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Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991–1992

U. Niermann, F. Bingel, A. Gorban, A. D. Gordina, A. C. Gücü, A. E. Kideys, A. Konsulov, G. Radu, A. A. Subbotin, and V. E. Zaika

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Two international surveys of anchovy eggs and larvae were carried out in the Black Sea at the beginning of the spawning season in June 1991 and during the main spawning period in July 1992. Horizontal tows demonstrated that the bulk of anchovy eggs and larvae were distributed in the upper 3-m layer, but in downwelling areas eggs and larvae were found down to 70 m depth. In contrast to earlier studies, vertical hauls obtained during the present investigation contained higher egg numbers in the southern and particularly south-eastern Black Sea than in the north-western region, which is known as the main spawning area of anchovy. Long-term sampling by the Institute of Biology of the Southern Seas, Sevastopol, shows that, in the northern Black Sea, the number of anchovy eggs and larvae found since the mid-1980s is lower than in the early 1960s. The sudden decline of anchovy ichthyoplankton in 1989, coinciding with the outburst of the recently introduced *Mnemiopsis* sp. (Ctenophora), supports the hypothesis that this gelatinous zooplankton species has played a role in diminishing the Black Sea anchovy fisheries, although the drastic changes in the Black Sea ecosystem (due to pollution, eutrophication, and heavy fishing) have also had an effect.

Key words: Black Sea, *Engraulis encrasicolus*, eutrophication, ichthyoplankton, *Mnemiopsis*.

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U. Niermann, F. Bingel, A. C. Gücü, and A. E. Kideys: Institute of Marine Sciences–Middle East Technical University, PO Box 28; TR 33731 Erdemli-Icel, Turkey. A. Gorban, and G. Radu: Romanian Marine Science Research Institute, Mamaia 300, RO 8700 Constanza 3/Romania. A. Konsulov: Institute of Oceanology, PO Box 52; Varna 9000, Bulgaria. A. D. Gordina, A. A. Subbotin, and V. E. Zaika: Institute of Biology of the Southern Seas–Ukrainian Academy of Science, Nachimov Ave., 2; Sevastopol, Ukraine.

Introduction

During the last few decades, one of the world's largest landlocked marine ecosystems, the Black Sea, has been subject to dramatic changes primarily as a result of increased nutrient input via the major rivers flowing into its northern region (Balkas *et al.*, 1990; Zaitsev, 1992; Volovik *et al.*, 1993; Kideys, 1994). In the 1940s this sea was classified as oligotrophic (Sorokin, 1983), but it has changed progressively to display, first, mesotrophic and, later, eutrophic, features (Caddy, 1993). The shallow north-western part of this sea has sometimes even shown dystrophic properties (Zaitsev, 1992).

Until recently, ever-increasing eutrophication levels, heavy fishing, and a large reduction in numbers of predators were probably the major factors for the steady rise in the biomass of small pelagic organisms in the Black Sea (Caddy, 1993), where anchovy is the dominant fish. The total catch of small pelagic fish doubled in the 1980s from the previous level of 350 000 tons in the late 1970s (Caddy, 1993). This occurred despite a large increase in the population of the jellyfish *Aurelia aurita* (estimated to be up to 400 million tons wet weight in the whole of the Black Sea in the early 1980s; Shushkina and Musayeva, 1983), which competes for zooplanktonic food with the small pelagic fish (Zaitsev, 1992; Caddy, 1993).

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In the beginning of the 1980s, the accidental introduction of the north-western Atlantic ctenophore *Mnemiopsis* sp., which originated from eutrophic lagoons in North America, radically affected the entire pelagic fauna of the Black Sea (Vinogradov *et al.*, 1989; Zaika and Sergeeva, 1991). The species was first described as *M. leidyi*, then redefined as *M. macradyi* (Zaika and Sergeeva, 1991). There is still some controversy as to whether these two species are separate or the same (M. R. Reeve, pers. comm.).

Reaching an estimated biomass of a remarkable 800 million tons wet weight in the summer of 1989 (Vinogradov *et al.*, 1989), this voracious ctenophore consumed a considerable fraction of the zooplankton which had been the food for pelagic fish and their larvae previous to the appearance of *Mnemiopsis* (Caddy, 1993). Since 1989 there have been sharp decreases in the fish catches of all the countries around the Black Sea (Kideys, 1994). The Turkish anchovy catch decreased from 295 000 tons in 1988 to 66 000 tons in 1990. Anchovy catches of the former USSR plummeted to 5800 tons in 1991 from 228 000 tons in 1988 (GFCM, 1993). Total catches of the Azov Sea fisheries dropped from 54 000 tons in 1988 to 8600 tons in 1990. Along the Romanian coasts anchovy have almost disappeared since 1989 (less than 100 tons), although in 1988 3171 tons were landed (GFCM, 1993).

In order to assess the impact of such a changing environment on the anchovy and its recruitment, monitoring of the egg and larval stages is essential. The first ichthyoplankton studies in the Black Sea started in the 1930s (Vodyanitsky, 1939; Dekhnik, 1954; Majorova and Chugunova, 1954) and systematic surveys were carried out by the Institute of the Biology of the Southern Seas (IBSS) during 1957–1965. Dekhnik *et al.* (1970) found that the peak spawning of anchovy took place in July, with temporal and spatial variations arising from physical features and condition factor of the parent stock. These authors also showed the abundance of anchovy eggs and larvae to be closely correlated with water temperature and available food. Similar results were obtained by Bulgarian authors (e.g. Dimov, 1968), but there are only a few surveys of the fish eggs and larvae in the southern Black Sea (Arim, 1957; Einarsson and Gürtürk, 1960; Mater and Cihangir, 1990). Egg and larvae samples taken from both inshore and offshore areas showed that anchovy spawn throughout the entire Black Sea (Majorova and Chugunova, 1954; Einarsson and Gürtürk, 1960), but the heaviest spawning occurs in the western (Einarsson and Gürtürk, 1960) or north-western region, close to the shore (Ivanov and Beverton, 1985).

This study examines the distribution of anchovy eggs and larvae with respect to changing environmental conditions in the Black Sea. Two basin-wide surveys were made by the coastal countries and the results obtained have been compared with those from previous studies.

Material and methods

Two joint international surveys were made in June 1991 and in July 1992. In both years the Institute of Marine Sciences (IMS), Middle East Technical University of Turkey, and the Institute of Biology of the Southern Seas (IBSS), Ukrainian Academy of Science, participated with their research vessels "Bilim" and "Prof. Vodyanitsky", respectively. Additionally, in July 1992 the Institute of Oceanology (BAS) of Bulgaria and the Romanian Marine Research Institute of Romania joined the survey with the Bulgarian RV "Akademik". During both cruises each vessel worked in its own exclusive economic zone (EEZ).

The ichthyoplankton was collected by vertical hauls at 116 stations in 1991 and at 241 stations in 1992 with the Hensen net, Bogorov Rass net (Rass and Kazanova, 1966), and the Djedi net. Additional horizontal tows were performed at 14 stations in July 1992 with the Melnikov's trawl (Melnikov, 1993) in the Ukrainian EEZ. Details of nets, vessels, and other information concerning the sampling procedure are given in Table 1.

Methodological differences, particularly between mesh sizes of the nets used by the co-operating organizations, were retained in order to obtain data comparable with studies previously carried out by each institute. Intercomparison attempts in 1991 and 1992 failed due either to bad weather conditions or insufficient numbers of eggs and larvae in the samples. However, more recently (August 1993) 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 towings using either net type (U. Niermann, unpublished data). We are aware that the anchovy larvae were not caught quantitatively by vertically-towed nets, but we believe that the main regional patterns of the larval distribution were recorded.

Area of investigation

The cyclonically meandering rim current constitutes the unique basin-scale feature of the Black Sea (Fig. 1). Along the axis of the rim current geostrophic currents attain speeds of 0.2–0.3 m s^{-1} (Oguz *et al.*, 1993). The interior of the rim current is formed by two separate cyclonic cells occupying the western (Western Gyre) and eastern halves (Eastern Gyre) of the basin. In addition to these features a series of mesoscale anticyclonic eddies is distributed between the rim current and the coast. The two most persistent eddies are the Batumi and the Sevastopol eddies. Along the Turkish coast three other

Table 1. Data collection scheme of the joint cruises. CIS = Commonwealth of Independent States.

Research vessel	Turkish EEZ RV "Bilim"	CIS EEZ RV "Prof. Vodyanitsky"	Bulgarian and Romanian EEZ RV "Akademik"
Vertical hauls			
Number of stations (1991)	66	50	—
Number of stations (1992)	143	65	33
Net type and mesh size	Hensen 0.3 mm	Bogorov Rass 0.5 mm	Djedi 0.15 mm
Diameter of net opening	70 cm	80 cm	36 cm
Hauling speed	1 m s^{-1}	1 m s^{-1}	?
Depth recording	Angle and cable length	Angle and cable length	Angle and cable length
Depth of haul in 1991	100 m → surface	100 m → surface	—
Depth of haul in 1992	*Anoxic layer → surface	100 m → surface	100 m → surface
Sorting large zooplankton	On board	On board	—
Sorting ichthyoplankton	In the Institute	On board	In the Institute
Conversion factor: 1 m^2	2.6	2	10
Fixation of the samples		4% buffered formalin	
Presentation of results		Numbers m^{-2}	
Horizontal hauls			
Net type and mesh size		Melnikov, 1 mm, closing net	
Number of stations 1992		14	
Depth ranges		1–3 m, 0–12 m, 20–30 m, 45–50 m, 70 m	
Towing speed		3–4 knots	
Duration of haul		10 min	
Surface area of net mouth		0.2 m^{-2}	
Fixation of the sample		4% buffered formalin	
Presentation of results		Numbers 100 m^{-3}	

*The depth of the anoxic layer varied between 80 m in the central gyers and about 200 m in downwelling regions.

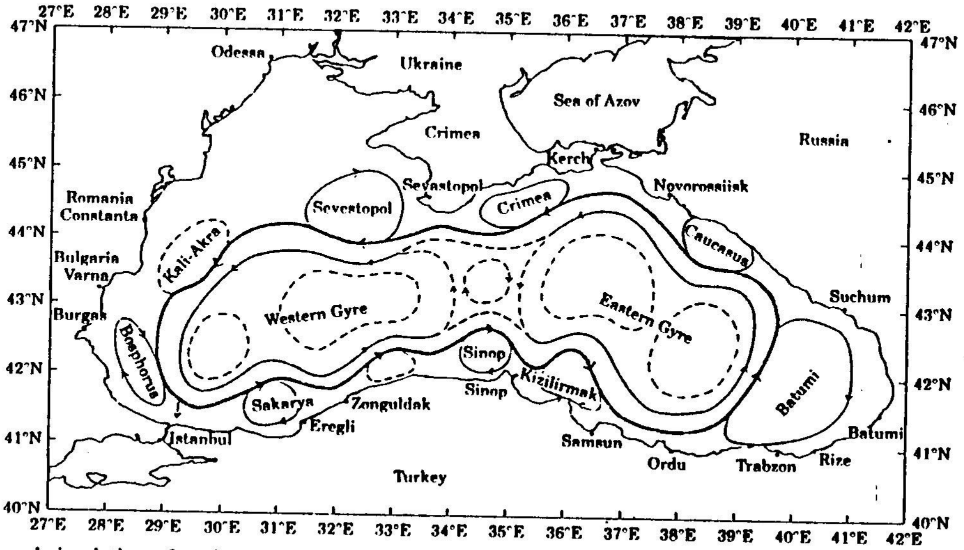

Figure 1. General circulation of surface currents in the Black Sea (redrawn from Oguz *et al.*, 1993). The bold line shows the rim current.

quasi-permanent anticyclonic eddies, related to regional topography, are situated in the south-western part of the basin (Bosphorus eddy), and off the Sakarya and Kizilirmak Rivers. Along the north-eastern coast, the Crimean and Caucasian eddies are the most pronounced quasi-permanent features of this region. An irregular offshore protrusion of the meandering rim current along the Caucasian coast is a common feature. Another apparently recurrent feature is the Kali-Akra eddy along the Bulgarian coast (Oğuz *et al.*, 1993).

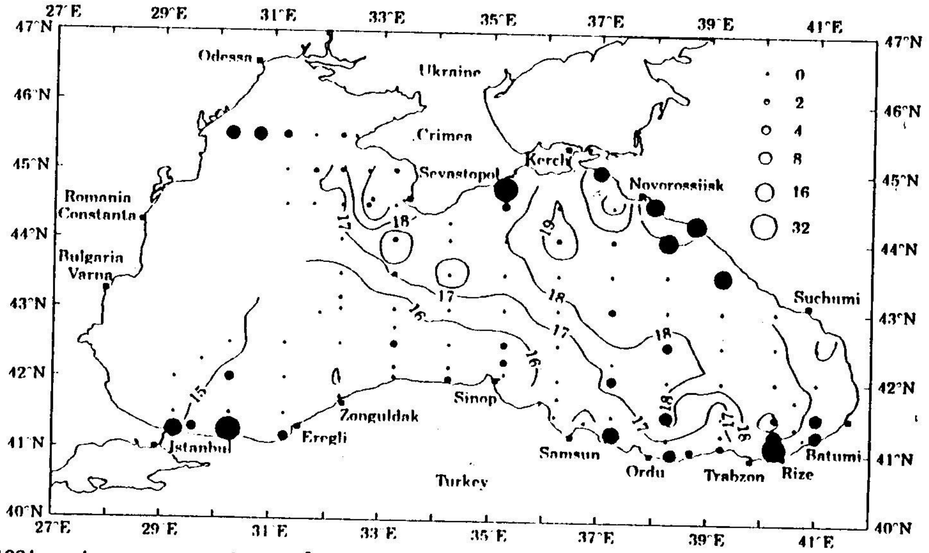

Figure 2. June 1991: anchovy eggs (number m^{-2}) and surface temperatures (°C; at 5 m depth) in the Black Sea. The largest circle is equal to 29 eggs m^{-2}. Numbers according to the area of the circle.

Results

Vertical distribution

In order to estimate differences between the hauls from the surface to the H_2S layer (120–180 m) and the hauls from the surface to the thermocline (20–45 m), comparative catches were carried out at four stations in the Turkish EEZ. No significant differences (U-test according to Mann and Whitney; Sokal and Rolf, 1973) were found between the deep and shallow hauls.

Horizontal tows performed by the Institute of Biology of the Southern Seas, Sevastopol, in the northern part of the Black Sea in 1992 (Ukrainian EEZ), showed that the majority of eggs and larvae were obtained from the surface layer (1–3 m), where the temperature was highest (range 20.1–24.6°C; Table 2).

Although the bulk of the anchovy eggs and larvae were above the thermocline, at seven stations some eggs and larvae were found below the thermocline at a depth of 45–70 m in July 1992 (Table 2). These stations were located at convergence zones along the outer edge of the rim current, in areas of the north-eastern part of the Black Sea and in the area of the quasi-stable anticyclonic Sevastopol eddy. In July 1992 about 18% (range 6–44%) of the total number of anchovy eggs found at the seven stations were below 40 m depth, far beneath the thermocline. All eggs of the development stages IV–VI (according to Dekhnik, 1973) were alive.

Larvae beneath the thermocline were found only at three stations (19, 30, 61). At the nearshore station 30 (Sevastopol Bay) the number of eggs and larvae were distributed unevenly down to 70 m with the bulk of larvae (n=28; 76%) concentrated below the thermocline. However, only larvae >6 mm, alive, and in good condition were found between the 50–70-m-depth range; smaller ones were dead.

Horizontal distribution

In June 1991 the water temperature was below 20°C (at 5 m depth) throughout the Black Sea (Fig. 2). The eastern part of the Black Sea, with temperatures varying between 17.8–19°C, was warmer than the western area, where surface temperatures were below 17°C. The lowest temperatures were found in the south-western region with temperatures under 16°C. Spawning had started mainly in the eastern part of the Black Sea in coastal areas (between east of Samsun and west of Rize, between east of Kerch and Suchumi and south of Odessa). Despite the low water temperatures of 15–16°C, spawning had also started by June in the Bosphorus area.

In this sampling period, overall egg abundance was very low; a total of 154 eggs at 66 stations in the Turkish EEZ and 286 eggs at 66 stations in the Ukrainian EEZ. The abundance of anchovy eggs in coastal areas was 10–30 eggs m^{-2}. In open waters egg numbers were usually zero, but, when eggs were present, their numbers were small (generally ≤ 2 eggs m^{-2}; Fig. 2) compared with those of coastal areas.

During the whole study period in June 1991 almost no anchovy larvae were found. Only at two stations situated between Novorossiisk and Suchumi, with relatively warm water (>19.5°C), were a total of two larvae found.

In July 1992 the surface temperatures (20.2–22.5°C) were higher than in June 1991 and relatively uniform

Table 2. Vertical distribution of anchovy eggs determined by horizontal tows from RV "Prof. Vodyanitsky" in the northern part of the Black Sea. (—): no haul made.

Date	Station	Lat (N)	Lon (E)	Egg number 1000 m $^{-3}$						Larvae number 1000 m $^{-3}$						Temperature °C					
				1–3 m	10–15 m	20–25 m	30 m	45–50 m	70 m	1–3 m	10–15 m	20–25 m	30 m	45–50 m	70 m	1–3 m	10–15 m	20–25 m	30 m	45–50 m	70 m
5.7	1	45°45	32°30′	204	55.0	0.0	—	—	—	0	9.0	0.0	—	—	—	20.1	20.0	17.8	—	—	—
8.7	13	43°49	31°15′	0	0.0	—	0	—	—	0	0.0	—	0	—	—	21.0	21.0	—	8.0	—	—
8.7	12	44°00	31°15′	694	74.0	83.0	—	—	139	0	27.0	0.0	—	—	0	21.8	21.8	16.0	—	—	6.5
10.7	19	45°00	32°15′	324	9.0	37.0	—	37	—	0	0.0	9.0	—	0	—	20.2	20.2	8.7	—	6.5	—
10.7	22	44°30	32°15′	120	9.0	—	0	—	—	0	0.0	—	0	—	—	21.9	20.6	—	8.5	—	—
10.7	25	44°01	32°15′	28	0.0	—	—	—	—	27	0.0	—	—	—	—	21.2	11.3	—	—	—	—
11.7	28	43°30	32°15′	130	18.0	—	—	9	—	0	0.0	—	—	0	—	21.5	21.4	—	—	7.1	—
12.7	30	44°50	33°15′	991	18.0	157.0	—	—	158	9	0.0	9.0	—	—	19	21.4	21.3	9.6	—	—	6.5
12.7	32	44°30	33°18′	74	9.0	0.0	—	—	27	0	0.0	0.0	—	—	0	21.1	20.6	10.2	—	—	6.6
12.7	34	44°00	33°15′	46	0.0	0.0	—	0	—	0	0.0	0.0	—	0	—	21.2	21.2	7.6	—	6.5	—
20.7	54	43°30	39°15′	172	134.0	55.0	—	55	—	9	0.0	0.0	—	0	—	24.2	22.0	10.2	—	7.3	—
21.7	57	42°10	40°15′	18	27.0	0.0	—	36	—	0	0.0	0.0	—	0	—	22.1	12.0	7.8	—	6.5	—
21.7	61	42°50	40°15′	778	0.0	55.0	—	0	—	0	0.0	9.0	—	0	—	24.6	23.6	9.4	—	6.9	—
21.7	63	43°09	40°15′	911	194.0	204.0	333	—	—	110	27.0	18.0	0	—	—	23.7	22.9	21.5	10.7	—	—
Sum				4490	547	591	333	137	324	155	63	45	0	0	19						
Sum (%)				70	9	9	5	2	5	55	22	16	0	0	7						

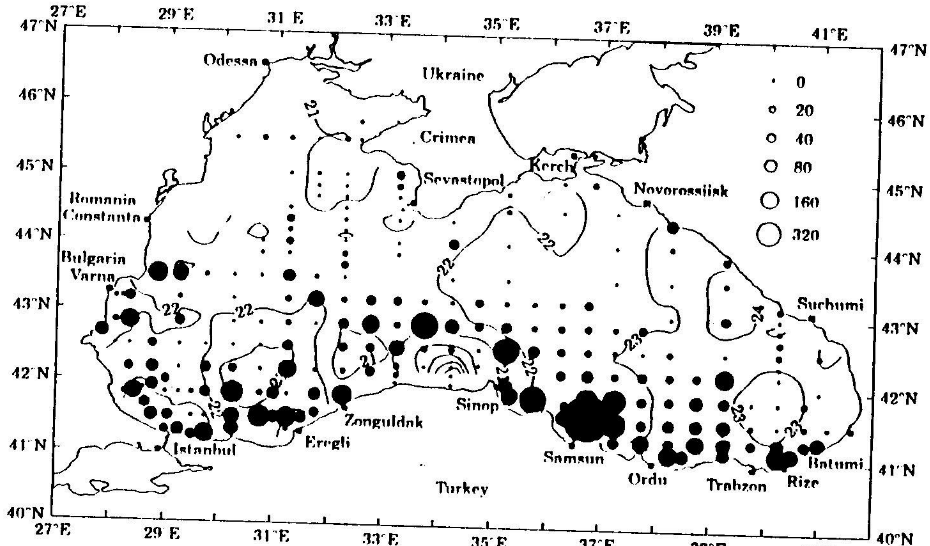

Figure 3. July 1992: anchovy eggs (number m^{-2}) and surface temperature (°C; at 5 m depth) in the Black Sea. The largest circle is equal to 1167 eggs m^{-2}. Numbers according to the area of the circle.

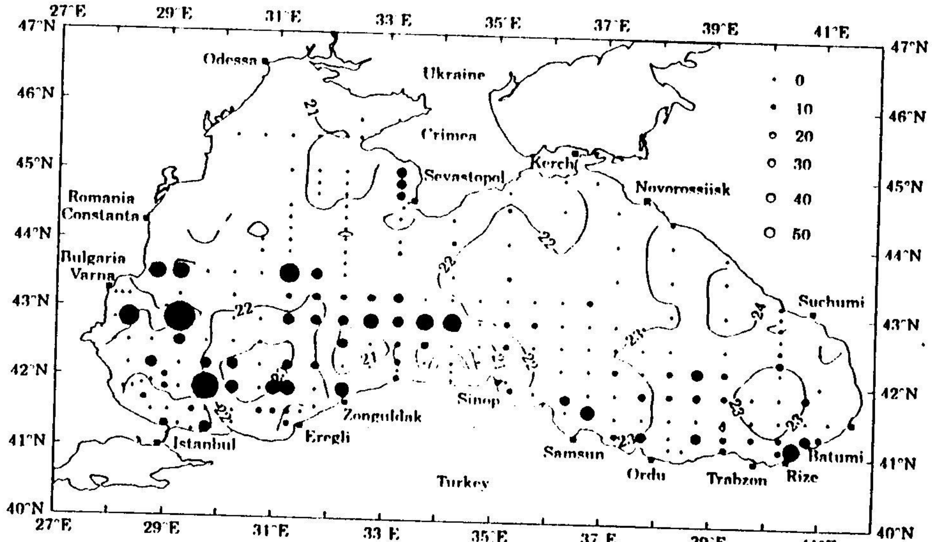

Figure 4. July 1992: anchovy larvae (number m^{-2}) and surface temperature (°C; at 5 m depth) in the Black Sea. The largest circle is equal to 55 larvae m^{-2}. Numbers according to the area of the circle.

throughout the whole Black Sea area (Fig. 3). Only in some areas of the eastern part the surface-water temperature was slightly elevated (23–24°C). In July 1992 a total of 4256 anchovy eggs at 241 stations were found. Maximum egg numbers occurred in the coastal waters of the south-eastern as well as in the south-western and western areas of the Black Sea (Fig. 3). No eggs were recorded in the cold waters of the upwelling area off Sinop.

Similar to the egg distribution, larval numbers were higher in the southern Black Sea in July 1992; however, their quantities were small (maximum 26 larvae m^{-2}; Fig. 4). In the southern Black Sea most larvae were found in the western basin, where they were distributed further offshore than the eggs. The bulk of larvae occurred at the inner border of the rim current (see Fig. 1). Similar to the egg situation, no larvae were recorded in the cold waters of the upwelling area of Sinop. In the northern part larvae occurred in moderate numbers only in the Sevastopol Bay. No larvae were found in the north-western shelf region and only one single larvae was obtained in the north-eastern Black Sea.

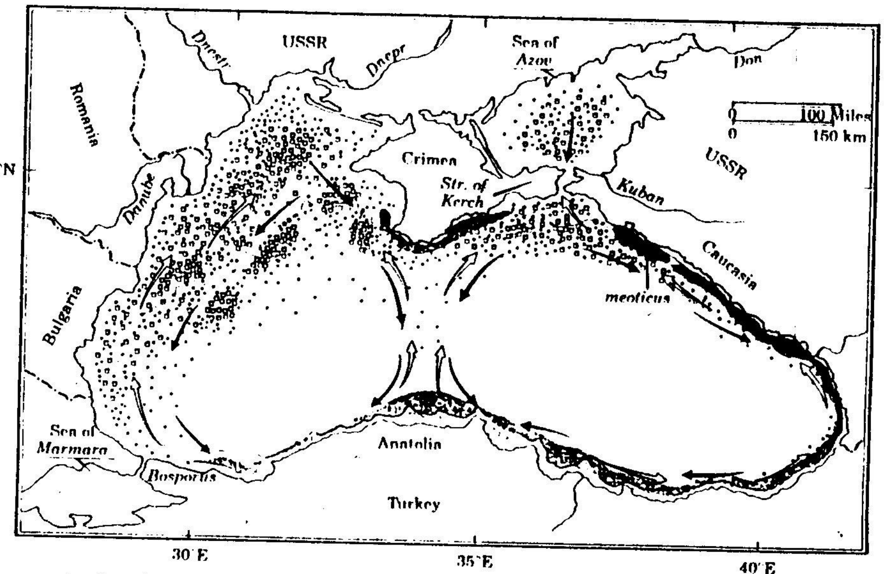

Figure 5. Spawning grounds of anchovy *Engraulis encrasicolus* in the Black Sea according to Ivanov and Beverton (1985). Squares: spawning areas. Circles: feeding areas. Dark grey: wintering areas. White arrows: migration to spawning and feeding areas. Black arrows: migration to wintering areas.

Discussion

The maturing of anchovy gonads starts at a minimum temperature of 13°C; spawning occurs between 13°C/14°C and 26°C, with maximal spawning activity at temperatures higher than 20°C (Dekhnik, 1954; Demir, 1959). During the survey in June 1991 the water temperatures in the upper 5 m were exceptionally cold, being 1.5–2.0 degC less than the average temperatures for this month in previous decades (Altman *et al.*, 1987). Thus, the low number of anchovy eggs and the scarcity of larvae found during the survey in June 1991 could be explained by delayed spawning due to the low water temperatures over the entire Black Sea.

In July 1992 the water temperature, due to the cold and late spring period, was 2.0–2.5 degC below the long-term average for previous years (Altman *et al.*, 1987). Yet the comparatively uniform surface temperatures of 20.2–22.5°C and above (Fig. 3) were high enough to lead to successful spawning. Spawning of anchovy in the Black Sea and in the Mediterranean occurs above the thermocline at a depth of 0–10 m (Dekhnik, 1973; Palomera, 1990, 1991). Eggs and larvae are distributed between 0–30 m. At night the larvae migrate close to the surface (Einarsson and Gürtürk, 1960). According to the present study the anchovy eggs are distributed within a narrow depth range, the majority of eggs occurring both day and night at a depth between 0–3 m below the surface (Table 2).

In regions of downwelling, anchovy eggs and larvae could sink below the thermocline. Gordina *et al.* (1990) found in areas of convergence of the Black Sea, usually at the outer border of the rim current, that live eggs and larvae of anchovy and horse mackerel were dispersed down to 100 m depth. In these downwelling areas in 1988, the number of anchovy eggs under the thermocline was up to 70% of the total number sampled per 1 m^2 (Gordina *et al.*, 1990). Similar results were found in the present survey. An average of 18% of eggs occurred under the thermocline below 40 m (Table 2). In July 1992, however, only larvae >6 mm, live, and in good condition were found in the 50–70-m-depth range, whilst smaller larvae were dead. Larger larvae (advanced stages), which undergo vertical migration, seemed less vulnerable to low temperature than younger stages (Gordina *et al.*, 1990).

According to the review of Ivanov and Beverton (1985), the two subspecies of the Black Sea anchovy undergo extensive migrations all over the Black Sea from the overwintering to the spawning areas (Fig. 5). These authors suggested that anchovy spawn throughout the whole of the Black Sea, but mainly in the northern half. However, this conclusion was based on surveys where the sampling was not adequate in the northern and southern part. Only one extensive survey on anchovy eggs and larvae has been carried out in Turkish waters, in July 1957 (Einarsson and Gürtürk, 1960), and is not included in the review of Ivanov and Beverton (1985). Einarsson and Gürtürk (1960) found the highest abundance of anchovy eggs in the south-western Black Sea and in the north-western shelf area in July 1957, whereas in the eastern Black Sea eggs were poorly distributed (Fig. 6). Changes in the spawning areas of anchovy were noticeable by 1988 (Gordina *et*

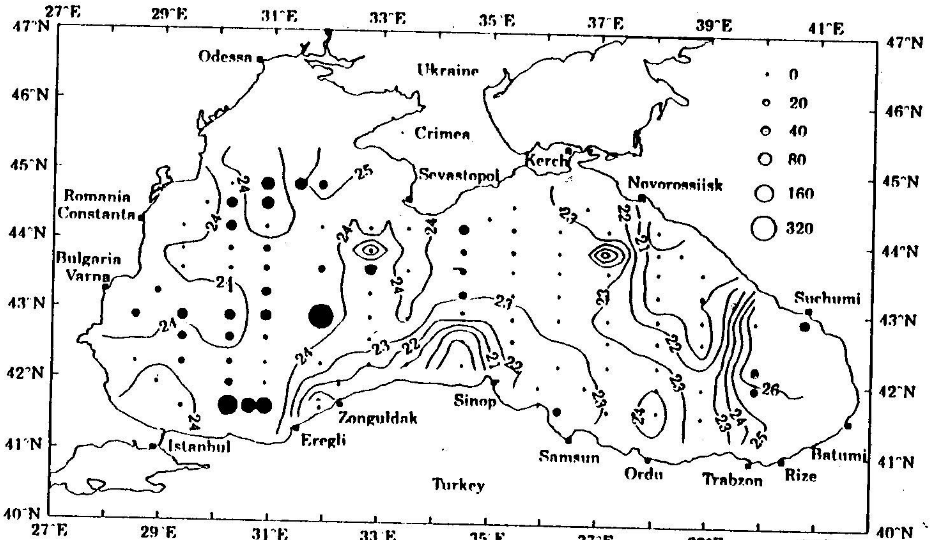

Figure 6. July 1957: anchovy eggs and surface temperature (at 10 m depth) in the Black Sea (redrawn from Einarson and Gürtürk, 1960). The largest circle is equal to 321 eggs m^{-2}. Numbers according to the area of the circle.

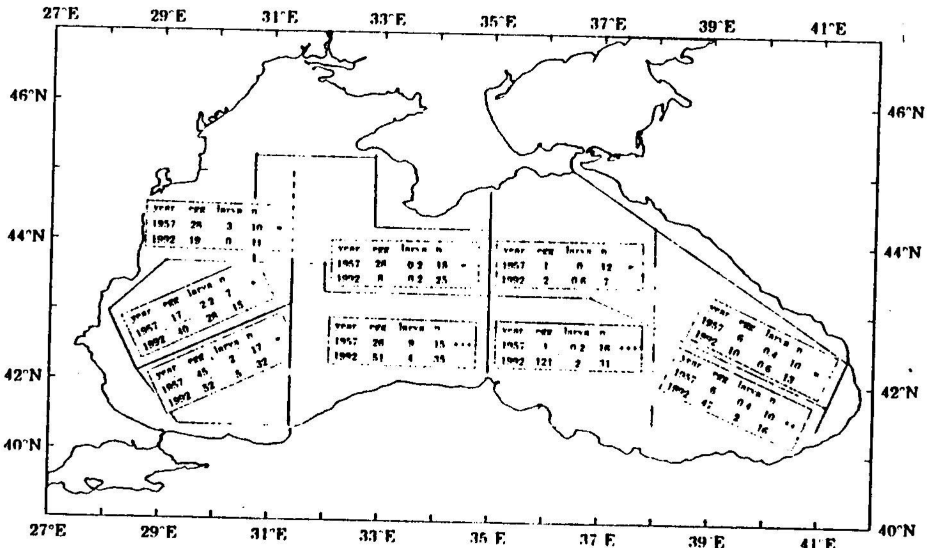

Figure 7. Comparison 1957/1992: numbers of anchovy eggs and anchovy larvae (number m^{-2}) in nine different areas of the Black Sea in 1957 (Einarson and Gürtürk, 1960) and in the joint survey of 1992. For statistical testing, the U-test (Sokal and Rohlf, 1973) was used. n=number of stations per area. =: not significantly different, *: significantly different, **: high significance, ***: very high significance.

al., 1990), when the areas observed to be most abundant with anchovy eggs and larvae were in the open sea along the offshore boundary of the rim current (Gordina *et al.*, 1990) rather than the typical distribution between shelf areas and the rim current found during 1950 to 1980 (Caddy and Griffiths, 1990; Gordina *et al.*, 1990; Arkhipov *et al.*, 1992).

Our survey during July 1992 showed that, in contrast to former studies (Einarsson and Gürtürk, 1960; Ivanov and Beverton, 1985), the bulk of anchovy eggs were obtained from the southern and particularly the south-eastern Black Sea (Figs 3, 5, and 6). Whilst the northern part of the Black Sea displayed nearly the same numbers of anchovy eggs in July 1957 and 1992 (Fig. 7), the egg numbers for the southern region were significantly higher in 1992 than in 1957 (Fig. 7). Thus, the July 1992 survey confirmed that pronounced spawning of anchovy occurs also in the south-eastern region of the Black Sea.

In June 1991 the spawning of anchovy had just started. A total number of only 340 eggs at 132 stations were found. For this reason it is difficult to compare the

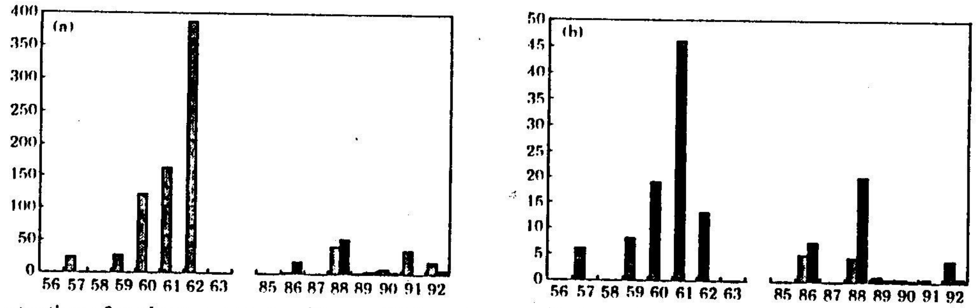

Figure 8. Fluctuation of anchovy eggs (a) and larvae (b) (numbers m^{-2}) along the Crimea peninsula (1957–1992). Grey columns: total water depth <100 m. Black columns: total water depth >100 m.

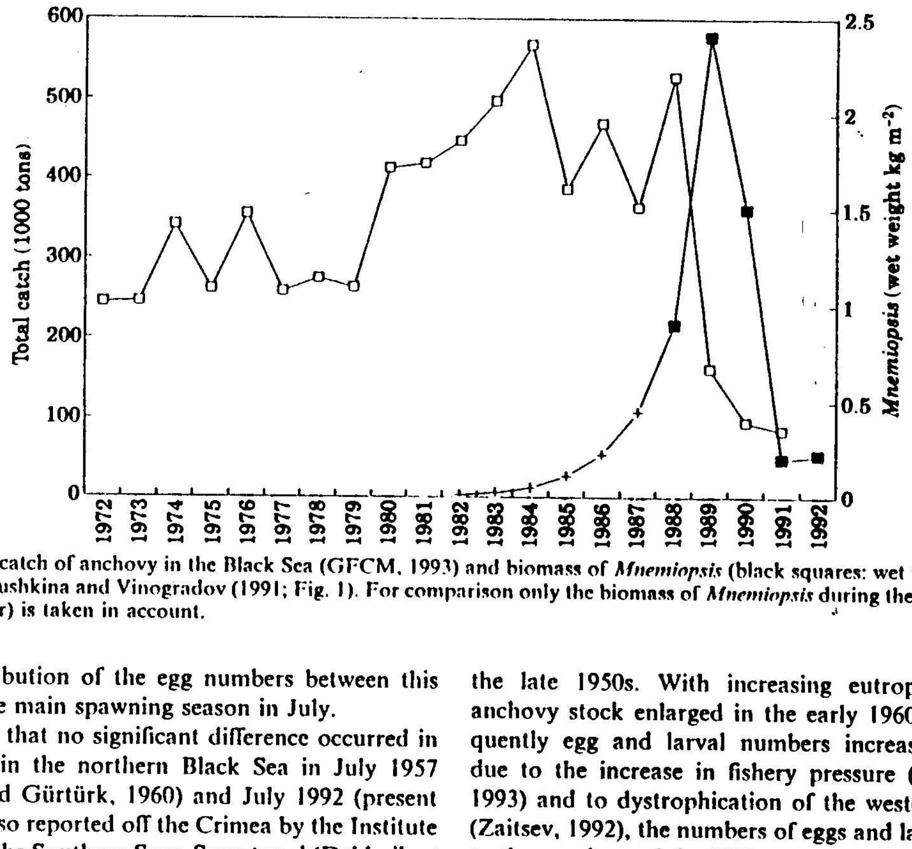

Figure 9. Total catch of anchovy in the Black Sea (GFCM, 1993) and biomass of *Mnemiopsis* (black squares: wet weight kg m^{-2}) according to Shushkina and Vinogradov (1991; Fig. 1). For comparison only the biomass of *Mnemiopsis* during the summer season (July–September) is taken in account.

regional distribution of the egg numbers between this period and the main spawning season in July.

The finding that no significant difference occurred in egg numbers in the northern Black Sea in July 1957 (Einarsson and Gürtürk, 1960) and July 1992 (present survey) was also reported off the Crimea by the Institute of Biology of the Southern Seas, Sevastopol (Dekhnik *et al.*, 1970; Dekhnik, 1973; A. D. Gordina, unpublished data), by employing identical net types and sampling procedure (Fig. 8). In the early 1960s the number of eggs increased continually (up to 390 eggs m^{-2} in 1962). From 1963 to 1986 no sampling was carried out. In the 1980s the egg and larvae numbers were low compared to the 1960s. In 1989 a significant decline in number of anchovy eggs and larvae, as compared to 1988 in inshore (depth <100 m) and offshore waters (depth >100 m), was noted (U-test, $p<0.005$; comparison of egg and larvae numbers in 1988/1989; 19 stations).

The low egg and larvae numbers in 1957 and 1959 possibly reflect the mesotrophic state of the Black Sea in the late 1950s. With increasing eutrophication, the anchovy stock enlarged in the early 1960s, and consequently egg and larval numbers increased. Probably due to the increase in fishery pressure (Bingel *et al.*, 1993) and to dystrophication of the western shelf area (Zaitsev, 1992), the numbers of eggs and larvae dropped to the numbers of the 1960s.

The sharp decline in anchovy eggs and larvae, reflecting the collapse of anchovy catches for the whole of the Black Sea in 1989, coincided with the mass development of the new invader *Mnemiopsis* since 1988 (Fig. 9). Laboratory experiments and *in situ* mesocosm studies on the predation and relative predation potential of *Mnemiopsis* in its native waters, showed that *Mnemiopsis* is an important potential predator of anchovy eggs, larvae, and, especially, of yolk-sac larvae (Burrell and Van Engel, 1976; Mountford, 1980; Cowan and Houde, 1993; Purcell *et al.*, 1993). *Mnemiopsis* could, therefore, be a threat to fishery year-class recruitment (Monteleone and Duguay, 1988).

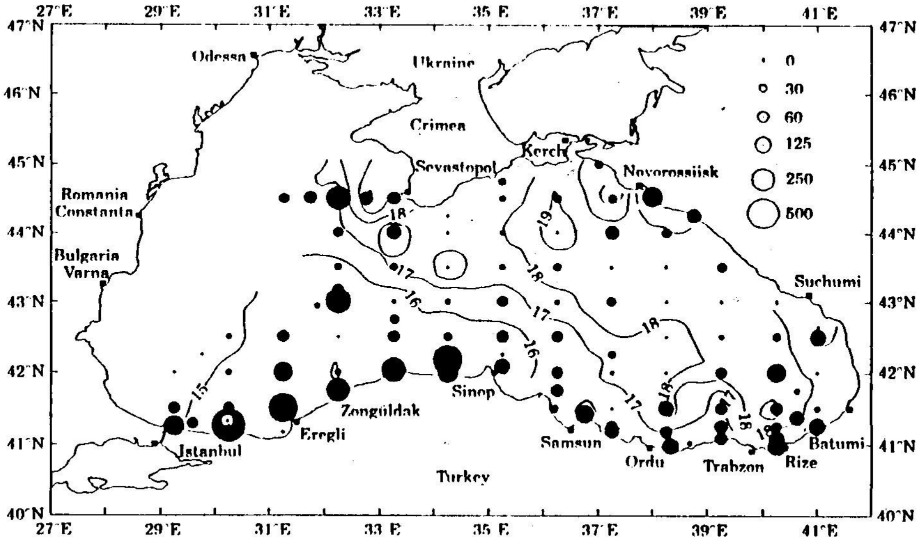

Figure 10. June 1991: *Mnemiopsis* (wet weight g m^{-2}) and surface temperatures (°C; at 5 m depth) in the Black Sea (according to Mutlu *et al.*, 1994). The largest circle is equal to 1.1 kg m^{-2}. Numbers according to the area of the circle.

The high fecundity (an average of 8000 eggs within 23 days) and the huge growth rates (up to daily doubling) observed in this ctenophore could only be sustained by high feeding rates, resulting sometimes in a sudden appearance of bloom proportions (Reeve *et al.*, 1978).

In the Black Sea *Mnemiopsis* competes for zooplanktonic food with anchovy, as well as preying on anchovy eggs and larvae (Sergeeva *et al.*, 1990; Tsikhon-Lukanina *et al.*, 1991; Tsikhon-Lukanina and Reznitchenko, 1991). Furthermore, the seasonal bloom of *Mnemiopsis* starts with the mean spawning season of the anchovy in July/August but continues until late autumn (Shushkina and Vinogradov, 1991). Nevertheless, in winter, high concentrations of *Mnemiopsis*, with a size of about 200 g wet weight, are present in coastal waters of Turkey (Mutlu *et al.*, 1994). Predation on anchovy larvae and the competition for food with juvenile and adult anchovies therefore continues the whole year.

In the Black Sea *Mnemiopsis* showed the typical pattern of a new colonizer: after mass development in the years 1989 and 1990 with 2 kg m^{-2} in the open sea and average numbers of 4.7 kg m^{-2} at the north-western shelf (Shushkina and Vinogradov, 1991), the numbers and biomass dropped to a moderate level by 1991 (Mutlu *et al.*, 1994; Vinogradov *et al.*, 1992). During the international Black Sea surveys in June 1991 and July 1992 the average *Mnemiopsis* biomass for the open Black Sea was 0.09 kg m^{-2} and 0.18 kg m^{-2}, respectively (Mutlu *et al.*, 1994). Unfortunately, no *Mnemiopsis* data could be collected for the north-western shelf area during these two surveys.

In both surveys during June 1991 and July 1992, the distribution of anchovy eggs (Figs 2, 3) and of *Mnemiopsis* (Figs 10, 11) showed similar patterns in coastal areas, which suggests that the distribution of both species is governed by nutritional and hydrographic features. In contrast to anchovy ichthyoplankton, *Mnemiopsis* was also found in the cold waters of the upwelling region off Sinop. Similar to the distribution of anchovy eggs, *Mnemiopsis* numbers were high in coastal regions in early summer (June 1991; Fig. 10), spreading into the open sea in mid-summer (July 1992; Fig. 11). A particularly high biomass of *Mnemiopsis* was found in the areas of Eregli and Samsun in July 1992, where high numbers of anchovy eggs also occurred. In July 1992 the highest concentrations of *Mnemiopsis* were obtained between Sinop and Rize, where heaviest anchovy spawning took place (Figs 3, 11). However, in these surveys no significant correlation between the occurrence of *Mnemiopsis* and anchovy eggs and larvae could be detected.

Conclusion

In contrast to the review of Ivanov and Beverton (1985), most anchovy eggs were found in the southern and south-eastern area of the Black Sea during the 1992 survey carried out in the main spawning season (July). The decrease in spawning in the northern Black Sea is consistent with the northern area of the Black Sea having become excessively eutrophic and more polluted than the southern area over the last two decades as a result of major rivers flowing into this region (Balkas *et al.*, 1990; Mee, 1992; Zaitsev, 1992; Volovik *et al.*, 1993). It may be suggested that the environmental deterioration of the shelf area due to dystrophication, and the improved food conditions in the open sea due to eutrophication (Zaitsev, 1992), has resulted in a shift of

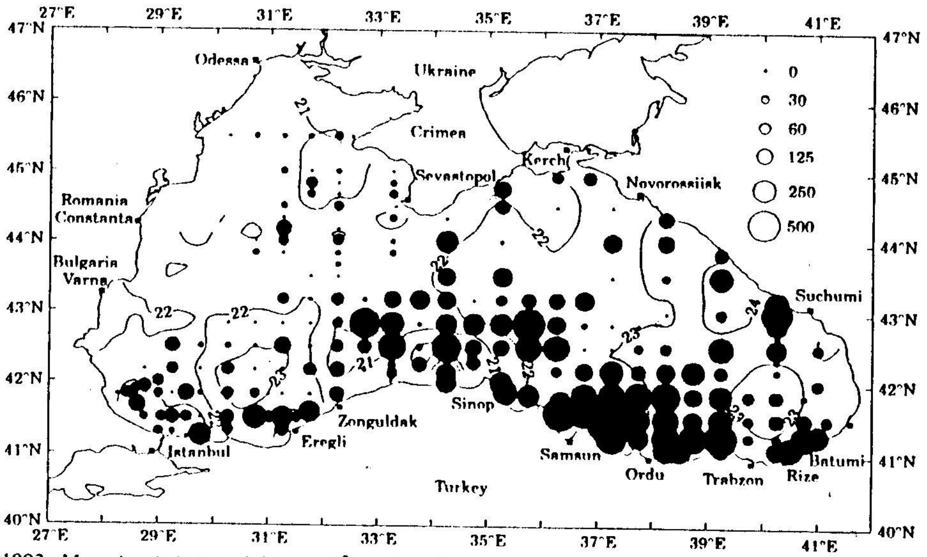

Figure 11. July 1992: *Mnemiopsis* (wet weight g m^{-2}) and surface temperatures (°C; at 5 m depth) in the Black Sea (according to Mutlu *et al.*, 1994). The largest circle is equal to 1.9 kg m^{-2}. Numbers according to the area of the circle.

the spawning grounds to the open sea. Increasing eutrophication of the former mesotrophic coastal areas of the southern Black Sea (Sur *et al.*, 1994) could also be assumed as a reason for the expansion of the spawning grounds from the Bosphorous area to the eastern Black Sea coast of Turkey.

The plankton-enriched water of the Black Sea created the basic conditions for the outbreak of the ctenophore *Mnemiopsis* observed in the years 1987 to 1989. It may be suggested that the outburst of *Mnemiopsis* during 1989/1990 had an impact on the anchovy stock of the Black Sea, and this ctenophore may continue to hamper the recovery of the severely over-fished anchovy stock.

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