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Introduced Species

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Abstract Due to increasing human activities such as shipping, deliberate stocking, and accidental introduction, a high number of alien species have become established in the Black Sea over the last century. In addition, global warming facilitates the population increase of thermophilic species and their northward expansion from the Mediterranean. As a result, the Black Sea became a pivotal recipient area for marine and brackish water aliens. It infects all other seas of the Mediterranean basin and the Caspian Sea as a donor. Species that have become abundant in all these seas are euryhaline and rather eurythermic, and are widely distributed in the coastal areas of the world's oceans. As a rule, they are abundant or dominant in their native habitats, where they sometimes cause outbreaks. Such species, with wide environmental tolerance and high phenotypic variability, have developed in high numbers and first became dominant in the Black Sea, and from here they spread to the Sea of Azov and became established in the Caspian and even the Aral Sea. The most euryhaline species also spread south to the Marmara and eastern Mediterranean (mainly the Aegean and Adriatic) Seas. They often greatly affected the recipient ecosystems, first of all the communities in the tropic level they occupy themselves, and thereafter some of them other trophic levels of the ecosystem; and finally, could cause changes in ecosystem functioning and a fundamental rearrangement of the original energy fluxes. The Black Sea became a natural laboratory for invasive biology as recipient and donor area. Some invasions were useful, like the intentional introduction of the gray mullet *Liza haematochila* and the accidental invasion of ctenophore *Beroe ovata*, some harmful, the most dramatic example of alien species effects documented was the invasion of a gelatinous predator, the polymorphic ctenophore *Mnemiopsis leidyi*.

Keywords Alien species · Black Sea · Ecosystem · Shipping

1 Introduction

In the 20th century, and especially in its second half, under the influence of climatic and anthropogenic factors, significant changes have occurred in the diversity of the flora and fauna of the Black Sea. Among the factors mentioned, the occasional and sometimes intentional introduction of alien species of animals and plants is a global phenomenon that has not avoided the Black Sea as well. As a result, the Black Sea became a basin for many alien species of different origins.

First, due to global warming, the process of penetration of Mediterranean species with the Lower Bosporus Current was intensified, representing an example of spreading of thermophilic species in the northern direction. Many of these species are recorded from time to time or are permanently present only in the near-Bosporus region. Their further expansion is most often hampered by the lower salinity of the main part of the Black Sea waters as well as the low winter temperatures. Therefore, most of the Mediterranean species that have penetrated the Black Sea but are found only in the near-Bosporus region are usually not regarded as assimilated established alien species. The near-Bosporus region represents a sort of an intermediate acclimation basin in the route of invasion of Mediterranean species into the Black Sea. Among such species there are representatives of various systematic groups such as phytoplankton, macrophytes, edible holozooplankton, and benthos [1–4]. Meanwhile, selected Mediterranean species of phyto- and zooplankton have been found off the Crimean and northwestern coasts, i.e., beyond the near-Bosporus region, as early as the 1960s and the beginning of the 1970s [5–7]. At present, this process is still ongoing [8, 9] and the number of penetrated and even established species increases each year.

Among the seasonal migrants from the Mediterranean Sea, there are several species of fishes that perform seasonal feeding or spawning migrations to the Black Sea. These species refer to migrants; meanwhile, they play or at least played a significant role in the trophic dynamics of the Black Sea ecosystem.

The penetration of Mediterranean migrants did not damage the Black Sea ecosystem; on the contrary, due to the insertion of these planktonic and benthic species, new edible organisms were added.

The present-day Black Sea, similar to many other seas, is an area of practical human activity. Changes in the composition of flora and fauna are caused by the unintentional delivery of new species with ships, by intentional introduction of commercial species and unintentional release of other species with them, by insertion by aquarium holders, and by the propagation and spreading of species over newly constructed canal systems that connect previously isolated basins. At present, among the above-listed ways (vectors) of penetration of accidental invaders, the principal ways are the transfer with the ballast ship waters and traveling with the fouling communities of ship hulls.

The successful establishment of such species in the Black Sea is favored by natural factors such as the diversity of habitats both in the sea proper and in its bays, lagoons, and river mouths; the favorable food conditions for benthofagous, planktivorous, and predator species; and the existence of free ecological niches because of the low species diversity of the Black Sea flora and fauna both in the near-shore benthic zone and in the pelagic area of the basin.

2 Microplankton

One of the most dangerous alien species of microfauna is the El-Tor strain, which causes epidemic outbursts of cholera; these strains were registered in Kerch and Odessa coastal waters in 1970. In contrast to classical cholera, the El-Tor strain is capable of long-term (over a few months) existence and, most likely, is able to reproduce in brackish-water basins [10]. The way of its penetration to the region is still not clear; meanwhile, starting from the moment of its appearance, has been often recorded in the near-shore waters off selected cities on the coast of the Black Sea and the Sea of Azov [11]. The social and economic losses caused by the El-Tor occurrence on the beaches are obvious, though no estimates have yet been made.

Selected species of the Mediterranean ciliates–tintinnids, which are representatives of microplankton, were found in the northwestern Black Sea in 2002 [12].

3 Marine Fungi

Marine fungi were found in bottom samples in Odessa Bay from northeastern Asia (two species) [13] and an additional five species were recorded in Odessa port in 2006 (Data of B. Alexandrov).

4
Phytoplankton

Phytoplankton species that are new for the Black Sea are annually reported from its various regions. A significant number of phytoplankton species that were previously unknown in the Black Sea (but usually occur in the Mediterranean Sea) were recorded in the near-Bosporus region of the Black Sea [4]. For example, the diatom algae *Fragillaria striatula* Lyngb. and *Thalassiothrix frauenfeldii*, the coccolithophorid *Calyptrosphaera incise* Schill., and the peridinea *Ceratium macroceros*, which are new species for the Black Sea, were registered in the near-Bosporus region as early as the beginning of the 1960s [14]. These species were found at a salinity of 34‰ and a temperature of 14 °C, that is, under the conditions significantly differing from those characteristic of the Black Sea waters.

L.V. Kuz'menko [5] listed a series of species previously unknown in the Black Sea but typical of the Mediterranean Sea, for example, *Dynophysis schuttii* Murr. et Whitt. and *Podolampas spinifer* Okatumura; they were sampled off the southern coast of the Crimea at a salinity of 18–18.5‰. At the beginning of the 1990s, selected species that were new for the Black Sea, such as *Katodinium rotundatum* (Lohm) Fott, *Achradina sulcata* Lohm., and *Pronoctiluca* sp., were found by L.G. Senichkina in the shallow-water area off Yalta. She also recorded *Distephanus octonarius* var. *Polyactis* (Jorg) Gleser and *D. speculum* var. *Septenarius* Jorg, which were previously unknown for the Black Sea [6]. Many of these species were recorded not only in the waters of a Mediterranean origin characterized by a high salinity but also in typical Black Sea waters. Their presence in the upper layers of the Black Sea may be related to the penetration of the waters from the Sea of Marmara followed by their subsequent mixing. As a result, 37 representatives of the Mediterranean phytoplankton were registered in the subsurface layers of the near-Bosporus region of the Black Sea, among them *Syracosphaera cornifera, Ceratium furca var. eugrammum, Pyrocystis hamulus, Pronoctiluca acuta*, and others [4].

In a coastal area of the northwestern Crimea during long-term observations (1968–2002) of phytoplankton development, new species for the Black Sea were recorded, among them diatoms—*Asterionellapsis glacilis* (Castracane) F.E. Round, *Chaetoceros tortissimus* Gran, *Thallassiosira nordenskioeldii* Cleve, *Lioloma pacificus* (Cupp) Hasle, *Pseudonitzschia inflatula* (Hasle), two subspecies of genus *Chaetoceros*, dynophytes—*Dinophysis odiosa* (Pavillard) Tai & Scogsberg [15].

A considerable number of phytoplankton species were recorded in port areas of the northwestern Black Sea [13, 16–18]. Only in the port of Odessa were 15 alien species of phytoplankton recorded, most of the species found were Dinophytes (8), and all of them most likely have a Mediterranean origin [13]. These species occur infrequently and in only a few locations.

In addition to the penetration of euryhaline salinophilic species of the flora, the penetration of freshwater phytoplankton is also occurring, especially in the northwestern part of the Black Sea subjected to the influence of major rivers such as the Danube, Dnieper, and Dniester [18]. However, not all of these species may be regarded as established alien species.

Among the alien phytoplankton species that has established itself and made a significant negative contribution to the phytoplankton community, we must note the diatom alga *Pseudosolenia calcar-avis* (=*Rhizosolenia calcar-avis*), first recorded in the northwestern part of the Black Sea in 1924 [19]. At present, *P. calcar-avis* is a abundant species widely spread in the northwestern part of the Black Sea, which sometimes demonstrates outbursts in its development. The occurrence of *Pseudosolenia calcar-avis* in the deposits of the Sarmatian age suggests its reintroduction to the Azov–Black Sea basin [20]. The diatom algae *Cerataulina pelagica* and *Chaetoceros socialis*, *C. tortissimus*, and *C. diversus*, which have settled in the Black Sea at the beginning of the 20th century, most probably from the North Atlantic, have also become abundant species of the Black Sea. Of them, *Cerataulina pelagica* and *Chaetoceros socialis* feature outbursts in their development in the spring and autumn over the entire sea basin [4]. The recent warm-water established alien *Leptocylindrus danicus* develops only in the summer in the northwestern part of the sea [21].

In all, among the alien phytoplankton species recorded, there are 19 species of diatoms, 19 species of Dinophyceae (of which *Alexandrium monilatum* and *Mantoniella squamata* are potentially toxic species), two species of the green algae, two species of Chrysophyceae, and one species of the Prymnesiophyceae *Phaeocystis pouchetii*. The brackish-water and freshwater phytoplankton species established in the brackish and freshwater bays and lagoons of the western part of the sea [16]. Some toxic alga species capable of forming cysts (resting stages) are among the most dangerous species supplied with ballast waters. The existence of cysts allows them to survive the unfavorable conditions both during transportation and in the new environment. Silty sediments are known to represent the most appropriate substrate for accumulation and maturation of the cysts settled. For the first time for the Black Sea, the quantitative parameters of the cysts of Dinophyta algae were determined when studying the silty grounds of the port of Odessa. Their abundance in the upper 5-mm layer of the sediments varied from from 1.6 to 105.6 million cells. m^{-2}. Most frequently recorded were the cysts of such alien dynoflagellates species as *Gonyaulax*, *Scrippsiella*, *Diplopsalis*, *Oblea*, *Protoperidinium*, and *Alexandrium*, which successfully germinated under laboratory conditions. Despite no *Alexandrium tamarense*, *A. affine*, and *A. acatenella* were recognized in plankton, they were assumed as potential established aliens, because cysts of these dinoflagellates were noted in the grounds of the port area [18]. In 2002, water “bloom” caused by the green alga *Prochlorococcus marinus* was registered; for the first time, this alga was observed in the lagoons of the northwestern sea area [22]. Therefore, at present, the process of penetration of alien phytoplankton species, mainly into the northwestern and western parts of the sea, is occurring due to their transfer both with the currents via the Bosporus Strait and with ballast waters. The process of establishment of the species that have already invaded into the sea is also proceeding. Selected species of this kind may temporarily become subdominant species, but, as a rule, they remain rare or are abundant only in selected years, which suggests a high stability of the phytoplankton community of the Black Sea with respect to establishment of alien species [22].

5 Macrophytes

Among macrophytes, the greatest number of Mediterranean species that have probably penetrated with the currents, succeeded in establishment in the near-shore waters of the Anatolian coast of Turkey (27 species). Their proportion reaches 26% of the total number of macrophyte species registered here. Among them, green algae Chlorophyceae, brown algae Fucophyceae, and red algae Rhodophyceae are represented by ten, five, and 12 species, respectively. Off the coasts of Romania and Bulgaria, six new species of Cladophora were recorded together with other green alga species; they refer to euryhaline and eurybiont species and, in addition, serve as indicators of eutrophic waters. These species were probably brought with ballast waters [23].

In 1990, in Odessa Bay, the near-shore euryhaline species of the brown algae *Desmarestia viridis* was found for the first time in the Black Sea [24]. By the winter months of 1994/1995, *D. viridis* had already become an abundant species of the near-shore zone of the bay. During recent years, especially in the cold ones, *D. viridis* was widely spread in the northwestern part of the Black Sea [25].

In the Danube River delta, in addition to marine macrophyte species, two alien species of freshwater ferns were recognized.

The brown alga *Ectocarpus caspicus* is also often referred as an alien species. About 40 years ago, *E. caspicus* was found and described on the Romanian coast in a brackish-water lake connected to the sea [26]; meanwhile, almost simultaneously, another author [27] regarded *E. caspicus* as an endemic species of the Caspian Sea. However, later, this species was referred to the Ponto–Caspian relics of the Black Sea basin [28]. Recently, *E. caspicus* was found off the southern coast of the Crimea as well [23]. In a series of papers [11, 29, 30], this species was mentioned as an invader from the Caspian Sea; this suggestion seems to be wrong, and the origin of this species requires special research, the more so as its habitat is presently expanding. Another example of this kind of error is the reference of the alga *Laurencia caspica* to

Caspian endemics [27]; later, this species was also recorded in the Black Sea on the shelf of Romania [26]. At present, A. Bogani also refers this species to the Ponto–Caspian relics of the Ponto–Azov basin [28].

From a comparison of the list of macrophytes of the Black Sea published in 1975 and the species that were found after 1975, N.A. Mil'chakova reported 38 new macrophyte species, of which 13, 10, and 15 species refer to green, brown, and red ceramian algae, respectively. The most significant change in the macrophyte flora of the Black Sea is related to the almost twofold increase in the number of species of the *Cladophora*, *Ulva*, *Ceramium*, *Polysiphonia*, *Cystoseira* and *Sargassum* genera; many of them play a key role in the bottom communities of the near-shore ecosystems of the Mediterranean Sea. Most of the new species are thermophilic organisms and serve as indicators of the transition zone between the boreal and tropical domains [23].

6 Zooplankton

In 1925, the hydromedusa *Blackfordia virginica*, which was brought from the Atlantic estuaries of North America, was for the first time recorded in the coastal waters of Bulgaria [31]. At present, it represents an abundant brackish-water species in the western part of the Black Sea and in the Sea of Azov. This medusa consumes small zooplankton and thus competes with fish larvae and fries; meanwhile, it never features significant outbursts in abundance and, therefore, is not harmful for the ecosystem. Later, in 1933, another hydromedusa species—the bougainvillea *Bougainvillea megas*—was found in Lake Varna and in the mouth of the Ropotamo River [32]. *B. megas* was also carried from the coastal Atlantic estuaries of North America. At present, it is widely spread in the form of bottom colonies that continuously cover rocks, port constructions, ship hulls, and pipelines in brackish areas of the Black Sea and the Sea of Azov. The negative effect of bougainvillea as a fouling agent is insignificant because of the high water content in the body of the polyp and its low strength [33].

In 1990, in the near-shore waters off the Crimea, five new hydromedusa (Hydrozoa) species (*Coryne pusilla*, *Eudendrium annulatum*, *E. capillare*, *Tiaropsis multicirrata* M.Sars, and *Stauridia producta*) were recognized. Meanwhile, the authors of [34], who found the former four species, were not absolutely sure in the correctness of the identification of at least two species—*Eudendrium annulatum* and *E. capillare* (the colonies encountered were without gonothecas). Later, N. Grishicheva reidentified *Tiaropsis multicirrata* as *Opercularella nana*. A colony of the fifth species, the polyp *Stauridia producta*, which refers to rare species, was found by T.V. Nikolaenko in September 2000 in a sample taken in the region of the exit from Sevastopol Bay. All five species seem to have a Mediterranean origin [29].

The ctenophore *Mnemiopsis leidyi* A. Agassiz was brought to the Black Sea with ballast waters from the near-shore regions of North America at the beginning of the 1980s (Fig. 1). By 1988, *M. leidyi* had spread over the entire Black Sea area and showed an enormous abundance outburst in the fall of 1989 [35]. During the subsequent years, sharp fluctuations in its abundance and biomass were observed caused by temperature and food conditions [36, 37] (Fig. 2).

The development of the *M. leidyi* population in the Black Sea ecosystem led to a decrease in the biomass, abundance, and species diversity of edible zooplankton, fish larvae, and eggs, which are the principal food objects of *M. leidyi* (Figs. 3, 4) [38–41].

Fig. 1 View of *Mnemiopsis leidyi*

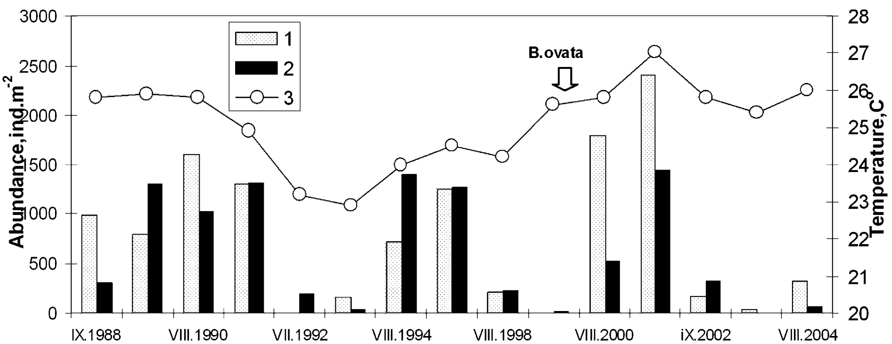

Fig. 2 Interannual variations of the abundance of *Mnemiopsis leidyi* (g m^{-2}) in August–September (abundance was estimated with coefficient for insignificant catchability (in mean 2) after Vinogradov [35]) and average surface water temperatures (direct measurements)

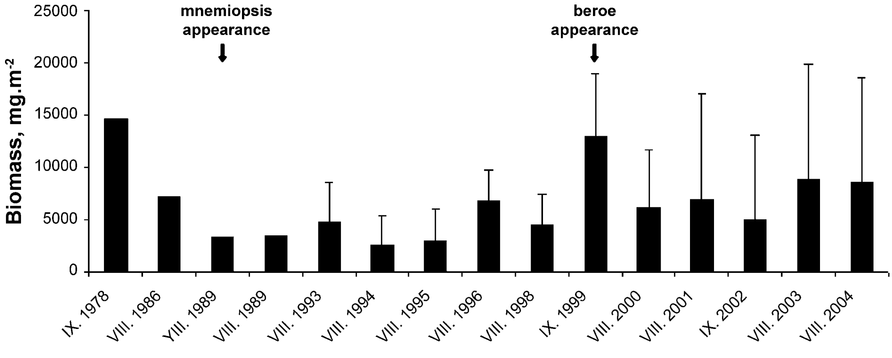

Fig. 3 Interannual variations of zooplankton biomass in August (g m^{-2})

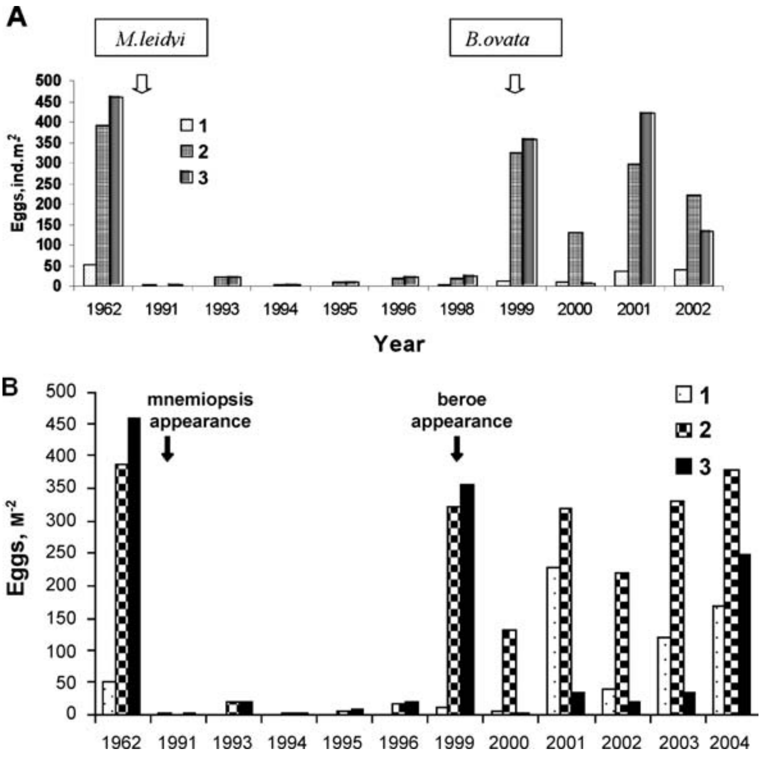

Fig. 4 Interannual variations in the abundance of **A** fish eggs (ind. m^{-2}), and **B** larvae in the northeastern Black Sea in July–August: 1 – scad; 2 – anchovy; 3 – other species

As a result, the commercial fish catches decreased; this especially refers to the planktivorous fishes that are food competitors of *M. leidyi* such as the anchovy *Engraulis encrasicolus ponticus*, the Mediterranean horse mackerel *Trachurus mediterraneus ponticus*, and, to a lesser extent, the sprat *Sprattus*

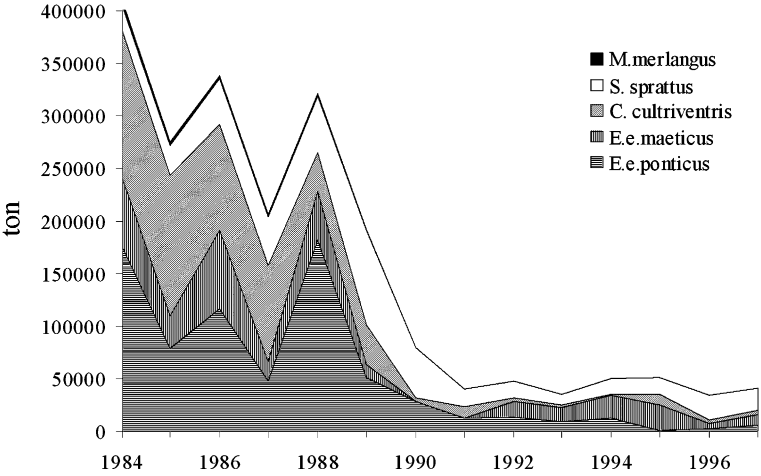

Fig. 5 Fish catch after *Mnemiopsis leidyi* outbreak but before *B. ovata* development

sprattus phalericus (Fig. 5). This also affected the representatives of higher trophic levels—predator fishes and dolphins, who feed mainly on anchovies and sprats [38, 42]. From the Black Sea, *Mnemiopsis leidyi* spread to the Azov and Marmara Seas and was periodically supplied with the Black Sea waters to the Aegean Sea [37, 43, 44]. In 1999, *M. leidyi* was introduced into the Caspian Sea as well, probably from ballast waters of oil tankers [45].

One of the reasons for the high abundance and biomass values of *M. leidyi* in the Black Sea that are never observed in its initial habitats—in the coastal waters of North America, is the absence of an appropriate predator to consume *M. leidyi* and control its abundance [46].

In 1997, a new invader—ctenophore *Beroe ovata* Mayer 1912 (Fig. 6)—was first found in the northwestern part of the Black Sea. This predator feeds on planktivorous ctenophores, first of all, on *M. leidyi* [47]. *B. ovata*, similar to its

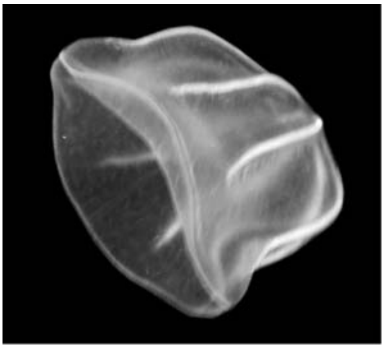

Fig. 6 View of *Beroe ovata*

predecessor *M. leidyi*, was carried with ballast waters from the Atlantic coast of the northern America [48]. In August 1999, the first outburst in the *B. ovata* development over the entire Black Sea was observed [49–51]. The studies of 1999–2006 showed that the development of the *B. ovata* population features a clear seasonal character. The first individuals appear in the middle or late August; in September–October, intensive reproduction proceeds, which leads to a sharp growth of the population; later, it gradually attenuates [52, 53]. The attenuation rate of the *B. ovata* development depends on the food (*M. leidyi*) availability. At significantly reduced *M. leidyi* abundances, the reproduction rate of *B. ovata* decreases and its population correspondingly reduces. Large adult individuals eliminate after spawning. In November, a minor part of the population consisting of individuals of new generation seems to sink down to the near-bottom layers; there, it rests over the winter until the subsequent outburst in the *M. leidyi* development. This kind of behavior is characteristic of the representatives of the *Beroe* genus in other regions as well.

With the appearance of the ctenophore *Beroe ovata* in the Black Sea ecosystem, a new previously absent level in the trophic web was formed. It was represented by a predator consuming *M. leidyi* and capable of significant decreasing the population of the latter. The results of the studies showed that *B. ovata* established in the Black Sea and occupied its niche in the ecosystem. Its seasonal development coincides with the cycling of this species in the near-shore waters of the North Atlantic: the appearance and starting reproduction at the end of the summer–beginning of the autumn and the decay in the late autumn [46].

Beroe ovata radically reduced the *M. leidyi* population and this resulted in the beginning of the process of restoration of the Black Sea ecosystem. The abundance and biomass of edible zooplankton significantly increased (Fig. 3). The species that have virtually disappeared after the *M. leidyi* invasion appeared again. Owing to the low abundance of *M. leidyi* in the first half of the summer, its pressure on the eggs and larvae of the summer-spawning fishes decreased (Fig. 4), while the winter-spawning species had enough time to spawn in the autumn and winter, when only isolated *M. leidyi* individuals existed. Therefore, other trophic levels started to be restored; first, this refers to small planktivorous fishes—anchovies, horse mackerel, and sprat—and their food rations [53].

Meanwhile, although with the appearance of *B. ovata* the pelagic ecosystem began to restore, in selected years, when *B. ovata* was seasonally absent, *M. leidyi* managed to reach high biomass values and significantly impaired the ecosystem under favorable feeding and temperature conditions. However, even in this case, the duration of its impact on the ecosystem was essentially lower: it lasted over one or two summer months instead of 8–9 months before the *B. ovata* invasion.

The most important alien species of mesozooplankton was probably the Copepoda representative *Acartia tonsa*, which was first recorded in the Black

Sea in 1994. Initially, it was regarded to be supplied from the Mediterranean Sea; meanwhile, the studies performed by A. Gubanova showed that *Acartia tonsa* appeared in the Black Sea before its appearance in the Mediterranean Sea (at the beginning of the 1970s) and was seemingly brought from the coastal waters of the North Atlantic. At present, the habitat of *Acartia tonsa* is extending and it was found off Kerch and off Novorossiisk, in the seas of Azov [54] and Marmara [7]. During the cold season of the year, from January to April, no *A. tonsa* is observed in the plankton of Sevastopol Bay, in contrast to the eurythermal Black Sea *A. clausi*. It appears at the end of May when the water temperature reaches 16 °C. From the end of June to August, *A. tonsa* quickly increases its abundance and starts to exceed *A. clausi* in quantitative parameters. According to the data of A. Gubanova, two peaks of *A. tonsa* are observed; they are more distinctly expressed than those of *A. clausi*. Thus, *A. tonsa* replenished the ecological niche of thermophilic zooplankton species in the Black Sea. It probably replaced two local Acarcia species—*A. latisetosa* and small *A. clausi*—but as itself it represents a valuable edible object.

In the coastal waters off the Crimea, the number of the alien planktonic species recorded goes on growing; all of them seem to have a Mediterranean origin. To date, it is not clear whether they will be capable of establishment. Among them, one finds the harpacticoids *Amphiascus tenuiremis*, *A. parvus*, *Leptomesochra tenuicornis*, *Idyella palliduta*, *Ameiropsis reducta*, and *Proameira simplex*, the planktonic copepods *Oithona brevicornis*, *O. plumifera*, *O. setigera*, *Clausocalanus arcuicornis*, and *Scolecetrix* sp., and the species of the Clausidiidae family, *Rhincalanus* sp. and *Oncaea minuta*. Some species were represented by a few specimens; of others, only single individuals were found [9]. Copepod *Oithona brevicornis* is establishing now and becoming abundant off Crimea (A. Gubanova, personal communication). Altogether only two species of ctenophores, two species of Copepoda, two (7) hydromedusae, which have also benthic stage, became established and 59 species of Copepoda were found in the near Bosphorus area, which we did not estimate as established aliens.

7 Benthos

The shipworm *Teredo navalis* (Linne 1758) seems to have performed the earliest penetration of invaders into the Black Sea, which was probably brought by the Greek vanquishers at the Attic times (750–500 B.C.) [55]. Shipworms are among the most widely spread and harmful invaders. Their intensive reproduction rate (up to 2 million larvae per cycle) and high resistance against unfavorable conditions represent the principal factors determining their wide propagation. They travel using wooden hulls of ships making holes with the help of endosymbiotic bacteria. Teredo may survive feeding on wood only, but it also filters and consumes plankton. Over 3 weeks, it may exist under anoxic conditions; it may survive in almost fresh water and in air and over-winter cold winters when wooden constructions are covered with ice. The mean length of the worms is 20–30 cm at a maximum value up to 60 cm. Teredo is a protandric hermaphrodite capable of self-fertilization.

This species was probably followed by spontaneous benthic invaders—the fouling acorn barnacles *Balanus improvisus* and *B. eburneus*, which penetrated into the Black Sea in the 19th century [56]. Balanuses were brought from the coastal Atlantic waters of North America. At present, both of these species, especially the former one, are mass organisms and are widely spread in the near-shore waters of the Black Sea. The negative effect of these species is related to the fact of their fouling over ship hulls, pipelines, piers, and dams. On the other hand, their pelagic larvae form a significant part of the near-shore edible meroplankton. Balanuses are hermaphrodites and, in conditions of the impossibility of cross-fertilization, *Balanus improvisus* are capable of self-fertilizing. In addition, eggs of all the balanuses are fertilized in the mantle cavity and develop there up to the stage of nauplius larva I, which is subsequently released to the water; this provides an additional protection of the progeny. The precipitation of larvae proceeds in a shoal mode, which provides the possibility of future cross-fertilization. Balanuses feature a high growth rate and 1-month-old individuals are already capable of reproducing [57]. These adaptation mechanisms provided the wide spreading and high abundance of *Balanus improvisus* and, to a lesser degree, of *B. eburneus*. One more species of acorn barnacles *Balanus amphitrite* was recorded in Odessa bay in 2001 [13].

The Polychaeta *Mercierella* (*Ficopomatus*) *enigmatica* was first recorded in 1929 in the brackish-water Lake Paliastomi near Poti (Georgia); later, it was also found in Gelendzhik Bay [58]. It dwells in curved calcareous tubes up to 4 cm long, from which it spreads a corolla of its branchial branches. Interlacing tubes form a quaint continuous cover over the surfaces of rocks and other underwater objects such as ship hulls. *M. enigmatica* precisely originates from the brackish-water coastal lakes of India. In 1923, it was found in the Seine River mouth and in the Adriatic Sea; from the Atlantic coasts of Europe or from the Adriatic Sea, it was brought to the Black Sea with ship-fouling organisms. Here, it became widely spread and penetrated into the Sea of Azov and the Caspian Sea. As a fouling organism, it damages ships and hydraulic structures, while its planktonic larvae serve as edible objects.

In 1937, in Dniester–Bug lagoon, A.K. Makarov found a crab species new for the Black Sea; it was identified as the Dutch crab *Rhitropanopeus harrisi tridentata*, which originates from Seider See Bay off the North Sea coast of Holland. Earlier, this species had been brought to Europe form the Atlantic coast of North America. At present, the Dutch crab is widely spread in desalinated areas of the Black Sea; in 1948, it was recorded in the Sea of Azov and in 1957 it was found as far as in the Caspian Sea [59]. It dwells over sandy and silty–sandy grounds of shoals and lagoons. It is intensely consumed by near-bottom fishes such as bullheads, flounders, Black Sea turbots, and sturgeons. It may be regarded as a useful species being an additional food object, the more so because it never competes with local species.

In 1947, off Novorossiysk, the gastropod mollusk *Rapana venosa* (=*R. thomasiana*) was recorded in the biocoenosis of mussels (Fig. 7). It is a predator feeding on oysters, mussels, and other bivalve mollusks. Rapa whelk inhabits the Japan and Yellow Seas, that is, in seas with a rather high salinity (25–32‰) and in relatively brackish waters. It was most likely brought to the Black Sea from the Japan Sea with a ship in the form of an egg clutch attached to its hull [60]. Rapa whelk has successfully reproduced, especially off the Caucasian coast, and in the 1950s it almost completely extinguished the community of the oyster *Ostraea edulis* on Gudauta Bank and then those of the mussel *Mytilus galloprovincialis* and scallops *Chlamys glabra*, that dwelled together with the oyster. Later on, rapa whelk started to destroy mussel colonies off the southern coast of the Crimea, then those off the coasts of Bulgaria, and reached a high abundance. By the beginning of 1970, rapa whelk had spread over almost the entire Black Sea area; at present, it is missing only from the most desalinated areas in its northwestern and western parts. In the 1980s, the intensive commercial fishing of rapa whelk as a valuable food object was initiated, first off the coasts of Turkey and then off Bulgaria. The unlimited commercial catch of the mollusk resulted in a decrease in its abundance; the drop was so crucial that the further fishery became unprofitable [61]. Later, fishing of rapa whelk was started on the Caucasian shelf and in the region of the Kerch Strait, where its total biomass was estimated at 2800 and 6000 t, respectively. The fishing of rapa whelk and the decrease in its stock due to the decrease of its food resources—small bivalves significantly reduced its abundance. The decrease in the stock of the food objects of rapa whelk such as small bivalves also continued with the development of the ctenophore *M. leidyi*, who consumed their pelagic larvae. At the end of the 1990s, the commercial catch of rapa whelk on the Russian shelf of the Black Sea was

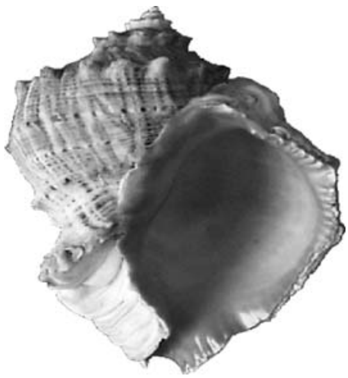

Fig. 7 View of *Rapana venosa*

performed only by a single enterprise [62]. After 2001, virtually no Russian organization has performed commercial fishery of rapa whelk. Bulgaria and Turkey continue their fishery activity and export rapa whelk meat to Japan and Korea. On the Turkish coast, there are several factories that specialize in the export production of rapa whelk meat. In the 1990s, the export of rapa whelk by Turkey alone exceeded 1000 t. The decrease in the commercial stress on the rapa whelk population in the mid-1990s seems to result in a growth in its abundance in the Russian part the Black Sea.

In 1995–1997, the studies of benthos in the northeastern part of the Black Sea showed a significant excess of the rapa whelk biomass over the biomass of other species of mollusks. In the Arkhipo–Osipovka–Kerch Strait region, the biomass of edible benthos was only 12 g m^2. The deterioration in the condition of food resources also affected the condition of benthofagous fishes. Only the Black Sea red mullet gut content mollusks were found. In the food of other fishes, benthos made up from 1 to 20% [62].

In 1999, during the survey of zoobenthos off the North Caucasian coast between Gelendzhik and Tuapse, a mass rapa whelk development was noted after the first outburst of the invader ctenophore *Beroe ovata* and the significant decrease in the *Mnemiopsis leidyi* population [63]. The total rapa whelk abundance reached 40 ind. m^2. This intensive rapa whelk development is comparable with its outburst in the 1950s, when the increase in its abundance proceeded under the availability of abundant food resources such as the oyster *Ostraea edilis* [1]. The outburst in the rapa whelk abundance in the 1990s was related to the growth in the provision of food resource such as brushes of the rock-dwelling variety of the mussel *Mythilus galloprovincialis*. In 2002, the abundance of rapa whelk continued to grow and reached its maximum in the near-shore waters of the northeastern part of the sea; later, in this region, because of the absence of food, rapa whelk remained the only representative of mollusks in the biocoenosis of zoobenthos and its abundance started to decrease. In 2005–2006, one could find numerous empty shells of rapa whelk that died from starvation on the coast of the sea. The main factor that restricts the rapa whelk development is the absence of food for its juvenile individuals [64].

No examples of consumption of adult representatives of rapa whelk by fishes or other hydrobionts are known; only its planktonic larvae may be consumed by planktivorous fishes. Rapa whelk is an active predator that consumes valuable representatives of benthos. It inserts significant changes into the structure of bottom biocoenoses and often is the dominating species of the bottom communities being itself an ecological dead-end. Therefore, its commercial extraction is extremely important for reducing the pressure on bivalve mollusks.

Another alien species—the gastropod mollusk *Potamopyrgus jenkinsi*—originates from New Zealand. Meanwhile, *P. jenkinsi* first appeared and inhabited the Atlantic near-shore waters off Europe and then penetrated into the Mediterranean and Black seas. In the Black Sea, it was recorded off the coast of Romania. Now, *P. jenkinsi* is observed in the lagoons of the northwestern part of the Black Sea [1].

In 1966, in the near-shore waters off Odessa, the bivalve mollusk *Mya arenaria* was found [65]. It is supposed that its larvae were brought to the Black Sea with ballast waters of ships either from the North Sea or from the coasts of North America. Mya widely spread over brackish areas of the Black Sea and the Sea of Azov and replaced the local species of the small bivalve *Lentidium mediterraneum*. During the first years after the mya invasion, its biomass had reached a value of 16–17 kg m^{-2} of the floor. The near-bottom oxygen deficiency at depths greater than 8–10 m represented a limiting factor for its further propagation. At lesser depths, where no hypoxy could restrict the mya development, its abundance was high and it often dominated over zoobenthos. Mya juveniles are consumed by near-bottom fishes—gobies, turbo, and sturgeons [29]. While estimating the significance of *Mya arenaria* as a new component of the Black Sea ecosystems, one can separate several aspects. On the one hand, its negative effect is represented by the significant replacement of the local species *Lentidium mediterraneum*, which served as a food for the fries of all the species of near-bottom fishes. On the other hand, mya juveniles proper became a food for adult fishes. In addition, this large alien species significantly enhanced the process of seawater filtration in the coastal zone, which is especially important under the conditions of eutrophication. One more factor has a positive effect. Every storm, when the wind blows from the sea, terminates in a high numbers throwing out of these mollusks from sea depths of 4–5 m onto the beaches, where they are consumed by sea birds—gulls, terns, and other species [25].

The blue crab *Callinectis sapidus*, one of the largest representatives of its order, was first found off Bulgaria in 1967; later, isolated specimens were encountered in the Kerch Strait in 1975, in Varna Bay, and in the Bosporus Strait. They were no more than single findings [25]. The blue crab originates from the Atlantic coastal waters of North America and was brought to the Black Sea and the Sea of Marmara with ballast waters of ships. At present, the blue crab seems to undergo establishment in the Black Sea. In recent years, it was recorded in the near-shore waters off Sevastopol and its abundance is increasing [66].

The nudibranchiate mollusk *Doridella obscura* was first found in the northeastern part of the Black Sea in 1980; later, it was also observed in Varna and Burgas bays in Bulgaria, in the Kerch Strait, and on the southern shelf of the Crimea. Doridella dwells off the Atlantic coasts of Canada and the United States. The studies of its food spectrum in the Black Sea showed that its main ration consists of the Bryozoa *Electra crustulenta* and *Conopeum seurati*. Having a food spectrum that narrow, this mollusk can hardly become an abundant species in the Black Sea and its influence on local fauna should not be significant [67].

One more alien species—the bivalve mollusk *Anadara inaequivalvis*,—was first found by V.E. Zaika on the Caucasian shelf in 1968. This species widely spread over the northwestern shelf of the Black Sea and the southern part of the Sea of Azov [68]. Due to the geometrically closing valves and the presence of hemoglobin in its tissues, anadara is capable of long-term existence under an oxygen deficiency in the near-bottom water layer and to survive hypoxy when other mollusks die. Adult individuals *Anadara inaequivalvis* can hardly serve as a food for fishes because of its thick massive shell; meanwhile, it helps sea purification as a filtrator. Anadara was brought to the Black Sea from the Adriatic Sea; there, it was inserted from the coastal waters of the Philippine Islands in the Pacific Ocean. In 1989, the anadara community almost completely replaced the community of *Chamelia gallina*; meanwhile, anadara was also noted in the bottom communities of the North Caucasian shelf as a subdominant species with a mean biomass of 70 g m^{-2} and an abundance of 10 ind. m^{-2}. In 2000, during a survey in the region between Gelendzhik and Tuapse, accumulations of anadara juveniles with abundances up to 3000 ind. m^{-2} were recorded at depths of 20–27 m. Judging from the size structure of the anadara population, the precipitation of juveniles observed was the first one over at least recent 8 years. In 2001, a high concentration of anadara (250–625 g m^{-2}) were observed in the northeastern part of the sea and intensive development of juveniles was also noted [55]. *Anadara inaequivalvis* is gradually becoming a natural component of the coastal biocoenoses off the Crimea [58].

In 2001, two new alien Bivalvia species were found in Odessa Bay: edible *Mytilus edulis* and *Mytilus trossulus* [13].

Altogether, among benthic alien species were recorded: Oligopaeta-1 species, Polychaeta-11, Mollusca-13, Cirripedia-3, Amphipoda-1, Decapoda-4.

8 Fishes

As mentioned before, selected Mediterranean species of fishes perform regular feeding and/or spawning migrations to the Black Sea. This refers, first of all, to valuable large predator species—the Mediterranean Atlantic horse mackerel *Trachurus trachurus trachurus* (Linnaeus), the Atlantic bonito *Sarda sarda* (Bloch), bluefish *Pomatomus saltatrix* (Linnaeus), the Atlantic mackerel *Scomber scombrus* (Linnaeus), and the Mediterranean mackerel *S. japonicus colias* Gmelin.

The swordfish *Xiphias gladius* Linnaeus (and even its spawning), the bluefinned tuna *Thunnus thynnus thynnus* (Linnaeus), the Mediterranean picarel *Spicara moena* (L), and the European pilchard *Sardina pilchardus* (Walbaum) were sometimes noted in the western and northwestern parts of the sea [69]. In the 1970s–1980s, the abundance of migrating species significantly decreased, and most of the species virtually stopped entering the Black Sea. Meanwhile, during recent years, the conditions for fattening have enhanced owing to increase in the stock of small pelagic fishes after the *Beroe ovata* invasion. As a result, some Mediterranean species again appeared both in the western part of the sea (the mackerels, the bonito, and the bluefish) [70] and in its northwestern part (the horse mackerel, the bonito, the bluefish, the Mediterranean picarel *Spicara moena* (L), the European pilchard *Sardina pilchardus* (Walbaum), the green wrasse *Labrus viridis* (Linnaeus), and triplefin *Tripterygion tripteronotus* (Risso) [71]. In addition, starting from 1999, their feeding area is expanded and new Mediterranean fish species appear; for example, in the near-shore waters off the Crimea, the dorado *Sparus aurata* Linnaeus, the salema *Sarpa salpa* (Linnaeus), and the thick-lipped gray mullet *Chelon* (=*Mugil*) *labrosus* (Risso) appeared and intensely reproduced [71]. Previously, in contrast to the gilthead bream, the thick-lipped gray mullet has never been recorded in the northwestern part of the Black Sea [69]. For the first time, a juvenile of *Chelon labrosus* was caught in October 1981 in Donzulav Bay. In October 1983, shoals of the thick-lipped gray mullet consisting of 10–15 fishes were observed in the waters off Sevastopol. Starting from 1999, the thick-lipped gray mullet has been repeatedly found in the areas off Sevastopol. A specimen of the salema off the Crimea was first noted in 1999 [71]. At present, its abundance in this region is rapidly increasing.

The dorado can be often recorded as single specimens or minor shoals in Balaklava Bay and adjacent near-shore waters. The dorado and the salema probably overwinter in the coastal waters off the Crimea [71].

The Mediterranean umbrine *Umbrina cirrosa* was once found in the Black Sea biospheric reserve in 1962 [72]. In the summer of 1999, one female with eggs with a length (L) of 43.5 cm was caught in Pshada Bay [73].

The common eel *Anguilla anguilla* may also be regarded as a migrant. E.I. Drapkin [74] reported 16 catches of eels in the region of Novorossiisk from 1946 to 1964; in 1958, an eel was caught off Anapa. Eels were also noted in the system of Kisiltash lagoons located on the Taman' Peninsula [75].

All the above-listed species are no more than seasonal Mediterranean migrants rather than invaders into the Black Sea. Among the alien species, three species of fishes previously not encountered in the Black Sea were found in the coastal waters of the Crimea. They include two specimens of the barracuda *Sphyraena obtusata* Cuvier 11.5 cm long caught with a bottom trawl in Balaklava Bay in August 1999. This is an Indian–Pacific species, which penetrated as a Lessepsian migrant via the Suez Canal to the Aegean Sea and then, probably, to the Black Sea [71].

A specimen of the northern blue whiting *Micromecisthis poutassou* 15.7 cm long was caught in January 1999 over a sea depth of 60 m off Balaklava (Crimea). It is a typical Atlantic–boreal species widely spread in the Mediterranean basin including the Aegean Sea and the Sea of Marmara; most likely, it penetrated from the Mediterranean Sea. Blue whiting performs long-lasting migrations; it is known as a stenohaline eurythermal species dwelling at salinities no less than 33‰, but was first encountered at a salinity of 18‰. There are two ways of explanation of the appearance of the above two species in the Black Sea: fishes might migrate from the Sea of Marmara or the Mediterranean Sea or, which seems more probable, might be brought with ballast waters. The third species is the coral-dwelling butterfly fish *Heniochus acuminatus*. A specimen 76 mm long was caught by a net in Balaklava Bay in October 2003. It is a typical tropical Indian–Pacific species and the conditions of Balaklava Bay are hardly favorable for it. This fish was most likely delivered with ballast waters [71].

The golden goby *Gobius auratus* Risso, which was first recorded in the communities of near-shore macrophytes off the Crimea in early 1970-s and now it regularly occurs in the northeastern part of the sea and may also be referred to Mediterranean invaders [76].

During the recent years, in the waters off Romania, centracant *Centracanthus cirrus*, which probably also penetrated from the Mediterranean Sea, was observed. To date, it has significantly increased its abundance and now represents a commercial fish in the littoral zone of Romania. In the central part of the sea, its developing eggs were first found in June 1982 [70].

In order to enhance the fishery potential of the basin, attempts to introduce 22 valuable commercial fishes were made; however, only a few of them managed to establish and became fishery objects [76]. The undoubtedly most significant event is the introduction of the large Far Eastern haarder *Liza haematochilos* (Temminck & Schlegel, 1945) (=*Mugil soiuy*) into the Black Sea and the Sea of Azov; it became a valuable commercial species for both of the seas.

The fry and juveniles of the haarder *Liza haematochilos* were brought from the estuaries of the Japan Sea in 1972–1980 and introduced to the lagoons of the Black Sea and the Sea of Azov and directly to the northwestern part of the Black Sea and to the open part of the Sea of Azov. In 1980, it became a widely spread commercial species in the regions off the coasts of Russia and the Ukraine; isolated specimens were also caught off Turkey, in the Sea of Marmara, and even in the Mediterranean Sea [77]. It was supposed that this fish would feed on detritus; meanwhile, its food spectrum widens and, in addition to detritus, it consumes small benthic organisms. In the Black Sea, this introduced species enters the food competition with local mullet species and reduces the abundance of the latter. In the Black Sea basin, the growth rates of the haarder changed; it reached significantly greater size and weight. Both a 1.3–3-fold increase in its growth rate (the corresponding values of mass and size are 3 kg and 65 cm in the Japan Sea and 4.5 kg and 71 cm in the Sea of Azov) and acceleration of its sexual maturation by a year were noted [78]. In 1992, the haarder was added to the list of commercial fishes of the Azov–Black Sea basin. In 1993, the allowable quota was established and the fishery began. The haarder fishery in the Sea of Azov and the Black Sea is performed by Russia, the Ukraine, and, starting from 1999, by Georgia.

Among the intentionally introduced sturgeon species, only the rainbow trout may occur in natural conditions. The environments in rivers and lagoons are favorable for the rainbow trout dwelling; they were episodically caught but their reproduction has never been observed. Most likely, no natural spawning of the rainbow trout proceeds and its population is replenished only owing to the individuals of a artificial origin [73].

Two sea bass species—the Japanese sea bass *Lateolabrax japonicus* (Cuvier) and the European bass *Dicentrarchus labrax* (Linnaeus) were brought for intentional introduction from desalinated waters of the Japan Sea. Both species are from time to time recorded in the northwestern part of the Black Sea. The European bass *Dicentrarchus labrax* is regularly caught in the Black Sea [79], although in small amounts.

In 1963, plecoglos *Plecoglossus altivellis* (Temminck & Schlegel) was brought from the Japan Sea with the purpose of intentional introduction to the western part of the Black Sea.

For commercial aquaculture, large freshwater fishes were brought to the ponds and lagoons of the Azov–Black Sea basin, among them the silver carp *Hypophthalmichthys molytrix* (Valenciennes, 1844), the speckled carp *Aristichthys nobilis* (Richardson, 1846), and two amur species—the black amur *Mylopharyngodon piceus* (Richardson) and the grass carp *Ctenopharyngodon idella* (Valenciennes, 1844). At present, carps became important commercial fishes. However, these fishes do not reproduce under the natural conditions.

In order to reduce the abundance of malarial mosquitoes in the swampy regions of Colchis, intentional introduction of the mosquito fish *Gambusia holbrooki* (Girard, 1859) was made. The mosquito fish was brought from freshwater regions of Italy in 1925 [57] and was successfully introduced into the wetlands of the Black Sea. The mosquito fish dwells in brackish estuaries; meanwhile, it behaved as an euryhaline species and expanded over the Azov–Black Sea basin. At present, it occurs in a wide salinity range from 0 to 15–17‰.

Together with the carp and amurs, the Amur River stone moroco *Pseudorasbora parva* (Schleg) was brought from the rivers of Far East to the Romanian freshwater basins, from which it spread via channel systems to other rivers of the Black Sea basin, then to the rivers of the basin of the Sea of Azov, and then farther to Europe. At present, it represents a widely spread species of weed fishes. This species is extremely eurybiontic and is capable of dwelling in various freshwater basins such as rivers, ponds, reservoirs, wastewater channels, and strongly eutrophicated basins. Its food spectrum is similar to that of juveniles of commercial fishes. Its larvae and fry feed mostly on planktonic crustaceans; adult individuals add benthic organisms to their ration. Thus, it competes with fish juveniles and adult planktivorous and benthofagous fishes. In addition, it extinguishes eggs of valuable commercial fishes [80].

Selected freshwater species penetrated to brackish-water estuaries and the Danube and Dnieper river deltas as a result of the activity of aquarium holders. Among this species is the aquarium sunfish *Lepomis gibbosus* (Linne, 1758), which was brought to Europe from North America as early as in the 18th century [69]. From the ponds into which it was released, it penetrated to major rivers such as the Rhine, the Oder, and the Danube and to related inner basins. In the Danube River delta, it was first noticed in 1949; then it gradually spread along the adjacent coasts of the Black Sea both to the south to the near-shore lakes of Romania and Bulgaria and to the northeast to selected basins between the Danube and the Dnieper Rivers [65]. At present, this fish occurs in the basins of the Tiss and Bug Rivers, in the lower reaches of the Danube, the Dniester, and the Dnieper, in Odessa Bay, and in Berezan lagoon; isolated individuals were recorded in significantly desalinated areas of the Black Sea. It is quite common in numerous channels of the Dnieper River, in the Kakhovka Reservoir, and in the Dnieper–Bug lagoon, from where it penetrated to the lower reaches of the Southern Bug River. At the end of September 2002, in an aquaculture pond located in the North Crimea, more than 200 individuals of sunfish were caught; they seemed to penetrate there from the Kakhovka Reservoir via the North Crimean Canal [79]. This species is euryhaline and eurythermal spreading in the near-shore waters with a salinity of 14–15‰; it survives equally well both the high summer temperatures and the under-ice wintering even in small basins. Its juveniles feed on crustaceans, while adult individuals consume insects and small fishes. It is harmful for the fishery both in natural and artificial basins because it consumes eggs, larvae, and fry of valuable species and is a food competitor for some of them [69]. In its turn, this species is characterized by a low growth rate; it refers to weed fishes and has no commercial value [79]. The process of introduction of the sunfish to the inland basins of the Ukraine and Russia is proceeding both because of the spontaneous expansion of its habitat and due to the occasional transport from fish nurseries with juveniles of valuable species. An analysis of the tendencies of its propagation allows one to expect its further penetration in the eastward direction to the rivers of the basin of the Sea of Azov (Don and Kuban') and related natural and artificial basins and its expansion up to the Volga River. Taking into account the high ecological plasticity of the sunfish and the availability of favorable conditions for it in the south of the Ukraine and Russia, one can suggest that in the forthcoming years it will be capable of making a negative impact on the ecosystems of the inland basins of this region and to cause economic losses in the fishing industry. This is another aggressive invader that requires an immediate monitoring of its propagation and elaboration of adequate measures in order to reduce its abundance [79].

Another aquarium fish—the Japanese oryzia *Oryzias latipes* (Temminck & Schlegel) was also occasionally released by its holders. It was brought from the estuaries of the Japan Sea, introduced, and is now is rather widely spread in the brackish and freshwater areas of the northwestern part of the Black Sea. This fish is also a widely distributed weed fish.

9
Pathways of Penetration of Alien Species

We have distinguished pathways of species penetration into the Black Sea on the base of analysis of the composition of the already established alien species and the regions donors from which they were brought (Figs. 8, 9).

The majority of the established accidental invaders were brought to the Black Sea from the near-shore Atlantic waters of North America; this mainly happened in the 1950s–1990s, although selected species had penetrated earlier. All the alien species of this group are neritic, rather eurythermal, and, most importantly, a euryhaline species widely distributed in the coastal waters of the world's oceans. This pathway is also characteristic of a group of brackish-water species that were accidentally introduced into the Black Sea; this group is represented by the inhabitants of near-shore brackish-water bays and estuaries of the same region. They established in the brackish western and northwestern areas of the Black Sea.

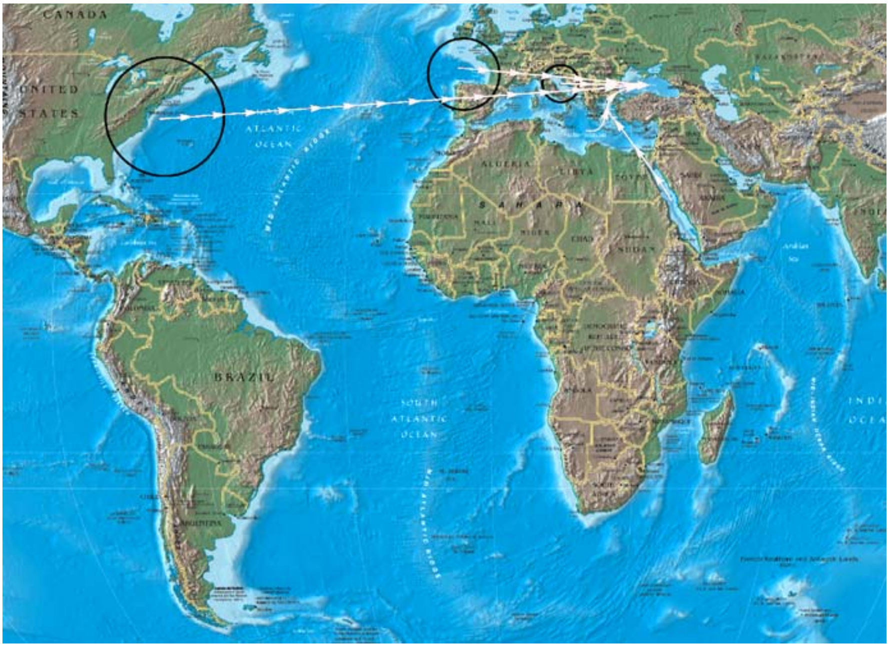

Fig. 8 Pathways of penetration of alien species to the Black Sea

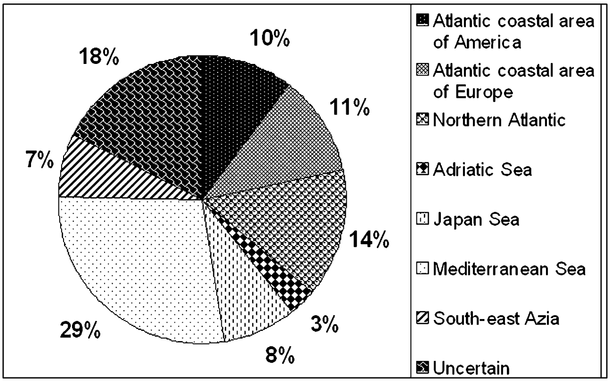

Fig. 9 Share of alien species in the Black Sea with respect to their donor area

One more group of alien species that were accidentally introduced into the Black Sea also features a northern Atlantic origin, although they arrived from the eastern part of the Atlantic Ocean—from the near-shore waters of Europe (Fig. 9).

The third group consists of alien species of a Mediterranean origin; their share is rather high and is gradually increasing over the recent years; meanwhile, not all of these species have already established. These organisms driven with currents and ballast waters represent phyto- and zooplankton, macrophytes, benthic or demersal organisms, and fishes. None of them became an abundant species; their greater number occur only in the near-Bosporus and southern parts of the Black Sea. Selected species penetrated to the near-shore regions off Bulgaria, Romania, and the Crimea also with currents, in the course of their migration, or with ship-ballast waters. Among them, one should note phytoplankton and zooplankton species, ciliates, macrophytes (whose greater part settled in the southern part of the sea), the crab *Sirpus zariquieyi* found off the Turkish coasts, the amphipod *Microprotopus maculatus* recorded off the Crimea, and three fish species, two of which may be regarded as already established species—the golden goby *Gobius auratus* and the centracant *Centracanthus cirrus*.

On the contrary, most of the species brought from the Adriatic Sea established in the Black Sea, created reproductive populations, and became abundant. Among them there are the bivalve mollusk *Anadara inaequivalvis* (*Cunearca cornea*), which was brought to the Adriatic Sea from the Pacific Ocean, and the oyster *Crassostrea gigas*, which was initially brought from the Japan Sea to the Adriatic Sea and then to the Black Sea. Later, the measures on the aquaculture of *Crassostrea gigas* in the Black Sea started; they are still going on [81]. The brown alga *Desmarestia viridis* could also penetrate not only from the near-shore waters of Europe but also from the Adriatic Sea [30]. Mosquito fish *Gambusia holbrooki* was brought for its intentional introduction from the Italian coasts of the Adriatic Sea, to where it had been previously brought from Central America. The fouling polychaete *Mercierella enigmatica* seems to have penetrated not only from the near-shore waters of Europe but also from the Adriatic Sea. The successful establishment of the species brought from the Adriatic Sea is explained, on the one hand, by the lower salinity of some of its regions as compared to other parts of the Mediterranean Sea and, on the other hand, by the winter and summer water temperatures close to those characteristic of the Black Sea; this allows the Adriatic invaders to overcome the conditions of the winter cooling in the Black Sea. In addition, the intensive shipping between the ports of the Adriatic and Black Seas favors the penetration of the organisms from this region. For example, according to the data of B. Aleksandrov, most of the 29 Mediterranean species recognized in the area of the port of Odessa was brought from the near-shore waters off the Italian coast of the Adriatic Sea [13].

The invasion of alien species via the three pathways mentioned is mainly implemented with ballast waters of ships or with the ship hull fouling communities.

The Japan Sea, with its estuaries and rivers, represents one more important source for alien species invasion to the Black Sea; several species were accidentally or intentionally introduced from this region. They are the spontaneously brought rapa whelk *Rapana venosa* and the intentionally introduced haarder *Liza haematochilos* (*Mugil soiuy*). Together with the haarder, three species of fish parasites were also introduced [11]. Aquarium holders occasionally released the aquarium fish Japanese oryzia *Oryzias latipes*, which originates from Japanese freshwater basins. The accidental introduction of alien species from the Japan Sea has become possible after the opening of the Suez Canal, when new navigation routes appeared. Meanwhile, except for rapa whelk, none of the species of the Japan Sea that spontaneously introduced into the Black Sea succeeded to establish in it. Of interest are the findings of Indian–Pacific fish species that might penetrate over this route with ballast waters and, probably, even in the course of their migration: initially to the Aegean Sea as Lessepsian migrants and then to the Black Sea; however, their further destiny is still unknown. During last years, other groups of species of Indo-Pacific origin began to appear in the Black Sea and they were most likely brought from the Mediterranean where they penetrated as Lessepsian migrants, but we cannot exclude their penetration with ballast waters from the Indo-Pacific area.

In addition to the species mentioned, there are others that also introduced from the near-shore waters of the Pacific or Indian oceans after the opening of the Suez Canal; initially, they established in the coastal waters of Europe and the Adriatic Sea and then were driven to the Black Sea. These are the polychaets *Capitellethus dispar* and *Glycera carpita*, the gastropod *Potamopyrgus jenkinsi*, and the decapod—Chinese mitten crab *Eriocheir sinensis*. However, these invaders have not become abundant species in the Black Sea.

The attempt of intentional introduction of five fish species from the estuaries of the Japan Sea, the Amur River, and other rivers of Southeast Asia was not successful: two sea bass species occur as isolated individuals and only the pond carps and amurs dwell in freshwater lagoons, rivers, and deltas of the Black Sea, but their populations are supported by artificial reproduction. Two fern species and strains of *Vibrio cholerae* were brought from the same regions.

One more route was mentioned—the penetration of the organisms from the Caspian Sea [11, 29], though it is hardly probable. For example, the algae mentioned in these publications (*Ectocarpus caspicus* and *Laurencia caspica*), were regarded as Caspian endemic species [27]; meanwhile, later they were recognized in the Black Sea waters off the coast of Romania [26] and referred to as the Ponto–Caspian relics of the Ponto–Azov province [28]. The same authors present the crustacean harpacticoid *Schizoptra neglecta* as an invader from the Caspian Sea; meanwhile, in addition to the Caspian Sea, this species is also mentioned as dwelling in the eastern part of the Black Sea and the Dnieper–Bug lagoon [82]. Thus, most likely, at present there is no invasion route from the Caspian to the Black Sea. Moreover, this route seems to be hardly possible because the species that were capable of establishing in the Ponto–Azov environment at its latest connection with the Caspian had already established in it and are now known as Ponto–Caspian relics. In the Ponto–Azov area, Ponto–Caspian species are common in origin with the autochthonous species of the Caspian and the species that could establish there, did it during the latest connection between the basins [83]. It is hardly probable that some other species from this group (particularly a Caspian-endemic species) is capable of penetrating into the Black Sea. These species were formed under the particular conditions of the Caspian Sea and can hardly establish under the conditions of the higher salinity of the Black Sea. Experimental studies showed that this fauna couldn't resist enhanced water salinity [84].

10
Vectors (Ways) of Alien Species Penetration

Various ways (vectors) of alien species penetration to the Black Sea may be distinguished: intentional introduction of commercial species, accompanied unintentional release of weed species during the latter operations, occasional release by aquarium holders, and penetration via straits, canals, and rivers. Meanwhile, the most important and largest vector whose significance increases each year is shipping. In so doing, while previously mostly the species of ship hull fouling communities invaded, in the recent years, a greater number of organisms are brought with ballast waters. The intensified shipping in the Black Sea increases the risk of appearance and establishment of new species accidentally brought if there is no control of ballast waters and ship fouling.

There are 92 (+32?) marine and brackish-water alien species brought with ships, which may be regarded as actually established. Among the 15 (17) fish species, ten are intentionally introduced, one species was a result of an accompanied unintentional release, and one more was released by aquarium holders; one fish species penetrated via canals and two more entered the sea via the Bosporus Strait. Thirty-seven more species have not established yet (regardless of parasites).

The currents via the Bosporus Strait delivered 59 species of zooplankton, 37 species of phytoplankton, 51 benthic species, and 23 species of macrophytes. Meanwhile, it seems probable that some of the species recognized during the recent years have not been noted previously because of the absence of appropriate studies in the near-Bosporus region aimed at the groups of species mentioned.

Summarizing, we may conclude that at present there are 152 established alien species (including freshwater species) in the Black Sea or 161 species including species doubtful with respect to their establishment. In addition there are 150 species that are recorded as isolated individuals or observed only in the near-Bosporus region; more than 37 species have not established yet. Probably, our generalization does not account for selected species, especially among those recorded as single specimens or observed only in the near-Bosporus region, if the specialists who studied these species did not report them as recent invaders from the Mediterranean Sea. Locally, in the northwestern and western parts of the sea, alien species were recorded whose status was not definitely determined. Among them, the same planktonic and meroplanktonic species brought from the Mediterranean Sea are noted in ballast tanks and port areas. It seems that some of the most euryhaline species of this group may soon establish in the Black Sea.

The invasion rate has been increasing over the last years. More and more Mediterranean species penetrate via the Bosphorus, are released from ballast waters, and establish due to global warming (Fig. 10).

Among the alien species one finds representatives of various ecological, systematic, and functional groups in the Black Sea (Table 1, Fig. 10).

The most negative effect on the Black Sea ecosystem was provided by the invaders–predators that formed abundant populations and featured abundance outbursts under favorable food and environmental conditions. Among them, one finds benthic species (such as rapa whelk, which consumes benthic organisms: oysters, mussels, and other bivalve mollusks) and pelagic species (ctenophore *Mnemiopsis leidyi*, which consumes edible holozoo–meroplankton, fish eggs, and larvae and indirectly affects all the trophic levels of the ecosystem). This group also includes the weed sunfish *Lepomis gibbosus*, which is widely spread and causes increasing damage to the ecosystems of the freshwater and brackish-water area of the Black Sea basin by consuming zooplankton, fish eggs, larvae, fries, as well as small adult fishes.

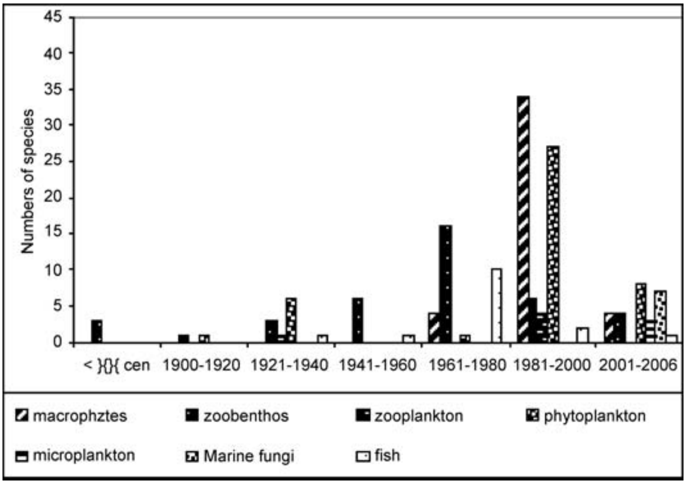

Fig. 10 Invasion rate of alien species in the Black Sea

Table 1 Taxonomical and ecological groups of alien species; *brackets* indicate species that were described as identified but whose status was still uncertain

	Established species	Species occurring only in the near-Bosporus area	Species not established yet
Fungi	7		
Bacteria	1		
Parasites of fish	3		
Infusorians	3 (>)		
Phytoplankton	43	37	
Macrophytes	42		
Kamptozoa	1		
Hydrozoa	2 (7)		
Ctenophora	2		
Polychaeta	11	29	
Copepoda	2	59	> 30
Decapoda	4	1	2
Amphipoda	1	4	
Cirripedia	3		
Bivalvia	8		
Gastropoda	5	18	
Pisces	15 (2)	2	5
Total	152 (161)	150	> 37

The proportions of the ecological groups of the species–invaders are similar to those of the aboriginal species of the Black Sea, especially if all the organisms both established and found as isolated individuals are taken into account. This may be explained, first of all, by the fact that in the course of the long-term geological evolution, particular conditions were formed in the Black Sea and the more the deviation from the normal environment setting the poorer its biological diversity (which depends on the number of species capable of adjusting to the existing conditions) and the higher the abundance and biomass of these species (productivity of the basin). Therefore, one may suggest that, under the existence of the limiting factors that strong (the low salinity, the continent climate, and the presence of the hydrogen sulfide layer), species that are ecologically similar to the aboriginal ones but stronger with respect to their competitive force may introduce into the community.

11 Conclusions

Let us try to analyze all the aliens that have established, both spontaneously and intentionally, in order to clarify which species (and why) became a large and widely spread species and which ones could not be established and are found as singular specimens.

The major part of the species that have established directly in the Black Sea are the widely distributed marine neritic, first of all euryhaline and, to a significant extent, eurythermal organisms. Their ability of inhabiting new areas is genetically provided. The progeny of widely distributed species features a phenotypic polymorphism. The habitats of species, especially of the widely spread ones, as well as the conditions existing in them, are irregular and "patchy" and change in space and with time; therefore, the species that are capable of both expanding their habitats and of existing under the given conditions can follow the best strategy. At the existence of the phenotypic polymorphism, two properties are coupled: the ability of migration and the genotypic variability. The expansion strategy is best manifested for the species existing in overpopulated communities, that is, for the species dominating in the communities or occur in high abundance and capable of providing outbursts. As a rule, these species feature a wide range of tolerance with respect to all the factors, which favors their wider expansion.

The species with the most complete set of the above-listed properties not only succeeded to establish but also became abundant species in the Black Sea and continued their further expansion. They expanded, first of all, to the brackish-water Sea of Azov with currents and ships via the Kerch Strait; selected species invaded to the Sea of Marmara via the Bosporus Strait and to the Aegean Sea via the Dardanelles or to the Caspian Sea with ballast waters or with ship fouling communities. Thus, the Black Sea became a donor basin for the further expansion of the alien species that have established in it to other southern seas.

The ctenophore *Mnemiopsis leidyi* is the most impressive representative of invaders; it is the most aggressive invader, which expanded over all the seas of the Mediterranean basin and over the Caspian Sea and affected their ecosystems. The subsequent introduction of *Beroe ovata* to the Black Sea provided the beginning of restoration of its ecosystem.

For 15 years after the spontaneous introduction of two lowly organized but adjustable gelatinous animals—the ctenophores *Mnemiopsis leidyi* and *Beroe ovata* the Black Sea ecosystem has changed significantly. As a result of the development of *Mnemiopsis leidyi*, the ecosystem, from the lowest trophic levels to the higher ones (fishes and dolphins), was significantly degraded. Meanwhile, after the introduction of the *Beroe ovata*, it started to recover. These events present a dramatic example of the impact on the ecosystem that is provided by the invasion of a single species and, undoubtedly, this process should be thoroughly controlled by man.

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