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The Invasion of *Beroe ovata* in the Black Sea a warning signal for ecosystem concern

Lyudmila Kamburska, Snejana Moncheva, Asen Konsulov, Anton Krastev, Kamen Prodanov

Institute of Oceanology, Bulgarian Academy of Sciences, Varna, Bulgaria; e-mail: cesum-bs@io-bas.bg

Introduction

Biological invasions as global environmental and economical problems have been well documented all over the world (W i n d l e, 1997; S h a r o v, L i e b h o l d, 1998; C o h e n, C a r l t o n, 1998). The dramatic effects of various plants and animals that have been already introduced (accidentally or intentionally) by human activity in the past 200 years have been catalogued (V i t o u s e k et al., 1996). The ecological economic impact analyses, empirical approaches, techniques and forecasting models have been developed to support the viable management strategies to protect the native land and aquatic ecosystems against the exotic species invasions (H i g g i n s et al., 1997; V o l o v i k et al., 1995).

According to the list given by Z a i t z e v, M a m a e v (1997), a lot of species of Atlantic and Pacific origin have been accidentally introduced during the 20th century into Black Sea basin. The invasion of non-indigenous species together with the anthropogenic eutrophication and overfishing during the last twenty years emerged to a key ecological problem for the ecosystem health (M e e, 1992; V i n o g r a d o v et al., 1992; K i d e y s, 1994; Z a i t z e v, A l e x a n d r o v, 1997).

An excellent example of the exotic invaders impact on the Black Sea ecosystem is

the successful adaptation of the ctenophore Mnemiopsis leidyi introduced into the Black and Azov Seas through the ship ballast waters from North Atlantic in the mid 80-ies (Vinogradov et Harbison, Volovik, 1993). M. leidyi became one of the major factors for the dramatic ecosystem alterations in the early 90ies, and it has been considered to contribute substantially in the reduce of the commercial fish stocks, zooplankton diversity and changes in the community structure (G u c u, 1997; Konsulov, Kamburska, 1998; Kideys et al., 1998; Kideys et al., 2000). Regardless of its seasonal and annual fluctuations, this species sustains a high population level and it has already become a current component of the Black Sea ecosystem due to the lack of predators (GESAMP, 1997). A lot of experimental, field and modelling research was conducted, with the aim to highlight the perturbations and forecast the functioning of the Black Sea pelagic system in "Mnemiopsis era" (H a r b i s o n, 1993; O g u z et al., 1999).

A strategy to control the expansion of the alien ctenophore in the Black and Azov Seas has been elaborated by GESAMP biodiversity working group (GESAMP, 1997). The advantages and disadvantages of different approaches and methods were discussed in

order to afford the negative impact once taking the dimension of biological pollution. It was suggested as the most realistic mode for success the ecological control approach (either by introduction of predator species or by parasites, pathogens, etc.). The international scientific community focused on the possible intentional introduction of *M. leidyi's* predators and the ctenophore *Beroe* was suggested as one of the most appropriate species (S w a n b e r g, 1970; R e e v e, W a l t e r, I k e d a, 1978).

In 1997 the dilemma was in a way solved, since the new for the Black Sea ecosystem Ctenophore Beroe ovata (M a y e r, 1912) was reported for the first time along the Bulgarian Kamburska, (Konsulov, interaction 1998a). The of Beroe ovata - Mnemiopsis leidyi Ctenophores in a typical predator prey mode, provokes many questions for the impact on the zooplankton dynamic and its adequate response to the new environment and for the future performance of the Black Sea ecosystem.

Initially the Black Sea ecosystem evolution has been subdivided into different phases, depending on the view point of the critical aspect of anthropogenic impact eutrophication, Jellyfish explosion, overfishing): pristine period (50-70-ies), period of intensive eutrophication (70-80-ies), recent period of relative relaxation (B e s i k t e p e, U n l u a t a, Bologa, eds. 1999). The pristine period – Rhizostoma pulmo prevailed (60-70-ies), period of Aurelia aurita expansion (70-80ies), recent period is nominated as *Mnemiopsis* era (Kideys, 1994; Niermann et al., 1999). These periods do not necessarily overlap due to the synergistic interaction between the environmental factors including global climatic changes (N i e r m a n n et al., 1999).

Our hypotesis is that the invasion of *Beroe* ovata is a warning for future ecological concern of the Black Sea. In order to target the problem the following aspects are discussed:

1) long-term overview of zooplankton dynamic alterations in relation to phytoplankton, *Mnemiopsis leidyi*, anchovy stock dynamic; 2) preliminary results on *Beroe* ovata—Mnemiopsis leidyi coupling; 3) cases within the World Ocean where these two ctenophores co-exist, as examples of ecosystem impact study.

Material and methods

Study area

The study is based on the long-term national monitoring data collected at a station 3 miles off Cape Galata along the Bulgarian Black Sea coast. Some investigations were carried out during the ComSBlack and NATO-TU international scientific cruises in September 1991 (HydroBlack '91), July 1992 (ComSBlack '92) and August (ComSBlack '95) in the Western Black Sea on board the R/V "Akademik" of the Institute of Oceanology -Bulgarian Academy of Sciences. The recent data were collected during 1996-1999 in the coastal zone off Cape Galata (1 station at 3 miles, depth 21 m), including Varna Bay (11 stations, max. depth 21 m). The latter was selected as one of the most eutrophicated region along the Black Sea coast (fig. 1).

Parameters

To overview the alterations in the Black Sea pelagic ecosystem a long term data serie is discussed including the following parameters: *Phytoplankton: data set 1967 1995

(Moncheva, 1991; Moncheva, Krastev, 1997) and unpublished data (1996-1998).

*Zooplankton: data set 1967 1995 (K o n s u l o v, K a m b u r s k a, 1998) and unpublished data (1996 - 1998).

*Flagellates: *Noctiluca scintillans* long-term spring summer abundance (1967 - 1998) (K o n s u l o v. K a m b u r s k a. 1997).

*Jellyfish: Mnemiopsis leidyi and Beroe ovata abundance and distribution-published (K i d e y s et al., 1998; K o n s u l o v, K a m b u r s k a, 1998) and unpublished data.

*Anchovy total biomass and total Black Sea catch: long term data (1967 - 1997) published.

Methods

Zooplankton samples were collected by a vertical plankton Jeddy type net (150 µm mesh size). Samples were fixed to 4% formalin solution after sorting out, counting and measuring the size of *M.leidyi*, *A.aurita* and *B.ovata*. The size groups ratio of *B.ovata* (M a y e r, 1912) and *M.leidyi* (M u t l u, 1994) was presented in order to determine the population age structure. Identification of the

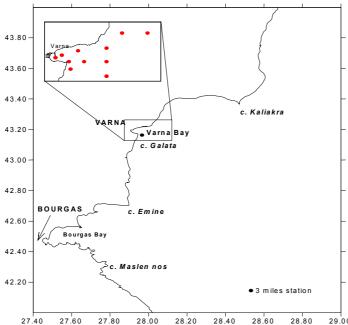


Fig. 1. Map of sampling stations along the Bulgarian Black Sea coast

samples to species level was done under a binocular microscope. The analysis of species abundance was performed according to Dimov's method (D i m o v, 1959). Biomass (mg·m⁻³) was estimated by using individual standard-wet weight (P e t i p a, 1959).

Results

Alterations of zooplankton dynamic in relation to phytoplankton, Mnemiopsis leidyi and anchovy stock variability during 1967-1990 The study of the long-term zooplankton data set has revealed significant fluctuations in the spring/summer dynamic of the fodder zooplankton biomass and community structure. During the period 1967-1975 (before the period of intensive eutrophication in the Black Sea) the average biomass was 296 mg·m⁻³±166 and the highest value was recorded in 1969 (fig. 2 A). During 1977-1981 (in the onset of anthropogenic eutrophication) the average value was 367 mg·m⁻³ with a maximum in 1981 of 683 mg·m⁻³. From 1982 till 1990 (period of intensive eutrophication) the average spring/summer zooplankton biomass dropped 3.5 times in comparison to the previous period and was kept at lower values with a minimum in 1987 (fig. 2 A),

accompanied by significant alterations in zooplankton community structure. diversity and biomass of Copepods-typical for the Black Sea ecosystem zooplankton group decreased substantially (fig. 3 Å). While in the early 70-ies this major group overdominated Cladocera species (in average 66 %, maintaining a share higher than 50 % of the biomass), oscillations of their spring-summer biomass ratio during the 80-ies is apparent The copepods Anomalocera (fig. 3 A). pattersoni, Pontella mediterranea, Centropages kroyeri and Oithona nana were common in 70-ies and rare in 80-ies. During 1973-1989 the average biomass of Q. nana and C. kroveri was 1.46 mg·m⁻¹ 2.37 mg·m⁻³ respectively, almost 6 times lower than that in the early 70-ies. On the contrary N.scintillans (an indicator species of dominant eutrophication) became frequent and massive blooms. In 1967-1975 its average abundance was low- 1364 ind·m⁻¹ while in the period of intensive eutrophication (1978-1988) it increased about 7 fold (9087 ind m³) with a higher range of spring/summer oscillations. Two extremely evident-in high maxima are

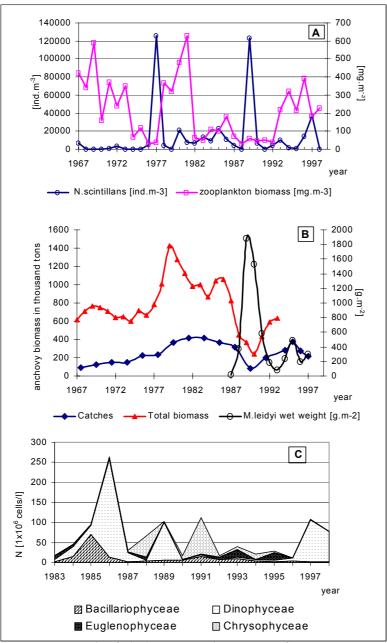


Fig. 2. Long-term dynamic of: A. Average spring-summer fodder zooplankton biomass [mg·m⁻³] and *N.scintillans* abundance [ind·m⁻³] at 3 miles station off cape Galata; B. Total anchovy biomass and catch in Black Sea, average *M.leidyi* biomass [g·m⁻²] in Black Sea (K i d e y s et al., 2000); C. Average spring-summer phytoplankton bloom abundance [1·10⁶ cells/l] at 3 miles station off cape Galata including Varna Bay

(125 619 ind·m⁻³) and in 1989 (123 424 ind·m⁻³) (fig. 2 A). The decrease of fodder zooplankton biomass during the 80-ies is concurrent with intensification of phytoplankton blooms and increased anchovy total biomass irrespective of the increased catches (fig. 2 B, C).

The onset of anthropogenic eutrophication (the 70-ies) marked the inversion in the

dominance of the major phytoplankton taxonomic groups especially in spring-summer, the opportunistic dinoflagelates overdominating the diatoms (fig. 3 B). During the 80-ies the increasing eutrophication induced further dramatic changes in phytoplankton communities structure, abundance and biological cycle, and phytoplankton blooms were a recurrent

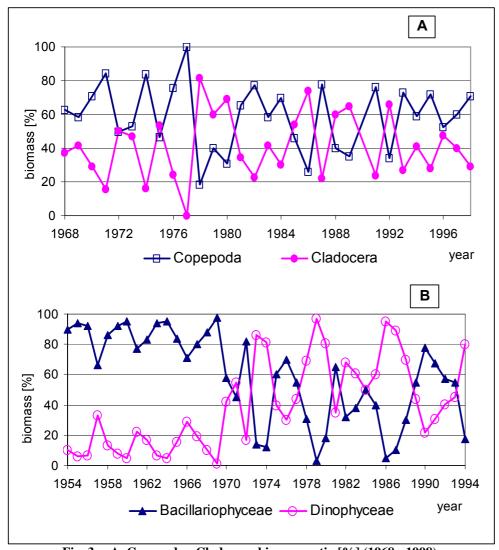


Fig. 3. A. Copepoda : Cladocera biomass ratio [%] (1968 - 1998); B. Bacillariophyceae: Dinophyceae biomass ratio [%] (1954 - 1997), in spring - summer at cape Galata including Varna Bay

phenomena. The enhanced outbursts of dinophytes and chrysophytes and the intensification of bloom frequency, duration and densities attained in spring-summer, as well as the diversification of the bloom species became the main features of phytoplankton dynamic (fig. 2 C).

Unlike the fodder zooplankton biomass, the total anchovy biomass in Black Sea was 2 times higher in 1977-1986 (1056 thousand tons) in comparison to 1967-1976 (683thousand tons) despite of intensification of total Anchovy catches which also may count for the depression of fodder zooplankton

biomass (fig. 2 B).

The biomass of Mnemiopsis leidyi presented a sharp increase in 1988-1990 with a value of 2000 g·m² in the Western Black Sea coastal area (fig. 2 B). The maximum value of 12 kg·m⁻² was found along the Bulgarian shelf 1990 April (Bogdanova, Konsulov, 1993). As a voracious predator of zooplankton and main food competitor of planktivore pelagic fishes and their larvae, the expansion of this ctenophore most likely contributed to the maintenance of the fodder zooplankton biomass at a lower level and to the sharp decline of anchovy biomass during 1988-1990.

Alterations of zooplankton dynamic in relation to phytoplankton, Mnemiopsis leidyi and anchovy stock variability during the 90-ies

Low biomass values of fodder zooplankton were found in 1991-1992 and a critical biomass of 40 mg·m⁻³ was observed at 3 miles off Cape Galata (fig. 2 A). Nevertheless, the general feature during the 90-ies (a period of relaxation of anthropogenic eutrophication) was the increase of biomass despite its small fluctuations. The average fodder zooplankton biomass for the period 1993-1998 was 259 mg·m⁻³±79, that is more than twice higher in comparisson to the 80-ies, but almost similar to that during 1967-1975 (fig. 2 A). Further changes in the zooplankton composition and taxonomic structure were observed during the 90-ies, Copepods dominated the fodder zooplankton biomass representing more than 50 % of zooplankton biomass (fig. 3 A). The Copepods and Cladocerans species are the major prey of M. leidyi (Reeve, Syms, Kremer, 1989). The oscillations in the percentage Copepoda: Cladocera biomass ratio in the late 80-ies-early 90-ies (fig. 3) could be related to either *Mnemiopsis* predation pressure or food availability especially in spring-summer. In contrast to the 80-ies after 1993 the ratio Copepoda: Cladocera biomass increased in favour of Copepods similar to the early 70-ies, indicating current changes in the pelagic food web.

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The cladocera *Pleopis polyphemoides* represented more than 60 % of zoobiomass during the 80-ies but it dropped twice in the 90-ies. On the contrary the cladocera *Penilia avirostris* was rare during the period of intensive eutrophication, while in the 90-ies it had the greatest contribution to the Cladocerans biomass (70 % in 1995). The structure and composition of *Copepods* was also significantly changed in the 90-ies. *Acartia clausi* had a frequency of distribution 100 % during the 80-ies, whereas in the 90-ies its contribution in the total zooplankton biomass decreased, although it was still a dominant species inshore.

Alternatively, the percentage share of N. scintillans in the total zooplankton biomass decreased. Only one bloom outburst was recorded in June 1997 (about 37000 ind·m⁻³) at a density about 4 times lower than the extremes during the 80-ies. The oscillations of its abundance in the 90-ies were of much lower amplitude than that in the 80-ies. Altogether these provide evidence for changes of zooplankton communities structure and dynamic contrasting to the period of intensive eutrophication. Thus the signs of recovery of fodder zooplankton biomass after 1993 correspond to a relative decrease of phytoplankton blooms and *N. scintillans* abundance and a relative increase of M. leidyi and anchovy biomass after the critical low values in 1991-1992 (fig. 2 B, C).

A characteristic feature of the 90-ies is the increase of phytoplankton species variety, involved in bloom episodes, typical for the period of intensive eutrophication. A lot of species have attained bloom densities, exceeding about 1.5 times that of the 80-ies, and about 5 times that of the 60-70-ies. Species like Detonula confervaceae, Chaetoceros curvisetus, Chaetoceros socialis, Cyclotella caspia, Pseudosolenia calcar-avis, Pseudonitzschia seriata (Bacillariophycea), typical for the 60-70-ies sustain bloom

abundance more frequently during the 90-ies, in comparison to the 80-ies. Although the blooms were frequent during this period, there was a decrease of both monospecific blooms and high abundance values were attained especially in spring-summer (fig. 2 C). During the period 1980-1990, were recorded 7 cases when a single microalgae reached concentration about 50·10⁶ cells/l and more (the highest attained by P. minimum-481·10⁶ cells/l) in comparison to only 3 during 1991-1998 (P. minimum outbursts during 1997-1998 were of densities within the range $100-200\cdot10^6$ cells/l). Some diatoms Ch. socialis $(35.5 \cdot 10^6 \text{ cells/l-summer}^2)$, dinoflagellate and the P. minimum (206·10⁶ cells/l–summer'97) continue generate high numbers but at much lower frequency than in the 80-ies. The maximum average density decreased slightly in spring, and about twice in summer, (132.2-76.5·10⁶) cells/l) on the account mainly of non-diatoms (two-fold reduction of the average abundance). In contrast to the 80-ies the ratio Bacillariophyceae: Dinophyceae has increased. ecosystem shifted towards harmonised seasonal dynamic-reduced amplitude of seasonal oscillations and year to year variations-a trend, which has been interrupted in 1997. Phytoplankton and zooplankton communities manifest parallel structural changes in terms of major taxonomic groups during the different phases of the Black Sea ecosystem evolution (fig. 3).

After the depression in 1989-1991 (critically low total and spawning biomass and respectively total catch) the anchovy biomass reached 637.1 thousand tons in 1993, followed by a very high anchovy catches in the recent period 1994-1997 (285.2 thousand tons), closed to the that found during 1977-1988 (fig. 2 B). The critically low biomass at the end of the 80-ies could well be attributed to *M. leidyi* explosion and overfishing, the *Mnemiopsis* predation and food competition pressure suggested to play an important role in the sharp decline of Black Sea pelagic fisheries

After its outburst in the late 80-ies, *M. leidyi* average spring/summer abundance along the Bulgarian Black Sea coast was the lowest in 1991-1992 (3-10 ind·m⁻³), and started to increase since 1993 (when the

fodder zooplankton biomass was about 230 mg·m⁻³). During summer, at 3 miles off Cape Galata its abundance in 1995 was 277 ind·m⁻³, in 1996 - 600 ind·m⁻³, reaching a maximum of 4 000 ind·m⁻³ in 1998 (in Varna Bay), despite the presence of the newly introduced ctenophore Beroe ovata (since 1997). Although the *M. leidyi* biomass has increased after 1993, the detected values were almost 4 times lower than the highest values observed in late 80-ies (fig.2 B). Weather this decrease was related to a reduction of the available (Shuskina, prey Vinogradov, 1991), to the different conditions environmental or parasites (M u t l u et al., 1994) or this is a performance typical for a period after initial invasion of a novel environment, cannot yet be stated. Possibly the 1991-1992 mark

Possibly the 1991-1992 marked a breakdown of the interaction pattern in the pelagic food web typical for the 80-ies, no matter that the underlying mechanisms might be various, not ignoring the possible role of global climatic signal too (N i e r m a n n et al., 1999). The forgoing analysis suggests that most likely the changed predator-prey interactions during the 90-ies evolved to the degree of an important controlling factor.

Preliminary results on Beroe ovata-Mnemiopsis leidyi coupling

In order to give an idea on the efficiency of Beroe predation pressure on M.leidyi the abundance and the age structure of their populations are analyzed (fig. 4). After a relatively high M. leidyi abundance in August 1996, the new for the Black Sea ecosystem ctenophore B. ovata was detected in October 1997 (12 ind·m⁻³) with mature (70 %) and nonmature (30 %) individuals along the Bulgarian Black Sea coast. In November 1997 B. ovata was recorded with only mature adult individuals of more than 70 mm length (32 ind·m⁻³), co-occurring with larval stages (33 %) and post-larvae (67 %) of *M. leidyi* at a low density (3 ind·m⁻³, fig. 4). In August 1998 B. ovata was not found, while larval (96 %) and post-larval (4%) stages of M. leidyi attained a high density of 671 ind·m⁻³ at Cape Galata and reached a maximum 4000 ind·m⁻³ in Varna Bay, that is more than 7 times higher than in August 1996. In September 1998 only M. leidyi larvae (88 %) and post-larvae (12 %) occurred at 3 miles off

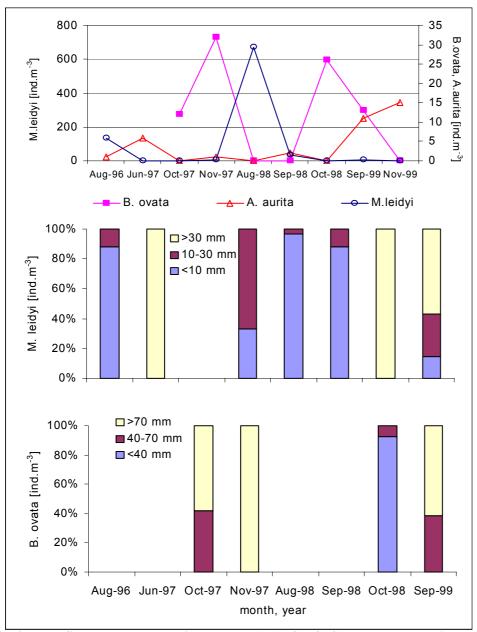


Fig. 4. Jellyfish abundance and size structure [%] of *M.leidyi*, *B.ovata* populations at 3 miles off cape Galata (1996-1999)

cape Galata, but at much lower abundance than in August (33 ind m⁻³). *B. ovata* was absent in the area, although few individuals of this ctenophore were randomly observed along

the Bulgarian coastline. In October 1998 a homogenous population of immature only *B. ovata* individuals (<70 mm) at a density about 26 ind·m⁻³ was recorded at Cape Galata,

while the average abundance in Varna Bay was 97 ind·m⁻³. At the same time *M. leidyi* abundance was only 1 ind·m⁻³. In September 1999 M. leidyi density was 7 ind·m⁻³ (57 % mature individuals, 29 % post-larvae and 14 % larvae stages), while B. oyata was recorded with a density of 13 ind·m⁻³ (62 % individuals more than 70 mm length). The ratio B. ovata/M. leidyi abundance was in favour of Beroe (5:1), while the ratio between the food competitors Aurelia aurita/M. leidyi was (3:1) in Varna Bay. In contrast to November'97, the ctenophores were not found in November'99. On the contrary, the jellyfish A. aurita dominated fully in Varna Bay and in front of Cape Galata (fig. 4).

Our data are consistent with the finding that the active reproduction period of *Mnemiopsis* in Black Sea coastal area occurs in July-September with a maximum in August and in October-November its biomass drops because of elimination of adult individuals after reproduction, as well the grazing by *Beroe*. The preliminary results on *Beroe* occurrence in the Eastern Black Sea coast suggest that the active reproduction period is September-November, although still uncertain. Altogether the results indicate a time-lag of their occurrence and reproduction period in coastal area, typical for predator-prey interaction, giving a prospect for flourishing of the jelly *A. aurita* (competitor of *M. leidyi*).

Discussion

According to our hypotesis, the invasion of the new ctenophore B. ovata is a warning signal for future Black Sea ecosystem health concern. The overview of the zooplankton communities structure and dynamic within the context of pelagic ecosystem interactions during the different phases of the Black Sea ecosystem evolution, provide arguments to suggest that the *M. leidyi* explosion could be considered as an important factor for the zooplankton community structure alterations. Furthermore, it seems that these changes could be related to the phytoplankton blooms expansion and the sharp decline of anchovy stock during 1988-1990, even if M. leidyi's effect was superimposed to the effects of eutrophication, overfishing and environmental deterioration, not ignoring the possible impact of global climatic changes too (Niermann et al., 1999). The main features of phytoplankton dynamic contrasting to the natural for the Black Sea succession pattern and seasonal cycle (Moncheva, Krastev, 1997) have contributed substantially to the dramatic alterations in zooplankton development no matter whether it was more due to the modification of the food web base or the resulting biomodulation of the marine environment (hypoxia conditions, changes in the viscosity, inhibition by the extrametabolites, etc.). It was suggested that M. leidyi may control also phytoplankton blooms indirectly through their predation on herbivorous zooplankton and directly by the nutrient excretion (Kremer, 1976; Deason, Smayda, 1982). The reduced grazing pressure was found to be important for the intensification and the increased frequency of exceptional phytoplankton blooms along the Bulgarian Black Sea coast (M o n c h e v a et al., 2000). Thus the feedback mechanisms between zooplankton/phytoplankton also may be important in determining the pattern of zooplankton abundance in spring-summer (F r a s e r, 1962; Kremer, 1979; Mountford, 1980).

During the recent period (the 90-ies) the Black Sea ecosystem emerged from the state of critical ecological instability (the 80-ies) into a phase of relative recovery, although still fragile. Most likely the collapse of the industrial and agricultural production of all Black Sea countries during the early 90-ies have contributed considerably to the signature of ecosystem improvement (I v a n o v, O g u z, Eds., 1998). As our results reveal, possibly the 1991-1992 marked a breakdown of the interaction pattern in the pelagic food web typical for the 80-ies, the changed predator-prey interactions evolving to the degree of an important controlling factor during the 90-ies. Thus under these conditions the introduction of the new ctenophore and the prey-predator coupling M. leidyi/B. ovata could at least exacerbate the Black Sea ecosystem ecological state.

The mechanism of introduction of *B. ovata* into the Black Sea is probably the same as for the *Mnemiopsis*, that is through the ballast waters, most likely transferred from the estuaries along the North Antlantic Ocean where this species is tolerant to lower salinity. It has been reported that *B. ovata* feeds only on *M. leidyi* (Nelson, 1925; Swanberg,

1970; Burrell, Van Engel, 1976). As it was also hypotesized for *M. leidyi* (GESAMP, 1997), it is quite possible that *Beroe* has been initially introduced earlier into the Black Sea basin, and after a period of adaption to have been successfully naturalized and produce the recent outbursts.

Naturally *Mnemiopsis* exhibits an excellent reproductive potential (several times during the year) and the ability to increase population biomass dramatically in a very short time (R e e v e, S y m s, K r e m e r, 1989). A few eggs might be produced by ctenophores even in immature stages. Some authors claim that the new generation of *M. leidyi* can emerge directly from the larvae (pedogenesis) (M a l a s h e v, A r c h i p o v, 1992). These "physiological advantages" rise the question to what level *Beroe* could control the *M.leidyi* population? Naturally *B. ovata* can grow at similar rates as *M. leidyi*, suggesting that *Beroe* may be able to reduce the initial growth of *M. leidyi* populations (G E S A M P,1997).

There are a lot of examples in the World Ocean where these two carnivorous Ctenophore species co-exist in the food web structure. Beroe ovata is abundant along the North Atlantic coast of the United States e.g. Chesapeake Bay, Narragansett Bay and Great Bahama Bank (Mayer, 1912; Fraser, 1962; B i s h o p, 1967; S w a n b e r g, 1970; Kremer, Nixon, 1976; Kremer, 1979; Deason, Smayda, 1982). In Narragansett Bay it has been found that M. leidyi reduces dramatically zooplankton stocks during June-August. By the end of August/September, when B. ovata is present and feeds on *M. leidyi*, zooplankton biomass increased sharply, mainly as a result of the reduced grazing pressure (K r e m e r, 1979; Deason, Smayda, 1982). It might be that July-August is the critical period for the ecosystem where these Ctenophores co-exist. In all, it was suggested that B. ovata can have a significant impact on zooplankton dynamic in the ecosystem by efficient feeding on *M. leidyi* in September. In York-River Estuary of Chesapeake Bay, M. leidyi reduced drastically the zooplankton biomass through the year except when it was actively preyed by B. ovata during summer and fall (B u r r e l l, V a n E n g e l, 1976).

The preliminary results on Beroe/

Mnemiopsis coupling presented in this paper indicate a time-lag between their occurrence and reproduction period in a coastal area, which is typical for predator-prey interaction, giving a prospect for flourishing of the medusa A. aurita. The maximum of B. ovata abundance was in September-November, while Mnemiopsis reproduction peak was detected in August, suggesting that Beroe will not be able to ignore the negative impact of M. leidyi in midsummer.

Our results suggest that these two ctenophores interact within an "ecological feedback system", an increase of Beroe population will result in a decrease of *Mnemiopsis*, followed by a successive increase of zooplankton and pelagic fish. This scenario is more efficient in autumn in Western Black Sea, as it is evident from the preliminary results. Besides B. ovata is a food web dead-end due to the lack of a natural enemy in the Black Sea. Thus either a direct or indirect effect through the entire food web could be expected e.g. copy *Mnemiopsis leidvi*'s history and further add to the problem of gelatinous species in Black Sea (Kideys, 1994). In any case the introduction of B. ovata in Black Sea is a sign for ecological concern.

Once *Beroe ovata* becomes acclimated, similarly to *Mnemiopsis* it will play the role of a "keystone species" or "ecological engineer" (C a r p e n t e r, C o t t i n g h a m, 1997) that may shape strongly the ecosystem processes and tolerance and it could be used as pelagic indicator for the assessment of the Black Sea ecosystem health.

It is quite possible that the population dynamic of *M. leidyi-B. ovata* (typical preypredator mode), in a very near future to get the dimension of an important controlling factor. In this case the trophic chain influencing the structure of Black Sea pelagic ecosystem will be similar to that described for Helgoland Bay: Ctenophore II-Ctenophore I-Mesozooplankton (Greeve, 1970). This can lead to a new disturbance of the Black Sea ecosystem as mass development of ctenophores dramatically modifies the structure of an otherwise stable community (Fraser, 1962; Bishop, 1967). From all the above it seems that the Black Sea could be considered as a natural lab for the assessment the role that an exotic nonindigenous ctenophore couple could play in the entire ecosystem.

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Инвазията на ктенофората *Beroe ovata* в Черно море – предупредителен сигнал за екосистемата

Людмила Т. Камбурска, Снежана П. Мончева, Асен Ст. Консулов, Антон И. Кръстев, Камен Б. Проданов

(Резюме)

Настоящото изследване прави обстоен ретроспективен анализ на измененията в пелагичната черноморска екосистема за периода 1967 – 1998 г. Анализирани са измененията в динамиката и структурата на зоопланктона по биомаса паралелно с динамиката на фитопланктона, експанзията на ктенофората Mnemiopsis leidyi, както и запасите и улови на черноморска хамсия. Черноморската екосистема индикира признаци на относително възстановяване през 90-те години в сравнение с периода на интензивна еутрофикация (70-те -80те). През 1991 – 1992 г. изглежда прекъсват типичните за 80-те години взаимоотношения в пелагичната трофична мрежа. Наскоро интродуцираната ктенофора Beroe ovata в Черно море (1997) и първоначалните данни за сезонната динамика на вида провокират редица въпроси и несигурности относно възможния ефект от нейната адаптация върху екосистемата. Инвазията на нов вид ктенофора увеличава проблемите на Черно море, свързани с желатиновите. Динамиката на популациите на двете ктенофори-пришълци (В. ovata и M. leidyi) е типична за трофичните взаимоотношения хищник-жертва и контролира както директно, така и индиректно динамиката на зоопланктона. Изказана е хипотезата, че в найблизко бъдеще взаимоотношенията на двойката ктенофори ще се окажат ключов, контролиращ фактор за развитието на пелагичната черноморска екосистема.