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Distribution of the new invader *Mnemiopsis* sp. and the resident *Aurelia aurita* and *Pleurobrachia pileus* populations in the Black Sea in the years 1991–1993

E. Mutlu, F. Bingel, A. C. Gücü, V. V. Melnikov, U. Niermann, N. A. Ostr, and V. E. Zaika

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Since the outburst of *Mnemiopsis* sp. in 1988–1990 in the Black Sea, two international cruises in June 1991 and in July 1992, and a subsequent survey in August 1993, have determined the distributions of both the invading *Mnemiopsis* sp. and the resident *Aurelia aurita* and *Pleurobrachia pileus*. *Aurelia aurita* and *Pleurobrachia pileus* displayed the lowest and the highest population densities of 3–14 individuals m^{-2} and 172–523 individuals m^{-2}, respectively. The abundances of *Mnemiopsis* sp. varied from 12–45 individuals m^{-2}. The lower ends of the ranges were found in June 1991, whilst the highest abundances occurred in July 1992 and August 1993. Despite the differences in abundance, the average biomass of all three species was about 200 g m^{-2} wet weight in July 1992 and August 1993, though in June 1991 biomass values were approximately half those found in succeeding years. The abundances and biomass of *Mnemiopsis* sp. were more than three times higher in the eastern than in the western Black Sea during 1992 and 1993. The biomass of *Mnemiopsis* sp. and *Aurelia aurita* decreased in 1992 and 1993 compared to its value in the 1980s, but the biomass of the deep-dwelling *Pleurobrachia pileus* doubled between 1990/1991 and 1993.

Key words: Black Sea, *Aurelia aurita*, *Mnemiopsis*, *Pleurobrachia pileus*, Ctenophora, scyphozoa, megazooplankton.

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F. Bingel, A. C. Gücü, E. Mutlu, and U. Niermann: Institute of Marine Sciences – Middle East Technical University, PO Box 28; TR 33731 Erdemli-Icel, Turkey. V. V. Melnikov, N. A. Ostr, and V. E. Zaika: Institute of Biology of the Southern Seas – Ukrainian Academy of Science, Nachimov Ave., 2, Sevastopol, Ukraine.

Introduction

Four species of gelatinous animals are common in the Black Sea: two scyphozoans, *Aurelia aurita* and *Rhyzostoma pulmo*, and two ctenophores, *Pleurobrachia pileus* and *Mnemiopsis* sp. While *Rhyzostoma pulmo* is most common in coastal areas, the three other species are distributed in all parts of the Black Sea.

Pleurobrachia pileus is found in the water column above the anoxic zone below the maximal pycnocline at depths between 60–170 m during the day at densities of 80–115 individuals m^{-3}. At night, this species migrates towards the surface. The adults reach a length of 2 cm in diameter, the biomass varying between 50–150 g m^{-2}. No major seasonal changes and annual fluctuations have been observed during the last few decades (Vinogradov *et al.*, 1990; Shushkina and Vinogradov, 1991).

Aurelia aurita is very common in the mixed layer down to the subthermocline region. Small animals are mostly found above the thermocline, while larger individuals, up to 40 cm, are found just below it. The biomass of *Aurelia aurita* fluctuates seasonally (Shushkina and Musayeva, 1990), being high in spring (March, April) and autumn (September–November). The biomass of *Aurelia aurita* has increased with increasing eutrophication of the Black Sea (Caddy and Griffiths, 1990). From 1950–1962, Shushkina and Musayeva (1983) found a biomass in the order of 30 million tons wet weight. In 1978 a much larger biomass, as large as 400 million tons wet weight for the whole of the Black Sea, was calculated by Gomoiu (1981). In spring 1984 and autumn 1985 the wet weight of *Aurelia aurita* was about 1 kg m^{-2}, averaged over the entire Black Sea (Flint *et al.*, 1989).

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At 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; Caddy, 1993). This species, up to 12 cm in total length, was first described as *M. leidyi*, then redefined as *M. mccradyi* (Zaika and Sergeeva, 1990). Because there is still some controversy as to whether these two species are separate or the same (Konovalov, pers. comm.; Reeve, pers. comm.), we have avoided the use of a species name.

Because *Mnemiopsis* inhabits the same depth range and utilizes the same food resources as *Aurelia aurita*, the large population of *Aurelia aurita* was nearly replaced by *Mnemiopsis* in 1989–1991. The average wet weight of *Aurelia aurita* dropped to 0.24 kg m^{-2} in September 1988 and 0.29 kg m^{-2} in September 1989 (Shushkina and Musayeva, 1990). The biomass of zooplankton such as *Sagitta*, *Paracalanus*, and *Acartia*, predated by *Mnemiopsis*, was 4.4 times lower in autumn 1989 than in the summer of 1978 (Vinogradov *et al.*, 1992). There was also a decrease in the anchovy catches of all the countries around the Black Sea, which coincided with the outburst of *Mnemiopsis* in 1989 (Caddy, 1993; GFCM, 1993).

The increase of *Mnemiopsis* started in the autumn of 1987, when the ctenophore spread from the northern coast of the Black Sea to the open sea, the mean biomass reaching 2 kg m^{-2} wet weight in the north-western area of the Black Sea in September 1988 (Shushkina and Vinogradov, 1991). The population of *Mnemiopsis* continued to increase rapidly. In the open sea the average total biomass was 3.5 kg m^{-2} in February 1989 (Shushkina and Vinogradov, 1991), and reached a maximum of about 4.7 kg m^{-2}, consisting of approximately 3000 mostly small individuals m^{-2}, in September 1989 in the north-western shelf area (Vinogradov *et al.*, 1992). In the autumn of 1989 a biomass of about 800 million tons wet weight of *Mnemiopsis* was estimated for the entire Black Sea (Vinogradov, 1990). After the spring of 1990 the biomass of *Mnemiopsis* in the open sea started to decrease from 3.8 kg m^{-2} to 0.1 kg m^{-2} in August 1990 (but still 1.5 kg m^{-2} in the coastal area around Gelendzik) and 0.6–0.8 kg m^{-2} in the spring of 1991 (Shushkina and Vinogradov, 1991).

Young specimens of *Mnemiopsis* occur the whole year round with a minimum in March/April and a peak in July/August. Their biomass is minimal in May/June and reaches its maximum in October/November. During winter the biomass remains high (Vinogradov *et al.*, 1992).

The aim of this study has been to monitor the further development of *Mnemiopsis*, *Aurelia aurita*, and *Pleurobrachia pileus* populations in the Black Sea for the years 1991–1993.

Material and methods

The distributions of *Mnemiopsis*, *Aurelia aurita*, and *Pleurobrachia pileus* in the Black Sea were studied during two joint cruises in June 1991 and in July 1992 and during an additional survey in the southern Black Sea in August 1993. In 1991 and 1992 the Institute of Biology of the Southern Seas (IBSS), Ukrainian Academy of Science, and the Institute of Marine Sciences (IMS), Middle East Technical University of Turkey, participated with their research vessels "Prof. Vodyanitsky" and "Bilim", respectively. The sampling in August 1993 was carried out with "Bilim". During the surveys each vessel worked in its own exclusive economic zone (EEZ).

All three species were collected using the Bogorov Rass net (Rass and Kazanova, 1966; used by IBSS) and the Hensen net (used by IMS). Samples were obtained by vertical hauls at 116 stations in 1991, 241 stations in 1992, and 134 stations in August 1993 (Fig. 2). Details of the nets and the sampling procedure are given in Table 1. The depth of the H_2S layer (according to sigma theta = 16.2; Tugrul *et al.*, 1992) was acquired by using a CTD probe (Seabird).

Regional classifications are as follows: inshore areas (<200 m depth), offshore areas (>200 m), western Black Sea (west of 35°E), and eastern Black Sea (east of 35°E). To estimate the biomass of the taxa for the total Black Sea area, sub-areas of 2 × 2 degrees latitude and longitude according to the GFCM (1993) grid for statistical purposes were chosen. The total biomass, the mean density for the whole Black Sea, and the standard deviation of the taxa were calculated using the methods for stratified sampling according to Saville (1977). The statistical significance of spatial and annual differences in the distribution of the species were tested with the U-test (Mann and Whitney, 1947; in Sokal and Rohlf, 1973).

An intercomparison for the sampling methods and for the catchability between the Hensen net and the Bogorov Rass net was made at two stations along the borderline of the EEZs in June 1991, and an additional comparison exercise was performed in the Turkish EEZ in August 1993. Both comparison exercises showed no significant differences in the catchability between the nets used. The variability between the nets was not higher than the variability in each single net.

Area of investigation

The Black Sea (423 000 km^2) is a deep basin with steep slopes of the order of 4–6°. A major shelf area exists only in its north-western region, comprising 27% of the total area of the Black Sea (Fig. 1). The shelf areas, especially in the south-eastern region of the Black Sea, are very narrow. The striking hydrodynamic

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

	Turkish EEZ RV "Bilim"	CIS EEZ RV "Prof. Vodyanitsky"
Number of stations (1991)	66	50
Number of stations (1992)	143	65
Number of stations (1993)	134	0
Net type and mesh size	Hensen 0.3 mm	Bogorov Rass 0.5 mm
Net opening diameter	70 cm	80 cm
Hauling speed	$1\ m\ s^{-1}$	$1\ m\ s^{-1}$
Depth recording	Angle and cable length	Angle and cable length
Sampling depth offshore		
Depth of haul in 1991	100 m→surface	100 m→surface
Depth of haul in 1992	*Anoxic layer→surface	100 m→surface
Depth of haul in 1993	Anoxic layer→surface	No sample
Sampling depth inshore		
by total depth <100 m	2 m above bottom→surface	
Evaluation of zooplankton	On board	On board
Convertion factor for 1 m²	2.6	2 and a filtration factor (1.6)
Presentation of results	Wet weight per m²; numbers per m²	
Investigated area (km²)		
June 1991	307 202	
July 1992	339 320	
August 1993	119 860	

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

features are the cyclonically meandering rim current together with two interior, western, and eastern gyres, and several mesoscale anticyclonic eddies (Oguz *et al.*, 1993; Oguz *et al.*, 1994). A permanent halocline exists at depths of 80–200 m (Oguz *et al.*, 1994). Below the halocline, hydrogen sulphide is present. Above the halocline, the salinity varies between S=18–18.5 in the central Black Sea. The areas between the rim current and coast have a lower salinity from S=17.5–18. In the western Black Sea the salinity drops below S=16 in near-shore areas due to the influence of the river Danube (Oguz *et al.*, 1993). In the open sea in summer the temperatures above the thermocline vary between 23–25°C, with a maximum of 27°C; the winter temperatures vary between 5–7°C, while in the north-western shelf area the temperature falls to 2°C in winter (Sur *et al.*, 1994).

Results

The overall results of the distributions of *Mnemiopsis*, *Aurelia*, and *Pleurobrachia* for each area investigated are

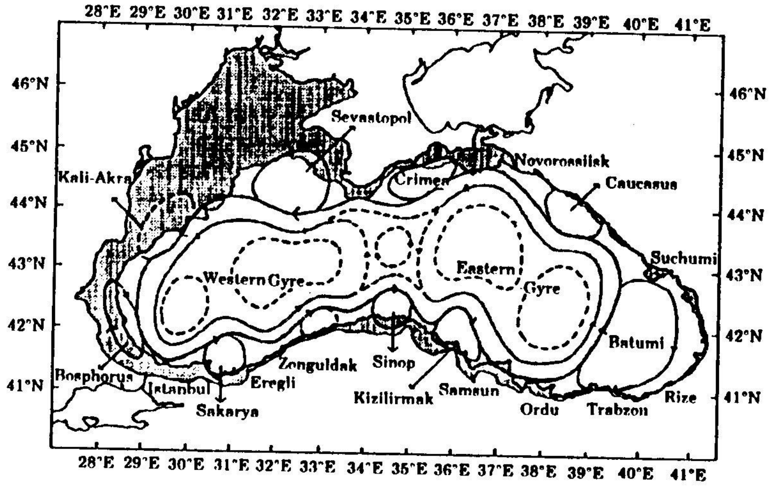

Figure 1. General circulation of surface currents in the Black Sea (redrawn from Oguz *et al.*, 1993). The bold line shows the rim current. Hatched area: shelf area with depth <200 m.

Table 2. Overall estimation of the abundance (numbers m^{-2}) and the biomass (wet weight: g m^{-2}) of *Mnemiopsis*, *Aurelia aurita*, and *Pleurobrachia pileus* in the Black Sea during 1991–1993. The biomass for the investigated area and for the total Black Sea (423 000 km^2) is presented as millions of tons.

	June 1991	July 1992	August 1993
Mnemiopsis sp.			
Maximum number of individuals (m^{-2})	89	546	371
Maximum wet weight (g m^{-2})	1040	1924	1430
Mean number of individuals (m^{-2})	12 ± 3	45 ± 11	38 ± 11
Mean wet weight (g m^{-2})	131 ± 35	192 ± 33	216 ± 35
Total biomass of the survey area (million tons)	40.3 ± 10.7	65.3 ± 11.0	25.9 ± 4.2
Estimated biomass for the total Black Sea (million tons)	55.400	81.216	91.368
Aurelia aurita			
Maximum number of individuals (m^{-2})	18	29	60
Maximum wet weight (g m^{-2})	2002	4380	1326
Mean number of individuals (m^{-2})	3 ± 2	5 ± 1	14 ± 2
Mean wet weight (g m^{-2})	86 ± 52	260 ± 68	222 ± 33
Total biomass of the survey area (million tons)	26.6 ± 15.9	88.3 ± 22.9	26.6 ± 4.0
Estimated biomass for the total Black Sea (million tons)	36.378	109.980	93.906
Pleurobrachia pileus			
Maximum number of individuals (m^{-2})	585	1638	1812
Maximum wet weight (g m^{-2})	988	871	1170
Mean number of individuals (m^{-2})	172 ± 23	436 ± 41	523 ± 44
Mean wet weight (g m^{-2})	100 ± 23	200 ± 21	264 ± 27
Total biomass of the survey area (million tons)	30.7 ± 6.9	67.8 ± 7.1	31.6 ± 3.2
Estimated biomass for the total Black Sea (million tons)	42.300	84.600	111.672

summarized in Table 2. The average number of individuals and the average biomass of each species were significantly lower in June 1991 than in July 1992 and August 1993. An average biomass of about 200–260 g m^{-2} was measured for all species in 1992 and 1993, about double that of June 1991.

Aurelia was least numerous (3–14 individuals m^{-2}), with highest numbers (172–523 individuals m^{-2}) belonging to *Pleurobrachia* (Table 2). The abundance of *Mnemiopsis* varied from 12–45 m^{-2}. Despite the differences in abundance the average biomass varied over a similar range for all species: 131–216 g m^{-2} for *Mnemiopsis*, 86–260 g m^{-2} for *Aurelia*, and 100–264 g m^{-2} for *Pleurobrachia*. The total biomass of these three dominant gelatinous species in the Black Sea amounted to 317 g m^{-2} in June 1991, increased to 652 g m^{-2} in July 1992, and to 702 g m^{-2} in August 1993.

Extrapolating these figures to the whole Black Sea area of 423 000 km^2, the biomass of each species was about 100 million tons in both 1991 and 1993 (Table 2). The total combined biomass was 134 million tons in June 1991, 276 million tons in July 1992, and 297 million tons in August 1993. For 1993 the estimate of biomass is approximate, since only the southern part of the Black Sea was investigated.

The spatial distribution of the individuals and the biomass of *Mnemiopsis*, *Aurelia*, and *Pleurobrachia* are shown in Figures 2–7. The figures for abundance and biomass values are also listed separately for the western and southern regions and for offshore and inshore areas in Table 3.

Mnemiopsis

In June 1991 *Mnemiopsis* was mainly distributed in waters between the outer edges of the rim current and the coast (19 individuals m^{-2}; Figs 2, 3; Table 3). High concentrations were observed in the near-shore anticyclonic eddies, namely the Sakarya, Sinop, Kizilirmak, Batumi, and Sevastopol eddies (see Fig. 1). The maximum wet weight observed (1040 g m^{-2}) was in the Sakarya eddy. In the centre of the Black Sea numbers of individuals and biomass were small (eight individuals m^{-2}), especially in the centre of the main eastern cyclonic gyre. The abundance and biomass were not significantly different between the western and eastern regions of the Black Sea (U-test, $p>0.05$).

In July 1992 the highest numbers of individuals and biomass were found in the eastern Black Sea, the average biomass for the whole eastern area (301 g m^{-2}) being about three times that of the western area (110 g m^{-2}). The abundances were about seven times greater in the eastern area (87 individuals m^{-2}) than in the western area (12 individuals m^{-2}). The area of main distribution in June 1991 had shifted from the western Sakarya region to the eastern Kizilirmak eddy region (station with maximum biomass of 1924 g m^{-2}) and to the offshore waters of Ordu (Figs 2, 3). In the eastern area large patches of *Mnemiopsis* were found offshore at the eastern and western edges of the main eastern cyclonic gyre. In contrast to June 1991, no significant difference was found between the inshore and offshore distribution of *Mnemiopsis* for the entire Black Sea.

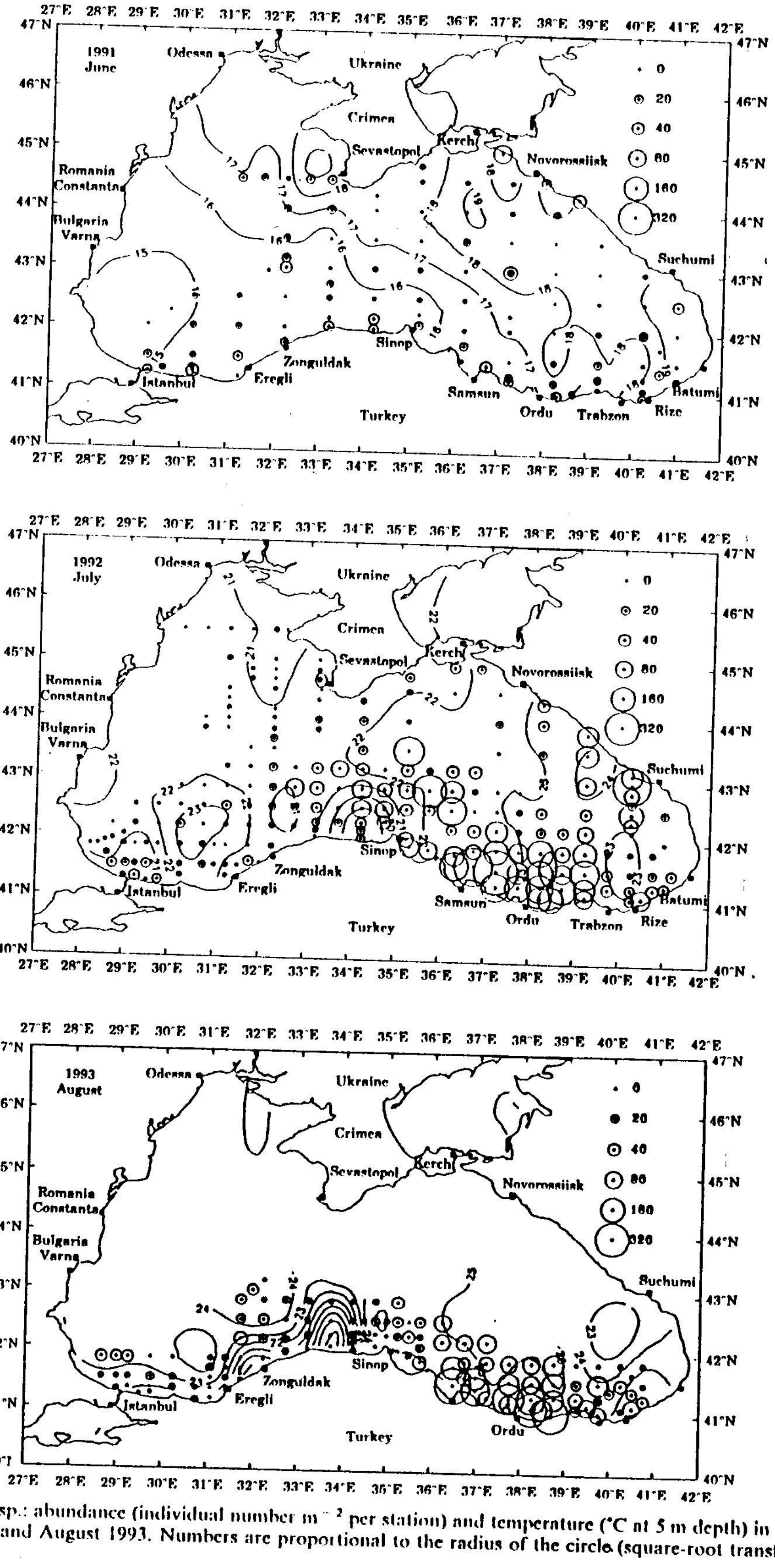

Figure 2. *Mnemiopsis* sp.: abundance (individual number m^{-2} per station) and temperature (°C at 5 m depth) in the Black Sea in June 1991, July 1992, and August 1993. Numbers are proportional to the radius of the circle (square-root transformation).

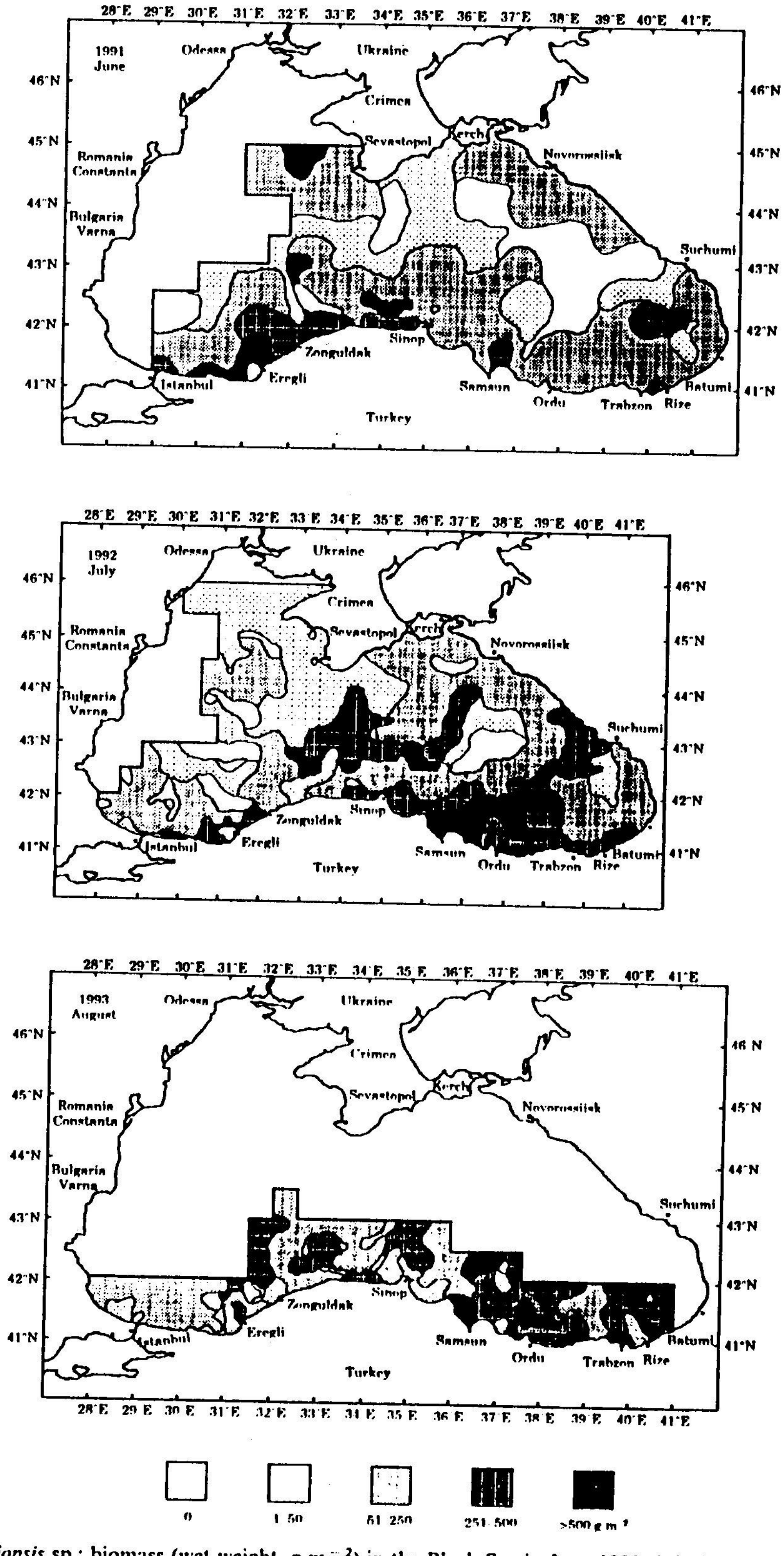

Figure 3. *Mnemiopsis* sp.: biomass (wet weight, g m^{-2}) in the Black Sea in June 1991, July 1992, and August 1993.

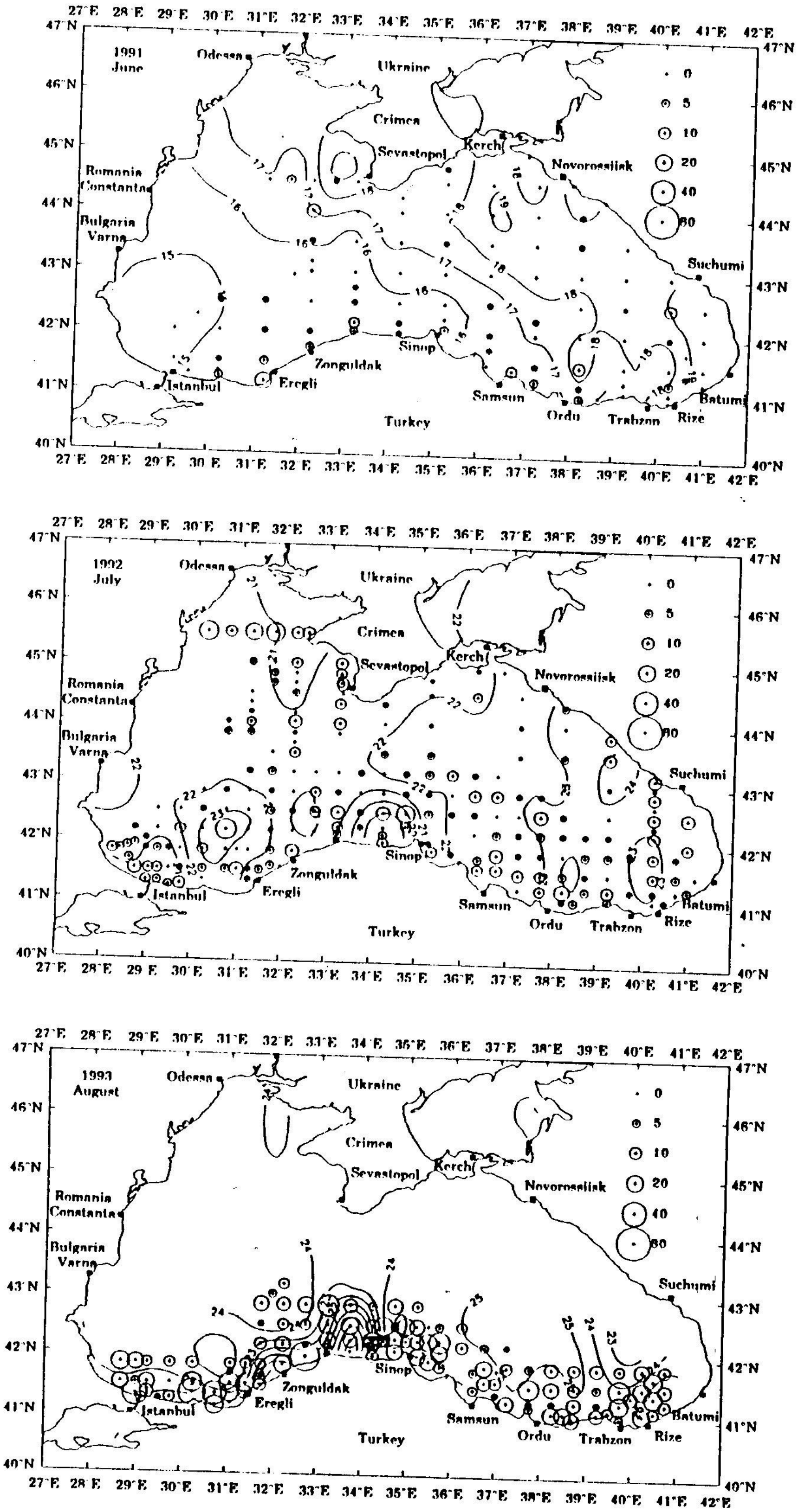

Figure 4. *Aurelia aurita*: abundance (individual number m^{-2} per station) and temperature (°C at 5 m depth) in the Black Sea in June 1991, July 1992, and August 1993. Numbers are proportional to the radius of the circle (square-root transformation).

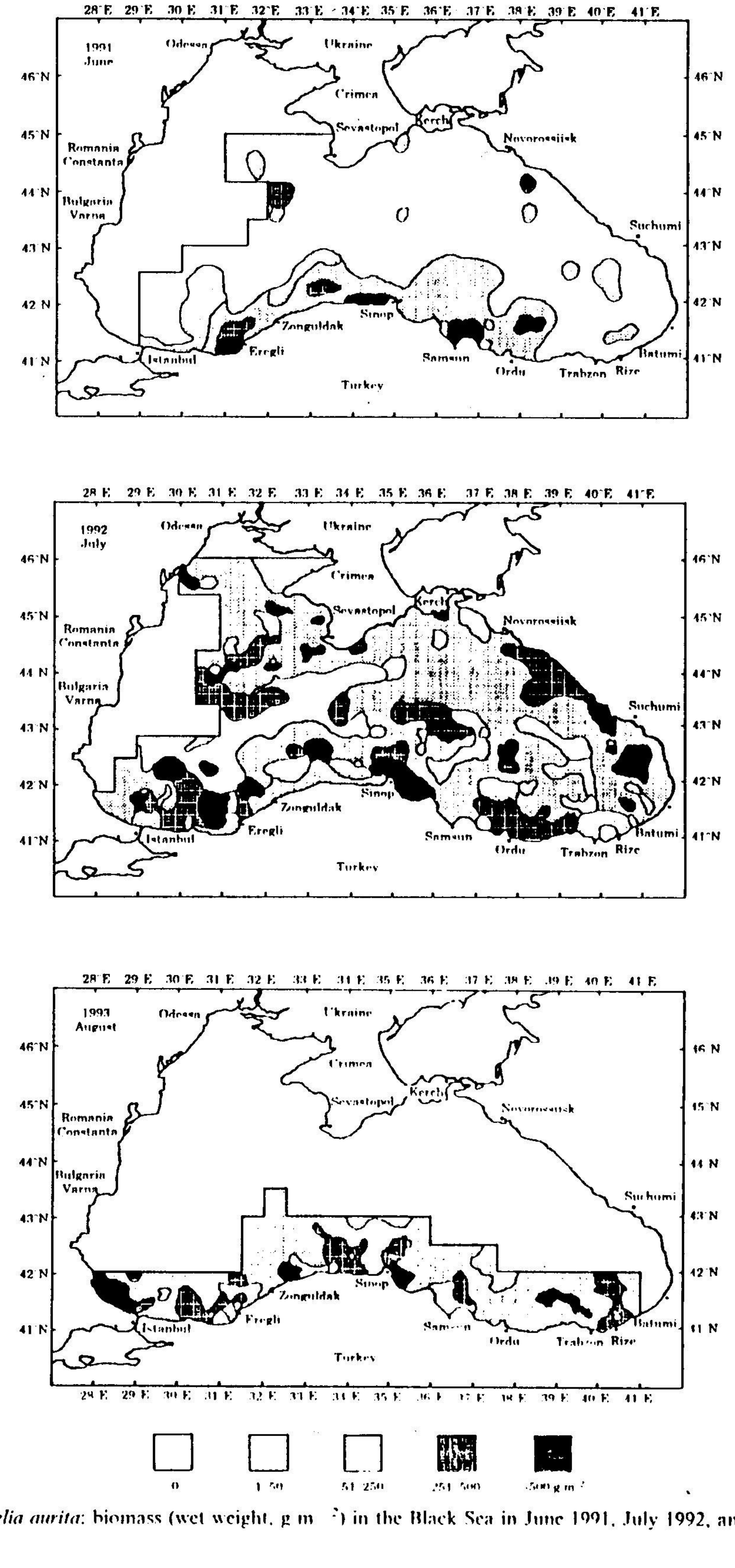

Figure 5. *Aurelia aurita*: biomass (wet weight, g m^{-2}) in the Black Sea in June 1991, July 1992, and August 1993.

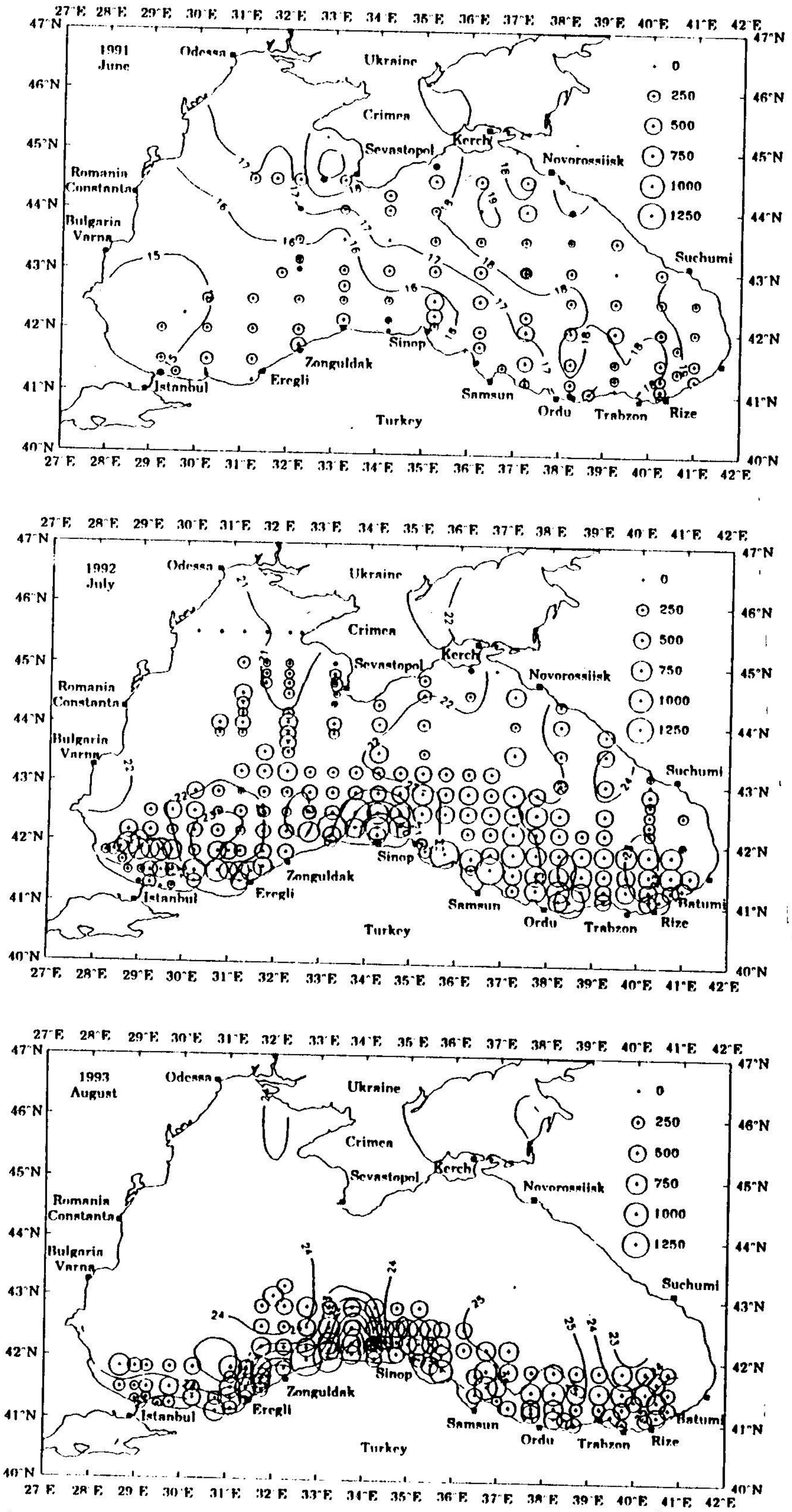

Figure 6. *Pleurobrachia pileus*: abundance (individual number m^{-2} per station) and temperature (°C at 5 m depth) in the Black Sea in June 1991, July 1992, and August 1993. Numbers are proportional to the radius of the circle (square-root transformation).

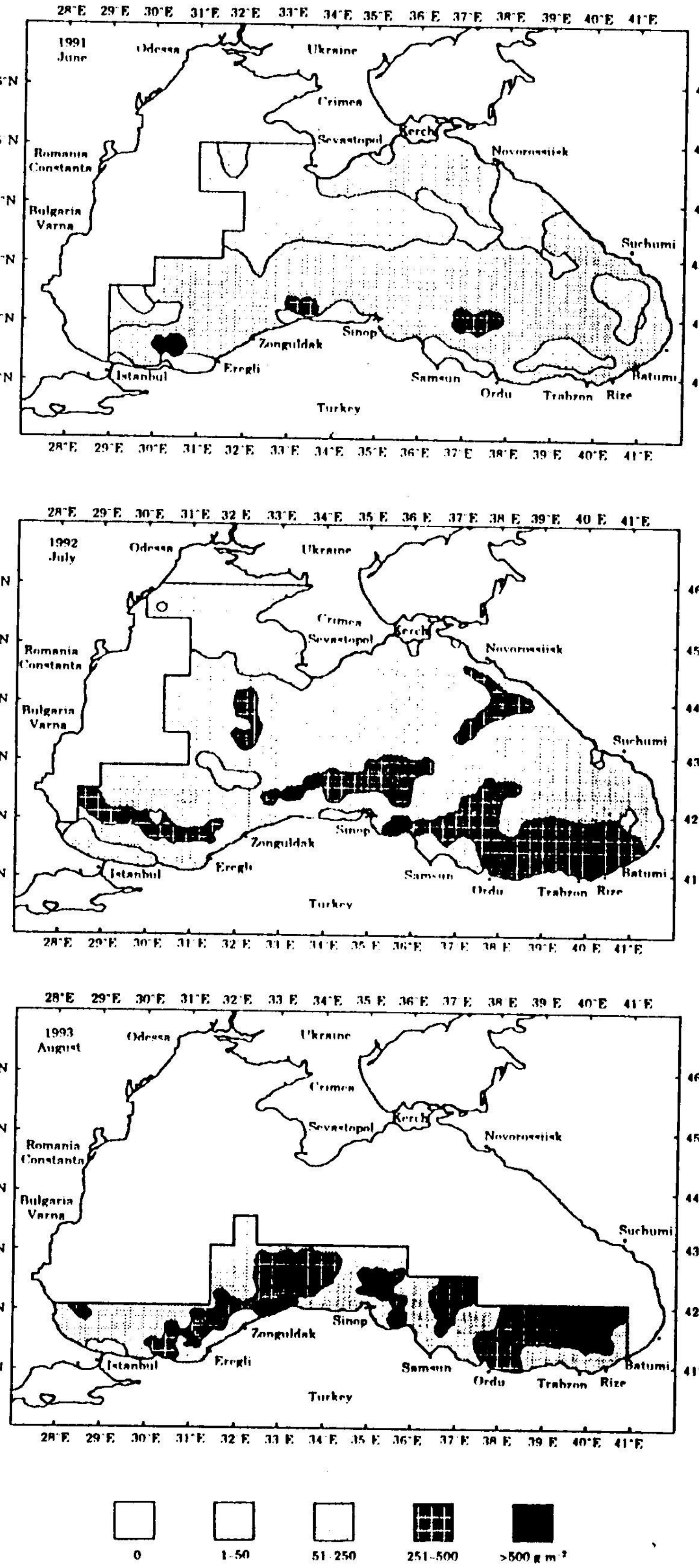

Figure 7. *Pleurobrachia pileus*: biomass (wet weight, g m^{-2}) in the Black Sea in June 1991, July 1992, and August 1993.

Table 3. Abundance and biomass of *Mnemiopsis*, *Aurelia aurita*, and *Pleurobrachia pileus* in the western and eastern area and in inshore and offshore areas of the Black Sea during 1991–1993. **Bold** numbers: significantly different (U-test, $p<0.05$).

	Western part						Eastern part						Total Black Sea			
	Inshore		Offshore		Total		Inshore		Offshore		Total		Inshore		Offshore	
	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}	n m^{-2}	g m^{-2}
Mnemiopsis																
June 1991	**19**	**345**	**8**	**98**	12	186	**19**	**142**	**8**	**68**	12	94	**19**	**227**	**8**	**80**
July 1992	6	72	15	128	**12**	**110**	**145**	**495**	**66**	**234**	**87**	**301**	58	229	39	177
August 1993	7	104	11	143	**10**	**133**	68	238	78	341	**77**	**329**	**24**	**140**	**42**	**235**
Aurelia																
June 1991	4	146	2	41	3	78	6	134	2	71	3	92	5	139	2	59
July 1992	**7**	203	**4**	260	5	241	5	482	4	217	5	286	**6**	306	**4**	240
August 1993	15	280	15	209	15	227	18	338	13	194	13	215	14	303	14	202
Pleurobrachia																
June 1991	117	127	156	86	141	101	**122**	**87**	**231**	106	192	100	**120**	103	**201**	98
July 1992	**208**	**82**	**460**	**218**	**376**	**172**	514	230	515	238	**515**	**236**	**321**	**137**	**485**	**227**
August 1993	**391**	**155**	**547**	**299**	508	264	**332**	**113**	**572**	**285**	542	264	**375**	**143**	**558**	**292**
Number of stations																
June 1991	15		27		42		21		40		61		36		67	
July 1992	39		78		117		23		66		89		62		144	
August 1993	19		58		77		7		50		57		26		108	

Only in the eastern area was the abundance and biomass of *Mnemiopsis* significantly higher for inshore waters.

In August 1993 the main area of distribution of *Mnemiopsis* shifted further to the east (Figs 2, 3), and in the region off Trabzon many small patches of *Mnemiopsis* occurred. In this region the station with the maximum biomass of 1430 g m^{-2} was found. The abundance (77 individuals m^{-2}) and biomass (329 g m^{-2}) of *Mnemiopsis* in the eastern area were in the same range as in 1992 (Table 3). In the western area *Mnemiopsis* was only present with a high biomass in two coastal regions (Sakarya and Sinop eddy). However, the abundance (10 individuals m^{-2}) and biomass (133 g m^{-2}) of *Mnemiopsis* for the whole western area had not changed from 1992 (12 individuals; 110 g m^{-2}). However, the biomass of *Mnemiopsis* was higher offshore (235 g m^{-2}) than inshore (140 g m^{-2}) in August 1993 than in 1991–1992 (Table 3).

Aurelia aurita

In June 1991 *Aurelia* was found to be mainly distributed in the southern inshore area of the Black Sea (Figs 4, 5). The locations of dense patches were well correlated with the anti-cyclonic (Sakarya, Sinop, and Kizilirmak) eddies, as already seen in the distribution of *Mnemiopsis*. In the northern Black Sea only two patches of *Aurelia* occurred, one off Novorossiisk and one south-west of the Crimea. The central Black Sea was virtually devoid of *Aurelia* in this season. Overall, the distribution of individuals and biomass did not differ between the western and eastern Black Sea (Table 3).

In July 1992, *Aurelia* was distributed over a wider area, with patches of high abundance and biomass being found throughout the entire basin (Figs 4, 5). Areas of low biomass existed at the centres of the western and eastern cyclonic gyres. As in 1991 the biomass and abundance were the same for the eastern and western areas, with highest abundances occurring in the western inshore areas (inshore: seven individuals m^{-2}; offshore four individuals m^{-2}; Table 3).

In August 1993 the main patches of *Aurelia* were present at the fronts of the anticyclonic eddies (Figs 4, 5). Whilst the abundance showed a three-fold increase from July 1992 (five individuals m^{-2}) to August 1993 (14 individuals m^{-2}), the total biomass remained unchanged (220 g m^{-2}), indicating the occurrence of a high number of small animals (Table 3). No statistical differences in abundance and biomass were found either between the western and eastern areas or between the inshore and offshore areas in 1993.

By comparing the distribution of abundance and biomass for *Aurelia* and *Mnemiopsis*, it is evident that in areas where *Aurelia* occurred in dense patches the abundance and biomass of *Mnemiopsis* was reduced, and vice versa (Figs 2–5).

Pleurobrachia pileus

In June 1991 the main patches of *Pleurobrachia* were found at the northern edges of the anticyclonic eddies (Sakarya, Kizilirmak eddy, and the eddy off Zonguldak) in the southern Black Sea (Figs 6, 7). No differences in abundance and biomass were obvious for the western and eastern Black Sea. Unlike the previously mentioned species, *Pleurobrachia* was present more frequently offshore (201 individuals m^{-2}) than inshore (120 individuals m^{-2}). However, the biomass of *Pleurobrachia* was not significantly different between offshore and inshore areas and varied from 86–106 g m^{-2} in June 1991 (Table 3).

In July 1992 the biomass of *Pleurobrachia* increased 1.5–2 times and the abundance increased by a factor of 2–3 in different areas of the Black Sea compared with 1991 (Table 3). Overall, the biomass and abundance of *Pleurobrachia* was significantly higher in the eastern area (515 individuals m^{-2}; 238 g m^{-2}) than in the western area of the Black Sea (376 individuals m^{-2}; 172 g m^{-2}). The main areas of distribution were found in the southern Black Sea at the northern edge of the anticyclonic eddies (Figs 6, 7). In the eastern Black Sea high abundances were also found in inshore areas off Ordu to Batumi. While no differences occurred between eastern inshore and offshore areas, the abundance and biomass was much higher offshore (460 individuals m^{-2}; 218 g m^{-2}) than inshore (208 individuals m^{-2}; 82 g m^{-2}) in the western Black Sea.

In August 1993 the bulk of *Pleurobrachia* was again distributed along the rim current, with highest densities in the open sea, but some patches extended to coastal areas (Figs 6, 7). The abundance and biomass were higher offshore than inshore. In offshore areas an average number of 558 individuals m^{-2} with an average biomass of 292 g m^{-2} was found (Table 3), and in inshore areas an average of 375 individuals m^{-2} with a biomass of 143 g m^{-2} was recorded. No difference in the distribution of *Pleurobrachia* was found for the western and eastern Black Sea.

Discussion

The estimated biomasses of *Mnemiopsis*, *Aurelia*, and *Pleurobrachia* for the whole of the Black Sea must be considered as approximate, since the western Black Sea and the north-western shelf area were either omitted, or only sparsely covered during the surveys. In the case of *Pleurobrachia*, estimates at some stations are only semi-quantitative because sampling depth was limited to 100 m for the entire sampling area in June 1991 and for the northern sampling area (EEZ of CIS) in July 1992. Thus, the sampling depth was not sufficient to catch *Pleurobrachia* quantitatively in the downwelling regions that occur in coastal areas where the main distribution of *Pleurobrachia* is below 100 m (Vinogradov *et al.*, 1985).

The distributions of *Mnemiopsis* (Figs 2, 3) and *Aurelia* (Figs 4, 5) follow the hydrographic features of the Black Sea (Fig. 1). High concentrations were always found at the edges of the anticyclonic gyres, while the centres of the western and eastern cyclonic gyres were generally poor in terms of biomass. The more homogeneous distribution of the deeper-dwelling *Pleurobrachia* could be related to the fact that the currents in these deeper layers are less pronounced than those in surface layers (Oguz *et al.*, 1993).

According to observations during 1988–1992, the mass spawning of *Mnemiopsis* is triggered by sea surface temperatures of about 23°C (Zaika, unpublished data). During the survey in June 1991 the water temperatures in the upper 5 m varied between 15–17°C in the western area and 17–21°C in the eastern area; no mass development of *Mnemiopsis* could therefore be expected at that time. However, water temperatures at 5 m depth in excess of 22°C in July 1992, and above 25°C in August 1993, were high enough for spawning. This was especially true in the eastern Black Sea where higher surface temperatures and dense patches of *Mnemiopsis* were observed (Figs 2, 3).

The higher abundance and biomass of *Aurelia* and *Mnemiopsis* in inshore waters, compared with offshore regions in June 1991 (Table 3, Figs 2–5), indicate that reproduction starts in coastal areas, which warm up earlier. Currents and a subsequent increase in temperature cause an expansion of the populations towards open waters. According to Vinogradov *et al.* (1992) the mass reproduction of *Mnemiopsis* and *Aurelia* is mainly confined to inshore waters of the Black Sea. *Pleurobrachia* did not show this pattern as clearly as the above-mentioned species during 1991–1993 (Figs 6, 7), but similarly in the North Sea reproduction takes place in coastal areas which warm up earlier than the open sea (Greve and Reiners, 1988).

The expansion of *Mnemiopsis* in the Black Sea from 1990–1993 could be related to the general route of the rim current (Fig. 1). With a speed of 0.2–0.3 m s^{-1} it is possible that the bulk of *Mnemiopsis* is carried about 20 km a day. In April 1990 a very high biomass (3 kg m^{-2}) with maximum values of 12 kg m^{-2} was found in the western Black Sea off Bulgaria (Vinogradov *et al.*, 1992). The area with the highest abundance and biomass of *Mnemiopsis* shifted eastward from the Sakarya area (in 1991) along the Turkish coast to the region off Ordu and Trabzon during 1991–1993 (Figs 2, 3). One reason for the high abundance of *Mnemiopsis* in the coastal regions off Samsun and Trabzon in 1992 and 1993 could be the combined effect of high temperature and river discharge, which leads to increased eutrophication in these areas (unpubl. data, Institute of Marine Sciences).

Our surveys were carried out in three subsequent years during three different months (June 1991, July 1992, August 1993). Consequently, it is difficult to evaluate the results fully since the abundance of *Mnemiopsis* sp. and *Aurelia aurita* shows great seasonal and annual fluctuations (Shushkina and Vinogradov, 1991; Volovik *et al.*, 1993). Despite this we have compared the results to former findings to get an overall view.

During the surveys in the summers of 1992 and 1993 a biomass of *Mnemiopsis* in the range of 200 g m^{-2} (total 55–91 million tons) was present for the whole Black Sea (Table 2). Compared to the high biomass of 2000 g m^{-2} in offshore regions and the huge biomass of 4500 g m^{-2} in the western Black Sea during the *Mnemiopsis* outbreak in 1989 (Shushkina and Vinogradov, 1991), the biomass had declined about 10-fold since the spring of 1990 (Fig. 8). This sequence exhibits the typical pattern of a new colonizer: after the explosion in 1988 until spring 1990 the numbers and biomass of *Mnemiopsis* fell in the summer of 1990 and remained at a moderate level during 1991–1993. Whether this decrease in *Mnemiopsis* is related to a reduction in its prey organisms since 1989 (Shushkina and Vinogradov, 1991), to the different environmental conditions compared with the original habitat, or due to parasites or disease, cannot as yet be stated.

The biomass of *Aurelia* (around 100 million tons; Table 2) was about four times lower during 1991–1992 than the stock estimates of 400 million tons for the whole of the Black Sea from 1978–1988 (Gomoiu, 1981). The explosion of *Mnemiopsis* caused a fall in the population of *Aurelia* in 1988 (Shushkina and Vinogradov, 1991). *Aurelia* and *Mnemiopsis* inhabit the same layer above and around the thermocline and compete for the same planktonic food. Since *Mnemiopsis* has a faster generation time and a higher production rate than *Aurelia* it was presumably successful in depressing *Aurelia* in the first two years (Kideys, 1994). After the decrease of *Mnemiopsis* in summer 1990 the biomass of *Aurelia* again increased, and since summer 1991 the biomass of both species has remained at the same level (Fig. 8).

If the biomass of *Mnemiopsis* and *Aurelia* are expressed in terms of carbon content, the increase in biomass of *Aurelia* after the main peak of *Mnemiopsis* in August 1989 is more apparent. According to Shushkina and Vinogradov (1991), 1 g wet weight is equivalent to 0.003 g carbon in *Aurelia* and 0.0007 g carbon in *Mnemiopsis*. During the explosion of *Mnemiopsis* the biomass of *Aurelia aurita* was about one half and one third (0.87 and 0.38 g carbon m^{-2}) of the biomass of *Mnemiopsis* (1.4 and 1.1 carbon m^{-2}) in August 1989 and in April 1990, respectively. After the decrease of *Mnemiopsis* the biomass of *Aurelia* was four–six-fold higher (0.78 and 0.67 g carbon m^{-2}) than that of *Mnemiopsis* (0.13–0.15 g carbon m^{-2}) in July 1992 and

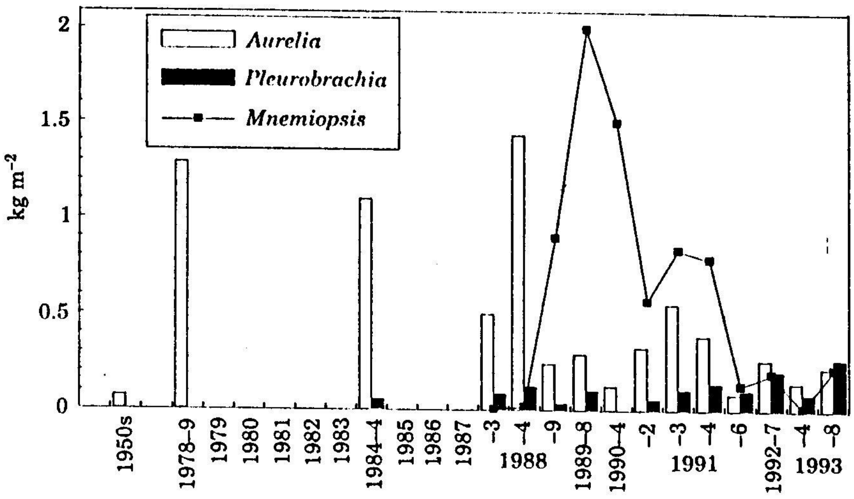

Figure 8. Fluctuation of the biomass (wet weight kg^{-2}) of *Mnemiopsis* sp., *Aurelia aurita*, and *Pleurobrachia pileus* in offshore areas of the Black Sea from 1958–1993. References: biomass of *Aurelia aurita* of 1950s, Shushkina and Musayeva (1983); biomass from 1958–April 1993, Shushkina and Vinogradov (1991, Table 2); biomass from April 1993, Mutlu (IMS), western Black Sea (49 stations), unpublished data; biomass from June 1991, July 1992, and August 1993, present survey.

August 1993. The reduction in the biomass of *Aurelia* during 1989–1993 was not so severe that the levels fell to those of the 1950s and early 1960s, when the total wet weight was about 30 million tons for the whole of the Black Sea (Shushkina and Musayeva, 1983), equivalent to 70 g m^{-2} wet weight or 0.21 g carbon m^{-2}.

The population of *Pleurobrachia* seemed not to be affected by *Mnemiopsis* since there is no competition between these species, *Pleurobrachia* inhabiting the deeper layers below the thermocline (Vinogradov *et al.*, 1985). *Pleurobrachia* remained at the same biomass level of 100 g m^{-2} during the epidemic of *Mnemiopsis* (Shushkina and Vinogradov, 1991). During our surveys in July 1992 and August 1993 the biomass of *Pleurobrachia* was in the same range of about 200–260 g m^{-2} as *Mnemiopsis* and *Aurelia* (Fig. 8).

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