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# A review of zooplankton investigations of the Black Sea over the last decade

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## Abstract

Investigations performed in the last decade indicate that there have been important changes in the zooplankton composition and structure in the Black Sea. However, contrasting events taking place in different regions of the Black Sea indicate a non-uniform structure of its ecosystem.

Several fodder zooplankton species have either disappeared from or substantially decreased in number at different sampling sites of the Black Sea over the last one or two decades. Some other species adapted to thrive in eutrophic conditions have either appeared or increased in quantity. Meanwhile the biomass of the fodder zooplankton has also fluctuated considerably through the years. However, there seems to be a reverse trend in the long-term variation of fodder zooplankton between the shallow western and deep eastern areas. Over the last few decades the abundance of fish larvae has decreased significantly when compared either to past records or with larval abundances of other seas. This was shown to be due mainly to malnutrition of larvae. One of the most striking changes in the ichthyoplankton has been the shift in the spawning areas of the main fish species, the anchovy *Engraulis encrasicolus* from the northwestern to the southeastern Black Sea. Even the invading ctenophore *Mnemiopsis* were found to be starving. The condition of other species (*Calanus euxinus* and *Pleurobrachia pileus*) disclosed the fact that cyclonic regions where chlorophyll and nutrient concentrations are high, provide better nutrition than anticyclonic regions. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Black Sea; zooplankton; ichthyoplankton; *Mnemiopsis*; anchovy; fisheries

## 1. Introduction

Adverse changes which have occurred in the Black Sea ecosystem in the last decade have taken a great attention from the scientific community (see Mee, 1992; Zaitsev, 1992; Kideys, 1994 for general reviews). The zooplankton of this sea is probably one of the most affected components of its pelagic ecosystem.

In the Black Sea, zooplankton studies first began about 150 years ago for faunistic purposes (e.g., species descriptions) (see Kovalev et al., 1998b). Later, studies concentrated on specific aspects (feeding, growth, reproduction and other physiological parameters) of zooplankton communities or species (Delalo, 1961; Petipa et al., 1970; Greze et al., 1971

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and others). These were coupled with temporal (mainly diurnal and seasonal) and spatial studies of zooplankton distribution (both horizontal and vertical) to understand the functioning of the ecosystem (Vinogradov et al., 1985; Konsulov, 1986,1990). The bulk of these earlier studies on Black Sea zooplankton were published in languages of former iron-curtain countries (Russian, Bulgarian or Romanian) and in a few cases in Turkish and therefore zooplankton science internationally could not benefit much. However, as a result of extensive collaboration among riparian countries in the framework of the TU-Black Sea Project during 1991–1996, numerous studies have been published in English. These recent studies have generally dealt with long-term changes in zooplankton composition due to anthropogenic factors (Konsulov and Kamburska, 1997; Niermann and Greve, 1997; Niermann et al., 1998; Shiganova, 1997,1998; Shiganova et al., 1998; Kovalev et al., 1998a,b,c,d, and several others). A few specific studies on zooplankton have also been carried out (Arashkevitch et al., 1998; Besiktepe, 1998; Shulman et al., 1998; and others). The aim of this paper is to do a synthesis of the most important findings of these recent zooplankton studies, evaluated separately under four main categories: (1) Fodder zooplankton, (2) Gelatinous zooplankton, (3) Ichthyoplankton, and (4) Physiological studies on zooplankton.

## 2. Material and methods

Long-term phytoplankton and fodder zooplankton data of the Southern Institute of Marine Fishery and Oceanography (YugNIRO, Ukraine) were obtained from the northwestern and the northeastern Black Sea during 1959–1988. The samples were collected annually in March, May, June, July and August at 24 stations in the northwestern shelf and at 25 stations in the northeastern offshore region with a nearest distance of 5 nautical miles from the coast (cf. Figs. 1A,B and 2). The phytoplankton samples were collected using a 1-l bathometer at standard depths (0, 10, 25, 50, 100 m). The zooplankton samples were collected with a Juday net ($d = 0.1$ m$^2$; mesh size = 168 microns) from 100 to 0 m (or bottom to 0 m). The monthly and subsequently annual average numbers and biomasses of the total zooplankton for each region (about 500 samples per year) were calculated. Unfortunately the published information did not present information about standard deviations of the average values.

From 1988–1996 the annual averages of fodder zooplankton were obtained using the data of the Institute of Biology of the Southern Seas (IBSS, Ukraine; cf. Fig. 1A–C) and the Institute of Marine Sciences (IMS, Turkey; 1991–1996; cf. Fig. 1D). The data were collected in shallow areas with water depth 50–200 m and in offshore areas ($> 200$ m water depth) from all over the Black Sea during national and international programs. IBSS and IMS used the same evaluation methodology for fodder zooplankton as YugNIRO. The large and rare animals were counted in all samples. Mass species were estimated by subsampling whereby duplicate subsamples of one or 2 ml were removed with a stempel pipette. The biomass was calculated by taking in account the abundance and individual weight of the species in accordance with the tables of Petipa (1959). The IBSS collected the samples by a Juday net (opening 0.1 m$^2$; mesh size 145 micron) in the layer 0–100 m (or 0–150 m). The IMS zooplankton samples were taken with a Hensen net (opening 0.385 m$^2$; mesh size 300 micron).

For the calculation of biomass percentage of copepods from the Sevastopol area (cf. Fig. 3), sampling was performed using different nets. In the Kamish Bay (maximum depth 50 m) the samples were taken by the IBSS over a 10 mile transect at four stations at depths of 0–40 m, 2–3 times per month during 1960–1969. More than 800 samples were collected from Kamish Bay. The horizontally towed Greze net (opening 158 cm$^2$, mesh-size $100 \times 70$ micron with a flow meter) was used. The samples were taken at 40, 30, 20, and 10 m depth. At each depth sampling continued for 2 min, after which the net was repositioned in the next layer. In total the net was towed for about 15 min. The total filtered volume of water varied between 4–9 m$^3$. The method of identification, counting and biomass estimation were the same as above. In Sevastopol Bay, zooplankton samples were taken twice monthly at one permanent station (12–17 m deep) during different time periods from January 1976 till May 1996 (1976: January to December; 22 samples; 1979/1980: December–November, 22 samples; five stations in 1981–1983, 150 samples; 1989/1990: October to September, 18 samples; 1995/1996: June to May, nine samples). These samples were collected with a vertically towed Juday net (opening: 0.1 $m^2$, mesh size: 145 micron). The hauls were performed from 10 m to the surface. In Vasilev Bay (Balaklava area) zooplankton samples were taken by the IBSS during 1981–1994. The samples were collected with a Juday net three times a year (spring, summer, autumn), at 5 permanent stations in an area of about 0.5 $km^2$, with a bottom depth of 10–50 m.

The ichthyoplankton and gelatinous plankton during 1991–1997 (cf. Figs. 4–6) were collected from a dense station grid in the Turkish Exclusive Economic Zone (TEEZ) covering the entire southern Black Sea with the R/V Bilim in 12 surveys. The average number of stations per cruise was 78. All samples were obtained via vertical tows from the anoxic zone (of which depth changes spatially, however, consistent at 16.2 in terms of sigma theta density unit) to the surface using a Hensen net (300 μm mesh size and 70 cm diameter of net opening). Bucket contents were filtered using a 2 mm sieve to retain and subsequently to quantify gelatinous organisms. The volume of each ctenophore *Mnemiopsis leidyi* was measured, whilst diameter measurements of the ctenophore *Pleurobrachia pileus* and the cnidarian *Aurelia aurita* were taken for all individuals. Using the conversion values (our unpublished data), biomass values were also calculated for the gelatinous zooplankton. The filtrates were then fixed with buffered formalin (final concentation of 4%) for ichthyoplankton analysis in the laboratory under a binocular microscope.

For the estimation of lipid content of *Calanus euxinus* and glycogen content of *P. pileus* (cf. Fig. 7) samples were collected in the southern Black Sea during 25 September–4 October 1996. Copepods were captured at night in surface waters using a Nansen plankton net (112 μm mesh size, 0.7 m diameter) and the ctenophore was caught with a Hensen net (300 μm mesh size, 0.7 m diameter) from the entire aerobic water column. The boundaries of the aerobic water column were determined for each station from the density depth of $\delta t = 16.20$ calculated from temperature and salinity profiles defined by means of a Sea Bird CTD probe. Ascend in the $\delta t = 16.20$ to 100–120 m depth was indicative of cyclonic activity and descend to 160–200 m depth was an anticyclonic one. The sea surface temperature was 18–21°C. Polysaccharide and glycogen content determinations were made in individual samples applying the spectrophotometric method. The polysaccaride content was calculated as μg per g of wet weight, glycogen in μg of wet weight and as a percentage of the total polysaccharide content. At each station concentrations of chlorophyll, nitrates and phosphates were measured at depth intervals of 15–20 m from the surface down to the $\delta t = 16.50$ density level. Profiles of chlorophyll, nitrate and phosphate contents were drawn, and integrated concentrations for the euphotic zone evaluated.

## 3. Fodder zooplankton

Fodder zooplankton are of great importance from a human point of view. Whilst feeding on primary producers, they filter suspended matter, which might have been increased due to eutrophication as in the northwestern shelf of the Black Sea, thus improving the water quality. They are, by definition, the food of higher trophic levels, including all stages of pelagic fishes. Since the catch of pelagic fishes makes up the bulk of total fishery (Leppakoski and Mihnea, 1996), this group of zooplankton is a subject of concern particularly for the Black Sea. The early developmental stages of demersal fish also feed on fodder zooplankton.

### *3.1. Species composition*

Copepods are the most important group of fodder zooplankton and hence the majority of investigations has been on this group. Zenkevitch (1963) reported 77 species of copepods in the Black Sea. However, at present, this value must have changed due to newcomers. Mediterraneanization is the most important process in the enrichment of Black Sea copepod fauna. This process was studied in detail by Kovalev et al. (1998a). They listed 60 copepod species originating from the Mediterranean Sea, most of them found only off the Bosphorus region. Five of these species, *Microcalanus pusillus, Aetideus armatus, Euchaeta marina*, *Metridia lucens,* and *Oncaea ob-*

*scura* were recorded for the first time in the Black Sea in samples collected from the Bosphorus region during 1995–1997. In this region as well as in all 14 stations sampled from different deep regions of the sea during September–October 1996, they also found *Acartia tonsa* which was previously reported only once in the Black Sea, near the Crimean coast (Belmonte et al. 1994). Kovalev et al.'s (1998a) study confirms that this species has now been naturalised in the Black Sea as had happened with several other non-indigenous copepod species in the past. According to Paffenhofer and Stearns (1988), *A. tonsa* is adapted to high food concentrations and therefore its appearance in the Black Sea is interesting though not surprising when the gradual increase in eutrophication over the last few decades is considered.

### 3.2. Long-term variations

Long-term changes in the biomass and composition of zooplankton, particularly for the fodder component have been the focus of various studies (Konsulov and Kamburska, 1997; Niermann and Greve, 1997; Niermann et al., 1998; Shiganova, 1997,1998; Shiganova et al., 1998; Kovalev et al., 1998c,d). Despite a few long-term data sets on the quantity of fodder zooplankton of the shallow regions (coastal waters of Bulgaria, Romania and the northwestern shelf), there is only one respective data set for the deep region ($> 200$ m) which exists for the northeastern Black Sea.

In all of these studies the fodder zooplankton has been found to fluctuate considerably through the years. However, there seems a reverse trend in the long-term variation of fodder zooplankton between the shallow western and deep eastern areas (Fig. 1). In the coastal area (e.g., the northwestern shelf), the fodder zooplankton biomass was high in the 1960's (up to 20.9 g $m^{-2}$ in 1960 and 27.6 g $m^{-2}$ in 1967), with a decreasing trend since then (except in 1980 when it was 22.5 g $m^{-2}$) until the early 1990's (Fig. 1A). In contrast to the coastal area, the quantity of fodder zooplankton in the deep eastern region gradually increased from the 1960's to the early 1970's. After a period when it decreased between the early and late 1970's, the trend was again positive until the 1990's (Fig. 1B). The increasing trend in the biomass of fodder zooplankton of the deep eastern region corresponds to that of the phytoplankton biomass (Fig. 2). Whilst there did not seem a clear trend in long-term variations in the phytoplankton biomass of the northwestern region, that of the deep eastern region increased substantially from the 1960's. This indicates that the deep eastern waters (including the southeastern Black Sea) became more productive through the years. which was also reflected by both the substantial increase in the fish catch of Turkey from this sea (Kideys, 1994; see Fig. 5) and the spawning behaviour of anchovy (see Section 7).

The decreasing trend seen for the fodder zooplankton of the coastal western Black Sea could be explained by the worsening ecological conditions in this region (Mee, 1992; Zaitsev, 1992; Kideys, 1994; Bologa et al., 1995). Among these conditions, harmful levels of pollution and increasing eutrophication which consequently results in an increase in the biomass of gelatinous organisms seem the most detrimental. One piece of evidence to support this statement is the negative changes seen in the composition of fodder zooplankton.

Analysing the long-term data, Kovalev et al. (1998c) observed similar changes in the composition of fodder zooplankton in the shallow northern and western regions of the Black Sea. While *Acartia clausi* (a species which prefers eutrophic conditions) became the most dominant copepod during the 1990's forming up to 85% of total fodder zooplankton biomass in the shelf areas of the Black Sea (Fig. 3), the biomass of other copepod species has decreased since the mid 1960's and indeed some (such as *Oithona nana*) have disappeared completely from the zooplankton community (Kovalev and Gubanova, 1995). In Sevastopol Bay the increase in *A. clausi* was so strong that this species was the only copepod found there in the summer months during June–August 1990–1994. The same was true for the shallow coastal area, close to the river Dniepr, where *A. clausi* was the sole species occurring in this area (Zagorodnyaya and Skryabin, 1995).

In 1976, 11 of the 13 common marine copepod species known for the Black Sea were present in Sevastopol Bay. By the 1990's only six species remained in this area. The disappearing species included the hyponeustonic copepods *Pontella mediterranea* and *Labidocera brunescens* (which are

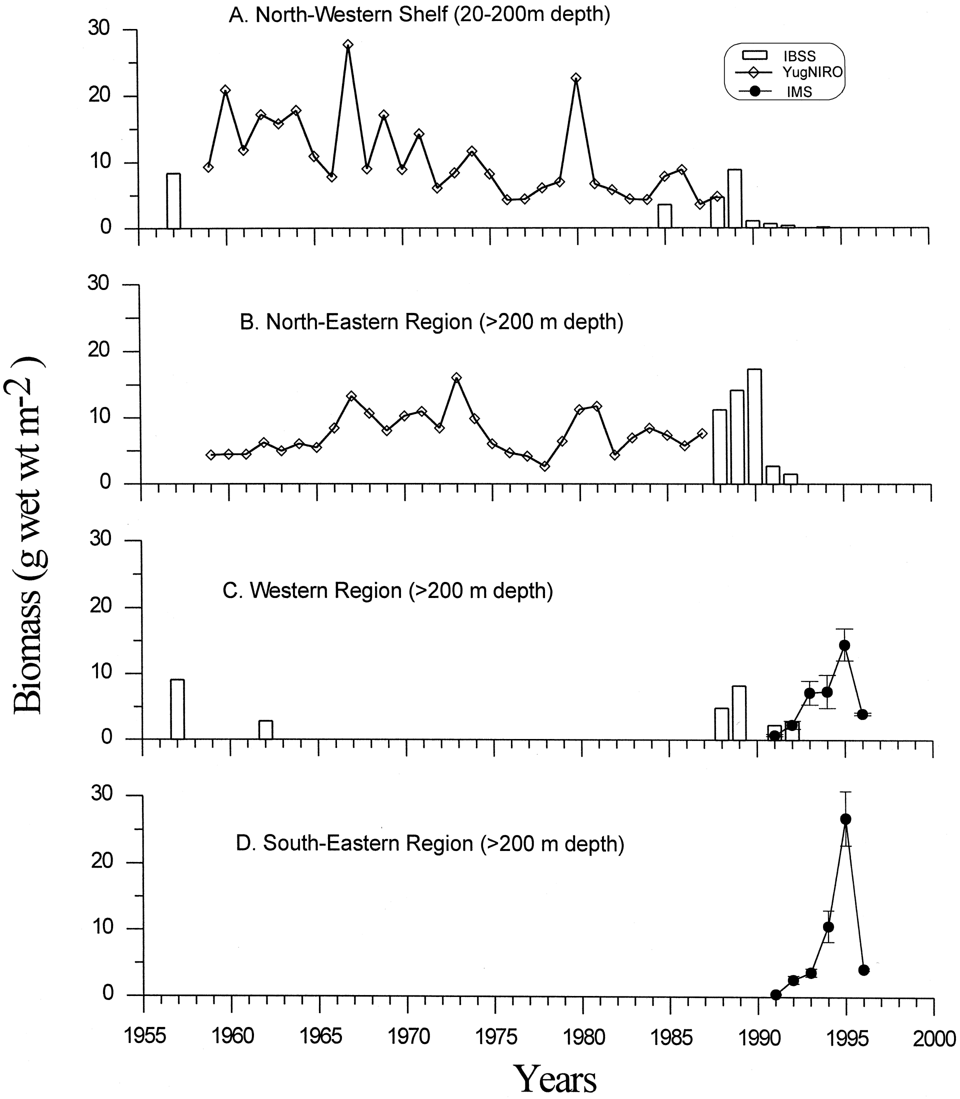

Fig. 1. Long-term changes (annual averages) in the fodder zooplankton biomass in different regions of the Black Sea (Kovalev et al., 1998d). Standard error values for Turkish data were plotted. (YugNIRO the Southern Institute of Marine Fisheries and Oceanography, IMS the Institute of Marine Sciences of Middle East Technical University, Turkey; IBSS the Institute of Biology for the Southern Seas, Ukraine).

highly sensitive to pollution at the microfilm layer of surface waters) which had not been recorded in the bay since 1976. In 1982–1983, the copepods *Anomalocera pattersoni* and *Paracartia latisetosa* were found for the last time (Belyaeva and Zagorodnyaya, 1988). During 1989–1990 the species *O. nana* and the small form of *A. clausi* also disappeared (Kovalev and Gubanova, 1995).

Similar changes were observed in the copepod composition of Vasilev Bay. *Paracalanus parvus* and *Centropages ponticus* have decreased drastically since 1987. *P. mediterranea* and *O. nana* had not been recorded in samples as for Sevastopol Bay while *A. clausi* constituted up to 90% of the total copepod biomass in the summer of 1990 (Zagorodnyaya and Skryabin, 1995). Similar changes were

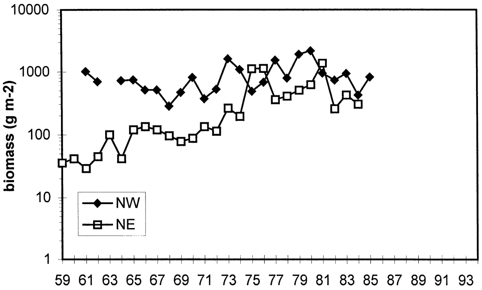

Fig. 2. Long-term changes in the average values of phytoplankton biomass in the northeastern (NE) and northwestern (NW) Black Sea (Data of YugNIRO; Kovalev et al., 1998d).

also reported for the Rumanian (Porumb, 1992) and Bulgarian coasts (Konsulov and Kamburska, 1997).

These remarkable changes did not only occur in the copepod community, but also in the composition of the total fodder zooplankton in the Sevastopol area. In Kamish Bay copepods constituted about 73% of the average total zooplankton biomass during 1960–1970, however, their percentage had decreased to 67% in Sevastopol Bay in 1976 and was only 14% in 1990 (Kovalev et al., 1998c).

Despite the decrease in biomass of the fodder zooplankton in the shallow northern and western regions, the total zooplankton biomass has increased during the period of increasing eutrophication of the Black Sea (Belyaeva and Zagorodnyaya, 1988; Zaitsev, 1992). This has occurred mainly due to the increase in the biomass of gelatinous organisms such as *Noctiluca scintillans, Pleurobrachia pileus, Aurelia aurita* and later *Mnemiopsis leidyi* (Zaitsev and Polischuk, 1984). Since these animals consume fodder zooplankton, the increased predation pressure has led to changes in the composition of the fodder zooplankton and a marked decrease in their biomass. The decrease in the fodder zooplankton biomass of both coastal and deep regions seen in the 1970's–1980's corresponds with the increase in the biomass of *Aur. aurita* (Kovalev et al., 1998d). However, the most dramatic decrease observed during the mass occurrence of *M. leidyi* in the early 1990's over the entire Black Sea (Fig. 1A,B; Kovalev et al., 1993). Even the production of *A. clausi,* which is the dominant species in the northern Black Sea, decreased 1.5–4-fold after the *Mnemiopsis* invasion (Ostrovskaya et al., 1998). However, Shiganova et al. (1998) suggested that with the recent decrease in *Mnemiopsis* since 1995 (see Fig. 4) the abundance and species diversity of fodder zooplankton started to increase which was also reflected by the Turkish data (Fig. 1C, D).

Kovalev et al. (1998d) and Niermann et al. (1998) compared the fluctuation of the plankton in different seas of the northern hemisphere and concluded hypothetically, that changes in the weather regime during the 1980's could have triggered the changes in the phyto- and mesozooplankton communities of the Black Sea, which caused the conditions that led to the outburst of *M. leidyi* and the subsequent decline in the anchovy stock during 1988–1990. A comparison of the weather regime of the 1980's with previous decades showed indeed that the 1980's were unique. The 1983–1990 period in particular was dominated by a positive phase of the North Atlantic Oscillation (NAO), which increased strongly after 1988 (Rodionov, 1994) resulting in an increase in the Black Sea surface temperature and a decrease in salinity and river discharges during the end of the 1980's, and the beginning of the 1990's. However, the effect of climate is difficult to gauge, since it is overshadowed, especially in the shelf regions, by pollution and eutrophication, resulting in the high fluctuation of the communities.

## 4. Gelatinous zooplankton

Gelatinous zooplankton of the Black Sea have been studied recently by Mutlu et al. (1994), Petran and Moldoveanu (1997), Shiganova (1997,1998), Anninsky et al. (1998), Konsulov and Kamburska (1998), Shiganova et al. (1998), Shulman et al. (1998). The last two studies are on physiological condition of animals whilst the former ones deal with their spatial and temporal distribution.

Four species of gelatinous animals are commonly present in the Black Sea, namely two scyphozoan medusae (*Rhizostoma pulmo* and *Aurelia aurita*) and two ctenophores (the indigenous *Pleurobrachia pileus* and the invader *Mnemiopsis leidyi*).

*R. pulmo* is most common in coastal areas and rarely penetrates into the open sea. They are generally encountered in single numbers. This species is the least abundant among gelatinous animals of the Black Sea, however, in the late 1960's–early 1970's

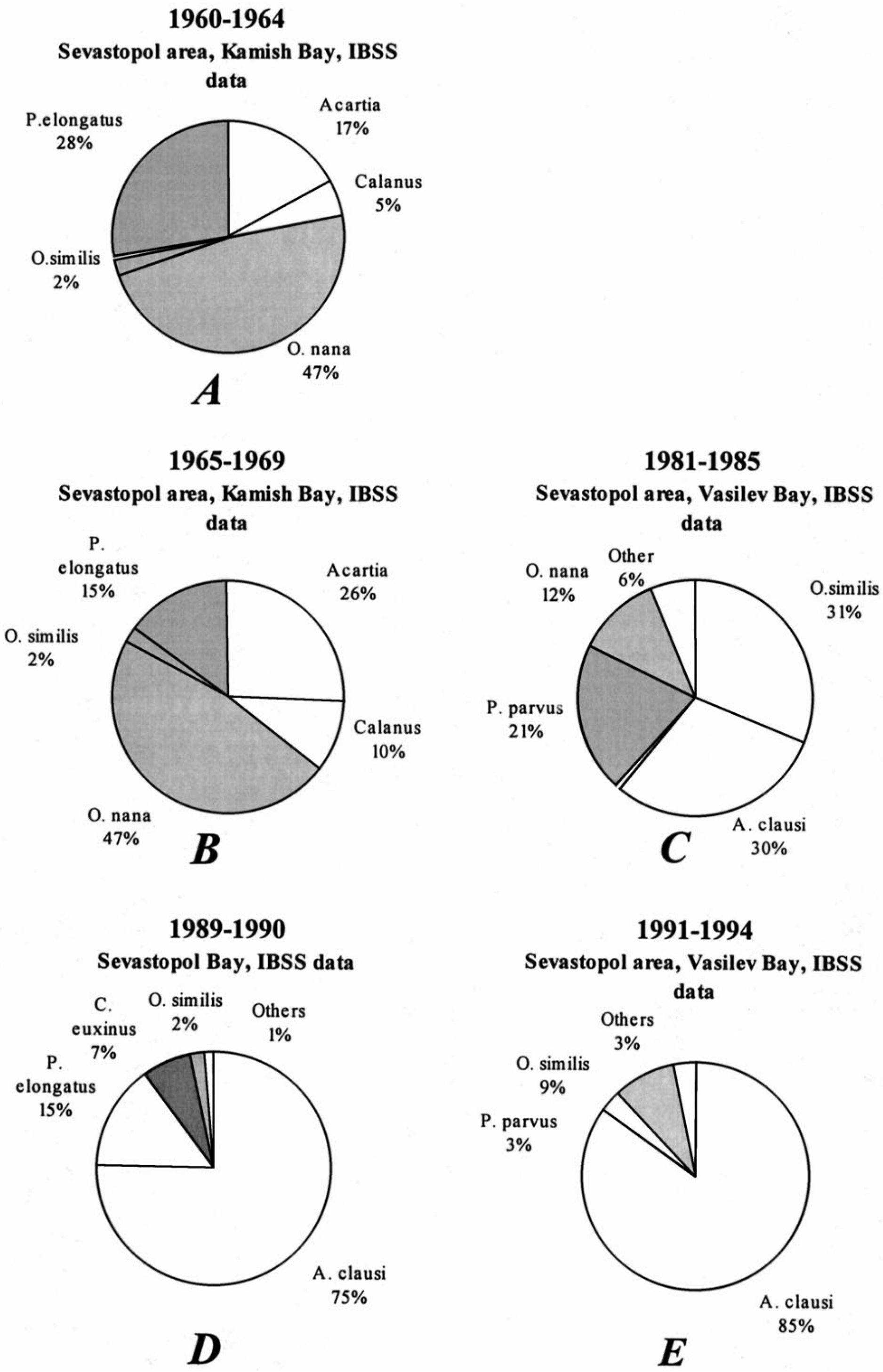

Fig. 3. Long-term variations in the biomass percentage of copepods in different bays off Sevastopol (Kovalev et al., 1998c).

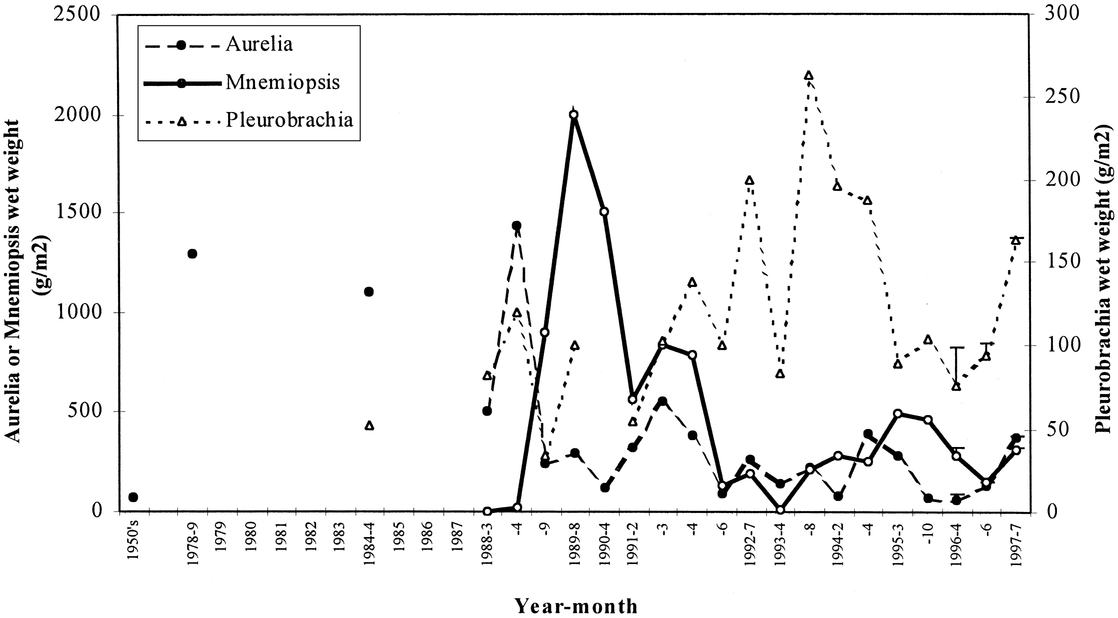

Fig. 4. Long-term dynamics of main gelatinous zooplankton species. Data after 1990 relate to the southern Black Sea (1991-2 to 1995-3 values from Mutlu et al. (1994) and Mutlu (1996); 1995-10 to 1997-8 values from unpublished data of A.E. Kideys et al., the standard error values of the latter were also drawn).

high abundances were reported (Zaitsev and Aleksandrov 1997).

*A. aurita* occurs throughout the sea but mostly in eutrophic inshore waters. Since the 1970's the population of *A. aurita* grew explosively and reached peak values (over 1 kg $m^{-2}$) during the 1980's (Fig. 4) when its total biomass for the total sea area was calculated to be 300–500 million tons (Shushkina and Musaeva, 1983). After the explosive development of *M. leidyi* in 1989, the abundance of *A. aurita* dropped (Fig. 4). Shiganova et al. (1998) found a significant negative correlation ($n = 14$, $r = -0.80$, $p = 0.005$) between the number of *M. leidyi* and the biomass of *Aur. aurita* indicating intense competition between these species whereby *M. leidyi* proved to be a successful competitor with *A. aurita*. The abundance of fodder zooplankton was reported to decrease during the 1980's due to grazing by *A. aurita* as was mentioned before. In the open sea, the maximum biomass ($> 2$ kg $m^{-2}$) values for *M. leidyi* were obtained in the 1989 autumn (Vinogradov et al., 1989; Fig. 4). After 1990 its biomass decreased almost steadily until 1993 when it dropped to its lowest value (14 g $m^{-2}$). In 1995 and 1996 the biomass of *M. leidyi* remained at moderate levels of 100–200 g $m^{-2}$. Shiganova et al. (1998) comparing the spatial distribution of *M. leidyi* and *A. aurita* observed that there were many more *M. leidyi* and *A. aurita* in the highly polluted inshore waters of the northeastern Black Sea than in its southern region.

The ctenophore *P. pileus* inhabits the layer between the seasonal thermocline and main pycnocline. Mutlu et al. (1994) observed a doubling in the biomass of this ctenophore between 1990/1991 and 1993. However, a sharp decrease in the biomass is striking between 1994 and 1995 (Fig. 4).

Overall, during the 1980's–1990's the abundance or biomass of gelatinous animals increased in the Black Sea.

## 5. Ichthyoplankton

### *5.1. Species composition*

According to Dekhnik (1973) ichthyoplankton of the Black Sea comprised a total of 56 fish species: 28 fish species producing pelagic eggs and larvae with another 28 species having pelagic larvae only. Gordina et al. (1998) observed eggs of 28 and larvae of 44 fish species in the Black Sea during their survey period of 1986–1996. During the most recent surveys (1991–1996), it was verified for the first time, that the Sea of Marmara anchovy (*Engraulis encrasicolus*) (Gordina et al., 1997), the mackerel *Scomber scombrus* and the blennid *Blennius ocellaris* spawn in the Black Sea (Gordina et al., 1998). These findings conclude the discussion of whether these species spawn in the Black Sea or not, which had been ongoing for a long time. Moreover, eggs of the far-eastern grey mullet *Mugil so-iuy* were found for the first time in the Black Sea. This finding proved that this species which was introduced into the northern lagoons during 1972–1986, now spawns along the Ukranian, Russian, Georgian and Turkish coasts.

### 5.2. Changes in the abundance

During the 1930's the northwestern Black Sea was characterised as having a considerable diversity of ichthyoplankton, up to 35 species in summer time. During the period between 1950–1970, the ichthyoplankton of four pelagic fish species, namely *E. encrasicolus*, *Trachurus mediterraneus*, *Mullus barbatus* and *Diplodus annularis* consisted 96% of the total egg and larva number (Dehknik, 1973). The average numbers of fish eggs and larvae in coastal waters were 216 $m^{-2}$ and 41 $m^{-2}$, respectively. Corresponding values for the offshore regions were 189 eggs $m^{-2}$ and 30 larvae $m^{-2}$.

Table 1 displays the larval abundance of the Black Sea in comparison to the rich Sea of Azov and and oligotrophic seas like the Red Sea and the Mediterranean Sea. Due to the changes in the Black Sea ecosystem the abundance of ichthyoplankton of the Black Sea decreased considerably and now appears to be at a low level, comparable to that of oligotrophic seas like the Mediterranean (Table 1).

Table 1
Average number of fish larvae in different seas (Gordina et al., 1998)

| Region | Period | Number of fish larvae (ind. $m^{-3}$) |
|---|---|---|
| Azov Sea | 1962–1963 | 570 |
| Mediterranean Sea | 1958–1962 | 17 |
| Red Sea and Gulf of Aden | 1966 | 75 |
| Black Sea | 1962–1963 | 160 |
| Black Sea | 1988 | 29 |
| Black Sea | 1989 | 7 |
| Black Sea | 1992 | 1 |
| Southern Black Sea | 1996 | 9 |

Compared with the previous years, in 1988 the number of eggs had decreased 2–4-fold, the number of larvae 2–9-fold, in both coastal and offshore waters in different regions of the Black Sea. During 1989, when *M. leidyi* reached its peak biomass (Vinogradov et al., 1989), a further 2-fold decrease in the ichthyoplankton abundance was observed over the entire Black Sea (Gordina and Klimova, 1996). The northwestern Black Sea, the main spawning area for many valuable fish species, suffered most.

### 5.3. Spawning areas

At the beginning of the 1970's, disturbances to the ecological condition of the Black Sea started, particularly in the shallow coastal waters of the north-western area. Over-regulation of river flows, the extensive use of fertilisers and chemicals in agriculture, industrial pollution and the removal of soil or sand along the coastal areas must have adversely affected the ichthyoplankton of the Black Sea in two ways. Firstly, it is known that 90% of fish species with a summer reproduction cycle spawn in the coastal waters of the Black Sea (Dekhnik, 1973; Gordina and Klimova, 1996) and hence the spawning population would inevitably be affected by changes in the water quality of these regions. Secondly, the highest mortality rate during the life cycle of fish occurs in the early stages of ontogenesis which usually take place in coastal areas.

Another profound change in the ichthyoplankton of the Black Sea has been caused by the recently introduced ctenophore *M. leidyi*, which very quickly became the dominant species in terms of biomass (wet weight) among zooplankton. This species is a voracious predator on zooplankton and became the main food competitor of plankton feeding pelagic fishes and their larvae. Besides this, it feeds on the eggs and particularly larvae of fish. In experimental conditions specimens of *M. leidyi* with a minimum length of 2–2.5 cm consumed larvae of the anchovy *E. encrasicolus* (Lipskaya and Luchinskaya, 1990). Yolk sack larvae were notably preferred. It was estimated that one individual can consume 4–8 fish larvae a day. During its spawning period in summer *Mnemiopsis* is able to consume 74% of the available fish larvae (Tsichon-Lukanina et al., 1992).

Such events must have resulted in significant changes in the abundance, composition and distribution of the Black Sea ichthyoplankton. The main spawning areas of many fish species are the coastal regions, especially at the northwestern shelf. At the end of 1980's/beginning of 1990's the importance of open waters as spawning grounds in the Black Sea increased considerably, when the environmental conditions of the coastal waters and the northwestern shelf became worse. These shifts of the spawning areas were observed for several pelagic fish species (Gordina and Klimova, 1996). At the beginning of 1988, besides coastal regions, offshore areas (on a scale of several km) containing a high number of eggs and larvae of *E. encrasicolus* and *T. mediterraneus* were observed in the Black Sea (Gordina et al., 1990).

The effects of these events which have occurred over the last few decades were particularly apparent for the most abundant fish species (the anchovy *E. encrasicolus*) of the Black Sea reflected as pronounced changes in its ecology. Initially anchovy abundance and catch gradually increased (up to approx. 500 thousand tonnes; Fig. 5). Besides new technology used in commercial fishing, this increase must also be due to several other factors, such as the beneficial effects of nutrient increase particularly in the northwestern shelf (Zaitsev, 1992; Kideys, 1994), decreasing predator pressure and disturbance in benthic/pelagic coupling (i.e., mass mortalities of benthic filter feeders in shallow regions caused by hypoxia resulted in more suspended organic matter available for zooplankton feeding). However, increasing eutrophication (for the northern or northwestern region) together with overfishing (mainly for the southern region) and the recent appearance of the competing invader *M. leidyi* caused an abrupt decrease (more than 5-fold) in the catch of this fish by the end of the 1980's (Kideys, 1994; Gücü, 1997) (see Fig. 5). After this sudden decrease the anchovy catch is now again increasing steadily (approaching levels seen in Turkey prior to the decrease; Maclennan et al., 1997). Besides its abundance, the reproductive strategy of anchovy (inferred from the long-term distribution of its early life stages) also displayed striking changes (Niermann et al., 1994). These authors were the first to notice the shift in the spawning region of anchovy (Fig. 6). In contrast to earlier studies, the southern Black Sea, particularly its southeastern region, contained higher egg numbers than in the northwestern region (Niermann et al., 1994) which was traditionally known as the main

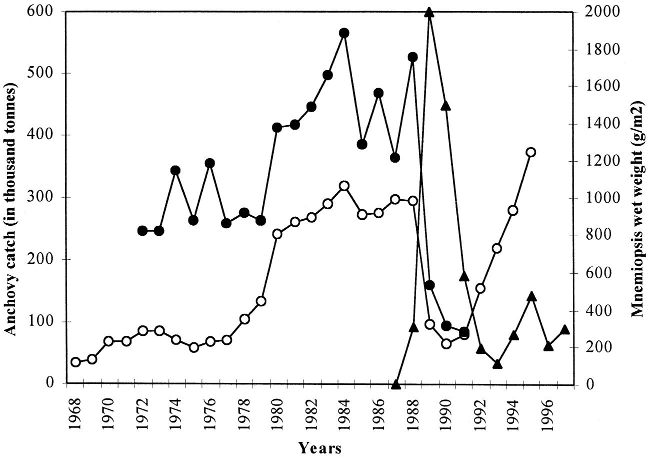

Fig. 5. Anchovy catches for the Black Sea. Open circles = Turkish catch, dark circles = total catch of all riparian countries, dark triangles: *Mnemiopsis* biomass. No total catch data available since 1991. Changes in the average *M. leidyi* biomass in the Black Sea are also shown (triangles) (after Kideys et al., 1998).

spawning area (Ivanov and Beverton, 1985). Monitoring the ichthyoplankton of anchovy in 1993 and 1996, Kideys et al. (1998) concluded that the southern Black Sea (i.e., Turkish coasts) has now been established as the most important spawning area. Moreover since egg numbers reflect the size of

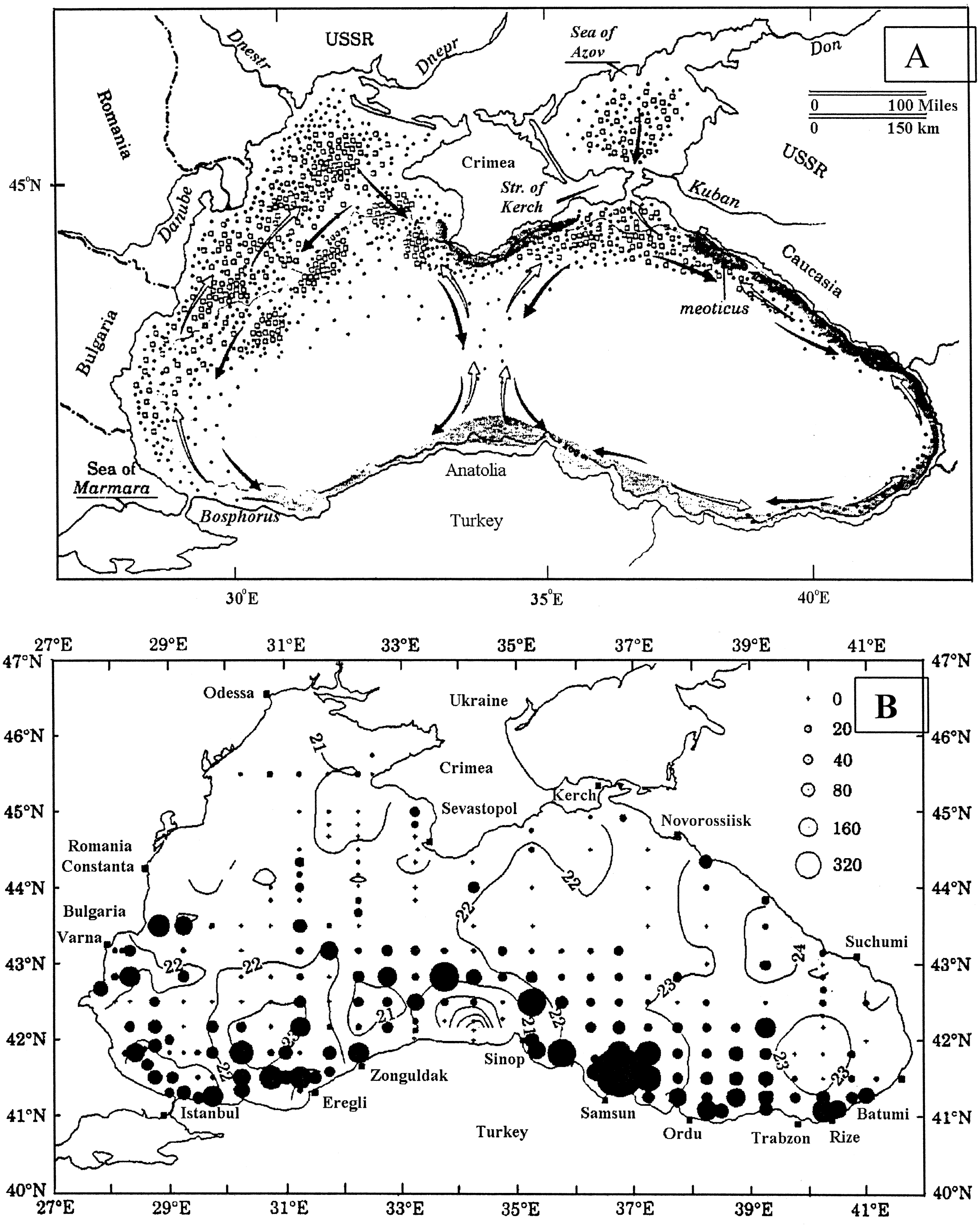

Fig. 6. Changes in the spawning grounds of anchovy. (A) Traditional spawning areas (shown with squares) according to Ivanov and Beverton (1985). Dark grey indicates wintering areas. (B) Distribution of anchovy eggs (numbers $m^{-2}$, scale is given on the upper right corner) and surface temperature (°C, at 5 m depth) in the Black Sea during July 1992 (modified from Niermann et al., 1994).

parent stock, they suggested that the high number of eggs and larvae obtained in June–July 1996 was an indication of improved conditions for anchovy at least for the southern Black Sea. Temperature, salinity and fodder zooplankton were among the most important ambient parameters in the distribution of anchovy eggs in this region.

Shiganova et al. (1998), comparing the abundance and species diversity in zooplankton, ichthyoplankton and fish catches between the northern and southern Black Sea, suggested the southern region to be richer in abundance and species diversity for these pelagic groups. The southern Black Sea became one of the most important areas for the spawning of a great number of commercial species, many of which had not previously been recorded there. Such changes in spawning locations may be attributed to favourable environmental conditions and food availability (fodder zooplankton) in the southern Black Sea in contrast to the northern part, in particular the barren northeastern area.

### 5.4. *Larval nutrition*

Tkach et al. (1998) analysed the data on the nutrition of the larvae of the main Black Sea fish species and found that the changes in the composition of plankton caused by anthropogenic impact considerably influenced the feeding of fish larvae. Food items which dominated in the 1950’s and 1960’s disappeared. Larvae began to eat organisms which were earlier considered to be of secondary importance for their nutrition.

In the past, all developmental stages of *O. nana* dominated the larval diet (Pavlovskaya, 1964); however, from 1989 to 1996 this species was almost absent in the digestive tract of different species of fish larvae (Table 2) concurrent with the disappearance of this copepod from the plankton. Another preferred food species, *Paracalanus parvus* is also now virtually non-existent, especially during the last few years (Table 2). Due to the near-absence of these small copepods, fish larvae have had to begin feeding on larger-sized organisms (in the intestine of a 10 mm long *E. encrasicolus* larva Tkach et al. (1998) observed *A. clausi* of 0.75 mm). The disappearance of *O. nana* and *P. parvus* from the guts of the early larval stages must have had an adverse effect on the survival of stage II–III larvae.

The number of larvae with empty guts increased, thus adversely affecting their survival. For example the percentage of *E. encrasicolus* larvae with empty intestines has increased substantially in recent years compared to the 1950’s and 1960’s (Tkach et al., 1998). Besides the increase in the number of empty guts, there were also many larvae with single food items in their intestines (e.g., eggs of *Synchaeta* or molluscs) which is far from sufficient to meet their nutritional demands.

Besides of the changes in the zooplankton community, another reason for the empty guts of the fish larvae must be the competition with *Mnemiopsis*. In the summer period, copepods, which are the main food for the larvae, made up 56.4% of the *Mnemiopsis* food uptake in coastal waters and 74.7% in open waters (Tsichon-Lukanina et al., 1995). With respect

Table 2
Stomach content of *E. encrasicolus* larvae for different years in the Black Sea. % = percentage of larvae with empty intestine, N = nauplii, E = eggs, C = copepodites

| Larva group | 1955–1965 | | 1986–1988 | | 1989–1991 | | 1992, 1996 | |
|---|---|---|---|---|---|---|---|---|
| | Food | % | Food | % | Food | % | Food | % |
| II–III < 6 mm | N&C of *Oithona* and *P. parvus* | 45–59 | copepod E<br>*O. nana* C | 90 | | 100 | copepod E<br>*A. clausi*<br>N&C<br>*P. elongatus* N | 91 |
| IV 6.1–12.0 mm | copepod N, C of *O. nana* and *P. parvus* | 51–61 | C of *O. nana* and *Par. parvus*, *C. euxinus* E | 91 | *A. clausi* | 97 | *A. clausi* | |
| V 12.1–25.0 mm | N&C of *A. clausi*, *O. nana* and *P. parvus* | 41–34 | *O. nana* C, *P. avirostris* | 74 | *A. clausi*, *C. euxinus* N | 84 | *A. clausi* | |

to the dominant food items, *Mnemiopsis* appear to be a significant food competitor for the larvae and juvenile fish. The quantitative and qualitative deterioration of food resulted in a decrease both in growth rate and survival rate, which led to a remarkable reduction in their number.

## 6. Eco-physiological studies on zooplankton

Besiktepe et al. (1997) studying some ecological and physiological characteristics of *C. euxinus* in the Black Sea calculated that the percentage of primary production grazed by the female copepods was 14.5% in April and 9.5% in September 1995. These results indicate that *Calanus* alone is one of the most important species in the transfer of primary production to pelagic fish. Later Besiktepe (1998) estimated the respective value for the total copepod community ($>300$ μm) to be 31.5% for September 1995.

Both Besiktepe (1998) and Araskevitch et al. (1998) confirmed that the diapausing copepodite stage V (CVs) of *Calanus* was not feeding, as opposed to the active feeding population. Moreover the active and diapausing CVs differed in their motor activity, respiration and excretion rates, with higher estimates for the former group.

Shulman et al. (1998) applied some biochemical indices in order to understand the state of food provision for Black Sea pelagic animals during September 1996. Total lipid content and the main lipid fractions (especially wax esters) of *C. euxinus*

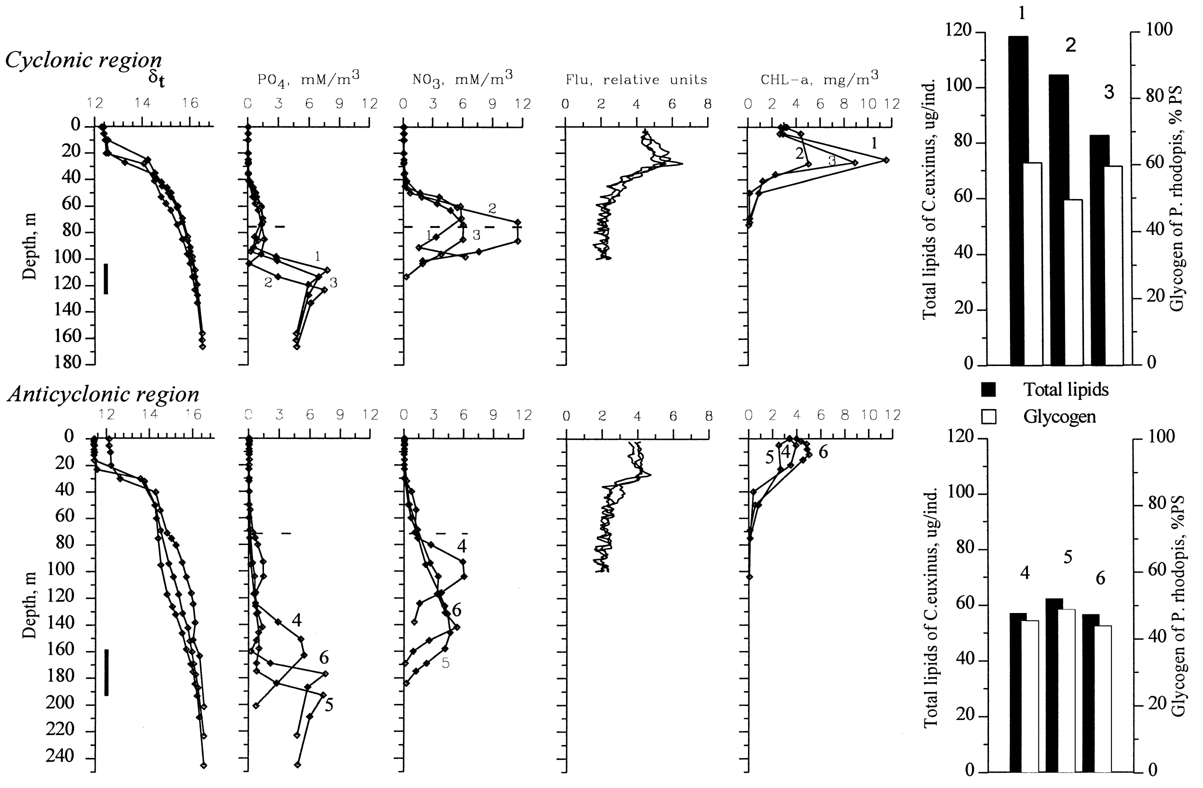

Fig. 7. Vertical profiles of sigma – t, phosphate, nitrate, in-situ fluorescence, chlorophyll-*a* concentrations and total lipids of *C. euxinus* females and glycogen content of *P. pileus* in cyclonic region (stations 1, 2 and 3) and in anticyclonic region (stations 4, 5 and 6) in the southern Black Sea. Bold lines on sigma – t profiles show oxygen minimum layer being the diapausing layer (sigma – t = 15.4 – 16.2) for *Calanus*. Dashed lines on $PO_4$ and $NO_3$ profiles indicate bottom border of the euphotic zone. PS = Polysaccharides (after Shulman et al., 1998).

females strongly correlated ($P < 0.005$) with mean integrated chlorophyll-a of the euphotic zone (see Fig. 7). Previously, for the 1991 cruise data, a highly significant correlation ($r = 0.82$; $n = 9$; $P < 0.005$) was also shown to exist between the chlorophyll-a concentration and biomass of phytoplankton within the size range of 10–50 μm (Yuneva et al., 1997). This indicates that the chlorophyll-a measurements alone may be sufficient for the evaluation of food availability for female *Calanus*. Indeed, highly significant correlations were also found between concentrations of chlorophyll-*a* (integrated mean) and of total lipid or its fractions (wax esters, phospholipids, triacylglycerols) of the feeding (and migrating) female *Calanus* (sampled at the surface layer during night-time) in 1991. The relationship between mean chlorophyll-a concentration and the content of wax esters (WE; being the major fraction of lipid in *Calanus*) was high ($r = 0.83$, $P < 0.005$). Thus, the level of lipids stored by *Calanus* clearly responds to changes in the chlorophyll-a concentration which in turn is related to the food availability being different in various regions of the sea.

As opposed to the lipid content of *Calanus*, the total mesozooplankton biomass, (akin to the biomass of *C. euxinus* being one of the principal contributors to the total mesozooplankton biomass) displayed no significant correlation (or even trend) with the integrated chlorophyll-a concentration (Shulman et al., 1998).

Furthermore, Shulman et al. (1998) observed a relationship (albeit not statistically high, $r = 0.79$, $P < 0.1$) between the total lipid content of female *Calanus* and glycogen content of its predator, the ctenophore *P. pileus* in September 1996. Moreover they found that animals from the cyclonic regions (where the main pycnocline is located at 100–120 m) contained almost double the lipid (for *Calanus*) and glycogen content than those obtained from the anticylonic regions (where the main pycnocline is located at 160–190 m) (Fig. 7). The euphotic zone of cyclonic regions was also richer in nutrients (phosphate and nitrate) and chlorophyll (indicating phytoplankton biomass and thereby the food of *Calanus*) compared to anticyclonic regions.

In September 1996, Anninsky et al. (1998) found that though the ctenophore *Mnemiopsis* still dominated the plankton in terms of biomass (276 ± 115 g $m^{-2}$), this estimate was significantly lower than corresponding estimates obtained for the same months in recent years. They suggested that a simultaneous reduction in the stock of small-sized fodder zooplankton and the large copepod *C. euxinus* since the early 1990's must have affected the nutrition of the ctenophore *Mnemiopsis* over the entire Black Sea.

By grazing zooplankton voraciously, ctenophores impoverish the surrounding environment. In turn, the chemical composition of ctenophores also is a reflection of feeding conditions. When there is sufficient food supply the metabolic rate of ctenophores increases as well as the activity of digestive enzymes (Hoeger and Mommsen, 1984). The storage of glycogen which often provides the main source of accumulated energy in ctenophores (Shulman, 1972) is also increased (Schneider, 1989). Under conditions of starvation the level of glycogen decreases. Data on the ctenophore's body glycogen content in 1996 varied from 21 to 44 $\mu g\ g^{-1}$ fresh weight and accounted for 52.5 ± 14.2% of total polysaccharide content on average. Thus the condition of *M. leidyi* observed during the conducted survey corresponded to that expected after a two-day fasting period (determined experimentally) implying that the ctenophores were starving, whereas earlier (in 1991–1992), they were found to be well fed (Anninsky, 1995).

An analysis of relationship between the condition of ctenophores and the availability of food has revealed a tendency towards a food preference for small forage mesozooplankton. Therefore the impact of *M. leidyi* predation is likely to be stronger on the younger (I–IV) stages of *C. euxinus*. That might explain the fact that in 1989–1990 when the outbreak of *M. leidyi* took place, the biomass of the copepod *C. euxinus*, unlike that of small mesozooplankton, remained at its usual level and later began to fall in 1991 (Vinogradov et al., 1992,1993). The scarcity of younger stages of *Calanus* compared to the older developmental stages observed in the samples since the 1990's (personal observation) could also be explained by such size selective feeding behaviour of *Mnemiopsis*. This fact is important from the fish larvae feeding point of view as they too feed on younger stages of copepods including that of *Calanus* (Tkach et al., 1998).

## 7. Conclusions

All these studies show that the Black Sea zooplankton, which as a group contains complex interwoven relationships, responds intimately to both natural environmental factors and anthropogenic impacts. However, the responses of zooplanktonic communities to these impacts differ among different areas of the Black Sea.

Eutrophication, being one of the main anthropogenic impacts, is a worldwide problem affecting all compartments of coastal marine ecosystems, including plankton (Cattani and Corni, 1992; Leppakoski and Mihnea, 1996). It should be noted that enclosed seas like the Black Sea are more susceptible to eutrophication (and to other types of human induced activities) due to very limited water exchange with the neighbouring seas. In these regions ‘‘problems’’ should not be exported elsewhere, but resolved within the system. The studies reviewed here only present a few examples on such resolutions.

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