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Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*

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Abstract The distribution of *Mnemiopsis leidyi* Agassiz, 1865 in the Black Sea was determined using plankton samples collected above the anoxic zone (maximum depth 200 m) in the summer, winter, and spring from 1991 to 1995. Distribution was patchy. Average biomasses of 15 to 500 g m^{-2} were measured, and abundances varied from 10 to 180 ind m^{-2}. Biomass and abundance peaked in winter, and there was a secondary peak in the summer. The distribution of *M. leidyi* was correlated with hydrographic features in the Black Sea with higher concentrations in anticyclonic gyres. The centers of the two main cyclonic gyres generally had a low biomass of *M. leidyi*. From July 1992 to March 1995, the populations were largely offshore. *M. leidyi* were confined to the upper part of the mixed layer both day and night. Some individuals displayed a negative taxis to daylight and were concentrated below the thermocline at night. Smaller *M. leidyi* (1.5 to 2 cm) were present in the winter, and individuals reached maximum size in the summer. Although reproduction was continuous throughout the year, there were two distinct peaks: the larger peak in the summer and the smaller peak in the winter. Microscopic analysis of stomach contents showed that copepods and molluscs form their main diet.

Introduction

Mnemiopsis leidyi was accidentally introduced into the Black Sea in the early 1980s, and since then dramatic changes in the ecosystem have been observed, perhaps because of eutrophication. Changes observed include continuous monospecific phytoplankton blooms, which have caused degradation of benthic macrophytes due to light limitation, declines in abundance of benthic organisms over broad regions of the shelf due to anoxia and high H_2S levels produced by decaying algae, massive settlement of phytoplankton blooms, mass mortalities of benthic organisms and demersal fishes due to hypoxia, rapid influx and spread of the scyphozoan *Aurelia aurita* (Semaeostomae) and the ctenophore *M. leidyi*, which have apparently occupied vacant niches in this eutrophied ecosystem (Anonymous 1993, 1994). Eventually, the rapid increase in abundance of *M. leidyi* caused a decrease in the abundance of *A. aurita* (Shushkina and Vinogradov 1991a). Paralleling a decrease in zooplankton due to competitive interactions with *M. leidyi*, the abundance of horse mackerel (*Trachurus mediterraneus*), anchovy (*Engraulis encrachicolus*), and red mullet (*Mullus barbatus ponticus*) also drastically declined (Anonymous 1994), although the causes of these decreases are unknown.

Four species of gelatinous zooplankton are common in the Black Sea: two scyphozoans, *Aurelia aurita* and *Rhizostoma pulmo*, and two ctenophores, *Pleurobrachia pileus* and *Mnemiopsis leidyi*. *R. pulmo* is the most common species in coastal areas, particularly along the southeastern coast, and the other species are distributed throughout the Black Sea (Anonymous 1993). Over the past couple of years *R. pulmo* abundance has increased offshore for unknown reasons.

In a preliminary study of the gelatinous zooplankton community from the Turkish side of the Black Sea (Mutlu et al. 1994), *Mnemiopsis leidyi* abundances increased from the summer of 1991 to the summers of 1992 and 1993, and these abundances were much higher in the eastern than western parts of the Black Sea. In the present study we examined the recent distribution of *M. leidyi*, and compared its abundances to 1991 to 1993 data. We also examined its morphology, and depth distribution, and made some observations about its food and relationships with other zooplankton groups.

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Materials and methods

Samples for studying the horizontal distribution of *Mnemiopsis leidyi* Agassiz were collected in the winter, spring, and summer of 1991 to 1995 as previously described (Mutlu et al. 1994; Mutlu and Bingel 1999). Vertical distributions were studied using discrete vertical hauls with a Nansen opening–closing net and from video observations using a camera mounted on a remote operated vehicle Mutlu and Bingel 1999).

On board ship *Mnemiopsis leidyi* were separated and counted. Aboral (AL; distance from statocyst to mouth), lobate (LL; from statocyst to end of lobe) and auricle lengths (ArL; from statocyst to end of auricle), and body widths (BW; the widest part of body) of individuals were measured with a millimeter scale, and individual displacement volumes (ml) were determined in finely graded cylinders. *M. leidyi* were classified into three different size classes (AL < 10 mm, larval, 10 to 30 mm, transitional, and AL > 30 mm, lobate stages; Baker and Reeve 1974). Monthly length-frequency distributions were sorted into 1-cm length classes. In the laboratory, stomach contents of 9709 individuals of *M. leidyi* were examined in individuals preserved in 5% formalin buffered with borax.

Results

Biomass and abundance

Horizontal distribution

Spatial distributions of *Mnemiopsis leidyi* followed hydrographic features of the Black Sea. High biomasses were always found in anticyclonic gyres and on the edges of cyclonic gyres, whereas centers of the western and eastern cyclonic gyres (Fig. 1 in Mutlu and Bingel 1999) generally had low *M. leidyi* biomass (Figs. 1, 2). The maximum abundance and biomass of *M. leidyi* were 510 ind m^{-2} and 2080 g m^{-2} in March/April 1995 (Table 1). The area with the highest abundance and biomass of *M. leidyi* shifted eastward from the Sakarya area (Fig. 2; June 1991) along the Turkish coast to the offshore regions of Ordu and Trabzon (Fig. 2; July 1992, August 1993). Shifts in the locations of *M. leidyi* aggregations during the year may be caused by small/large-scale changes in the surface circulation in the Black Sea. The biomass and abundance of *M. leidyi* were significantly higher in the eastern area than in the western area of the Turkish Black Sea. The higher abundance and biomass of *M. leidyi* in inshore waters compared to offshore regions indicate that reproduction occurs in coastal areas, which warm up earlier (Figs. 1, 2; Table 2). Currents moving warm water offshore, and a subsequent increase in temperature in offshore areas, may cause the expansion of offshore populations.

Vertical distribution

Mnemiopsis leidyi was confined to a narrow depth range in the upper parts of the mixed layer, at depths of 20 to 30 m during both day and night. No individuals were observed beneath the thermocline in summer (August 1993; Fig. 3). A few individuals were collected below the thermocline at 60 to 80 m at night in March 1995 (Fig. 3). Throughout the entire sampling, *M. leidyi* comprised at least 50 to 55% of the total abundance and biomass of all taxa reaching 70 to 80% above the Cold Intermediate Layer (CIL), where a peak in biomass and abundance was observed within the first 15 m. During the day, they were concentrated within a narrow layer above 40 to 50 m depth. At night, abundance of *M. leidyi* in the layer below the CIL was less than that above the thermocline. A few individuals of *M. leidyi* were found at about 130 m depth.

Fig. 1 *Mnemiopsis leidyi*. 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})

Visual observations of vertical distribution

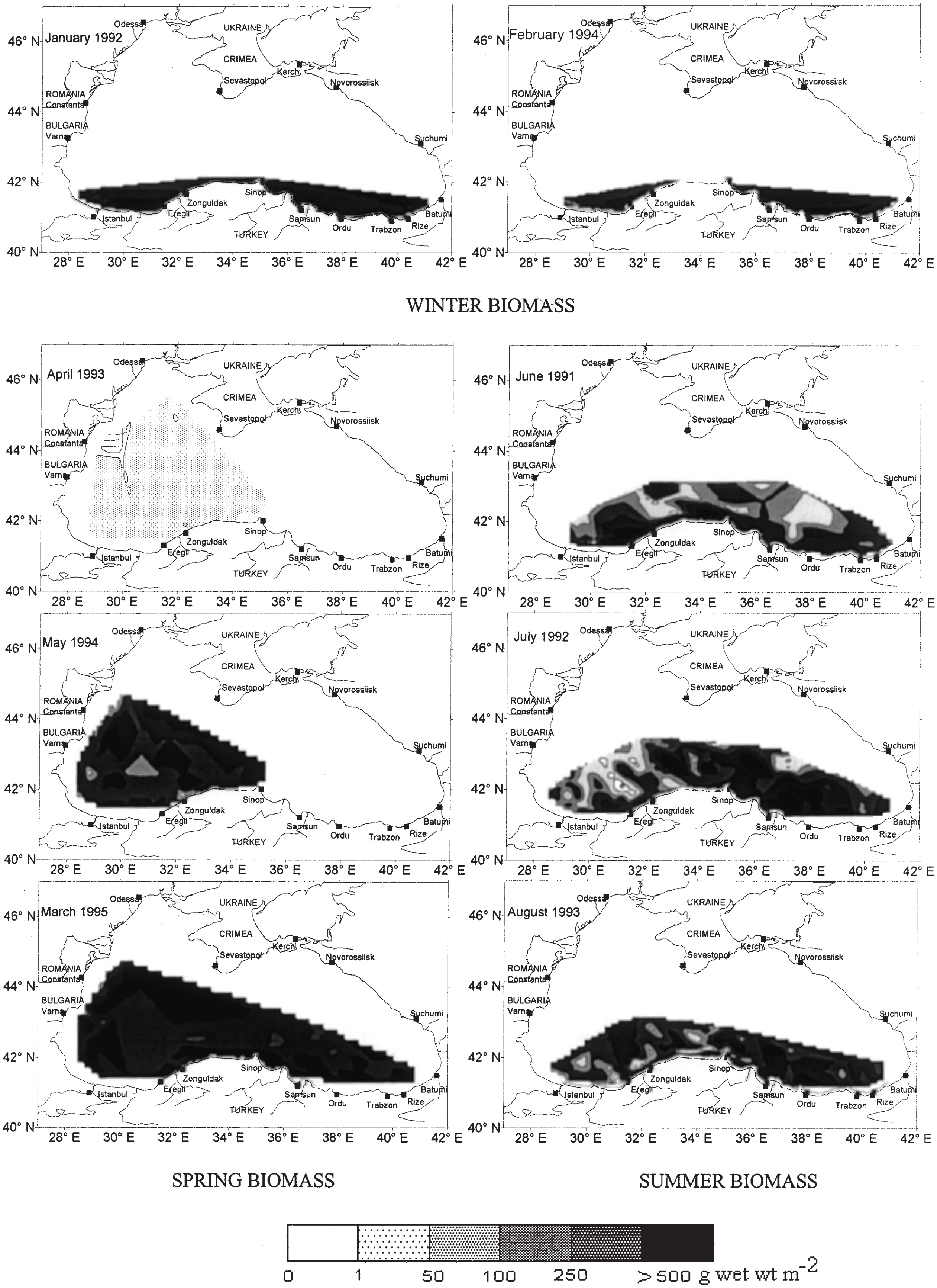
In situ visual inspection using a Mini-ROVER (Remote Operated Vehicle, Benthos Inc.) in July 1992 and August 1993 showed that the organisms were distributed throughout the water column. *Mnemiopsis leidyi* was homogeneously distributed in the mixed layer (12 to 15 m). The surface waters were warmer in August (25 to 26 °C; Fig. 5, Mutlu and Bingel 1999), when individuals of *M. leidyi* were found at greater depths (down to 20–25 m) compared to those measured in July 1992. No *M. leidyi* or *Aurelia aurita* were observed below the thermocline at 25 to 30 m (Fig. 5 in Mutlu and Bingel 1999).

Temporal fluctuations

The mean abundance and biomass of *Mnemiopsis leidyi* peaked between January and March. It was apparently followed by a spring decrease and a subsequent summer minimum (Fig. 6 in Mutlu and Bingel 1999). Temporal variation in biomass and abundance was especially pronounced in the coastal region. Abundance and biomass of *M. leidyi*, on the average, were significantly lower in April 1993. The annual cycles in biomass and abundance of *M. leidyi* differ from those of *Aurelia aurita* and *Pleurobrachia pileus,* and the spatial distributions of the three species also differ.

Morphometric characters

Individual displacement volume and live weight were fitted to length measurements using regression analysis. Linear regression gave a better fit for relationships between different linear measurements. Additionally, the relationship between the wet weight and displacement volume of fresh individuals of *Mnemiopsis leidyi* was obtained using a generated linear function. All relationships were highly significant at $p < 0.01$ (Table 3).


January 1992
February 1994
WINTER BIOMASS
April 1993
June 1991
May 1994
July 1992
March 1995
August 1993
SPRING BIOMASS
SUMMER BIOMASS
Odessa
UKRAINE
CRIMEA
Sevastopol
Kerch
Novorossiisk
ROMANIA
Constanta
BULGARIA
Varna
Suchumi
Sinop
Zonguldak
Eregli
Istanbul
Samsun
Ordu
Trabzon
Rize
Batumi
TURKEY
46° N
44° N
42° N
40° N
28° E
30° E
32° E
34° E
36° E
38° E
40° E
42° E
0
1
50
100
250
>500 g wet wt m-2

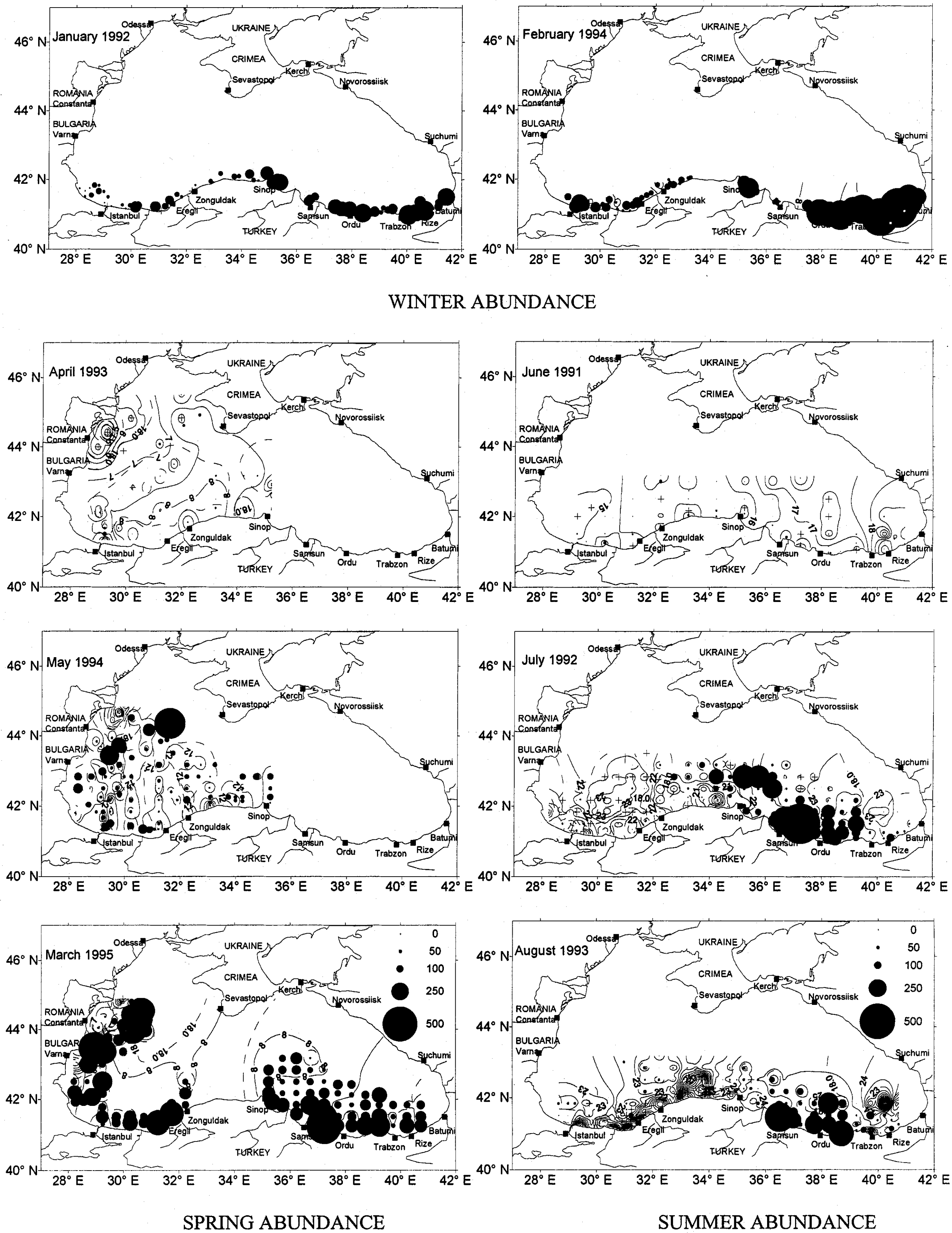


Fig. 2 *Mnemiopsis leidyi*. Spatio-temporal abundance distribution (ind m^{-2}) from June 1991 to March 1995 (*solid contour* is temperature at 5 m; *dashed line* represents salinity at 5 m)

Table 1 *Mnemiopsis leidyi*. 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	Feb 1994	May 1994	Mar 1995
Max. no. (ind m^{-2})	47	281	569	57	408	561	442	510
Mean no. (ind m^{-2})	11 ± 1	97 ± 9	54 ± 7	12 ± 2	40 ± 6	158 ± 15	68 ± 7	152 ± 10
Max. wet wt (g m^{-2})	1039	780	1924	52	1430	1039	962	2080
Mean wet wt (g m^{-2})	176 ± 27	291 ± 21	226 ± 21	14 ± 2	212 ± 16	339 ± 29	253 ± 21	485 ± 34

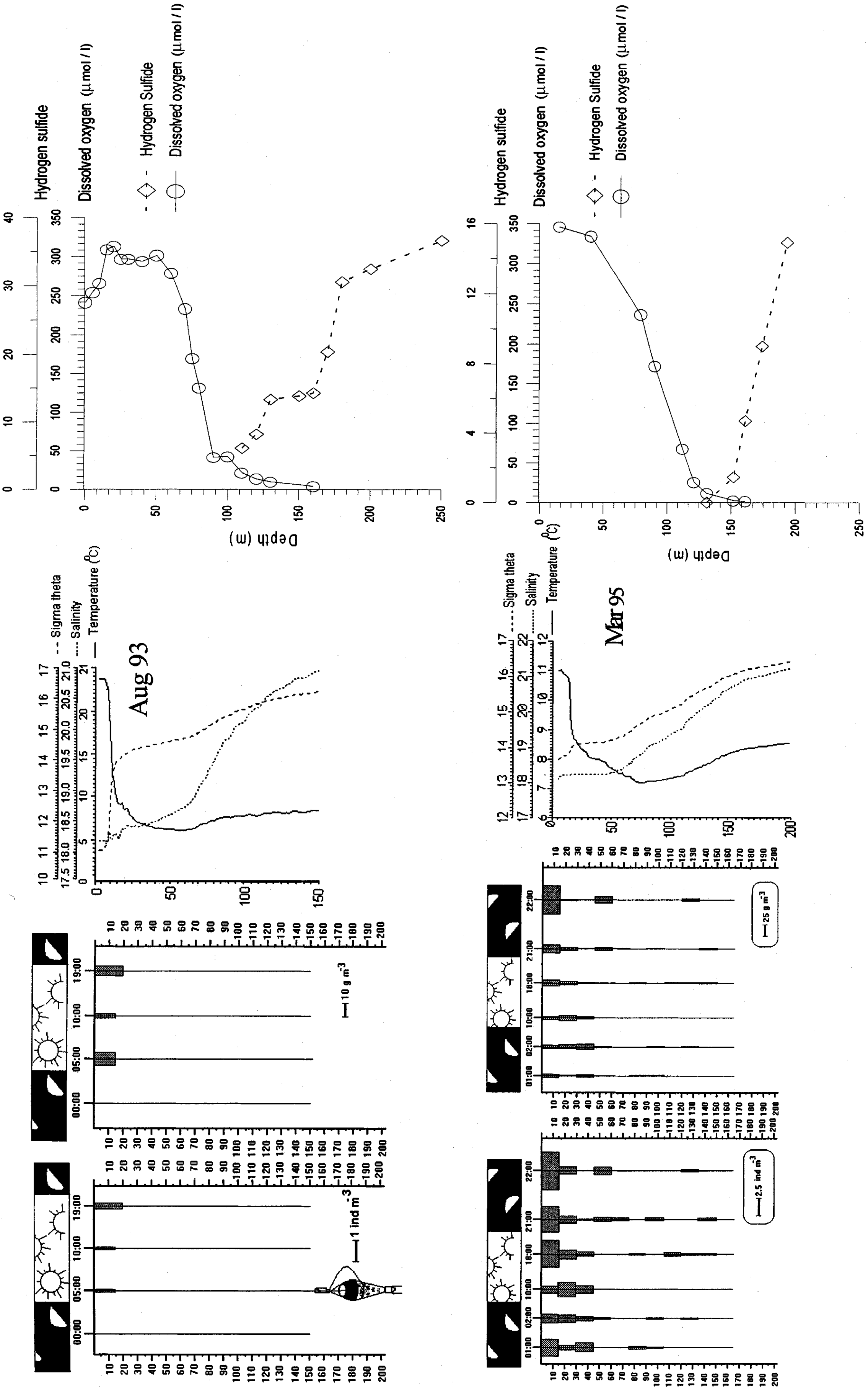
Table 2 *Mnemiopsis leidyi*. Abundance (ind m^{-2}) and biomass (g wet wt m^{-2}) in western, eastern, inshore and offshore areas of the Black Sea during 1991 to 1995. **Bold numbers** indicate significant difference between inshore and offshore areas inside the specified areas of the Black Sea (non-parametric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

Area, sampling date	Inshore			Offshore			Total		
	Abund.	Biomass	(n)	Abund.	Biomass	(n)	Abund.	Biomass	(n)
Western Black Sea									
Jun 1991	21	431	(6)	11	208	(24)	12	243	(29)
Jan 1992	58	269	(30)	56	291	(7)	**57**	273	(37)
Jul 1992	12	119	(14)	18	133	(67)	**17**	**130**	(81)
Aug 1993	7	**104**	(19)	15	**148**	(75)	**14**	**139**	(94)
Jan/Feb 1994	88	191	(25)	77	268	(10)	**84**	**214**	(35)
Mar/Apr 1995	145	**337**	(28)	177	**550**	(23)	159	433	(51)
Eastern Black Sea									
Jun 1991	16	146	(4)	9	124	(35)	10	126	(39)
Jan 1992	**95**	**212**	(20)	**185**	**424**	(17)	**137**	309	(37)
Jul 1992	114	529	(3)	101	341	(59)	**102**	**350**	(62)
Aug 1993	68	238	(7)	84	342	(51)	**82**	**329**	(58)
Jan/Feb 1994	210	443	(29)	277	477	(9)	**226**	**451**	(38)
Mar/Apr 1995	**373**	**1634**	(3)	**131**	**470**	(53)	144	532	(56)
Area studied (see Fig. 2)									
Jun 1991	19	317	(10)	10	152	(58)	11	176	(68)
Jan 1992	**73**	**246**	(50)	**148**	**385**	(24)	97	291	(74)
Jul 1992	30	191	(17)	57	230	(126)	54	226	(143)
Aug 1993	**24**	**140**	(26)	**43**	**227**	(126)	40	212	(152)
Jan/Feb 1994	153	329	(54)	171	366	(19)	158	339	(73)
Mar/Apr 1995	167	463	(31)	145	494	(76)	152	485	(107)
Turkish EEZ									
Apr 1993	5	11	(4)	**13**	18	(26)	17	12	(30)
Apr/May 1994	74	225	(6)	57	234	(53)	58	233	(59)
Mar/Apr 1995	196	664	(11)	143	504	(68)	151	**526**	(79)
Bulgarian, Romanian and Ukranian EEZ									
Apr 1993	7	6	(10)	**16**	14	(10)	12	10	(20)
Apr/May 1994	95	253	(12)	86	336	(14)	90	298	(26)
Mar/Apr 1995	151	352	(20)	162	410	(8)	154	**368**	(28)
Area studied (see Fig. 2)									
Apr 1993	**6**	**7**	(14)	**14**	17	(36)	12	14	(50)
Apr/May 1994	88	244	(18)	63	255	(67)	68	253	(85)
Mar/Apr 1995	167	463	(31)	145	494	(76)	152	485	(107)

The ratios of aboral length to auricle and lobe lengths were 0.69 and 0.65, and the auricle-to-lobe length ratio was 0.94. The aboral-to-auricle length ratio increased during development from larval to lobate stages. Lobe length-to-body width ratio was <1 only in the larval stage.

Spatial and temporal size distribution

Using aboral length (AL) as a measure of size, the size structure of *Mnemiopsis leidyi* in the Black Sea showed marked seasonal fluctuations (Fig. 4). Comparison of the mean lengths obtained from 1992 to 1995 revealed that the smallest mean length was found within winter periods (January 1992 and February 1994, Fig. 5). The mean length increased slightly in spring (2.20 cm in April/May 1994 and March/April 1995) and reached 2.38 cm in July 1992 and 2.88 cm in August 1993. Aboral length generally did not exceed 70 mm (11.5 cm lobe length). The relative abundance of larval individuals increased from west to east, whereas lobate stages appeared in high abundance mostly in the southwestern part of the Black Sea. *M. leidyi* >30 mm (AL) rarely exceeded 12 to 13% of the total population of *M. leidyi* (Fig. 4). In this study, two seasonal peaks (winter and



Hydrogen sulfide
Dissolved oxygen (µ mol / l)
Hydrogen Sulfide
Dissolved oxygen (µ mol / l)
Depth (m)
Sigma theta
Salinity
Temperature (°C)
Aug 93
Mar 95
10 g m-3
1 ind m-3
25 g m-3
2,5 ind m-3

◀

Fig. 3 *Mnemiopsis leidyi*. Vertical abundance and biomass distribution at station 41°30′N; 31°15′E in August 1993, and station 41°54′N; 29°51′E in March 1995. Vertical lines indicate maximum depth of sampling at 15-m intervals, and corresponding profile of temperature, salinity, density gradients, dissolved oxygen (μ*M*), and hydrogen sulphide (H_2S in μ*M*)

summer) of young individuals were observed in coastal waters (Fig. 5). Winter reproduction was less pronounced than that of summer, where it was very high in the eastern region. In winter and summer, when *M. leidyi* was reproducing intensively, two or more separate size classes were detected (indicating that younger and older age-classes co-existed), while in spring, when *M. leidyi* reproduced minimally, only one cohort could be found (Fig. 5).

Vertical size composition

Observations at station 41°30′N; 31°15′E in August 1993, and station 41°54′N; 29°51′E in March 1995 were conducted to determine vertical size distribution in the Black Sea. In August 1993, when the surface water temperature reached its yearly maximum, all the individuals of *Mnemiopsis leidyi* were found in the upper mixed layer just above the well-formed thermocline. In March 1995, when the mean aboral length of *M. leidyi* was found to increase slightly from the surface to between 45 and 75 m depth, where it peaked, and then decreased in individuals at greater depths (135 m). Young or, perhaps, shrunken individuals due to starvation (Kremer 1976) were found at greater depths. In the upper 50 m, individuals with lengths varying from 2.5 to 4.5 cm and with lengths < 1.5 cm occurred. Small individuals (AL ≈ 1 cm) of *M. leidyi* were observed at depths of 105 and 150 m, where large individuals were not generally found. During the day (10:00 hrs), most individuals were concentrated in the upper layer (0 to 50 m). Only adult specimens were observed at greater depths at 18:00 hrs. Mean aboral length of the individuals increased between the CIL and 150 m depth as time approached midnight. After midnight the reverse process was observed.

Stomach contents

Overall, the gastrovascular cavities of *Mnemiopsis leidyi* individuals contained the following food components, in descending order of frequency: Copepoda (50%), Mollusca (40%), fish eggs and larvae (1%), Cladocera (%1) and others (8%). Of the five most important copepod species (*Calanus euxinus*, *Acartia clausi*, *Pseudocalanus elongatus*, *Oithona similis*, and *Paracalanus parvus*), *C. euxinus* was most frequently consumed (35%) by this lobate ctenophore in the Black Sea. Following *C. euxinus*, food consumed were *A. clausi* (33%), *P. elongatus* (22%), *O. similis* (9%), and *P. parvus* (1%) in frequency of occurrence. In numerical occurrence, *A. clausi* (37%) ranked first and *C. euxinus* was 35% during the 1992 to 1995 study period. The greatest number of individual food items in the stomach of one *M. leidyi* was 94 in February 1994 (Table 4). In comparison with the stomach contents in April 1993, the proportion of copepods was lower at 75%, whereas molluscans comprised 15 to 20% of the diet in May 1994. Fish eggs were observed in the stomach of *M. leidyi* at the maximum frequency and abundance (4% each) in the May 1994 samples. During the summer, the consumption of bivalve larvae by *M. leidyi* was minimal, while no specimens of *O. similis* were encountered. Throughout the present study, when *M. leidyi* was confined to the upper mixed layer, the most abundant food items in the guts were *A. clausi* (44% in April 1993; 14% in August 1993). In *M. leidyi* collected from greater depths to 130 m, the proportion of *C. euxinus* in the diet increased (*C. euxinus* 19%, *A. clausi* 12% in March/April 1995). By winter and early spring, the consumption of Mollusca, mainly bivalve larvae and juveniles, by *M. leidyi* was observed (Table 4).

Table 3 *Mnemiopsis leidyi*. Biometric relationships of (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 (g) vs Aboral length (cm)	Power	0.928	2.231	0.91	214
Wet wt (g) vs Lobe length (cm)	Power	0.393	2.163	0.94	214
Wet wt (g) vs Auricle length (cm)	Power	0.460	2.471	0.92	50
Wet wt (g) vs Width (cm)	Power	0.334	3.237	0.91	50
Displacement vol. (ml) vs Lobe length (cm)	Power	0.485	2.174	0.96	50
Displacement vol. (ml) vs Aboral length (cm)	Power	1.436	2.081	0.96	50
Displacement vol. (ml) vs Auricle length (cm)	Power	0.619	2.402	0.94	50
Displacement vol. (ml) vs Body width (cm)	Power	0.429	3.148	0.92	50
Wet wt (g) vs Displacement vol. (ml)	Linear	−0.249	0.886	0.98	50
Aboral length (cm) vs Lobe length (cm)	Linear	0.199	0.598	0.97	214
Auricle length (cm) vs Lobe length (cm)	Linear	0.496	0.664	0.97	50
Body width (cm) vs Lobe length (cm)	Linear	1.114	0.389	0.92	50
Aboral length (cm) vs Auricle length (cm)	Linear	−0.167	0.889	0.97	50
Body width (cm) vs Auricle length (cm)	Linear	0.932	0.547	0.90	50
Body width (cm) vs Aboral length (cm)	Linear	1.086	0.599	0.92	50

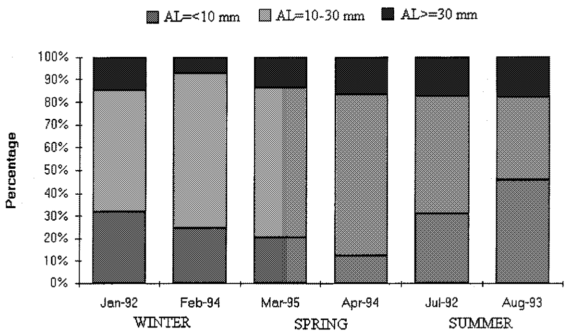


Fig. 4 *Mnemiopsis leidyi*. Temporal changes in size-frequency distributions of larval (aboral length; AL < 10 mm), transitional (AL = 10 to 30 mm) and lobate(AL > 30 mm) stages

Correlation with ambient zooplankton abundance

In July 1992, *Mnemiopsis leidyi* abundance was positively correlated with both *Pleurobrachia pileus* and *Aurelia aurita* at the same level ($p < 0.05$, $r = 0.3$, $n = 143$), but there was no correlation between *P. pileus* and *A. aurita* abundance. *M. leidyi* was more closely correlated with *P. pileus* ($p < 0.05$, $r = 0.6$, $n = 50$) in April 1993 as compared with previous years. In August 1993 and February 1994, the abundance of *M. leidyi* was not significantly correlated with *P. pileus* and *A. aurita* abundances. In contrast to the previous correlations in abundance from June 1991 to February 1994, *A. aurita* abundance was significantly negatively correlated with *M. leidyi* abundance ($p < 0.05$, $r = -0.25$, $n = 85$) and with *P. pileus* ($p < 0.05$, $r = -0.2$, $n = 85$) in May 1994. In March 1995, there were no significant correlations in abundance among these organisms. Comparison of the spatial distributions of abundance and biomass of *A. aurita* and *M. leidyi* reveals that in areas where *A. aurita* is in dense patches, the abundance and biomass of *M. leidyi* is reduced, and vice versa.

Discussion and conclusions

Spatial patterns of *Mnemiopsis leidyi* abundance and biomass appeared to be associated with surface circu-

Fig. 5 *Mnemiopsis leidyi*. Seasonal aboral length-frequency distributions

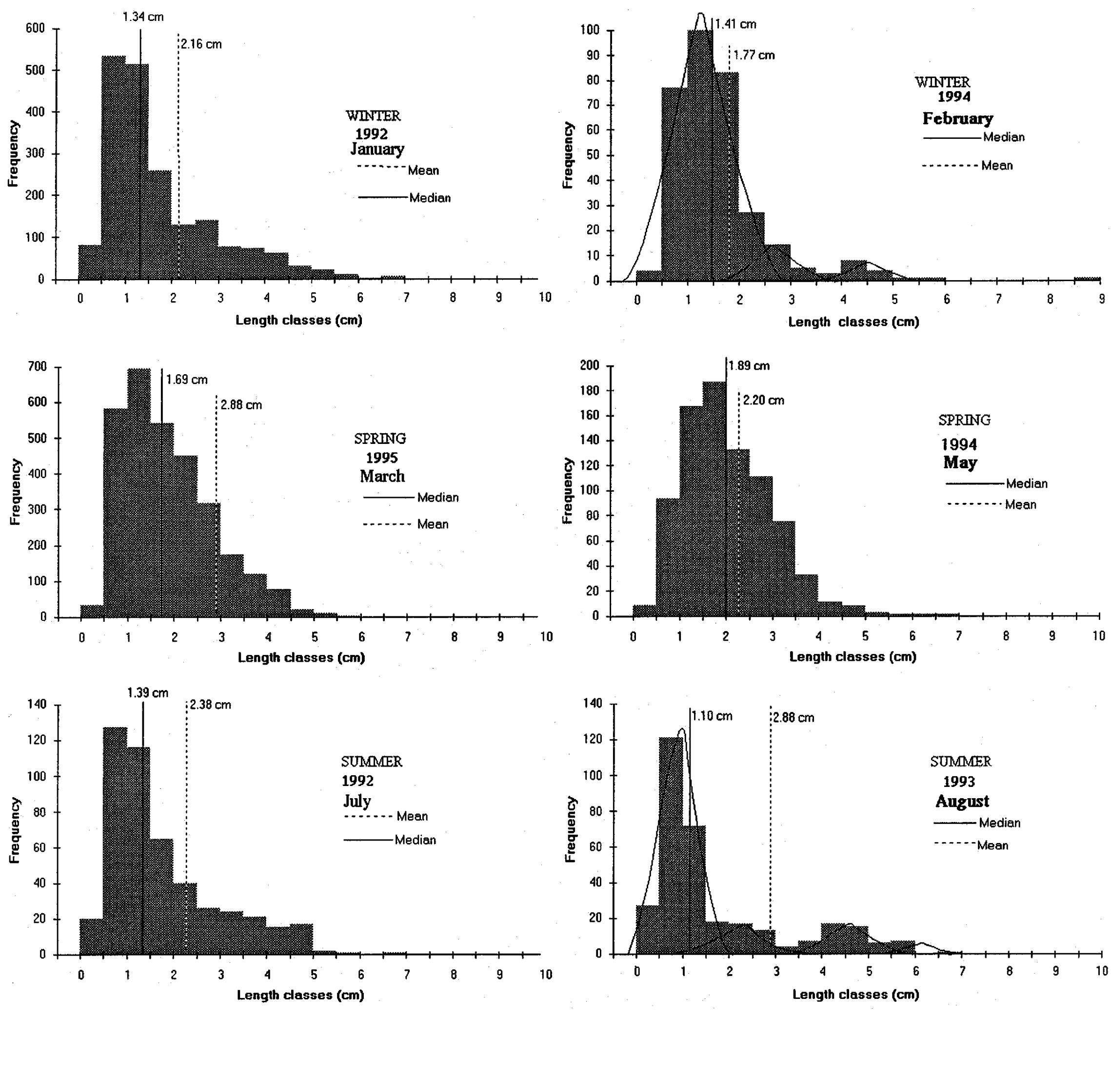


Table 4 *Mnemiopsis leidyi*. Percent frequency of occurrence (*FO*, as %) and numerical occurrence (*NO*, as %) of food items in July 1992 to March 1995 (0 = <1%)

Food items	July 1992		April 1993		Aug 1993		Feb 1994		May 1994		March 1995	
	FO	*NO*	*FO*	*NO*	*FO*	*NO*	*FO*	*NO*	*FO*	*NO*	*FO*	*NO*
Pseudocalanus elongatus			33	33	11	10	15	3	12	9	14	6
Acartia clausi	34	26	34	44	19	13	8	0	27	17	11	3
Calanus euxinus	50	63	17	11	6	3	18	3	27	13	18	3
Oithona similis			17	11			8	0	1	0	8	3
Paracalanus parvus											5	1
Unidentified copepod					25	38	21	6	16	14	19	11
Appendicularia							1	0				
Fish eggs and larvae					4	4	0	0	1	0		
Podon leucarti (Cladocera)					1	0	3	0			3	1
Bivalve larvae					4	5	19	84	11	36	15	69
Ostracoda							1	0				
Pleurobrachia pileus					3	0						
Sagitta setosa									7	8		
Crab larvae	17	13										
Mysidacea											0	1
Unidentified food					28	24	6	0	1	0	3	1
Total no. individuals examined		311		46		641		4422		1124		3165
No. individuals with food items in gut	6		6		66		343		48		110	
Max. no. of prey ind^{-1}	4		2		9		94		46		61	
Total no. food items	8		9		132		3985		223		1257	

lation of the Black Sea, perhaps because most individuals occur in the upper mixed layer. Relatively higher biomasses were observed in patches in coastal anticyclonic eddies. Other parts of the Black Sea had low biomasses. Zhong (1988) previously suggested that the horizontal distribution of Ctenophora is dictated by currents, water temperature, and salinity. Anticyclonic gyres, in which the water mass downwells, continuously accumulate planktonic individuals in the core of the eddies, resulting in high biomasses (Fig. 1 in present paper; Fig. 1 in Mutlu and Bingel 1999). Cyclonic gyres with upwelling waters force *M. leidyi* towards the perimeter and cause aggregations at the edges. Interactions of local, small-scale anticyclonic eddies in the region also affect distributions (Fig. 1). These complex interactions cause patchy distributions of organisms on the outskirts of cyclonic gyres (Fig. 1). Biomasses and abundances differed among regions: higher accumulations were found in the eastern and inshore areas compared with western and offshore areas. In June 1991, the water temperature in the upper 5 m varied between 15 to 17 °C in the western area and 17 to 21 °C in the eastern area: which is below optimal temperature (24 to 25 °C, Zaika 1992). Low abundances of *M. leidyi* during that time corresponded with the sub-optimal temperatures (Fig. 1). However, in 1992, water temperatures at 5 m depth exceeded 22 °C in July (Fig. 1), and were >25 °C in August 1993 (Fig. 1), which was high enough for spawning (Mutlu et al. 1994). The high abundance of *M. leidyi* in coastal regions may be caused by the synergetic effects of high temperature and eutrophication. This pattern seems to affect other taxa such as anchovy (Niermann et al. 1994) and *Pleurobrachia pileus* (Mutlu and Bingel 1999).

Mnemiopsis leidyi were distributed over a narrow depth range both day and night, in and above the thermocline. Vinogradov et al. (1989) first observed a similar vertical distribution in late September 1987, and this pattern has been seen repeatedly (Vinogradov 1990; Bogdanova and Konsoulov 1993). In March 1995, a few individuals were observed below the thermocline, spreading down to the pycnocline at night. Shushkina and Vinogradov (1991b) showed that the *M. leidyi* population was distributed over the entire thermocline and above the pycnocline in winter 1991. The reason for the presence of a few individuals of *M. leidyi* in the deeper layer at night in the Black Sea remains unexplained. However, Miller (1974, in Kremer and Nixon 1976) found *M. leidyi* in the Pamlico River, North Carolina, to be homogeneously distributed from surface to bottom at night, in contrast to their accumulation in near surface waters during the day. Visual inspection of the vertical distribution of *M. leidyi* agreed well with results obtained using the standard opening–closing net (Fig. 3 in present paper; Fig. 5 in Mutlu and Bingel 1999).

Temporal variation in abundance and biomass of *Mnemiopsis leidyi* was characterized by a primary peak in winter, and a secondary peak in summer. Depending on atmospheric temperature conditions, the winter/spring phytoplankton bloom occurs in January or even February. Cold-water copepod populations increase synchronously with increased mixing and input of allochthonous nutrients in winter. Mass reproduction of *Calanus euxinus* in winter takes place in shallow waters (Vinogradov et al. 1992). This increase in food supply may cause the subsequent winter population explosion of *M. leidyi* in the Black Sea. *M. leidyi* grazed intensively during the winter and summer and starved with the beginning of fall. The decrease in biomass and abundance (Fig. 6 in Mutlu and Bingel 1999) may be due to the depletion of its food source.

Small individuals (< 10 mm) were observed throughout the year, and mean lengths of individuals increased from winter to summer, when large individuals dominated the population. Young individuals (AL < 10 mm) were abundant primarily in summer and secondarily in winter. In winter, temperature of the upper 5 m varies between 6.5 and 10 °C which is far below the optimal temperature, and so temperature is not the cause of changing rates of reproduction in *Mnemiopsis leidyi*. Food availability probably plays a more important role in the reproduction of *M. leidyi*. Vinogradov et al. (1992) and Volovik et al. (1993) found similar seasonal changes in size composition of *M. leidyi*. Summer reproduction may be associated with the combined effects of food and higher temperature (> 23 °C) on spawning of *M. leidyi*.

Mnemiopsis leidyi showed no evidence of a layered size distribution in the water column. It was strictly confined within the upper 20 m (above the thermocline) in August 1993. In March 1995 it was found at greater depths, as Shushkina and Vinogradov (1991a) had shown. Vinogradov et al. (1992) stated that large individuals were found near the upper boundary of the thermocline, and the offspring lived mainly in the upper part of the mixed layer.

Mnemiopsis leidyi ingests practically any organism that it captures with its oral lobes, including holoplanktonic organisms, the planktonic larvae of benthic organisms, and the eggs and larvae of fishes (Monteleone and Dugay 1988). Tsikhon-Lukashina et al. (1991) found that *Acartia clausi* and *Calanus euxinus* were abundant in gastrovascular cavities of *M. leidyi*, as the present study confirms. In *M. leidyi* from deeper water (130 m), the proportion of *C. euxinus* in the diet increased. This grazing by *M. leidyi* may contribute to the decline in *C. euxinus* biomass in spring to autumn (Vinogradov and Shushkina 1992). In winter and early spring samples we observed a high consumption of molluscs, mainly bivalve larvae. Kremer (1976) stated that bivalve veligers were one of the predominant foods of *M. leidyi* in waters from New England to the Gulf of Mexico.

In the summer, winter, and spring months, *Mnemiopsis leidyi* abundances were either negatively correlated (r = −0.5 to −0.7) or less significantly positively correlated (r = 0.25 to 0.3) with *Acartia clausi* abundance. Mountford (1980) found a strong inverse relationship between *M. leidyi* and *Acartia* sp. abundances in Barnegat Bay, New Jersey.

In conclusion, the spatial distribution of *Mnemiopsis leidyi* is controlled by sea surface circulation in the Black Sea. High concentrations were found in downwelling regions, while smaller concentrations were found in the main cyclonic gyres. The biomass and abundance of *M. leidyi* peaked in winter. *M. leidyi* occupied a narrow range of vertical depths, being confined to the upper part of the mixed layer by day and night. A few individuals were found below the thermocline at night, showing negative phototaxis. Smaller individuals (AL = 1.5 to 2.0 cm) occur in winter, and maximum size is reached in summer. Although they continuously reproduce, *M. leidyi* reproduction peaks twice annually, in the winter and summer, the largest peak being in summer. Analysis of stomach contents of *M. leidyi* has shown that copepods and bivalve larvae form the main diet.

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