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Summer ichthyoplankton, food supply of fish larvae and impact of invasive ctenophores on the nutrition of fish larvae in the Black Sea during 2000 and 2001

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Qualitative composition and abundance of both ichthyoplankton and small forms of zooplankton were evaluated by field studies in the northern (the Crimea near Sevastopol) and southern (Sinop region and TEEZ) Black Sea during the summers 2000 and 2001. A tendency of increasing the species richness, abundance of fish eggs and larvae as well as zooplankton (which is the food for fish larvae) was observed over a period of *Mnemiopsis leidyi* and *Beroe ovata* co-existence. The eggs and larvae of the Mediterranean migrants—bonito and bluefish appeared again in the coastal waters near Sevastopol, which testified to favourable conditions for the spawning and nutrition of these fish species and their larvae. Aborigen copepod *Oithona nana* was found in the Crimean coastal waters although earlier in the 1990s it had completely vanished. Although rare in the 1990s copepods *Centropages ponticus* and *Paracalanus parvus* appeared in inshore waters as well as Pontellids species. Observed increases in species number and abundance of both ichthyoplankton and small zooplankton (≤500 μm), which promoted survival and development of fish larvae, were attributed to reduced predatory impact of *Mnemiopsis* on prey zooplankton after *the* arrival of *Beroe* in the late 1990s. However, the influence of *Mnemiopsis* continued to be significant during the short period of its peak occurrence in late summer. When this period coincided with the appearance of fish larvae, a negative impact on their survival could be predicted due to a low concentration of food items for larvae feeding.

INTRODUCTION

The invasion of the ctenophore *Mnemiopsis leidyi* combined with an unfavourable ecological situation in the Black Sea led to a sharp decrease in fish abundance during the 1980s (Boltachev et al., 2001; Prodanov et al., 2001; Gucu, 2002; Boltachev & Zuev, 2003; Bilio & Nirmann, 2004). Anchovy played a special role in the Crimean coastal catches in the 20th century. The average catch by the USSR fishing fleet from 1975 to 1989 was 138.9 thousand tons (with a maximum catch of 214.7 thousand tons) in the Black Sea. The main catches were made in the Ukraine. In some years anchovy catches by all the Black Sea countries exceeded 0.5 million tons (Rass, 1992; Chashchin, 1997). Catches of anchovy in the Sevastopol region in 1989 consisted of only 2.6 tons, which was 367 times less than in 1986. Catches of horse-mackerel were similarly affected. Its catches near Sevastopol in 1989 decreased 121 times compared with 1986. Considerable changes in the Black Sea ecosystem took place due to several natural and anthropogenic factors (Vinogradov, 1991; Zaitzev, 1992; Zaidiner & Popova, 1997; Kideys, 2002; Dascalov, 2003; Oguz, 2003). These changes were reflected in the structure of planktonic communities. The abundance of fodder zooplankton sharply decreased in the 1990s (Vinogradov, 1991; Zaitzev, 1992; Zagorodnyaya & Skryabin, 1995; Kovalev et al., 1996, 1998; Pavlova et al., 1999). The share of fish larvae with empty guts increased because of the absence or extremely low abundance of food for pelagic fish larvae (Tkach, 1993; Tkach et al., 1998, 2002). The low food concentration considerably affected the survival of fish larvae. As a result, at the end of the 1980s and the beginning of the 1990s, a significant fall in ichthyoplankton abundance took place in the Black Sea (Gordina et al., 1998, 2001, 2003, 2004). As a result of the sharp decline in ichthyoplankton abundance, the stock of commercial fish species decreased dramatically. Whilst the total catch of the Black Sea countries varied from 746 to 926 thousand tons in 1980–1988, it was reduced by 2–3 fold, to 363 and 284 thousand tons, respectively in 1990 and 1991 (Lisovenko et al., 1997; Zaidiner & Popova, 1997). The harsh decline of the Black Sea fishery is directly connected with the survival of young fish stages. The purpose of this study is to present the results of the ichthyoplankton and zooplankton community structure in the Black Sea during 2000 and 2001 with respect to the nutrition of fish larvae.

MATERIALS AND METHODS

In this study, we used material obtained in two regions of the Black Sea: from the northern part in the summers 2000–2001 and from the southern part in summer 2000 only. In the northern Black Sea (i.e. Ukrainian waters), the samples were collected only from the coastal areas off Sevastopol, the Crimea. The data from the southern Black Sea (i.e. Turkish waters) is based on samples obtained in the Turkish Exclusive Economic Zone (TEEZ) both from offshore waters and on the samples collected in inshore waters, off Sinop. Location of ichthyoplankton sampling stations in Ukrainian and Turkish waters is given in Figure 1.

Sevastopol area

Ichthyoplankton samples were collected via vertical tows from 10 m to the surface using Bogorov–Rass net (opening diameter: 0.5 m^2, mesh size: 500 µm) at four permanent stations off Kruglaya Bay. Two stations were located at 15–20 m depth and the other two at 50–60 m (Figures 1 & 2). Additionally horizontal tows were also carried out with the same net at the surface layer for five min. The samples were taken every two weeks from June till August. There were totals of 40 samples in 2000 and 32 in 2001. Simultaneously with ichthyoplankton sampling, zooplankton was sampled for the estimation of fish larval food at two stations (Stations 1 & 3) which were the same as in the ichthyoplankton investigation. The vertical layer 0–10 m was towed with a planktonic Judey net (opening diameter: 0.1 m^2, mesh size: 145 µm). The samples were preserved in 4% borax buffered formaldehyde and then identified in the laboratory using a Bogorov camera and an MBS microscope. Large and rare species were counted for half or the whole sample. Mass species were sorted by taking duplicate sub-samples of one or two millilitres using a Stempel pipette. Nauplii and copepodite stages of copepods were identified to species level. Meroplankton species were analysed only to higher taxonomic groups. The length of all organisms in the zooplankton was measured individually. The organisms equal to or less than 0.5 mm were assumed to be the food for fish larvae upto 7 mm length. The nutrition spectrum of these size group larvae consisted of eggs, nauplii and copepodite stages of small copepods and harpacticoids, two cladoceran species, larvae of cirripedians, polychaetes and bivalve molluscs, rotifers and theirs eggs, tintinnoides (Gordina et al., 2003). The estimation of fodder zooplanktonic organisms for fish larvae was carried out for the period of early June to middle September.

Turkish shelf

In the southern part of the sea ichthyoplankton was collected from a dense grid in the TEEZ covering the entire southern Black Sea with the RV 'Bilim' during July 2000 where 43 stations were sampled with a vertically towed Hensen net (300-µm mesh size and a net opening of 70 cm diameter) from the anoxic zone to the surface. The sampling method was as described in Niermann et al. (1994). In coastal waters off Sinop, additional samples were collected during the summer of 2000 from June until August at two permanent stations: A (maximum depth 75 m) and B (maximum depth 400 m). Samples were collected using a plankton net (112-µm mesh size and 50 cm diameter net opening) and two different methods: by vertical hauls from 77 to 0 m (Station A) and from 180 to 0 m (Station B) and by horizontal hauls, which were made by towing the net for 10–15 min at a vessel speed of 2 miles h^{-1}. More details of this method are described in Satilmis et al. (2003). Analyses of samples were the same as given above for Ukranian waters. All samples in Ukrainian and Turkish coastal waters were collected between 0900 and 1200.

Methodological differences, particularly between the models and mesh sizes of the net used in the northern and southern Black Sea, nevertheless permits us to obtain comparable results among samples. An intercomparison study of the Hensen net and Bogorov–Rass net revealed that the variability between these two nets was not greater than that for successive vertical towing using either net type (Niermann et al., 1994).

RESULTS

Based on the vertical and horizontal samples of ichthyoplankton, a total of 25 species of fish were found from June to August 2000 in Ukrainian coastal waters in the Sevastopol area (Tables 1 & 2). There were 15 species of eggs and 12 species of fish larvae. Average abundance of eggs was 15.4 ind m^{-2} in the vertical samples and 88.8 ind 100 m^{-3} in the horizon-

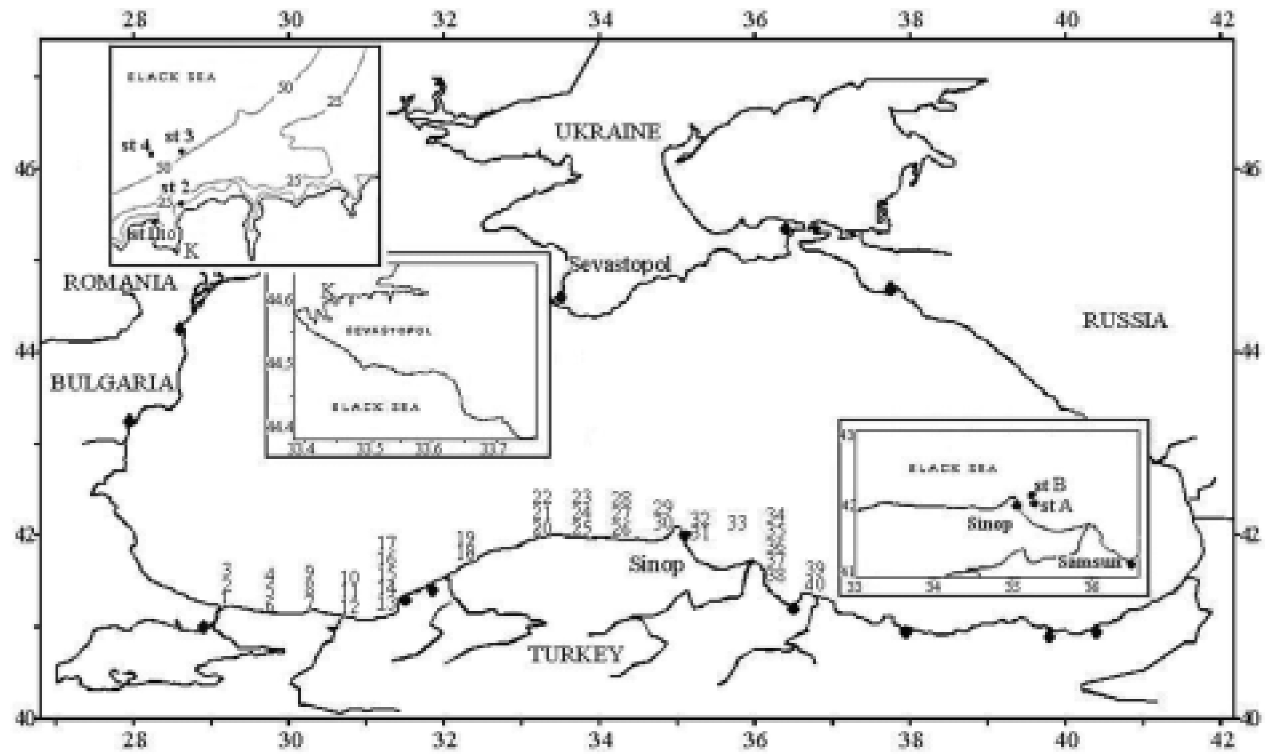

Figure 1. Location of sampling stations (Stations 1–40) in TEEZ during July, 2000 cruise (Stations 31, 32 were the same Stations as A, B in the Sinop area) and in the coastal waters of Sevastopol near Kruglaya bay (K) at Stations 1–4 in 2000–2001.

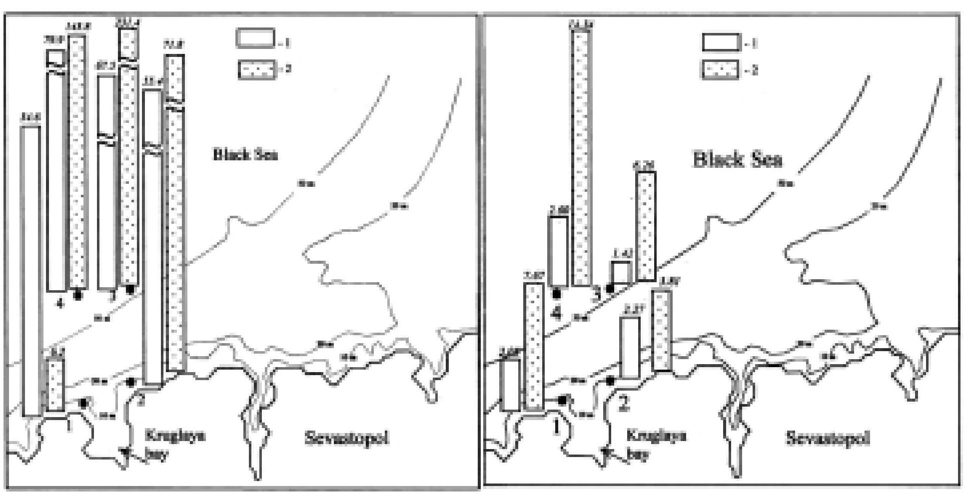

Figure 2. Location of the stations and average number of fish eggs (left) and larvae (right) in the coastal areas of Sevastopol (the Black Sea) in 2000 (1) and 2001 (2).

tal catches. Average number of larvae was 1.1 ind m^{-2} and 1.9 ind 100 m^{-3} accordingly. In terms of eggs, four fish species, *Engraulis encrasicolus, Trachurus mediterraneus, Mullus barbatus ponticus* and *Diplodus annularis* had a share of 96.1% in the vertical and 96.2% in the horizontal tows. With respect to larvae, *E. encrasicolus* and *D. annularis* were rare, while *T. mediterraneus* and *M. barbatus ponticus* were at all absent. These four species dominated in plankton during the 1950s to 1970s. The qualitative composition of ichthyoplankton was poorer in the southern Black Sea. Here only nine species (egg species: 5 and fish larvae: 7) were presented in both the vertical and horizontal tows. At the same time ichthyoplankton abundance was richer in Turkish waters, where the average number of fish eggs was 4.6 fold higher than in the Ukrainian coastal waters. Anchovy eggs dominated and formed 95% of the total number of eggs. Other fish species eggs were few. Fish

Table 1. *Qualitative composition and average number of fish eggs in the Black Sea in the summers of 2000 and 2001, from vertical (ind m*$^{-2}$*) and horizontal (ind 100 m*$^{-3}$*) tows.*

	2000					2001	
	Ukrainian waters, June–August		Turkish waters (TEEZ), July	Turkish waters, Sinop area, June–August		Ukraine waters, June–August	
Species	ind m^{-2}	ind 100 m^{-3}	ind m^{-2}	ind m^{-2}	ind 100m^{-3}	ind m^{-2}	ind 100m^{-3}
Engraulis encrasicolus (L.)	10.2	62.5	68.7	31.7	104.6	31.6	116.6
Merlangius merlangus euxinus (Nordmann)			1.3	8.3			
Ophidion rochei Muller		0.2					0.4
Mugil so-iuy Bas		0.4					0.1
Mugil cephalus L.		0.1	0.1				
Serranus scriba (L.)					0.2		0.1
Pomatomus saltatrix (L.)		0.2					1.9
Trachurus mediterraneus (Staindachner)	0.2	2.1	0.1	0.8		3.4	16.2
Diplodus annularis (L.)	2.1	10.4				6.2	44.8
Mullus barbatus ponticus Essipov	2.3	10.5	1.3		1.7	5.0	25.1
Ctenolabrus rupestris (L.)	0.2	0.5					1.0
Trachinus draco L.	0.3	0.4				0.6	5.6
Uranoscopus scaber (Linné)							0.3
Sarda sarda (Bloch)		0.1					0.1
Callionymus pusillus Delaroch		0.1					
Scorpaena porcus L.		1.1			0.2	0.2	1.7
Psetta maxima maeotica (Pallas)		0.1					0.1
Solea lascaris nasuta (Pallas)	0.1	0.1			0.1		
Total number of eggs	15.4	88.8	71.5	40.8	106.8	47.0	214.4
Standard deviation	5.2	27.8	10.9	9.3	20.8	11.6	55.6
Number of species	7	15	5	3	5	6	14

larvae were not numerous in the samples. Average abundance of anchovy larvae was only 1.9 ind m^{-2}, but that was 2.7 times more than in the northern part of the sea.

Near Sinop eggs and larvae of 11 fish species were recorded in the summer of 2000 among them egg species: 7 and fish larvae: 6. The average number of fish eggs was 40.8 ind m^{-2} in vertical tows and 106.8 ind 100 m^{-3} in horizontal catches; fish larvae 7.5 ind m^{-2} and 3.2 ind 100 m^{-3} respectively (Tables 1 & 2).

All species of eggs and fish larvae presented in Tables 1 & 2 were recorded in coastal waters to the limit of 100-metres isobate, whereas in the Turkish offshore waters in summer only some species were registered : the eggs of *E. encrasicolus, T. mediterraneus, Merlangius merlangus euxinus, Ctenolabrus rupestris* and fish larvae of *E. encrasicolus, T. mediterraneu, Lipophrys pavo, Parablennius zvonimiri* and unidentified Gobiidae.

There were eggs and larvae of 26 fish species (eggs of 14 and larvae of 17 species) from the coastal areas of the Crimean peninsula in the summer spawning period of 2001. Average numbers of ichthyoplankton increased three fold for eggs and four fold for larvae in 2001 compared with the previous year. A similar tendency was detected with ichthyoplankton abundance in the horizontal tows (Tables 1 & 2). Increases in fish eggs and larvae were recorded at all stations (Figure 2). Anchovy eggs dominated the ichthyoplankton. The average egg number of other commercial fishes: *T. mediterraneus, Mullus barbatus ponticus* and *D. annularis* also increased (Table 1). The larvae of these three species appeared in ichthyoplankton samples in 2001, while in summer 2000 they were absent (Table 2). Non-commercial fish larvae from the family Blenniidae, Gobiidae dominated. Eggs of fish migrating from the Sea of Marmara, such as the common

Table 2. *Qualitative composition and average number of fish larvae in the Black Sea in the summers of 2000 and 2001, from vertical (ind m-2) and horizontal (ind 100 m-3) tows.*

	2000					2001	
	Ukrainian waters, June–August		Turkish waters (TEEZ), July	Turkish waters, Sinop area, June–August		Ukraine waters, June–August	
Species	ind m^{-2}	ind $100m^{-3}$	ind m^{-2}	ind m^{-2}	ind $100m^{-3}$	ind m^{-2}	ind $100m^{-3}$
Engraulis encrasicolus (L.)	0.7	0.9	1.9	2.5	0.2	1.2	0.9
Merlangius merlangus euxinus (Nordmann)			0.2				
Syngnatus schmidti Popov			0.3				
Mugil cephalus L.			0.1				
Trachurus mediterraneus (Staindachner)			0.1			0.6	0.9
Diplodus annularis (L.)		0.1			0.1		1.0
Mullus barbatus ponticus Essipov			0.1		0.5	0.6	2.7
Symhodus cinereus (Bonnaterre)							0.8
Symphodus ocellatus Forsskal	0.1	0.1				1.0	0.5
Symphodus tinca L.		0.1					
Gobius niger jozo L.						0.2	0.4
Pomatoschistus marmaratus (Risso)		0.1					
P. minutus elongatus (Canestrini)							0.1
Pomatoschistus sp.					1.8		
Gobiidae unidentified	0.2	0.1	0.8	5.0	0.2	0.4	0.4
Callionymus sp.							0.5
Lipophrys pavo (Risso)		0.1				0.4	0.8
Parablennius sanguinolentus (Pallas)		0.1					0.1
P. tentacularis (Brunnich)	0.1	0.1				0.2	0.9
P. zvonimiri (Kolombatovic)		0.1			0.4		1.4
Blennius sp.							0.1
Scorpaena porcus L.							0.3
Diplecogaster bimaculata euxinica Murgoci							0.1
Lepadogaster lepadogaster lepadogaster (Bonnaterre)		0.1					
Total number of larvae	1.1	2.9	3.5	7.5	3.2	4.6	11.9
Standard deviation	0.32	0.68	0.65	1.3	0.27	1.46	3.23
Number of species	4	11	7	2	6	8	17

bonito *Sarda sarda* and bluefish *Pomatomus saltatrix,* appeared near the Crimean coast in 2000–2001. The number of *P. saltatrix* eggs increased in summer 2001 about nine fold (Table 1).

The spawning effectiveness of species like *E. encrasicolus, T. mediterraneus, M. barbatus ponticus* and *D. annularis* formed the annual variability of fish egg abundance. Comparative analysis of the numbers of these species of fish eggs from the coastal areas of Sevastopol in 1998–2001 showed that their abundance was the poorest in 1998. A more favourable year for *E. encrasicolus, M. barbatus ponticus* and *D. annularis* spawning was 1999 and for *T. mediterraneus* 2001 (Gordina et al., 2001). The changes in correlation between fish larvae and eggs in our ichthyoplankton catches were shown as indices of larvae survival. Percentage of the commercial fish larvae of their available eggs in the sea varied noticeably during 1998–2001 (Table 3). Compared to these years it was noticed that larvae of *E. encrasicolus, T. mediterraneus, M. barbatus ponticus* and *D. annularis* had minimum percentages in 1998. The percentages of *T. mediterraneus, M. barbatus ponticus* and *D. annularis* larvae were zero and anchovy only 0.17% from their eggs. That year was found to be the worst period for fish larvae survival. The percentages of commercial fish larvae from their available eggs in

Table 3. *Percentage of the commercial fish larvae from their available eggs in the sea in the Crimean inshore waters.*

Years of investigation	Fish larva species			
	Engraulis encrasicolus	*Trachurus mediterraneus*	*Mullus. barbatus ponticus*	*Diplodus annularis*
1998	0.17	0	0	0
1999	1.73	6.90	0.70	1.88
2000	2.00	1.45	0	1.06
2001	1.31	5.44	6.26	1.54

2001 were higher, so this year was predicted to be better for commercial fish larvae survival. As a result the fish larvae of older age groups appeared in plankton in contrast with the 1990s, when only earlier stages were present in our catches (Tkach et al., 2002). The average size of fish larvae varied from 2.3–4.5 mm for anchovy, 2.1–5.5 for *T. mediterraneaus* and 2.1–3.5 for *D. annularis*.

Indices of fish catches show the positive changes in ichthyoplankton communities structure. The end of 1980s and beginning of 1990s were characterized by the Ukraine economic crisis, which led to a sharp decrease in fish catches in this region of the Black Sea. Average year catch in 1988–1993 was 382 tons, (the minimum being only 160 tons). Inter-annual fluctuations of anchovy and horse-mackerel and total catches in the area of water near Sevastopol are presented in Table 4. The data on fish catches in this region were taken from the paper (Boltachev, 2003). Beginning in 1994 the local fishery began to recover from the crisis. The relative fish catch by Sevastopol fishermen also increased sharply. Sprat increased from 86.1 to 98.3% of the general yearly catch and became a dominating species in catches in the region of Sevastopol. Anchovy increased from 0.7 to 12.3% its catches remained low until 2000. The same took place in the catches of horse-mackerel, which over 12 years remained low, and in some years there were practically none in the catches. The Turkish anchovy catch data as well as fish catches in Russia and Georgia sector of the Black Sea showed a systematic decreasing trend after 1995 (Oguz et al., 2003).

Mesozooplankton abundance also remained at a low level during the same period (Kovalev et al., 1996, 1998). Below we give the data about the state of the food base for the fish larval nutrition in the region of the investigation in 2000–2001. Over the two years of observation copepods and cladocerans concomitant with benthic larvae were the dominant group in the zooplankton. The population of the small sized copepod *Paracalanus parvus* has been recovering since 1999. In summer 2000 in the Crimean coastal waters another important copepod *Centropages ponticus* became numerous, a lot of its nauplii appeared in the sea. Pontellids were again found in plankton after some years of absence (Zagorodnyaya & Kovalev, 2001). In 2000–2001 single individuals of the copepod *Oithona nana* were found in the Black Sea again. In 2000 during the summer months (June to September) average abundance of zooplankton organisms less or equal to 0.5 mm was calculated for both stations and consisted of 3464 ±761 ind m^{-3}. Nauplii of calanoid copepods dominated in that size group. Together with copepodite stages of copepods they dominated in that size group. They made up about 50% of the zooplankton, which may potentially be consumed by fish larvae. Acartiid nauplii were the most numerous and their share in abundance of copepod nauplii was 65%. Bivalve mollusc larvae were the second largest group but usually their role in fish larval feeding was small. Cladocerans were the third in abundance (Figure 3A). The nearshore station (Station 1) differed from the offshore station (Station 3) with a higher abundance of food organisms for fish larvae nutrition and a larger number of harpacticoid nauplii (with the average density 621 ind m^{-3}). Nauplii of both harpacticoid and

Table 4. *Dynamics of fish catches in the Black Sea near Sevastopol from 1986 to 2002 (in tons).*

Years	1986	1987	1988	1989	1990	1991	1992	1993	1994
Anchovy	956	1748	209	2.6	0.5	4.1	0.5		68
Horse-mackerel	341	148	6.5	2.8	2.2	0.6	0.2	0.5	
Total catch	2173.8	3560.8	408.2	426.5	701.9	182.9	412	159.5	2397.9

Years	1995	1996	1997	1998	1999	2000	2001	2002
Anchovy	164	117.8	228.5	69.4	263	1456.99	961.3	1888.2
Horse-mackerel	0.8	0.8	2.2	0.5	1		10.8	
Total catch	4432.3	6006.6	6195.9	9692.9	11580.8	12007	20576.6	23337

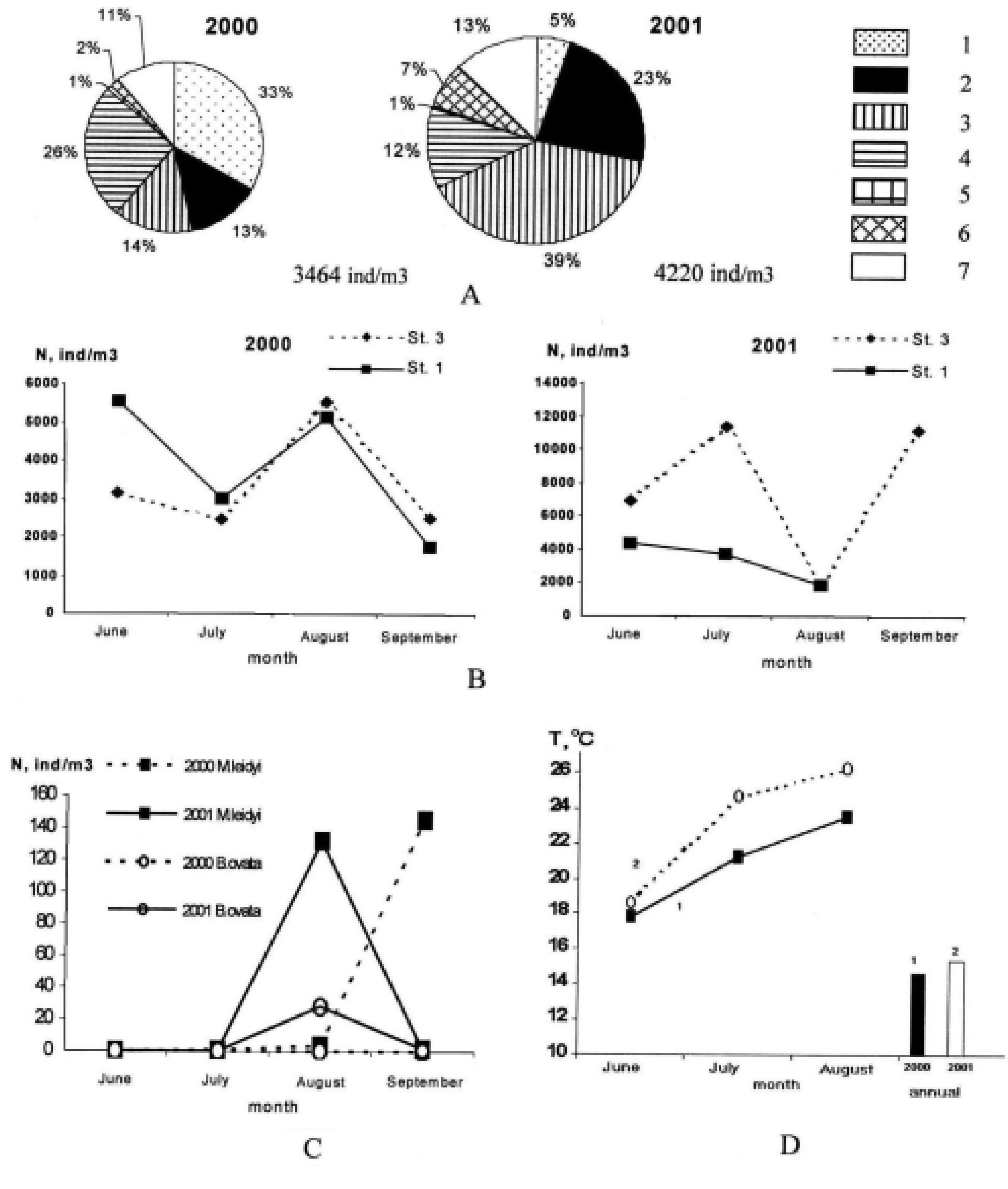

Figure 3. (A) Average abundance (N, ind m^{-3}) of zooplankton organisms for fish larvae nutrition and percentage of copepoda nauplii (1), copepoda copepodites (2), cladocers (3), mollusc larvae (4), harpacticoids (5), rotifers (6), Cirripedia nauplii (7) in it; (B) seasonal dynamics of zooplanktonic organisms <0.5 mm, (ind m^{-3}); (C) abundance of alien ctenophores (ind m^{-3}) at the same stations by Z.A. Romanova (Finenko et al., 2003); and (D) monthly and annual temperature in the sea in the Sevastopol area in the summers of 2000 and 2001.

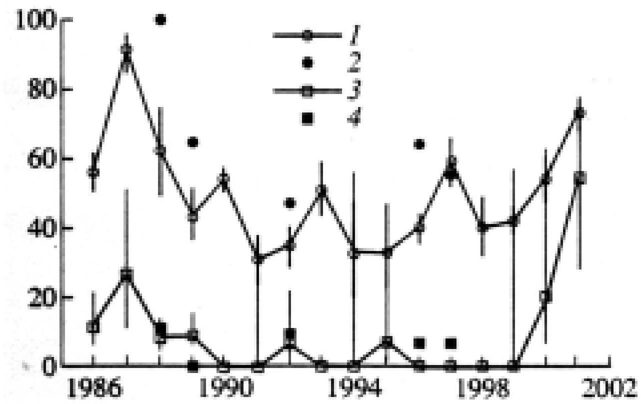

Figure 4. Percentages of fish larvae with food in their guts in the Black Sea during 1986–2001. Blenniidae and Gobiidae (1), anchovy (3) in the northern part; Blenniidae and Gobiidae (2), anchovy (4) in the southern part after (Gordina et al., 2004).

Table 5. *Monthly abundance of fish larvae (ind 100 m⁻³) in the surface layer and zooplankton (≤500 μm) organisms (ind m⁻³) in the 10 m layer in inshore waters in the Sevastopol area at the same stations in 2000 and 2001 and inter-annual variability of fish larvae food in this region.*

Years	Parameters	June	July	August
1995*	Zooplankton organisms	734	326	278
2000	Zooplankton organisms	4367	2760	5355
	Fish larvae	2.0	2.1	4.4
2001	Zooplankton organisms	5664	7660	1966
	Fish larvae	16.1	5.8	10.2

*, Fish larvae data are absent for this region.

small copepod species were always the main food for the fish larvae of the earlier size group (Duka, 1988; Tkach et al., 2002; Gordina et al., 2003).

In the same period of 2001 (June to September) the average number of zooplankton organisms less or equal to 0.5 mm had increased 1.2 fold compared with the previous year and was 4220 ±1790 ind m^{-3} in the region of investigation. In contrast to 2000 cladocerans dominated and made up 39% of total organisms registered as fish larval food. They were represented mostly by a small cladoceran *Pleopis polyphemoides*. Together with nauplii and copepodites they comprised 67% in abundance of the total organisms for fish larval nutrition. *Pleopis polyphemoides* prevailed in biomass and formed 78% of the fish larval food. So crustacean zooplankton prevailed greatly (Figure 3A). There was a noticeable difference between two stations both qualitative and quantitative. Cladocerans prevailed in open waters (station at 50–60 m depth) while meroplankton (Cirripedia + Polychaeta) was more numerous at the nearshore station (at 15–20 m depth). Food supply of fish larvae was better at the off-shore station, where during the whole summer higher numbers of zooplankton (≤500 μm) were found and its average abundance reached 6709 ±4170 ind m^{-3}. During a period of mass appearance of fish larvae in the plankton and their feeding in July, zooplankton abundance multiplied by 1.2 at Station 1 and 4.5 at Station 3 compared with the same period of 2000 and was respectively 3826 and 11,494 ind m^{-3}. In these two years the total share of all small crustaceans was 60 and 67% in zooplankton abundance, correspondingly (Figure 3A).

During the summer months the fish larvae food items sharply decreased in September 2000 and in August 2001 (Figure 3B). In both cases it coincided with mass *Mnemiopsis* appearance in the sea near Sevastopol (Figure 3C). Biomass of small sized zooplankton had recovered the month after the *Mnemiopsis* peak. By analysing the peak occurrence of this ctenophore near the coast it was observed that its abundance depended on temperature regime (Figure 3D) and the appearance of its predator *Beroe ovata*.

Monthly fluctuation of the food organisms in the period of fish larvae feeding showed the difference between years (Table 5). In 1995 their abundance steadily dropped in number during the summer months. In 2000–2001 zooplankton did not show this pattern. The decline shifted from July 2000 to August 2001. During both years of our investigation, crustaceans, which before had usually been the preferred food for fish larvae, dominated the zooplankton in contrast with the 1990s. In the middle of the 1990s in this region crustaceans were found in very few numbers during the period of fish larvae feeding, but also the total number of organisms ≤500 μm was low (Table 4).

Considerable increases in food for fish larvae as a whole and crustaceans, in particular, caused improvements in the fish larvae nutrition (Figure 4). Almost all larvae of families Gobiidae and Blenniidae had food in the intestines in 2000–2001. Average index food uptake reached 94% (Tkach et al., 2002; Gordina et al., 2004).

DISCUSSION

Bilio & Niermann (2004) put forward four hypotheses to explain variability of pelagic fish stocks: (1) predation on fish eggs and larvae by *Mnemiopsis*; (2) food competition between *Mnemiopsis* and fish larvae; (3) overfishing; and (4) climatic and hydrological shifts of regime. Although a lot of factors regulate fish population abundance in the sea, food supply to the larvae and carnivorous pressure are a must for establishing favourable conditions for their survival during the early life history of fish (Vodyanitsky, 1941; Ahlstron & Moser, 1976). The dynamics in fish population abundance is determined by intensity of recruitment and losses. In fish with a short life cycle, to which anchovy belongs, greatest fluctuations in population abundance are determined by recruitment, formed under natural reproductive conditions. Changes in food supplies of fish larvae is one of the main reasons for fluctuation of their stocks (Kostuchenko & Pavlovskaya, 1979).

Anchovy larval abundance remained low upto 2000 and horse-mackerel upto 2001, undoubtedly due to qualitative and quantitative lack of food (Gordina et al., 2004). In the middle 1990s, in spite of decreased levels of *M. leidyi*, which is undoubtedly a major food competitor for fish larvae, abundance of small epipelagic copepods, which are the main food items, remained very low (Vinogradov, 1991; Zagorodnyaya et al., 2003; Gordina et al., 2004). The percentage of Blenniidae and Gobiidae larvae with food in their digestive track was 30–55%, while among anchovy larvae it was lower and varied from 0 to 10% (Figure 4). Based on data received in 1992 and 1996 in Ukraine and Turkish waters, essential differences in feeding of *Engraulis encrasicolus*, *Trachurus mediterraneus*, Blenniidae and Gobiidae larvae were not noticed (Tkach et al., 1998). The fish larvae of the earlier size groups with length less than 4 mm especially suffered from absence of preferred food items for their nutrition (Tkach et al., 1998, 2002).

In the 1990s, after the population explosion of the invasive ctenophore *Mnemiopsis leidyi* in the late 1980s, the food base of fish larvae was disturbed. Zooplankton communities inhabited the shelf zone and formed by epipelagic complex species, were reduced in quality and quantity. Abundances of copepods and cladocerans became low especially in the summer months (Zagorodnyaya & Skryabin, 1995; Kovalev et al., 1998; Finenko & Romanova, 2000). Pronounced changes in zooplankton would inevitably reflect on fish larval nutrition. From the late 1980s and early 1990s, significant changes occurred in fish larval feeding concomitant with the zooplankton community. The food spectrum of larval nutrition decreased. Preferred food species, such as *Oithona nana*, *Paracalanus parvus*, which had dominated in larval nutrition before the arrival of *Mnemiopsis*, became rare or absent (Zagorodnyaya & Skryabin, 1995; Kovalev et al., 1996, 1998; Goubanova et al., 2001). The percentage of fish larvae with empty guts increased and ranged from 80 to 100% depending on species and size (Tkach, 1993; Tkach et al., 1998). The overall effect of the worsening conditions in larval nutrition was a sharp decrease in larval abundance of dominant fish species including *E. encrasicolus*, *T. mediterraneus* and *Mullus barbatus ponticus* (Gordina & Klimova, 1993, 1996; Gordina et al., 1998). But at the end of the 1980s, beginning of the 1990s, low abundance was registered not only in food fish species: anchovy, horse-mackerel, red-mullet, but also in fish of no interest for fisheries from the families Blenniidae, Gobiidae, Labridae, Gobiesocidae. Average abundance of larvae of all registered fish species all over the Black Sea was 7 ind 100 m^3 and only 1 ind 100 m^3 in 1992. The negative situation for larval nutrition of anchovy, Blenniidae and Gobiidae continued until 2000. In spite of an increase in number of anchovy eggs in the sea in 1995, its larvae were of low abundance in plankton. An analogous situation was observed in August 1995 near Bulgarian shores (Prodanov et al., 2001). Low abundance of anchovy larvae in the sea resulted in reduced stock of fish after 1995.

Based on our data of zooplankton abundance and results of fish larvae feeding investigations (Tkach et al., 1998, 2002) we note the improvement of the fish larvae nutrition in the 2000–2001. The total number of food organisms for fish larvae nutrition increased almost by one order compared with the mid 1990s (Table 4). The qualitative component of small zooplankton changed for the better too. Whilst in the 1990s bivalve larvae prevailed in the plankton (Gordina et al., 2001), in 2000–2001 crustaceans were dominant in the zooplankton community. Changes in qualitative composition and an increase in zooplankton abundance were detected in the background of low *Mnemiopsis* abundance as in the northern and southern parts of the Black Sea. In 1989–1990 *Mnemiopsis* biomass reached 1500–2000 g m^{-2} both in the northern and southern parts of the sea (Kovalev et al., 1996; Kideys et al., 1999). In 2000–2001 these magnitudes didn't exceed 500 g m^{-2}, in the region of our investigation in the northern part (Finenko et al., 2003) as well as near Sinop in the southern part (Satilmis et al., 2003). The abundance and biomass of other voracious feeders on zooplankton *Aurelia aurita* remained at a low level and was 1.83 ind m^{-2}, 6.9 mg m^{-2} in 2000 and 0.25 ind m^{-2}, 26.1 mg m^{-2} in 2001 at the same site in July–August (data provided by Z.A. Romanova).

The stock of young fish for a given year directly depends on syncronization between the period of hatching and abundance of food supply (Gerbilsky, 1954). Therefore, the number of surviving larvae increased in the sea when the fish larvae appearance coincided with the period of mass development of zooplankton forms, which are vital for their feeding. As expected, fish stocks were low in the years of poor zooplankton levels for larval feeding (Kostuchenko & Pavlovskaya, 1979). The larvae of warm spawning fish species (mainly the anchovy) usually appears in mass numbers during the second half of June and July. The conditions of their nutrition were more favourable in 2001 compared with the same period in 2000. The fish larvae survival directly depends on the nutritional state of the fodder zooplankton base. Survival of the larvae was not counted. But presence of larvae of the older age groups, absent earlier in the plankton gives us an indication that they survive.

This positive shift was noticed after the occurrence of the ctenophore *Beroe ovata* in the late 1990s, resulting in the decline of *Mnemiopsis* biomass by a 3.5 fold in the Sevastopol area (Finenko et al., 2003). As a response to the reduced *Mnemiopsis* pressure on zooplankton, epipelagic copepods and cladoceran abundance increased. The improvement of zooplankton composition includes the increase in small sized crustacean zooplankton. Decreased food competition with *Mnemiopsis* resulted in improvement of food conditions for pelagic fish larvae. The share of fish larvae with food in their guts was 54.5% of anchovy and 73% of species from the family Blennidae and Gobiidae in 2000–2001 (Figure 4). The copepod *O. nana* was again found in the larval gut after its disappearance in the beginning of the 1990s (A.V. Tkach, personal communication). Our investigations carried out in the southern and northern Black Sea showed an increase in fish eggs and larvae abundance as well as in zooplankton, that had been voraciously consumed by the invasive ctenophore *Mnemiopsis leidyi* during its peak occurrence in the Black Sea in the early 1990s. Later both due to decreased *M. leidyi* levels and then due to the appearance of its predator (i.e. the ctenophore *Beroe ovata*) in the late 1990s, an improvement in fish larvae nutrition has been observed. Observed positive changes in the plankton community suggested that on the whole the situation in the pelagic ecosystem of the Black Sea has been improving. The positive changes in zooplankton and ichthyoplankton communities were observed in different regions of the Black Sea (Shiganova et al., 2001; Kideys, 2002; Kamburska et al., 2003; Satilmis et al., 2003; Gordina et al., 2004).

Nevertheless, in certain periods of the year, *Mnemiopsis* has still been significantly influencing the food base of fish larvae. In 2000–2001 during the peak occurrence of this ctenophore in late summer, just before the *Beroe ovata* appearance, the concentration of food items for the fish larvae fell to low levels, but such a decrease was not long lived and the zooplankton biomass recovered relatively quickly.

CONCLUSION

Abundance of small zooplankton organisms being the most important factor for fish larval nutrition increased in 2000–2001. With the positive changes in the zooplankton community the feeding conditions of fish larvae improved and this resulted in greater larval survival. Simultaneously, both fish eggs and larvae increased reliably in number compared with the mid 1990s. Positive shifts took place when the *Mnemiopsis* biomass fell and its presence became very seasonal after the appearance and mass development of its predator, the ctenophore *Beroe ovata,* by the end of the 1990s in the Black Sea. Food concentration was considered the main factor controlling fish larvae abundance in the 1990s. Some positive changes in ichthyoplankton and zooplankton abundance, a significant increase in the fish larvae with food in the guts are the important evidence, confirming recovery of the Black Sea pelagic ecosystem.

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