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Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources

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We describe the effect of gelatinous plankton – *Aurelia aurita* and invaders *Mnemiopsis leidyi* and *Beroe ovata* – on fish (eggs, larvae, feeding, and stocks) in the Black Sea and Sea of Azov, based on field data and the relevant literature. Representatives of three ecological groups of fish were chosen as examples: planktivorous anchovy typical of warm-water conditions, planktivorous sprat of temperate waters, and benthivorous and piscivorous Black Sea whiting of temperate waters. Changes were noticeable in all three groups, particularly after the invasion of the ctenophore *Mnemiopsis leidyi*. When the density of the latter decreased, some improvements in fish stocks were recorded, which increased after the invasion of *Beroe ovata*, predator of *Mnemiopsis*.

Key words: Azov Sea, *Beroe ovata*, Black Sea, fish feeding, fish stocks, gelatinous plankton, ichthyoplankton, *Mnemiopsis leidyi*, zooplankton.

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Introduction

Among European semi-closed and coastal seas, the Black Sea and Sea of Azov are the most isolated from the ocean and have the largest enclosed catchment basin, obtaining fresh water and sediment input from rivers draining half of Europe. These seas were among the most productive for pelagic and demersal fish (Rass, 1992). The Black Sea began to change in the 1960s under the influence of various anthropogenic factors, the most important in terms of large-scale ecological consequences being a decreased freshwater run-off, eutrophication, overfishing, and the introduction of alien species (Ivanov and Beverton, 1985; Caddy and Griffith, 1990).

These events were most pronounced in the northern part of the Black Sea, where the outflow of the great rivers determined the hydrological and hydrochemical regimes. Until the mid-1970s, this northern part was the most important spawning area for all commercial fish species, including the predator species *Sarda sarda*, *Pomatomus saltatrix*, *Scomber scombrus*, *S. japonicus*, and *Trachurus trachurus*, which migrated for spawning or feeding from the Mediterranean, the demersal species *Psetta maxima maeotica*, *Arnoglossus kesleri*, *Platichthys flesus luscus*, *Solea lascaris nasuta*, and planktivorous species. As a result of the decrease in freshwater discharge since 1970, the extent of the migrations and numbers of migratory fish in this region has greatly declined. Heavy fishing by all countries during the 1970–1980s has also contributed to the decline in all stocks of these valuable species. As a consequence of the reduced pressure caused by predators, the pelagic fish communities of the entire Black Sea changed to a dominance of small pelagic fish: anchovy (*Engraulis encrasicolus*), Black Sea horse mackerel (*Trachurus mediterraneus ponticus*), and sprat (*Sprattus sprattus phalericus*); Ivanov and Beverton (1985); Caddy and Griffiths (1990). The decrease in Don and Cuban discharges in the 1970s caused an increased salinity in the Sea of Azov.

At the same time, nitrogen and phosphorous inputs from river run-off increased dramatically and caused eutrophication in the coastal ecosystem of the north-western part of the Black Sea and Sea of Azov (Zaitsev and Aleksandrov, 1997; Aleksandrova *et al.*, 1996). The most pronounced changes occurred after the invasion of the ctenophore *Mnemiopsis leidyi* (Vinogradov *et al.*, 1992). Another remarkable event is the invasion of its predator *Beroe ovata* (Shiganova *et al.*, 2000). We review the observed ecological changes.

Table 1. Number of stations by survey and gear type (PT: pelagic trawl, J: Juday net, BR: Bogorov-Rass net).

Data	Black Sea NW	Black Sea NE	Sea of Azov S
Jun–Jul 1987	18 PT		
May–Aug 1988	35 PT		
Jun 1989	10 PT		
Jun–Aug 1990	41 PT		
Jul 1992	56 BR	56 BR	
Mar, Aug, Nov 1993		134 BR, 48 J	86 BR
Aug, Sept 1994		60 J, 60 BR	
Mar, Jun–Aug, Sept 1995		50 J, 50 BR	32 PT
Jun–Jul 1996		50 J, 25 BR	16 PT
May 1997	5 PT, 24 J, 24 BR	42 BR, 66 J	
Aug 1998		98 J, 59 BR, 1 PT	
Aug, Sept 1999		96 J, 52 BR, 5 PT	

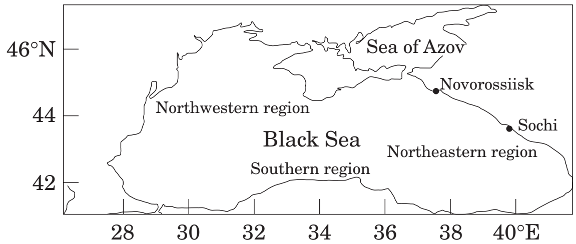

Figure 1. Chart of the Black Sea and Sea of Azov with the survey regions.

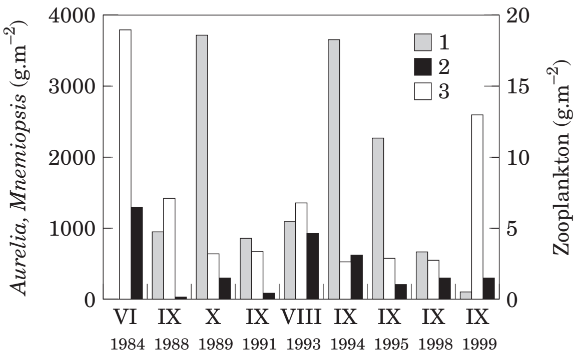

Figure 2. Long-term fluctuations in biomass (wet weight, g m^{-2}) of *Mnemiopsis leidyi* (1), *Aurelia aurita* (2), and edible zooplankton (3) in the open sea (data up to 1992 from Vinogradov *et al.*, 1992).

Material and methods

Survey data from 1987 to 1999 (Table 1, Fig. 1) were used for analyses. Gelatinous plankton, fish eggs, and larvae were sampled using the Bogorov-Rass net (square net opening of 1 m^2, mesh size 500 μk) by vertical hauls from the anoxic layer (150 m) to the surface and from the thermocline (15–25 m) to the surface. Mesozooplankton was sampled with the Juday net (square net opening of 0.1 m^2, mesh size 200 μk) by vertical hauls from the thermocline to the surface, from the pycnocline (70–80 m) to the thermocline, and from the anoxic layer to the pycnocline. Adult fish for stomach content analyses were collected by pelagic trawl.

Results and discussion

Gelatinous zooplankton

As a result of eutrophication, changes occurred in the structure of the planktic and benthic community. Blooms of the dinoflagellate *Noctiluca miliaris* had been observed since the late 1960s. During the 1970–1990s, this species sometimes comprised more than 99% of the total zooplankton biomass in the north-western area (Petran, 1997). In the early 1980s, an explosive development of jellyfish (*Aurelia aurita*) began (Fig. 2), reaching an average biomass of 0.6–1 kg · m^{-2} (Lebedeva and Shushkina, 1991), which may have been provoked by eutrophication. In the 1970s, *A. aurita* appeared in the Sea of Azov after the salinity increased in the 1970s (Zakhutsky *et al.*, 1983).

In the early 1980s, an invader ctenophore (*Mnemiopsis leidyi*) was recorded in the Black Sea which had spread over the entire sea in the autumn 1988 (Vinogradov *et al.*, 1989). It reached peak abundance in autumn 1989, followed by interannual variations in density (Fig. 2). *Mnemiopsis* increased markedly in 1994–1995 and decreased again in 1996–1997 in correspondence with temperature and food availability (Shiganova, 1998; Thikhon-Lukanina *et al.*, 1993). Since August 1988 the species has also been observed in the Sea of Azov, where it reaches high densities. However, it can live there only during the warm season and is re-introduced every spring or summer (Volovik *et al.*, 1993).

In 1997, the ctenophore *Beroe ovata* was recorded for the first time in the Black Sea (Konsulov and Kamburska, 1998); it most likely penetrated from the Mediterranean Sea. In 1999, *Beroe* had spread over the entire sea and its first bloom was recorded, with 1.1 ind. m^{-2} and an average biomass of 31 g m^{-2}. Consequently, biomass and numbers of *Mnemiopsis* decreased greatly to 155 g m^{-2} owing to grazing by *Beroe* (Shiganova *et al.*, 2000). *B. ovata* was recorded in the Sea of Azov in September 1999.

Mesozooplankton

The structure of the zooplanktonic communities began to change in the 1960s in response to eutrophication, which had an indirect effect on zooplankton species diversity through its impact on phytoplankton. The abundance of detritivorous and herbivorous zooplankton species increased; the biomass of *Acartia clausi* and *Pleopis poliphemoides* increased fivefold; and biomass of *Centropages ponticus*, *Paracalanus parvus*, and *Oithona nana* declined in the 1980s (Petranu, 1997). The growth of the *Aurelia* population in the early 1980s led to increased grazing and a continued decrease in abundance of zooplankton (Vinogradov *et al.*, 1992).

Since the summer of 1988, great changes have occurred in the plankton community, coinciding with the development of *Mnemiopsis*. Biomass declined sharply because zooplankton is the main food. Since the summer of 1989, the abundance of *P. parvus*, *Oithona similis*, *A. clausi*, all species of Cladocera, *Oicopleura dioica*, and larval Polychaeta and Gastropoda has decreased, particularly in the upper layer and coastal areas. *O. nana*, *Sagitta setosa*, and representatives of the family Pontellidae disappeared completely from the samples (Kovalev *et al.*, 1998). In 1990, the abundance of *Calanus euxinus* began to decrease (Vinogradov *et al.*, 1992). Overall, edible zooplankton was largely replaced by gelatinous plankton (Fig. 2). However, the abundance of *Aurelia* decreased after the invasion, *Mnemiopsis* apparently being a more successful food competitor. The changes were more pronounced in the northern region, which had already suffered a severe anthropogenic impact (Shiganova *et al.*, 1998).

When the density of *Mnemiopsis* declined in 1992–1993, zooplankton abundance began to rise. First, *C. euxinus*, *P. elongatus*, and *S. setosa* recovered. In 1996, the biomass of zooplankton, particularly *C. euxinus*, increased significantly. The biomass of other copepods remained low, but their number and species diversity increased. During all years of investigations, biomass, number, and species diversity of mesozooplankton were higher in the southern area than in the northern. For instance, the biomass of edible zooplankton in 1996 was 6.1 g m^{-2} in the north-eastern part and 9.5 g m^{-2} in the southern part.

After the introduction of *Beroe*, the edible zooplankton biomass increased to about 11 g m^{-2} in the open north-eastern area and to 13 g m^{-2} in the inshore area, much higher than it had been in the 10 years since the *Mnemiopsis* invasion (Fig. 2). The biomass of *C. euxinus* and *P. elongatus* hardly changed, while in other copepods, particularly species inhabiting the surface layer, it increased threefold. *S. setosa* greatly increased to 6–15 thousand ind. m^{-2}, while representatives of the meroplankton also increased greatly. Cladocera increased to 150–300 thousand ind. m^{-2}, *Penilia avirostris* being the most abundant. After many years of absence, *Pontella mediterranea* and *Centropages ponticus* were again recorded in samples. Mediterranean species appeared around the same time, mainly in the southern and north-western areas (Kovalev *et al.*, 1998).

Ichthyoplankton

In the 1970s, species diversity and numbers of summer ichthyoplankton began to decrease. The eggs and larvae found belonged mainly to planktivorous species (anchovy and horse mackerel in summer; sprat and whiting in winter). Eggs and larvae of valuable species (*S. sarda*, *P. saltatrix*, and *P. flesus*, *P. maxima*, *S. lascaris*) were found mostly in the southern area and in small numbers also in the north-west (Archipov, 1993; Gordina and Klimova, 1995). However, in the 1980s they were almost completely absent in the north-eastern area.

After the *Mnemiopsis* explosion in 1989, even anchovy eggs and larvae greatly decreased in number. They gradually increased in 1992 and again in 1996, when abundance of this ctenophore decreased. Measured by their eggs and larvae, Black Sea horse mackerel, *Mullus barbatus ponticus*, and *Diplodus annularis* were, consecutively, the most abundant species in both the northern and southern regions. After 1996, eggs of *Mugil cephalus*, *M. siouy*, *Ctenolabris rupestris*, *Ophidion rochei*, and *Scorpena porcus*, which had been completely absent during 1992–1995, appeared again in samples from the north-eastern part. The abundance of ichthyoplankton was inversely correlated with that of *Mnemiopsis* (cf. Figs 2 and 3).

Since the early 1980s, the changes in the Black Sea plankton community in relation to eutrophication, *Aurelia* outbursts, and the *Mnemiopsis* invasion in later years have had a considerable effect on the nutrition of fish larvae. The percentage of starving larvae increased and reached high values during the first years of intensive blooms of *Mnemiopsis*. Owing to the absence of the small copepods, larvae had to feed on bigger-sized organisms, which are less suitable and may cause mortality (Tkach *et al.*, 1998).

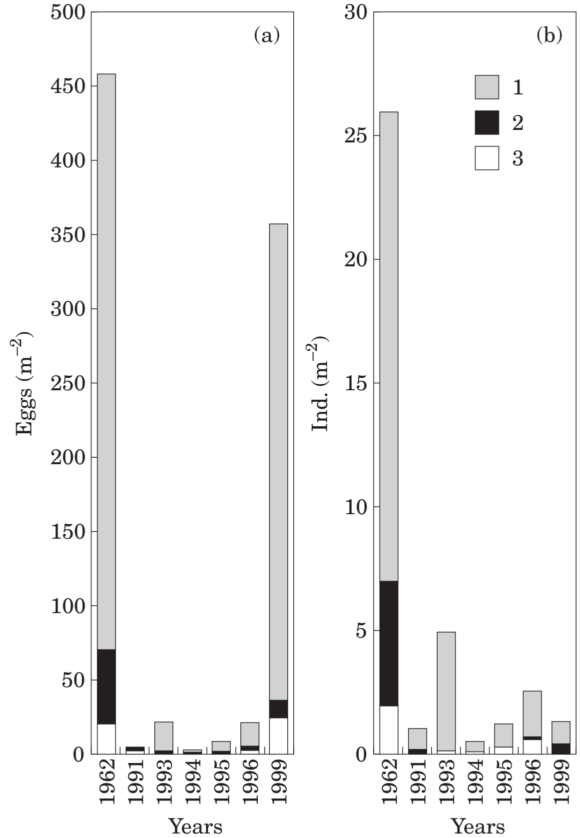

Figure 3. Fluctuations in numbers of (a) fish eggs and (b) larvae in the northern Black Sea (1: anchovy; 2: Mediterranean horse mackerel; 3: other species; data for 1962 from Dekhnik, 1973).

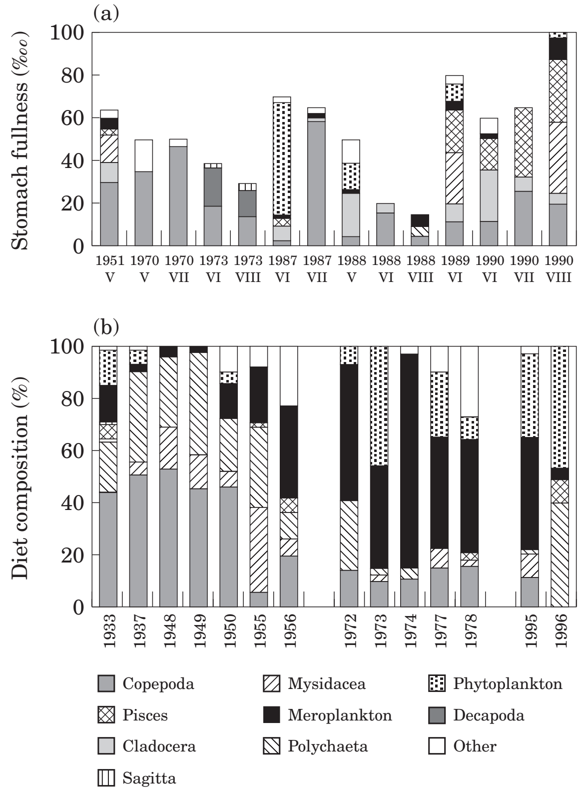

Figure 4. Diet composition of (a) *Engraulis encrasicolus ponticus* in the north-western part of the Black Sea (data: 1954: Chajanova, 1954; 1970: Sirotenko and Danilevskij, 1973; 1973: Sirotenko and Budnichenko, 1975). and (b) *E. e. maeoticus* in the Azov Sea (data: 1933: Smirnov, 1938; 1937: Okul, 1941; 1948–1949: Longivnovich, 1951; 1950–1956: Kornilova, 1955, 1960; 1972–1974: Mikhman and Romanovich, 1977; 1977–1978: Lutz *et al.*, 1981).

In mid-August 1999, after the *Beroe* invasion, ichthyoplankton was very rich in numbers compared to previous years and species diversity was high (24 species of eggs and larvae). Anchovy eggs were the most abundant ($323\ m^{-2}$), followed by eggs of horse mackerel ($11\ m^{-2}$) and of *Mugil saliens* and *D. annularis* ($1.2\ m^{-2}$). Such a high abundance of anchovy (Fig. 3) and horse mackerel had not been recorded since the introduction of *Mnemiopsis*.

Fish

During the first years of *Mnemiopsis* blooms in the Black Sea and Sea of Azov the stocks and catches of all planktivorous species declined greatly. The most severe decline was recorded for warm-water species spawning during summer – Black Sea anchovy (*E. encrasicolus ponticus*) and Sea of Azov anchovy (*E. encrasicolus maeoticus*). Their diet compositions and rations were adversely affected owing to the decrease in zooplankton abundance. Copepoda had always been the main food of the Black Sea anchovy, but in the 1970s their share began to decrease. They were replaced by Cladocera (mainly *Pleopis poliphemoides*) and phytoplankton. In the summer of 1988, when the numbers of anchovy were very high and there was a lack of food, stomach fullness indices declined. *A. clausi* and *P. poliphemoides* were its main food. When *Mnemiopsis* abundance increased towards the end of the summer, about 30% of the food comprised larvae of Cirripedia, Ostracoda, and Bivalvia, which have a low calorie content. As a consequence, growth rate, weight-at-age, fecundity, and frequency of spawning of anchovy decreased (Lisovenko *et al.*, 1997). During the following years the anchovy population decreased from 235 000 t in 1988 to 32 000 t in 1989. Thus, food competition declined and, while zooplankton biomass was low in the summers of 1989 and 1990, feeding intensity was high because the diet changed from zooplankton to epibenthos and fish, including its own larvae (Fig. 4a).

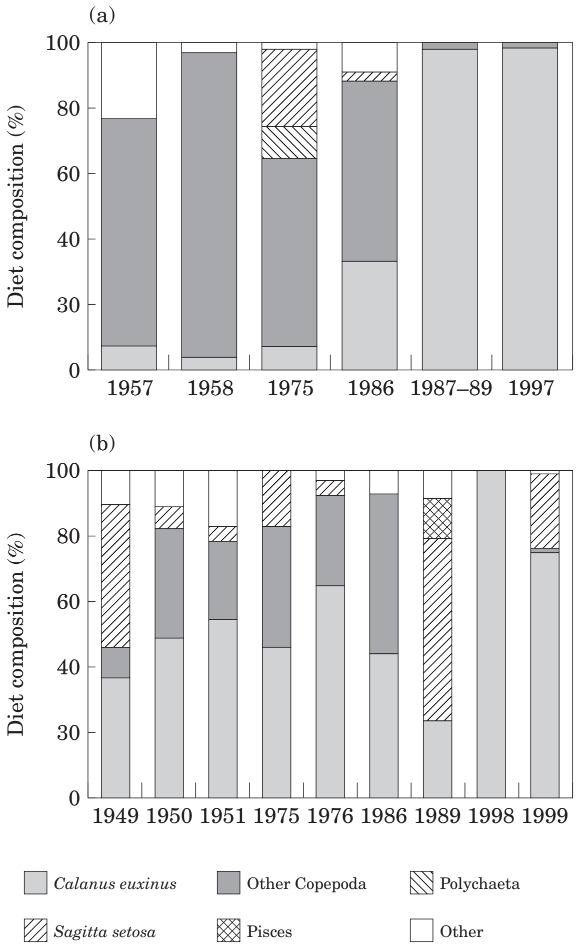

Figure 5. Diet composition of *Sprattus sprattus* (a) in the north-western and (b) in the north-eastern Black Sea (data: 1948–1951: Chajanova, 1958; 1957–1958: Lipskaia, 1960; 1975–1976: Sirotenko and Sorokolit, 1979; 1986: Gapishko and Malyshev, 1990; 1987–1989: Oven *et al.*, 1996).

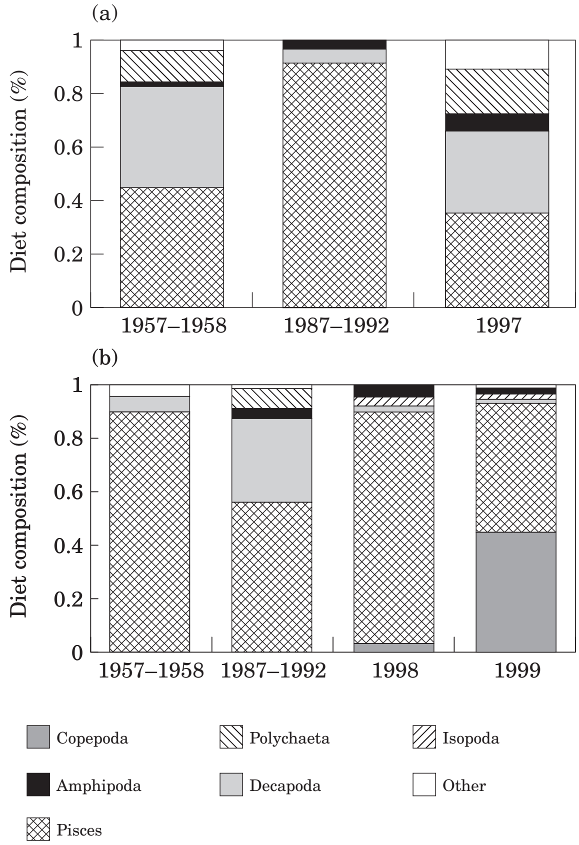

Figure 6. Diet composition of *Merlangius merlangus* (a) in the north-western and (b) in the north-eastern Black Sea (data: 1957–1958: Burdak, 1960; 1987–1989: Oven *et al.*, 1996).

During the *Mnemiopsis* outbreak in 1989–1991, the biomass of sprat and whiting, species typical of more temperate waters, declined greatly, but increased again after the first decline in *Mnemiopsis* abundance in 1992–1993 (Prodanov *et al.*, 1997). Sprat diet composition changed in the north-western region, where eutrophication influence was stronger. The share of warm-water Copepoda, which was its main food, dropped greatly in the 1970s and sprat became almost monophagous, consuming only *C. euxinus* (Fig. 5a). Eutrophication effects on sprat feeding were not noticeable in the north-eastern part, but Copepoda disappeared from its diet and only *C. euxinus* remained after the invasion (Fig. 5b).

A similar influence was noted in the diet composition of Black Sea whiting. The share of Ampipoda, Decapoda, and Polychaeta in the stomach contents decreased from 55% to less than 10% in the north-western region, whereas the share of sprat increased. Epibenthos decreased in abundance as a result of *Mnemiopsis* grazing on their larvae. In May 1997, when ctenophore abundance declined, the diet spectrum recovered (Fig. 6a). In the north-eastern region, whiting diet recovered only in 1999 (Fig. 6b), when *Beroe* controlled *Mnemiopsis*.

The situation is worse for Sea of Azov fish. Since the 1970s, there has been a gradual decline in pelagic fish stocks. After the re-introduction every spring, *Mnemiopsis* completely removes all edible zooplankton during the first summer months (Budnichenko *et al.*, 1999). After an early introduction, the Sea of Azov anchovy and Azov kilka (*Clupeonella cultriventris*) do not have enough food to produce sufficient eggs and their larvae do not have enough food to survive. Spawning stocks are therefore very low. After a late re-introduction in June or July, spawning stocks during summer are higher (Volovik *et al.*, 1993). For several decades, the share of Copepoda and Polychaeta in the diet has been decreasing and the share of low-calorie meroplankton larvae (Cirripedia, Ostracoda, Bivalvia) has increased (Fig. 4b).

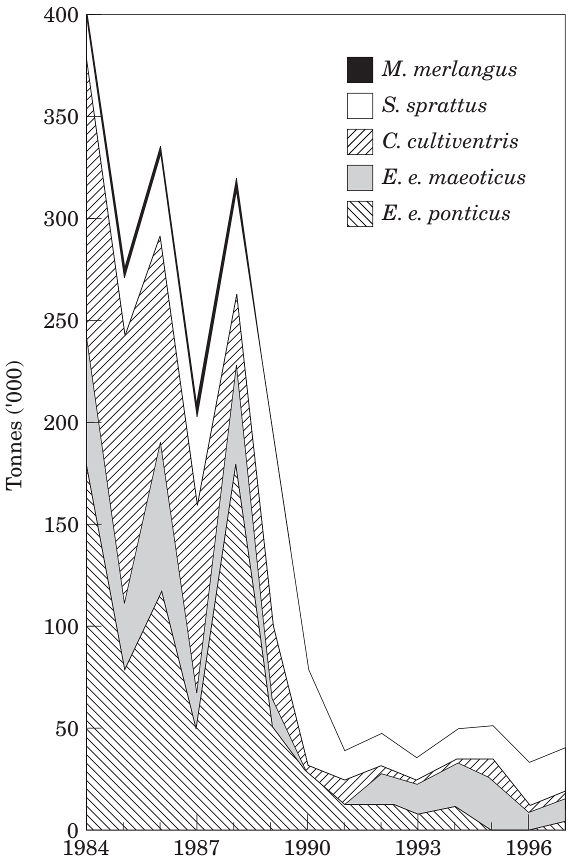

Figure 7. Catches of main commercial fish by Russia, Ukraine, and Georgia in the northern Black Sea and Sea of Azov (data from FAO, AzNIIRKH, Russia).

In 1996, Copepoda were not found at all in stomachs, and, as a result, average length, weight, and fat contents have decreased and mortality increased during winter.

The volume and species diversity of the commercial catches showed the same tendency. Catches of planktivorous species dropped greatly in 1989–1991 after the explosive development of *Mnemiopsis* in the Black Sea (Fig. 7). However, since 1992 catches of planktivorous species, particularly the Black Sea anchovy with its short life cycle, have increased gradually (Shiganova, 1998; Prodanov *et al.*, 1997).

The most abundant species in the 1995–1997 Russian and Ukraine catches were Azov anchovy and kilka (Fig. 7). The Russian catch is now the lowest in weight and the poorest in species diversity, although species such as scrited mullet and mullets have appeared again. Species diversity is highest in Turkish catches: *S. Sarda*, *P. saltatrix*, *S. scombrus*, *S. japonicus*, *T. trachurus*, *P. maxima maeotica*, *S. lascaris nasuta*, *M. barbatus*, *M. surmuletus*, and *E. engrasicolus ponticus* increased in 1993–1994. *P. saltatrix* was found in the catches of Rumania, Bulgaria, and the Ukraine. The demersal species *P. maxima maeotica* and *S. lascaris nasuta* were recorded in the catches of Bulgaria and Romania in low numbers in 1995. *P. maxima maeotica* was recorded in very low numbers in Ukrainian and Russian catches only in 1995.

Conclusions

The gelatinous plankton food-web in the Black Sea comprises the omnivorous dinoflagellate *Noctiluca*, the carnivorous jellyfish *Aurelia*, and the comb jelly *Mnemiopsis*. *Noctiluca* competes with zooplankton for living and detritus particles. *Mnemiopsis* and *Aurelia* compete between each other and with planktivorous fish for edible zooplankton. The effect of gelatinous plankton on the fish and their food resources was most pronounced after the introduction of *Mnemiopsis*. Major effects have been recorded on edible zooplankton, fish eggs, and larvae and on the diet composition of small pelagic fish belonging to both warm-water and temperate-water species with different feeding spectra. Grazing of ichthyoplankton by the ctenophore, as well as food competition, resulted in drops of stocks and catches of pelagic fish. After *Mnemiopsis* density decreased, some improvements in the pelagic ecosystem of the Black Sea have occurred, particularly in the southern part. Smaller improvements have also been recorded for Sea of Azov fish populations. The most positive changes were recorded in the Black Sea after the invasion of *Beroe*, which apparently restructured the food web. There is a chance that the ecosystem will recover further if *Beroe* persists.

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