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Invasion note

Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora)

Vladimir P. Ivanov[1], Andrey M. Kamakin[1], Vladimir B. Ushivtzev[1], Tamara Shiganova[5], Olga Zhukova[1], Nikolay Aladin[2], Susan I. Wilson[3], G. Richard Harbison[4] & Henri J. Dumont[6,*]
[1]*CaspNIRH, Astrakhan, Russia;* [2]*Brackish Water Laboratory, Russian Academy of Sciences, St.-Petersburg, Russia;* [3]*School of Biology and Biochemistry, Queens University, Belfast, UK;* [4]*Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA;* [5]*P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia;* [6]*Laboratory of Animal Ecology, Ghent University, Belgium;* [*]*Author for correspondence (e-mail: Henri.Dumont@rug.ac.be)*

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We document the invasion of the Caspian Sea by the large estuarine Western Atlantic ctenophore (comb jellyfish) *Mnemiopsis leidyi* (hereafter *Mnemiopsis*), and speculate on its potential impact on the diverse endemic fauna of the Caspian, and especially upon the Caspian Seal, *Phoca caspica.*

Mnemiopsis was first seen in the Black Sea in 1982 (Pereladov 1983). It was restricted to coastal areas of the northwest Black Sea, where it was found in low numbers, until the summer and fall of 1988, when it became the dominant planktonic organism reaching an estimated biomass of 1.10^9 t wet weight (WW) in the entire Black Sea, a number larger than the world's annual fish landings (Sorokin 2001). Its success then and now was facilitated by a combination of its reproductive biology (*Mnemiopsis* is a self-fertilizing, simultaneous hermaphrodite), abundant food resources, suitable temperature and salinity, and lack of predators (and perhaps of parasites and diseases) that it had in the Americas.

Mnemiopsis is found in American estuaries from 40° N to 46° S, and tolerates a wide range of salinity (3.4 to 75.0‰) and temperature (1.3 to $32\,^\circ$C). It can survive for weeks without feeding, and responds to increased food levels with rapid reproduction. All these factors make it an excellent organism for transport in ships' ballast water (Harbison and Volovik 1994).

That *Mnemiopsis* would invade the Caspian Sea from the Black Sea, unless stringent measures on the movement of ballast water between the two seas were taken, had been predicted (Dumont 1995). Rumors of fishermen in Turkmenistan catching 'strange jellies' in their fishing nets were circulating since 1996, prompting one of us (H.J.D.) to spend a week looking for them in Krasnovodsk Bay, but only the small hydromedusan *Moerisia pallasi* was found at that time. In November 1999, two of us (V.B.U. and A.M.K.) carried out a survey of crayfish along the east coast of the middle part of the Caspian Sea, in the Turkmen and Kazakh sector. At $40^\circ 58'$, $52^\circ 45'$, on a coastal plateau zone of 40 m depth, jellies were videotaped at depths ranging from 10–15 to 30–40 m. These pictures proved to be the first records from the Caspian Sea of the ctenophore *Mnemiopsis*, as well as of the scyphozoan medusa *Aurelia* sp. cf. *A. aurita* (which we discuss further below). We suggest that both of these jellies were transported with ballast water taken aboard in the Black Sea or the Sea of Azov (where *Mnemiopsis* occurs in the spring and summer) 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.

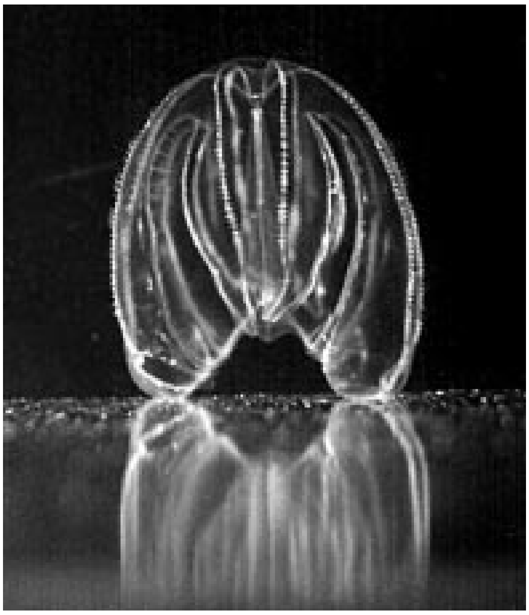

Figure 1. Mnemiopsis leidyi (photograph by Tamara Shiganova).

In summer 2000, we documented that a stunningly rapid expansion of *Mnemiopsis* had taken place. This increase in the Caspian Sea within 1 year of its sighting stands in contrast to the apparent lag time between the first detection of this species in the Black Sea (1982) and its population increase (1988). In early July 2000 *Mnemiopsis* was not found in the northern region of the Caspian, where salinity ranges from 2‰ to 10‰. But by late July it had become abundant in central open Caspian waters, at a salinity of 4–13‰ and temperatures of 24–29 °C. Density varied from 3–5 to more than 100 ind. m^{-2}. The largest specimens reached 9–10 cm, and high numbers of small-sized (less than 10 mm) individuals suggest active reproduction. In August, a survey of the northern Caspian revealed that *Mnemiopsis* had moved up close to the Volga delta, in waters with salinity 2–4‰. The situation remained more or less the same in September. Less than 1 year after its initial sighting, *Mnemiopsis* therefore now effectively occurs over most of the Caspian. By analogy with previous events in the Black Sea, we predict a major population explosion in the Caspian Sea will now occur.

The salinity in the central and southern parts of the Caspian Sea (12–13‰) appears to be ideal for *Mnemiopsis*. The shallow northern third of the sea freezes in winter; like the Sea of Azov, this area will almost certainly not support continuous populations of *Mnemiopsis*. Although this region makes up about one-third of the total area of the Caspian Sea, it represents only 0.5% of its volume. The more saline, deep central and southern basins are much warmer, and do not freeze. South of 40° latitude, surface temperature rarely goes below 10 °C, and thus these areas should provide a favorable environment for *M. leidyi* year round.

Aurelia aurita, previously known from the Black Sea, was not seen again in any of the 2000 surveys and thus it seems to have disappeared after what may have been an ephemeral incursion. In the late 1980s, as populations of *Mnemiopsis* exploded in the Sea of Azov, the biomass of *Aurelia aurita* fell to 1.10^8 t or less (Shiganova et al. 1998), and thus *Aurelia* in the Caspian may not have survived in the face of the increasing population of *Mnemiopsis* as well.

Mnemiopsis is an actively hunting carnivore feeding on zooplankton (including meroplankton, the larvae of benthic animals), fish eggs and fish larvae (Tzikhon-Lukanina et al. 1993). It often feeds superfluously, regurgitating excess ingested food, and it can consume up to ten times its own weight per day (Kremer 1979). Thus not surprisingly its effect on the pelagic fisheries of the Black and Azov Seas was clear-cut and devastating: the fisheries collapsed in the Black Sea on zooplanktivorous fish species such as anchovy (*Engraulis encrasicolus ponticus)*, Mediterranean horse mackerel (*Trachurus mediterraneus ponticus*) and sprat (*Sprattus sprattus phalericus*), and in the Sea of Azov on Azov anchovy (*Engraulis encrasicolus maeticus*) and Azov kilka (*Clupeonella cultriventris*). Landings of anchovy dropped to one-third of their previous levels, and many fishermen abandoned fishing. This catastrophic decline was caused by both the elimination of the zooplankton, the normal food of pelagic fish, and by predation by *Mnemiopsis* on floating fish eggs and early larvae (Shiganova and Bulgakova 2000).

What impacts will the invasion of *Mnemiopsis* have on the Caspian Sea, an ecosystem that is extremely different from that of the Black Sea (Dumont 1998; Sorokin 2001)? We distinguish two categories of effects: a qualitative one and a quantitative one.

A qualitative effect of this invasion may be comparable to that of the impact of the Nile perch in Lake Victoria, where hundreds of species of endemic haplochromine fish were driven to extinction by this introduced predator (Witte et al. 1992). A large number (possibly over 400) of endemic species also occur in the Caspian Sea, most of which are pelagic, benthic or semi-benthic crustaceans of the orders Amphipoda, Mysidacea, Cumacea, Copepoda and Onychopoda (Zaitsev and Mamaev 1997). A similar fate may thus be in store for the endemic flock of onychopod (cladoceran-like) zooplankton, and for the numerous endemic amphipods, mysids, and cumaceans. Many of these are benthic species, but move into the water column at night during vertical migrations.

A quantitative effect will likely be a sharp decline in the zooplankton stocks and pelagic fish eggs and larvae, similar to that which also occurred coincident with the invasion of *Mnemiopsis* in the Black Sea. In the Caspian Sea the main stock of pelagic fish (which have been overfished, as in the Black Sea) consists of three species of small pelagic clupeids, mainly *Clupeonella cultriventris caspia and C. engrauliformes*, known as kilka (Kosarev and Yablonskaya 1994). Kilka feed exclusively on zooplankton, mostly copepods (55–77% by weight), cladocerans and meroplankton. If these stocks collapse, the last economically exploitable fisheries resource of the Caspian will disappear.

But the top predator of the Caspian is not a fish but a seal. Like the severely depleted sturgeon fish, the endemic Caspian Seal *Phoca caspica* is a flagship species of the Caspian biota. Its main prey in the central and southern Caspian is kilka. We predict that if the population of *Mnemiopsis* in the Caspian Sea grows and remains large, depletion of the food base of kilka, and predation by *Mnemiopsis* on the eggs and larvae of kilka, will occur, and thus lead to (and repeat) the collapse of small pelagic fish previously seen in the Black Sea (Zaitsev and Mamaev 1997; Shiganova 1997, 1998).

The Caspian seal population is already under considerable stress. The population size in the year 2000 is not known, but was estimated at about 350,000–400,000 in the mid-1980s (Khuraskin and Pochoyeva 1997). Female fertility has been extremely low at least since the early 1980s (Krylov 1990). This reproductive failure may be linked to high levels of organochlorine pesticide residues found in seal tissues in recent years (Watanabe et al. 1999). As in Lake Baikal, Caspian seals have also suffered from viral infections, such as canine distemper virus (Forsyth et al. 1998). Finally, there is annual commercial hunting of pups on the northeast Caspian ice in the winter. The entry of *Mnemiopsis* into this complex equation of population stress and demise could prove to be the final straw for the Caspian seal.

There are many fewer species in the Caspian Sea than in the Black Sea, so the list of the potential predators on *Mnemiopsis* is even shorter than it is for the Black Sea, where we have earlier noted that the general lack of predators facilitated its establishment and increase. It is extremely unlikely that a predator capable of feeding on and thus controlling the population of *Mnemiopsis* exists in the Caspian.

A GESAMP working group suggested that one method of control of *Mnemiopsis* populations in the Black Sea that could be investigated was the introduction of a commercially valuable fish that feeds specifically on gelatinous zooplankton, or of another gelatinous species, feeding only on ctenophores, and preferably mainly on *Mnemiopsis* (GESAMP 1997). One candidate gelatinous-eating fish suggested was the American butterfish *Peprilus triacanthus*. This fish evolved with *Mnemiopsis*, and is able to survive under similar environmental conditions. It feeds voraciously, although not exclusively, on *M. leidyi* and *Aurelia aurita,* and is a commercially valuable species (Harbison 1993). The extent to which it would feed on native ctenophores in the Black Sea is not known. A candidate ctenophore-eating ctenophore suggested by GESAMP was *Beroe ovata,* which feeds specifically on *Mnemiopsis leidyi* in American coastal areas (GESAMP 1997).

Interestingly, *Beroe ovata* appeared in the Black Sea in 1997, probably arriving from the Mediterranean Sea through the Sea of Marmara. During 1997 and 1998 *B. ovata* occurred in some coastal areas in autumn (Konsulov and Kamburska 1998; Shiganova et al. 2000a). In August 1999, the first bloom of *Beroe* was recorded, with average numbers and biomass 1.1 ind. m^{-2} and 31 g WW m^{-2}, respectively. The abundance of *M. leidyi* suddenly declined (from 7000 ind. m^{-2} and 3–5 kg WW m^{-2} in 1988–89 to 17.3 ind. m^{-2} and 155 g WW m^{-2}). In September 1999, a few specimens of *Beroe ovata* were collected in the Sea of Azov (Shiganova et al. 2000b, 2001a). In April 2000, *M. leidyi* was found solely in some warm locations and its density was only 1.2 ind. m^{-2} and biomass only 28 g WW m^{-2} (Shiganova et al. 2000a,b). Concomitantly, in the fall of 1999 the biomass of the zooplankton greatly increased, the density of fish eggs greatly increased, and the number of species increased four times compared to species richness following earlier *Mnemiopsis* blooms (Shiganova et al. 2000b, 2001b).

The intentional introduction of one exotic species to control another is an extraordinarily complex issue. In the Caspian Sea, any such introduction would require taking into account a broad number of variables. One challenge in the case in hand is the immediate threat to the potential survival of many endemic Caspian species versus the possibility that a species introduced for bio-control could directly or indirectly impact those same species.

However, the present situation in the Caspian Sea – including the potential impact of *Mnemiopsis* on the Caspian seal – is sufficiently dire that we propose that research on this subject, or other avenues of control, should proceed with the greatest urgency.

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