Gelatinous invaders in the macroplankton of the Ponto-Caspian basin

H.J. DUMONT

Introduction

Physical background

The Black Sea, the world's largest mesohaline meromictic lake (SOROKIN 2002), and the Caspian Lake, a holomictic lake with a gradient in salinity from fresh in the north to mesohaline in the south (KOSAREV & YABLONSKAYA 1994), are remnants of the Tethys ocean. With the opening of the Bosphorus around 6-7,000 BP, the Black Sea became reconnected to the marine world, and lost most of the endemic biota it had acquired across the Tertiary (ZAITSEV & MAMAEV 1997). The Caspian, in contrast, remained a closed basin throughout its history and, in spite of considerable fluctuation in size and salinity, accumulated an impressive endemic fauna, with molluscs and crustaceans dominant (DUMONT 1998).

One of the feeder rivers of the Black Sea, the Don, emptying in the Sea of Azov in the NE (fig. 1), runs north close to the Volga, the main river debouching in the Caspian. In the 20th century, under the Soviet regime in the USSR, the Lenin canal, uniting both rivers, was dug (fig. 1). This canal made it possible for ocean-going vessels to leave, say, the Caspian ports of Iran, and dock in New York or Chesapeake Bay. Alternatively, ships might take advantage of the Caspian-Baltic waterway, totally renovated by 1964, and by navigating through the canals linking the Volga, through lakes Onega and Ladoga, to end up in the Baltic or in the White Sea. The first route opened a possibility for dispersal by ship ballast water (see further). The second allowed the Caspian, for the first time since the mid Tertiary, to act as a source for emigrating species, as well as a target for invading species.

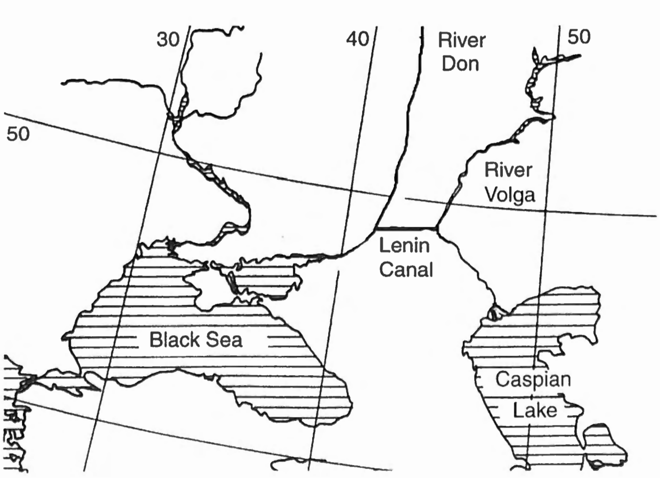

Fig. 1 — The Ponto-Caspian basin, showing the major rivers and the Lenin Canal uniting the Black Sea to the Caspian Lake.

Background to the success of the jelly invaders: growing economies, growing populations, and overfishing of the pelagic carnivorous fish

Since the 1960s, the economies of the countries bordering the Black and Caspian Seas to the north, and especially the countries of the Danube basin, started growing at an accelerating rate. To the south, the human populations of Turkey and Iran were in expansion. Both contributed to increase the pressure on the resources of the Ponto-Caspian.

As of the 1970s, the Black Sea ecosystem, and especially the shallow shelf areas to the north-west, started changing: algal blooms appeared, and benthic forests of macro-algae began shrinking. Increased fishing pressure eliminated one large pelagic species after the other: tuna, bonito, bluefish, and mackerel, migratory fish that seasonally immigrated the Black Sea in search of abundant food, were fished to extinction or near-extinction one after the other (fig. 2).

Interestingly, small sized species like anchovy, sprat, and horse-mackerel reacted to this predatory release by expanding in numbers and biomass. So did the Turkish fishing fleet, which specialised in these relatively small fish, and prospered as never before, especially in the 1980s, when peak fish landings of well over 600.10^3t were reached. Anchovy, with up to 525.10^3 t, represented the bulk of that, and Turkey became the biggest producer. More fishermen than ever before entered the business, and many took out loans with commercial banks to start up or expand their business.

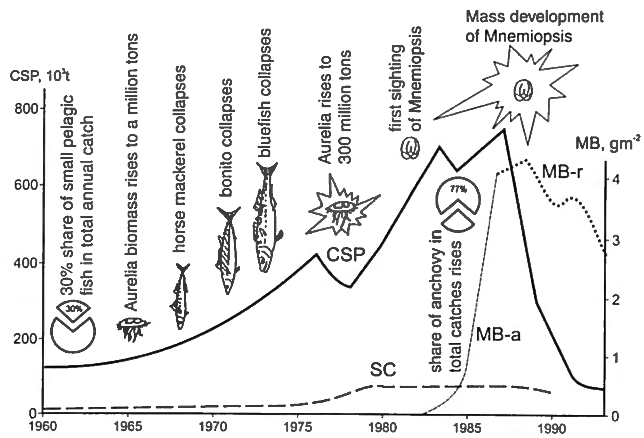

Fig. 2 — The sequence of ecological disturbances affecting the Black Sea over most of the last four decades. CSP = total fish landings; SC = annual catch of sprat; Mb-a, Mb-r = mean biomass of *Mnemiopsis* in grammes per square meter (a: estimated, before 1986; r: recorded, after 1986). Based on data by Yuvenali ZAITSEV (Odessa), figure borrowed from SOROKIN (2002) (reproduced with permission of Backhuys publishers).

Jellies dominate the scene in three phases

In the 1970s, there was little awareness about the connectivity of the food web of the Black Sea. The demise of the large predatory fish was regretted, but for economic reasons only. Typical of the ecological short-sightedness of that time, the fact that their disappearance, coupled to a mounting eutrophication, might release not only small fish but also some elements of the macro-zooplankton from predation, was hardly noticed.

The first major species to expand to bloom proportions was the scyphozoan *Aurelia aurita*, a planktivorous medusa with an inconspicuous vegetative polyp stage. The sexual stage, a medusa, has an average diameter of about 10 cm, although some specimen may reach up to 30 cm in size. Several cryptic species exist, and the Black Sea one is perhaps not the true *A. aurita* (DAWSON & MARTIN 2001), but that name shall be used here by convenience. In the pristine Black Sea, *Aurelia aurita* typically built biomasses of the order of 20-50 g m^{-2} of fresh weight. By the early 1980s, it had expanded twenty-fold, reaching up to 1 kg m^{-2} (30-60 specimens m^{-2}), and consuming about half of the non-jelly zooplankton production (fig. 2). Its consumption of zooplankton was about 20 times that of fish, and its consumption pattern completely masked the stimulating effect of eutrophication on that zooplankton. This *Aurelia* bloom, in hindsight, would only prove to be phase one of a series of three jelly invasions.

Mnemiopsis spoils the party

In autumn 1982, scuba divers off the SE coast of Crimea recorded the first few specimens of a ctenophore (fig. 3), identified – erroneously as it turned out – as *Bolinopsis* sp. (PERELADOV 1983). The observation was published in Russian in the proceedings of a Russian conference on marine biology printed in Ukraine, and was hardly noticed. The GESAMP report (1997) gives a tabular overview of the expansion of this ctenophore, meanwhile correctly assigned to the genus *Mnemiopsis*, although its specific status remains clouded to date (either *leidyi* or *mccradyi).* By 1988, its expansion had reached catastrophic dimensions, with a biomass of 1.5 kg m^{-2} fresh weight (VINOGRADOV *et al.* 1989). A peak was reached the next year with biomasses in the open sea reaching 4 kg m^{-2} and numeral abundances of ca 7,000 ind m^{-2} (VINOGRADOV *et al.* 1992), representing a biomass of 1.10^9t, more than the planet earth's yearly fish landings.

It is now generally agreed that *Mnemiopsis* was imported with ballast water (fig. 4) from (a) ship(s) coming from the East Coast of the Americas, where the species is native and inhabits estuaries where it is exposed to diurnally fluctuating salinities and temperatures.

Being estuarine, the species is euryhaline and eurythermic (survival possible at temperatures as low as 1-2°C, but top performance only reached at about 20°C). Likewise, it may tolerate salinities down to 3.5 and up to 75 (GESAMP 1997), although it is not doing well close to these extremes (but see further: Caspian lake) and might be over its optimum (which is situated at 10-15) in the open water of the Black Sea, which explains its success in the fresher Sea of Azov.

How could such a rapid expansion occur? I see at least three reasons:

1) An intrinsic factor: the reproductive machinery of Mnemiopsis

The reproductive biology of *Mnemiopsis* predestines it for rapidly colonising new environments. It is a selfing her-

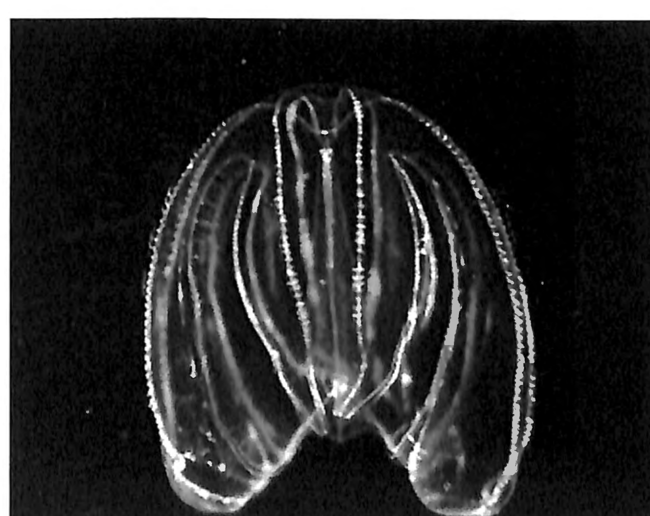

Fig. 3 — *Mnemiopsis leidyi* photographed in an aquarium by Dr Tamara SHIGANOVA (Moscow).

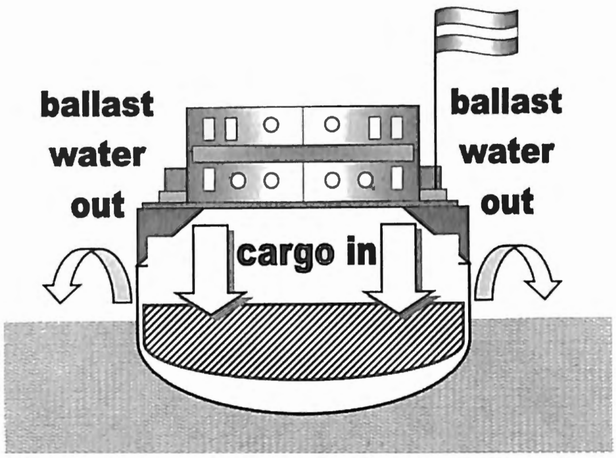

Fig. 4 — Modern ships take in ballast water when not fully loaded with cargo, and discharge this when taking in cargo. Even when loaded, the cargo tanks cannot be considered to be free of organisms, however. Ballast water is thus currently one of the most powerful means of animal and plant dispersal across the planet.

maphrodite (whether cross-fertilisation ever occurs in the genus is an open question) that spawns at 10-20 days intervals, and releases 100-10,000 eggs at a time, depending on food availability. The life span of an individual may last for an entire spring-summer, thus quite a few spawning events may take place, concentrated in summer. Embryonic development is, of course, time dependent, but takes only one day at 23°C, and larvae grow to reproductive size in about two weeks (SHIGANOVA *et al.* 2000a,b).

In the native range of the species, estuaries along the east coast of North, Central, and South America (PURCELL *et al.* 2001), this tremendous fertility is counterbalanced by the two severe ecological constraints discussed hereafter. These were not or no longer operative in the Black Sea in the 1980s.

2) No predators, weak competitors: ''if you can't join them, eat them''

One might raise the academic question what would have happened had *Mnemiopsis* arrived in the Black Sea while it was still in a pristine condition. In fact, it is quite conceivable that it did arrive not one, but many times. Under this multi-introduction hypothesis, the inescapable conclusion is that all but the last attempt failed. Why could this be? Quite possibly, early attempts at invading were checked by the large predatory fish that used to populate the Black Sea, and which are known to eat jellies. In their absence, unchecked reproduction thus became much easier, and was facilitated by the fact that *Aurelia* proved only a poor competitor to *Mnemiopsis*. Fish eating jellies are affected by parasites that mature inside the fish (PURCELL & ARAI 2001). The disappearance of such fish, by rupturing the parasitic cycle, may have conferred an additional advantage to the ctenophore

3) An abundance of food

Mnemiopsis is a versatile, opportunistic, occasionally cannibalistic animal that feeds superfluously (several times its own body weight per day) as long as food presents itself to the mouth opening. Wasteful killing is common, and stomachs full of dead but undigested prey are at times regurgitated. One factor that has not been widely recognised, but may explain the rapid decline of *Aurelia* after the bloom of *Mnemiopsis*, is that the latter may have used the ephyrae and young medusae of *Aurelia* as a source of food. There are no hard data to support this statement, but circumstantial evidence is also available from the Caspian invasion in 1999 (see further). This unusual form of winning a competition by actually eating the competitor in its young stages is probably more common in nature than generally thought and also applies to *Mnemiopsis*' habit of eating fish eggs and larvae. The net result was that, as long as sufficient food, including crustacean zooplankton, chaetognaths, other jellies, and fish eggs, was available, *Mnemiopsis* could continue its ''photocopying'' style of reproductive behaviour.

The Black Sea fisheries collapse at the end of 1988

By the summer of 1988, all but the strongest vertical migrators – almost exclusively calanoid copepods – of the Black Sea zooplankton had been reduced to levels as low as to be unobservable by ordinary sampling methods. This included *Aurelia* and pelagic fish eggs and larvae. Fish therefore found little to eat, and their recruitment was destroyed. As a result, the pelagic fisheries, which had overshot 600.10^3 tons in 1988, collapsed. They halved in 1989, and fell to 100.10^3 tons in 1991. Numerous, mostly Turkish, fisherman went bankrupt and left the fishing business between 1989 and 1992 (SOROKIN 2002, KIDEYS 2002).

Beroe, a third player, appears on the scene

It is ironical that in 1997, the report of the GESAMP experts on the *Mnemiopsis* problem in the Black Sea was printed. Among possible actions to counter the effect of the jelly invader, it was proposed to introduce another Ctenophora, *Beroe*. Species of *Beroe* are specialist carnivores, that only eat other jellies. Exactly that year, the first specimens of a *Beroe* were spotted in the coastal zone of the northern shelf (KONSULOV & KAMBURSKA 1998). To date, confusion continues to reign as to what species is involved, although it is now usually cited as *Beroe ovata* MAYER (SHIGANOVA *et al.* 2001a). Earlier in the 1990s, a *Beroe* had been spotted in the Sea of Marmara (SHIGANOVA *et al.* 2000a) and, possibly, it is this Mediterranean species that expanded into the Black Sea in search of its favourite food, *Mnemiopsis*, which had become superabundant here. However, exactly as *Mnemiopsis* has so far failed to expand significantly from the Black Sea to the Mediterranean because of a supra-optimal salinity here (SHIGANOVA *et al.* 2001b), the Mediterranean *Beroe* might be prevented to settle in the Black sea on account of its infra-optimal salinity. Hence, many consider that the *Beroe* of the Black Sea is another recent arrival from the coastal USA, transported by ballast water.

Beroe ''*ovata*'', larger than *Mnemiopsis*, quickly turned out to be an efficient antidote against it: as of 1998, *Mnemiopsis* abundance collapsed, although it took until 2000 for *Beroe* to penetrate the (much fresher) Sea of Azov. By 1998, therefore, it can be said that a biological control of *Mnemiopsis* had installed itself in the Black Sea. The outcome of this is expected to be a coexistence of *Beroe* and *Mnemiopsis*, both at population levels sufficiently low to be tolerable by the zooplankton (KIDEYS 2002).

The Caspian lake: the next domino to fall

The Caspian, the largest lake in the world, has a salinity gradient from the Volga estuary in the North (essentially zero salinity) to 13-14 in the South-East. This enclosed lake used to produce about 90 % of the world's caviar, and has a level of endemicity comparable to that of Lake Baikal (DUMONT 1998). Like in Lake Baikal, its top predator is a seal, *Pusa caspica*, of which the population size varies between 200,000 and 500,000 specimens (KHURASKIN & POCHOYEVA 1998).

Sturgeon and seal are clearly flagship species of the Caspian, but, in addition, it harbours about 400 endemic species of crustaceans and molluscs. Many of the crustaceans are benthic, but quite a làrge fraction is partly or exclusively planktonic.

Around the middle of the past decade, I summarised the environmental problems of the Caspian (DUMONT 1995) and warned of the possibility that *Mnemiopsis* would, sooner or later, cross the Lenin canal (with ballast water or by other means). I predicted that it would find in the Caspian -especially the deep south basin- an environment that, by temperature and salinity, suits it even better than the Black Sea. Its food would be the numerous endemic crustaceans which -totally naïve to a destructive alien predator- could be expected to get decimated.

This prediction, sadly, was confirmed earlier than I thought. By 1996, rumours started circulating that fishermen in Turkmenistan and Iran had noted ''strange jellies'' in their nets. I undertook a cruise off the coast of Turkmenbashi in Turkmenistan in June, but could not find *Mnemiopsis*. Apparently, the population was still in its lag phase, with specimens hard to come by, especially from shipboard. Late in 1997, the World Bank called a meeting of experts to discuss the Caspian Environment in Bordeaux (DUMONT *et al.* 1998). Little was said here about *Mnemiopsis*: all efforts still concentrated on saving the sturgeon fishery, which slightly later collapsed anyway. But things would soon change.

In late 1999, at a conference in Astrakhan (Russia), two students of Caspian crayfish, Vladimir USHIVTSEV and Andrey KAMAKIN, presented a video of their fieldwork on a littoral plateau in the middle of the east coast of the Caspian. Nikolay ALADIN from St Petersburg, who also attended the meeting, was struck, not by the astacids being shown, but by the unmistakable presence on the tape of two jellies: *Aurelia aurita,* and a *Mnemiopsis*.

ALADIN obtained the tape, and sent it to me. I discussed its content with Richard HARBISON from Woods Hole and with a number of Russian colleagues, and we agreed that several specimens of *M. leidyi* could be identified on the tape. But although alarmed, we did not fully anticipate how rapidly the events would now move: by next July, there was an outbreak in the middle and south Caspian and by late summer, large numbers had moved north into salinities of 2-4, reputedly the lower limit of tolerance of the species but also the zone of the Caspian where most zooplankton food is available! Locally, especially in the SE, biomasses of the order of 0.5 kg m^{-2} were recorded. The paper relating this story up to the end of 2000 was published early in the next year (IVANOV *et al.* 2001). But by the summer of 2001, a threshold of 1 kg m^{-2} was overshot in many locations, and effects of *Mnemiopsis* became incisive: the zooplankton was decimated, with the marine cladoceran group of the Onychopoda, largely endemic, apparently extinct, and the main pelagic fish, small sardine-like clupeids collectively known as ''kilka'', collapsing. History repeated itself: many fishermen in Iran stopped their activities. The top predator, the seal, fully dependent on kilka for its feeding, had suffered from canine distemper virus in the 1990s (FORSYTH *et al.* 1998), but now became deprived of its food as well. In 2002, a dramatic drop in the pregnancy rate of the females was recorded.

It should be noted, finally, that *Aurelia*, prominently present on the videotape, has not been seen since. Clearly, *Mnemiopsis*, like in the Black Sea, has completely overtaken it, apparently by the same combination of competition and predation that gave it an edge in the Black Sea.

Beroe *in the Caspian: to introduce or not to introduce?*

In view of the Black Sea experience, it seems straightforward to intentionally introduce *Beroe* to the Caspian, in order to limit further damage. The United Nations GEF project on the Caspian called two expert meetings in Baku (a third one is scheduled for early July 2002), which I had the honour to chair, to discuss the rationale of this move. It was agreed to ask the governments of the five littoral countries to endorse introduction as soon as a threshold of 1 kg m^{-2} would be reached. This happened – in fact the threshold was surpassed in many places and on many occasions – in summer 2001. Introduction, however, requires the agreement of ALL littoral states, and approval by the FAO. The procedures to obtain both are currently underway, and it is hoped that introduction of specimens airlifted or speed-boated from the sea of Azov will be possible in July 2002.

There is, however, some resistance to introduction, based on failed introductions, or introductions that went wrong in the past. There are claims that we do not know enough of *Beroe* to introduce it. Opposed to this is the quasi-certainty that, if we do nothing, we may loose a substantial part of the endemic biological diversity of the Caspian. Moreover, we may never know enough of *Beroe* to establish beyond any doubt that nothing will go wrong if it is introduced.

Another argument which was tabled could be describe as *ostrich politics*: since *Beroe* arrived ''spontaneously'' in the Black Sea, it will also, sooner or later, reach the Caspian. Let us, therefore, allow nature to take its course. Opposed to this position is the fact that, until this happens, the losses will be terrible and irreparable. I should also mention that there exists a proposal not to introduce *Beroe* but a specialised fish predator of jellies. The butterfish, *Peprilus triacanthus*, from coastal North America has been nominated, because it is a tasty species that might create a new resource to the already badly affected Caspian economies (HARBISON 1993). Such a win-win situation indeed seems quite attractive. However, and sadly, too little is currently known about the biology of the butterfish (where and how does it reproduce?) to make it reasonably safe to attempt its release in the Caspian.

With our current ecological wisdom, introducing *Beroe* therefore seems the only viable option. The prospect is that both (*Beroe* and *Mnemiopsis*) will live side by side in the Caspian in the future, until such time as a predator of both (*Peprilus*, for example) can be added to the system. *Beroe* can thus buy us some time, but time is the scarcest resource we have: the option of doing nothing might mean that the summer of 2002 might cause havoc, worse than in the Black Sea in 1988!

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Henri J. DUMONT
Animal Ecology
Ghent University
K.L. Ledeganckstraat 35
B-9000 Ghent