Marine Biology (1999) 135: 589–601 © Springer-Verlag 1999

E. Mutlu · F. Bingel

Distribution and abundance of ctenophores, and their zooplankton food in the Black Sea. I. *Pleurobrachia pileus*

Received: 1 November 1997 / Accepted: 30 August 1999

Abstract The distribution of *Pleurobrachia pileus* Müller, 1776 in the Black Sea was determined using plankton samples collected above the anoxic zone (maximum of 200 m) in the winter, spring, and summer of 1991 to 1995. The summer samples were collected in 1991 to 1993 (for a previous) and are included in this paper for comparative purposes. High concentrations of *P. pileus* were found at the northern edges of anticyclonic eddies along the southern coastal regions. The biomass and abundance of *P. pileus* increased from winter through spring to a peak in summer. The highest mean wet weight during a sampling period was 250 g m^{-2}, while the maximum wet weight was 1429 g m^{-2}. *P. pileus* was mostly found in a layer extending from the lower parts of the thermocline down to the anoxic zone, where the temperature was < 8 °C. The vertical distribution of *P. pileus* biomass had two clear maxima at night: an upper maximum at 20 to 40 m was less pronounced than the lower maximum at 90 to 120 m depth. Mean body length of *P. pileus* did not exceed 12 mm. Smaller individuals (9 to 10 mm length) occurred in winter. *P. pileus* had two length classes in early spring (March 1995) and late summer (August 1993), indicating the presence of both newly hatched and larger individuals. Overall, the stomach contents of *P. pileus* consisted mainly of Copepoda (90%), Cladocera (1%), Mollusca (1%), fish eggs and larvae (1%), and other taxa (7%). The preferred food of *P. pileus* (frequency of occurrence) was: *Calanus euxinus* (39%), *Pseudocalanus elongatus* (30%), *Acartia clausi* (28%), *Oithona similis* (2%), and *Paracalanus parvus* (1%). The endoparasite *Hysterothylacium aduncum* was commonly found in *P. pileus*. Abundances of *Mnemiopsis leidyi* and *P. pileus* were either negatively correlated ($r = -0.5$ to -0.7) or positively correlated at a low significance level ($r = 0.25$ to 0.3) with abundance of *A. clausi* in different months of the year. *Aurelia aurita* abundance was correlated mainly with the abundance of *C. euxinus* from June 1991 to March/April 1995. Over the same period the abundance of *P. pileus* was significantly correlated with the abundance of *P. elongatus*, an important prey species.

Communicated by J.P. Grassle, New Brunswick

E. Mutlu (✉) · F. Bingel
Institute of Marine Sciences,
Middle East Technical University,
P.O. Box 28, TR-33731, Erdemli-İçel, Turkey

Introduction

The drastic changes in the ecosystem of the Black Sea after the introduction of *Mnemiopsis leidyi* in the early 1980s have stimulated numerous recent studies. Plankton studies in the Black Sea have mainly dealt with horizontal and vertical distributions, morphology, trophic relationships, predation, ecological roles, and methods for controlling the *M. leidyi* population (Shushkina and Musayeva 1983; Vinogradov et al. 1989; Zaika and Sergeeva 1991; Harbison and Volovik 1993; Zaitsev 1993; Lebedeva and Shushkina 1994). Early efforts to study gelatinous zooplankton by the Commonwealth of Independent States (CIS) date back to the mid-1980s, with additional studies since the end of the 1980s. Vinogradov et al. (1985) first reported the extensive vertical distribution of *Pleurobrachia pileus* in the open water of the Black Sea. Following this, researchers from the CIS focused on various sectors of the Black Sea, especially the Novorosyisk, Odessa, Sevastopol, and Crimean coasts, and the open Black Sea (Vinogradov et al. 1989; Shushkina and Musayeva 1990a, b; Vinogradov 1990; Shushkina and Vinogradov 1991a, b; Zaika and Sergeeva 1991; Vinogradov et al. 1992; Volovik et al. 1993).

There were no studies of the Turkish region of the Black Sea until Mutlu et al. (1994) described the spatial distributions of gelatinous zooplankton in this area in June 1991, July 1992, and August 1993. This study found that the average biomasses of *Mnemiopsis leidyi*, *Pleurobrachia pileus*, and *Aurelia aurita* were approximately the same (200 g wet wt m^{-2}) in 1992 and 1993. *P. pileus* biomass doubled between 1990/91 and 1993.

The present study was conducted to fill the gap in the knowledge about the recent ecological state of *Pleurobrachia pileus* in the southern Black Sea and to compare these data to those for the rest of the Black Sea, since most researchers ignored this species while focusing on *Mnemiopsis leidyi*. *P. pileus*, like *M. leidyi*, is an important predator on the copepod community. The objective of the present study was to determine the vertical and horizontal distribution, and the temporal fluctuation in biomass and abundance of the plankton caught in net tows, especially the gelatinous zooplankton. The biometry of *P. pileus*, spatio-temporal and vertical size composition of the population, stomach contents, occurrence of parasites, and the abundance in relation to the abundance of other zooplankton species were examined.

Materials and methods

Samples for studying the distribution of *Pleurobrachia pileus* Müller, 1776 in the Black Sea were collected in the winter (January 1992 and February 1994), spring (April 1993, May 1994, March 1995), and summer (June 1991, July 1992, August 1993). The areas investigated during the winter and summer surveys were restricted to the Turkish Exclusive Economic Zone (TEEZ; Fig. 1), but spring cruises also included the Bulgarian and Romanian EEZs. Data from the summer cruises were published previously (Mutlu et al. 1994), but they are included here for comparison with data for the winter and spring.

The horizontal distribution (abundance and biomass) of *Pleurobrachia pileus* was studied by collecting the ctenophores with a Hensen net (0.7 m net diameter, 300 μm mesh). Samples were obtained by hauling the net at each station vertically from above the anoxic zone to the surface. The depth of the H_2S layer (according to sigma theta, $\delta = 16.2$; Tugrul et al. 1992) was determined with a SeaBird CTD. To estimate the diel vertical distribution of the organisms, a single Nansen opening–closing net (0.7 m net diameter, 200 μm mesh) was used. A series of discrete vertical hauls was made at a speed of 1 cm s^{-1} from the top of the anoxic layer to the surface (0 to 150 m) at 15-m intervals in August 1993 and March 1995. In addition, more than ten dives were conducted at four stations in July 1992 and August 1993, using the Benthos Inc., Mini-ROVER (Remotely Operated Vehicle), equipped with a PAL-color video camera. Further, live specimens of *P. pileus* were collected outside the harbor of the Aquatic Resources Research Institute in Yomra-Trabzon in September 1993 to establish biometric relationships for the species (Table 1).

On board ship, gelatinous organisms were separated from the other meso-zooplankton using a 2-mm mesh sieve. The total number of individuals and total wet weight of *Pleurobrachia pileus*, measured with a simple hand balance, were determined. Body lengths and widths of individuals were measured with a millimeter scale and individual displacement volumes (ml) were determined in finely graded cylinders. *P. pileus* were classified into three different size classes (< 10 mm, 10 to 20 mm, and > 20 mm). Monthly length-frequency distributions were sorted into 2-mm length classes.

Gelatinous organisms were preserved in 5% formalin buffered with borax. Preservation was good although there was some shrinkage in size and weight loss (Mutlu 1996). In the laboratory, stomach contents of 27 424 individuals of *Pleurobrachia pileus* were examined. The gastrovascular cavity of each specimen was dissected under a stereoscopic binocular microscope by making an incision with a dissecting needle from the mouth through the cavity. Stomach contents were identified to the lowest possible taxonomic level and individual food items were enumerated. The frequency of occurrence and numerical abundance (Holden and Raitt 1974) were calculated to provide estimates of the qualitative and quantitative importance of the prey. The presence and abundance of the endoparasitic nematode *Hysterothylacium aduncum* (Køie 1993) in ctenophores were also recorded.

The study area was divided into seven sub-regions in order to test for differences (using the non-parametric Kruskal–Wallis test) in abundance, biomass, and size distribution: on-shelf or inshore areas (< 200 m depth), off-shelf or offshore (> 200 m), western Black Sea (west of 35°E), eastern Black Sea (east of 35°E) in the TEEZ (below 43°N in the western Black Sea), and in the EEZs of other riparian Black Sea countries (Bulgaria, Romania, and Ukraine) lying above 43°N in the western Black Sea (Fig. 1).

Abundances of the gelatinous species (*Mnemiopsis leidyi*, *Pleurobrachia pileus* and *Aurelia aurita*) and the abundances of copepods, ichthyoplankton, chaetognaths, and phytoplankton etc. were subjected to a non-parametric Spearman's rank correlation

Fig. 1 General circulation of surface currents in the Black Sea (redrawn from Oguz et al. 1993). Area below the bold line is the Turkish Exclusive Economic Zone (TEEZ) (*hatched area* shelf area with depth < 200 m)

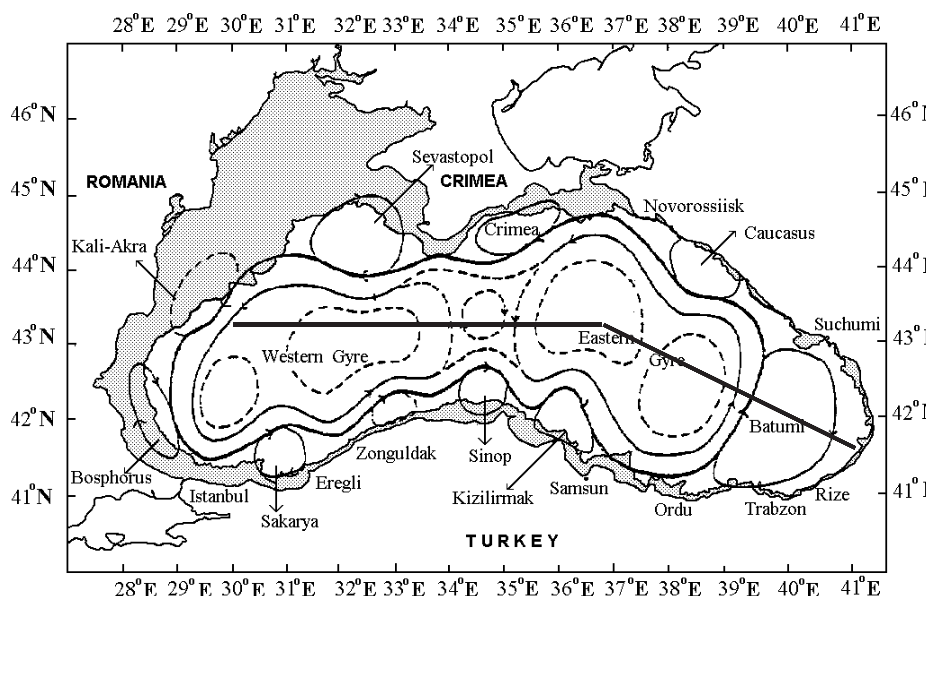


Table 1 Purpose of gelatinous zooplankton studies and number of stations in the sampling periods

	Number of stations for sampling depth:							
	100 m to surface		Anoxic layer					
	Jun 1991	Jan 1992	Jul 1992	Apr 1993	Aug 1993	Feb 1994	May 1994	Mar 1995
Horizontal abundance and biomass	68	74	143	50	152	73	85	107
Vertical abundance and biomass					1			1
Visual inspection			2		2			
Horizontal size distribution		33	44		22	57	41	45
Vertical size distribution					1			1
Biometry					1			
Stomach content and parasites			15	12	60	38	32	41
Correlation structure	68	74	143	50	152	73	85	107

analysis (Sokal and Rohlf 1968). Abundances of copepods, ichthyoplankton, chaetognaths, etc. were obtained from unpublished data from the Institute of Marine Sciences, Middle East Technical University (IMS-METU).

Results

Biomass and abundance

Horizontal distribution

The spatial distribution of *Pleurobrachia pileus* in the Black Sea was not closely related to the general surface circulation. Instead, the main concentrations of *P. pileus* were found at the northern peripheries of anticyclonic eddies in the TEEZ (Figs. 2, 3). The mean wet weight of *P. pileus* at the study sites never exceeded 250 g m^{-2}, while the maximum wet weight (1429 g m^{-2} off Ordu) was recorded for June 1991 and March 1995 (Table 2; Fig. 2). In contrast to the winter distribution, the mean biomass and abundance were significantly higher in the eastern than western Black Sea in summer. The TEEZ had higher biomass and abundance than the Bulgarian, Romanian, and Ukrainian EEZs (Table 3; Figs. 2, 3).

Vertical distribution

Pleurobrachia pileus exhibited a well-marked diel migration in response to daily light conditions. During the day, *P. pileus* was found mostly below the thermocline down to the anoxic layer, where the temperature was <8 °C. The distribution pattern of the total biomass of *P. pileus* throughout the oxygenated zone of the open Black Sea showed two peaks in biomass, most clearly observed at night. In August 1993, the upper peak at 20 to 40 m depth had lower abundances than the lower maximum at 90 to 120 m depths during the day, while the layer between 70 and 90 m was devoid of *P. pileus*. At midnight and before dawn, abundance peaked both at 30 m and in a layer at 70 to 100 m, being more abundant at 30 m. In the deeper layer, *P. pileus* abundance apparently increased between midnight and dawn, and remained high at 10:00 hrs. During this period, most individuals were in the halocline. Early in the morning, some individuals seemed to ascend to the surface at 15 to 30 m. A significant proportion of individuals was aggregated in the upper 15 m in the evening (Fig. 4). In March 1995, 70 to 80% of total biomass and abundance of *P. pileus* was encountered below the cold intermediate layer during the night. During day there is only a slight indication of vertical aggregation. By night, most of the individuals were concentrated between 90 and 130 m, where the water temperature was constant at about 7 °C (Fig. 4).

Visual observations of vertical distribution

Using a mini-ROVER underwater video-camera, marine snow in high concentration was observed at 3 m and 30 to 40 m (12:00 hrs in July 1992; 13:30 hrs in August 1993; Fig. 5). The deeper layer overlapped with the upper portion of the Cold Intermediate Layer (temperature <8 °C, CIL). *Pleurobrachia pileus* was present in the upper portion of the thermocline (10 to 12 m), but there were few individuals with extended tentacles (12:00 hrs in July 1992; 13:30 hrs in August 1993; Fig. 5). Below this layer between 20 and 25 m, *P. pileus* had their tentacles retracted. At 10 to 25 m depth at deep stations, *Aurelia aurita* and *Mnemiopsis leidyi* were also present. In August 1993 thermocline depths were different at deep and shallow stations. Only *M. leidyi* and *A. aurita* were present above the CIL at deep stations, whereas at shallow stations *P. pileus* (with retracted tentacles) and *A. aurita* were found. In the pycnocline (70 to 110 m), high abundances of *P. pileus* with extended tentacles were observed. Below 110 m and down to 140 m, *P. pileus* was found very rarely and all individuals had retracted tentacles (Fig. 5).

Temporal fluctuations

The abundance and biomass of *Pleurobrachia pileus* peaked in summer (411 ind. m^{-2} and 204 g m^{-2}; means for three summers), being about four times higher than

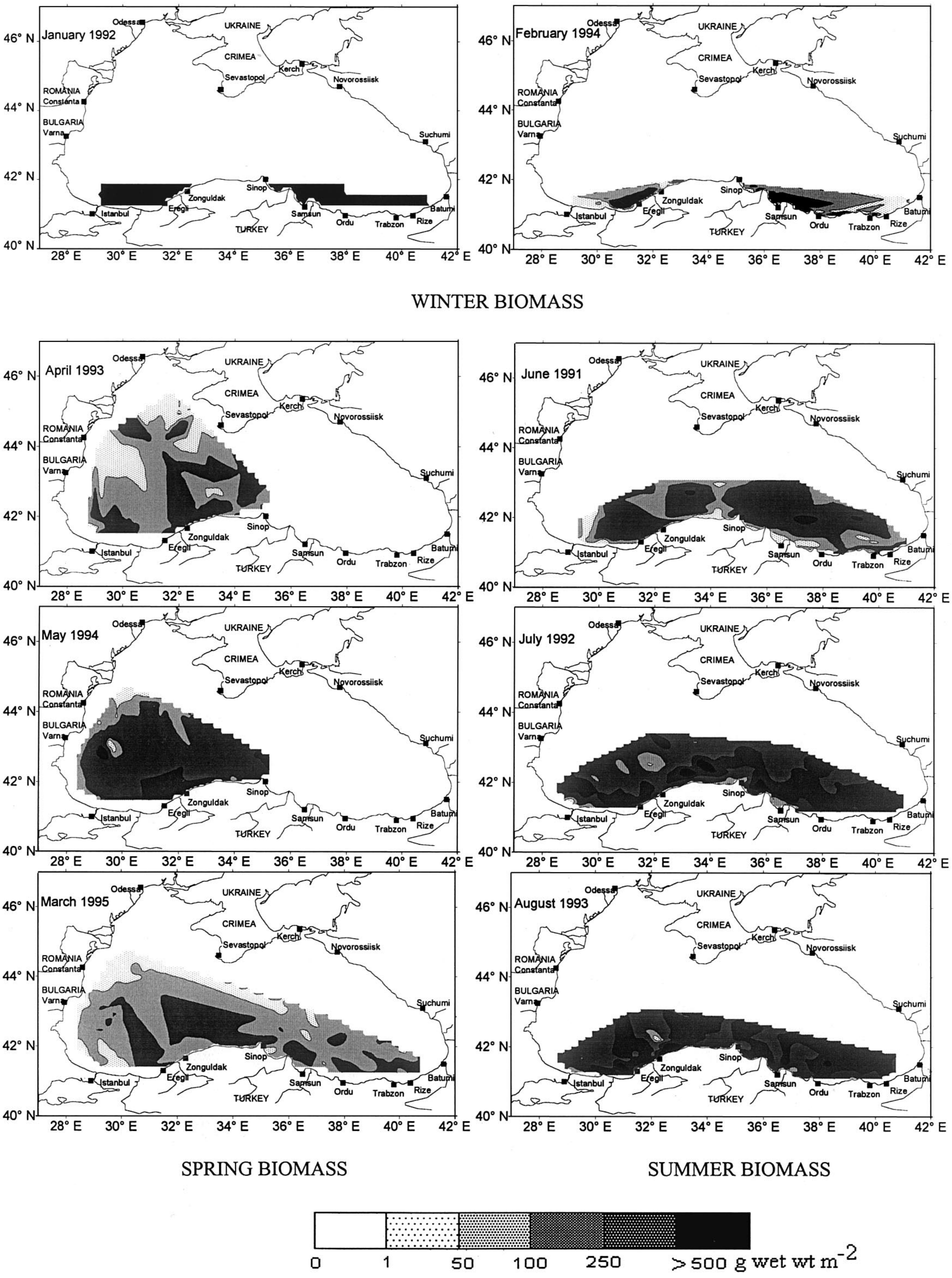


Fig. 2 *Pleurobrachia pileus*. Biomass distribution (g wet wt m^{-2}) from June 1991 to March 1995 (*no shading* within area studied represents 0 to 1 g wet wt m^{-2})

in winter, and about twice as high as in spring (Fig. 6). During the summer, the mean wet weight and abundance increased rapidly from June (109 g m^{-2} and 203 ind. m^{-2} in 1991) to July (244 g m^{-2} and 523 ind. m^{-2} in 1992, while the numbers remained unchanged between July and August (258 g m^{-2} and 503 ind. m^{-2} in 1993). Because these data were obtained in different years this may have been due to between-year variation (Fig. 6).

Morphometric characters

Individual displacement volume and live weight were fitted to length measurements by regression analysis. The relationship between body length and width was represented by a linear regression model (Table 4). The average ratio of body length to body width was 1.10. The ratios remained unchanged with size class (< 10 mm, 10 to 20 mm, and > 20 mm body length).

Spatial and temporal size distribution

Although individuals with lengths as much as 30.6 mm were observed, *Pleurobrachia pileus* with lengths > 20 mm formed < 1% of the population on any date. Young individuals (< 10 mm body length) constituted 50 to 60% of the population of *P. pileus* in January 1992, but accounted for only 8 to 10% in April/May 1994 (the minimum observed). Specimens < 10 mm in length formed 40% of the population in the summer months (July 1992 and August 1993; Fig. 7). *P. pileus* displayed two separate length classes in early spring (March 1995) and late summer (August 1993), due to the presence of newly hatched specimens and larger individuals (Fig. 8). Thus, there appeared to be at least two generations per year. Small specimens of *P. pileus* were widely distributed in the western Black Sea. The abundance of larger individuals apparently increased from west to east and from inshore to offshore. Small *P. pileus* species were also found along the southern edges of the Batumi anticyclonic eddy in the eastern Black Sea.

Vertical size composition

Pleurobrachia pileus showed diel changes in vertical size distribution. In summer (August 1993), smaller individuals (< 10 mm) were mostly in the upper 40 m, particularly around the thermocline (10 to 15 m) and in the seasonal pycnocline (Fig. 9). The *P. pileus* did not, however, show a significant difference in vertical size distribution due to diel vertical migration. During the night, some larger individuals ascended up to the depth of the core of the CIL. By midnight, mean (± SE) body length increased from 10.3 ± 1.73 mm below the thermocline to 13.7 ± 0.5 mm from 40 to 100 m depth in the CIL. The length of *P. pileus* increased slightly with the slight increase in salinity from surface to deeper waters (Fig. 9).

Stomach contents

The stomach contents of *Pleurobrachia pileus*, classified by higher taxonomic categories, consisted mainly of Copepoda (90%), Cladocera (1%), Mollusca (1%), fish eggs and larvae (1%) and others (7%). The five most abundant copepod species in the guts were *Calanus euxinus* (39%), *Pseudocalanus elongatus* (30%), *Acartia clausi* (28%), *Oithona similis* (2%), and *Paracalanus parvus* (1%). The primary prey of *P. pileus* were the small planktonic Crustacea (*P. parvus*, *A. clausi*, *O. similis*, *P. elongatus*, and Cladocera), the larvae of benthic invertebrates, Appendicularia, and arrowworms. In terms of numerical occurrence, *P. pileus* fed on *P. elongatus* (38%) more than *C. euxinus* (32%). In the years 1992 to 1995, the greatest number of organisms found in the stomach of one *P. pileus* was 84 in May 1994. The individual food items were *P. elongatus* (22 females), *A. clausi* (21 males), digested copepods (20), *A. clausi* (16 females), *P. elongatus* (2 males), *C. euxinus* (2 copepodites) and one *Podon leucarti* (Table 5). In the years 1992 to 1995 the lowest percent of individuals with food items in the guts was 0.5%, found in July 1992.

Parasite

The parasitic nematode *Hysterothylacium aduncum* was found in different parts of the body of *Pleurobrachia pileus*. Throughout the Black Sea, the highest (65 to 73%) occurrence of the parasite occurred in the summer (July 1992, August 1993). In late winter, the occurrence decreased to 32%, then increased again to 54% in early spring. Occurrence of the parasite was very low (6%) in the late spring.

Correlation with ambient zooplankton abundance

In early and late summer (June 1991 and August 1993), *Pleurobrachia pileus* abundance was positively correlated spatially with a few species of copepods, such as *Pseudocalanus elongatus* and *Calanus euxinus*. In July 1992, in addition to these species, *P. pileus* was negatively correlated with *Acartia clausi* at a level of $p < 0.05$ ($r = -0.4$) and positively correlated with the ctenophore *Mnemiopsis leidyi* ($r = 0.3$). In the winter, there was an increase in the number of species with which *P. pileus* had a significant correlation. During the winter months of January 1992, February 1994, and March 1995, *P. pileus* was significantly positively correlated with *Sagitta setosa* (Chaetognatha), *C. euxinus*, and *P. elongatus*, respectively. In spring, *P. pileus* had correlations similar to those of winter, except in late spring

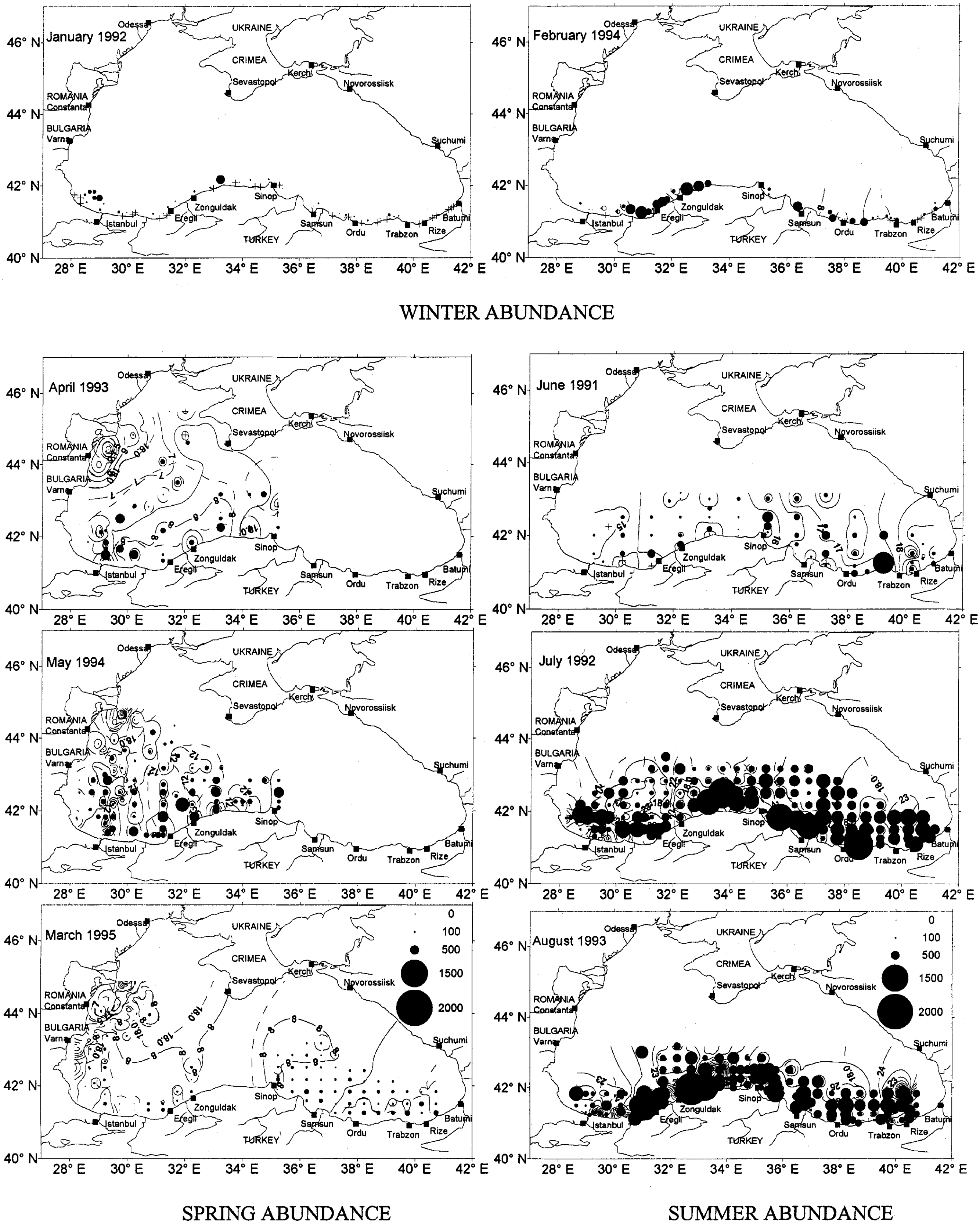


Fig. 3 *Pleurobrachia pileus*. Spatio-temporal abundance distribution (ind m^{-2}) from June 1991 to March 1995 (*solid contour* is temperature at 5 m depth; *dashed line* represents salinity at 5 m)

Table 2 *Pleurobrachia pileus*. Maximum and mean ± SE abundance (ind m^{-2}) and biomass (g wet wt m^{-2}) in the Black Sea, 1991 to 1995

	Jun 1991	Jan 1992	Jul 1992	Apr 1993	Aug 1993	Jan/Feb 1994	Apr/May 1994	Mar/Apr 1995
Max. no. ind. (m^{-2})	1154	481	1638	520	1812	696	757	289
Mean no. ind. (m^{-2})	203 ± 21	55 ± 10	523 ± 25	160 ± 21	506 ± 21	137 ± 21	229 ± 15	111 ± 7
Max. wet wt (g m^{-2})	312	234	871	234	1170	1429	416	546
Mean wet wt (g m^{-2})	109 ± 9	27 ± 5	244 ± 13	84 ± 10	258 ± 13	83 ± 22	162 ± 10	77 ± 6

(May 1994) when it was negatively correlated with *A. clausi*. Correlations between *P. pileus* abundances and ambient zooplankton varied in time. There was never any significant correlation between abundances of *P. pileus* and *Aurelia aurita*.

Discussion and conclusions

The spatio-temporal horizontal distribution of *Pleurobrachia pileus* was found to be related to the general current circulation of the Black Sea, with high concentrations found at the northern peripheries of anticyclonic eddies in the TEEZ. It is hypothesized that slowly swimming organisms are aggregated toward the center of the eddies (Zhong 1988; Shushkina and Vinogradov 1991a). The area of the anticyclonic eddies is well-known as a downwelling region. In addition to the effect of the circulation on shaping patches of ctenophores, vertical distribution must be taken into consideration. *P. pileus* individuals dwell below the thermocline, or within the CIL, which is characterized by temperatures < 8 °C. Most individuals, especially larger ones which contribute much to the wet weight biomass, were found where the maximum density stratification occurred. The pycnocline is well-formed in the northern periphery (including

Table 3 *Pleurobrachia pileus*. Abundance (ind m^{-2}) and biomass (g wet wt m^{-2}) in western, eastern, inshore and offshore areas of the Black Sea during 1991 to 1995. Bold numbers indicate significant difference between inshore and offshore areas inside the specified areas of the Black Sea (non-parametric Kruskal–Wallis ANOVA, $p < 0.05$) (*n* number of stations sampled)

Area	Inshore			Offshore			Total		
Sampling date	Abund.	Biomass	(*n*)	Abund.	Biomass	(*n*)	Abund.	Biomass	(*n*)
Western Black Sea									
Jun 1991	**45**	**30**	(6)	**167**	**111**	(24)	**146**	97	(29)
Jan 1992	**53**	**25**	(30)	**212**	**108**	(7)	**83**	**40**	(37)
Jul 1992	**198**	**95**	(14)	**503**	**205**	(67)	**450**	**211**	(81)
Aug 1993	**391**	**155**	(19)	**508**	**281**	(75)	**484**	255	(94)
Jan/Feb 1994	**39**	**16**	25	**60**	**33**	10	164	72	(35)
Mar/Apr 1995	**28**	**43**	(28)	**126**	**90**	(23)	**72**	**64**	(51)
Eastern Black Sea									
Jun 1991	**168**	**62**	(4)	**254**	**124**	(35)	**246**	118	(39)
Jan 1992	**9**	**4**	(20)	**51**	**26**	(17)	**28**	**14**	(37)
Jul 1992	**216**	108	(3)	**639**	297	(59)	**618**	**288**	(62)
Aug 1993	**332**	**113**	(7)	**569**	**283**	(51)	**540**	262	(58)
Jan/Feb 1994	**60**	**33**	(29)	**278**	**283**	(9)	111	94	(38)
Mar/Apr 1995	**68**	48	(28)	**152**	91	(23)	**147**	**88**	(51)
Area studied (see Fig. 2)									
Jun 1991	**94**	**43**	(10)	**220**	**120**	(58)	203	109	(68)
Jan 1992	**35**	**16**	(50)	**98**	**50**	(24)	55	27	(74)
Jul 992	**201**	**97**	(17)	**566**	**264**	(126)	523	244	(143)
Aug 993	**375**	**144**	(26)	**533**	**282**	(126)	506	258	(152)
Jan/Feb 1994	**50**	**25**	(54)	**382**	**247**	(19)	137	83	(73)
Mar/Apr 1995	**32**	**44**	(31)	**144**	**90**	(76)	111	77	(107)
Turkish EEZ									
Apr 1993	**64**	**31**	(4)	**226**	**106**	(26)	**205**	96	(30)
Apr/May 1994	**79**	**56**	(6)	**296**	**207**	(53)	**274**	**191**	(59)
Mar/Apr 1995	**35**	**76**	(11)	**148**	**93**	(68)	**132**	**91**	(79)
Bulgarian, Romanian and Ukranian EEZ									
Apr 1993	**32**	**31**	(10)	**155**	**99**	(10)	**93**	65	(20)
Apr/May 1994	**69**	**55**	(12)	**176**	**129**	(14)	**127**	**95**	(26)
Mar/Apr 1995	**30**	**26**	(20)	**111**	**70**	(8)	**53**	**38**	(28)
Area studied (see Fig. 2)									
Apr 1993	**41**	**31**	(14)	**206**	**104**	(36)	160	84	(50)
Apr/May 1994	**73**	**56**	(18)	**271**	**191**	(67)	229	162	(85)
Mar/Apr 1995	**32**	**44**	(31)	**144**	**90**	(76)	111	77	(107)

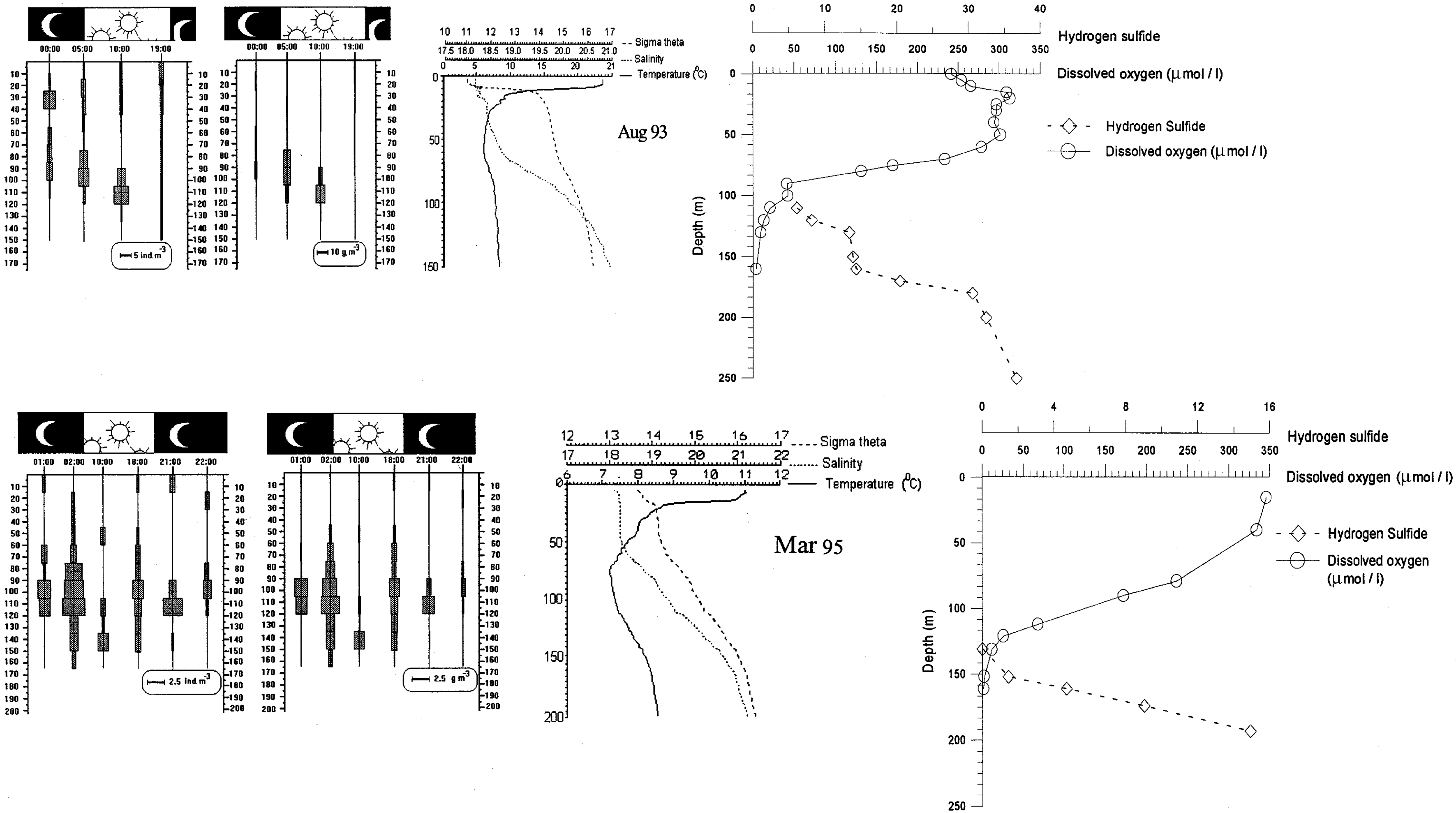


Fig. 4 *Pleurobrachia pileus*. Vertical distribution with respect to daily light conditions, temperature, salinity, density gradients, dissolved oxygen (µ*M*), and hydrogen sulphide (H_2S in µ*M*), August 1993, station 41°30′N; 31°15′E, and March 1995, station 41°54′N; 29°51′E

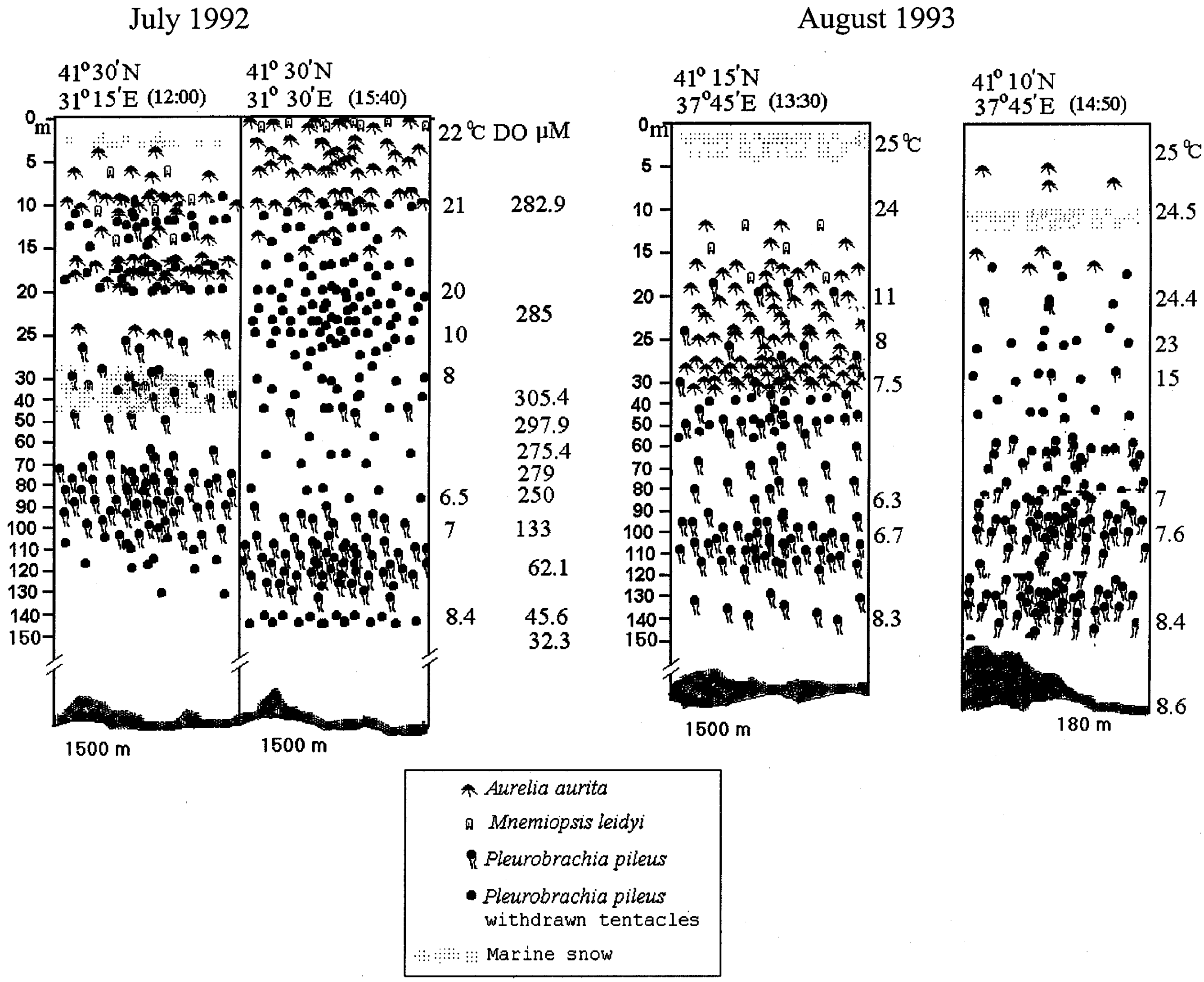


Fig. 5 *Pleurobrachia pileus*, *Mnemiopsis leidyi*, *Aurelia aurita*. Vertical distribution from video records for station 41°30′N; 31°15′E, and 41°30′N; 31°30′E, July 1992, and station 41°15′N; 37°45′E and 41°10′N; 37°45′E, August 1993

deep water) of anticyclonic eddies along the Turkish coast. Except for the winter, the occurrence of higher biomass and abundance both in offshore and eastern waters of the Turkish Black Sea may be a result of early warming, which triggers spawning and accelerated growth of the *P. pileus*, and the late cooling of the waters, which permits an extended growth period.

With two distinct depth maxima at 20 to 40 and 90 to 120 m, most *Pleurobrachia pileus* were observed below the thermocline, where relatively cold water occurs. This observation supports Ivanov and Beverton (1985) who classified *P. pileus* into a cold-water group of plankton occupying the water from the thermocline down to the H_2S zone in summer, and the surface during the transition to the cold season. Vinogradov et al. (1985) found similar trends in vertical distribution of *P. pileus* in the Black Sea in April/May 1984, and Vinogradov et al. (1992) and Vinogradov and Nalbandov (1990) stated that the overwhelming majority of individuals migrated vertically upward at night. A second group did not migrate and remained at depth. The second group remaining at the pycnocline could be related to the vertical migration of *Calanus* spp. (their main food). The *P. pileus* resting at the pycnocline may save metabolic energy by remaining motionless.

The distribution of marine snow patches in this study was in good agreement with a visual study by Kempe et al. (1989). Marine snow particles occurred at all depths of the mixed layer of the Black Sea, with occasionally higher concentrations at 20 to 30 and 70 to 80 m depths. Visual observation by underwater video camera allowed us to clarify the vertical distribution of *Pleurobrachia pileus* with respect to the physical characteristics of the water column and to observe the appearance of the ctenophores in the water column. Vinogradov et al. (1985) observed that in the layer of deep Ctenophora-maxima they were suspended and "inactive" in the water with widely outstretched tentacles. This inactive appearance of *P. pileus* with outstretched tentacles sug-

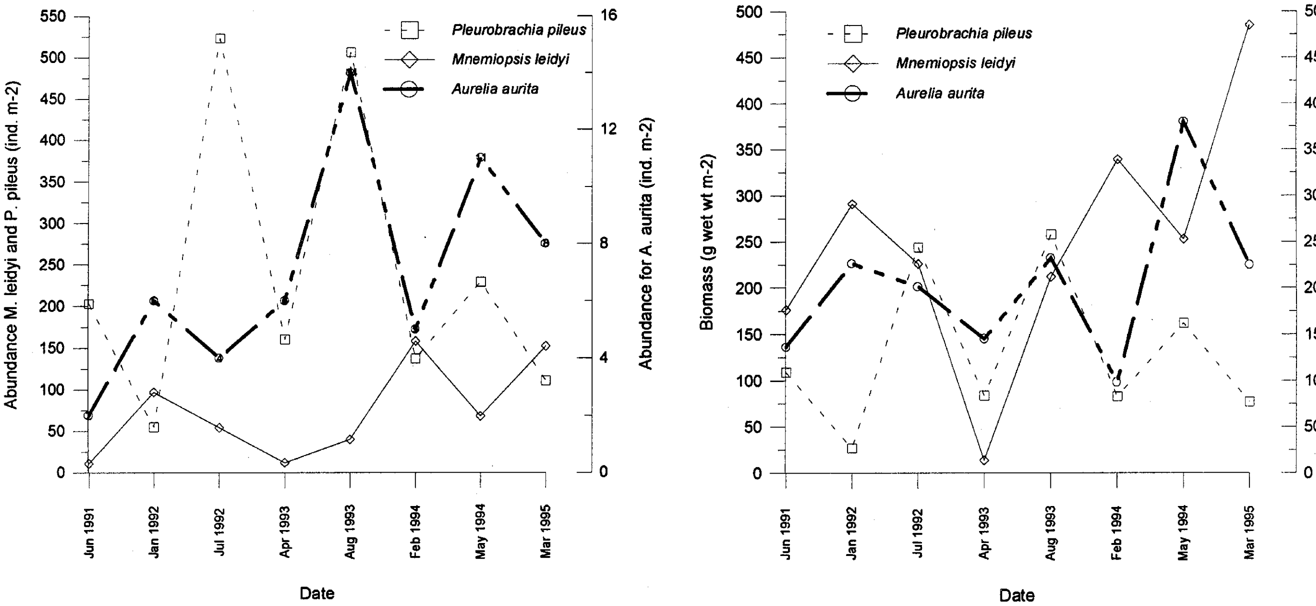


Fig. 6 *Pleurobrachia pileus*, *Mnemiopsis leidyi*, *Aurelia aurita*. Fluctuation in mean abundance (ind. m^{-2}) and mean biomass (g wet wt m^{-2}) from June 1991 to March 1995

gests that individuals were, in fact, in a feeding mode, gathering prey with the tentacles. The tentacles catching the prey are coiled in helical fashion and then contracted to bring the food to the mouth (mini-ROVER observation, IMS-METU video recording, 1996).

An evaluation of inter-annual biomass and abundance variations could not be done because there were too few sampling months each year, and an average over the sampling times would not provide a meaningful annual mean. Nevertheless, *Pleurobrachia pileus* displayed regular monthly variation in biomass and abundance from January to August, regardless of the year. Starting in winter, when the lowest values were observed, *P. pileus* showed marked increases in biomass and abundance up to the summer, when the maximum values occurred. A significant increase in weight and number between June and July suggests that reproduction of *P. pileus* began in March/April and continued to increase until July, ceasing in July to August. Vinogradov and Shushkina (1992) found a parallel trend in the seasonal biomass of *P. pileus*.

Co-existence of newly hatched specimens and larger individuals suggested that reproduction of *Pleurobrachia pileus* in the Black Sea occurred in winter and summer. Vinogradov and Shushkina (1992) also observed cydippid ctenophores 5 to 10 mm in diameter dominating the winter population and 10 to 20 mm individuals predominating in summer.

With respect to the vertical physical structure in the sampling area, smaller individuals (< 10 mm) were observed around the thermocline and just above the pycnocline. With increasing depth, ctenophore length increased. Vinogradov et al. (1992) found a very narrow (1 to 2 m) layer of small *Pleurobrachia pileus* (5 to 10 mm length) just below the maximal pycnocline gradient. This suggests that *P. pileus* distribution is largely controlled by density stratification which enables the organisms to make passive vertical movements with a minimum energy expenditure, or to accumulate in layers where they are nearly neutrally buoyant. Vinogradov et al. (1985) found that large individuals (> 10 mm) of *P. pileus* were concentrated in a deeper layer at 100 to 140 m, a few meters above a high abundance of *Calanus euxinus* in a thin layer of relatively higher oxygen content. Vinogradov et al. (1986) observed them suspended, motionless, and with outstretched tentacles in April/May 1984.

Copepoda, Cladocera, Mollusca, and fish eggs and larvae formed the main zooplankton food of *Pleurobrachia pileus* as Greve (1972) previously stated. The five most abundant copepod species observed in the guts were *Calanus euxinus*, *Pseudocalanus elongatus*, *Acartia clausi*, *Oithona similis*, and *Paracalanus parvus*. Vinogradov et al. (1986) stated that *P. pileus* preys upon *C. euxinus* in the Black Sea.

Table 4 *Pleurobrachia pileus*. Biometric relationships (*Y* dependent variable; *X* independent variable; *a* intercept; *b* slope; *r* correlation coefficient, significant at $p < 0.01$ level; *n* sample size)

Relationship (*Y* vs *X*)	Type of function	a	b	*r*	*n*
Wet wt (mg) vs Length (mm)	Power	0.682	2.522	0.91	256
Width (mm) vs Length (mm)	Linear	0.166	0.904	0.99	1215
Displacement vol. (ml) vs Length (mm)	Power	0.002	2.185	0.83	1215
Displacement vol. (ml) vs Width (mm)	Power	0.002	2.163	0.83	1215

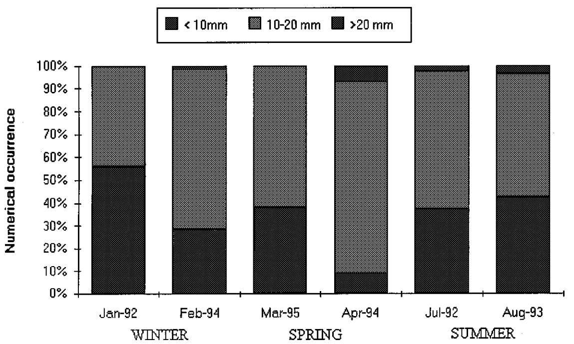
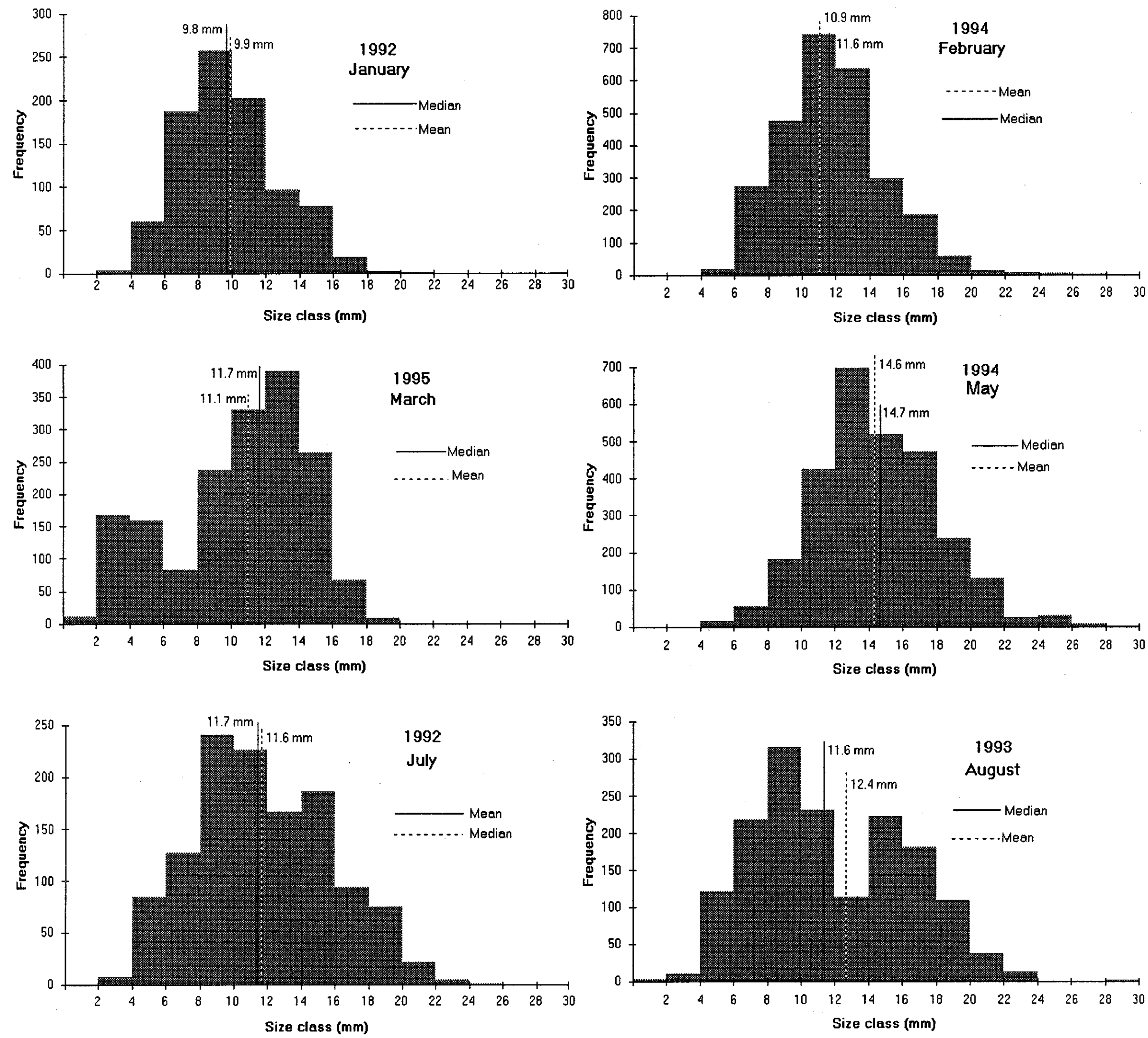


Fig. 7 *Pleurobrachia pileus*. Seasonal changes in frequency of three size classes from January 1992 to March 1995

Occurrence of the parasitic nematode *Hysterothylacium aduncum* in the body of *Pleurobrachia pileus*, which is classified as an intermediate host of *H. aduncum* (Kinne 1984; Køie 1993), increased from winter (the minimum observed) to summer (the maximum observed). These changes could be related to the life cycle, or reproductive period, of this worm (Kinne 1984) and to the reproductive cycle of *P. pileus* and the time taken to infect new individuals.

In conclusion, the highest concentrations of *Pleurobrachia pileus*, measured as wet weight, were found in offshore waters (outside the continental shelf of the Black Sea) at the edge of anticyclonic eddies. At these locations large individuals, whose contribution to wet biomass was very high, lived in deeper water above the anoxic zone. The biomass of *P. pileus* increased markedly from winter to summer. This species was mostly found in a layer extending from the lower parts of the thermocline down to the anoxic zone, where the temperature was <8 °C. The vertical distribution of the total biomass of *P. pileus* throughout the oxygenated layer had two maxima, which were most evident at night. Abundance in the upper

Fig. 8 *Pleurobrachia pileus*. Length-frequency distribution for six sampling dates from January 1992 to March 1995. Data from multiple stations are averaged to reflect winter, spring, and summer conditions



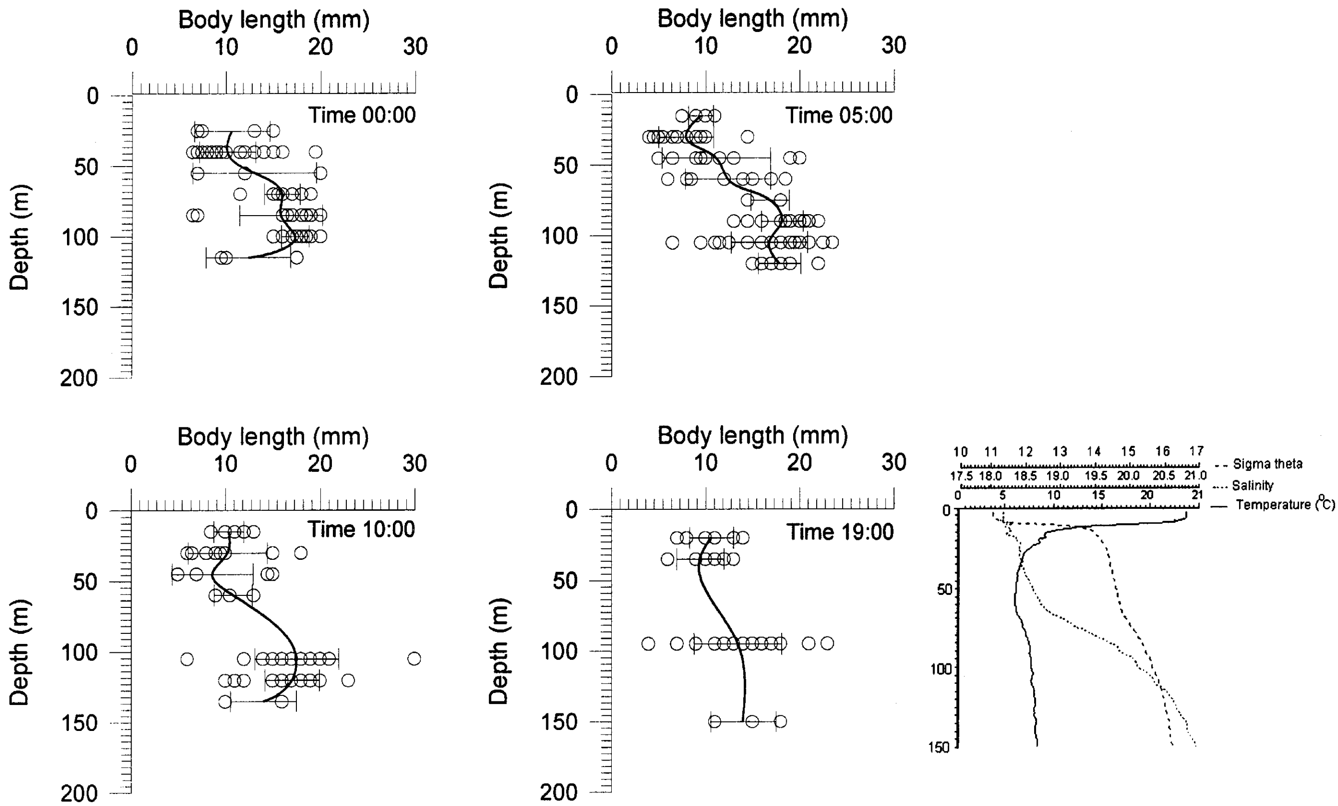


Fig. 9 *Pleurobrachia pileus*. Depthwise change in mean body length over 1 d and in environmental parameters (salinity, temperature, and density) in August 1993 at station 41°30′N; 31°15′E

maximum at 20 to 40 m depth was less than in the lower maximum at 90 to 120 m depth. Smaller body lengths were measured in winter months. The *P. pileus* population had two distinct length classes in early spring and late summer, indicating that newly hatched ctenophores and larger individuals were present. Overall, the stomach contents of *P. pileus* consisted mainly of copepods. High abundances of *P. pileus* were correlated with high abundances of *Pseudocalanus elongatus* and fewer *Acartia clausi*.

Table 5 *Pleurobrachia pileus*. Frequency of occurrence (*FO*, as %) and numerical occurrence (*NO*, as %) of food items in July 1992 to March 1995 (0 = < 1%)

Food items	Jul 1992		Apr 1993		Aug 1993		Feb 1994		May 1994		Mar 1995	
	FO	NO	FO	NO	FO	NO	FO	NO	FO	NO	FO	NO
Pseudocalanus elongatus	9	10	30	39	17	19	21	38	16	18	25	26
Acartia clausi	27	30	24	33	18	19	3	0	21	22	8	5
Calanus euxinus	18	20	15	7	23	20	34	25	32	28	33	26
Oithona similis	0	0	2	1	6	3	1	0	2	0	0	0
Paracalanus parvus	0	0	2	1	1	0	0	0	0	0	2	0
Unidentified copepods	9	10	14	15	19	24	22	29	13	25	22	35
Appendicularia					1	0			0	0		
Fish eggs and larvae	18	10	4	1	1	1	1	0	0	0	0	0
Cladocera	0	0	1	0	1	0	3	0	2	0	0	1
Bivalve larvae					1	0	4	1	0	0	2	1
Cerianthula mediterranea			1	0								
Peachia hastata	9	10	2	0	1	0	0	0			2	0
Sagitta elegans									2	0	0	0
Cumacea			1	0								
Polychaeta larvae	9	10	1	0	1	0	0	0	0	0		
Unidentified food item			1	0	11	8	10	3	8	2	2	2
Total no. individuals examined	2319		603		14 875		3396		3370		2861	
No. individuals with food items in gut	12		99		276		460		415		201	
Max. no. prey ind^{-1}	11		35		9		3		84		8	
Total no. food items	451		296		732		10		1215		317	

Acknowledgements This work was funded by the Scientific and Technical Research Council of Turkey (TUBITAK), and by the Scientific Affairs Division of NATO within the framework of the Science for Stability Programme. We are indebted to the crews of the R.V. "Bilim". Our thanks also go to friends who assisted during sampling cruises. Our special thanks go to Dr. P. Wiebe for giving valuable suggestions in various ways, and for correcting the English of this manuscript.

References

Greve W (1972) Ecological investigations on *Pleurobrachia pileus*. II. Laboratory investigations. Helgoländer wiss Meeresunters 23: 141–164

Harbison GR, Volovik SP (1993) Methods for the control of populations of the ctenophore, *Mnemiopsis leidyi*, in the Black Sea and Azov Sea. GFCM technical consultation on stock assessment in the Black Sea, Ankara, Turkey, 15 to 19 February 1993, p 21

Holden MJ, Raitt DFS (1974) Manual of fisheries science. Methods of resource investigation and their application. FAO Fish tech Pap 115: 1–92

Ivanov L, Beverton RJH (1985) The fisheries resources of the Mediterranean Sea. Part II. Black Sea. Stud Rev gen Fish Coun Mediterr 60: 1–135

Kempe S, Diercks AR, Liebezeth G, Prange A (1989) Geochemical and structural aspects of pycnocline in the Black Sea. In: Izdar E, Murray J (eds) Black Sea oceanography. Vol. 351. Kluwer Academic Publisher, Dordrecht, The Netherlands, pp 89–110

Kinne O (1984) Diseases of marine animals. Vol. IV. Pisces. Biologische Anstalt Helgoland, Hamburg

Køie M (1993) Aspects of the life cycle and morphology of *Hysterothylacium* (Rudolphi, 1802) (Nematoda, Ascaridoidae, Anisakidae). Can J Zool 71: 1289–1296

Lebedeva LP, Shushkina EA (1994) Modeling the effect of *Mnemiopsis* on the Black Sea plankton community. Oceanology 34: 72–80

Mutlu E (1996) Effect of formaldehyde on the gelatinous zooplankton (*Pleurobrachia pileus*, *Aurelia aurita*) during preservation. Turk J Zool 20: 423–426

Mutlu E, Bingel F, Gücü AC, Melnikov VV, Niermann U, Ostr NA, Zaika VE (1994) 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. ICES J mar Sci 51: 407–421

Oguz T, Latun VS, Latif MA, Vladimirov VV, Sur HI, Markov AA, Ozsoy E, Kotovshchikov BB, Eremeev VV, Unluata U (1993) Circulation in the surface and intermediate layers of the Black Sea. Deep-Sea Res 40: 1597–1612

Shushkina EA, Musayeva EI (1983) The role of jellyfish in the energy system of the Black Sea plankton communities. Oceanology 23: 92–96

Shushkina EA, Musayeva EI (1990a) Structure of the planktonic community of the Black Sea epipelagic zone and its variation caused by invasion of a new ctenophore species. Oceanology 30: 225–228

Shushkina EA, Musayeva EI (1990b) Increasing abundance of the immigrant ctenophore *Mnemiopsis* in the Black Sea (report of an expedition by the R/Vs Akvanavt and Gidrobiolog in April 1990). Oceanology 30: 521–522

Shushkina EA, Vinogradov MYe (1991a) Long-term changes in the biomass of plankton in open areas of the Black Sea. Oceanology 31: 716–721

Shushkina EA, Vinogradov MYe (1991b) Plankton changes in the open Black Sea for many years. Oceanology 31: 973–980

Sokal RR, Rohlf FJ (1968) Biometry: the principles and practise of statistics in biological research. WH Freeman and Company, San Francisco

Tugrul S, Bastürk O, Saydam C, Yilmaz A (1992) Changes in the hydrochemistry of the Black Sea inferred from the water density profiles. Nature 359: 137–139

Vinogradov MYe (1990) Investigation of the pelagic ecosystem of the Black Sea (44th cruise of the R/V Dimitry Mendeleyev), 4 July–17 September 1989. Oceanology 30: 254–256

Vinogradov MYe, Flint MV, Shushkina EA (1985) Vertical distribution of mesoplankton in the open area of the Black Sea. Mar Biol 89: 95–107

Vinogradov MYe, Nalbandov RYu (1990) Effects of changes in water density on the profiles of physicochemical and biological characteristics in the pelagic ecosystem. Oceanology 30: 567–573

Vinogradov MYe, Sapozhnikov VV, Shushkina EA (1992) The Black Sea ecosystem. Nauka, Moscow

Vinogradov MYe, Shushkina EA (1992) Temporal changes in community structure in the open Black Sea. Oceanology 32: 485–491

Vinogradov MYe, Shushkina EA, Flint MV, Tumantseva NI (1986) Plankton in the lower layers of oxygen zone in the Black Sea. Oceanology 26: 222–228

Vinogradov MYe, Shushkina EA, Musayeva EI, Sorokin PYu (1989) A newly acclimated species in the Black Sea: the ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). Oceanology 29: 220–224

Volovik SP, Myrzoyan ZA, Volovik GS (1993) *Mnemiopsis leidyi* in the Azov Sea: biology, population dynamics, impact to the ecosystem and fisheries. Int Counc Explor Sea Comm Meet (Biol Oceanogr Comm) L:69: 1–11

Zaika VE, Sergeeva NG (1991) Diurnal dynamics of population structure and vertical distribution of ctenophore *Mnemiopsis mccradyi* Mayer in the Black Sea. Zh obshch Biol 27: 15–19

Zaitsev PYu (1993) Impact of eutrophication on the Black Sea fauna. Stud Rev gen Fish Coun Mediterr 64: 59–83

Zhong Z (1988) Marine planktonology. China Ocean Press and Springer-Verlag, Beijing