The catastrophic invasion of the Black Sea by *Mnemiopsis leidyi* : is it only doing what other ctenophores did long ago ?

G. Richard Harbison

Woods Hole Oceanographic Institution, Woods Hole, USA. Email: gharbison@whoi.edu

Mnemiopsis leidyi Agassiz, 1865 is a member of a small phylum of exclusively marine carnivores, the Ctenophora. A single polymorphic species was, until the 1980's, restricted to the eastern seaboard of the Americas, with a continuous range extending from Cape Cod, USA (41°N, 70°W) in the north to Peninsula Valdez, Argentina (43°S, 64°W) in the south (Harbison and Volovik, 1994). It is most common in bays and estuaries, and does not occur very far from shore, since it seems to do best in environments with high levels of food (Reeve and Baker, 1975). It forms massive blooms over its entire home range. It was apparently transported to the Black Sea in the ballast water of ships, and was first reported in 1982. In 1988, massive blooms of this animal captured the attention of fishermen and biologists. By 1989, pelagic fisheries in the Black Sea had dropped precipitously (GESAMP, 1997). The two fisheries that were most effected were those of the anchovy (*Engraulis encrasicolus*) and the Azov Sea kilka (*Clupeonella cultriventris*).

In hindsight, it is obvious that *Mnemiopsis leidyi* has the characteristics of an ideal invasive species :
1 - it is a simultaneous self-fertilizing hermaphrodite (*e.g.*, Martindale, 1987), which means that only a single animal is needed to establish a population;
2 - it is a feeding generalist, ingesting a wide spectrum of food, ranging from algae and microzooplankton to crustaceans, fish eggs and fish larvae;
3 - it tolerates a wide range of environments, with salinities ranging between 3.4 (Miller, 1974) and 75 (Simmons, 1957) and temperatures ranging between 1.3°C (Burrell and Van Engel, 1976) and 32°C (Baker, 1973);
4 - at optimal temperatures (above 20°C), it develops rapidly, reaching full sexual maturity in 12 days. Dissogony (precocious production of gametes) can occur as early as 6 days after hatching (Martindale, 1987);
5 - it releases copious quantities of eggs (up to 2 to 3 thousand per day), and sexual reproduction is only a minor component of its carbon budget (Reeve *et al.*, 1989);
6 - it responds to elevated food concentrations with rapid growth and reproduction (Reeve *et al.*, 1989).

Although *Mnemiopsis leidyi* needs high concentrations of food for optimal growth and reproduction, it can also live for weeks without feeding, by simply de-growing (Reeve *et al.*, 1989). Thus, it is difficult to imagine an organism that is better adapted to colonize new eutrophic marine environments (particularly through the vector of ships' ballast water) than *M. leidyi*.

In the 1990's another ctenophore from the Americas, *Beroe ovata sensu* Mayer (1912), was also introduced, also probably in ships' ballast water. This ctenophore is a specific and highly

voracious predator on other ctenophores, and has most of the invasive characteristics listed above for *M. leidyi*. It is now functioning as a biological control agent there, appearing to be dramatically reducing populations of *M. leidyi* in the Black Sea (*e.g.*, Vostokov *et al.*, 2001), as predicted by Harbison and Volovik (1994).

In fact, when one looks at the phylum Ctenophora as a group, one finds that many of the more common species in the Mediterranean also share most of those invasive characteristics of *Mnemiopsis leidyi* listed above. Of the 17 species from the Gulf of Naples listed by Chun (1880), all (with the exception of the problematic species *Euchlora filigera*) are found over broad areas of the Atlantic and Pacific. Thirteen species form large aggregations under appropriate conditions. Extremely large blooms of the following "Mediterranean" species have been reported on numerous occasions in different regions of the world: *Pleurobrachia pileus, Euplokamis stationis, Bolinopsis vitrea, Eurhamphaea vexilligera, Leucothea multicornis, Cestum veneris, Velamen parallelum* and *Beroe ovata sensu* Chun (1880). One is forced to conclude that most ctenophores have the characteristics of highly invasive species, and that these worldwide invasions occurred long before there were marine biologists to document them.

It should be noted that, before the *Mnemiopsis leidyi* invasion, only a single species of ctenophore, *Pleurobrachia pileus*, inhabited the Black Sea. Now there are three. As the salinity of the Black Sea increases due to human activities, other Mediterranean species will enter, and ctenophore faunal diversity will increase.

Thus, it appears that the invasion of the Mediterranean, Black and Caspian seas by *Mnemiopsis leidyi* occurred through a combination of human activities and the evolutionary peculiarities of the species. In contrast to most other ctenophores, *M. leidyi* is apparently unable to reproduce in oligotrophic environments. In the Americas, it is mostly found close to shore in bays and estuaries, and is not found around coral reefs, for example, which frequently have blooms of *Bolinopsis vitrea* and *Eurhamphaea vexilligera* instead. Thus, before the use of ship's ballast water, *M. leidyi* was unable to cross the Atlantic. It is interesting that *M. leidyi* is not found on the Pacific seaboard of the Americas. This indicates either that it evolved after the Isthmus of Panama was formed (about three million years BP), or that environmental conditions are unfavorable for its establishment along the western coasts of the Americas.

Since most of the Mediterranean is oligotrophic, it is unlikely that catastrophic blooms such as have occurred in the Black Sea will occur here. Although large concentrations of *Mnemiopsis leidyi* have been observed in the Sea of Marmara, the Aegean Sea and Mersin Bay (Kideys and Niermann, 1994), it is likely that its distribution in the Mediterranean will be restricted to eutrophic areas. Should *M. leidyi* become established in the Mediterranean, its distribution will probably resemble that of the American blue crab, *Callinectes sapidus* (Fischer *et al.*, 1987), which has environmental preferences similar to those of *M. leidyi*. Thus, one would expect to find blooms of *M. leidyi* in the Nile delta and in the upper Adriatic, for example. The situation in the Caspian Sea is quite different, since this sea has environmental conditions that more closely resemble the preferred habitats of *M. leidyi*. The potential for a catastrophic decline in endemic zooplankton and fishes is therefore much higher in the Caspian Sea.

Beroe ovata sensu Mayer (1912) may be more successful in the Mediterranean than *Mnemiopsis leidyi*. It appears to be better able to reproduce in oligotrophic conditions, and feeds on a wide variety of ctenophores (Swanberg, 1974). In contrast to *M. leidyi*, it is found on coral reefs. Although it is only rarely collected in the open ocean and is regarded as neritic (Harbison *et al.*, 1978), it will probably become more widespread and abundant in the Mediterranean than will *M. leidyi*. Mediterranean plankton biologists should be on the alert for both *M. leidyi* and this "new" species of *Beroe*. Whether or not *B. ovata sensu* Mayer (1912) will reach the Caspian Sea will depend on whether or not ballast water controls in the Volga-Don Canal are promptly put in place. Should it enter the Caspian, its long-term survival will depend on the success of *M. leidyi*, since this ctenophore will be its only source of food there.