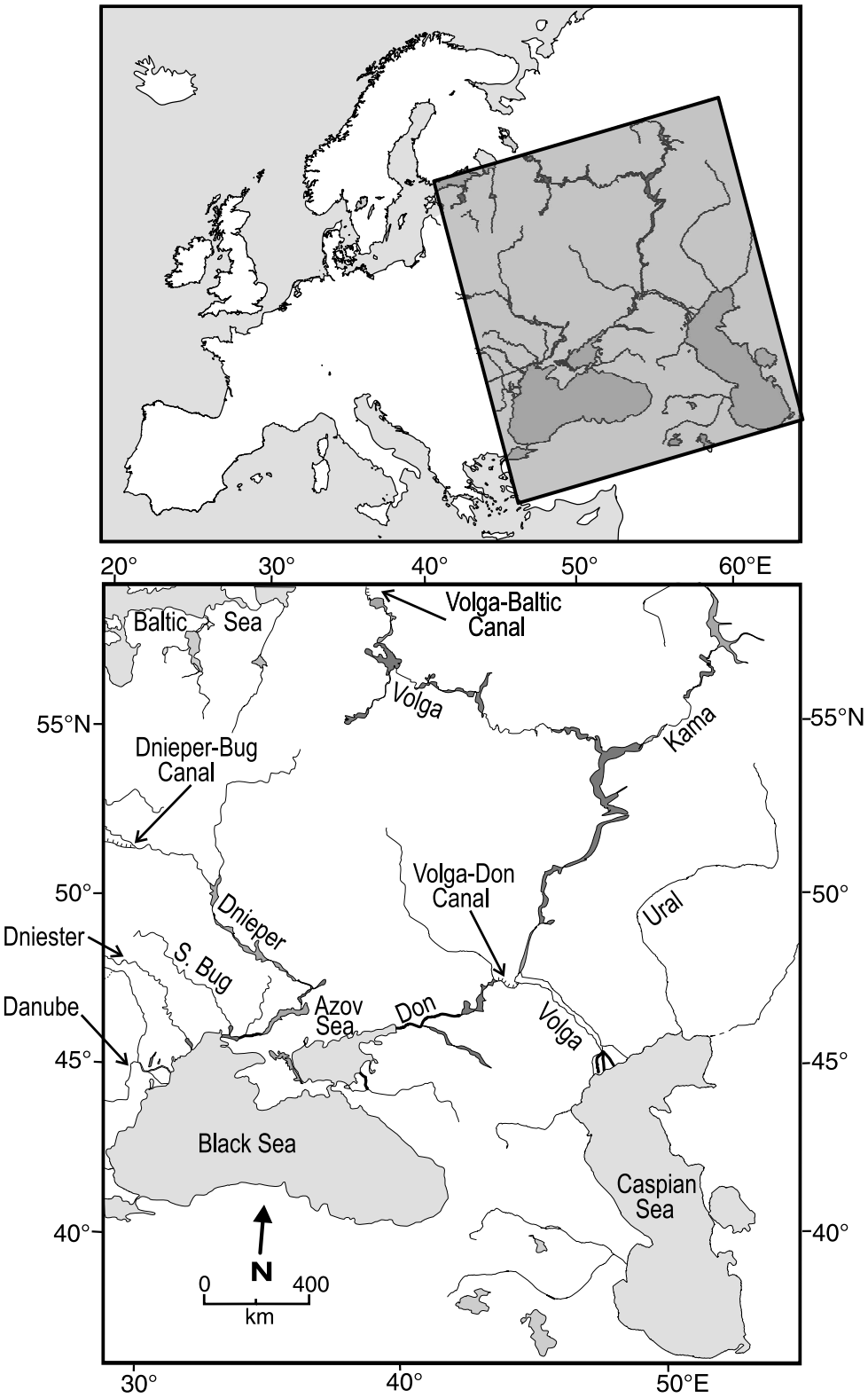
Fig. 1. Map of the Ponto-Caspian region.



Locality of introduction (i.e., human-mediated invasion after Carlton 1996) was defined as the first site, outside of the historic range, where a species successfully colonized owing to human activities. We attempted to discern the native geographic distribution of NIS in the Ponto-Caspian region. The following geographic regions were recognized as native areas of NIS: boreal European–Siberian (i.e., northern and temperate latitudes of Europe and western Siberia within the boreal forest zone), Ponto-Caspian (i.e., Black, Azov, and Caspian seas, including their estuarine regions, limans (i.e.,

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lagoon-like estuaries), and inlets), Pontic (i.e., northern Black Sea, including its estuarine regions, limans, and inlets), North Atlantic (i.e., Atlantic coasts of Europe or North America), Atlantic–Mediterranean (i.e., Lusitanian region of Atlantic Ocean, Mediterranean Sea, and Black Sea), Atlantic–Pacific (i.e., Atlantic and Pacific oceans including adjacent waters of the Arctic Ocean), Pacific (i.e., Pacific coasts of Asia and Australasia), Amur (i.e., the Amur River drainage and adjacent Far-East Asian watersheds), Interior North American (i.e., North American interior basin including the Laurentian Great Lakes), Indian–Pacific (i.e., Indian and Pacific coast of Asia including adjacent estuaries), Baikal, Caucasian (i.e., inland drainages between the Caspian and Black seas), and Australian (i.e., Australian interior basin).

Entry mechanisms were defined as the most probable means by which a species was first introduced outside of its native range. Entry mechanisms were categorized as follows: (*i*) deliberate releases (i.e., cultivation on fishery farms and stocking); (*ii*) accidental releases, including those from aquaria, escape from cultivation, and releases of nontarget species with aquaculture; (*iii*) shipping activities, including transport in solid or liquid ballast as well as fouling on hulls; (*iv*) hydrotechnical development (i.e., river damming and construction of canals and reservoirs); (*v*) multiple vectors that involve more than one entry mechanism. We did not distinguish among several entry mechanisms acting jointly. Parasites were given the same entry mechanism(s) as that of the host species, except in instances where they were unintentionally introduced as contaminants with stocked hosts.

The principal limitation of our data set is the paucity of information pertaining to introduction and occurrence of NIS in the Ponto-Caspian region during the 1980s and 1990s. We are aware that intentional stocking (i.e., "acclimatization" after Karpevich 1975*a*) of invertebrates and fishes continued in the former U.S.S.R. into the 1980s, and possibly the 1990s. However, results and consequences of these efforts are difficult to trace since many records are not readily accessible in the refereed literature, but rather occur in conference proceedings, collected abstracts, and bulletins of various institutions in the Commonwealth of Independent States (CIS) (see Yanushevich (1966) for a list of institutions).

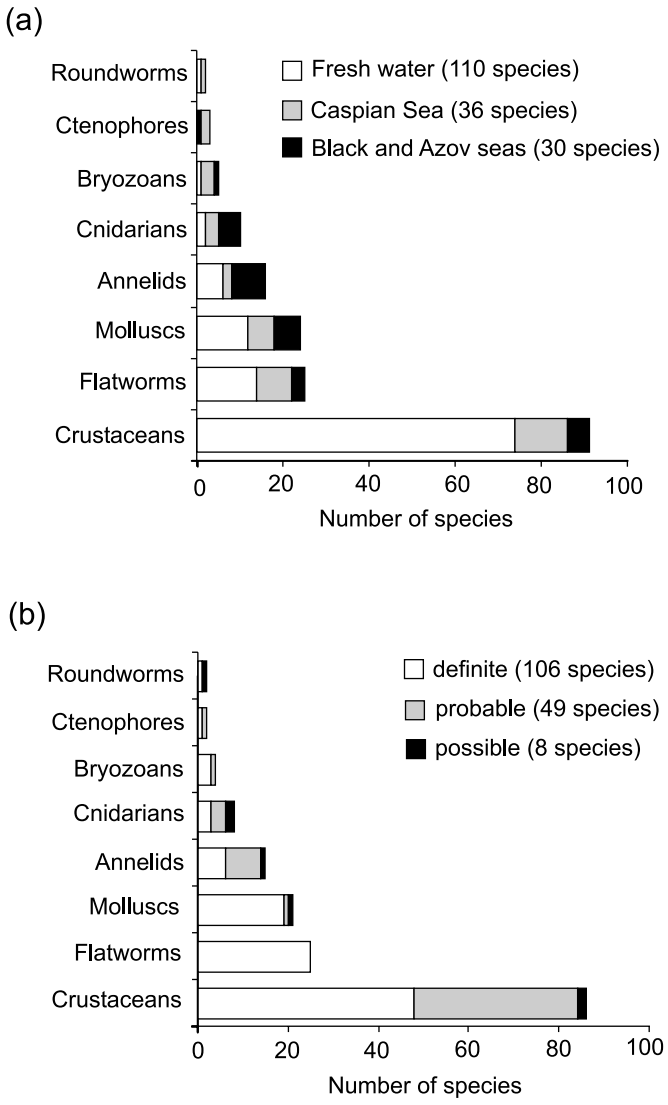
Results and discussion

Composition and status of NIS

One hundred and sixty-three invertebrate species were identified as introductions in freshwater, estuarine, and marine habitats of the Ponto-Caspian region since the late 1800s (Fig. 2*a*).

Free-living invertebrate NIS in the Ponto-Caspian region are dominated by crustaceans (53%), molluscs (13%), and annelids (9%), whereas flatworms dominate among parasitic fauna, composing nearly 15% of the total introduced species (Fig. 2*a*). Free-living cnidarians, bryozoans, roundworms, and ctenophores collectively represent ca. 9% of the NIS recorded in the Ponto-Caspian region (Fig. 2*a*). The composition of nonindigenous fauna in freshwater habitats differs from that in estuarine and marine ones in that there is a considerably higher proportion of crustaceans and by the absence or reduced frequency of ctenophores and cnidarians in fresh water (Fig. 2*a*).

Fig. 2. (*a*) Taxonomic diversity of nonindigenous invertebrates established in the Ponto-Caspian region, sorted by habitat. (*b*) Status of introduced species in the Ponto-Caspian region, sorted by taxonomic group.



One hundred and six (65%) of the 163 introduced species in our analysis were considered definite introductions (Fig. 2*b*). These species were transferred to new habitats in the Ponto-Caspian region with direct involvement of humans, including deliberate stocking, unintentional releases, and by shipping activities. Examples include the bivalves *Dreissena polymorpha*, *Dreissena bugensis*, and *Hypanis colorata*, which are demonstrably distinct in morphology from resident taxa. The bulk of these introductions are represented by crustaceans. Another 49 species (30%) were considered probable introductions; an indirect by-product of human activities including alteration of hydrological regimes or canal and reservoir construction (Karpevich 1975*a*; Mordukhai-Boltovskoi and Dziuban 1976). Finally, eight species (~5%) were classified as cryptogenic. Examples include nematode and copepod species (see below) that

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are poorly differentiated taxonomically, with no information available regarding their native distribution.

Native regions of NIS

NIS that have been successfully introduced to Ponto-Caspian waterbodies are native to 13 geographic zones, including 37% of identified NIS, which are native to different areas of the Ponto-Caspian basins (Fig. 3). In early Holocene, the native range of many Ponto-Caspian species encompassed the Black Sea coast and the Azov and Caspian seas, as well as estuarine regions, and in some cases, lower reaches of the rivers draining into these seas (Mordukhai-Boltovskoi 1960). Ponto-Caspian species have extended their ranges into inland freshwater basins primarily because of human activities. Most of the introduced Ponto-Caspian species are crustaceans (Fig. 3).

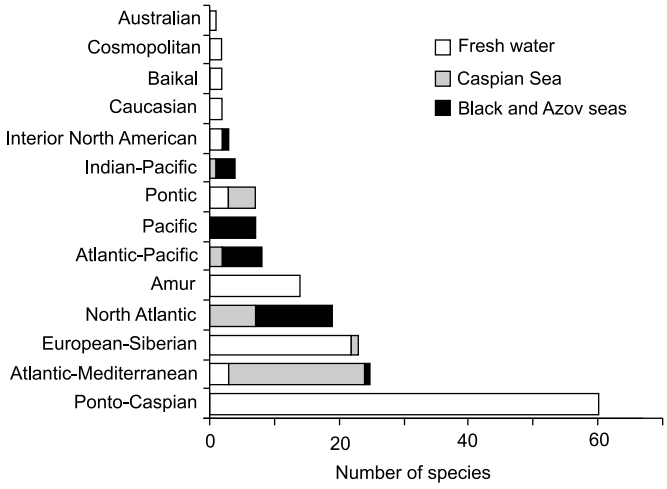
Atlantic–Mediterranean species, which accounted for 15% of total NIS in the region, were introduced mainly from shipping activities. Freshwater species native to European–Siberian zoogeographic province make up another 14% of invaders; these species were derived from the northern habitats following reconstruction of Ponto-Caspian rivers and established naturally reproducing populations in man-made habitats in middle and lower portions of these rivers (Mordukhai-Boltovskoi and Dziuban 1976). Other geographic regions that contributed species to the Ponto-Caspian region include Amur (9%), North Atlantic (7%), Atlantic–Pacific (5%), Pacific (4%), and Pontic (3%). Oceanic species have established only in estuarine and marine habitats in the Ponto-Caspian region (Fig. 3). Conversely, species originating from Interior North America, the Amur River, Lake Baikal, and boreal European–Siberian province have invaded only freshwater habitats. Species native to other geographic regions collectively account for nearly 5% of introduced species in the Ponto-Caspian region (Fig. 3). *Craspedacusta sowerbii* and *Eurytemora affinis* are regarded as cosmopolitan across the Northern Hemisphere (e.g., Protasov et al. 1981).

The majority of introduced species in our analysis are originated from other areas of the Ponto-Caspian region. Although these species are native to specific areas or watersheds within the Ponto-Caspian region, there exists little or no evidence of natural range expansion. Rather, human activities, such as deliberate stocking, hydrotechnical development, and shipping, were apparently responsible for dispersal and establishment of most of these species in new habitats.

Entry mechanisms and time scales

Since the late 1800s, the long-term average rate of introductions to the Ponto-Caspian region averages ca. 1.5 species per year. This value approximates the long-term average invasion rate in the Great Lakes (e.g., Ricciardi and MacIsaac 2000). Nonindigenous invertebrates in the Ponto-Caspian region have been introduced through an array of mechanisms (Fig. 4*a*), although the importance of individual vectors has varied tremendously over time and across habitat types. The rate of invasions reached its zenith between 1940 and 1960 (Fig. 4*a*), and was highest during the 1950s. At that time, government authorities in Europe (and later in North America) promoted invertebrate stocking to enhance

Fig. 3. Geographic origin of nonindigenous aquatic invertebrates established in the Ponto-Caspian region, sorted by habitat. See text for descriptions of geographic regions.



fish production and harvest (Ioffe 1968; Karpevich 1975*a*). Many of the species that were introduced intentionally during this period expanded their ranges subsequent to establishment at the colonization site.

Deliberate introduction by humans historically played an important role in invertebrate invasions of Ponto-Caspian habitats, composing 29% of the total number of established species introductions (Figs. 4*a*, 4*b*). Freshwater habitats were differentially targeted for intentional introductions, with many fewer species introduced to marine and estuarine habitats (Karpevich 1975*a*). Failure to establish reproducing populations discouraged continued stocking of invertebrates for commercial reasons in the former Russian Empire during the 19th century (see below). Subsequent extensive stocking the fishes during the 1930s fostered development of programs to improve food supply for fishes, often through deliberate introduction of forage invertebrates. However, the rates of fish stocking was at least one order of magnitude greater than that of invertebrates (Figs. 5*a*, 5*b*). Many invertebrates became established elsewhere in the Ponto-Caspian region by 1960, although stocking programs continued throughout the decade. By the late 1970s, stocking was greatly reduced or eliminated in many areas (Pligin and Yemelyanova 1989). The number of new, documented invasions declined steeply after the 1960s, following a reduction in the frequency of deliberate introductions (Figs. 4*a*, 6).

Shipping activities account for 22% of the total invertebrate introductions (Figs. 4*a*, 4*b*), likely through a combination of discharge of contaminated ballast water and fouling of ships' hull surfaces and anchors. Shipping was a particularly important vector in estuarine and marine environments, paralleling in importance the roles of hydrotechnical development and intentional stocking in freshwater ecosystems. The majority of the recognized introductions to Ponto-Caspian waterbodies during the 1980s and 1990s have been attributed to ballast-water transport, illustrating the growing importance of this mechanism in association with increased volume of shipping traffic. This pattern parallels that in the Laurentian Great Lakes, where ballast-water transport by commercial vessels has been invoked to explain the origin of

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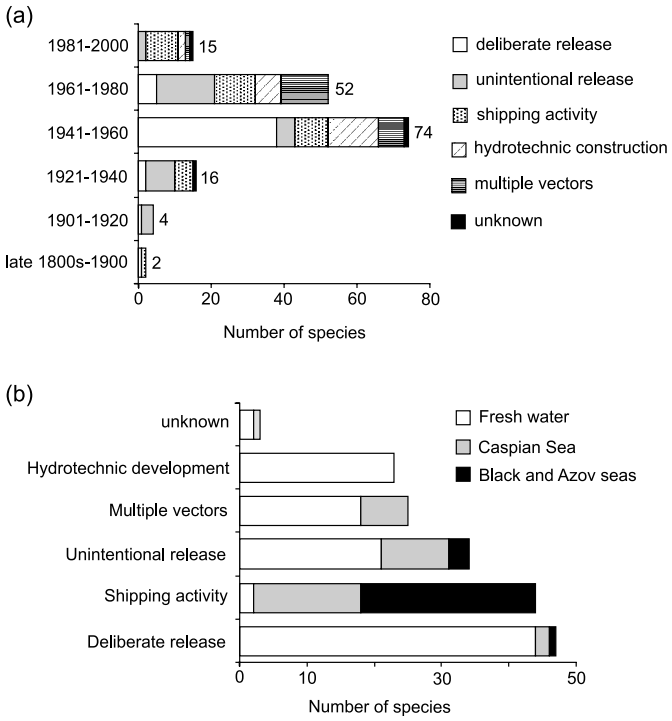
Fig. 4. (*a*) Time trends in introductions of nonindigenous aquatic invertebrates established in the Ponto-Caspian region, sorted by entry mechanism. (*b*) Entry mechanisms of nonindigenous aquatic invertebrates established in the Ponto-Caspian region, sorted by habitat.



a majority of recent animal NIS introductions (Ricciardi and MacIsaac 2000).

Unintentional release was implicated as the entry vector for 21% of the introduced species, mainly parasitic flatworms. The relative importance of unintentional release was temporally variable. Massive translocations of the Amur cyprinid fishes (*Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, and *Aristichthys nobilis*) during the late 20th century inadvertently introduced numerous helminthes in several freshwater habitats in Europe (Appendix A). Unintentional releases have added to the species complement of marine and freshwater systems with almost equal frequency (Figs. 4*a*, 4*b*).

Hydrotechnical construction contributed 14% of the NIS introduced to the Ponto-Caspian region, primarily through canal and reservoir construction (Fig. 4*b*). Reconstruction of Ponto-Caspian rivers and construction of other canals and reservoirs in the Volga, Dnieper, and Don watersheds during the 1940s and 1950s facilitated range expansion of numerous northern freshwater and southern Ponto-Caspian species (Mordukhai-Boltovskoi 1979; see below for examples). Since that time, however, the significance of this entry mechanism has waned.

Between 1940 and 1980, a combination of multiple and often interacting vectors became progressively more important as a source of introductions. In total, 13% of the introduced species were associated with multiple vectors. Construction of reservoirs and canal networks enabled commercial ships to move between previously isolated basins, thereby facilitating the entry of NIS. For example, the Volga–Don canal was opened in 1952 to permit direct maritime navigation to the Caspian Sea from the Azov Sea. This canal, linking these systems via their major rivers, the Volga and Don, served as a dispersal pathway for entry of NIS (Zevina 1965; Zevina and Kuznetsova 1965). Subsequent to the canal's creation, nearly 23 invertebrate species established the Caspian Sea and the Volga River delta (see below). Invasions by the bivalve *Hypanis colorata* and gastropod *Lithoglyphus naticoides* most likely were jointly facilitated by the Volga–Don canal and shipping traffic. Three parasitic trematode species were most likely introduced with their host, *L. naticoides*, using multiple vectors (Biserova 1990, 1996). In a similar manner, river–canal networks and boat traffic were jointly responsible for invasion of the Dniester, Severskii Donets, and Volga river drainages and northern Caspian Sea by the bivalve *D. bugensis*, originally endemic to the Southern Bug River Estuary (e.g., Kharchenko 1995; Grigorovich and Babko 1997).

Historical perspective on introductions in the Ponto-Caspian river drainages

Historical records of introductions and transplantation of invertebrates for commercial purposes, like the long-clawed crayfish *Astacus leptodactylus*, date back to the 1820s (Karpevich 1975*a*, 1975*b*). In the late 1800s, the wide-clawed crayfish *Astacus astacus colchicus* was successfully introduced to the Kura River drainage, Georgia (Birshtein and Vinogradov 1934). In the following years, commercial stocking of invertebrates continued steadily (Fig. 5*a*).

During the 1940s and 1950s, large reservoirs were constructed in major Ponto-Caspian river drainages, including the Volga, Don, Dnieper, Dniester, and Southern Bug (see Fig. 1). Physical and chemical conditions of many of these reservoirs were suitable for invasions by boreal planktonic crustaceans derived from northern habitats of the European CIS (Table 1). These conditions included low water velocity and development of a seasonally stratified water column with a cool hypolimnion (Mordukhai-Boltovskoi and Dziuban 1976). For example, at least five species including *Bythotrephes longimanus*, *Cyclops kolensis*, *Eudiaptomus gracilis*, *Daphnia cristata*, *Bosmina coregoni*, and *Bosmina longispina* spread through the Volga reservoir system and became established in its most southern Volgograd reservoir (Mordukhai-Boltovskoi and Dziuban 1976).

Beginning in the 1940s and continuing through the 1970s, massive efforts to introduce aquatic invertebrates were made in the former U.S.S.R. for the purposes of aquaculture and to improve the food supply for fishes (Ioffe 1968; Karpevich 1975*a*). The wide-clawed crayfish *Astacus astacus astacus* is one species that was successfully introduced in the upper reaches of Volga River for commercial harvest (Yanushevich 1966). A closely related species, the long-clawed crayfish *A. leptodactylus*, was successfully introduced in the Shatsk lakes (Volyn region, Ukraine) and Ural waterbodies in the 1950s (Yanushevich 1966).

Extensive aquaculture and intentional stocking activities increased the potential and provided the mechanism for unintentional releases (see Tseeb and Olivari 1958). Clearly, some of the unintentional introductions included parasites

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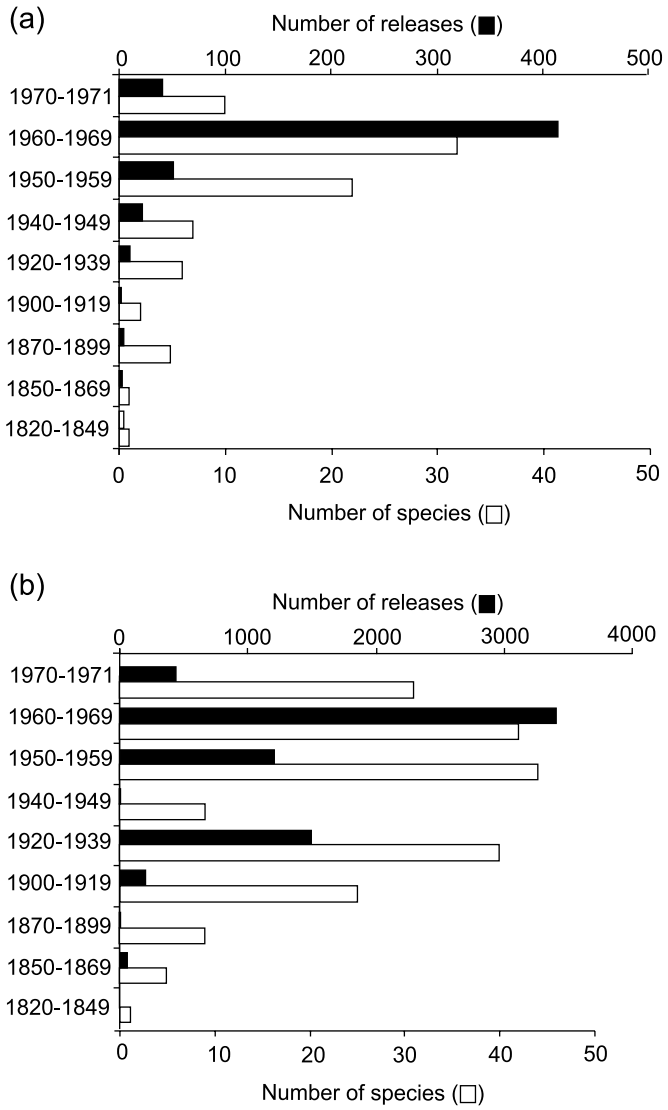
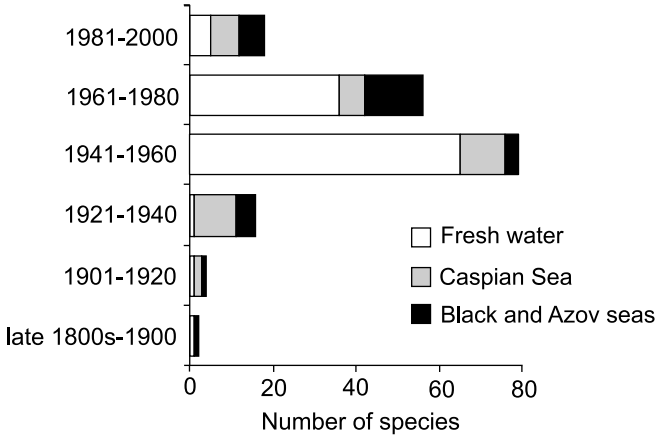
Fig. 5. Rates of stocking (*a*) invertebrates and (*b*) fishes in fresh waters in the former U.S.S.R. Number of species (open bars) involved in stocking and number of releases (solid bars) are indicated for each time period. Data from Karpevich (1975*a*). Notice that scales differ for fish and invertebrate releases.



and other nontarget species with close associations with those that were intentionally stocked. For example, three species of southern, Ponto-Caspian onychopods (*Cercopagis pengoi*, *Cornigerius maeoticus*, and *Podonevadne trigona ovum*) that commonly occur in the Kakhovka reservoir probably originated as stock contaminants during the late 1950s (Gusynskaya and Zhdanova 1978). Several parasitic invertebrates, including monogeneans *Dactylogyrus solidus* and *Cleidodiscus pricei*, and cestodes *Bothriocephalus gowkongensis* and *Khawia sinensis*, were likely transported to the Ponto-Caspian region with stocked fish hosts (Malevitskaya 1958; Kulakovskaya and Krotas 1961; Karpevich 1975*b*). These parasites originated from the Amur River drainage and North America (Appendix A).

During the 1960s, a number of NIS initially introduced for commercial purposes continued to expand their nonnative distribution and established new populations within, or

Fig. 6. Timeline of established aquatic invertebrates in the Ponto-Caspian region, sorted by habitat.



outside of, the Ponto-Caspian region (Fig. 5*a*). However, most of these species were recorded elsewhere in the Ponto-Caspian region by 1960 (Fig. 6). For example, two of the aforementioned onychopod species, *C. maeoticus* and *P. t. ovum*, dispersed into reservoirs built on the Dnieper, Volga, Don, and Manych rivers (Mordukhai-Boltovskoi and Galinskii 1974; Mordukhai-Boltovskoi and Dziuban 1976; Gusynskaya and Zhdanova 1978). We did not consider these recent introductions, as the species had already been recorded outside of their natural ranges. Consequently, the percentage of new introductions associated with intentional releases appears remarkably low since the 1960s (Fig. 4*a*).

During the 1960s and 1970s, many introductions in the Ponto-Caspian region resulted from multiple vectors, particularly hydrotechnical construction and shipping activities (Figs. 4*a*, 4*b*). The construction of reservoirs and canals provided new artificial habitats and promoted dispersal of numerous Ponto-Caspian calanoid and harpacticoid copepods in the Dnieper River watercourse (Table 1). Copepods occurring in waters associated with shipping traffic probably gained access to and spread through newly created reservoirs (e.g., Monchenko 1995). One of these calanoid copepods, *Heterocope caspia*, also extended its range to Volga reservoirs, while a second, *Calanipeda aquae-dulcis*, spread extensively in reservoirs created on Ponto-Caspian rivers and invaded the Aral Sea (Karpevich 1975*a*; Mordukhai-Boltovskoi and Dziuban 1976).

During the 1960s and 1970s, a complex network of canals was constructed and rendered operational in southern Ukraine. These canals permitted many invertebrates to spread into adjacent basins, where they had never been present previously (see Table 1). For example, a number of gammarid and corophiid amphipods dispersed outside their natural ranges in the southern Ukrainian canals (e.g., Kaftannikova 1975; Dediu 1980).

By the mid- to late 1970s, invertebrate-stocking efforts declined or ceased in some areas. It is possible, however, that our analysis understates recent introductions because of limitations in acquiring data. Establishment of new nontarget species that were inadvertently introduced during stocking efforts continued to be recorded into the 1980s, after populations had grown large enough to be detected (Pligin and Yemelyanova 1989).

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Table 1. Summary of introduced free-living aquatic invertebrates in the Ponto-Caspian river drainages.

Taxonomic group	Species name	Status	Date	Location	Native region	Entry vector	Nonnative occurrence	References
Cnidarians	*Cordylophora caspia*	D	1948	Veselovsk reservoir	Ponto-Caspian	S	Globally dispersed	1, 2, 3
	Craspedacusta sowerbii	C	1928	Don River	Cosmopolitan?	?	Globally dispersed	4
Bryozoans	*Urnatella gracilis*	C	1954	Danube River basin	North American?	S?	Globally dispersed	5
Annelids	*Hypania invalida*	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS; Transcaucasia; central Asia	3, 6, 7
	Hypaniola kowalevskyi	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS	8, 9, 10
	Manayunkia caspica	P	<1963	Oktiabrsk reservoir	Ponto-Caspian	H	Ingulets River basin	2, 8, 11
	Psammoryctides deserticola	P	1989	Severskii Donets–Donbass Canal	Ponto-Caspian	H	Severskii Donets basin	12
	Cystobranchus fasciatus	P	1974	Kremenchug reservoir	Ponto-Caspian	H	Reservoirs and canals of Ukraine	13, 14
	Archaeobdella esmonti	P	1980s	Upper Volga River	Ponto-Caspian	H	Volga River basin	15
Crustaceans	*Leptestheria dahalacensis*	P	1960s	Kuban River basin	South European	A	Volga and Kuban basin	16
	Eocyzicus orientalis	P	1970s	Dniester River basin	Transcaucasian	A	Ponds of European part of CIS	17
	Limnosida frontosa	P	<1955	Rybinsk reservoir	North European	H	Volga reservoirs; Norway lakes	18
	Daphnia cristata	P	1958	Kuibyshev reservoir	North European	H	Volga and Dnieper reservoirs	18, 19, 14
	Bosmina longispina	P	1956	Kuibyshev reservoir	North European	H	Volga and Dnieper reservoirs	14, 18
	Bosmina coregoni	P	<1955	Rybinsk reservoir	North European	H	Volga and Dnieper reservoirs	14, 18, 20
	Bosmina obtusirostris	P	1957	Kuibyshev reservoir	North European	H	Volga and Dnieper reservoirs	14, 18, 20
	Bosmina crassicornis	P	1958	Kuibyshev reservoir	North European	H	Volga and Dnieper reservoirs	14, 18
	Bosmina kessleri	P	1957	Kuibyshev reservoir	North European	H	Volga reservoirs	18
	Cornigerius maeoticus maeoticus	P	1959	Kakhovka reservoir	Ponto-Caspian	M	Reservoirs and canals of European part of CIS	19, 21, 22
	Cornigerius bicornis	P	1966	Dnieper–Krivoi Rog Canal	Ponto-Caspian	H	Dnieper and Don basins	22, 23
	Cornigerius lacustris	P	1970	Tsimlyansk reservoir	Ponto-Caspian	M	Dnieper and Don reservoirs	22, 23
	Podonevadne trigona ovum	P	1959	Kakhovka reservoir	Ponto-Caspian	M	Reservoirs of European part of CIS	2, 24, 25
	Bythotrephes longimanus	P	1952	Tsimlyansk reservoir	North European – Siberian	H	Volga and Don reservoirs; Rhine River basin	18, 21, 26
	Cercopagis pengoi	P	1959	Kakhovka reservoir	Ponto-Caspian	M	Reservoirs of European part of CIS; Baltic Sea basin	19, 27, 28
	Eurytemora affinis	P	1955	Kakhovka reservoir	Cosmopolitan?	H	Reservoirs of European part of CIS	20, 14, 29
	Heterocope appendiculata	P	1957	Kuibyshev reservoir	North European	H	Volga and Dnieper reservoirs	14, 18, 19
	Heterocope caspia	D	1962	Kremenchug reservoir	Ponto-Caspian	M	Dnieper and Volga reservoirs	2, 14, 18
	Calanipeda aquae-dulcis	P	1967	Volgograd reservoir	Ponto-Caspian–Mediterranean	M	Reservoirs of European part of CIS; Aral Sea	18, 30, 31
	Eudiaptomus gracilis	P	1950s	Kakhovka reservoir	North European	H	Volga and Dnieper reservoirs	14, 18
	Eudiaptomus graciloides	P	1955	Kakhovka reservoir	North European	H	Volga and Dnieper reservoirs	18, 20

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Cyclops kolensis	P	1956	Kuibyshev reservoir	European–Siberian	H	Volga reservoirs	18
Limnocletodes behningi	P	1970s	Kakhovka reservoir	Ponto-Caspian	M	Kakhovka reservoir	32
Ectinosoma abrau	P	1970s	Kakhovka reservoir	Mediterranean–Ponto-Caspian	M	Dnieper reservoirs	32
Schizopera borutzkyi	P	1970s	Kakhovka reservoir	Ponto-Caspian	M	Dnieper reservoirs	32
Paraleptastacus spinicaudata triseta	P	1970s	Kakhovka reservoir	Ponto-Caspian	M	Dnieper reservoirs	32
Nitocra incerta	P	1970s	Kakhovka reservoir	Ponto-Caspian?	M	Dnieper reservoirs	32
Onychocamptus mohammed	P	1970s	Kakhovka reservoir	North Atlantic – Mediterranean	M	Dnieper reservoirs	32
Paramysis baeri bispinosa	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS	9, 10, 33
Paramysis kessleri sarsi	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Dnieper reservoirs	8, 14, 34
Paramysis ullskyi	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and canals of Don and Volga basins	9, 10, 35
Paramysis lacustris	D	1948–1949	Karachunovsk reservoir	Ponto-Caspian	D	Reservoirs and lakes of CIS; Baltic Sea basin; Crimea; Transcaucasia; Lake Balkhash	6, 8, 36
Paramysis intermedia	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and lakes of CIS; Transcaucasia; Lake Balkhash	6, 30, 37
Katamysis warpachowskyi	D	1955–1956	Dubossary reservoir	Ponto-Caspian	D	Dniester reservoirs	2, 9, 11
Limnomysis benedeni	D	1947–1949	Zaporozhie reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS; Crimea; Rhine basin	8, 9, 38
Hemimysis anomala	D	1957	Zaporozhie reservoir	Ponto-Caspian	D	Reservoirs and lakes of CIS; Baltic Sea and Rhine River basins	8, 2, 39
Pterocuma pectinata	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and lakes of CIS	1, 3, 33
Pterocuma rostrata	P	<1965	Ingulets Canal	Ponto-Caspian	D	Canal of Dnieper basins	8, 40
Pterocuma sowinskyi	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs of Don basins	1, 6, 33
Stenocuma tenuicauda	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs of Don basins	1, 6, 33
Pseudocuma cercaroides	D	1947–1949	Zaporozhie reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS	3, 8, 41
Schizorhynchus eudorelloides	D	1956–1964	Tsimlyansk reservoir	Ponto-Caspian	D	Tsimlyansk reservoir	9, 41
Caspiocuma campylaspoides	D	1955–1956	Dubossary reservoir	Ponto-Caspian	D	Dubossary reservoir	9, 42
Jaera sarsi	D	1969	Lower Kama reservoir	Ponto-Caspian	M	Volga and Dnieper reservoirs	18, 13, 43
Gammarus lacustris	D	1961–1964	Irikla reservoir	European–Siberian	D	Irikla reservoir; Ural lakes; Lake Pskov-Chud	9, 44
Gmelinoides fasciatus	D	1962–1965	Gorkii reservoir	Lake Baikal	D	Lakes and reservoirs of Volga and Ural River basins, Lake Ladoga	6, 9, 41
Micruropus possolskii	D	1962–1965	Gorkii reservoir	Lake Baikal	D	Reservoirs of the Volga and Ural River basins	6, 9

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Table 1 (*concluded*).

Taxonomic group	Species name	Status	Date	Location	Native region	Entry vector	Nonnative occurrence	References
	Dikerogammarus haemobaphes	D	1955, 1959	Simferopol reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS; Vistula and Rhine basins	8, 9, 45
	Dikerogammarus villosus	D	1955, 1959	Simferopol reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS; Rhine basin	3, 8, 45
	Pontogammarus aralensis	D	<1956	Veselovsk reservoir	Ponto-Caspian	M	Dnieper and Don River basins	1, 3
	Pontogammarus maeoticus	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Reservoirs of Dnieper River basin; Crimea	3, 8, 9
	Pontogammarus subnudus	P	1981	Kremenchug reservoir	Ponto-Caspian	A	Dnieper reservoirs	3
	Pontogammarus robustoides	D	1950–1951	Dnieper near Buchak	Ponto-Caspian	D	Reservoirs and canals of CIS; Transcaucasia; Baltic Sea basin	6, 8, 36
	Pontogammarus crassus	D	1955, 1959	Simferopol reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS	3, 8, 46
	Pontogammarus obesus	D	1950–1951	Middle Dnieper River	Ponto-Caspian	D	Reservoirs and canals of CIS	6, 8, 46
	Stenogammarus carausui	P	1977	Kremenchug reservoir	Ponto-Caspian	A	Dnieper reservoirs	3, 14
	Echinogammarus ischnus	D	1955, 1959	Simferopol reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS; Baltic Sea and Rhine River basins	8, 34, 46
	Echinogammarus trichiatus	D	<1998	Kiev reservoir	Ponto-Caspian	M	Dnieper reservoirs	12
	Echinogammarus warpachowskyi	D	1953	Zaporozhie reservoir	Ponto-Caspian	D	Reservoirs and canals of European part of CIS	3, 8, 11
	Iphigenella shablensis	P	<2000	Volga River delta	Pontic	H	Volga delta, Caspian Sea	47, 48
	Iphigenella andrussowi	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Dnieper reservoirs	14, 34
	Gmelina kusnetzowi	P	1982	Zaporozhie reservoir	Ponto-Caspian	A	Dnieper reservoirs	3, 14
	Gmelina pusilla	P	<1965	Ingulets Canal	Ponto-Caspian	H	Canals of southern Ukraine	46
	Gmelina costata	P	<1965	Ingulets Canal	Ponto-Caspian	H	Canals of southern Ukraine	46
	Amathillina cristata	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Reservoirs and canals of Dnieper River and Don River basins	8, 14, 46
	Corophium nobile	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Reservoirs and canals of Dnieper River basin	8, 34, 46
	Corophium robustum	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Reservoirs and canals of Dnieper River basin	3, 8, 49
	Corophium chelicorne	D	1956–1957	Kakhovka reservoir	Ponto-Caspian	D	Reservoirs and canals of Dnieper River basin	6, 8, 46
	Corophium curvispinum	D	1951–1956	Veselovsk reservoir	Ponto-Caspian	D	Reservoirs and canals of CIS; Baltic Sea and Rhine River basins	6, 8, 9, 50
	Corophium mucronatum	P	<1969	Ingulets Canal	Ponto-Caspian	H	Canals of southern Ukraine	46

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	Corophium maeoticum	P	<1969	Severskii Donets–Donbass canal	Ponto-Caspian	H	Canals of southern Ukraine	46
	Astacus leptodactylus	D	<1963	Shatsk lakes	Ponto-Caspian	D	Ponds of Belarus and northwestern Ukraine; western Siberia	10, 30, 33
	Astacus astacus astacus	D	1950s	Upper Volga reservoirs	North European	D	Upper Volga drainage; Barabinsk lakes; Scandinavia	10, 49, 51
	Astacus astacus colchicus	D	Late 1800s	Kura River basin	Transcaucasian	D	Rioni River and Chorokh River drainages	10, 51
Molluscs	*Pettancylus petterdi*	D	1969	Pshada River basin	Inland Australian	A	Krasnodar Territory	52
	Theodoxus fluviatilis	D	1955	Simferopol reservoir	European	D	Crimean reservoirs	9, 10, 53
	Theodoxus pallasi	P	1960	Volgograd reservoir	Ponto-Caspian	M?	Volgograd reservoir	54
	Viviparus viviparus	D	1955	Simferopol reservoir	European	D	Crimean reservoirs	9, 10, 53
	Viviparus ater	C	<1987	Kiev reservoir	European?	?	Dnieper reservoirs; Crimea; Transcaucasia	55
	Lithoglyphus naticoides	D	1955	Simferopol reservoir	European	D	Crimean reservoirs; Volga delta	10, 53, 56
	Dreissena polymopha	D	1953	Veselovsk reservoir	Ponto-Caspian	M	Reservoirs and canals of Europe	1, 18, 31
	Dreissena bugensis	D	1941	Zaporozhie reservoir	Bug River estuary	M	Reservoirs and canals of European part of CIS; North Caspian Sea	2, 57, 58
	Hypanis colorata	D	1951–1956	Veselovsk reservoir	Pontic	D	Canals and reservoirs of CIS	1, 2, 59
	Sphaerium corneum	D	1955	Simferopol reservoir	European–Siberian	D	Crimean reservoirs	10, 53
	Sphaerium rivicola	D	1955	Simferopol reservoir	European–Siberian	D	Crimean reservoirs	10, 53
	Pisidium sp. (NS)	D	1955	Simferopol reservoir	European–Siberian	D	Crimean reservoirs	10, 53

Note: Nonindigenous species status: D, definite; P, probable; C, possible. Time intervals are provided for stocked species. Vectors of introduction: D, deliberate releases; A, accidental releases; S, shipping activities; H, hydrotechnical construction; M, multiple vectors; ?, unknown or uncertain. Reference sources: 1, Kruglova (1961); 2, Zhuravel (1969); 3, Pligin and Yemelyanova (1989); 4, Protasov et al, (1981); 5, Vodianitskii (1968); 6, Ioffe et al, (1968); 7, Dziuban and Slobodchikov (1980); 8, Zhuravel (1965); 9, Ioffe (1968); 10, Yanushevich (1966); 11, Zhuravel (1974); 12, I.A. Grigorovich, unpublished data; 13, Pligin (1985); 14, Shcherbak (1989); 15, Bakanov (1994); 16, T.I. Dobrynina, Institute for Inner Water Biology, Borok, Russia, personal communication; 17, Dobrynina (2001); 18, Mordukhai-Boltovskoi and Dziuban (1976); 19, Gusynskaya and Zhdanova (1978); 20, Tseeb (1964); 21, Glamazda (1969); 22, Mordukhai-Boltovskoi and Galinskii (1974); 23, Basilevich (1972); 24, Kaftannikova and Basilevich (1972); 25, Grigorovich and Frinovskaya (1991); 26, Rivier and Grigorovich (1999); 27, Volvich (1978); 28, Grigorovich et al. (2000); 29, Shevtsova and Primak (1990); 30, Karpevich (1975*a*); 31, Mordukhai-Boltovskoi (1979); 32, Monchenko (1995); 33, Karpevich (1975*b*); 34, Tseeb and Olivari (1958); 35, Milovidov and Yegereva (1985); 36, Sergeeva and Tskhomelidze (1968); 37, Zhuravel (1961*a*); 38, Lubyanov (1953); 39, Zhuravel (1960); 40, Shevtsova (1968); 41, Ioffe (1973); 42, Yaroshenko (1964); 43, Lyakhov and Mordukhai-Boltovskoi (1973); 44, Grandilevskaya-Deksbakh (1968); 45, Shevtsova (1991); 46, Dediu (1980); 47, Vodianitskii (1969); 48, Grigorovich at al. (2002); 49, Kruglova et al. (1972); 50, Kaftannikova (1975); 51, Birshtein and Vinogradov (1934); 52, Kafanov and Starobogatov (1971); 53, Zhuravel (1961*b*); 54, Kirpichenko and Lyakhov (1963); 55, Anistratenko (1998); 56, Pirogov (1972); 57, Zhuravel (1967); 58, Grigorovich and Babko (1997); 59, Zhuravel (1975). CIS, Commonwealth of Independent States; NS, no species identity provided.

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Table 2. Summary of nonindigenous free-living aquatic invertebrates established in the Black and Azov seas.

Taxonomic group	Species name	Status	Date	Location	Native region	Entry vector	Nonnative occurrence	References
Cnidarians	*Blackfordia virginica*	C	1925	Black Sea	North American Atlantic?	S?	Black, Azov, and Caspian seas	1, 2
	Bougainvillia megas	C	<1933	Black Sea	North Atlantic?	S	Black, Azov, and Caspian seas	2, 3
	*Eudendrium annulatum**	P	1990	Black Sea	North Atlantic – Pacific	S	Black Sea	4
	*Eudendrium capillare**	P	1990	Black Sea	North Atlantic – Pacific	S	Black Sea	4
	*Tiaropsis multicirrata**	P	1990	Black Sea	North Atlantic – Pacific	S	Black Sea	4
Ctenophores	*Mnemiopsis leidyi*	D	1982	Black Sea	North and South American Atlantic	S	Black, Azov and Caspian seas; Donuzlav estuary	5, 6, 7
	Beroe ovata	P	1997	Black Sea	North and South American Atlantic – Mediterranean	S?	Black and Azov seas	8, 9
Bryozoans	*Urnatella gracilis*	C	1962	Azov Sea	North American?	S?	Globally dispersed	10
Annelids	*Mercierella enigmatica*	D	1929	Black Sea	Indian–Pacific	S	Black, Azov, and Caspian seas	11, 12
	Nephthys ciliata	C	<1972	Black Sea	Atlantic–Pacific	S?	Black Sea	10
	Polydora limicola	D	1962	Sukhoi Liman	Pacific	S	Northwestern Black Sea	13
	Streblospio shrubsolii	P	<1957	Black Sea	North Atlantic	S?	Black Sea	2, 14
	Streptosyllis varians	P	<1972	Black Sea	North Atlantic	S?	Black Sea	10
	Ancistrosyllis tentaculata	C	<1964	Black Sea	North American Atlantic?	S?	Black Sea	15
	Capitellethus dispar	P	<1972	Black Sea	Indian–Pacific	S?	Black Sea	10
	Glycera capitata	P	<1968	Black Sea	Atlantic–Arctic–Pacific	S?	Black Sea	2, 14
Crustaceans	*Acartia tonsa*	D	<1976	Black Sea	North and South American Atlantic	S	Black, Caspian, and Baltic seas	16
	Balanus improvisus	D	Late 1800s	Black Sea	North Atlantic – Pacific	S	Black, Azov, and Caspian seas	17, 18
	Balanus eburneus	D	1933	Black Sea	North American Atlantic	S	Black, Azov, and Caspian seas	18
	Rhithropanopeus harrisi	D	<1936	Dnieper-Bug Liman	North American Atlantic	S	Black, Azov, and Caspian seas	19
	Callinectes sapidus	D	1967	Black Sea	North Atlantic	S	Black and Mediterranean seas	20, 21
Molluscs	*Potamopyrgus jenkinsi*	D	1951	Dnieper-Bug Liman	Australasian Pacific	S	North Black Sea estuaries	22

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Rapana thomasiana	D	<1946	Black Sea	Asian Pacific	S	Black and Azov seas	23, 24
Doridella obscura	D	1986	Black Sea	North American Atlantic	S	Black Sea	25, 26
Crassostrea gigas	D	Early 1900s	Black Sea	Pacific	D	Black Sea	10, 26
Cunearca cornea	D	1968	Black Sea	Indian–Pacific	S	Black Sea	27, 26
Mya arenaria	D	1966	Black Sea	North American Atlantic	S	Caspian Sea	28

Note: Nonindigenous species status: D, definite; P, probable; C, possible. Vectors of introduction: D, deliberate releases; S, shipping activities; ?, unknown or uncertain. Reference sources: 1, Valkanov (1936); 2, Vodianitskii (1968); 3, Paspalev (1933); 4, Grishicheva and Shadrin (1999); 5, Pereladov (1988); 6, Vinogradov et al. (1989); 7, GESAMP (1997); 8, Konsulov and Kamburska (1998); 9, Shiganova and Bulgakova (2000); 10, Vodianitskii (1972); 11, Annenkova (1930); 12, Karpevich (1975*a*); 13, Losovskaya and Nesterova (1964); 14, N.B. Shadrin, unpublished data; 15, Kiseleva (1964); 16, Belmonte et al. (1994); 17, Rass (1978); 18, Marinov (1990); 19, Makarov (1939); 20, Bulgurkov (1968); 21, Zaitsev and Mamaev (1997); 22, Markovskii (1954); 23, Drapkin (1953); 24, Ivanov (1968); 25, Roginskaya and Grintsov (1990); 26, Zolotarev (1996); 27, Gomoiu (1984); 28, Beshevli and Kolyagin (1967).

*Species identity designated preliminary.

Historical perspective on introductions in the Black and Azov seas

During the first and second Mediterranean phases, Atlantic–Mediterranean species immigrated naturally to the Black and Azov seas (see Zenkevich 1963). As a result, Atlantic and Mediterranean biota dominate the contemporary fauna in the Black and Azov seas, including at least 1790 and 200 species, respectively (Vodianitskii 1972; Gomoiu 1975). In addition to their natural biodiversity, the Black and Azov seas support a large number of human-mediated introductions from remote geographic regions (Zaitsev and Mamaev 1997). Shipping activities have played a major role in these introductions, probably because many introduced taxa possess life history traits that make them prone to being transported on ships' hulls or in ballast tanks.

The Black Sea has frequently served as a secondary source of introduced species for the Azov Sea and beyond. These basins, in turn, may be donor regions for invasions of the Caspian Sea (e.g., *Mnemiopsis leidyi*). In this manner, NIS may sequentially disperse from one invaded site to another. For example, the barnacles *Balanus improvisus* and *Balanus eburneus* were likely introduced to the Black Sea during the late 19th and early 20th centuries, respectively (Karpevich 1975*a*; Zaitsev and Mamaev 1997). Both species originated from the Atlantic coast of North America, and are now firmly established in both the Black and Azov seas and their estuaries and inlets (Karpevich 1975*a*). The cnidarian *Blackfordia virginica*, a North American Atlantic coast native, was first observed in the Black Sea in 1925, although it subsequently spread into the Azov Sea (Zenkevich 1963). Likewise, the decapod *Rhithropanopeus harrisi* was discovered in the Black Sea in 1936, although by the 1940s it had spread from the northwestern Black Sea and its estuaries into the Azov Sea and Don River Estuary (Makarov 1939; Zaitsev and Mamaev 1997). The gastropod *Rapana thomasiana*, a native of the Japan Sea, was observed invading the Black Sea during 1947 and the Azov Sea in 1956 (Drapkin 1953; Zolotarev 1996). During the 1960s two additional molluscs were discovered in the Black Sea, including the bivalve *Mya arenaria* in 1966, and *Cunearca cornea* (as *Scapharca inaequivalvis*) in 1983 (Beshevli and Koliagin 1967; Gomoiu 1984; Zolotarev 1996). In 1986, one additional nudibranch mollusc, *Doridella obscura*, was found in the Black Sea (Roginskaya and Grintsov 1990).

In 1982, the ctenophore *Mnemiopsis leidyi* (reported as *Bolinopsis*) was discovered in the Black Sea (Pereladov 1988; GESAMP 1997). By 1988, it had spread across much of the Black Sea, into the Azov Sea, and recently, the Caspian Sea (Vinogradov et al. 1989; Ivanov et al. 2000; Shiganova and Bulgakova 2000). During the 1990s, three new cnidarian species were found invading the Black Sea (Table 2). In 1997, the ctenophore *Beroe ovata*, a native of the Mediterranean Sea, was reported for the first time in the Black Sea (Table 2). In subsequent years, it spread throughout the sea and into the Azov Sea (Shiganova and Bulgakova 2000). Ships likely dispersed this ctenophore, abetted by abundant populations of *Mnemiopsis* prey (Shiganova and Bulgakova 2000). Several other invertebrates have also invaded the Black Sea basin (see Table 2 for species list).

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Historical perspective on introductions into the Caspian Sea

Introductions of invertebrates into the Caspian Sea for commercial reasons began as early as 1897 (e.g., Karpevich 1975*a*). Initial efforts involving the Black Sea oyster *Ostrea edulis* and bivalve mussel *Mytilus galloprovincialis* were not successful. Between 1917 and 1920, the bivalve mussel *Mytilaster lineatus* was accidentally transferred to the Caspian Sea, possibly on the bottom of boats carried from the Black Sea by rail (Rass 1978). By the time of its discovery in 1928, this mussel had already established and dispersed throughout the sea (Zenkevich 1963). A few Atlantic–Mediterranean nematode species were believed to have been introduced with their bivalve host (Chepalyga and Tarasov 1997).

Two Atlantic–Mediterranean shrimps, *Palaemon adspersus* and *Palaemon elegans*, were introduced between 1930 and 1934 as nontarget species during stocking of mullet (*Mugil auratus* and *Mugil saliens*) taken from the Black Sea (Table 3). Moreover, several trematode species and one parasitic copepod species may have been transported with the mullet stocking effort (Appendix A).

Between 1939 and 1941, the polychaete *Nereis* was transferred to the Caspian Sea from the Azov Sea on a substantial scale. Subsequent study of bottom sediments in the Caspian Sea revealed that an additional nontarget Atlantic–Mediterranean bivalve, *Abra ovata* (synonym: *Abra segmentum*), was successfully introduced as a result of this stocking effort, even though it remained undetected until 1955 (Chepalyga and Tarasov 1997).

The Volga–Don Canal circumvented the geographic barrier that had previously kept vessels from passing from the Black and Azov seas into the Caspian Sea. During the late 1950s and 1960s, several Atlantic and Atlantic–Mediterranean species have arrived on ships' hulls or in ballast water and established large populations in the Caspian Sea (Zevina 1965; Zevina and Kuznetsova 1965; Karpevich 1975*a*).

Our findings suggest that the vectors associated with shipping shifted from the hull fouling to that associated with ballast water discharge during the 1981–2000 period. For example, two planktonic crustaceans of the Atlantic–Mediterranean origin (*Podon intermedius* and *Acartia tonsa* (as *A. clausi*)) and one benthic crustacean (*Gammarus aequicauda*) invaded the Caspian Sea during the 1980s (Table 3). Most recently, in 1999 or more likely in 1998, the Atlantic ctenophore *Mnemiopsis leidyi* was discovered in the Caspian Sea, most likely owing to discharge of contaminated ballast water from the Black–Azov basin (Ivanov et al. 2000; Grigorovich, unpublished data). Several other invertebrates have also invaded the northern basin of the Caspian Sea adjacent to the Volga River delta (see Table 3 for species list).

Implications for water resource management

Over the last century, some 47 invertebrate species have naturalized in new aquatic habitats in the Ponto-Caspian region as a result of stocking programs, while other human activities inadvertently promoted the establishment of nearly 116 species. Most of these species became integrated into their new ecosystems. Several of these species, including the ctenophore *Mnemiopsis leidyi*, gastropod *Rapana thomasiana*, and bivalve *Mytilaster lineatus*, have established enormous populations and contributed to food web alterations in recipient communities. These invaders have had profound ecological impacts in invaded habitats and strong economic and social consequences on human populations dependent on aquatic resources from these habitats (Karpevich 1975*a*; GESAMP 1997; Zaitsev and Mamaev 1997). These impacts are best established for the Atlantic ctenophore *Mnemiopsis leidyi*, which has profoundly affected the Black and Azov sea ecosystems via predation on, and competition for food with, planktivorous fishes (GESAMP 1997). Establishment of this species in the Caspian Sea portends further ecological and economic impacts. The gastropod *Rapana thomasiana* has profoundly affected mussel community structure in the Black Sea and caused economic impacts as a result of depletion of cultivated oyster stocks (Karpevich 1975*a*). *Mytilaster lineatus* invasion into the Caspian Sea resulted in extinction of two endemic mussels, *Dreissena elata* and *Dreissena caspia*, and changes in resident species interactions (Karpevich 1975*a*). Anchovy fisheries are nearly extinct in the northwestern Black and Azov seas as a consequence of the cumulative or interactive effects of biological invasions and other stressors, including intensive commercial fishing and habitat modification (GESAMP 1997).

Authorities in the CIS are becoming increasingly aware of the consequences of biological invasions (e.g., Zaitsev and Mamaev 1997). Because shipping is the largest vector for NIS introduction to estuarine and marine environments of the Ponto-Caspian region, a key challenge exists to develop treatment technologies to prevent release of viable NIS in ballast water. The United Nations International Maritime Organization has developed voluntary guidelines for ballast water management, which include open-ocean exchange of ballast water before entering coastal zones. This procedure appears to afford significant if not absolute protection to the Great Lakes (Locke et al. 1993), although it appears less effective in preventing transfer of NIS among marine habitats (Ruiz et al. 2000).

Geographic patterns of introductions in the Ponto-Caspian region

The ecological integrity of Ponto-Caspian ecosystems has been challenged by invading NIS from various parts of the world. Many of the species successfully colonizing Ponto-Caspian ecosystems are native to other areas of the Ponto-Caspian region, whereas others originate from distant geographic localities. Three general invasion patterns are evident in the European CIS between 60° and 40°N (Rass 1978; Nikolaev 1979). First, there are numerous examples of southern introductions of boreal European–Siberian species and of northern introductions of Ponto-Caspian and Pontic species. These patterns are consistent with geographic pathways provided by large eastern European rivers including the Volga, Don, Dnieper, and possibly Dniester, which flow in north–south directions. Second, humans have transferred large numbers of NIS from the Black–Azov basins to the Caspian Sea, but no invertebrates have spread in the opposite direction. Third, NIS originating from distant localities often use secondary "staging" areas, which serve as the source of individuals to invade new areas in the Ponto-Caspian region. For example, the Black Sea has frequently served as a secondary source for invaders to the Azov and Caspian seas.

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Table 3. Summary of nonindigenous free-living aquatic invertebrates established in the Caspian Sea.

Taxonomic group	Species name	Status	Date	Location	Native region	Entry vector	Nonnative occurrence	References
Cnidarians	*Bougainvillia megas*	D	1960	Caspian Sea	North Atlantic?	S	Black, Azov and Caspian seas	1
	Blackfordia virginica	D	1956	Caspian Sea	North American Atlantic	S	Black, Azov and Caspian seas	2
	Moerisia maeotica	C	1959	Caspian Sea	Pontic?	M	Caspian Sea	
Ctenophores	*Mnemiopsis leidyi*	D	<1999	Caspian Sea	North and South American Atlantic	S	Black, Azov and Caspian seas; Donuzlav estuary	3
Roundworms	Nematoda (NS)	C	<1920	Caspian Sea	Mediterranean	A	Caspian Sea	2
Bryozoans	*Electra crustulenta*	D	1958	Caspian Sea	Atlantic–Mediterranean	S	Caspian Sea	4
	Conopeum seurati	D	1958	Caspian Sea	Atlantic–Mediterranean	S	Caspian Sea	2, 4
	Barentsia benedeni	D	1962	Caspian Sea	North Atlantic – Pacific	S	Caspian Sea	4
Annelids	*Nereis diversicolor*	D	1939–1940	Caspian Sea	Atlantic–Mediterranean	D	Caspian Sea	5
	Mercierella enigmatica	D	1961	Black Sea	Indian–Pacific	S	Black, Azov and Caspian seas	1, 5
Crustaceans	*Pleopis polyphemoides*	D	1957	Caspian Sea	Atlantic–Pacific	S	Caspian Sea	6
	Podon intermedius	D	1985	Caspian Sea	Atlantic–Mediterranean	S	Caspian Sea	
	Acartia tonsa	D	1981	Caspian Sea	North Atlantic	S	Caspian Sea	
	Balanus improvisus	D	1955	Caspian Sea	North American Atlantic – Pacific	S	Black, Azov and Caspian seas	1, 2
	Balanus eburneus	D	1956	Caspian Sea	North American Atlantic	S	Black, Azov and Caspian seas	1, 2
	Gammarus aequicauda	D	<1996	Caspian Sea	Mediterranean	S	Caspian Sea	7
	Iphigenella shablensis	P	<1969	Caspian Sea	Pontic	M	Caspian Sea	6, 7
	Corophium orientalis	C	<1951	Caspian Sea	Atlantic–Mediterranean	?	Caspian Sea	
	Palaemon elegans	D	1931–1934	Caspian Sea	Atlantic–Mediterranean	A	Caspian and Aral seas	5, 6, 8
	Palaemon adspersus	D	1930–1934	Caspian Sea	Atlantic–Mediterranean	A	Caspian and Aral seas	5, 6
	Rhithropanopeus harrisi	D	1958	Caspian Sea	North American Atlantic	S	Black, Azov and Caspian seas	6
Molluscs	*Lithoglyphus naticoides*	D	1983	North Caspian Sea	European	M	North Caspian Sea; Volga delta	9
	Tenellia adspersa	D	1989	Caspian Sea	Atlantic–Mediterranean	S	Caspian Sea	
	Mytilaster lineatus	D	1917–1920	Caspian Sea	Atlantic–Mediterranean	A	Caspian Sea	
	Dreissena bugensis	D	1996	North Caspian Sea	Bug River estuary	S	North Caspian Sea; Volga delta	
	Hypanis colorata	D	1959–1956	North Caspian Sea	Pontic	M	North Caspian Sea; Volga delta	
	Abra ovata	D	1939–1940s	Caspian Sea	Atlantic–Mediterranean	D	Caspian and Aral seas	5

Note: Nonindigenous species status: D, definite; P, probable; C, possible. Vectors of introduction: D, deliberate releases; A, accidental releases; S, shipping activities; M, multiple vectors; ?, unknown or uncertain. Reference sources: 1, Zevina (1965); 2, Chepalyga and Tarasov (1997); 3, Ivanov et al. (2000); 4, Zevina and Kuznetsova (1965); 5, Karpevich (1975*a*); 6, Vodianitskii (1969); 7, Grigorovich at al. (2002); 8, Zenkevich (1963); 9, Biserova (1990); See Grigorovich at al. (2002) for addtional references.

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Management of the invasion problem must identify key staging areas that allow NIS to spread to geographically remote regions, as well as those areas where numerous invasive NIS occur. At present, aquatic ecosystems across Europe and North America are being inundated with aquatic invertebrate species, many of which are native to the Ponto-Caspian region (Ricciardi and MacIsaac 2000). Particular attention should be focused on vectors and pathways allowing dispersal of NIS from this area, such that treatment options could be developed to reduce the rate of new introductions.

During the publication of this paper we became aware of three additional NIS in the Ponto-Caspian region. The tropical snail *Melanoides tuberculata*, native to the Middle East and Eastern Africa, was recorded from the cooling reservoir of Yuzhnoukrainsk nuclear power station, southern Ukraine, during 1997–2000 (A.N. Protasov, NAS of Ukraine, Institute of Hydrobiology, Kiev, Ukraine, unpublished data). We observed this snail during September 2001, confirming the species' establishment in this habitat. This introduction most likely resulted from an aquarium release. Native of Far-Eastern Asia, the unionid bivalve *Synanodonta woodiana* was inadvertently introduced with Asian cyprinid fishes stocked in the Danube–Sasyk, southern Ukraine. The glochidia and free-living adults of this species were first discovered during 1999 (A.V. Korniushin, NAS of Ukraine, Institute of Zoology, Kiev, Ukraine, personal communication). Finally, the dark false mussel *Mytilopsis leucophaeata*, native to the Atlantic Ocean, has recently invaded the northwestern Black Sea coast (unpublished data). During 2001 we recorded a *M. leucophaeata* population in Dniester Liman (unpublished data). *Mytilopsis leucophaeata* was also recently recorded as present in the Baltic Sea. Commercial ships were the most plausible mode of *M. leucophaeata* introduction. All these species have apparently become self sustaining.

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(Appendix A follows.)

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Appendix A

Table A1. Summary of nonindigenous parasitic invertebrates established in Ponto-Caspian region.

Taxonomic group	Parasite name	Host name	Date	Habitat	Native region	Entry vector	Nonnative occurrence	References
Flatworms	*Dactylogyrus extensus*	*Cyprinus carpio haematopterus*	<1953	Ukraine FWF	Amur province	A	Eastern Europe	1
	Dactylogyrus vastator	*Cyprinus carpio haematopterus*	1950s	Ukraine FWF	Amur province	A	Eastern Europe	2
	Dactylogyrus achmerovi	*Cyprinus carpio haematopterus*	1960s	Russia FWF	Amur province	A	Eastern Europe; Hungary, Uzbekistan	3, 4
	Dactylogyrus ctenopharyngodonis	*Ctenopharyngodon idella*	<1959	Russia FWF	Amur province	A	Eastern Europe; Hungary	3, 4
	Dactylogyrus lamellatus	*Ctenopharyngodon idella*	1960s	Russia FWF	Amur province	A	Eastern Europe; Hungary	3, 4
	Dactylogyrus hypophthalmichthys	*Hypophthalmichthys molitrix*	<1967	Russia FWF	Amur province	A	Eastern Europe; Hungary	3, 4
	Dactylogyrus nobilis	*Aristichthys nobilis*	<1967	Russia FWF	Amur province	A	Eastern Europe; Hungary	3, 4
	Dactylogyrus chenshuchenae	*Hypophthalmichthys molitrix*	1960s	Russia FWF	Amur province	A	Eastern Europe; Uzbekistan	3, 4
	Dactylogyrus skrjabini	*Hypophthalmichthys molitrix*	1960s	Russia FWF	Amur province	A	Eastern Europe; Uzbekistan	3, 4
	Dactylogyrus suchengtai	*Hypophthalmichthys molitrix*	1960s	Russia FWF	Amur province	A	Eastern Europe; Uzbekistan	3, 4
	Gyrodactylus ctenopharyngodonis	*Ctenopharyngodon idella*	1960s	Russia FWF	Amur province	A	Eastern Europe; Hungary	3, 4
	Gyrodactylus mugili	*Mugil soiuy*	1970s	Black Sea	Asian Pacific	A	Black Sea	5
	Gyrodactylus zhukovi	*Mugil soiuy*	1970s	Black Sea	Asian Pacific	A	Black Sea	5
	Ligophorus kaohsinghsieni	*Mugil soiuy*	1970s	Black Sea	Asian Pacific	A	Black Sea	6
	Cleidodiscus pricei	*Ictalurus nebulosus*	Early 1900s	Volyn lakes	North America	A	Ukraine; Belarus; Hungary	1
	Ancyrocephalus vanbenedenii	*Mugil saliens*	1930s	Caspian Sea	Black Sea	A	Caspian Sea	2
	Wlassenkotrema longicollum	*Mugil saliens*	1930s	Caspian Sea	Black Sea	A	Caspian Sea	2
	Haploporus longicolum	*Mugil saliens*	1930s	Caspian Sea	Black Sea	A	Caspian Sea	7
	Haplosplanchnus pachysoma	*Mugil saliens*	1930s	Caspian Sea	Black Sea	A	Caspian Sea	7
	Saccocoelium obesum	*Mugil saliens*	1930s	Caspian Sea	Black Sea	A	Caspian Sea	7
	Apophallus muehlingi	*Lithoglyphus naticoides*	1970s	Caspian Sea	European	M	Caspian Sea	8
	Rossicotrema donicum	*Lithoglyphus naticoides*	1970s	Caspian Sea	European	M	Caspian Sea	9
	Nicolla skrjabini	*Lithoglyphus naticoides*	1970s	Caspian Sea	European	M	Caspian Sea	9
	Khawia sinensis	*Cyprinus carpio haematopterus*	1950s	Ukraine FWF	Amur province	A	Eastern Europe; Central Asia	10, 11
	Bothriocephalus gowkongensis	*Ctenopharyngodon idella*	1950s	Ukraine FWF	Amur province	A	Eastern Europe; Hungary, Uzbekistan	1, 12
Roundworms	*Philometroides lusiana*	*Cyprinus carpio haematopterus*	1960s	Belarus FWF	Amur province	A	Belarus and Lithuania	11
Crustaceans	*Ergasilus* sp.	*Mugil saliens*	1930s	Caspian Sea	Black Sea?	A	Caspian Sea	7

Note: Status of *Ergasilus* sp. was assigned to the category cryptogenic taxon; status of all other species was assigned to the category definite nonindigenous species. Vectors of introduction: A, accidental releases; M, multiple vectors. Reference sources: 1, Malevitskaya (1958); 2, Yanushevich (1966); 3, Osmanov (1971); 4, Hoffman and Schubert (1984); 5, Maltsev (1997); 6, Dmitrieva (1996); 7, Mikailov (1958); 8, Biserova (1990); 9, Biserova (1996); 10, Kulakovskaya and Krotas (1961); 11, Karpevich (1975*b*); 12, Yukhimenko (1970). FWF, freshwater fishery farm.

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