TEMPORAL (SEASONAL AND INTERANNUAL) CHANGES OF ECOSYSTEM OF THE OPEN WATERS OF THE BLACK SEA

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Abstract. The pelagic ecosystem of the open part of the Black Sea was analyzed from the point of view of its temporal changes on interannual and seasonal basis. The material was collected during interdisciplinary expeditions to the Black Sea, between 1978 - 1996. The observed interannual variability is discussed for all plankton groups except protozooplankton. During 1980 - 1993 a gradual decrease of mean air temperature in winter and an increase in phytoplankton biomass in summer were observed. The lowest and the highest phytoplankton biomasses corresponded to high and low temperatures in 1980 and 1992 respectively. The climatic quasi-periodic 20-years oscillations of winter air temperature determine the general intensity of Black Sea current system and, as a result, favorable conditions for growth of phytoplankton. The analysis of historical phytoplankton data corroborates this hypothesis. According to surface chlorophyll "a" satellite measurements the interannual variations were seen in winter and spring during the period from 1978 to 1986.

The intrusion of *Mnemiopsis leidyi* to the Black Sea in 1989 led to radical changes in the structure and functioning of the ecosystem. After its outbreak, the biomass of phytoplankton increased in summer-autumn; the abundance of bacterioplankton was higher in spring; protozoan biomass did not changed. The fodder mesozooplankton as well as jelly-fishes biomasses sharply decreased. Within the jellies group, a significant decrease in the *Aurelia* biomass was compensated partly by developing of *Mnemiopsis.* The role of different groups of plankton in the community also changed significantly. As an example, the percentage of gelatinous macroplankton increased from 10-20% to 72-78% of the total zooplankton biomass. The decrease of biomass of mesozooplankton resulted in sharply diminishing of catches of pelagic fish.

The characteristics of the plankton community in temperate regions exhibit regular seasonal oscillations of a relatively high range, the biomass values varying by factors of 5-10 during the year. Two different seasonal scenarios of phytoplankton succession (with winter or spring blooms) for open waters of the Black Sea were considered. The spring phytoplankton mass development starts in the upper mixed layer after the seasonal pycnocline appearance, while the winter bloom ends with the formation of the seasonal pycnocline.

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Due to the radical changes in the zooplankton communities, associated with the intrusion of *Mnemiopsis leidyi,* the seasonal pattern has changed. The seasonal variations of zooplankton indicate that the grazing pressure of *Mnemiopsis leidyi* is the principle factor that determines these changes. The variations in the biomasses of its potential preys were the most pronounced. Influence of *Mnemiopsis* towards *Aurelia aurita* was the competitive one. It appears that the typical pattern of *Aurelia* seasonal development has not changed, however, the absolute values of its biomass has decreased.

1. Introduction

The earlier investigations of the seasonal dynamics of the plankton communities in the Black Sea were all carried out in coastal regions [1, 9, 13, 35]. The seasonal changes of the different groups of organisms illustrate the typical pattern for temperate and subtropical areas [18]. The formation of seasonal thermocline was followed by the development of the spring bloom of phytoplankton. The subsequent steps of ecological succession are also typical for all pelagic communities: the increase of zooplankton biomass and decrease of the phytoplankton, till its rise again in late autumn. The mechanism of this pattern seems to be clear and has been well studied [8, 16]. In contrast to the shelf areas, data on seasonal changes of plankton communities in the deep sea waters are virtually absent. The few available observations show that due to the characteristics of the current system, the seasonal pattern of ecosystem in the deep areas could well be different from the coastal ones. For example, unusual blooms of phytoplankton have been observed during the winter in the temperature homogenous upper mixed layer [10, 23].

The interannual changes of the Black Sea ecosystem have received special attention during the last few years. These changes are associated with the drastic changes in the main ecosystem parameters, which occurred in the early 90s [34]. It is assumed that the main reason of the changes was the anthropogenic impact.

The anthropogenic impact on marine ecosystems is manifested in various forms: toxic contamination, controlled river flows which decrease inflows affecting the salinity and water stratification, eutrophication, i.e. overfertilization, of the sea with nutrients and dissolved organic substance, fisheries, and finally, accidental or deliberate introduction of new species. The anthropogenic impact is often distorted by natural fluctuations of environmental parameters such as water supply and intensity of circulation, with mixing and temperature contrasts influencing water stratification. However, it is obvious that during the recent 15-25 years anthropogenic effects have resulted in profound alterations of the Black Sea ecosystem in the north-western part of the Sea [34]. In the deep areas of the basin, the observed changes in the productivity level of plankton community which in turn led to changes in the optical and chemical properties, were recorded by many authors in the late 80s - early 90s [25, 33]. At the same time, the mass development of a newcomer ctenophore *Mnemiopsis leidyi* in the last few years has been followed by drastic drops in stocks of small herbivorous fish (particularly, brisling and anchovy) [15, 19, 28, 35]. Nevertheless, the role of the anthropogenic factor in these changes is not evident for the deep part of the Black Sea.

In the present paper we describe the patterns of seasonal and the interannual changes of ecosystem of the deep waters of the Black Sea.

2. Material and methods

The material was collected during interdisciplinary expeditions to the Black Sea. It covers the period from 1978 to 1996. For the present analysis, only stations with depths greater than 200 m were used. The distribution of stations is shown in Figure 1.

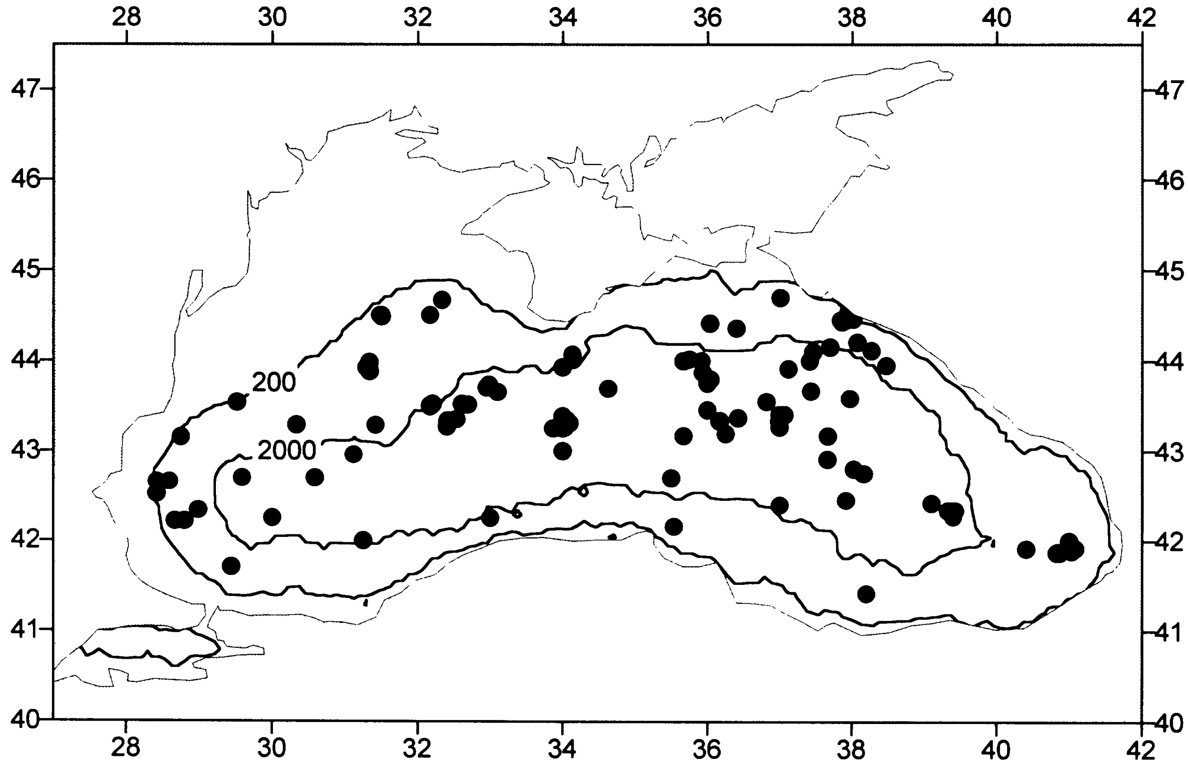

Figure 1. Map of stations of the cruises of P. P. Shirshov Institute of Oceanology RAS in the open part of the Black Sea (depth > 200 m).

At each station the following parameters were measured: vertical hydrological profiles (CTD soundings), nutrient contents, light penetration, biomass and the species composition of phytoplankton, bacterioplankton, ciliates, zooflagellates, mesozooplankton, macrozooplankton, fish eggs and larvae, the chlorophyll "a" concentration and the primary production. The detail description of methods used may be found in the literature cited in the following.

3. Results and discussion

3.1. INTERANNUAL VARIATIONS

The clearest indication of interannual changes is the pattern of fluctuations of phytoplankton biomass. The mean value of phytoplankton biomass in summer-autumn (June - October) changed several times during the period from 1978 to 1995 (Figure 2). These changes are inverse to oscillations in air temperature in winter (Figure 2, curve 1).

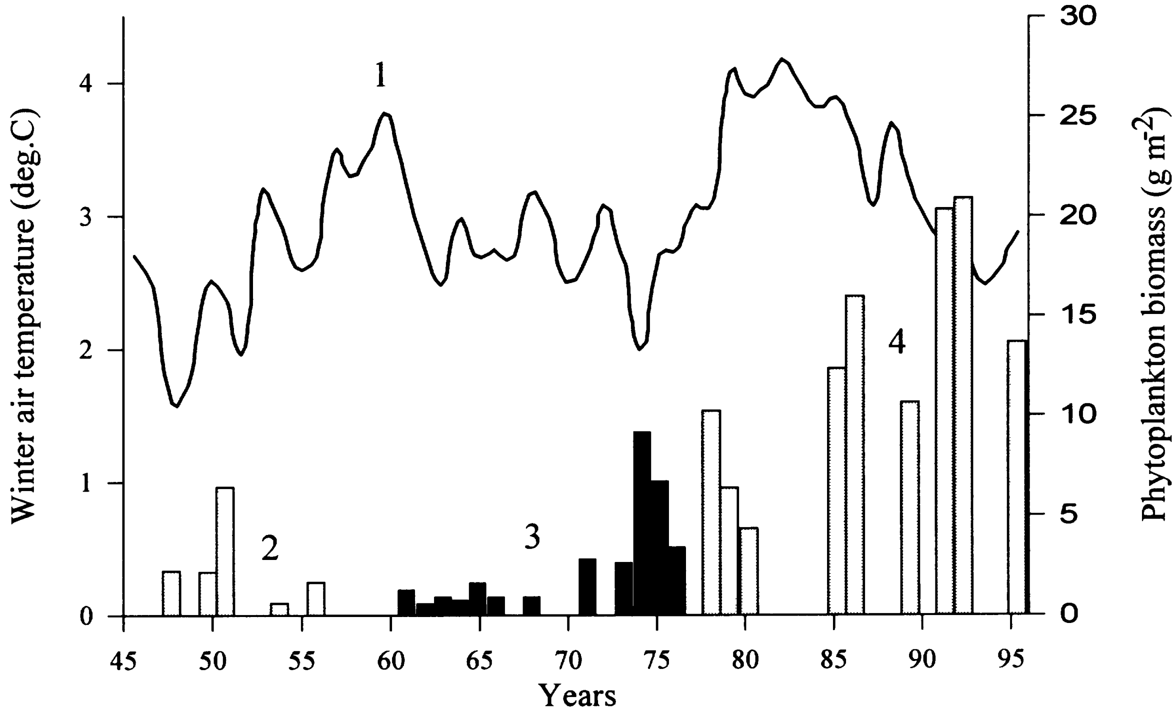

Figure 2. Average winter temperature (1) (from [17], modified] and total phytoplankton biomass in summer. (2) - from [4]; (3) - from [9]; (4) - from [11].

The general hydrological state of the Black Sea is well known to depend on the intensity of winter convection [3], which, in turn, depends on air temperature in winter. According to Ovchinnikov and Osadchiy [17] the average winter air temperature undergoes a quasi-periodic 20-years oscillation. During the coldest years of the observed period the low winter temperature causes intense water uplift in the centers of both gyres ("Black-Sea upwelling") and intensifies the circulation of the Rim Current. Such an intensification takes place both in winter and in summer. In summer this leads to more intensive penetration of the nutrients to the upper mixed layer in the center of the Sea, and, hence, creates favorable conditions for phytoplankton growth.

The variations in the phytoplankton biomass seem to corroborate this hypothesis. In the period from 1980 to 1993 a gradual decrease of mean air temperature in winter and an increase in phytoplankton biomass in summer were observed (Figure 2). The lowest and the highest phytoplankton biomasses corresponded to high and low temperatures in 1980 and 1992 respectively. The decrease in biomass from 1978 to 1980 and from 1992 to 1995 corresponded to inverse changes in air temperature. While the earlier data (2 and 3 in Figure 2) can not be compared directly with the more recent data, due to differences in methods of collection and treatment of phytoplankton samples, the position of peaks in the biomass data does indicate the inverse relationship between the phytoplankton biomass and air temperature. Data on phytoplankton biomass obtained in the eastern part of the sea from 1961 to 1976 [9] confirm the correspondence of low winter air temperatures and maximum of algae abundance in summer (Figure 2, curve 3). A similar pattern is also seen in the data for the period 1948 to 1956 [4]. Cold winter periods from 1948 to 1952 corresponded to highest summer-autumn phytoplankton biomasses (Figure 2, curve 2).

The next warm and cold extremes are expected in 1998-2000 and 2010-2012 respectively. Hence, the level of productivity of the sea observed in 1980 should be compared with 2000, and the same should be done for the 1990 and 2010 data.

The changes between the years could be expected also during the winter and spring seasons. Due to lack of the field observations during these periods, the data on surface chlorophyll "a" from the CZCS radiometer of the satellite "Nimbus-7" were used [2]. During 1978 to 1986 large variations in surface chlorophyll concentration were seen in winter: October-December (10 times), January - February (5 times) (Figure 3, curves 1 and 2). The spring bloom period (March-April) also shows the wide range in surface pigment content (Figure 3, curves 1 and 2). It is interesting that in contrast to summer phytoplankton biomass, the highest chlorophyll values corresponded to the most warm winters.

The interannual changes are seen not only in biomass but in size and taxonomic structure of phytoplankton (Figure 4). These changes are illustrated by the percentage of picophytoplankton (small algae with cell size under 2 μm), nanophytoplankton (algae with cell size from 2 to 15 μm), and microphytoplankton (over 15 μm) in the summer phytoplankton biomass. The taxonomic composition is presented by the percentage of two main taxonomic groups of algae: diatoms and dinoflagellates. It is evident that after 1991 the structure of phytoplankton community of the Black Sea essentially differs from that observed earlier. The role of large cells of diatoms significantly increased. It could be supposed that before 1991 these large cells of diatoms were grazed by mesozooplankton, but after 1991 the biomass of mesozooplankton decreased due to the influence of *Mnemiopsis leidyi* and the abundance of large diatoms increased. It will be recalled, that the total value of phytoplankton biomass varied under the influence of other factors (Figure 2), zooplankton grazing being not crucial.

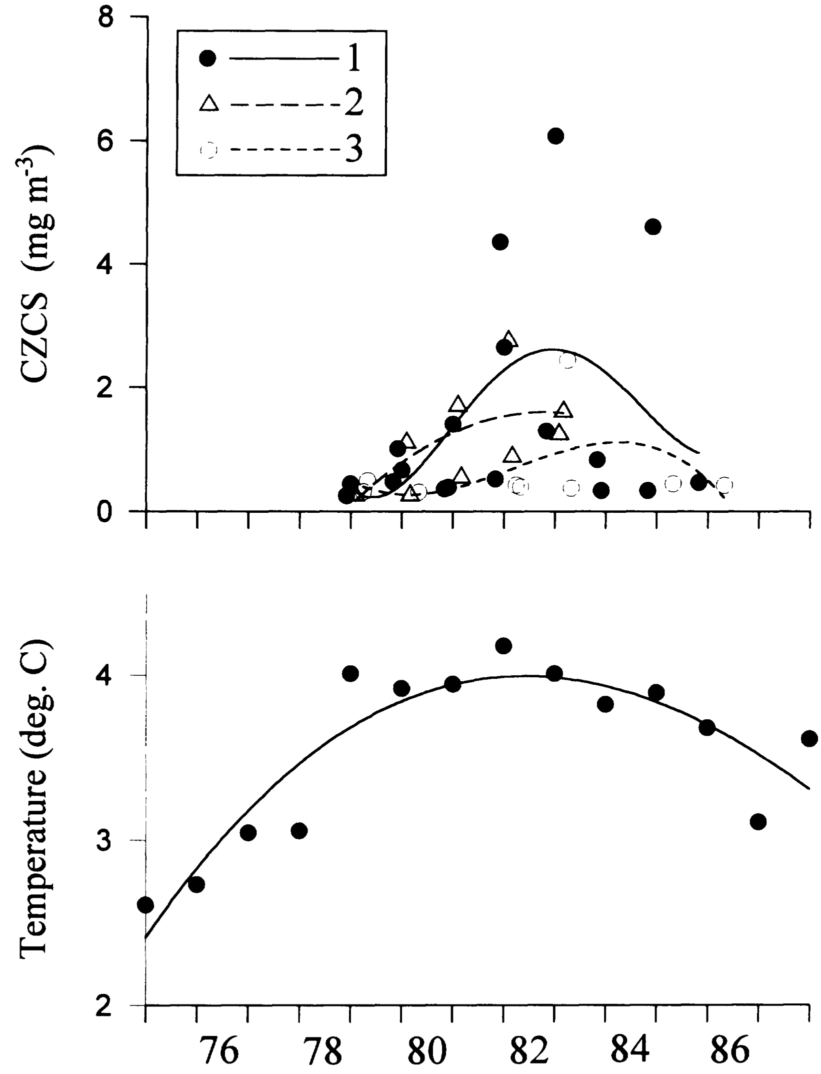

Figure 3. Interannual variation of CZCS-measured surface chlorophyll *a* concentration (Y-axis, mg m^{-3}) during cold season (October-April) in the open part of the Black Sea (depth >200 m) during 1978-1986. (1) - October-December, (2) - January-February, (3) - March-April The values of mean winter air temperature (degrees C) are also given.

Variations of summer chlorophyll "a" and in the level of primary production were observed from the 1960's to early 1990's [25] (Figure 5). During this period both parameters varied *ca* 3 times. The significant increase in chlorophyll "a" concentration in the early 90's is evident and corresponds well with the changes in phytoplankton biomass (Figure 2). The sharp peak in primary production observed in 1986 (Figure 5) is not in coincidence with phytoplankton biomass and chlorophyll "a" dynamics as well as with the changes in optical water transparency. The latter showed the sharp decrease in disk Secchi transparency since 1990 [33]. Unfortunately, it is impossible to compare earlier peaks of phytoplankton biomass with chlorophyll "a" concentration and with primary production changes. These parameters were not measured during the phytoplankton peaks of 1951 and 1974.

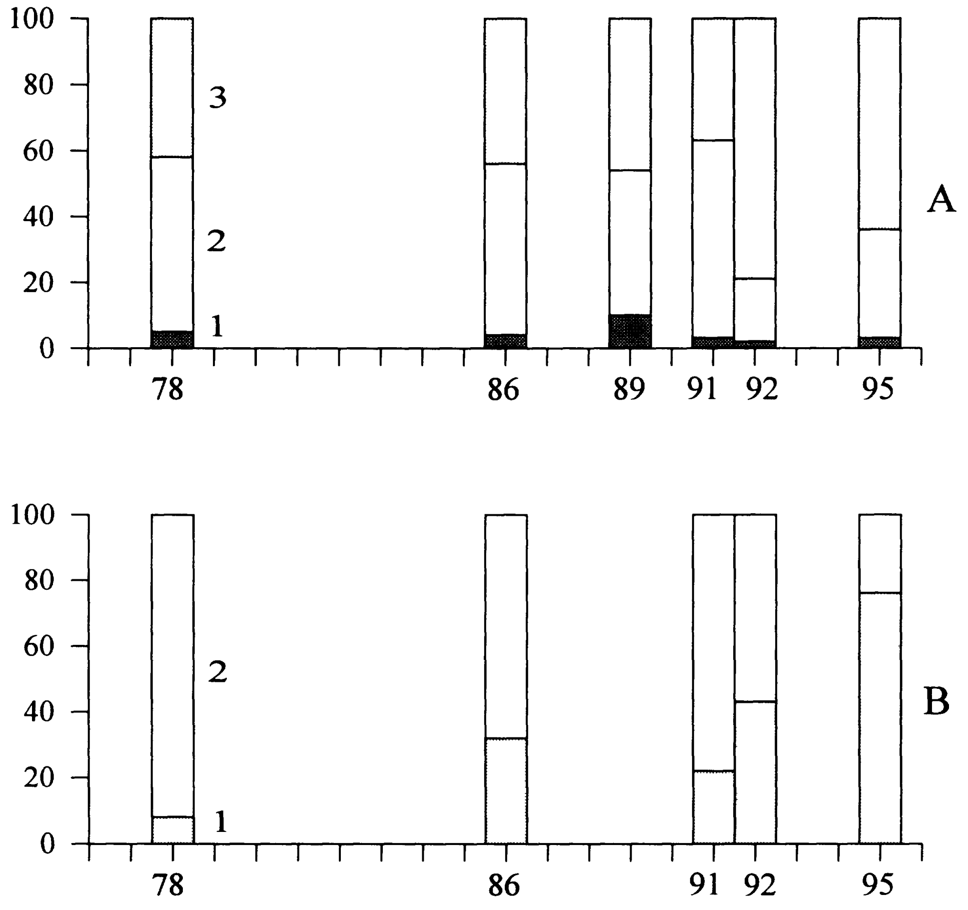

Figure 4. Changes in (A) percentage (%) of 3 size groups ((1) - pico-, (2) - nano-, and (3) - microplankton) in the total phytoplankyon biomass, (B) percentage (%) of biomass of (1) diatoms and (2) dinoflagellates

However the recent changes in phytoplankton community are not as drastic as in the zooplankton community. The latter resulted from the development of newcomer ctenophore *Mnemiopsis leidyi* in late 1980s. This species is a voracious predator [24]. It is believed that *Mnemiopsis leidyi* reached the Black Sea in the ballast water of ships cruising between the western North Atlantic and the Black Sea.

The mass development of *Mnemiopsis leidyi* in the Black Sea started in 1987 (Figure 6) and, at first, covered the bays, gulfs and coastal waters. Since the spring of 1988, its juveniles were encountered in all open sea areas and in the autumn of that year its biomass reached 1.5 kg m^{-2} [31]. During the summer of 1989, the biomass of *Mnemiopsis* considerably grew and its total value for the whole sea attained 1 Gt [21]. In 1990, the development of *Mnemiopsis* remained at the same rate (Figure6). Its abundance reached 10-12 kg m^{-2} at several coastal areas (Anapa, the south-western Bulgarian coast), but did not exceed 1.5-3 kg m^{-2} in the open sea.

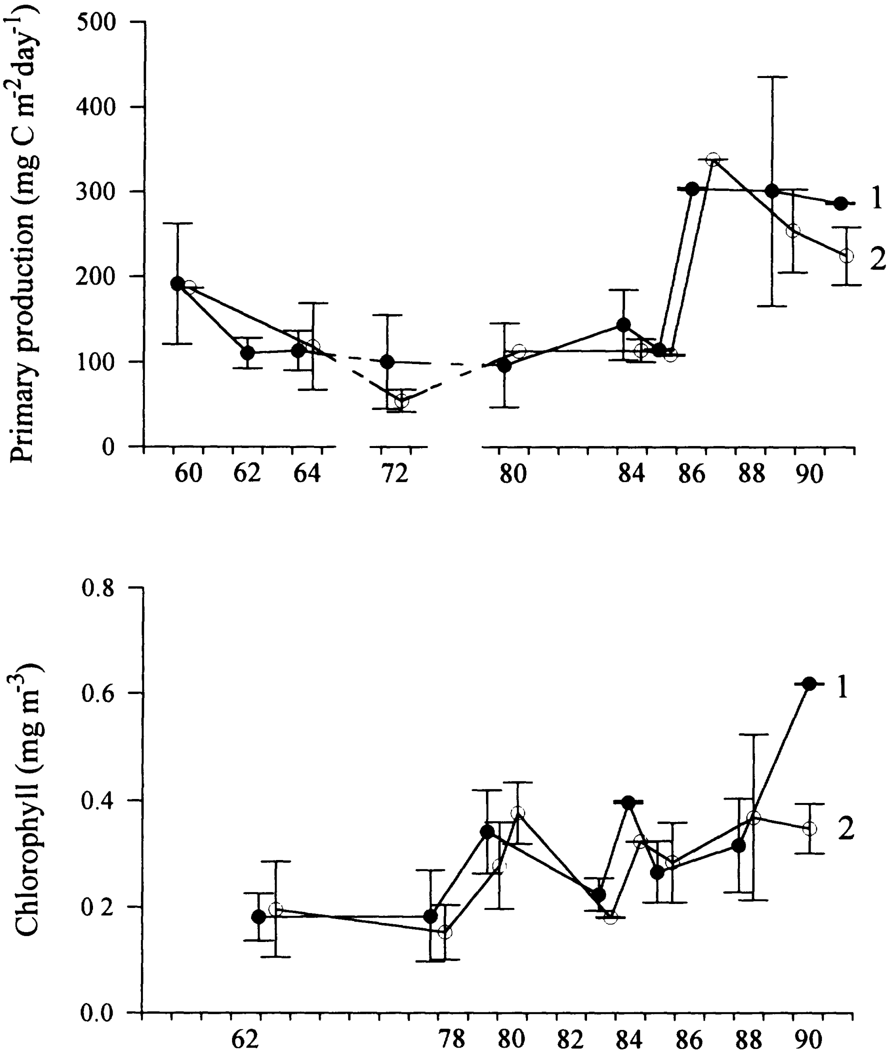

Figure 5. Variations of summer (May-September) values (mean±SD) of primary production in water column and mean chlorophyll *a* concentration in photosynthetic layer in the western (1) and eastern (2) parts of the deep part (depth>1500 m) of the Black Sea (from [25]).

During summer 1991, the biomass began decreasing and in the autumn months it dropped sharply, reaching values 4-6 times lower compared to 1989. In autumn 1992 (September-October) the *Mnemiopsis* biomass remained at the level of 1991. It is likely that the ctenophore development passed its peak at the end of 1989 and in 1990, and its place in community will be more modest in the future.

Another species which determined the level of community biomass before the *Mnemiopsis* appearance, was jellyfish *Aurelia aurita*. Its abundance sharply increased in the 1970s and exceeded the estimates of the 1950s - early 1960s by more than two orders of magnitude. The jellyfish probably occupied the ecological-trophic niche that became vacant as a result of abrupt decrease in the stock of plankton-feeding fish. It can be considered as an indicator of profound changes in the Black Sea ecosystem in the 1970s. Jellyfish biomass varied slightly since the late 1970s and its autumn peak was on average *ca* 1 kg m^{-2} in the open sea. A sharp drop in its abundance followed the mass development of *M. leidyi*. Changes in the biomass of *A. aurita* from 1978 to 1991 are shown in Figure 6. Against the background of seasonal variations, a sharp decrease in their abundance can be clearly seen after summer of 1988. While the wet biomass of the jellyfish, averaged over the period of 1978-1988, was about 1 kg m^{-2} (*ca* 400 Mt for the whole sea area), in the summer of 1989, it decreased to 0.14 kg m^{-2} i.e. to about one-seventh of its former value and was as low as 60 Mt for the whole sea area. At the same time, changes in the size structure of *A. aurita* population were observed. The mean size of organisms decreased. It seems that the jellyfish were incapable of attaining larger sizes because of sharp food competition with *M. leidyi*. It is interesting also that the biomasses of *M. leidyi* and *A. aurita* during peaks of their outbreak, were approximately the same in terms of organic carbon (Figure 6), although their wet weights differed by several orders of magnitude

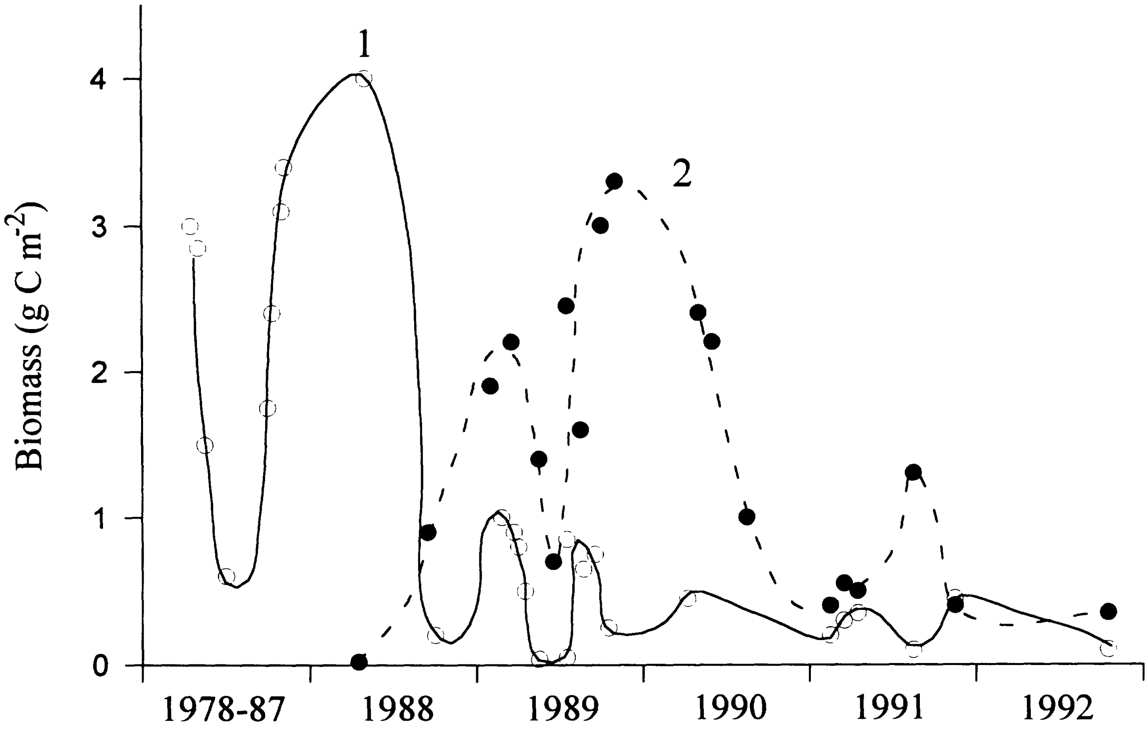

Figure 6. Interannual variations of the biomass (gC m^{-2}) of *Aurelia aurita* (1) and *Mnemiopsis leydyi* (2) during 1978-1992 according to observations in expeditions of P. P. Shirshov Institute of Oceanology (from [22, 27], modified).

The taxonomic structure of zooplankton community has been deformed. The species which are permanent inhabitants of the upper mixed layer, the initial basic biotope of *M. leidyi*, and those regularly moving up there prove to be easily accessible, whereas the species remaining in the deep water layers (*C. euxinus, P. elongatus*) were biotopically isolated from *M. leidyi* and, therefore, were less exposed to grazing pressure.

Due to this reason, the changes in zooplankton communities, first of all, concerned the mesozooplankton inhabiting the layer over intermediate cold waters [20, 22]. In

1989 its abundance declined in 2-2.5 times on average, as compared to the previous period. Biomass of some species and groups decreased 3-10 times or even more (Figure 7).

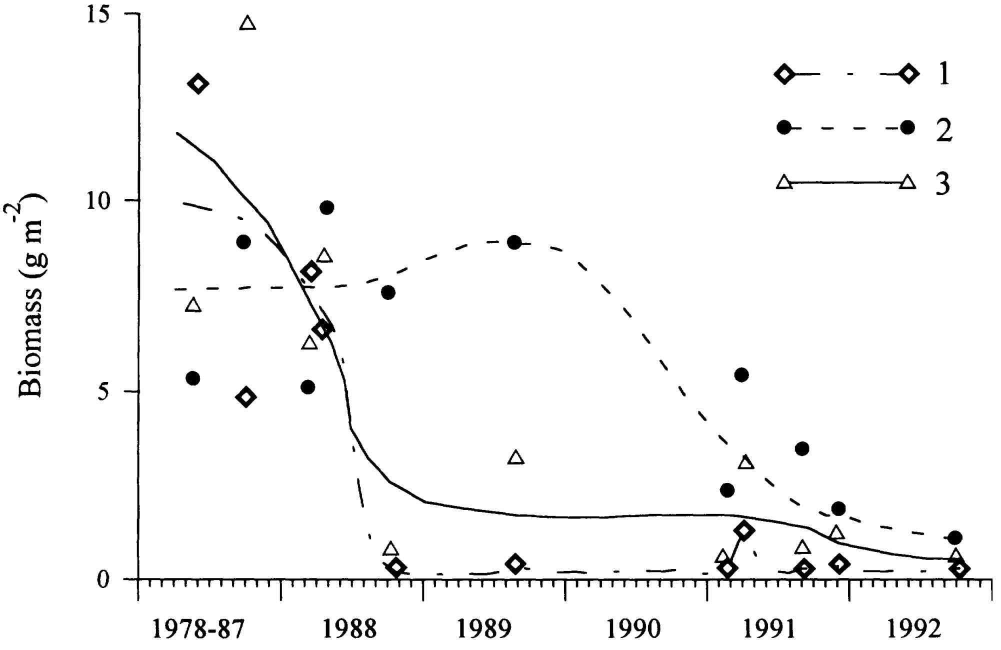

Figure 7 Interannual variations of the biomass (g wet weight m^{-2}) of *Sagitta setosa* (1), *Calanus euxinus* (2) and other zooplankton (3) during 1978-1992 according to observations in expeditions of P. P Shirshov Institute of Oceanology (from [22, 27], modified).

Such a significant decrease in biomass, and, consequently, in production of the main food for *Mnemiopsis leidyi* in the upper layer in the Black Sea might have led to more explicit decay in the ctenophore biomass than occurred in reality. The reason, probably, is that the dwelling zone for Mnemiopsis became extended and new mass food objects were introduced into its ration.

During the first period of development *Mnemiopsis leidyi* was strictly limited to the upper mixed layer over the thermocline and its assemblages often occurred just under the surface. However, in autumn 1989, we observed from the submersible "Osmotr" large-size ctenophore individuals in the under-thermocline layer as well. During the observations from submersible "Argus" in spring 1991 the penetration of the bulk of ctenophore population below the upper boundary of pycnocline was recorded. During the summer periods of 1991 and 1992, unlike 1989, only a few individuals were encountered in the surface layer, while the whole population inhabited the thermocline layer and underneath. In the under-thermocline layer the ctenophore, probably, began to feed on the population of *Calanus euxinus*, which lifts up from the deep waters at night time. During this period, the biomass of *C. euxinus* exceeded that of other zooplankton which were less than in summer 1989 by factors of 2.5 - 3.5. At all stations in 1991 and 1992 the biomass of *C. euxinus* was less by 1.7-8.3 times as compared with the values observed at the same sampling sites in 1989.

The intrusion of *Mnemiopsis leidyi* led to radical changes in the structure and functioning of the ecosystem. Such a strong carnivore pressure caused the decrease in the population density of *C. euxinus*. The data obtained in summer and autumn 1991 and in autumn 1992 evidently corroborated this fact. The biomass of *C. euxinus* in 1991 and 1992 changed significantly. Evident differences could be seen between two periods: before and after the *Mnemiopsis* appearance (Table 1). After the outburst of Mnemiopsis the biomass of phytoplankton increased in summer-autumn; the abundance of bacterioplankton was higher in spring; protozoan biomass did not change. The fodder mesozooplankton as well as jelly-fishes biomasses sharply decreased. Within the jellies group the significant decay of *Aurelia* biomass was partly compensated by development of *Mnemiopsis*.

TABLE 1. Averaged biomasses (B±S.E., g C· m^{-2}) and percentages of total community biomass of the main elements of planktonic communities in the open part of the Black Sea (depth >1000 m) during different seasons before the bloom of newcomer ctenophore *Mnemiopsis leidyi* (1978-1988) and after the bloom (1989-1992).

	Winter (February)		Spring (March-April)		Summer-autumn (May-November)	
	before	after	before	after	before	after
Phytoplankton	-	5.06±1.36 (64%)	3.31±0.54 (36%)	4.02±0.54 (48%)	0.87±0.10 (12%)	1.72±0.15 (31%)
Bacteria	-	0.68±0.07 (9%)	0.54±0.04 (7%)	0.89±0.07 (11%)	0.60±0.07 (8%)	0.71±0.04 (13%)
Protozoa	-	0.22±0.04 (3%)	0.21±0.04 (3%)	0.22±0.03 (3%)	0.20±0.03 (3%)	0.23±0.03 (4%)
Mesozooplankton	-	0.25±0.04 (3%)	1.48±0.11 (16%)	0.56±0.18 (7%)	1.64±0.46 (22%)	0.68±0.10 (12%)
Jelly-fishes *(Pleurobrachia pileus* *+ Aurelia aurita* *+ Mnemiopsis leidyi)*	-	1.71±0.31 (22%)	3.46±0.60 (38%)	2.61±0.51 (31%)	4.04±0.28 (55%)	2.24±0.19 (40%)
Aurelia aurita	-	1.01±0.29 (13%)	2.98±0.54 (32%)	1.57±0.32 (19%)	3.67±0.22 (50%)	0.98±0.18 (18%)
Mnemiopsis leidyi	-	0.43±0.07 (5%)	0.00±0.00 (0%)	0.50±0.15 (6%)	0.00±0.00 (0%)	0.78±0.08 (14%)

The role of different groups of plankton in the community also significantly changed (Figures 8 and 9). Before the introduction of Mnemiopsis bacterioplankton contributed from 5 to 10% to the total zooplankton biomass. This rate was similar to this ratio in the ocean ecosystems. After outburst of Mnemiopsis the role of bacteria sharply increased (Figure 8). The role of gelatinous macroplankton increased as well. Earlier, they comprised from 10 to 20% of the total zooplankton biomass. After the development of *Mnemiopsis leidyi*, the portion of jelly organisms in the Black Sea zooplankton (including macroplankton) amounted to 72-78% in carbon content and more than 99% in the wet weight units. Thus, the thin aerobic layer of the Black Sea, the only dwelling place for all its inhabitants (except bacteria), turned to be conqured by mucilaginous zooplankton - the trophic deadlock in the food chains of the sea. It should be mentioned that in undisturbed marine ecosystems the percentage of jellies usually does not exceed 10%.

The elimination of fodder mesoplankton, which consumes microplankton (phytoplankton, bacteria, protozoa) removed its pressure from microplankton and its role in total plankton biomass. The changes of production of the main groups of the community were also important. After the outburst of Mnemiopsis the production of total mesoplankton decreased about two-fold, especially the fodder zooplankton (Figure 9).

The decrease of biomass of mesozooplankton resulted in sharp decline of catches of pelagic fish in the Black Sea (Figure 10). The dominant fish (about 70% of total catch) was anchovy (*Engraulis encrasiccolus*), the fish with the shortest life cycle. Immediately before *Mnemiopsis leidyi* mass development (1985-88) the total (for all countries of the Black Sea region) catch values varied from 360 to 530 thousand tons per year (average 435). After the bloom of *Mnemiopsis* the catch dropped to $161 \cdot 10^3$ tons. During 1990-1991 the abundance of ctenophore decreased, but the catches continued to decrease as well.

The life duration of the horse mackerel (*Trachurus mediterraneus*) is longer. Thus the generation of 1985-1988 continued to share in the catch during 1989. The slump in catches occurred in 1990-1991 [29]. In the northern part of the sea the decrease of catches occurred in 1986 (Figure 10) and was not connected with *Mnemiopsis*, but in 1988-1989 the catches of horse mackerel decreased 10 times (from 2.5 to 0.3-0.4 thousand tons). In 1990-1991 this species disappeared from the official statistical reports, and appeared again only in 1992, when the biomass of *Mnemiopsis* started to decrease.

At the beginning of mass development population of *Mnemiopsis* was rather strictly confined to warm upper mixed layer, but as early as 1990 its main aggregations were concentrated in the thermocline while some specimens penetrated even deeper. Hence the *Mnemiopsis* population came in contact with the population of *Calanus euxinus,* which resulted in sharp decrease in its abundance and biomass [32]. Hence the food resources of sprat (*Sprattus sprattus*) were undermined. The catches of this fish started to decrease in 1990. The total catch in the basin was maximum in 1987-1989 (66-105 thousand tons). In 1991 it was as low as 16.9 thousand tons. In 1986-1988 the catch of USSR was 43-54 thousand tons. In 1989 the fleet tried to compensate the fall of anchovy catch by the intensified fishery of sprat. That year its catch rose to 89 thousand tons. However since 1990 the catch dropped; in 1991-1992 the catch values were as low as 15.0-14.8 thousand tons.

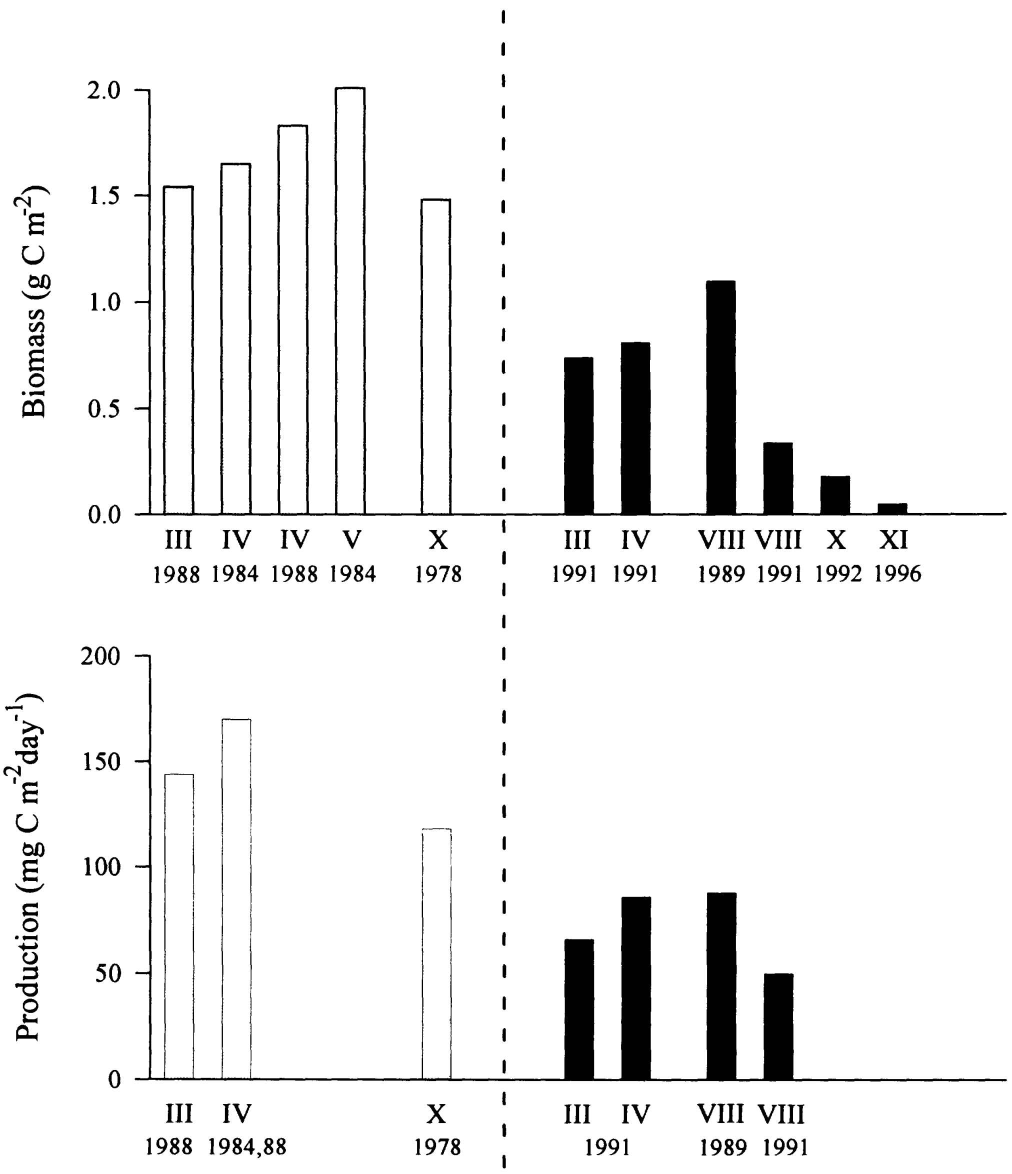

Figure 8 Biomass of fodder mesozooplankton and production of total mesozooplankton before(left) and after (right) the outburst of *Mnemiopsis leidyi* in the Black Sea.

It thus appears that the impact of introduction of *M. leidyi* on the biological communities of the pelagic zone and on fishery for plankton-feeding fishes has been more catastrophic than the effect of other anthropogenic factors to which the Black Sea ecosystem has been exposed in recent years.

Nevertheless, it seems impossible to separate the influence of climatic and anthropogenic factors on the Black Sea ecosystem in the early 1990's. At least, for low trophic level (phytoplankton, bacterioplankton and mesozooplankton) the influence of both climatic oscillations and *Mnemiopsis* development can be said to be equally important.

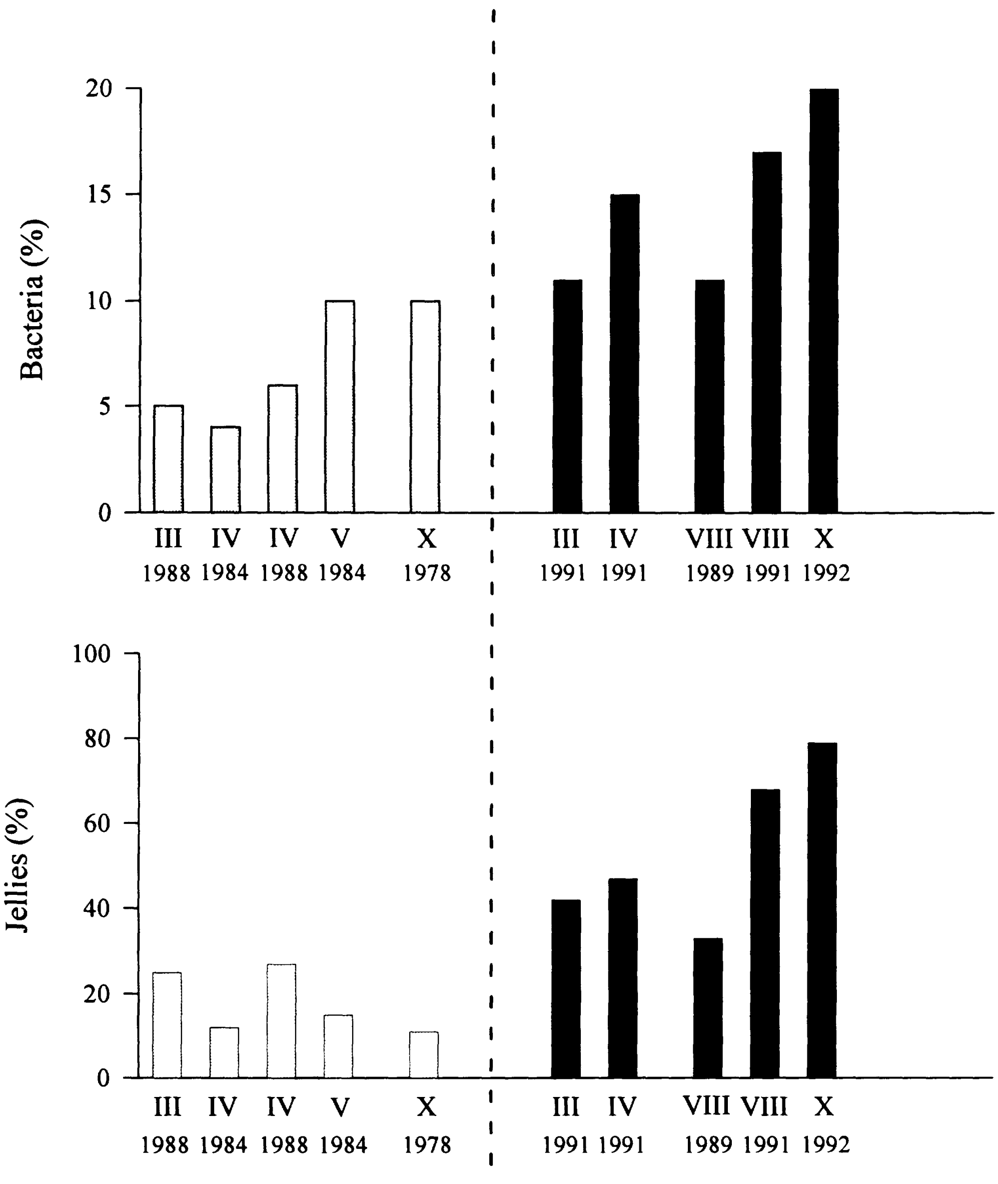

Figure 9. Role of bacteria and gelatinous animals in total zooplankton biomass before (left) and after (right) the outburst of *Mnemiopsis leidyi* in the Black Sea.

3.2. SEASONAL CHANGES

In the coastal regions of the Black Sea the values of primary production, chlorophyll concentration, phyto- and zooplankton biomasses change according to typical pattern of seasonal variations of temperate and subtropical areas [18]: spring bloom (March) of phytoplankton is followed by its decrease in summer due to depletion of nutrients. At the same time in the open regions the bloom of diatom phytoplankton occurs in winter (January-February). The reason is that during cold winter time with the absence of seasonal thermocline the main pycnocline in the centers of the cyclonic gyres rises as close to surface as 25-30 m. This phenomenon is called "Black-Sea upwelling" [27]. As a result the whole upper mixed layer apparently becomes located within the euphotic zone that favors primary production. This leads to the phytoplankton bloom. As an example, in 1988 and 1991 the biomass of diatom *Nitzschia delicatula* was observed as high as 120 g m^{-2} [10, 12].

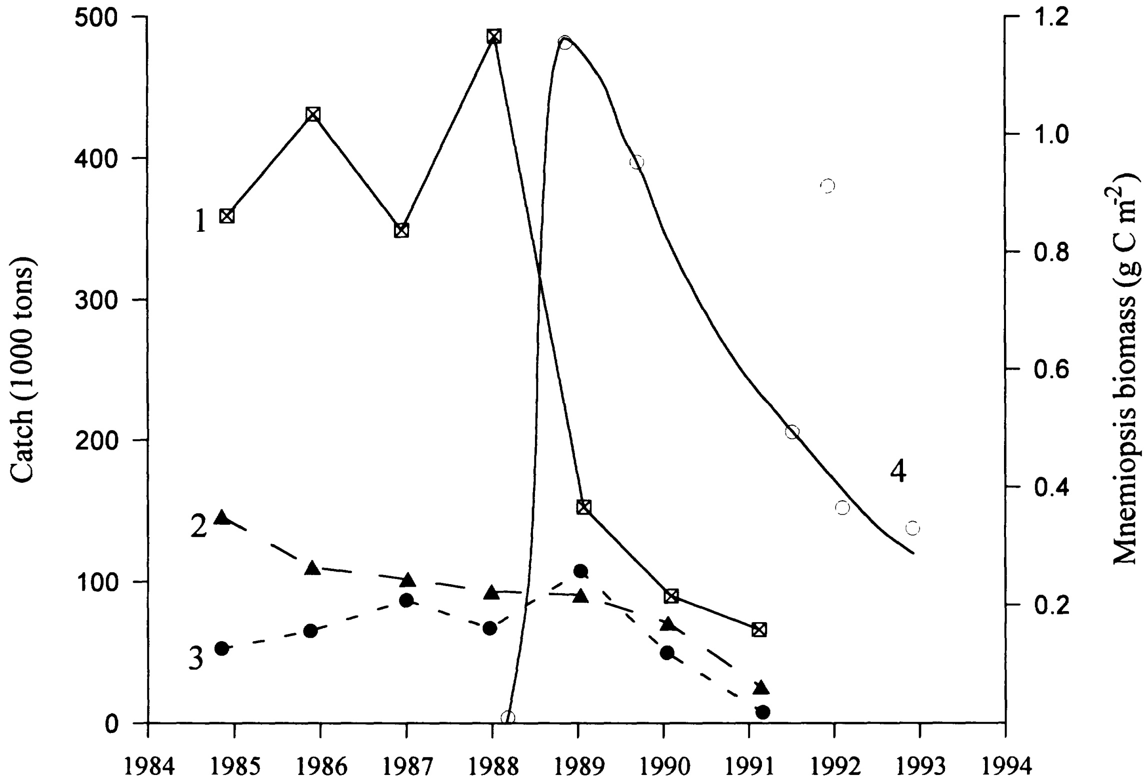

Figure 10 Total catchs of anchovy (1), sprat (2) and horse-mackerel (3) in the Black Sea, and mean biomass of *Mnemiopsis leidyi* during summer months (4) (from [29]).

It should be noted, that the lifting up of pycnocline does not take place every year. In normal winters the pycnocline is located at depths of 50-60 m, which prevents the development of phytoplankton. In these years, the seasonal pattern in the open waters with spring bloom in March is similar to that in the coastal areas. The spring phytoplankton mass development starts in the upper mixed layer after the seasonal pycnocline appearance. The winter bloom, on the other hand, ends when the seasonal pycnocline is formed. This processes is clearly seen in changes of vertical distribution of phytoplankton biomass (Figure 11). At the end of March during a few days cells of diatoms sink down to seasonal pycnocline, cleaning up the upper mixed layer [23].

Thus, two different seasonal scenarios (with winter or spring blooms) for open waters of the sea, should be considered. Unfortunately, the very scarce data for winter season do not permit to construct these patterns separately. Usually, the data have been averaged over many years, which results in mixing the two types of blooms .For example, the primary production percentage averaged for many years for the whole open regions of the Black Sea is distributed as follows: 35% - winter, 30% - spring, 16% - summer and 19% - autumn, the total winter-spring period being two-fold productive than the summer-autumn one [25]. During the year with the winter bloom, over 60% of total year primary production is created in winter [6].

During the winter or spring bloom, the areas of high average chlorophyll concentrations (0.4-2.7 mg m^{-3}) were spread over a large part of the open sea. The primary production value reached 1300 mg C m^{-2} day^{-1} [25].

The further steps of ecological succession are typical for all pelagic communities: increase of zooplankton biomass and decrease of the phytoplankton one, till the new increase in late autumn. The mechanism of this pattern seems to be evident, thus this process was successfully modeled [8, 16].

In March-April, the phytoplankton "blooming" declines and the steady summer-early autumn (April-October) state with low level of phytoplankton development sets in. The phytoplankton biomass in summer-autumn varies from 4 to 10 g m^{-2}. According to long-term oscillations (see above) in some years it increased up to 20-30 g m^{-2} . The main bulk of phytoplankton biomass in this period is located in the seasonal pycnocline layer (Figure 11). In November-December due to mixing the upper boundary of the seasonal pycnocline becomes eroded. The upward nutrient transport into the euphotic zone enhances favoring of growth of algae in this well illuminated zone and the biomass of phytoplankton increases. The values of chlorophyll concentration increases up to 0.5-1.6 mg m^{-3}[25].

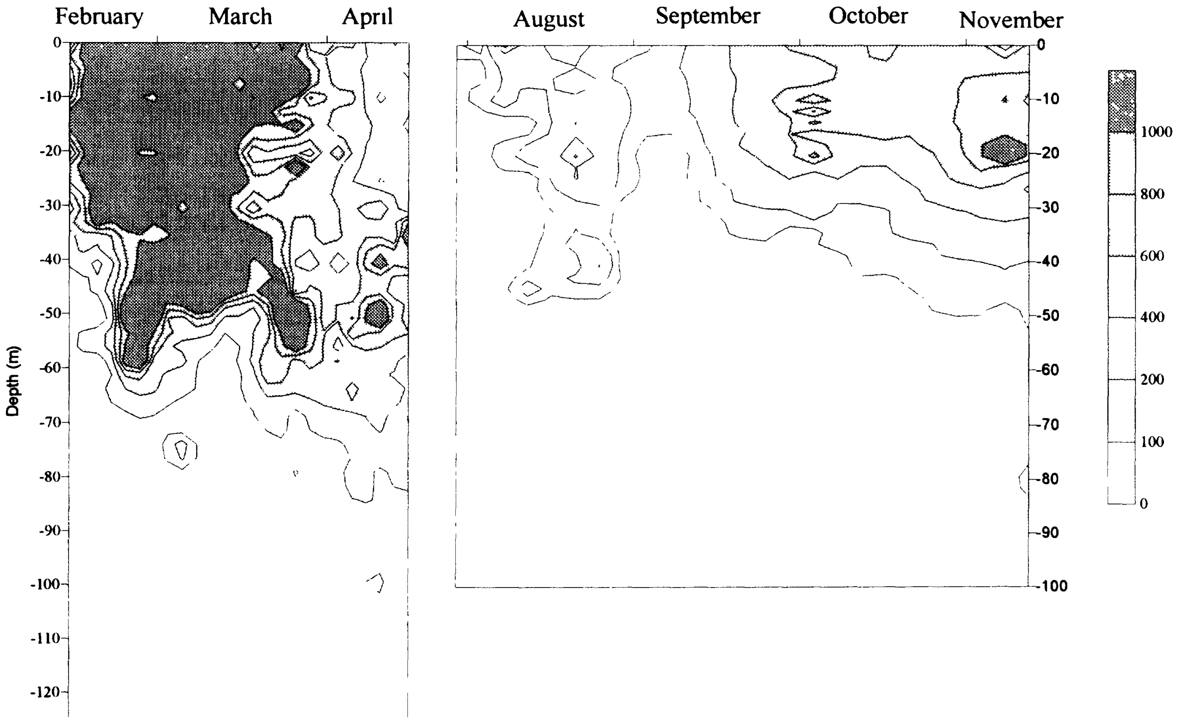

Figure 11. Seasonal variation of phytoplankton biomass(mg m^{-3}) in the open part of the Black Sea (depth >1000 m)

Due to the radical changes in the zooplankton communities, connected with the intrusion of *Mnemiopsis leidyi* (see above), the seasonal pattern today is different today than in the past. The averaging of long-term data for construction of seasonal zooplankton changes makes no sense. Instead, here we present the seasonal variability of zoocene structure that has been monitored during 1991 at five representative points in the open sea [28].

The seasonal trend in the biomass of the ctenophore *Mnemiopsis leidyi*, edificator of the open sea communities, is presented in Figure 12A. In winter (February) its quantity was minimum over the entire area and did not exceed 200-800 g m^{-2}. Most of its population was composed of medium-sized individuals. In spring (March-April), the biomass rapidly increased at the periphery of the gyres while it remained at the same level.in the centers. In summer, abundance of the population along with juvenile individuals number increased, which resulted in high total biomass. In autumn (November) the biomass of the population decreased to values typical for winter.

Fluctuations of biomass of jellyfish *Aurelia aurita* were synchronous over the entire sea area and had two peaks in spring (March-April) and autumn and two minima in winter and summer (Figure 12B). These changes were determined by biological cycles of this jellyfish. It has been analyzed and successfully modeled [7].

The seasonal changes of *Pleurobrachia pileus* (Figure 12C) were similar to that of *Mnemiopsis*. Biomass of *P.pileus* significantly increased from winter to summer and sharply decreased by late autumn. The increase of the biomass was the result of growth of animals. During winter the specimens of 5-10 mm size predominated, during summer the average diameter was twice higher (10-20 mm).

The seasonal trends in biomass of the species consumed by jelly carnivores seem to be determined by the trophic pressure of the latter. This is evident from the pattern of seasonal variations of total biomass of *Mnemiopsis* prey (Figure 12D). This group consists of small crustacean plankton (*Paracalanus, Acartia, Oithona, Pseudocalanus, Cladocera*), larvae of benthic animals and appendicularia (*Sagitta setosa* and *Calanus euxinus* which are also the potential food for ctenophores will be considered separately). The bulk of these animals consists of small-sized species-opportunists with rather short life cycle. These species are capable of increasing their biomass when the limiting factors slacken. Biomass of these species in winter was minimum over all the sea surface. They began reproducing, growing and increasing their biomass only during spring, after phytoplankton bloom, when the seasonal thermocline was established. At the same time a lot of larvae of benthic animals appeared in plankton. The total biomass of zooplankton that seems to be potential prey of *Mnemiopsis* grew rapidly reaching in some areas 9 g m^{-2}. The amounts of *Mnemiopsis, Aurelia* and *Pleurobrachia* increased concurrently, and the strong pressure of these carnivores led to decay of the biomass of their potential food by end of summer: in August it was as low as in winter. It is likely that this substantial decrease in food resources caused decay of *Mnemiopsis* biomass in the autumn. The autumn weakening of the carnivores' pressure caused the counter-phase increase in biomass of this group.

The affect of carnivores (*Mnemiopsis*) on seasonal variations of biomass of *Sagitta setosa* was also evident (Figure 12F). The early spring rise in *Sagitta* biomass was related to rapid growth of population consisting of large, mature specimens. Death of the large-size animals and consumption of juveniles by *Mnemiopsis* led to the sharp reduction of the population. Its biomass in summer declined to the values about 10 mg m^{-2}. In contrast to small opportunist species, the population of *Sagitta* has slow growth rate; hence the abundance of its population failed to grow during autumn weakening of the pressure of carnivores, therefore the biomass increase of *Sagitta* was very low.

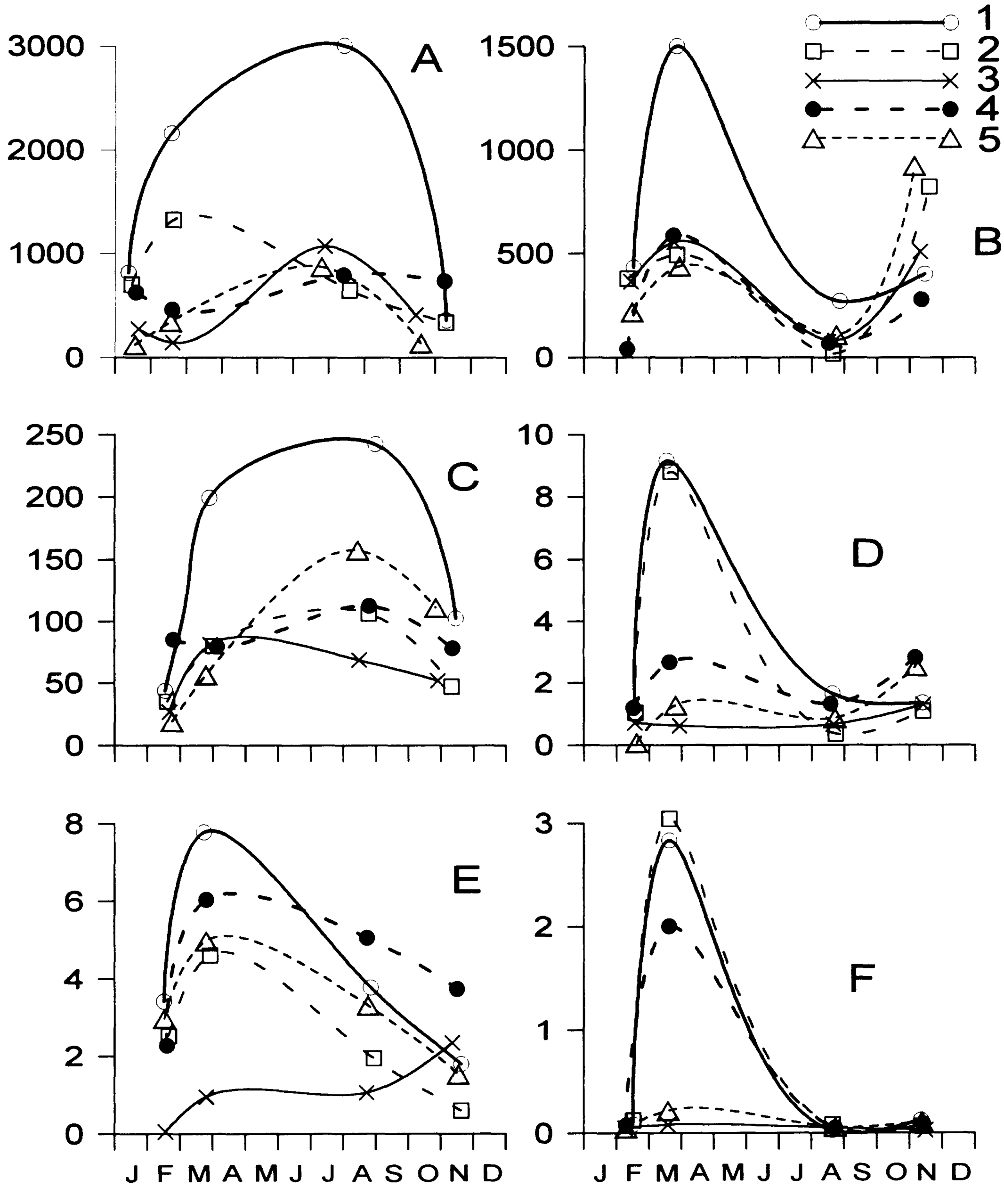

Figure 12 Seasonal variation of the biomasses (g m^{-2}) of main compounds of zooplankton during 1991 (from [28]) (A) - *Mnemiopsis leydyi*; (B) - *Aurelia aurita*; (C) - *Pleurobrachia pileus*; (D) - small zooplankton (prey of *Mnemiopsis*), (E) - *Calanus euxinus*; (F) - *Sagitta setosa*. (1) - south-eastern region; (2) - outer periphery of the Rim Current near Gelendzhik; (3) - eastern cyclonic gyre; (4) - convergence south of Yalta, (5) - western cyclonic gyre

It is interesting to note that in the 1960-80s before the introduction of *Mnemiopsis* the mesoplankton biomass reached maximum in summer months - July-August [5].

The seasonal variations in biomass of *Calanus euxinus* should be considered separately (Figure 12 E). The bulk of its population is associated with the under-thermocline layer and the upper main pycnocline waters [26]. Existence of the population in the open sea is considerably determined by replenishment from the shoals, primarily from the north-western shelf where mass reproduction occurs during late winter [30]. Thus, the seasonal cycle of this species in the Black Sea is determined by both temporal and spatial redistribution of the population.

The seasonal changes in biomass of *Calanus euxinus* in the open sea region, 90-95% of which consisted of V and VI, and less by IV copepodits were synchronous during the whole period of observations over the entire sea area. In winter the biomass of *C. euxinus* was low. In the open sea the amount of nauplii and early (I-II) copepodits was not high in March or during other seasons. It increased later in spring, obviously, due to migration of quickly growing juveniles from the shoals. Maximum in *C.euxinus* concentration was observed in March-April. Then it gradually decreased till November to the values lower than that at the beginning of the year. The reason of this decrease seems to be primarily the feeding off by *Mnemiopsis, Pleurobrachia*, and some pelagic fishes.

The described pattern of seasonal variations of zooplankton illustrates that the grazing pressure of *Mnemiopsis leidyi* is the principle factor that determines these changes. Thus, the variations of the biomasses of its potential preys were the most pronounced. Influence of *Mnemiopsis* towards *Aurelia aurita* was the competitive one. It apparently did not change the typical pattern of *Aurelia* seasonal development, but decreased its absolute biomass values. *Noctiluca miliaris* was not influenced by *Mnemiopsis*. *Pleurobrachia pileus* has the similar pattern of seasonal variations as *Mnemiopsis*. It seems to be strange because these two species are the competing ones. However the cores of the populations of these species are separated vertically: *Mnemiopsis* inhabits the upper mixed layer, and the *Pleurobrachia* occurs in the cold intermediate waters below the thermocline.

The seasonal variations in the deep part of the sea are the least known part of the temporal ecosystem variations. As was shown before, significant interannual variability occurs and the seasonal patterns differ between the years. Undoubtedly, it should be taken into account during the elaboration of the scheme of studying of the seasonal changes in the open waters of the Black Sea. Evidently, this study should be primarily based on the monitoring of the ecosystem within the same year.

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