Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure

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ABSTRACT

A short synthesis of the present state of the ctenophore, *Mnemiopsis leidyi*, invasion in the Black Sea is given, together with a brief review of its status in other areas of the Mediterranean basin. The impact of *M. leidyi* on the main components of the pelagic community, mesozooplankton, ichthyoplankton and fish resources, based on published data and new field studies (1992–1997) are analysed. This assessment showed sharp fluctuations in the interannual abundance of *M. leidyi*. The main factors controlling the spatial distribution of *M. leidyi* were temperature and, to a lesser degree, salinity, whereas its abundance was controlled by food availability. An analysis of the main constituents of the pelagic ecosystem of the Black Sea before the *M. leidyi* outbreak showed that a reduction in numbers of planktivorous fishes, the main competitors of *M. leidyi*, could be a possible reason for the upsurge in abundance of *M. leidyi*. Following the increase of *M. leidyi*, there was a decline in the abundance and species diversity of ichthyoplankton and mesozooplankton. An assessment of data collected during the period 1992–1997 showed that the number of fish eggs and larvae and of zooplankton was negatively related to *M. leidyi* abundance. After the recent decrease of *M. leidyi* in the period 1995–1997, there has been an increase in abundance and diversity of fish eggs, fish larvae, and zooplankton, which together with an increased catch of planktivorous fish indicates that there has been a recovery of the ecosystem.

Key words: biodiversity, fish catch, ichthyoplankton, invader, *Mnemiopsis leidyi*, zooplankton

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INTRODUCTION

The Black Sea was characterized until the mid 1970s as a highly productive ecosystem at all trophic levels, which by the 1990s had degraded to an ecosystem with a low biodiversity dominated by a 'dead-end' gelatinous food web (Vinogradov *et al.*, 1992). A number of factors, such as climate change, interannual natural biological fluctuations, anthropogenic impacts, including changes in river discharge quality resulting in a rise in eutrophication and pollution (Zaitsev and Aleksandrov, 1997), overfishing of selective species (Ivanov and Beverton, 1985; Rass, 1992) together with the accidental introduction of exotic species from aquaculture projects, have resulted in great structural changes in the food web of the Black Sea (Caddy and Griffiths, 1990). The pelagic community was the first to respond to these changes (Shiganova *et al.*, 1998a).

Anthropogenic introduction of exotic species into the Black Sea, either accidentally or intentionally, began in the 19th Century, but the greatest problems occurred during the latter half of the present century. The introduction of a new species, often inadvertently from aquaculture developments, can be harmful to an ecosystem; semi-enclosed seas being more sensitive to impacts than the open sea (Caddy, 1993). The Black Sea, with its decreased biological diversity, has been the target of opportunistic invasions by temperate and subtropical animals and plants. Of 26 'exotic' species now occurring in the Black Sea, six have had a significant impact on its ecology. These are the crustacean, *Rhithopanopeus harrisi*; the molluscs, *Rapana thomasiana*, *Mya arenaria* and *Cunearca cornea* and the fish, *Mugil soiuy*. The most dramatic effects have followed the invasion of the ctenophore *Mnemiopsis leidyi* (A. Agassiz), a gelatinous predator. It was introduced into the Black Sea in the early 1980s, possibly in ballast water of ships from the north-western Atlantic coastal region. Being a rapidly reproducing, self-fertilizing hermaphrodite, it possessed the ideal reproductive strategy for rapid colonization. As a generalized feeder (Tzikhon-Lukanina and Reznichenko, 1991), it is not prey specific and occurs over a broad range of inshore, hydrographic conditions

Figure 1. The Black Sea and surrounding areas.

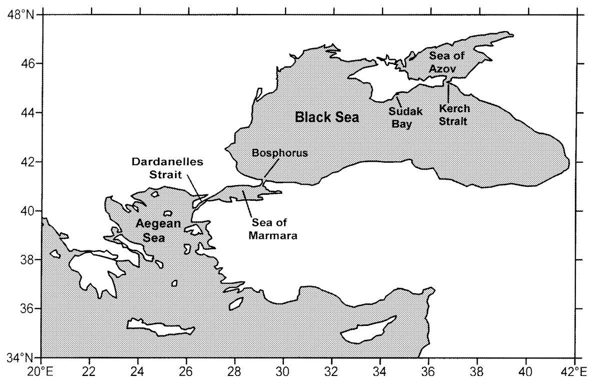
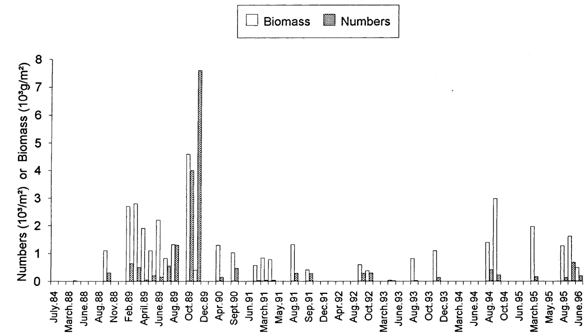


Figure 2. Long-term fluctuations of M. *leidyi* numbers and biomass in the Black Sea.



(Harbison and Volovik, 1994). The Black Sea represented an ideal environment for M. *leidyi* as an opportunistic species.

METHODS

In this paper we describe data collected on 12 cruises from 1992 to 1997. Sampling methods are described by Shiganova (1997). The main area of investigation was the north-eastern part of the Black Sea (Fig. 1). The southern and north-western areas were studied on some cruises as well as the Sea of Marmara (in 1992) and the eastern Mediterranean (in 1993). In addition, data published by the Institute of Oceanology (Vinogradov *et al.*, 1989, 1992) have been used.

Species diversity was analysed following Margalef (1992).

RESULTS AND DISCUSSION

Long-term development of Mnemiopsis leidyi *in the Black Sea*

M. *leidyi* first appeared in the Black Sea in 1982 (Pereladov, 1988), occurring only in inshore waters of Sudak Bay. Only during the autumn of 1988 did it start to spread throughout the Black Sea (Vinogradov *et al.*, 1989), and then seems to have been assimilated into the biotope, reaching peak abundance in the autumn of 1989 (Fig. 2). Thereafter, its abundance decreased steadily until the summer of 1993 (Vinogradov *et al.*, 1992; Shiganova *et al.*, 1998b) when a second increase began, reaching a peak in autumn 1994, at which level it remained until August 1995 (Shiganova, 1997). In 1996 its abundance again decreased (Fig. 2), this decrease continuing in 1997 (when observations were made only in the north-western area).

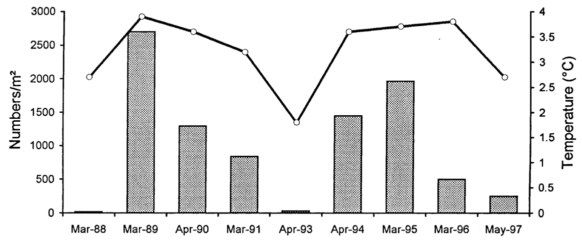
M. *leidyi* from the Black Sea also penetrated into adjacent basins. In August 1988 it was observed for the first time in the Sea of Azov. As the organism can only survive in the Sea of Azov during the warmer times of the year (> 4°C), it must re-invade during the spring or summer months through the Kerch Strait. Initially, it occurs in the southern area adjacent to the Kerch Strait; later, in August/September, it spreads throughout the Sea of Azov and reaches its peak biomass. The variation in the timing and extent of the penetration of M. *leidyi* into the Sea of Azov depends largely on wind-driven currents (Volovik *et al.*, 1993).

In 1989–90, M. *leidyi* appeared in the Sea of Marmara and later in the eastern Mediterranean (Shiganova, 1993, 1997; Kideys and Niermann, 1994), where its pattern of occurrence and temporal variations in abundance suggests that it was introduced to these areas with the surface outflow from the Black Sea through the Bosphorus and Dardanelles Straits. Optimal conditions for the maintenance of M. *leidyi* may exist continually in the surface waters of the Sea of Marmara, which originate in the Black Sea. It is not surprising that M. *leidyi* survives in the Aegean and eastern Mediterranean Seas during the spring and autumn, when the temperature is no higher than 26°C, although it is difficult to understand how it can survive the high summer temperatures in these areas and consistently high salinity of about 39.

Seasonal dynamics of M. leidyi

In February the abundance of M. *leidyi* in the Black Sea is dependent on temperature conditions over the winter (Fig. 3). Moderate-sized individuals predominate from February to June, when this species occurs mainly in the open sea and there is only somatic growth of the overwintering individuals. In June and early July, the biomass and numbers remain relatively low and the population consists mainly of adults. Re-

Figure 3. Relationship between abundance of M. *leidyi* and minimum winter temperature.



production starts in some inshore areas during the second half of July or August (as observed in 1991, 1992 and 1994) or later in August/September (1993 and 1995) when temperatures reach 23°C. Reproduction peaks during August/September or September/October, first in the inshore waters and then in the open sea when temperatures reaches 24–25°C. At this time, mean individual biomass decreases due to the appearance of high numbers of small individuals. During October or November, overall biomass decreases as adult individuals die after reproduction. Reproduction continues until October/November when numbers reach a maximum. From the middle of November, there is only somatic growth, which ceases when the temperature decreases. During the winter the population consists of moderate-sized individuals, which can survive in the open sea in warmer water (>4°C) at depths below the cold surface layers.

Changes in the pelagic community prior to the M. leidyi invasion

Changes in the Black Sea ecosystem began in the north in the 1970s, some years before the M. *leidyi* invasion. Most changes occurred in species diversity within the main pelagic groups of Black Sea fish and to a lesser degree in the mesozooplankton.

Until the mid 1970s, the northern part of the Black Sea was the most important area for spawning of commercial fish species, including valuable pelagic species such as *Sarda sarda* and *Pomatomus saltatrix*, and demersal species including *Psetta maxima maeotica*, *Arnoglossus kesleri*, *Platichthys flesus luscus* and *Solea lascaris nasuta*. The northern Black Sea was also the main spawning area for the Black Sea anchovy (*Engraulis encrasicolus ponticus*) and the 'hibernation' area for the Black Sea and Azov Sea anchovy *Engraulis encrasicolus maeoticus* (Chazchin, 1995; Svetovidov, 1964).

During the 1970s, unregulated diversion of fresh water for irrigation and power generation resulted in a decrease of fluvial input and changes in the hydrological regime. The greatest effects occurred in the north, where the influence of rivers such as the Danube, Dnieper, Dniester, Don and Cuban determined the hydrochemical regime. The surface currents in the Black Sea are generated by inflow from these rivers and inflow through the Strait of Kerch from the Sea of Azov. These inflows also affect the velocity of the rim current in the west (Rumelian current) and central Black Sea, which is directed towards the Bosphorus, particularly during the spring flood. These currents determine the extent of migration of pelagic species (*Scomber scomber*, *Sarda sarda*, *Pomatomus saltatrix* and *Trachurus trachurus*) in the spring from the Sea of Marmara to the northern Black Sea (Ivanov and Beverton, 1985). A decrease in current velocity resulted in a limitation of the extent of migration of these species to the north and a decrease in the number of migrating fish (Rass, 1992). A simultaneous input of nutrients and toxic substances from a large catchment basin caused changes in the hydrochemical regime with consequent eutrophication.

Eutrophication had an indirect effect on zooplankton species diversity through its impact on the phytoplankton. The abundance of *Noctiluca miliaris* and herbivorous zooplankton species increased, but the abundance of other large crustacean species decreased. Stocks of many commercial demersal fish species, including *Psetta maxima*, *Arnoglossus kesleri*, *Platichthys flesus luscus* and *Solea lascaris nasuta*, were reduced significantly due to changes in benthic conditions and a decrease in water transparency related to the eutrophication (Zaitsev and Aleksandrov, 1997). Overfishing by international fleets during the period 1970–1980 also contributed to a reduction in the number of valuable species (Ivanov and Beverton, 1985; Caddy and Griffiths, 1990). By the beginning of the 1980s, a considerable increase in the population of the jellyfish *Aurelia aurita* had occurred (Lebedeva and Shushkina, 1991), this probably being related to the eutrophication.

In contrast to the northern area, there are no large rivers draining into the southern Black Sea. Turkish rivers discharging into the southern Black Sea were not utilized for energy generation, their nutrient load and industrial or domestic waste content were far less than those of the north (Balkas *et al.*, 1990) and consequently, the anthropogenic impacts on the hydrological regimes in the south were less significant than in the northern Black Sea.

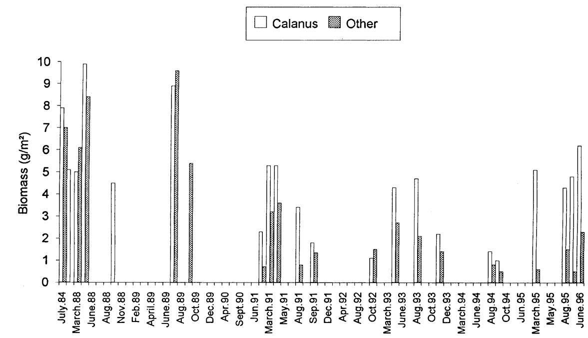
The species diversity of communities representing the secondary (mesozooplankton) and higher (fish) trophic levels decreased significantly at the end of the 1970s and during the 1980s, particularly in the northern Black Sea. The pelagic fish community of the Black Sea as a whole became dominated by the planktivorous species, *Engraulis encrasicolus*, *Trachurus mediterraneus ponticus* and *Sprattus sprattus phalericus*. In the southern Black Sea, pelagic species decreased in number and became randomly distributed (Rass, 1992). During the 1980s, fishing pressure increased on the Black Sea anchovy. Prior to 1984, the anchovy catch made up 50–53% of the total pelagic biomass, subsequently increasing to 60–80% (Chazchin, 1995) with small individuals dominating the catch from 1984 to 1991 (Shiganova, 1997). Despite intensive fishing, anchovy abundance remained high throughout the late 1980s, reaching a maximum in 1988 (Chazchin, 1995) and constituting more than 60% of the total catch for the Black Sea (Shiganova, 1997). After such a high catch in 1988, the spawning stock in 1989 declined to a level only about 15% of that of the previous year (YugNIRO data).

Changes in the pelagic community following the M. leidyi invasion

In the Black Sea during 1989, following the overfishing of anchovy in the previous year, the biomass of zooplankton increased, probably due to reduced grazing pressure. The resulting favourable feeding conditions allowed a rapid and explosive development of M. *leidyi*. This signalled a pronounced change in the Black Sea ecosystem (Vinogradov *et al*., 1989).

A rapid decline in ichthyoplankton and mesozooplankton abundance and species diversity followed, owing to predation on zooplankton and fish eggs and larvae by M. *leidyi*. These changes were most notable in the northern region of the Black Sea, which was already subject to severe anthropogenic damage. Some mesozooplankton species (copepods: Pontellidae and *Oithona nana*; *and* chaetognath: *Sagitta setosa*) virtually disappeared during the period 1990–1992 (Vinogradov *et al*., 1992). The comparison of interannual fluctuations of M. *leidyi*, zooplankton, eggs and larvae of summer-spawning fish (mainly anchovy) and the species diversity of zooplankton and ichthyoplankton clearly demonstrate a negative correlation between M. *leidyi* abundance and the population abundance of these groups (Figs 2 and 4; Shiganova *et al*., 1998a). The same negative correlation was also apparent with winter-spawning fish species (sprat and whiting; Shiganova and Bulgakova, 1998) although the total number of sprat eggs and larvae did not decline to the same extent as those of the summer-spawning species. This may be because both of these species inhabit the intermediate water layer during the warmer seasons, while M. *leidyi* occurs mainly in the upper layer; additionally, sprat and whiting spawn during the winter when M. *leidyi* is relatively scarce.

Figure 4. Long-term fluctuations in biomass of *Calanus euxinus* and other copepods.



Since 1992, when the numbers of M. *leidyi* decreased to the lowest values, the number and species diversity of summer ichthyoplankton and zooplankton began to increase, and with the recent decline of M. *leidyi* in the period 1995–96, the abundance of ichthyoplankton and zooplankton and species diversity have increased to higher levels than in the period 1992–93 (Figs 4 and 5). Higher abundance and species diversity of zooplankton and ichthyoplankton were also recorded in the southern Black Sea (Shiganova *et al*., 1998a).

In contrast to the previous situation described by Ivanov and Beverton (1985), the highest numbers of eggs and larvae of anchovy during the period 1991–1996 were found in the southern Black Sea (Niermann *et al*., 1994). Eggs and larvae of the pelagic fish species such as *Sarda sarda*, *Pomatomus saltatrix* and *Scomber scomber*, and the demersal species, *Platichthys flesus luscus*, *Psetta maxima maeotica* and *Solea lascaris nasuta*, were found off the Antalian coast, although their spawning area was previously reported as being generally in the northern Black Sea (Svetovidov, 1964; Ivanov and Beverton, 1985). The eggs and larvae of these species occurred in low numbers in the north-western area (Arkhipov, 1993; Gordina and Klimova, 1995; Radu *et al*., 1994, 1995), but were almost completely absent in the north-east in the period 1992–1996). This change in the location of the population and of spawning may be due to the better environmental conditions and food availability in the southern Black Sea compared with the north.

A comparison of ichthyoplankton data with the species diversity of the fish catch demonstrates the same trends. The catch of planktivorous fish dropped after the explosive development of M. *leidyi* in the Black Sea and in the Sea of Azov. During recent years,

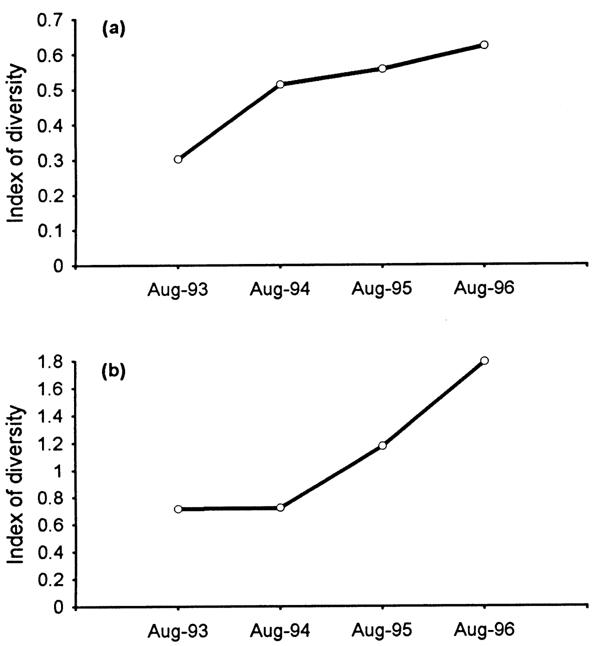


Figure 5. Annual changes in species diversity in the summer in the north-eastern Black Sea for (a) mesozooplankton and (b) ichthyoplankton.

the catches of planktivorous species have increased, particularly the Black Sea anchovy with its short life cycle (Fig. 6).

The species diversity of the Turkish fish catch is the highest in the Black Sea. Based on Turkish data, the following fish species all increased in numbers during the period 1993–94 (St. Bull, 1997): *Sarda sarda*, *Pomatomus saltatrix*, *Scomber scomber*, *S. japonicus*, *Trachurus trachurus*, *Psetta maxima maeotica*, *Solea lascaris nasuta*, *Mullus barbatus*, *M. surmuletus* and *Engraulis encrasicolus ponticus*.

Pomatomus saltatrix, *Psetta maxima maeotica* and *Solea lascaris nasuta* were recorded in the fish catches of Bulgaria and Romania in low numbers in 1995 (St. Bull, 1997) and *Psetta maxima maeotica* was recorded in particularly low numbers in the catches of the Ukraine and Russia in 1995. The area of 'hibernation' of the Black Sea anchovy currently occurs only in the south and south-east, and as a consequence it is now only recorded in Turkish catch statistics. The most abundant species in the catches of Ukraine and Russia during the period 1990–1995 were the Azov Sea anchovy, sprat and whiting. The total catch by Russia in the Black Sea is now the poorest with regard to quantity and species diversity. One of the most important commercial fish now landed by Russia is a species that invaded the region, the mullet, *Mugil soleiy*.

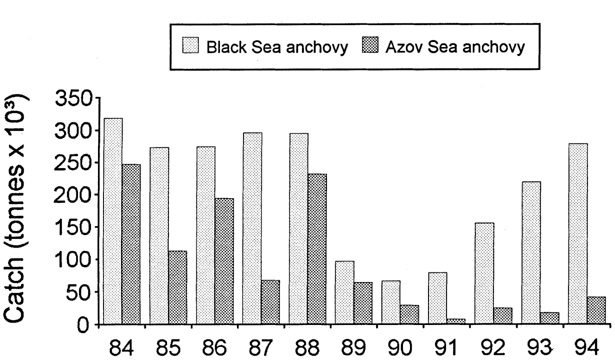


Figure 6. Annual changes in the catch of the Black Sea and the Azov Sea anchovy.

The species diversity and abundance of eggs and larvae of small pelagic fish and zooplankton, which decreased after the M. *leidyi* explosion, have risen concurrently with its decline during recent years. This is much more noticeable in the southern Black Sea. Many commercially valuable species which have disappeared from the northern area are now found in the south, particularly in the catches and ichthyoplankton samples of Turkey. This may indicate that the Black Sea pelagic ecosystem, as a mature system, is now more resistant to the influence of an invader species. After the 'invasion', the ecosystem performs an inner reconstruction in order to compensate for the influence of the invader. Due to this process and following a decrease in invader abundance, the ecosystem recovers and becomes more resistant to further outside influences. This process proves most effective in the areas of less disturbed environmental conditions, such as in the southern Black Sea.

Both the indigenous, gelatinous carnivore *Aurelia aurita* and the invader M. *leidyi* still dominate in the Black Sea pelagic community. Although there are signs of improvement in the state of the ecosystem, these should not prevent the demand for practical measures to restore the environment and aid recovery of fish resources.

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