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Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin

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Abstract In the last two decades of the twentieth century, the ctenophore *Mnemiopsis leidyi* (A. Agassiz) has invaded the Black, Azov, Marmara and Aegean Seas, and, recently, the Caspian Sea. Here, we compare its spatial and temporal distribution, seasonal dynamics and the time and duration of reproduction. We also discuss factors that control its abundance throughout its invasive range and its effect on ecosystems. Observations are based on the long-term field data collected by three research institutes. An analysis of the effects of temperature, salinity, prey (zoo- and ichthyoplankton) availability and predation (by ctenophores of the genus *Beroe*) on *M. leidyi* population size, and the effects of *M. leidyi* on zoo- and ichthyoplankton, and on fish populations in the Black and Azov Seas is also provided. With the Black Sea current, *M. leidyi* spreads to the upper layers of the Sea of Marmara, where it now occurs around the year. At regular intervals, the Black Sea current also takes it to the northern Aegean Sea. In contrast, it has to re-invade the Sea of Azov every spring or summer, dying out during winter when the temperature drops below 4°C. The warm summer and mild winter temperatures, relatively low salinity and abundance of prey in the Black Sea are close to optimal for *M. leidyi*, while they are suboptimal in the northern Aegean Sea, where salinity and temperature are often too high. In the Black Sea the absence of gelatinous and other predators led to an enormous ctenophore abundance for a decade, but with the appearance of *Beroe ovata* in 1999, *M. leidyi* abundance greatly decreased. Analysis of seasonal dynamics of *M. leidyi* in the Black Sea and in other seas of the Mediterranean basin indicates similarities in the timing of maximum abundance and biomass, in spite of some differences in the initiation and duration of reproduction. A peak biomass and density occurred in 1989 in the Black and Azov Seas and in 1990 in the other seas. The *M. leidyi* invasion negatively affected the ecosystems of the Black Sea and the Sea of Azov. The zooplankton, ichthyoplankton and zooplanktivorous fish stocks all underwent profound changes. Similar effects, but less pronounced, were recorded in the Sea of Marmara. Effects on Mediterranean food chains have, so far, remained insignificant. Salinity is probably supraoptimal here, and several predators prevent *M. leidyi* from reaching outbreak levels.

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Introduction

The Mediterranean is a system of semi-enclosed seas connected by straits (Fig. 1). Semi-enclosed seas are more sensitive to impact than open seas, and anthropogenic introduction of alien species is more likely to be successful here (Caddy 1993). The Black Sea, with its truncated biological diversity, had been damaged in the past by opportunistic invasions of temperate and subtropical animal and plant species. Recently, it was invaded by a predatory ctenophore of the genus *Mnemiopsis*, assigned to the polymorphic species *M. leidyi* (A. Agassiz) (Seravin 1994). It was accidentally introduced in the early 1980s, possibly with ballast water from the northwestern Atlantic coastal region (Vinogradov et al. 1989). This species is a self-fertilizing

Fig. 1 *Mnemiopsis leidyi*. Patterns of occurrence in the Mediterranean basin (scheme) as of summer, 1999 (*dark areas* present all year; *light areas* seasonal occurrence). Russian monitoring area in the Black Sea

hermaphrodite, preadapted to rapid colonization (Kremer 1976). Pianka (1974) reported that up to 100% normal development has been repeatedly obtained from self-fertilized eggs of single ctenophores, and the significance of outbreeding in ctenophores is controversial. An individual first sheds sperm, briefly disperses them, and releases oocytes into its own sperm.

In addition, *M. leidyi* has an ability to regenerate from fragments larger than one-quarter of an individual (Coonfield 1936). It is also a generalist carnivorous feeder (Tzikhon-Lukanina and Reznichenko 1991), and occurs over a broad range of salinity conditions (Harbison and Volovik 1994). From the Black Sea, it spread north to the Sea of Azov, south to the Sea of Marmara and perhaps even to the eastern Mediterranean (Studenikina et al. 1991; Shiganova 1993, 1997). In 1999, it reached the Caspian, where it is currently expanding at an even more rapid rate than in the Black Sea (Shiganova et al. 2001).

A steep decline in ichthyo- and mesozooplankton abundance and change in species composition followed in its wake (Vinogradov et al. 1989, 1992, 1995; Shiganova 1997; Konsulov and Kamburska 1998; Kovalev et al. 1998). The catches of zooplanktivorous fish sharply dropped (Volovik et al. 1993; Prodanov et al. 1997; Shiganova 1997, 1998). By the late 1980s the pelagic ecosystem of the Black Sea had become a dead-end gelatinous food-web (Vinogradov et al. 1992).

The goal of the present study is to review the distribution and dynamics of *M. leidyi* in the Black and Azov Seas, compare patterns with those in the Sea of Marmara, the Aegean Sea and the eastern Mediterranean, and identify the reasons for the species' success.

Materials and methods

Data were collected from 1992 to 1999 by 16 Black Sea cruises of the P.P. Shirshov Institute of Oceanology, three international cruises on the Black Sea (August and November 1993, and May 1997), one survey of the Sea of Marmara (October 1992) and one survey of the Mediterranean Sea (September–October 1993).

The Sea of Azov was surveyed on a monthly basis from May to October–November 1989 and 1999 by the Research Institute of the Azov Sea Fishery Problems, 32 cruises in all.

Methods of sampling were the same for the P.P. Shirshov Institute of Oceanology and the Research Institute of the Azov Sea Fishery Problems. Gelatinous plankton, fish eggs and larvae were sampled with a Bogorov–Rass net (a square net with an opening of 1 m^2 and a mesh size of 500 μm), taking vertical hauls from the anoxic layer (120–150 m) to the surface, and from the thermocline (15–25 m) to the surface. In shallow zones and in the Sea of Azov, vertical hauls were from the bottom to the surface. Mesozooplankton was collected using a Juday net (net opening 0.1 m^2, mesh size 200 μm) by vertical hauls from thermocline to surface, from pycnocline (70–80 m) to thermocline and from the anoxic layer to the pycnocline.

A correction factor (k) for differential catchability was used for gelatinous plankton [*Mnemiopsis leidyi*: size <10 mm, 10–45 mm – $k=2$; size >45 mm – $k=2.3$ (Vinogradov et al. 1989); *Aurelia aurita*: size <50 mm – $k=2$, size 50–100 mm – $k=2.3$; >100 mm – $k=3$; *Pleurobrachia pileus*: $k=2$ for all sizes of specimens (Vinogradov and Shushkina 1992)].

In the northern Aegean Sea, samples were collected during seven cruises (March, May and September 1997, March and June 1998, September 1999 and March 2000) of the National Centre of Marine Research, Athens. During these cruises mesoplankton sampling used a WP net (mesh size 200 μm), while ctenophore sampling was performed with a WP-3 net (500 μm). Mesoplankton samples were also collected in Saronikos Gulf monthly from 1990 to 2000, in Elefsis Bay seasonally, and at Lesvos Island seasonally (May 1995–May 1996).

Biomass of *M. leidyi* was estimated using a regression equation derived from field measurements, $y=0.0056x^{1.85}$, where x is length (including oral lobes) in millimeters, and y is wet weight in grams (Shiganova 2000).

Older data on the Black Sea (1989–1992), published by the Institute of Oceanology (Vinogradov et al. 1989, 1992; Khoroshilov 1993) were used for comparison.

Characteristics of the receiving environments

The eastern Mediterranean, including the Aegean Sea, has a salinity ranging from 38.7‰ to 39.1‰, and surface temperatures of 13.3–14.1°C in winter, and 24–29°C in summer (Arkhipkin and Dobrolubov 1999). The seas in its north basin are estuarine in nature, with lower salinity and colder winter temperatures.

The brackish Black Sea is the largest semi-enclosed basin in the world. The Bosphorus Strait connects it with the Sea of Marmara, and Kerch Strait with the Sea of Azov. Because of restricted water exchange with the Mediterranean, and abundant inflow of freshwater via a number of rivers, of which the Danube is the most important, the Black Sea is a net exporter of water (the surface current), and, in the sea itself, a saline stratification exists. All water below the permanent halocline (87% of total volume) is anoxic.

The surface water is aerated, with an upper mixed layer above the seasonal thermocline at 15–25 m depth. Salinity at the surface is, on average, only 18‰, but rises to 21.9–22.3‰ at greater depths. The surface is warmed to 24–27°C in summer, cooling to 2–8°C and usually freezes in the shallow northwest in winter. A cold intermediate layer with a temperature of 6–8°C occurs between the permanent halocline and the summer thermocline. In winter, an isothermal layer extends from the surface to 70–80 m (Ovchinnikov and Titov 1990).

The Black Sea began to change in the 1960s because of anthropogenic stress, including a decrease in fresh-water runoff, pollution, bottom-trawling, over-fishing and the introduction of alien species (Caddy and Griffiths 1990; Caddy 1993). The effects were greatest in the north, where the Danube, Dnieper and Dniester Rivers determine the hydrological and hydrochemical regime. Nitrogen and phosphorus inputs dramatically increased in the 1960s, causing eutrophication in the coastal northwest. Eutrophication led to changes in zooplankton structure and blooms of *Noctiluca scintillans* Kofoid and Swezy, 1921 (Zaitsev and Aleksandrov 1997). An outburst of *Aurelia aurita* (L) followed in the early 1980s (Lebedeva and Shushkina 1991).

The Sea of Azov is shallow (4–14.5 m depth) and even less saline than the Black Sea. In the 1970s, decreases in discharge from the Don and the Kuban Rivers caused an increase in salinity (Kuropatkin 1998), which later recovered and currently ranges from < 1‰ to 16‰ according to area. Temperature varies from –0.8°C to 1.2°C in winter and from 24°C to 30.0°C in summer (Kuropatkin 1998). Prior to the 1980s, the Black Sea and the Sea of Azov were rich in zooplankton and had the most productive fishery in the world (Ivanov and Beverton 1985; Rass 1992; Kovalev et al. 1998).

Results

Distribution and abundance of *M nemiopsis leidyi* in the Black Sea

Interannual variation

Mnemiopsis was first discovered in the northwest in November 1982 (Pereladov 1988). By summer/autumn 1988, it was found everywhere, at an average biomass of ca. 1 kg wet weight (WW) m^{-2} (40 g WW m^{-3}) and an average abundance of 310 ind. m^{-2} (12.4 ind. m^{-3}) (Vinogradov et al. 1989) (Fig. 2). In autumn 1989, the greatest mean biomass ever in the open sea, 4.6 kg WW m^{-2} (184 g m^{-3}), and greatest abundance, 7600 ind. m^{-2} (304 ind. m^{-3}), were measured (Vinogradov et al. 1989). In spring 1990, abundance was still very high, but by summer, it began to decrease (Vinogradov et al. 1992). This decreasing trend reversed in September 1994, with an average biomass of 2.7 kg WW m^{-2} (108 g WW m^{-3}) in the open sea, but much higher values in inshore waters (maxima 9.7 kg WW m^{-2}, 176 g WW m^{-3}; averages 4.5 kg WW m^{-2}, 180 g WW m^{-3}). A second peak in biomass was observed in spring and summer 1995 (Fig. 2), followed by a second decrease. In 1998, a third increase in offshore waters produced an average biomass of 876 g WW m^{-2} (35 g WW m^{-3}) and an average abundance of 463 ind. m^{-2} (18 ind. m^{-3}).

Vertical distribution

M. leidyi mainly lives above the thermocline (from 0 to 15–25 m) during the warm season. A few large specimens venture below the thermocline, but remain above the pycnocline (60–80 m). In winter, *M. leidyi* is found throughout the isothermal layer above the pycnocline, with most of the population above 50 m. In March 1998 the R.V. ‘‘Bilim’’ survey identified small specimens at depths of 105–150 m, where low oxygen concentrations were found (Mutlu 1999). Adults feed and reproduce above the thermocline (15–25 m) at night (Shiganova, unpublished data).

Seasonal dynamics and factors controlling population size

M. leidyi, as most ctenophores, is annual and does not survive Black Sea winters if water temperatures decrease below 4°C. Experiments showed that *M. leidyi* dies in Black Sea water if it spends 4–6 h at a temperature of 4°C, and faster when the temperature is lower (Shiganova, unpublished data). Body size is smaller in spring

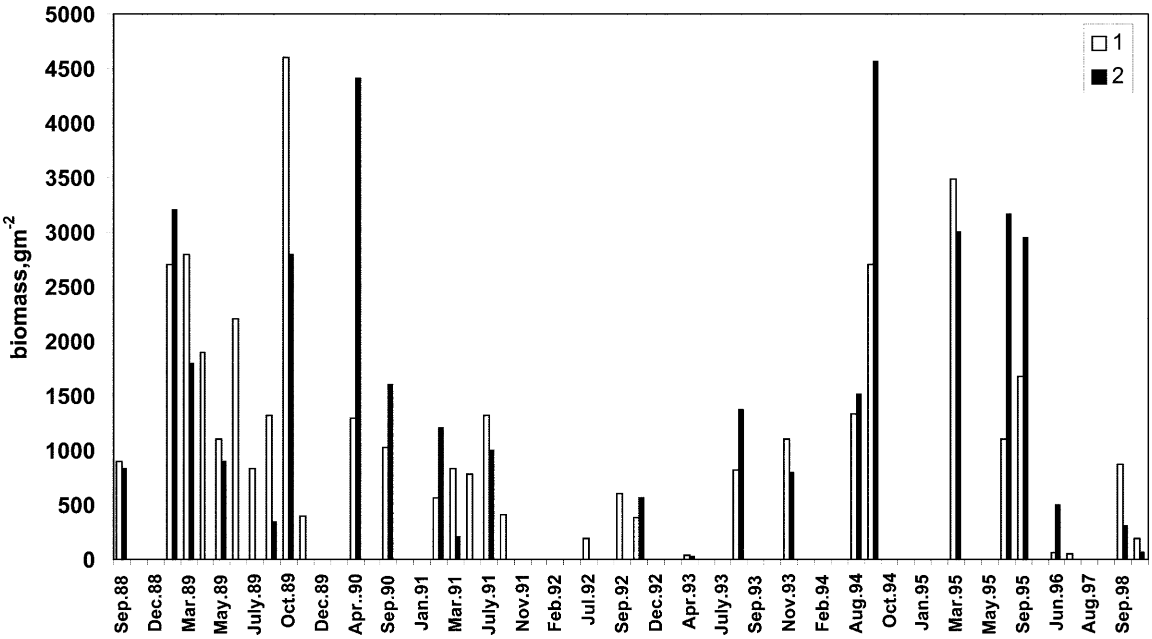

Fig. 2 *Mnemiopsis leidyi*. Long-term variations in biomass (g WW m^{-2}) in the offshore (*1*) and inshore (*2*) areas of the Black Sea (data before 1992: Vinogradov et al. 1989, 1992; Khoroshilov 1993)

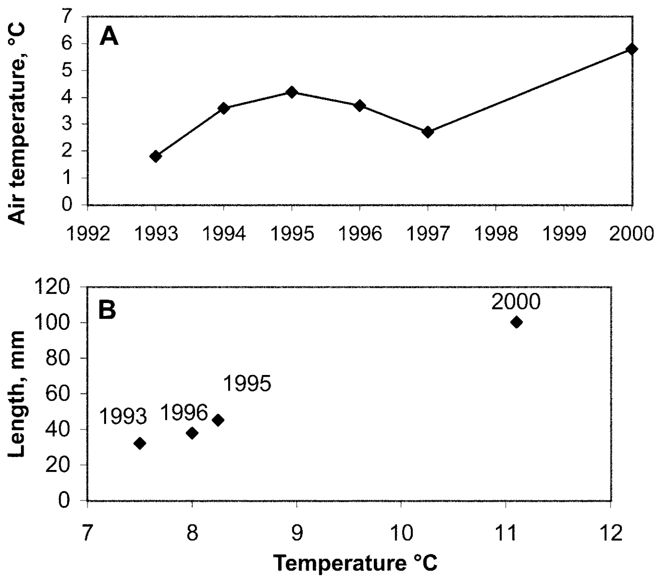

Fig. 3 *Mnemiopsis leidyi*. Average length relative to temperature. In March of 4 years in the Black Sea

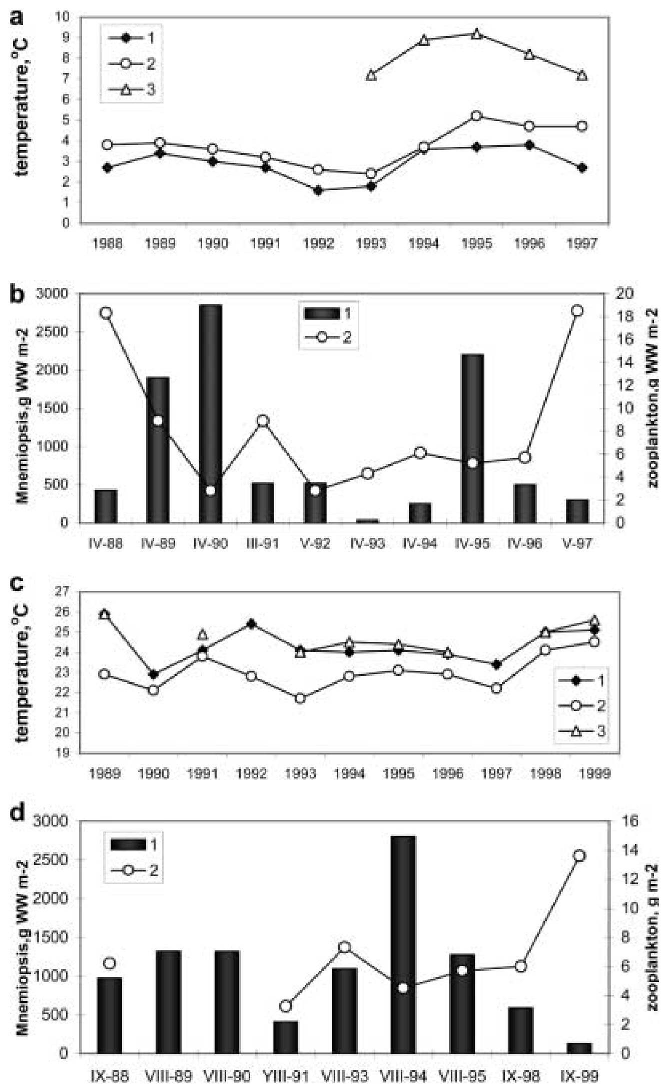

Fig. 4a–d Long-term variations in *Mnemiopsis leidyi* biomass (g WW m^{-2}) (*1*), zooplankton biomass (g WW m^{-2}) (*2*), and temperature (°C) in the Black Sea since 1988 (data before 1992: Vinogradov et al. 1989, 1992; Khoroshilov 1993). **a** Minimal winter air temperature; *2* mean winter air temperature; *3* spring surface water temperature. **b** Spring biomass of *M. leidyi* and zooplankton. **c** Mean air temperature in August; *2* mean air temperature in summer; *3* surface water temperature in August. **d** Biomass of *M. leidyi* and zooplankton in summer

after a cold winter (Fig. 3), and population size after cold winters is low (Fig. 4). The relative size of the spring population determines that later in the year: the high abundance of *M. leidyi* in March and August 1995 reflects a previous warm winter (Fig. 5). The spatial distribution of *M. leidyi* in spring also depends on the previous winter's temperatures. After a cold winter *M. leidyi* is practically absent from inshore waters, where a stronger cooling of the water column occurs. After a warm winter it is found in inshore waters, but is more abundant in the open sea (Fig. 5).

Between February and June, overwintering specimens increase size (weight) by somatic growth only. By June–July, they reach adulthood (Fig. 6). Episodic reproduction first begins where zooplankton is abundant and temperature higher than 21°C. Mean individual weight reaches a maximum in June–July (Fig. 6), such that biomass peaks in August–September. Density, however, peaks in September–November when reproduction is greatest and the population contains many larvae and small individuals (Fig. 7). Reproduction in the inshore waters becomes intense in mid-July to mid-August, and continues until October–November. It requires temperatures of 23.5–24°C, and peaks at 24.5–25.5°C. Food supply is also critical (Tzikhon-Lukanina et al. 1993), and the main areas of reproduction are inshore waters with abundant mesozooplankton in August–September, the time of the so-called "second peak" of zooplankton, composed of warm-water species and larvae of benthic organisms (meroplankton). However, reproducing ctenophores also spread to the open sea, where spawning continues (Fig. 7a).

During October–November, biomass decreases due to the presence of numerous young individuals (< 3 g WW) and to the death of large individuals after reproduction. In late October to early November, reproduction gradually comes to a standstill, at first in the inshore waters, where temperature drops quickest (Fig. 7b).

Effects on zooplankton

Feeding in *M. leidyi* is directly proportional to prey concentration over an extremely wide range of prey densities (Miller 1974; Reeve and Walter 1978; Kremer 1979), except at densities below 3 ind. m^{-2} (Tzikhon-Lukanina et al. 1992). Ctenophores often face a deficiency of food in the sea. In such areas with low zooplankton concentrations, most of them have an

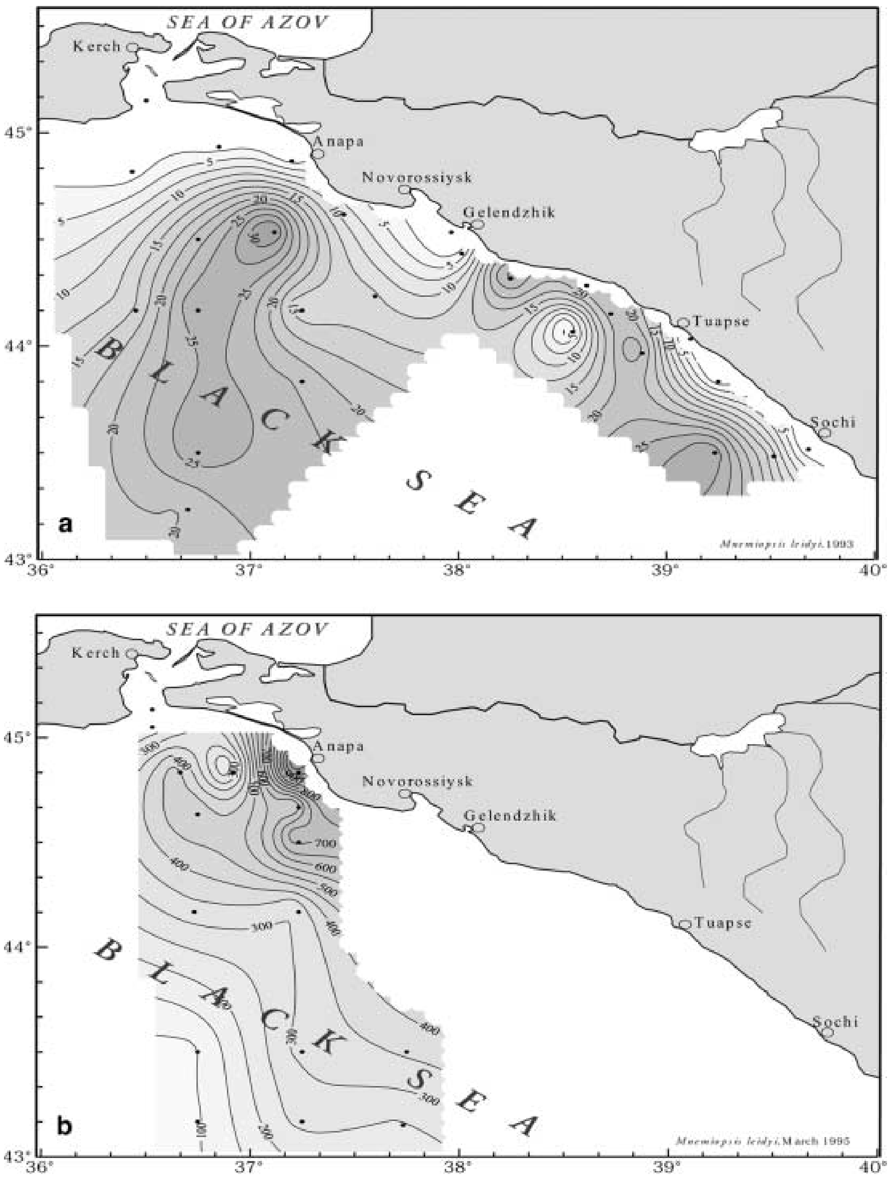

Fig. 5a, b *Mnemiopsis leidyi*. Abundance (ind. m^{-2}) **a** in spring after a cold winter (March 1993) and **b** after a warm winter (March 1995)

empty gastrovascular cavity (Tzikhon-Lukanina et al. 1991). In summer, *M. leidyi* feeds mainly on planktonic crustaceans. Small ctenophores prefer cladocerans, larger ones copepods together with fish eggs and larvae (Tzikhon-Lukanina and Reznichenko 1991; Tzikhon-Lukanina et al. 1991, 1992). Mean size of prey varies between 0.75 and 1 mm. Ctenophores in coastal waters have a more varied diet than those in the open sea (Sergeeva et al. 1990; Tzikhon-Lukanina and Reznichenko 1991); their diet includes more copepods and fish eggs, fish and invertebrate larvae. Among the latter, mussel veligers usually predominate.

The main food of *M. leidyi* is zooplankton, but fish eggs and larvae ("ichthyoplankton") directly follow this. In the Black Sea, plankton varies with season, area and time of day. Feeding intensity is maximal around midnight (Sergeeva et al. 1990).

At high food concentrations (*Acartia*) of 20–200 ind. l^{-1}, the food ration varied between 120% and 1500% of body weight per day (Finenko et al. 1995). But in natural conditions, the ration is more often close to 70%, which is below saturation. Digestion in adult ctenophores takes 2–3 h at a temperature of 20–23°C (Sergeeva et al. 1990; Tzikhon-Lukankina et al. 1992, 1993). Digestion time is longer with increasing food and at lower temperatures.

M. leidyi triggered an unprecedented decline in the density, biomass and species composition of the mesozooplankton (Fig. 4) of the Black Sea. In summer 1989, the copepods *Paracalanus parvus* Boeck and *Centropages ponticus* Karaw almost disappeared; *Oithona nana* Giesbrecht and the Pontellidae completely disappeared in the first years of the *M. leidyi* bloom (Kovalev 1993; Kovalev et al. 1998). The standing stock of *Oithona similis* Claus and *Acartia clausi* Giesbrecht, cladocerans, appendicularians, polychaetes and gastropod larvae, particularly in the upper water layers and in coastal areas, collapsed but did not become extinct. A planktonic zooplanktivore, the chaetognath *Sagitta setosa* Müller, also virtually disappeared, possibly by a combination of reduced prey availability and predation pressure by the ctenophore. By autumn 1989, zooplankton biomass in the open sea was 4.4 times lower than in 1988. In 1990, the abundance of one previously little affected copepod species, *Calanus euxinus* Hulsemann, also began to decrease (Vinogradov et al. 1992).

The fluctuations between ctenophores and zooplankton were antagonistic (Fig. 4). In years with high *M. leidyi* density, zooplankton biomass had strongly declined by autumn. When *M. leidyi* density was lower, zooplankton biomass remained higher (Fig. 4). During low ctenophore years, such as 1992–1993 and after 1996, zooplankton, and particularly *C. euxinus,* showed signs of a recovery. Copepod species diversity increased; some species, which had disappeared in 1990–1992, reappeared. The most striking comeback was that of *P. parvus*.

In late August 1999 after *Beroe ovata* first bloom, a recovery in zooplankton numbers and biomass was noted (Fig. 4). The biomass of mesozooplankton

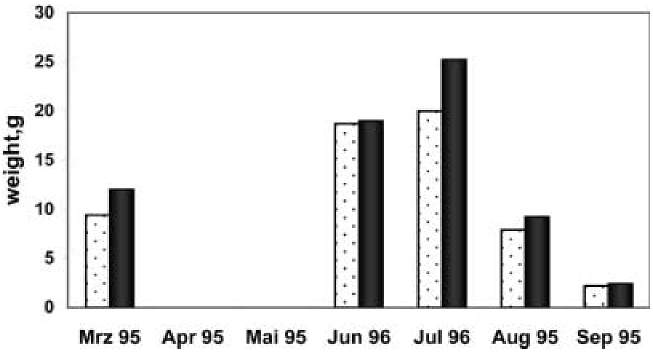

Fig. 6 *Mnemiopsis leidyi*. Seasonal change of average individual weight (g WW) in the inshore (*gray bars*) and offshore (*black bars*) areas (1995–1996) in the Black Sea

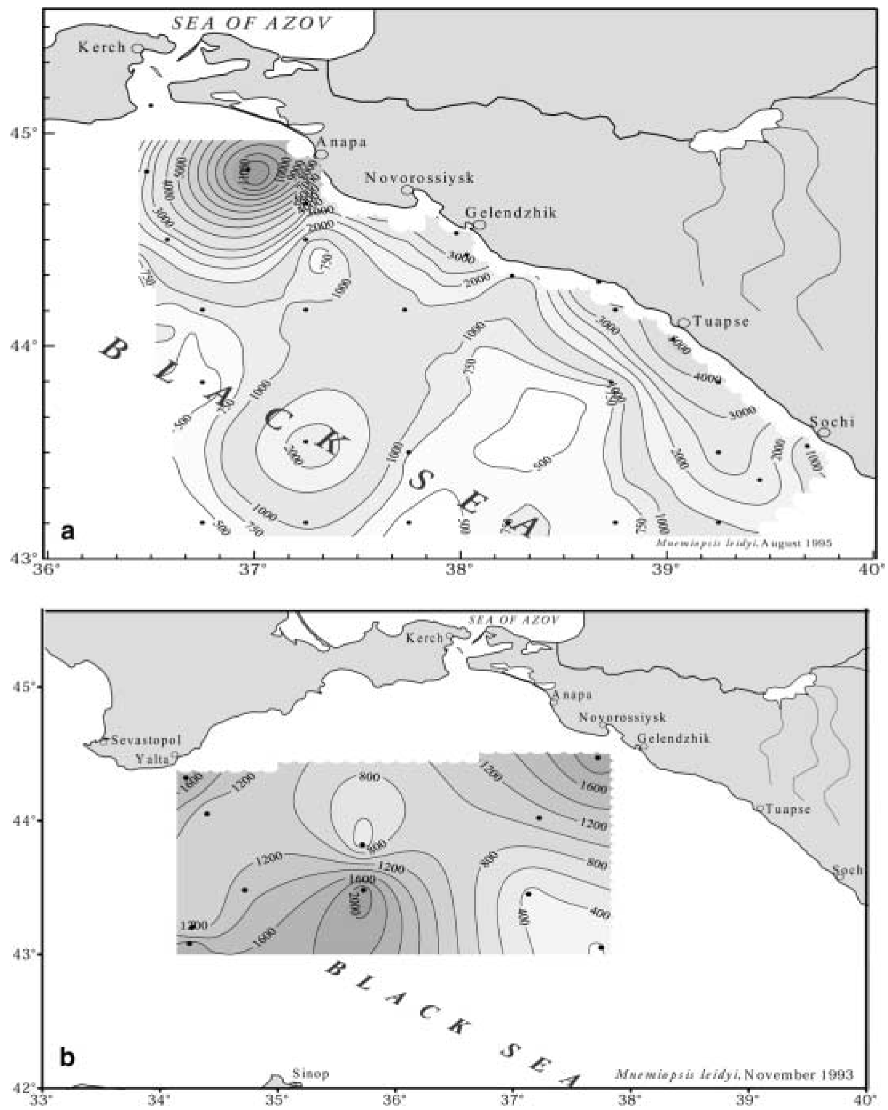

Fig. 7a, b *Mnemiopsis leidyi*. Abundance (ind. m^{-2}) **a** in summer (August 1995) and **b** in autumn (November 1993) in the Black Sea

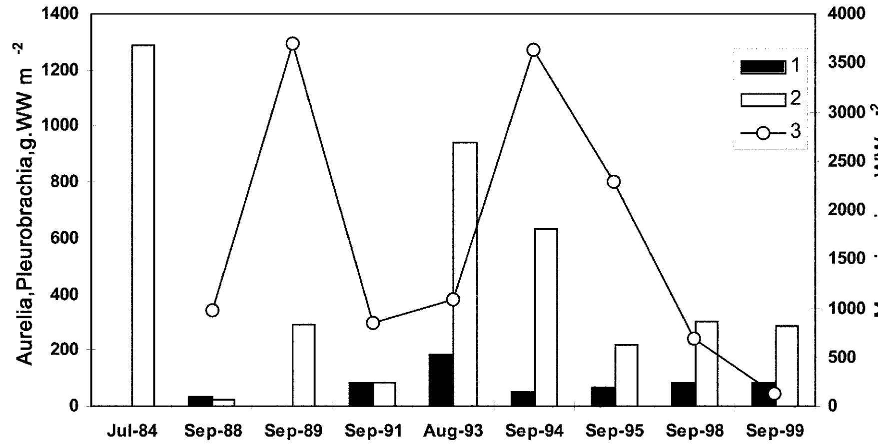

Fig. 8 Interannual variation of *Pleurobrachia pileus* (*1*), *Aurelia aurita* (*2*) and *Mnemiopsis leidyi* (*3*) biomasses (g WW m^{-2}) in the Black Sea (data before 1992: Vinogradov et al. 1989, 1992; Khoroshilov 1993)

increased to ca. 11 g WW m^{-2} in the open northeast and to 13 g WW m^{-2} in inshore areas, a much higher value than during the ten previous years. The biomass of *Calanus euxinus* and *Pseudocalanus elongatus* was almost invariant, but that of other copepods, primarily in the surface layer, increased threefold, reaching 1.4 g WW m^{-2}. Cladocerans increased to 150–300×10^3 ind. m^{-2}, with *Penillia avirostris* most abundant. *Pontella mediterranea* Claus and *Centropages ponticus* Karaw, which had not been seen since the early 1990s, returned. The meroplankton increased greatly too. All these changes were exactly paralleled by the appearance of a new ctenophore, *Beroe ovata*.

Competitors

M. leidyi competes with other gelatinous species, planktivorous fish and pelagic fish larvae. Three gelatinous zooplanktivorous organisms are indigenous to the Black Sea: the scyphozoans *Rhizostoma pulmo* (Macri, 1778) and *Aurelia aurita*, and the ctenophore *Pleurobrachia pileus* (O.F. Miller, 1776). *R. pulmo* mainly inhabits contaminated coastal areas. *P. pileus* inhabits the intermediate layer from 15–25 to 150 m, and its abundance is generally uncorrelated with that of *M. leidyi* (Fig. 8) (Shiganova et al. 1998). Only *A. aurita* overlaps spatially and temporally with *M. leidyi*. It occurs throughout the sea, but reaches its greatest abundance in inshore waters. It reached a peak in the early 1980s at an average biomass of 0.6–1.0 kg WW m^{-2} and total biomass of 3–5×10^8 tons (Lebedeva and Shushkina 1991). After the arrival of *M. leidyi*, it collapsed (Fig. 8). A significant negative correlation between *M. leidyi* and *A. aurita* ($n=14$, $r=-0.80$, $P=0.005$) was established (Shiganova et al. 1998).

There are three predominantly zooplanktivorous fish species in the Black Sea: the Black Sea anchovy (*Engraulis encrasicolus ponticus* Aleksandrov), the Mediterranean horse mackerel (*Trachurus mediterraneus ponticus* Aleev) and sprat (*Sprattus sprattus phalericus* Risso, 1827). They became the main commercial species in the 1980s, after the demise of the large pelagic piscivorous fish and dolphins (Caddy and Griffiths 1990). But their stocks and catches declined dramatically during the bloom of *M. leidyi* (Fig. 9). The most severe decline was in Black Sea anchovy and Mediterranean horse mackerel, which spawn during summer and suffered from decreased zooplankton abundance. Copepoda had been the main food of Black Sea anchovy, but in 1989 these sharply decreased. Copepods in the diet were replaced (~30%) by larvae of Cirripedia, Ostracoda and Bivalvia, all with a low caloric content. Consequently, growth rate, weight-at-age, fecundity and frequency of spawning of anchovy decreased (Shiganova and Bulgakova 2000), while the Mediterranean horse mackerel completely disappeared from Russian commercial catches.

There was also an adverse effect on moderate to cold water fish (e.g. sprat), in spite of their spawning in autumn and winter. These co-occurred with *M. leidyi* in the surface layer in winter and only occasionally in summer (Shiganova and Bulgakova 2000).

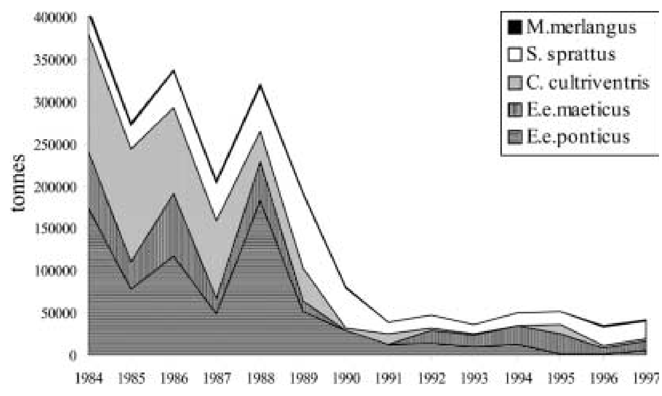

Fig. 9 Catches of zooplanktivorous species (Russia, Ukraine and Georgia) in the Black and Azov Seas (data FAO's Statistical Bulletin, nominal catches 1985–1994, and data AzNIIRKH): *Merlangus merlangus euxinus* (Black Sea), *Sprattus sprattus phalericus* (Black Sea), *Clupeonella culttriventris* (Sea of Azov), *Engraulis encrasicolus maeticus* (Sea of Azov) and *Engraulis encrasicolus ponticus* (Black Sea)

M. leidyi affected the food base of all fish larvae. The percentage of starving larvae increased to high values during the bloom of *M. leidyi*. Due to the absence of small copepod species, larvae had to switch to a diet of larger organisms, which were less suitable and caused heavy mortality (Tkach et al. 1998).

Effects on ichthyoplankton

According to Dekhnik (1973), 28 species and subspecies of Black Sea fish have pelagic eggs and larvae, and 28 others have only pelagic larvae. This fauna is diverse by ecology and origin. It includes summer-spawning, warm-water species of subtropical origin and winter-spawning, cold-water boreal species.

The spawning of warm-water species begins in late spring and lasts until July–August or August–September. The highest density of *M. leidyi* coincides with the reproduction of these populations of summer-spawning fish, among which are important commercial species such as anchovy and Mediterranean horse mackerel. The ctenophore is particularly destructive to these. Tzikhon-Lukanina et al. (1993) estimated the consumption of fish larvae by one *M. leidyi* in the coastal Black Sea at 5 specimens day^{-1} or 74% of all ichthyoplankton at peak periods. In periods between bursts, this level of consumption dropped to 7% daily (Tzikhon-Lukanina et al. 1993). These levels may be overestimates. Our observations in situ in coastal areas showed that 1% of *M. leidyi* population had fish larvae in gut content and 2–10% of population had eggs. Larvae are very active and *M. leidyi* consumes them only with difficulty. However, *M. leidyi* can have a disastrous effect if it encounters an aggregation of eggs. One ctenophore in our samples had eight eggs of Mediterranean horse mackerel in its gut (Shiganova, unpublished data). As a result, in 1989 the density of eggs and larvae of summer-spawning fish greatly decreased, with a particularly great decline in ichthyoplankton species like anchovy (*Engraulis encrasicolus ponticus*) and Mediterranean horse mackerel (*Trachurus mediterraneus*). Since 1992, the numbers of anchovy eggs and larvae gradually began to rise as *M. leidyi* declined, but their total density remained low in the northern area, and only significantly increased in the southern and particularly in the southwestern area (Niermann et al. 1994; Shiganova et al. 1998). In 1999, after the appearance *Beroe ovata*, the numbers of eggs increased greatly, and above all other species those of anchovy, Mediterranean horse mackerel and *Diplodus annularis* (Shiganova et al. 2000).

Predators

For a decade or so after its outbreak in the Black Sea, *M. leidyi* encountered no predator limitation here. The only potential fish predators were mackerel (*Scomber scombrus* Linnaeus, 1758 and *S. japonicus* Houttuyn, 1782) and Black Sea whiting, *Merlangus merlangus euxinus* (Linnaeus, 1758). These eat gelatinous species elsewhere (GESAMP 1997). However, their numbers had been decimated before 1980 by over-fishing (Caddy and Griffiths 1990; Rass 1992).

There also were no gelatinous predators of *M. leidyi* in the Black Sea, until the ctenophore *Beroe ovata* spontaneously appeared. In 1997 and 1998, *B. ovata* was first seen in some coastal areas in autumn (Konsulov and Kamburska 1998). In August 1999, a first bloom was recorded, with average numbers and biomass 1.1 ind. m^{-2} and 31 g WW m^{-2}, respectively. The abundance of *M. leidyi* immediately dropped (17.3 ind. m^{-2} and 155 g WW m^{-2}), and, in April 2000, *M. leidyi* was found only in some of the warmest locations, at a density of 1.2 ind. m^{-2}. and biomass of 28 g WW m^{-2}.

Distribution and abundance of *M. leidyi* in the Sea of Azov

M. leidyi made its first appearance in the Sea of Azov in August 1988 (Studenikina et al. 1991); a first peak followed in September 1989 (Fig. 10), with a biomass of 936 g m^{-2} (103 g m^{-3}). From that point onwards it bloomed there every summer–early autumn, with peaks in July–August (higher as a rule in August) in the case of early arrival and in August–October in the case of late arrival (Fig. 11). In August 1991, biomass reached 812 g m^{-2} (91.2 g m^{-3}), to decrease in 1992–1994 to a low in August 1992 of 362 g m^{-2}, or 53.9 g m^{-3}. In 1995, a new rise began from 610 g m^{-2} (74.5 g m^{-3}) in August 1995 to the greatest biomass ever of 1075 g m^{-2} (131.5 g m^{-2}) in August 1999 (Fig. 10).

M. leidyi only occurs during the warm seasons, and reinvades every year through the Kerch Strait. The time and dynamics of its penetration correlate with wind-driven currents. Under southwestern and southern winds in April, it arrives in spring (April–May); failing these, it does not appear until June–July (Fig. 11). As a

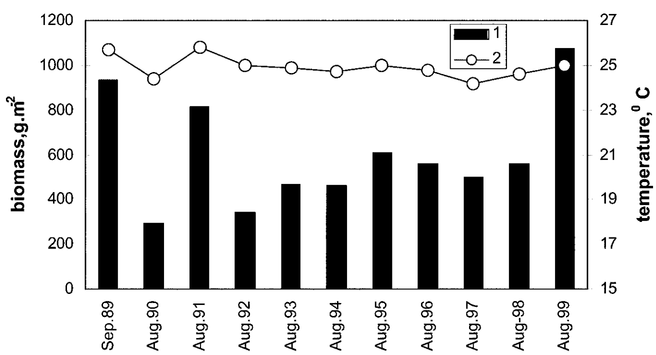

Fig. 10 *Mnemiopsis leidyi*. Interannual variations in biomass (g WW m^{-2}) in the Sea of Azov (*1*) and mean surface water temperature (°C) (*2*)

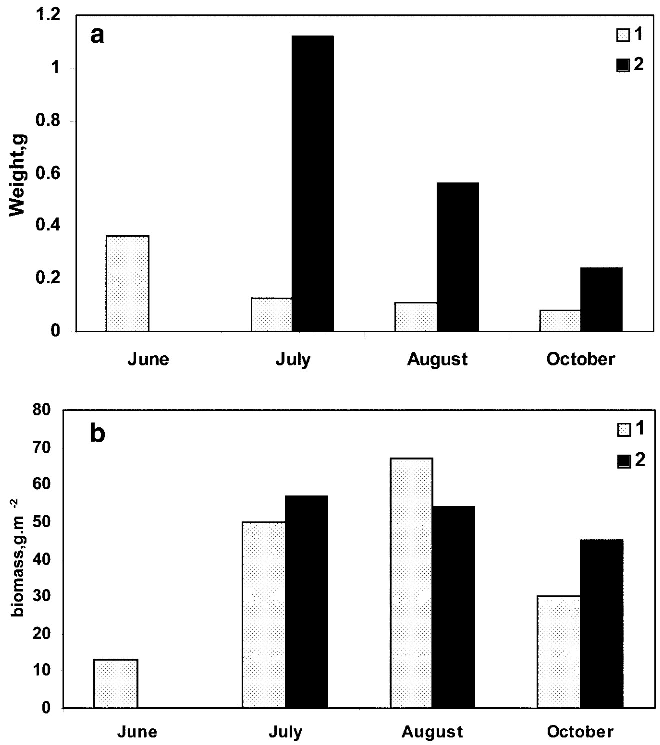

Fig. 11a, b *Mnemiopsis leidyi.* Seasonal changes in **a** individual weight and **b** biomass (g·m^{-2} WW) in the Sea of Azov in the case of early arrival (1996) (*1*) and later arrival (1993) (*2*)

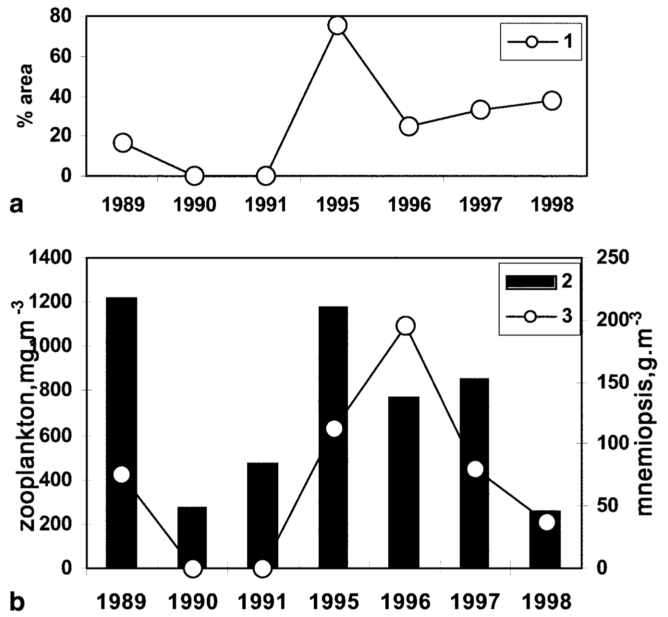

Fig. 12a, b Interannual variations of **a** *Mnemiopsis leidyi* area of distribution (%) (*1*) and **b** zooplankton (mg WW m^{-2}) (*2*) *M. leidyi* biomass (g WW m^{-3}) (*3*), in the Sea of Azov in June

result, a population may form as early as May. In May and June, winds determine the pattern of its distribution and the size of its distribution area (Fig. 12). It first occurs in the south, adjacent to Kerch Strait. Then it spreads to the south and southeast. In June it reaches the central and southwestern areas (Fig. 13). A predominance of eastern winds inhibits its spread. In 1998, for example, its area of distribution was three times smaller than normal. Alternatively, northern and northeastern winds prevent its distribution to the eastern and central areas. But in August or September *M. leidyi* is usually found everywhere, including in Taganrog Bay (Fig. 13), where salinity is as low as 3‰ (Studenikina et al. 1991; Volovik et al. 1993). The abundance of *M. leidyi* in the Sea of Azov depends on the timing of the annual re-invasion, on the number of invading specimens, on the size of the area that becomes occupied, on available zooplankton biomass and water temperature (Figs. 10, 11, 12, 13, 14). High biomasses of *M. leidyi* occurred in August/September 1989, 1991, 1995, 1999, years of early re-introduction as well as high mean water temperatures in July (26°C) and August (25–26.2°C) (Figs. 10, 11).

When *M. leidyi* appears in the Sea of Azov, its size and individual weight are typical of those of the spring Black Sea population (e.g. length 30–50 mm). Juveniles and larvae are usually absent. In the case of late arrival, their sizes and individual weights are larger, as in the Black Sea at that time (Figs. 6, 11a).

Initiation of reproduction depends on time of arrival, and on available food (Fig. 12) (Volovik et al. 1993). Reproduction occurs usually in June, in the case of early arrival, or between July and October, peaking in August–October. It is not restricted to certain temperatures, although it is greatest at high temperatures. *M. leidyi* remains relatively small (1.5–2.5 cm) in the Sea of Azov (Fig. 11a). The invading specimens are larger (about 5.0 cm), and die after reproduction. By September, they are very rare. In November, when temperature drops to 4°C, the entire population dies.

Effects on zooplankton and ichthyoplankton

In late spring, zooplankton is very abundant in the Sea of Azov. This is the period when *Acartia clausi*, *Centropages ponticus, Paracalanus parvus, Oithona similis* and *Lebidocera bruences* reproduce, and the community abounds with naupliar and copepodid stages. After each invasion of *M. leidyi*, zooplankton was decimated: from 79×10 m^{-3} to 0.43×10 m^{-3}. In the most productive areas, where zooplankton biomass attained 200 mg WW m^{-3} in July, it was reduced to 10% of its initial standing stock, and in August it dropped to zero (Fig. 14). If *M. leidyi* invaded here in spring, it consumed a high percent of eggs and larvae of Azov anchovy, *Engraulis encrasicolus maeticus* Pusanov, and Azov kilka, *Clupeonella cultriventris* (Nordmann, 1840). In such cases, their spawning stocks were very poor. In case of a late arrival in June or July, larvae have time to grow and spawning stocks were higher.

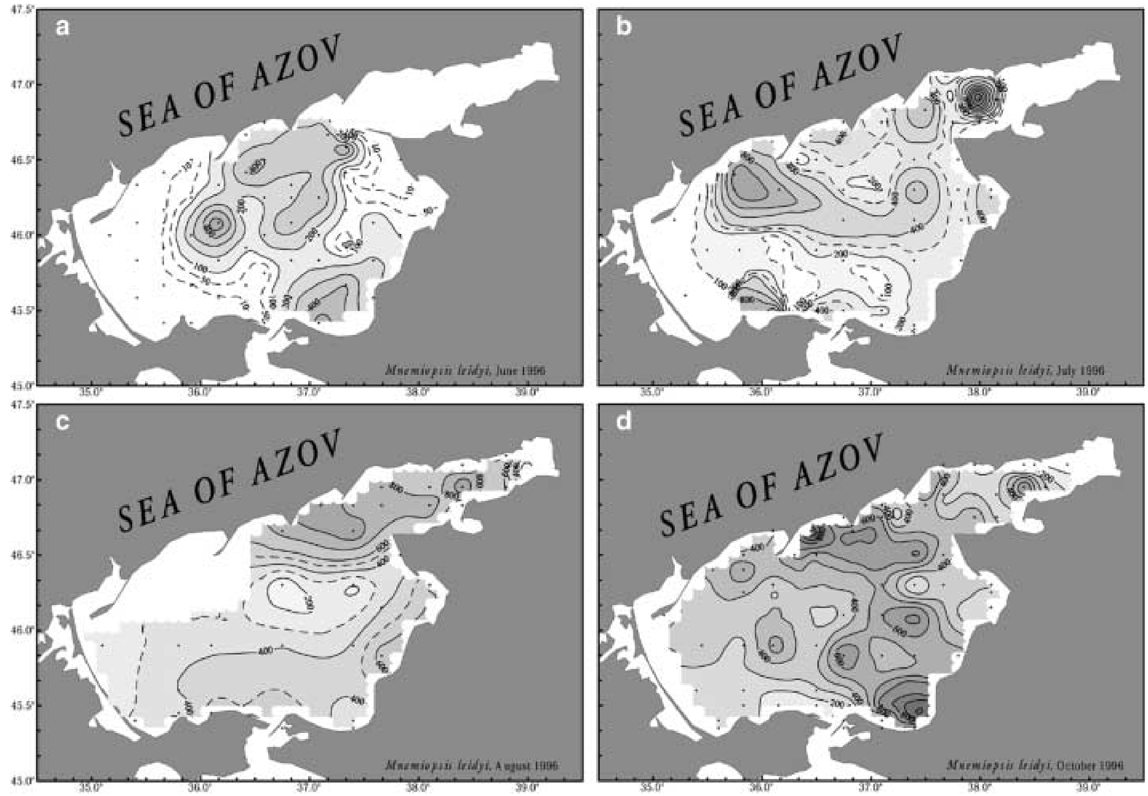

Fig. 13a–d *Mnemiopsis leidyi*. **a** Spatial distribution (g m^{-2}) in the Sea of Azov in **a** June 1996, **b** July 1996, **c** August 1996, **d** October 1996

Competitors

The gelatinous *Aurelia aurita* and *Rhisostoma pulmo* first penetrated the Sea of Azov at the end of the 1960s when a decrease in Don and Kuban River discharge caused a salinity upsurge (Zakhutsky et al. 1983). However, *M. leidyi*, soon reduced both species to rarities.

The stocks of planktivorous Azov anchovy, *E. encrasicolus maeticus*, and Azov kilka, *C. cultriventris*, had been in decline since the 1970s. After the appearance of *M. leidyi,* they collapsed (Fig. 9). Interannual variation depends on the time of arrival of *M. leidyi*. If it arrives early in spring, fish have insufficient food to spawn, and their larvae starve because *M. leidyi* consumes all mesozooplankton during early summer (Fig. 14). If *M. leidyi* does not arrive until June or July, spawning stocks do better (Volovik et al. 1996; Volovik and Chikharev 1998). During the last decades, the diet of the Azov anchovy switched from copepods and polychaetes to low-calorie meroplankton. Consequently, its average length, weight and fat content decreased, while winter mortality increased (Shiganova and Bulgakova 2000).

Predators

There is no native predator of *M. leidyi* in the Sea of Azov. In 1999, a few specimens of *Beroe ovata* arrived for the first time, but these were too few to have an effect on *M. leidyi* density. *M. leidyi* density and biomass were the highest ever (Fig. 10).

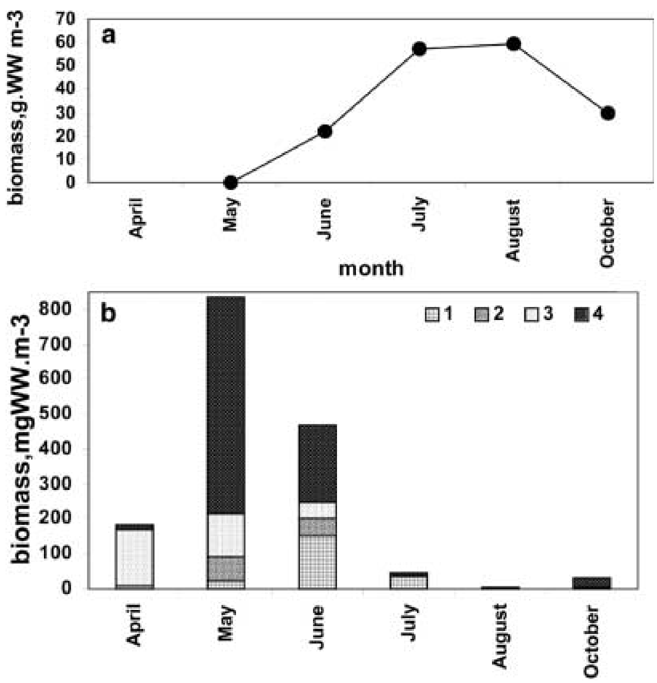

Fig. 14 **a** Seasonal changes *Mnemiopsis leidyi* biomass (g m^{-3}) and **b** seasonal changes of zooplankton (mg WW m^{-3}) biomass (1990–1996) in the Sea of Azov (*1* Copepoda; *2* Cladocera; *3* Rotatoria; *4* meroplankton)

Distribution in the Sea of Marmara

Probably, *M. leidyi* penetrated the Sea of Marmara with the upper Bosporus current in 1989–1990. It now occurs year-round in the upper water layer. Intense reproduction was recorded in early October 1992, when mean biomass was 4.2 kg m^{-2} (152 g WW m^{-3}) and density was 27 ind. m^{-3} (Shiganova 1993). In July 1993, its density was about 40 times lower than in the previous year (Kideys and Niermann 1994). Its size (with lobes) was approximately the same as in the Black Sea. The largest specimen had a length of 105 mm.

Effects on zooplankton and ichthyoplankton

Data are scarce, but during a survey in 1992 zooplankton density was drastically lower than in 1977 (Cebeci and Tarkan 1990), from 257 to 33 ind. m^{-3} in the north, and from 360 to 35 ind. m^{-3} in the south. The density and species composition of fish eggs and larvae were also low (Shiganova 1993; Shiganova et al. 1995).

Competitors

Several Black Sea gelatinous species also inhabit the Sea of Marmara: *Rhizostoma pulmo, Aurelia aurita* and *Pleurobrachia pileus*; but *A. aurita* was not found here in 1992, reflecting the great density of *M. leidyi.*

Near the Dardanelles, a Mediterranean gelatinous species (*Bolina* sp. = *Bolinopsis* sp.?) was found in 1992.

Predators

The Mediterranean ctenophore *Beroe ovata* (size 2.5–4.8 cm) was collected at six stations near the Dardanelles, and in the central part of the sea, but it was not abundant (Shiganova et al. 1995).

Distribution in the Aegean Sea and in the eastern Mediterranean

M. leidyi was first recorded during late spring–summer 1990 in Saronikos Gulf (45–75 ind. m^{-2}), as well as in the neighboring, eutrophic Elefsis Bay (Fig. 15). In the littoral of the gulf, *M. leidyi* abundance decreased (1.5 ind. m^{-2}) until 1996, when it was mainly found in spring. A large swarm (up to 10 ind. m^{-3} or 150 ind. m^{-2}) was observed in January 1998, but after 1996 it became rare in this area.

M. leidyi was rather abundant (3 ind. m^{-2} or 0.3 ind. m^{-3}) in May 1995 in Kalloni Bay (Lesvos Island), but it was less abundant there in September 1995 and May 1996. In June 1998 its abundance varied between 1.5 and 2.5 ind. m^{-2} (or 0.3 and 0.5 ind. m^{-3}) in the northeastern Aegean, and in September 1998 its greatest abundance

Fig. 15 *Mnemiopsis leidyi*. Sightings in the Aegean Sea

was close to the Dardanelles Strait: 2.5 ind. m^{-2} and 45.5 g WW m^{-2} (0.5 ind. m^{-3} and 9.09 g WW m^{-3}). Swarms were observed during summer in several coastal areas of the Aegean Sea (Skyros, Limnos and Alonissos Islands, Halkidiki Peninsula) between 1991 and 1996. No specimens (adults or juveniles) were collected in the northern Aegean Sea, even at the mouth of the Dardanelles, during cruises in March 1997, 1998 and 2000 or in September 1997 and 1999. Furthermore, *M. leidyi* populations were rare along the Limnos coasts in summer 1997, 1998 and 1999. The size of individuals collected in the Aegean Sea and in the Saronikos Gulf was 2.5–6.5 cm. These *M. leidyi* may have been carried to the northern Aegean Sea by the Black Sea currents. Here, they may spread independently of the Black Sea current.

Further east, *M. leidyi* appeared in Mersin Bay in spring 1992 (Uysal and Mutlu 1993; Kideys and Niermann 1994), and in Syrian coastal waters in October 1993 (Shiganova 1997). The specimens may represent invasions with ballast water of Black Sea origin, as supported by the fact that they were found near Mersin and Latakia ports.

Effects on zooplankton

Mesozooplankton in Saronikos Gulf did not decrease after the appearance of *M. leidyi* in the area. Only in

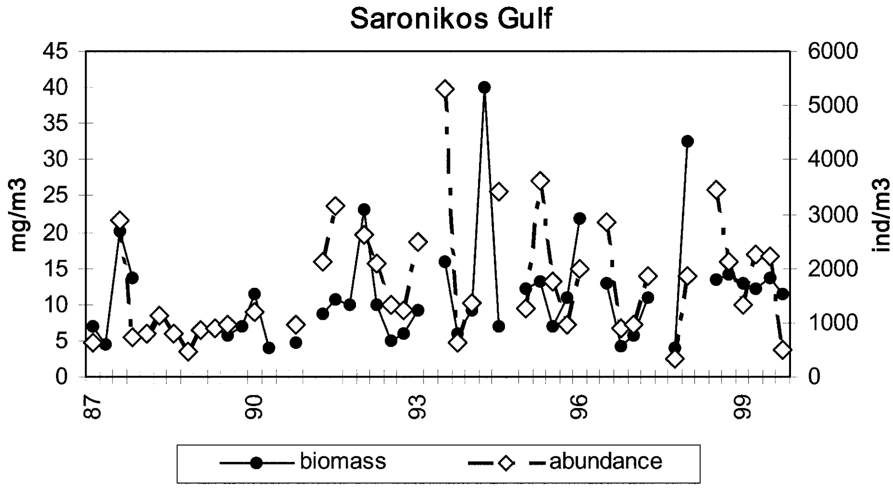

Fig. 16 Interannual variability (1987–1999) of mesozooplankton biomass and abundance in Saronikos Gulf

1990, when *M. leidyi* was most abundant, were zooplankton biomass and abundance somewhat lower (Fig. 16). There is no time series of data for the northern Aegean Sea, but we could compare data obtained in 1988 (before the *M. leidyi* invasion) and in 1997 and 1998 (when *M. leidyi* was present) for the 0–50 m layer. Total mesozooplankton was 765 ind. m^{-3} in September 1988 versus 2534 ind. m^{-3} in September 1997.

Competitors

In the Aegean Sea *Aurelia aurita* occurs (Papathanassiou et al. 1986), but the abundance of *A. aurita* is much lower when *M. leidyi* is present. Furthermore, *A. aurita* was absent in Elefsis Bay in the summer of 1990, when *M. leidyi* was abundant there; it reappeared the following year. There was no noticeable effect of *M. leidyi* on the zooplanktivorous fish in the Aegean Sea.

Predators

At least two species of *Beroe* occur in the Mediterranean Sea (Tregouboff and Rose 1957). During our survey several ctenophores (3.0–4.6 cm) were found in the Syrian coastal area. Specimens of the genus *Beroe* were also found in the northern Aegean Sea in March 2000. The presence of *Beroe* may be among the reasons for the persistent low density of *M. leidyi* in the eastern Mediterranean Sea.

Discussion

In light of the current, enormously expanded maritime traffic, the arrival of *Mnemiopsis leidyi* in the Black Sea was probably unavoidable. In fact, the structure of the Black Sea zooplankton had begun to change as early as the late 1960s. These changes were greatest in the northern region, which was severely affected by eutrophication and predation by a first jelly fish, *Aurelia aurita* (Lebedeva and Shushkina 1991; Petranu 1997; Shiganova et al. 1998).

The introduction of *M. leidyi* to the Black Sea allowed it to secondarily expand its range to the adjacent seas of Azov, Marmara, the Aegean and perhaps the eastern Mediterranean (Fig. 1). However, nowhere were conditions as optimal and perennial as in the Black Sea and the surface waters of the Sea of Marmara. It has to re-invade the Sea of Azov each year. Low numbers take advantage of the Black Sea current to reach the northern Aegean Sea, where they disperse according to the dominant circulation patterns (Stergiou et al. 1998; Theocharis et al. 1999). But its presence in Saronikos Gulf and Elefsis Bay could be also due to ballast water release as elsewhere in the eastern Mediterranean Sea (Fig. 1). The fact that, unlike in the northern Aegean Sea, it has also been found in winter, might suggest that the population of Saronikos Gulf is distinct from that in the northern Aegean. In the latter area no specimens have been observed from October to April.

In the Black Sea *M. leidyi* mainly lives above the thermocline (0 to 20–25 m). In the Sea of Marmara it inhabits only the upper layer, composed of Black Sea water. In the Aegean Sea too it was found in the upper layer only.

These observations suggest that the Black Sea environment suits *M. leidyi* best, while conditions seem worst in the eastern Mediterranean with its combination of high salinity (about 39‰), high summer temperature (24–29°C), and significant predation levels.

How does all this compare with conditions in its native range?

The native habitats of *M. leidyi* are temperate to subtropical estuaries along the Atlantic coasts of North and South America. Its population dynamics here shows differences in seasonal patterns according to area. Narragansett Bay is near the northern end of its range. This temperate estuary has an annual temperature range of 1–25°C, with temperatures >20°C from June to September. Salinity ranges from 21‰ to 32‰. Abundance is low during winter and spring, and increases by several orders of magnitude during summer, peaking in late summer or early autumn (August–September), with high biomass lasting about 2 months (Kremer and Nixon 1976; Deason and Smayda 1982). High ctenophore biomass correlates strongly with that of crustacean zooplankton in early summer (Deason and Smayda 1982).

Chesapeake Bay (Maryland) is a large and complex estuarine system. Temperatures typically range from 2°C to 26°C annually, and are >20°C from June to October. Salinity ranges from 5‰ to 16‰. *M. leidyi* biomass peaks during July and August, with a sharp drop in autumn. Reproduction begins in spring, and is most intense in July and August. In summer, the peaks of copepod and ctenophore biomass coincide (Miller 1974; Olson 1987; Purcell et al. 1994).

Biscayne Bay, Florida, is a shallow subtropical estuary with a temperature range of 18–32°C, and salinities ranging from mesohaline (<20‰) to hypersaline (>40‰), depending on season and location. Here, *M. leidyi* is scarce in summer and peaks in late autumn or early winter (October–November). Its abundance correlates with times and areas of high prey availability (Baker 1973; Reeve 1975; Kremer 1994).

Coastal areas along the Gulf of Mexico with shallow subtropical waters, with temperatures ranging from 10°C to 30°C and salinity from 20‰ to 33‰, have *M. leidyi* present for much of the year, and abundant at variable times, with several biomass spikes but without clear seasonal variations. Mesozooplankton also peaks several times a year (Kremer 1994).

A consensus therefore emerges that temperature, salinity, food availability and predators combine to determine seasonal abundance of *M. leidyi* (Raymond 1988; Kremer 1994), whatever the location. In temperate mesohaline estuaries, high abundance falls in summer, with a peak between August and September (Narragansett Bay, the Black Sea). In estuaries with lower salinity, the peak occurs from July to August, with a sharp decrease in autumn (Chesapeake Bay, the Sea of Azov in the case of early arrival). In subtropical hypersaline areas *M. leidyi* dynamics are similar to those in the Mediterranean Sea, depending on season and location (Biscayne Bay, the Gulf of Mexico). In the Mediterranean, *M. leidyi* abundance is lower in summer and higher in winter, autumn or spring, depending on location.

In the Black Sea, *M. leidyi* reached extremely high mean densities (7600 ind. m^{-2}), biomass (4.6 kg m^{-2}) and became larger (8–15 cm, maximum 18 cm) than in its native range (Vinogradov et al. 1992; Shiganova 1997). In the Sea of Marmara the average size of *M. leidyi* was as in the Black Sea, but the largest individual found was only 10.5 cm. Mature individuals in the Sea of Azov (0.5–2.5 cm and maximum 3 cm) and in the Aegean Sea were much smaller than in the Black Sea (2.5–6.5 cm average size).

The peak of *M. leidyi* abundance in autumn 1989 in the Black and Azov Seas not only coincided with high summer temperatures, but also with zooplankton abundance (Figs. 4, 12) (Vinogradov et al. 1992; Shiganova 1997). The peak of abundance in other seas was later. There are no exact data for the Sea of Marmara, but most likely *M. leidyi* appeared there between 1989 and 1990; a bloom was recorded in October 1992. The highest density in the Aegean Sea, in 1990, was from late July or August until October or early November, with a maximum in August–September. Together these data not only indicated to favorable temperatures, but also periods with high zooplankton and meroplankton biomass.

In the Sea of Azov reproduction occurs from June, in the case of early arrival, or July to October, peaking between July and September in the case of early arrival, and between August and October in the case of late arrival. However, initiation of reproduction depends on time of penetration to the Sea of Azov, prey availability (Figs. 12, 14) and temperature (Fig. 10).

Timing of reproduction in the Sea of Marmara is probably as in the Black Sea. In the Aegean Sea *M. leidyi* specimens are found mainly in inshore waters, bays and gulfs. Reproduction here is yet to be confirmed, since no larval stages have been collected.

The strong effect of *M. leidyi* on the Black and Azov Seas also reflects an absence of predators. Black Sea mesozooplankton was decimated by *M. leidyi*. Planktivorous fish suffered from competition and consumption of their pelagic eggs and larvae due to the great numbers of *M. leidyi*, unchecked by predators of their own. After the appearance of *Beroe ovata,* the situation took a new, spectacular turn: *M. leidyi* numbers plummeted, and the ecosystem began to recover.

The situation was most extreme in the Azov Sea. During the first months of summer *M. leidyi* consumed almost all of the zooplankton. The stocks of planktivorous fish dropped and recovered little, due to a persistent summer abundance of *M. leidyi* (Figs. 9, 12, 14). Up until 2000, no effect of *Beroe* has been recorded here.

In the Sea of Marmara zooplankton biomass was lower than before *M. leidyi* appeared; ichthyoplankton density and species composition both declined in 1992, but not as catastrophically as further north.

There were no measurable changes in the pelagic ecosystem of the Aegean Sea under the influence of *M. leidyi*. Only in 1990 was there a drop of zooplankton biomass and abundance in Saronikos Gulf, but it remains to be seen whether this was really due to *Mnemiopsis* (Fig. 16), which never really managed to reach bloom levels here.

In conclusion, the Black Sea is a main habitat of *M. leidyi*, and from the Black Sea *M. leidyi* has continuously spread to other seas of the Mediterranean basin, the current abundance in the Black Sea determining the abundance in the other seas.

M. leidyi was such a success in the Black Sea because: (1) it was not preyed upon, (2) it successfully competed with *Aurelia aurita* and (3) it undercut zooplanktoneating fish by using their eggs and larvae as food, which *M. leidyi* transferred into jelly biomass at a rate that fish could not match. When finally, after a decade, a jelly predator, *B. ovata*, appeared (in 1997), this rapidly began to control the density of *M. leidyi*.

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References

Arkhipkin VS, Dobrolubov SA (1999) Steric variation of the Mediterranean and Black Sea level. In: Balopoulos ET, Iona A (eds) Oceanography of the eastern Mediterranean and Black Sea. Sakellariou, Athens, pp 5–6

Baker LD (1973) The ecology of the ctenophore *Mnemiopsis mccradyi* Mayer in Biscayne Bay, Florida. Technical report, Resenstied School of Marine and Atmospheric Science, University of Miami, Miami

Caddy JF (1993) Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. Rev Fish Sci 1:57–95

Caddy JF, Griffiths RC (1990) A perspective on recent fishery-related events in the Black Sea. Stud Rev Gen Fish Counc Mediterr 63:43–71

Cebeci M, Tarkan N (1990) A perspective on recent fishery related events in the Black Sea. Stud Rev Gen Fish Counc Mediterr 63:43–71

Coonfield BR (1936) Regeneration in *Mnemiopsis leidyi* Agassiz. Biol Bull (Woods Hole) 71:421–428

Deason EE, Smayda TJ (1982) Ctenophore–zooplankton interactions in Narragasett Bay, Rhode Island, USA, during 1972–1977. J Plankton Res 4:203–217

Dekhnik DV (1973) Ichthyoplankton of the Black Sea. Naukova Dumka, Kiev

Finenko GA, Abolmasova GI, Romanova ZA (1995) Intensity of the nutrition, respiration and growth of *Mnemiopsis mccradyi* in relation to grazing conditions (in Russian). Biol Morya (Kiev) 21:315–320

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection) (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. Rep Stud GESAMP 58:1–84

Harbison GR, Volovik SP (1994) The ctenophore *Mnemiopsis leidyi* in the Black Sea. In: Proceedings of the conference on nonindigenous estuarine and marine organisms (NEMO). Maryland University, pp 25–26

Ivanov LR, Beverton JH (1985) The fisheries resources of the Mediterranean, part 2. Black Sea. GFCM, FAO, Rome

Khoroshilov VS (1993) Seasonal dynamics of the Black Sea population of ctenophore *Mnemiopsis leidyi*. Oceanology 33:558–562

Kideys AE, Niermann U (1994) Occurrence of *Mnemiopsis* along the Turkish coast. ICES J Mar Sci 51:423–427

Konsulov AS, Kamburska LT (1998) Ecological determination of the new ctenophore – *Beroe ovata* invasion in the Black Sea. Oceanology. Proc Inst Oceanol Varna 2:195–198

Kovalev AV (1993) Mesozooplankton. In: Kovalev AV, Finenko ZZ (eds) Plankton. Naukova Dumka, Kiev, pp 144–165

Kovalev AV, Besiktepe S, Zagorodnyaya J, Kideys A (1998) Mediterraneanization of the Black Sea zooplankton is continuing. In: Ivanov L, Oguz T (eds) Ecosystem modeling as a management tool for the Black Sea, vol 47. Kluwer, Dordrecht, pp 199–207

Kremer P (1976) Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley ML (ed) Estuarine processes, vol 1. Academic, New York, pp 197–215

Kremer P (1979) Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. Estuaries 2:97–105

Kremer P (1994) Patterns of abundance for *Mnemiopsis* in US coastal waters: a comparative overview. ICES J Mar Sci 51:347–354

Kremer P, Nixon S (1976) Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley M (ed) Estuarine processes, vol I. Academic, New York, pp 197–215

Kuropatkin AP (1998) Changes in salinity and in the vertical stability of the Azov Sea water in the present day conditions. In: Makarov EV (ed) The main problems of fisheries in the Azov Sea basin. AzNIIRHK, Rostov-on-Don, pp 30–33

Lebedeva LP, Shushkina EA (1991) The estimation of population characteristics of *Aurelia aurita* in the Black Sea. Oceanology 31:434–441

Miller RJ (1974) Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). Chesapeake Sci 15:1–8

Mutlu E (1999) Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. Mar Biol 135:603–614

Niermann U, Bingel F, Gerban A, Gordina AD, Gugu AC, Kideys AE, Konsulov A, Radu G, Subozin AA, Zaika VE (1994) Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv) in the Black Sea in 1991–1992. ICES J Mar Sci 51:395–406

Olson MM (1987) Zooplankton. In: Heck KL (ed) Ecological studies in the middle reach of Chesapeake Bay. Springer, Berlin Heidelberg New York, pp 38–81

Ovchinnikov IM, Titov VB (1990) Anticyclonic eddies of currents in the coastal area of the Black Sea. DAN USSR 314:739–746

Papathanassiou E, Panayotidis P, Anagnostaki K (1986) Reproduction and growth of *Aurelia aurita* in Elefsis Bay. Nova Thalassia 8[Suppl 2]:83–88

Pereladov MV (1988) Some observations of biota in Sudak Bay of the Black Sea (in Russian). In: Third All-Russian conference of marine biology, vol 1. Naukova Dumka, Kiev, pp 237–238

Petranu A (1997) Black Sea biological diversity. Romania. BSEP 4, UN Publications, New York

Pianka HD (1974) Reproduction of marine invertebrates, vol 1, chap 4. In: Giese AC, Pearse JS (eds) Ctenophora. Academic, New York, pp 201–265

Prodanov K, Mikhailov K, Daskalov G, Maxim K, Chashchin A, Arkhipov A, Shlyakhov V, Ozdamar E (1997) Environmental impact on fish resources in the Black Sea. In: Ozsoy E, Mikaelyan A (eds) Sensitivity of North Sea, Baltic Sea and Black Sea to anthropogenic and climatic changes. Kluwer, Dordrecht, pp 163–181

Purcell JE, White JR, Roman MR (1994) Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay. Limnol Oceanogr 39:263–278

Rass TS (1992) Changes in the fish resources of the Black Sea. Oceanology 32:197–203

Raymont D (1988) Plankton and ocean productivity, vol 2. Moscow Agroprom, Moscow

Reeve MR (1975) The ecological significance of the zooplankton in the shallow subtropical waters of South Florida. Estuar Res 1:352–371

Reeve MR, Walter MA (1978) Nutritional ecology of ctenophores – a review of recent research. Adv Mar Biol 15:249–287

Seravin LN (1994) Systematic revision of the genus *Mnemiopsis* (Ctenophora, Lobata) (in Russian). Zool Zh 73:9–18

Sergeeva NG, Zaika VE, Mikhailova TV (1990) Nutrition of ctenophore *Mnemiopsis mccradyi* (Ctenophora, Lobata) in the Black Sea (in Russian). Zool J Ecologia Morya 35:18–22

Shiganova TA (1993) Ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Sea of Marmara in October of 1992. Oceanology 33:900–903

Shiganova TA (1997) *Mnemiopsis leidyi* abundance in the Black Sea and its impact on the pelagic community. In: Ozsoy E, Mikaelyan A (eds) Sensitivity of North Sea, Baltic Sea and

Black Sea to anthropogenic and climatic changes. Kluwer, Dordrecht, pp 117–130
Shiganova TA (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. In: Coombs S (ed) Fish Oceanogr 7[Spec Issue]:305–310
Shiganova TA (2000) Some results of studying the invader *Mnemiopsis leidyi* (A. Agassiz) in the Black Sea. In: Volovik SP (ed) Ctenophore *Mnemiopsis leidyi* (A. Agassiz) in the Azov and Black Seas: its biology and consequences of its intrusion. AzNIIRHK, Rostov-on-Don, pp 33–75
Shiganova TA, Bulgakova YV (2000) Effect of gelatinous plankton on the Black and Azov Sea fish and their food resources. ICES J Mar Sci 57:641–648
Shiganova TA, Tarkan AN, Dede A, Cebeci M (1995) Distribution of the ichthyo-jellyplankton and *Mnemiopsis leidyi* (Agassiz, 1865) in the Marmara Sea (October 1992). Turk J Mar Sci 1:3–12
Shiganova TA, Kideys AE, Gucu AS, Niermann U, Khoroshilov VS (1998) Changes of species diversity and their abundance in the main components of pelagic community during last decades. In: Ivanov LI, Oguz T (eds) Ecosystem modeling as a management tool for the Black Sea. Kluwer, Dordrecht, pp 171–188
Shiganova TA, Bulgakova JV, Sorokin PY, Lukashev YF (2000) Investigation of a new invader, *Beroe ovata* in the Black Sea. Biol Bull (Woods Hole) 27:247–255
Shiganova TA, Kamakin AM, Zhukova OP, Ushivtzev VB (2001) Result of investigation of new invader *Mnemiopsis* sp. and its effect on zooplankton. Oceanology 41 (in press)
Stergiou K, Christou ED, Georgopoulos D, Zenetos A, Souvermezoglou C (1998) The Hellenic seas: physics, chemistry, biology and fisheries. Oceanogr Mar Biol Annu Rev 35:415–538
Studenikina EI, Volovik SP, Miryozan IA, Luts GI (1991) The ctenophore *Mnemiopsis leidyi* in the Sea of Azov. Oceanology 3:722–725
Theocharis A, Balopoulos E, Kioroglou S, Kontoyannis H, Iona A (1999) A synthesis of the circulation and hydrography of the South Aegean Sea and the Straits of the Cretan Arc (March 1994–January 1995). Prog Oceanogr 44:469–509
Tkach AV, Gordina AD, Niermann U, Kideys AE, Zaika VE, et al (1998) Changes in the larval nutrition of the Black Sea fishes with respect to plankton. In: Ivanov L, Oguz T (eds) Ecosystem modeling as a management tool for the Black Sea. Kluwer, Amsterdam, pp 235–248
Tregouboff G, Rose M (1957) Manual de Planctonologie Mediterraneenne. Ordre des Nus (Nuda). Centre Nat. de la Rech. Sci, Paris, pp 405–415
Tzikhon-Lukanina EA, Reznichenko OG (1991) Feeding peculiarities of different size speciments of ctenophore *Mnemiopsis* in the Black Sea. Oceanology 3:442–446
Tzikhon-Lukanina EA, Reznichenko OG, Lukasheva TA (1991) Quantitative aspects of feeding in the Black Sea ctenophore *Mnemiopsis leidyi*. Oceanology 31:272–276
Tzikhon-Lukanina EA, Reznichenko OG, Lukasheva TA (1992) What ctenophore *Mnemiopsis* eats in the Black Sea inshore waters? Oceanology 32:724–729
Tzikhon-Lukanina EA, Reznichenko OG, Lukasheva TA (1993) Ecological variation of comb-jelly *Mnemiopsis leidyi* (Ctenophora) in the Black Sea (in Russian). Zh Obshch Biol 54:713–724
Uysal Z, Mutlu E (1993) Preliminary note on the occurrence and biometry of ctenophore *Mnemiopsis leidyi* finally invaded Mersin Bay. Turk J Zool 17:229–236
Vinogradov ME, Shushkina EA (1992) Concentration estimations of the Black Sea jellyfishes, Ctenophora and *Calanus* based on the observations from Argus submersible. Oceanology 22:473–479
Vinogradov ME, Shushkina EA, Musaeva EI, Sorokin PY (1989) Ctenophore *Mnemiopsis leidyi* (A. Agassiz) (Ctenophora: Lobata) – new settler in the Black Sea. Oceanology 29:293–298
Vinogradov ME, Sapozhnikov VV, Shushkina EA (1992) The Black Sea ecosystem (in Russian). Nauka, Moscow
Vinogradov ME, Shushkina EA, Bulgakova YuV, Serobaba II (1995) The consumption of zooplankton by comb-jelly *Mnemiopsis leidyi* and pelagic fishes in the Black Sea. Oceanology 35:569–573
Volovik SP, Chikhachev AS (1998) Man-provoked transformations of the ichthyophauna in the Azov Sea basin. In: Makarov EB (ed) The main problems of fisheries in the Azov Sea basin. AzNIIRHK, Rostov-on-Don, pp 7–22
Volovik SP, Mirzoyan IA, Volovik GS (1993) *Mnemiopsis leidyi*: biology, population dynamics, impact to the ecosystem and fisheries. Int Counc Explor Sea Comm (Biol Meet Oceanogr Comm) 69:1–11
Volovik SP, Mirzoyan ZA, Studenikina EI (1996) Estimation of effects of invader ctenophore *Mnemiopsis* in the Sea of Azov. Rybn Khoz 1:48–51
Zaitsev YP, Aleksandrov BG (1997) Recent man-made changes in the Black Sea ecosystem. In: Ozsoy E, Mikaelyan A (eds) Sensitivity of North Sea, Baltic Sea and Black Sea to anthropogenic and climatic changes. Kluwer, Amsterdam, pp 25–32
Zakhutsky VP, Lutz GI, Shishkin VM (1983) The numbers and biomass of jelly fish in the Sea of Azov (in Russian). Rybnoe Khozyaistvo 8:33–34