THE COMB JELLY *MNEMIOPSIS LEIDYI* IN THE BLACK SEA

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Abstract
Following its transportation in ballast waters, the western Atlantic ctenophore *Mnemiopsis leidyi* caused a striking damage to the ecosystem of the Black Sea in the early 1990s. The concentration of food zooplankton and simultaneously catches of anchovy and other pelagic fishes sharply decreased during the peak levels of the ctenophore. There have been many studies on the distribution and physiology of this ctenophore in its new environment due to its substantial impact on the marine ecosystem. Later in mid 1990s its biomass was at moderate levels till the appearance of its predator, another ctenophore *Beroe* sp. in 1997. The predator decreased *Mnemiopsis* biomass to very low levels which was confirmed by both laboratory and field observations. Now *Mnemiopsis* is causing very similar problems in the Caspian Sea following its transport from the Black Sea.

1 History and impact of *Mnemiopsis* invasion in the Black Sea

The North American comb jelly *Mnemiopsis leidyi* (also identified as *M. mcradyii*, Zaika & Sergeeva 1990; Fig. 1) is a member of phylum ctenophora (order Lobata, family Bolinopsidae). The invasion case of this species in the Black Sea is one of the most drastic among marine bioinvasions. It caused a great damage to the entire pelagic ecosystem of the Black Sea at the end of 1980s and at the early 1990s devastating valuable pelagic fishery. As a matter of fact similar events are now taking place in the Caspian Sea after *Mnemiopsis* inadvertently transported here from the Black Sea.

It is believed that *Mnemiopsis* reached the Black Sea in the ballast waters of ships. In the spring of 1986, this ctenophore was first recorded off the Bulgarian coast (Bogdanova & Konsoulov 1993), then in offshore waters (Vinogradov et al. 1989). Increasing substantially following years, the total biomass of *Mnemiopsis* in the Black Sea was calculated as 800 million tons (live weight) in 1989 summer (Vinogradov 1990). A great alteration of the structure in the planktonic community has resulted from this mass development (Kideys 1994; Niermann et al. 1994; Kovalev et al. 1998a,b; Kideys et al. 1999, 2000). The sharp decrease in the concentration of anchovy eggs and larvae observed since 1989 has been suggested to be due not only to overfishing, eutrophication or pollution but also to *Mnemiopsis* predation on fish eggs and larvae or competition for food in the northern Black Sea (Niermann et al. 1994). The catch of anchovy (*Engraulis encrasicolus*), being the most abundant fish species of the Black Sea, decreased sharply too in this period (Fig. 2), as well as other pelagic fish species. The economic loss for fishermen of the Black Sea was hundreds million dollars during this period.

2 Biology and ecology of *Mnemiopsis*

Mnemiopsis is a transparent animal with gelatinous soft body. The locomotory apparatus is composed of eight symmetrical comb rows, distinguished by fused ciliary plates (ctenes) on the body surface (Mianzan 1999). Bioluminescence is a common feature in

E. Leppäkoski et al. (eds.), Invasive Aquatic Species of Europe, 56–61.

ctenophores occurring along the comb rows. Its body is laterally compressed, with large lobes arising near stomodeum. It may reach to a total (lobe) length of 14 cm in the Black Sea. Early life stages of this ctenophore are shown in Fig. 3.

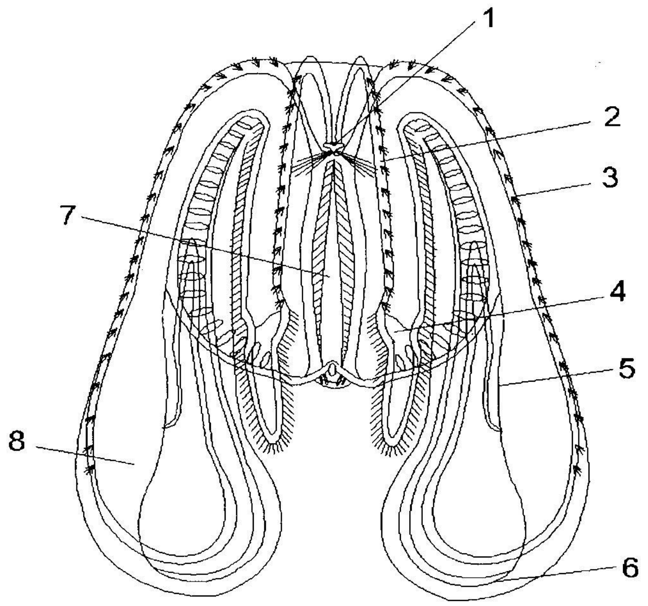

Figure 1. Mnemiopsis leidyi. (1) aboral organ, (2) subtentacular row of comb flappers, (3) subsagital row of comb flappers, (4) auriculus, (5) subsagital tube, (6) translobal tube, (7) tentacular tube, (8) lobe (from Shiganova 2000).

2.1 FEEDING

Mnemiopsis is a voracious predator on zooplankton. Unlike medusae, *Mnemiopsis* is a macrophage capable of consuming fairly large prey (up to 1 cm or more in length). *Mnemiopsis* has also been shown to feed on eggs and larvae of fishes in the Black Sea (Tsikhon-Lukashina et al. 1992; Mutlu 1999). Mutlu (1999) observed the following groups in the stomach of *Mnemiopsis* from 1991 to 1995 in the southern Black Sea: copepods (50%), mollusks (40%), cladocerans (1%), fish eggs and larvae (1%), and others (8%). *Calanus euxinus* was the most frequently consumed copepod.

2.2 GROWTH AND REPRODUCTION

Mnemiopsis, like all other ctenophores, are hermaphroditic with a very high reproductive capacity. *Mnemiopsis mccradyi* is able to produce 8,000 eggs within 23 days, after 13 days of its own birth (Baker & Reeve 1974). The growth rate of this species is comparable to that of phytoplankton (daily doublings, Reeve et al. 1978). Naturally such high growth rates can only be achieved with a high feeding rate.

In the Black Sea, mature specimens of *Mnemiopsis* spawn at night (Zaika & Revkov 1994) in summer temperatures of 19 to 23 °C. Embryonic development takes about 20 h (Fig. 3). The maturing of gonads and the subsequent spawning can take place only at a reasonably high food concentration of medium size copepods (up to 100 copepods l^{-1}).

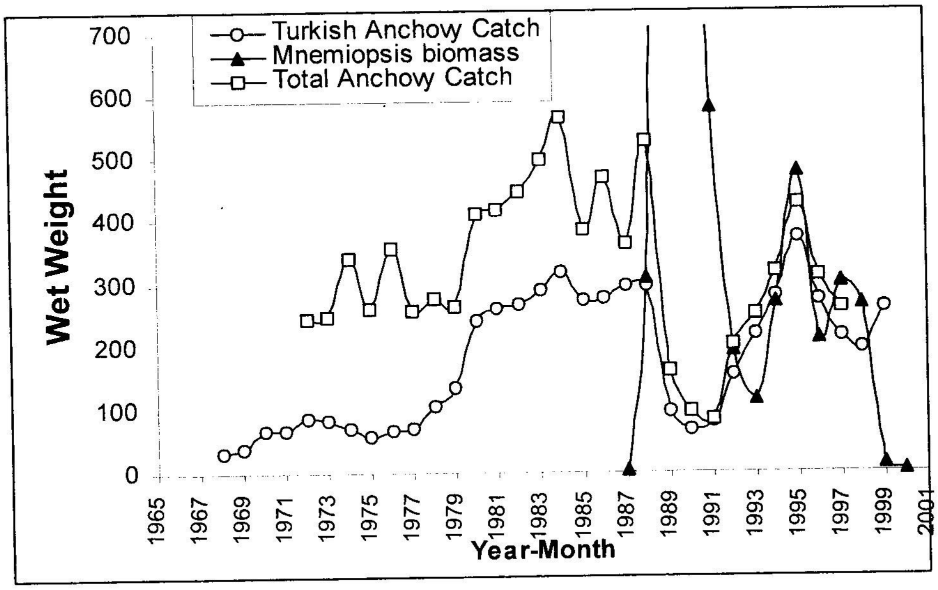

Figure 2. Relationship between *Mnemiopsis* biomass (g m^{-2}) and anchovy catch (as thousand tons) values from the Black Sea (modified from Kideys et al. 1999).

2.3 RESPIRATION

Minkina & Pavlova (1995) determined an equation of R (µl O_2 h^{-1}) = 3.20 dry wt $(g)^{0.89}$ for 23 °C for the Black Sea *Mnemiopsis*. Kideys's (1996) equation obtained for 20 °C (R (µl O_2 h^{-1}) = 2.88 dry wt $(g)^{0.86}$) was close to this one, but lower rates for 8 °C (R (µl O_2 h^{-1}) = 1.48 dry wt $(g)^{0.87}$). Anninsky et al. (1998) described the respiration rate of *M. leidyi* with the equation R (µl O_2 h^{-1}) = 6.73 wet wt $(g)^{0.83}$) for freshly captured ctenophores at 22 °C. Rate of respiration is important in explaining nearly absence of *Mnemiopsis* from the suboxic water layers in the Black Sea. For example, the intercept value obtained for *Mnemiopsis* is much lower than that obtained for the other ctenophore occurring in suboxic layers, (i.e. *Pleurobrachia pileus* R=1.2 to 2.2 $W^{0.625}$ measured at 17-20 °C; Lazareva 1961). This indicates a higher metabolism in *Mnemiopsis* compared with *P. pileus*. Keister et al. (2000) also reported that when the dissolved oxygen levels were below 1 mg l^{-1} (approx. 30 µM), *Mnemiopsis* were nearly absent in the bottom layers of Patuxent River, Chesapeake Bay.

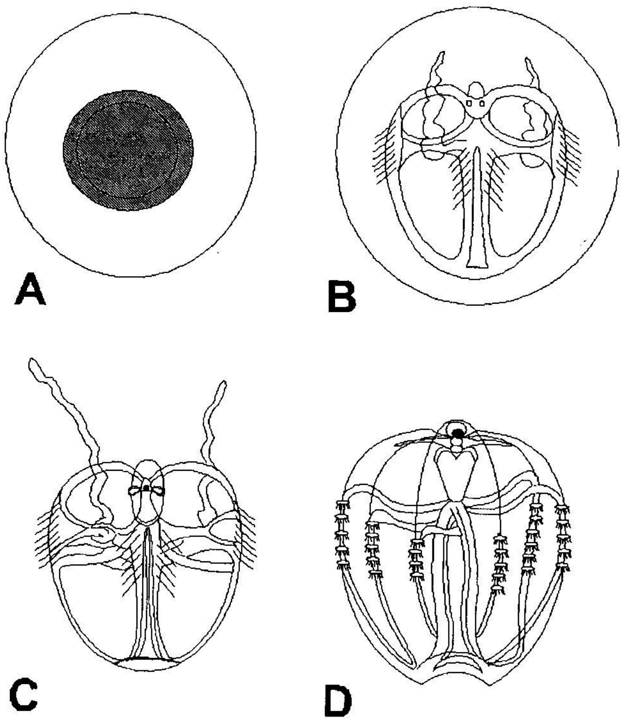

Figure 3. Early life stages of *Mnemiopsis.* (A) newly laid egg, (B) embryo with tentacles, about 30 hours old, still within the egg envelope, (C) newly hatched embryo in cydippid stage, (D) embryo about 32 hours old showing muscular strands (from Shiganova 2000).

3 Spatial and temporal distributions

In the shallow well mixed northeastern American waters (e.g. Narragansett Bay) *Mnemiopsis* was usually fairly evenly distributed vertically (Kremer & Nixon 1976). In the Black Sea, where the oxic layer may extend below 200 m, *M. leidyi* was usually in the upper mixed layer, or in and above the seasonal thermocline, with only a few individuals found in deeper layers (Mutlu 1999; Kideys & Romanova 2001). The major reason for the very low occurrence of this ctenophore in deeper layers could also be the low levels of oxygen concentration (< 20-30 μM) as pointed out above.

Horizontal distribution of *Mnemiopsis* in the Black Sea is much more patchy compared to the native ctenophore *P. pileus*. There are hot spots for the abundance of *M. leidyi*, mainly occurring in the coastal regions. Overall density of *Mnemiopsis* seems higher in the northern Black Sea compared to the south.

Abundance of *Mnemiopsis* has been observed to fluctuate throughout the year in USA waters with higher values in summer (Kremer & Nixon 1976). In the Black Sea too, high values are generally observed in summer-autumn though a considerable stock was present during the winter months until the appearance (i.e. 1997) of its predator *Beroe* in the Black Sea. Since then, winter population of *Mnemiopsis* is very low both in northern and southern Black Sea.

In the open sea, the maximum biomass values for *Mnemiopsis* (1.5-2 kg m^{-2}) were obtained in autumn 1989 (Vinogradov et al. 1989; Fig. 2). After 1990, the biomass decreased sharply. Comparing data only from the warm period (summer and early autumn when these ctenophores are known to increase their abundance and biomass) to eliminate seasonal variability, one can see that after the high values at the end of the 1980s, the biomass of *Mnemiopsis* was very low with a mean value of 131 g m^{-2} in June 1991. There was again an increasing trend during the summers of 1992, 1993 and 1995 when the biomass increased steadily up to 465 g m^{-2}. However, another decrease trend has occurred since 1995, that is prior to the appearance of the predator *Beroe*. One of the most important factors for the decrease in the biomass of *Mnemiopsis* in this period was the food limitation as was demonstrated by Anninsky et al. (1998). Under conditions of starvation, the level of glycogen, which is accumulated energy in ctenophores (Shulman 1972), decreases and this characteristic can be used to understand the condition of ctenophores. Glycogen content of *Mnemiopsis* in 1996 varied from 21 to 44 µg/g fresh weight and accounted for 52.5 ± 14.2% of total polysaccharide content. Thus the condition of *M. leidyi* observed during the conducted survey corresponded to that expected after a two-day fasting period (determined experimentally) implying that the ctenophores were starving. Earlier measurements (in 1991-1992) displayed high glycogen levels for *Mnemiopsis* indicating that the Black Sea had provided the ctenophores with a good food supply (Anninsky 1995).

4 Control of *Mnemiopsis*

The unprecedented impact caused by *Mnemiopsis* in the Black Sea attracted great attention from the scientific community so that UNEP intervened to develop a strategy to control this ctenophore in the Black Sea (GESAMP 1997). *Beroe* arose as one of the best agents for the aim. Interestingly, by October 1997, this ctenophore (*Beroe ovata*) had already appeared in shallow waters of the Black Sea (Konsoulov & Kamburska 1998), in September 1998 in the Sea of Marmara (A. E. Kideys, unpubl.) and in August-September 1999 in Sevastopol Bay and adjacent water regions as well as in the north-eastern Black Sea (Finenko et al. 2000). Since genus *Beroe* occurs in the Mediterranean, there is a possibility that this invasion was a spontaneous one from the Mediterranean.

Several studies performed since then have shown that *Beroe* feed entirely on *Mnemiopsis* (Shiganova et al. 2000; Finenko et al. 2001). The latter investigators calculated the mean daily ration as 45% of *B. ovata* wet weight.

Since the appearance of *Beroe* in the Black Sea, population of *Mnemiopsis* decreased gradually to almost zero values as found during the most recent (May-June 2001) cruise to the Black Sea (Fig. 3). This shows the effectiveness of *Beroe* in controlling *Mnemiopsis* in the Black Sea ecosystem. This is a very important event displaying that the impact of a holoplanktonic alien species could be reverted via biological control.

Mnemiopsis appeared in the Caspian as was expected (Dumont 1995; GESAMP 1997) since 1997 (pers. comm. with Caspian fishermen). Ivanov et al. (2000) suggested that this ctenophore was transported with ballast water taken aboard in the Black Sea or the Sea of Azov (where *Mnemiopsis* occurs in warm months) and released after ballast-loaded ships passed through the Volga-Don Canal and the shallow freshwater North Caspian Sea, into the saltier Central or South Caspian (Ivanov et al. 2000). In 2001 summer abundance of *Mnemiopsis* was as high as 1,393 ind m^{-2} in the southern Caspian Sea (Kideys et al. 2001), and about 50% reduction in kilka fishery compared to two-three years earlier. Kideys et al. (2001) suggested introducing *Beroe* to control *Mnemiopsis* in Caspian Sea after necessary laboratory experiments performed and conditions set by the FAO guidelines on the precautionary approach on inland fisheries and species introduction as well as the ICES (1995) code of practice on the introductions and transfers of marine organisms.

Acknowledgements

The present investigation was carried out with the support of a NATO Linkage Grant (ENVIR.LG.974491) and by the Turkish Scientific and Technical Research Council (TUBITAK YDABÇAG 100Y017).