Marine Biology (2001) 139: 535–547
DOI 10.1007/s002270100602

A.E. Kideys · Z. Romanova

Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996–1999

Received: 18 September 2000 / Accepted: 4 April 2001 / Published online: 21 July 2001

Abstract In this study, spatial and temporal distributions of three gelatinous macrozooplankton, the scyphozoan *Aurelia aurita* and the ctenophores *Pleurobrachia pileus* and *Mnemiopsis leidyi*, were evaluated using the data obtained from seven southern Black Sea cruises carried out from 1996 to 1999. A comparison of nets used for the sampling of gelatinous macrozooplankton illustrated the superiority of the Hensen net with a larger mesh size (300 µm) over the Nansen net (112 µm). *P. pileus* was mainly concentrated below the mixed layer, while *A. aurita* and *M. leidyi* were generally confined to surface waters. Horizontally, *P. pileus* was associated with deep, offshore waters. *P. pileus* also displayed the least interannual variation of the three species. Biomass of *A. aurita* and *M. leidyi* varied substantially seasonally and inter-annually. In September 1999, the average biomass of *M. leidyi* was at its lowest level (12 g wet weight m^{-2}) since its explosive development at the end of the 1980s. This was associated with the appearance of the new predatory ctenophore *Beroe ovata*, which appeared in the Black Sea at the end of the 1990s.

Introduction

Gelatinous zooplankton may substantially affect pelagic food webs by exerting a top-down control on their ecosystems (Deason and Smayda 1982; Mountford 1980; Greve 1994). This has been well documented for estuaries and enclosed seas (Kremer and Nixon 1976; Mountford 1980), the most notable example being the Black Sea. The arrival of the ctenophore *Mnemiopsis leidyi* (A. Agassiz) from the western Atlantic to the Black Sea at the end of the 1980s escalated several adverse events. In the summer of 1989 peak biomass levels of this ctenophore were up to 1.5–2 kg wet weight m^{-2} totaling close to 1 billion tons for the entire sea (Vinogradov et al. 1989). Simultaneously there were sharp decreases in the quantity of prey zooplankton (Kovalev et al. 1998a,b; Kideys et al. 2000), and in commercial fishery catches (Kideys 1994; Kideys et al. 1998, 1999). These enormous biomass levels of *M. leidyi* steadily decreased in subsequent years (Mutlu et al. 1994), however.

Until very recently, four species of gelatinous macrozooplankton were present in the Black Sea: two scyphozoan medusae [*Rhizostoma pulmo* (Macri) and *Aurelia aurita* (L.)] and two ctenophores (the indigenous *Pleurobrachia pileus* O.F. Müller and the invader *M. leidyi*). All but *R. pulmo* are common in the Black Sea. By October 1997, a predator of *M. leidyi*, the beroid ctenophore *Beroe ovata* Bosc appeared both in shallow and open waters of the Black Sea (Konsulov and Kamburska 1998).

A critical step in evaluating the impact of these jellyfishes is to document their distribution pattern, both in space and time. Despite the abundance of substantial studies on the physiological aspects (respiration, excretion, feeding, etc.) of these animals (Lazareva 1961; Tsikhon-Lukashina and Reznichenko 1991; Tsikhon-Lukashina et al. 1991; Anninsky et al. 1998; Shulman et al. 1998; Finenko and Romanova 2000; Finenko et al., 2001), there are only a few studies on the distribution of gelatinous macrozooplankton, which cover wide areas of the Black Sea (Shushkina and Arnautov 1985; Shushkina and Musayeva 1990). Some of these studies pertain to the southern Black Sea (Mutlu et al. 1994; Mutlu 1999; Mutlu and Bingel 1999), but there are no

---

Communicated by R. Cattaneo-Vietti, Genova

A.E. Kideys (✉)
Institute of Marine Sciences, P.O. Box 28,
Erdemli 33731, Turkey

E-mail: kideys@ims.metu.edu.tr
Tel.: +90-324-5213434
Fax: +90-324-5212327

Z. Romanova
Institute of Biology of the Southern Seas,
Nachimov Ave. 2, Sevastopol, Ukraine

published data for this region after 1995. We present here results from seven cruises (1996–1999), to evaluate inter-annual changes in biomass and abundance levels of these gelatinous species in the Black Sea, including both vertical and horizontal distributions (Fig. 1).

Materials and methods

In the present study a total of 484 samples were obtained using vertical tows from the anoxic layer (or from the bottom in shallow areas) to the surface (Table 1). For the sampling, a Hensen net (mouth diameter 70 cm) with a 300 μm mesh size was used most often. In July 1997, successive Hensen tows were performed at one station (stn 26), in order to determine the variation within samples. Besides the Hensen net, a Nansen closing net (mouth diameter 70 cm) with a 112 μm mesh size was also utilized, mainly for the sampling of zooplankton from different depth substrata, as well as for the sampling of smaller zooplankton. Deployment of both nets at several stations enabled us to compare their relative efficiency. Unfortunately a flowmeter was not utilized for calculating the filtering efficiency of the nets. Vertical distributions of gelatinous macrozooplankton were evaluated using the data obtained from the June–July 1996, April 1998 and September 1999 cruises. During these cruises the water column was sampled over five different depth strata chosen by density level, because major biochemical characteristics of the water column may affect plankton distribution in the Black Sea (Vinogradov et al. 1992; Saydam et al. 1993; Besiktepe et al. 1998). These depth strata were as follows: (1) from the thermocline to the surface (this stratum is almost saturated with dissolved oxygen, DO); (2) from the depth of sigma-theta (σ_t) equals 14.6 (corresponding to the upper boundary of the oxycline with about 250–300 μM DO) to the thermocline; (3) the depth range between $\sigma_t = 15.4$ (corresponding to the lower boundary of the oxycline with about 20 μM DO) and 14.6; (4) the depth range between $\sigma_t = 15.8$ and 15.4; and (5) the depth range between $\sigma_t = 16.2$ (onset of anoxic waters) and 15.8. The latter two substrata are situated in the so-called oxygen minimum zone (OMZ), where DO concentrations are < 10 μM (Bingel et al. 1993). According to Vinogradov et al. (1992), the last depth substratum is the daytime aggregation layer for late copepodite stages and adults of *Calanus euxinus* (Hulsemann), one of the most important copepod species of the Black Sea.

At the end of each tow, nets were washed from the exterior, and their cod ends were passed through a 2 mm sieve to retain the gelatinous organisms which were immediately enumerated. Planktonic organisms < 2 mm were fixed with 4% buffered formaldehyde for subsequent qualitative and quantitative analyses of mesozooplankton; the same was true for jellyfishes < 2 mm. However, only a few small jellyfishes were identified upon microscopic examination in preserved samples, which was not unexpected. It is well known that, in general, gelatinous plankton do not preserve well (Purcell 1988), and therefore an underestimation of small size groups is possible in the present study.

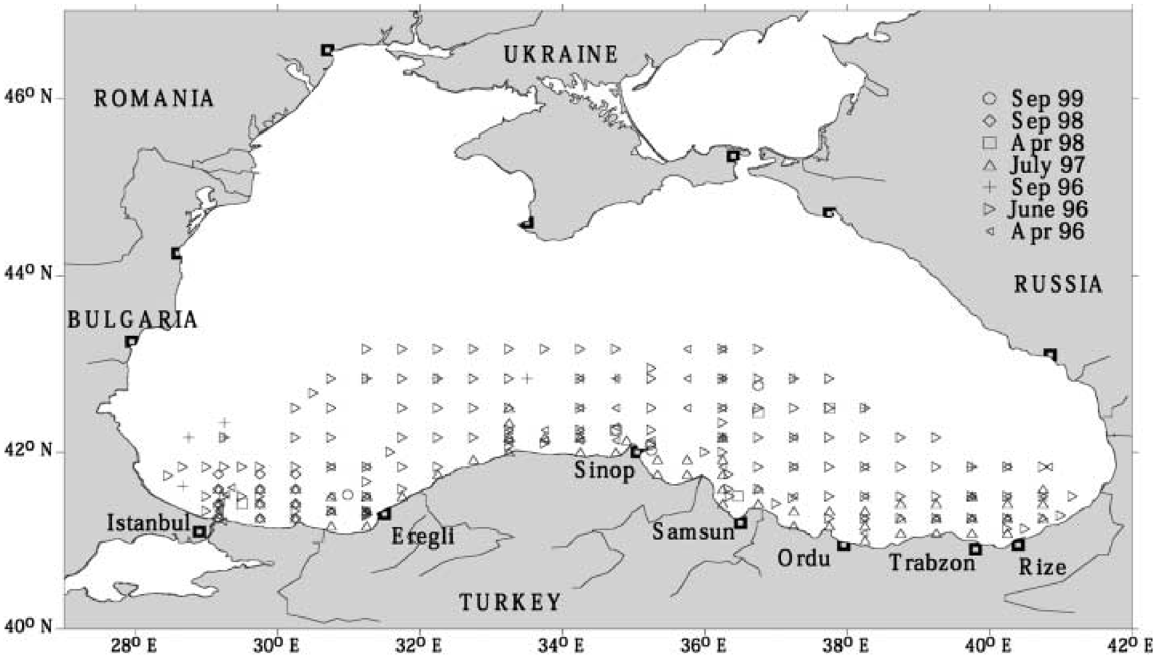
The density of gelatinous macrozooplankton was calculated from the diameter of the net without taking the tow depth into account to express results per unit surface area. This type of presentation is suitable for the Black Sea as a permanent anoxic zone exists below 150–200 m; thus almost all plankton studies use this methodology.

From a total of 32,555 gelatinous macrozooplankton specimens caught in these samples, the size of 20,236 were measured individually (Table 2). Individual weighing of these animals was not practical at sea. Weight of these animals was therefore calculated from size measurements using a conversion formula. Previously,

Table 1 Number of samples analyzed

Cruise	Year	Sampling period	Total no. of: stations	Total no. of: samples
1	1996	8–16 Apr	49	50
2	1996	20 Jun–10 Jul	120	252
3	1996	28 Sep–2 Oct	14	14
4	1997	10–20 Jul	60	66
5	1998	25 Mar/20–24 Apr	5	37
6	1998	13–15 Sep	12	17
7	1999	23–28 Sep	5	48
Total			265	484

Fig. 1 Stations sampled during 1996–1999 in the southern Black Sea



Mutlu (1996) had determined that the umbrellar diameter of *Aurelia aurita*, length of *Pleurobrachia pileus* and volume of *Mnemiopsis leidyi* gave the best fits for prediction of individual weight for these species. Therefore, in this study, the umbrellar diameter was measured on a tray to the nearest centimeter for *A. aurita*, and the length of *P. pileus* was measured to the nearest millimeter using a ruler. Sometimes, *A. aurita* specimens, which were much more fragile than the other gelatinous organisms, were broken in samples, and in these cases the half diameter of specimens were measured and multiplied by two. For the measurement of individual volume of *M. leidyi* and *Beroe ovata*, 2, 5, 10, 20 and 50 ml capacity cylinders were used depending on the size of the animal. When there was a bulk of specimens sufficient for taking accurate weight determination using a balance, we determined the total weight (termed "direct weighing") of each species from each tow. These total weights were later compared with those calculated from individual measurements. Additionally, individual wet weights and volumes of 54 *M. leidyi* specimens having a wide size range (0.7–26 ml) were taken at a station (stn 27) where the sea was very calm during the 1997 cruise. The largest *M. leidyi* were measured to be 46 ml in the present study; however, only 0.5% of all *M. leidyi* caught were >26 ml in size.

Results

Variabilities between Hensen and Nansen nets and within Hensen nets

In this study all tows were vertical; either from the depth of the upper H_2S boundary or from the bottom to the surface (in shallow areas). Although the mouth diameters of both nets were the same (70 cm), their mesh sizes were different, the Hensen net having a larger mesh size (300 µm) than the Nansen net (112 µm). Comparisons of average abundance and weight data for the 1996 cruise from these two nets revealed the superiority of the larger mesh size. The Hensen net was observed to retain on average 2.7 times more specimens for all three species studied (Table 3). Some variance is to be expected due to patchy distribution of plankton and changes in the water actually sampled between successive tows. In order to understand the degree of this variability, six successive tows were performed in 1997 at one station (stn 27) with the same Hensen net. The average coefficient of variation among these tows was about 50% (Table 4).

Table 2 Number of individuals used in analyses

Species	Total no. of individuals: caught	size measured
Aurelia aurita	1,201	916
Mnemiopsis leidyi	14,309	7,622
Pleurobrachia pileus	17,045	11,698
Total	32,555	20,236

Converting measurements to weight

In order to test the equations used to calculate the weight of animals using length or other easily measured characteristics, the values from "direct weighing" (see "Materials and methods") were compared with those from the "calculated weights" based on Mutlu's (1996) equations:

for *P. pileus*:

$$\text{Wet Weight(mg)} = 0.682 + \text{Length(mm)} \times 2.522; \quad n = 33, r^2 = 0.95$$

for *A. aurita*:

$$\text{Wet Weight}(g) = 0.12 + \text{Umbrellar Diameter (cm)} \times 2.582; n = 58, r^2 = 0.95, \text{and}$$

for *M. leidyi*:

$$\text{Wet Weight}\,(g) = -0.249 + \text{Volume (ml)} \times 0.886; \quad n = 33, r^2 = 0.95.$$

It is worth noting that the measurement techniques of Mutlu and those of the present study were the same. The relationship between "direct weight" (y) and "calculated weight" (x) was expressed with the equations: $y=0.56x$ ($n=58$) for *A. aurita*, $y=1.08x$ ($n=54$) for *M. leidyi*, and $y=1.02x$ ($n=33$) for *P. pileus*. Correlation coefficients for these equations were very good ($r^2=0.95$ for *P. pileus*, 0.97 for both *A. aurita* and *M. leidyi*). Predictions were close to unity for the ctenophores but only 0.56 for the medusa. During collection, *A. aurita* was often sampled as broken pieces, while ctenophores were intact. Moreover, for *M. leidyi* our own equation (Wet Weight (g) = 0.962 × Volume (ml), $n=54$) gave an even higher correlation ($r^2=0.99$, $y=0.95x$, $n=54$) with direct weighings than the equation of Mutlu (1996).

Vertical distribution and diel migration

Vertical distributions of these three species are shown in Fig. 2a–c for cruises during which depth-stratified tows were performed. The sampling for vertical distribution of animals was designed by taking into account differences in the water column reflected in terms of

Table 3 Comparison of catchability of (*Aurelia aurita*, *Mnemiopsis leidyi*, *Pleurobranchia pileus*) between Nansen and Hensen nets (June–July 1996, $n=20$). All values as per haul

	A. aurita		*M. leidyi*		*P. pileus*	
	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)
Mean Nansen	2.6	28.9	11.1	34.5	24.4	13.0
Mean Hensen	3.2	71.6	25.9	85.1	75.3	42.7
Hensen/Nansen ratio	1.5	3.1	2.6	2.7	3.1	3.3
Overall ratio	2.7					

Table 4 Variation in catches of (*Aurelia aurita*, *Mnemiopsis leidyi*, *Pleurobranchia pileus*) among successive vertical tows (Hensen net, July 1997, stn 27, $n = 6$). All values as per haul

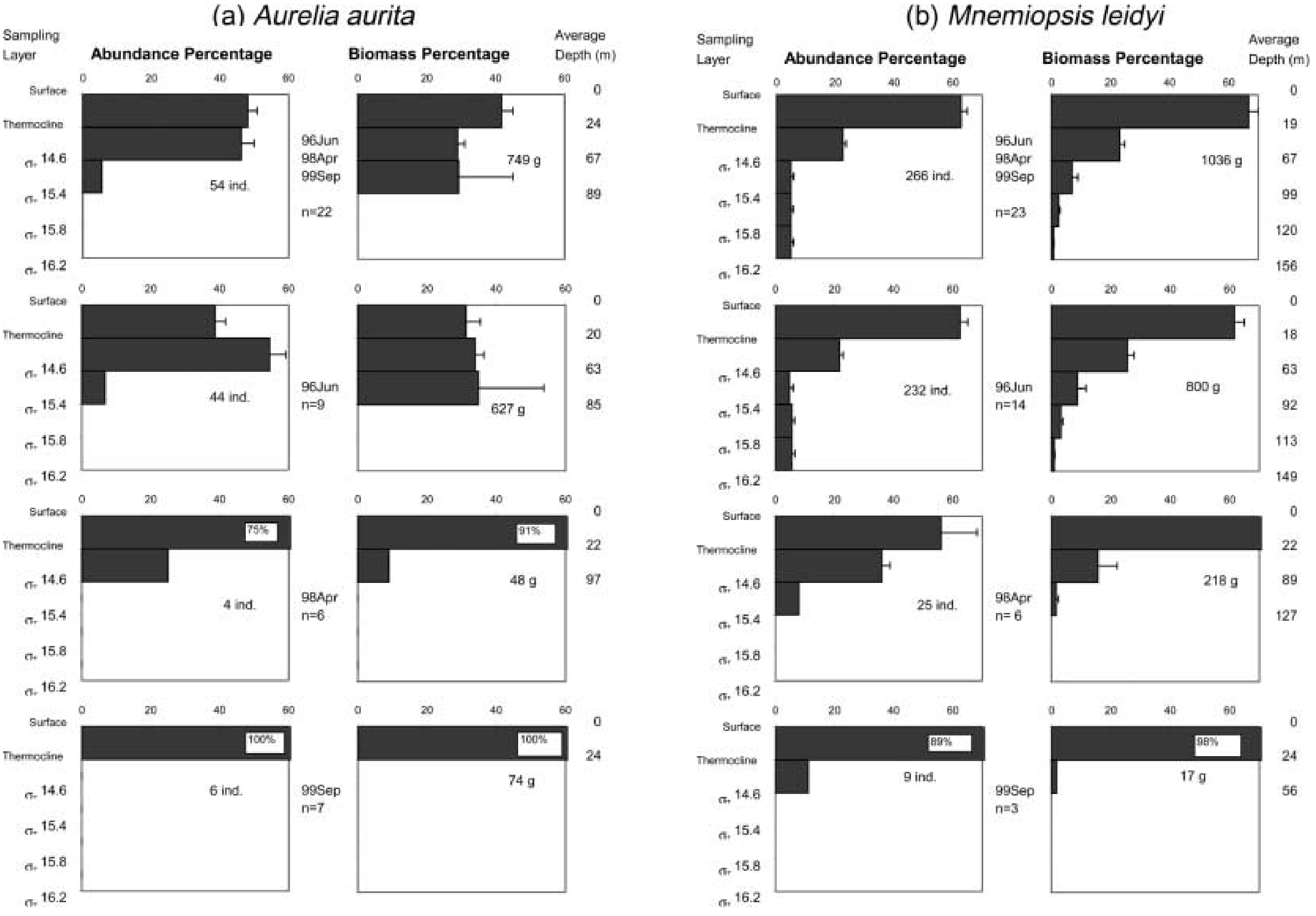
	A. aurita		*M. leidyi*		*P. pileus*	
	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)
Mean	2.8	115.7	24.7	117.3	46.8	44.4
Coeff. variation	41.3%	61.7%	43.9%	49.9%	42.6%	55.5%
Overall variation	49%					

density (Saydam et al. 1993; Besiktepe et al. 1998). Temperature, salinity and density profiles for three contrasting regions sampled during the June–July 1996 cruise are presented in Fig. 3. As seen in this figure, for example, anoxic waters start at ~100 m in the cyclonic, ~150 m in the peripheral and ~230 m in the anticyclonic regions, whereas in all these regions, the anoxic zone starts at $\sigma_t = 16.2$ sigma theta density level. For the analysis of vertical distribution of plankton data collected from different regions of the Black Sea, it is better to relate the results to density and not to absolute depth.

A. aurita was never found below $\sigma_t = 15.4$ (i.e. upper layer of the suboxic zone), its bulk being restricted to the stratum between the surface and $\sigma_t = 14.6$. From the combined data of the three cruises, it should be noted, however, that this species was able to penetrate below the thermocline (both in 1996 and in 1998; Fig. 2a). The vertical distribution of *M. leidyi* displayed a similar distribution to that of *A. aurita*. Although primarily in the surface waters, these ctenophores were always present below the thermocline down to $\sigma_t = 14.6$ (Fig. 2b). Unlike *A. aurita,* in the summer of 1996 specimens of *M. leidyi* were obtained from lower layers (at 11 stations) down to the anoxic zone. The vertical distribution of *P. pileus* was completely different from the other two species (Fig. 2c). The minority of individuals were in surface waters, the bulk occurring below the thermocline down to the anoxic zone.

Since the two ctenophore species were found in all layers in the summer of 1996, data were analyzed to see

Fig. 2a–c Vertical distribution of gelatinous macrozooplankton (**a** *Aurelia aurita*, **b** *Mnemiopsis leidyi*, **c** *Pleurobranchia pileus*) in the southern Black Sea during three different cruises and for combined data. Abundance values are given as individuals per haul and biomass values are given as grams wet weight per haul. Standard deviations of average percentage values are also shown



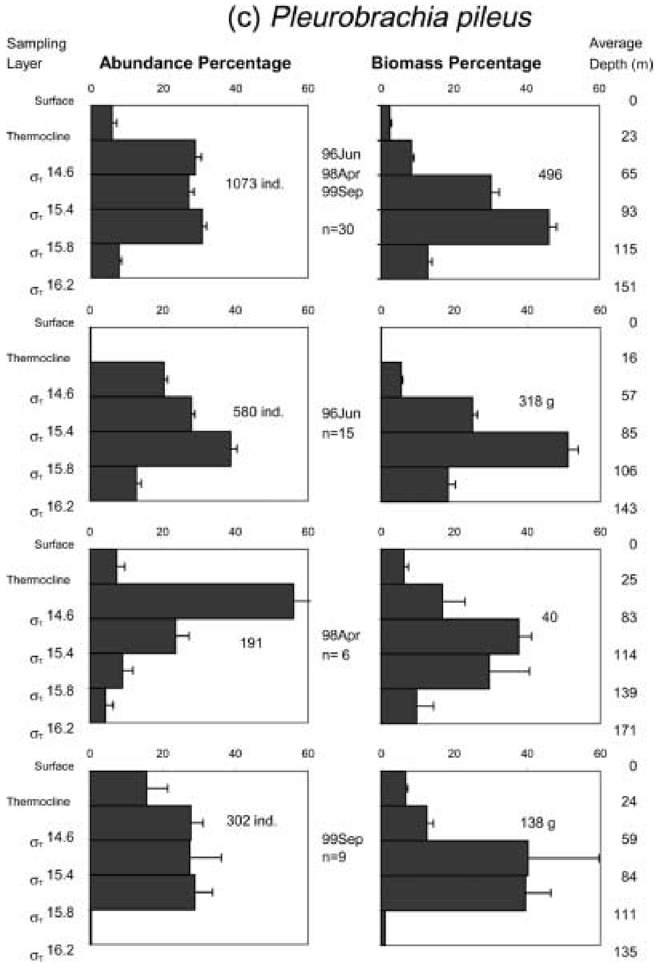


Fig. 2a–c (continued)

if these species were exhibiting diel vertical migration, as in the case of a few other mesozooplankton species in the Black Sea (Vinogradov et al. 1985; Besiktepe et al. 1998). The vertical distribution pattern compiled for 4-h intervals did not show a clear migration trend for either *M. leidyi* or *P. pileus* (Fig. 4a,b).

Horizontal distribution

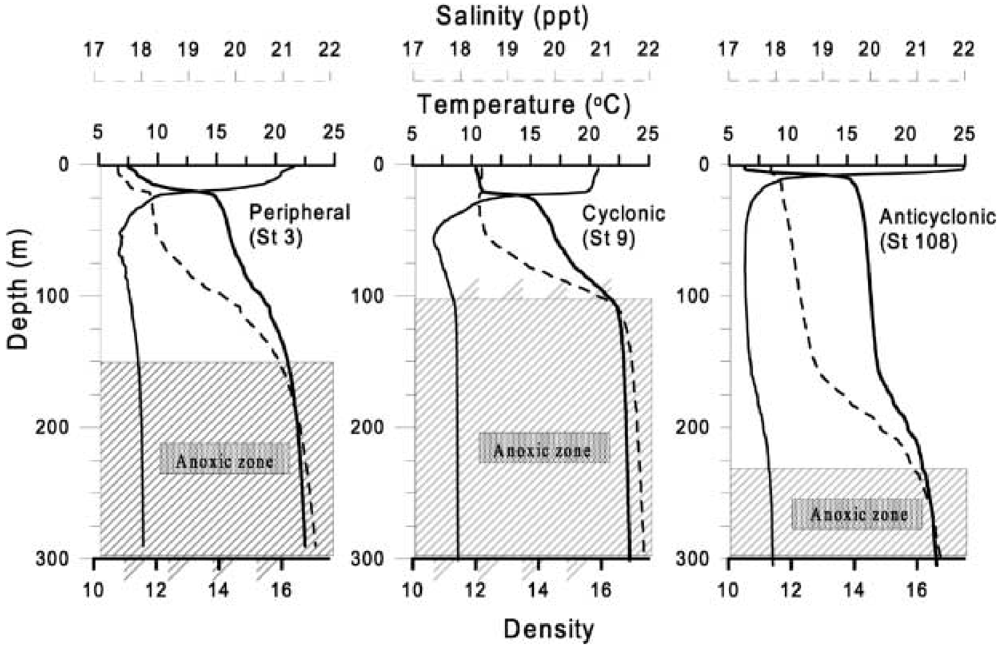
Horizontal distributions (both in abundance and biomass) of three gelatinous species are shown along with surface temperatures in Fig. 5 for three different sampling periods. It should be noted that the spatial coverage during the summer 1996 survey was the best of all cruises.

A. aurita abundances were low in offshore areas (Fig. 5a). The coastal waters of the western Black Sea displayed highest abundances (up to 468 ind. m^{-2} in April 1996) compared to the east, presumably due to a few high recruitment sites off Istanbul and Eregli. Centers of offshore cyclonic regions as well as the upwelling region (for June–July 1996) were low both in abundance and biomass (Fig. 5a,b) of *A. aurita*.

Similar to *A. aurita, M. leidyi* was also rare in centers of offshore cyclonic regions as well as in the coastal upwelling area in the summer of 1996 (Fig. 5c,d). Generally *M. leidyi* occurred more in coastal regions, along the rim current. In 1997, a high abundance (1,604 ind. m^{-2}) consisting of very small individuals (<0.2 ml) was obtained off Eregli.

Compared to the other two species, *P. pileus* showed a more homogeneous distribution (Fig. 5e,f); however, deep offshore regions were generally richer than the coastal areas. The upwelling area in the summer of 1996 also displayed high abundance and biomass values (up to 497 ind. m^{-2} and 295 g m^{-2}) of this ctenophore.

Fig. 3 Temperature (*thin continuous line*), salinity (*broken line*) and density (*thick continuous line*) profiles from the three contrasting stations (stns 3, 9, 108) of the southern Black Sea in June–July 1996



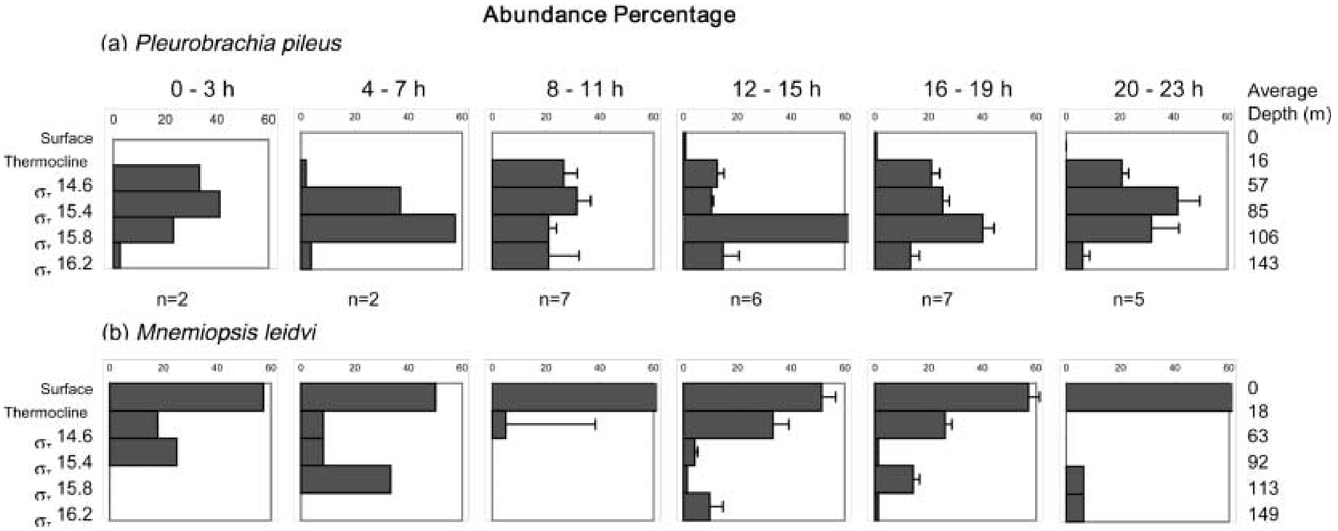


Fig. 4a, b Vertical distribution (for evaluating the diel migration) of ctenophores (**a** *Pleurobrachia pileus*, **b** *Mnemiopsis leidyi*) in different water strata during the course of 24 h, during the June–July 1996 cruise. Values are average abundances in terms of percentage. Standard deviations of average percentage values are also shown; *n* is the number of stations at which five different layers of the water column were sampled

Temporal distribution

Long-term variations in the biomass of these three species, plus that of *Beroe ovata* from the last cruise (i.e. September 1999), are shown in Fig. 6. Here it should be noted that the data after 1990 are limited to the southern Black Sea.

In the past, high biomass values (averaging ~1,500 g m^{-2} for samples taken from mainly inshore waters of different regions of the Black Sea) for *A. aurita* have been reported (Shushkina and Arnautov 1985); however, with the mass development of *M. leidyi* in 1989, its biomass decreased sharply to average levels of 125 g m^{-2}. Since then, the biomass of *A. aurita* has been recorded to be between 553 g m^{-2} (in March 1991) and 32 g m^{-2} (in September 1996) (Fig. 6).

After its peak values (up to 2 kg m^{-2}) in the summer of 1989, *M. leidyi* displayed a remarkable decreasing trend until April 1993, during which time its average biomass fell to only 14 g m^{-2} (Fig. 6). After that it gradually increased again (to 493 g m^{-2}) until 1996. From this year on, another decreasing trend started, and the biomass of *M. leidyi* had dropped to 178 g m^{-2} by the summer of 1996. Although biomass values for the next three consecutive warm periods (i.e. September 1996, July 1977 and September 1998) were a little higher, the very low biomass value of 12 g m^{-2} for the last cruise in September 1999 is striking. As a matter of fact, this was the lowest average biomass value for *M. leidyi* since its mass development in the southern Black Sea. During this cruise, we noted for the first time in our samples the presence of a new invasive predator of *M. leidyi*, the ctenophore *B. ovata*, with an average biomass value of 12 g m^{-2}. Since *B. ovata* first appeared in the Black Sea in October 1997, it is possible that we overlooked this species in our 1998 cruises.

The biomass of *P. pileus* showed the least fluctuation in the Black Sea compared to the other two species (Fig. 6). The biomass of *P. pileus* was always lower in colder months compared to warmer periods within the same year. After the mass occurrence period of *M. leidyi* (summer 1991), the average biomass of *P. pileus* was 100 g m^{-2}. However, while the biomass of *M. leidyi* was decreasing, the biomass of *P. pileus* increased to 200 g m^{-2} in July 1992 and to 264 g m^{-2} in August 1993. After that the biomass of *P. pileus* remained at moderate levels (around 100 g m^{-2}) during the summers of 1995, 1996 and 1997. Although a doubling was observed in the biomass value of this species in September 1998, the last figure (91 g m^{-2}) obtained in 1999 was again close to moderate levels.

Discussion

Sampling at sea always involves some degree of error; and in the present study this was documented once more. Although the average variation caused by patch distribution of the three gelatinous macrozooplankton was only 50%, on average a 2.7-fold difference occurred between the 112 μm Nansen and 300 μm Hensen nets, with the Hensen net consistently collecting more jellyfish. A similar 50% coefficient of variation found among replicate tows is close to the value (40%) of Kremer and Nixon (1976) from 31 replicate hauls using mesh sizes of 3–10 mm in Narragansett Bay and comparable with the range of 22.4–44.7% usually found in plankton sampling (Cassie 1963). The large difference in capture efficiency between the two nets used in the present study is attributed to clogging of the net material by gelatinous matter from the animals. Similar differences (three- to fourfold) in the catchability of *Mnemiopsis leidyi* have been observed between the BR (mouth opening 80 cm,

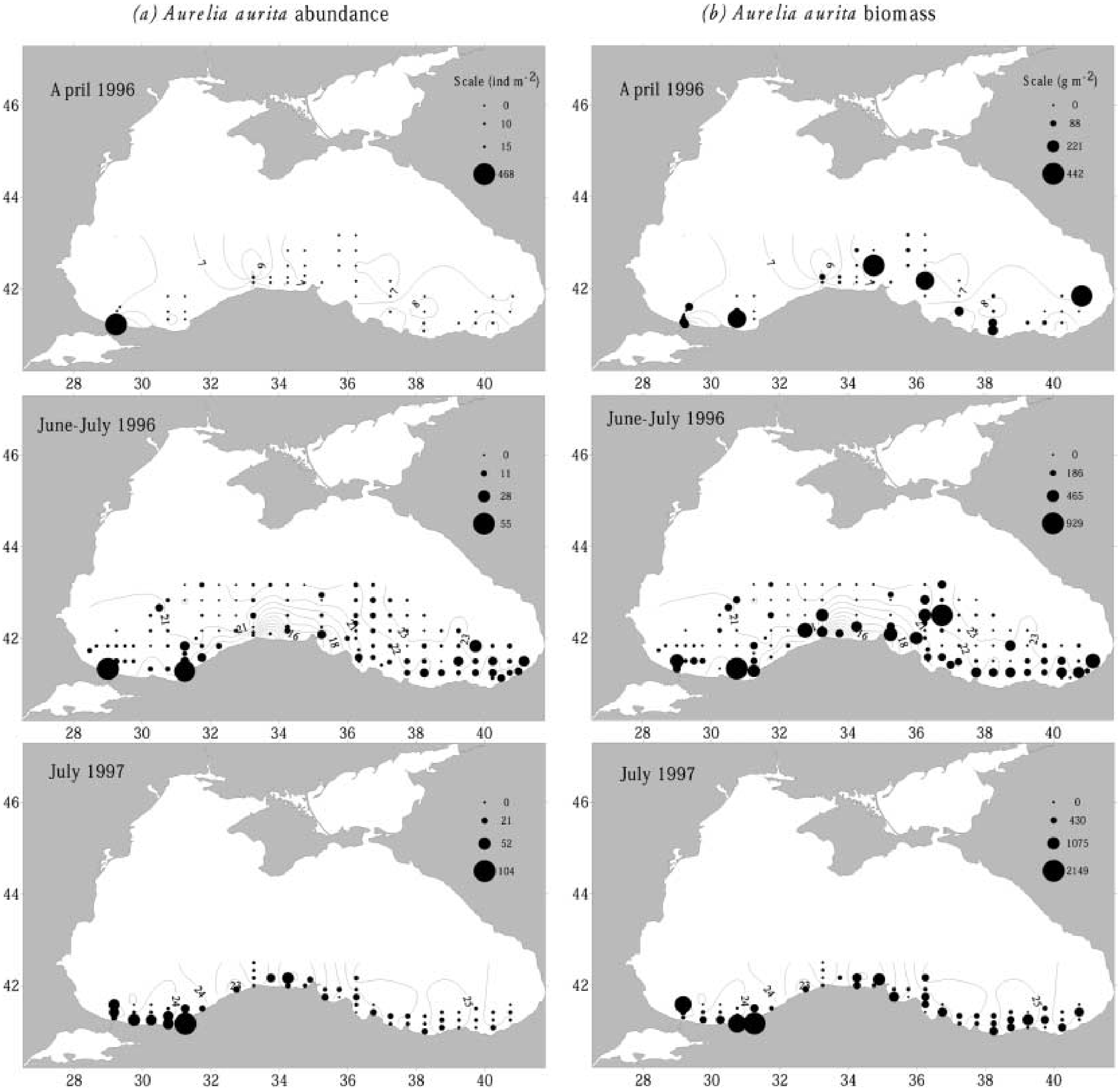


Fig. 5a–f Horizontal distribution according to abundance (**a**,**c**,**e**) and biomass (**b**,**d**,**f**) of gelatinous macrozooplankton (**a**,**b** *Aurelia aurita*; **c**,**d** *Mnemiopsis leidyi*; **e**,**f** *Pleurobrachia pileus*) in the southern Black Sea during three different cruises with wide spatial coverage. Contours show the temperature distributions in degrees Celsius. Maximum values obtained are shown in the keys

mesh size 500 μm) and Juday nets (mouth opening 50 cm, mesh size 200 μm) by Shushkina and Musayeva (1990). Both their study and our study clearly demonstrate the importance of mesh size of nets used. Moreover, Shushkina and Musayeva (1990) obtained higher values for medusae and ctenophores from direct observation using a submersible than those obtained by either of these nets. Thus, they suggested that the BR net could catch on average only one-third or one-fourth of organisms present in the sampled layer. In the present study, during all cruises, the main net used was the Hensen, whilst the Nansen net was used for auxiliary aims only. Thus, except data for vertical distribution, all comparative (horizontal and temporal) data were obtained by the Hensen net. However, it should be noted that in future studies a flowmeter must be employed to evaluate the filtering efficiency of the nets used.

In the literature, the length of *M. leidyi* (as well as other gelatinous macrozooplankton species) is one of the most commonly measured variables to calculate biomass (Purcell 1988). However, both Mutlu's (1996, 1999) and Kremer and Nixon's (1976) results clearly show that volume of this species (as well as that of *Beroe*; our unpublished data) is a better variable to calculate its

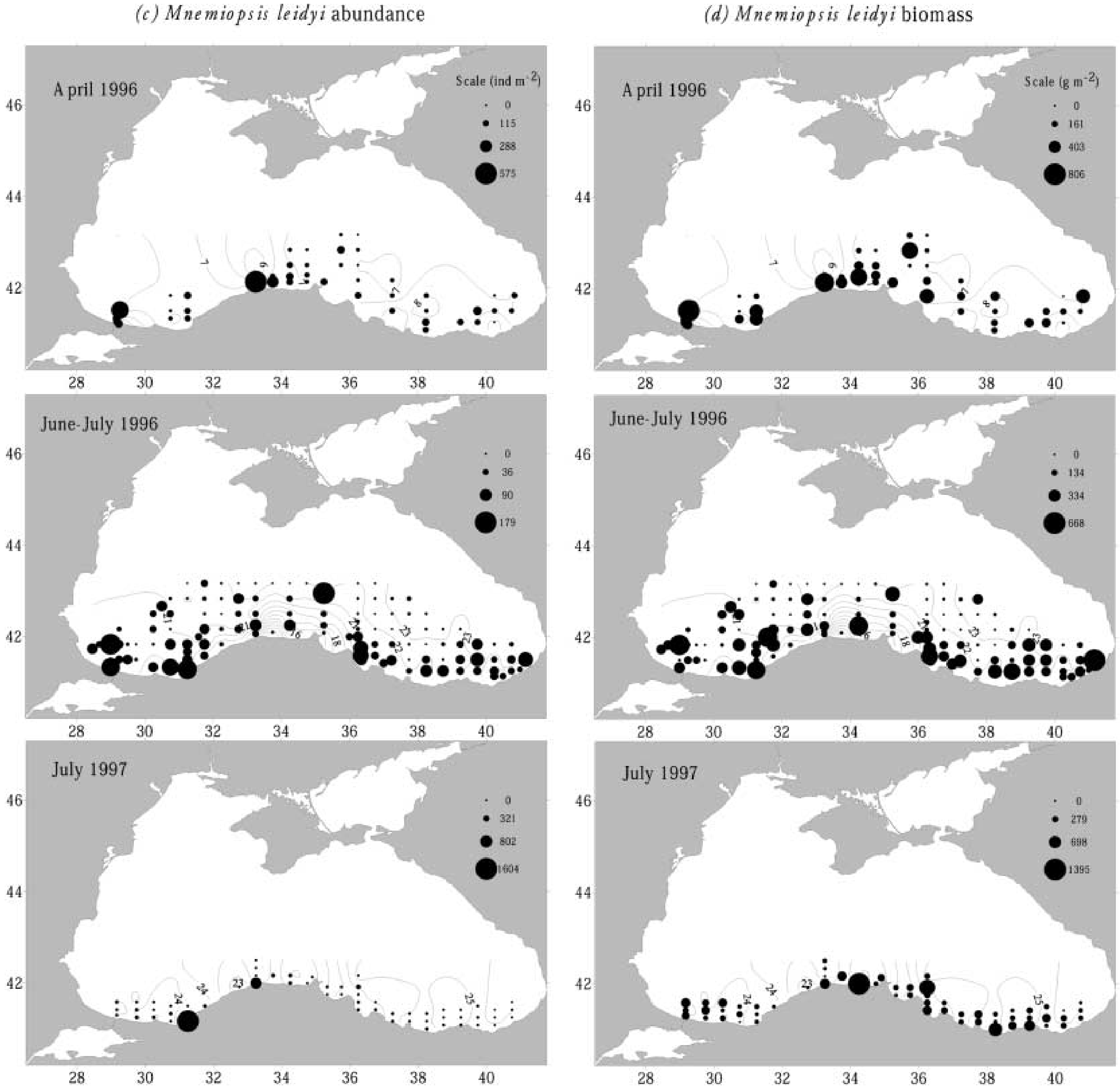
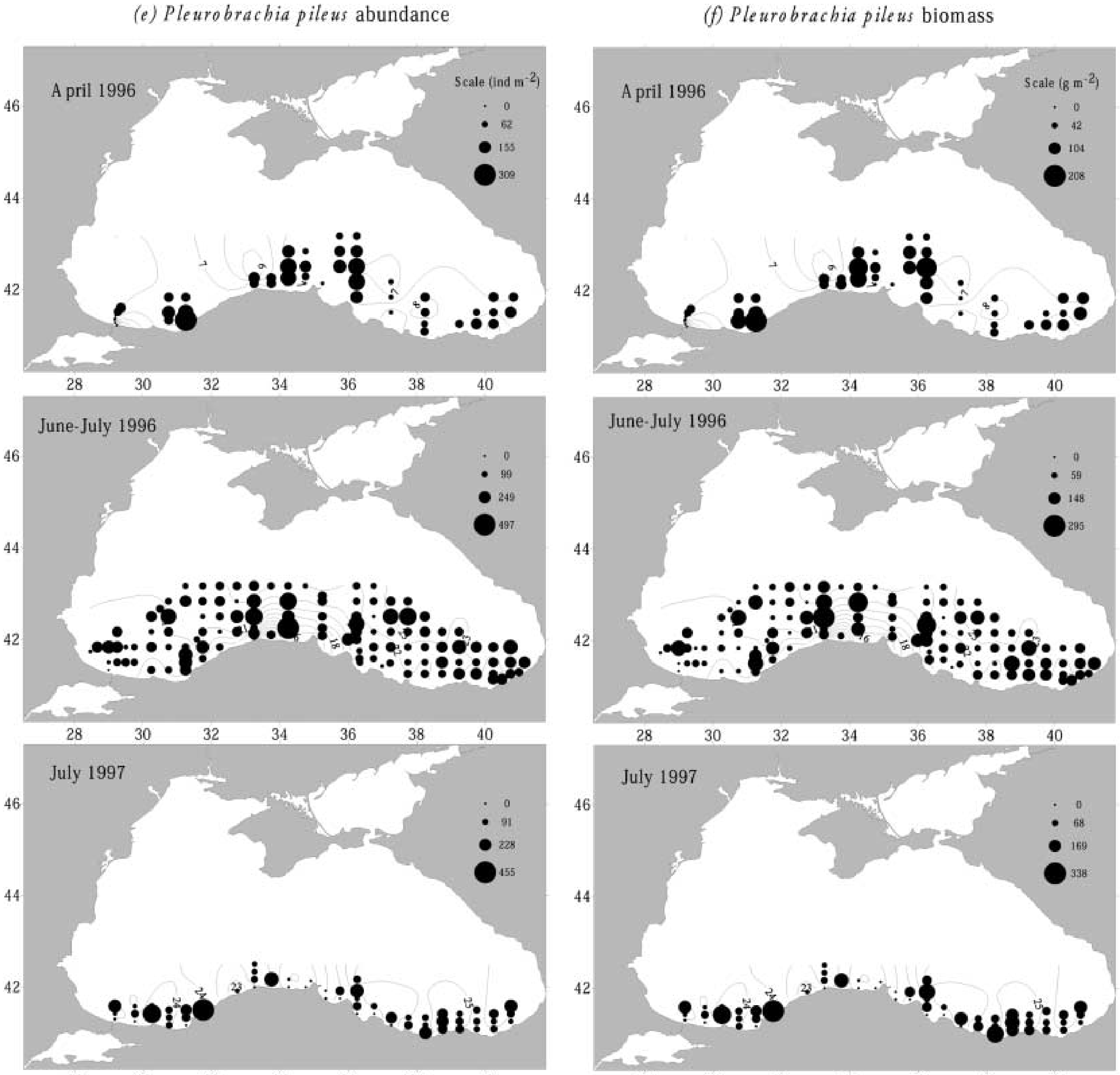


Fig. 5a–f (continued)

weight. Moreover, our simpler equation for the relationship between wet weight and volume of *M. leidyi* gave an even better correlation than that of Mutlu (1999).

Except when *M. leidyi* individuals decend a few meters deeper because of windy conditions, the results from Kremer and Nixon's (1976) study with a luminescent meter suggested that in most areas in the shallow, well-mixed Narragansett Bay (northeastern US waters) *Mnemiopsis* was fairly evenly distributed vertically. Similarly Miller (1974) found that this ctenophore was homogeneously dispersed from surface to bottom at night, in contrast to an accumulation near the surface during the day in the Pamlico River, N.C. In the Black Sea, where the oxic layer may extend below 200 m, *M. leidyi* was usually in the upper mixed layer, or in and above the seasonal thermocline, with only a few individuals found in deeper layers (Vinogradov et al. 1989; Shushkina and Musayeva 1990; Bogdanova and Konsulov 1993; Mutlu 1999). We also usually observed them in surface waters, but also below the thermocline, down to the onset of the oxycline, confirming that *M. leidyi* prefers warm and well-oxygenated surface waters. Despite the fact that *M. leidyi* is a euryhaline and eurythermic species (Kideys and Niermann 1994), its optimum temperature for spawning in the Black Sea is



(e) *Pleurobrachia pileus* abundance

(f) *Pleurobrachia pileus* biomass

Fig. 5a–f (continued)

above 20°C (Zaika and Revkov 1994), which correlates with the high annual biomass during the summer and autumn months (Finenko and Romanova 2000). *M. leidyi* may also be quite abundant in winter in the Black Sea, when surface temperatures are around 7–8°C (Mutlu 1999), yet it does not usually occur in deeper waters (e.g. cold intermediate waters) having similar temperatures. Since the salinity of the oxic zone does not change much (only 3 ppt difference between the upper and lower layers of the oxic zone), the major factor for the very low occurrence of this ctenophore in deeper layers could also be the low levels of oxygen concentration. In the Black Sea, the dissolved oxygen concentration is nearly saturated (up to 450 μM) in surface waters (Yilmaz et al. 1998). The concentrations decrease gradually to 200–250 μM at depths of $\sigma_t = 14.2$ to 14.8 and steeply to 20–30 μM at depths of $\sigma_t = 15.4$ to 15.6. Unfortunately, up until now, there have been no published studies investigating the effect of low oxygen levels on the physiology of this ctenophore. However, comparison of oxygen consumption rates of this ctenophore with *Pleurobrachia pileus*, which mainly dwells in the oxycline and suboxic zone in the Black Sea, may provide a clue. Anninsky et al. (1998) described the respiration rate of *M. leidyi* with the equation $R(\mu\mathrm{l\ O_2\ h^{-1}}) = 6.73\,\mathrm{Wet\ Weight(g)}^{0.83}$ for freshly captured ctenophores

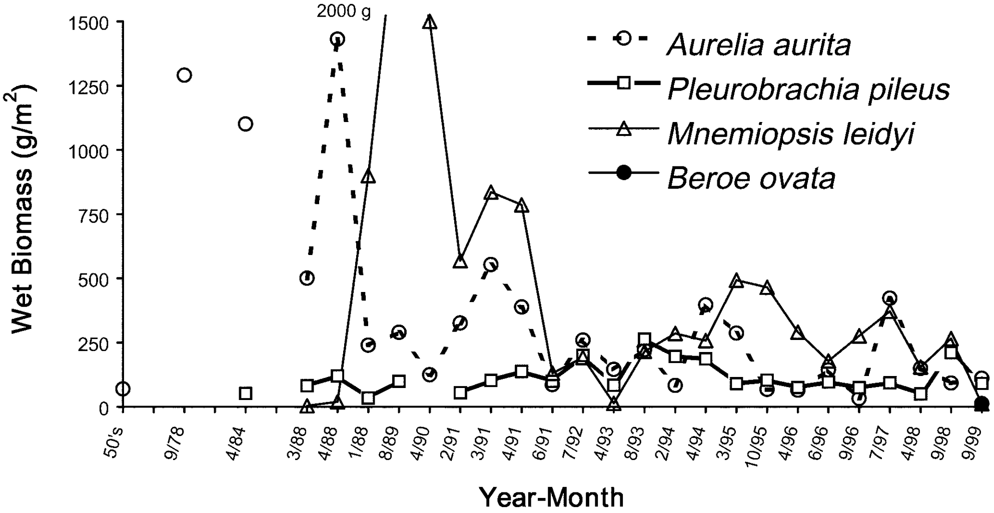


Fig. 6 Long-term changes in the biomass of gelatinous macrozooplankton (*Aurelia aurita*, *Mnemiopsis leidyi*, *Pleurobranchia pileus*, *Beroe ovata*) in the Black Sea. Data after 1990 belong to the southern Black Sea

at 22°C. Whilst the slope value was the same as that for 22°C, the intercept value was significantly lower (about 4.5) for 12–14°C. The intercept value was much lower in the equation $R = 1.2$ to $2.2W^{0.625}$ obtained for *P. pileus* measured at 17–20°C (Lazareva 1961), indicating a lower respiration rate in this ctenophore compared with *M. leidyi*. It should be pointed out that *M. leidyi* (as well as the scyphomedusa *Chrysaora quinquecirrha*) has been reported to be occasionally abundant in the bottom waters, with low dissolved oxygen concentrations, of the Chesapeake Bay (Breitburg 2000), which is much shallower than the oxic layer of the Black Sea. However, Keister et al. (2000) reported that when the dissolved oxygen levels were < 1 mg l^{-1} (approx. 30 μM), *Mnemiopsis* were nearly absent in the bottom layers of the Patuxent River, Chesapeake Bay.

It must be noted that in June–July 1996, several specimens were also obtained from the oxycline and the suboxic zone at 11 stations sampled during both day and night. The occurrence of this ctenophore in deeper layers, with reduced oxygen levels, could not be explained solely by eddy activity (e.g. downwelling), as these stations were situated both in anticyclonic and cyclonic regions. Vertical distribution of prey zooplankton could also be important for the presence of *M. leidyi* in waters with low oxygen. Besiktepe (2001) showed that in this period there was a clear stratification in the distribution of copepods (all species and stages combined) which were concentrated at the surface during night and in deep waters (down to anoxic zone) during daytime. It could also be speculated that the specimens obtained from deeper layers were sedimenting, unhealthy organisms. Mutlu (1999) also observed a few individuals below the thermocline spreading down to the main pycnocline in March 1995. He also noticed some individuals displayed a negative taxis to daylight, accumulating below the thermocline at night. Our results differ from his as Fig. 4b does not show any clear migration pattern despite the diel stratification in prey zooplankton.

Except for a total of three individuals, obtained from the layer between $\sigma_t = 14.6$ and 15.4 in June–July 1996, *Aurelia aurita* was exclusively restricted to the well-oxygenated surface layers (down to $\sigma_t = 14.6$). This is similar to the findings of previous studies (Shushkina and Musayeva 1983; Vinogradov et al. 1989; Mutlu 1999), although *A. aurita* has been reported to show diel vertical migration (sometimes the usual nocturnal migration but sometimes reverse migration) in other parts of the world (Arai 1997).

In contrast to the two previously mentioned species, *P. pileus* was found to dwell mainly below the seasonal thermocline down to the upper boundary of the H_2S zone; these findings are similar to those of previous studies (Vinogradov et al. 1985, 1989; Mutlu and Bingel 1999). However, whilst Vinogradov et al. (1985, 1989) observed that *P. pileus* migrate to the upper layers during night, our results from the June–July 1996 cruise did not suggest a clear vertical migration pattern (as also reported by Mutlu and Bingel 1999). The main prey items of this ctenophore are late stages of the copepod *Calanus euxinus* (Vinogradov and Shushkina 1992; Mutlu and Bingel 1999). Since these copepods also migrate to surface waters at night (Besiktepe et al. 1998), a migration pattern by *P. pileus* could be expected.

Horizontal distributions of *A. aurita* and *M. leidyi* were much more patchy than that of *P. pileus*. The more homogeneous distribution of the deeper-dwelling *P. pileus* is partly related to the fact that the currents in deeper layers are less pronounced than those in surface layers (Oguz et al. 1993). As mentioned above, the main food item (39%) of *P. pileus* is the late stages of the copepod *Calanus euxinus* which is also mainly restricted to the deep, offshore regions due to their demand for suboxic conditions (Yuneva et al. 1999). Moreover, Shulman et al. (1998) showed the concentration of energy-storage compounds, lipids in *C. euxinus* and glycogen in *P. pileus*, to be higher in animals obtained from cyclonic regions compared to those from anticyclonic regions due to a more efficient nutrient-pumping potential of the former region which supports a higher primary production. This explains the high abundance and biomass values of *P. pileus* obtained in the Sinop upwelling region. In contrast to *P. pileus*, smaller copepods and meroplanktonic mollusk larvae constitute the main diet of *M. leidyi* and *A. aurita* (Anninsky et al. 1998; Mutlu and Bingel 1999), and these mesozooplankton are generally more abundant in coastal regions. It is worth noting that an affinity with coastal regions by the younger *A. aurita*, presumably due to the distribution of its benthic stage, is expected. There were hot spots for the abundance of both *A. aurita* and *M. leidyi* in the Black Sea, and some of these are undoubtedly due to reproduction and food availability. These spawning areas include the waters off Istanbul (29°E) for *A. aurita* in April 1996 (Fig. 5a) and off Eregli (31.5°E) for *M. leidyi* in 1997 (Fig. 5c). The precise conditions leading to such high spawning in these specific regions are yet unknown.

As with the homogeneity of its horizontal distribution, *P. pileus* displayed the least temporal variability in biomass among the gelatinous macrozooplankton sampled over the years. This is partly due to the more stable conditions of offshore areas where this ctenophore mainly dwells compared to the coastal areas in the Black Sea. Mutlu et al. (1994) observed a doubling in the biomass of this ctenophore between 1990/1991 and 1993. However, after 1994, its biomass was generally at moderate levels of around 50–100 g m^{-2} (Fig. 6).

Since the 1970s the population of *A. aurita* has been suggested to show an increasing trend, reaching peak values (> 1 kg m^{-2}) in the 1980s (Fig. 6) when its overall biomass for the total sea area was calculated to be 300–500 million tons (Shushkina and Musayeva 1983). After the explosive development of *M. leidyi* in 1989, the abundance of *A. aurita* dropped (Fig. 6). Shiganova et al. (1998) found a significant negative correlation ($n = 14$, $r = –0,80$, $P = 0.005$) between the number of *M. leidyi* and the biomass of *A. aurita*, indicating a potential for intense competition between these species. In the open sea, the maximum biomass values for *M. leidyi* (1.5–2 kg m^{-2}) were obtained in autumn 1989 (Vinogradov et al. 1989; Fig. 6). The abundance of fodder zooplankton, as well as of planktivorous fishes, was reported to decrease sharply during the 1990s following the outbreak of *M. leidyi* throughout the entire Black Sea (Kideys 1994; Niermann et al. 1994; Kideys et al. 1999, 2000; Kovalev et al. 1998a,b). After 1990, the biomass of *M. leidyi* decreased sharply. Comparing data only from the warm period (summer and early autumn when these ctenophores are known to increase their abundance and biomass) to eliminate seasonal variability, one can see that after the high values at the end of the 1980s, the biomass of *M. leidyi* was very low with a mean value of 131 g m^{-2} in June 1991. An increasing trend resumed during the summers of 1992, 1993 and 1995, when the biomass values of *M. leidyi* rose steadily up to 465 g m^{-2}. However, another decreasing trend has occurred since 1995. Given the lack of predators (until 1997; see below) and parasites, one of the most important factors for the decrease in the biomass of *M. leidyi* was likely to have been food limitation.

Glycogen storage is the main mechanism for energy accumulation in ctenophores (Shulman 1972). Under conditions of starvation, therefore, the level of glycogen decreases; this characteristic can be used to help understand the condition of ctenophores. Data on the body glycogen content of *M. leidyi* in September 1996 recorded levels between 21 and 44 μg g^{-1} wet weight and accounted for $52.5 \pm 14.2\%$ of total polysaccharide content on average (Anninsky et al. 1998). Thus, the condition of *M. leidyi* obtained from the field corresponded to that expected after a 2-day fasting period (determined experimentally), implying that the ctenophores were starving. Earlier (in 1991–1992), a greater expanse of the Black Sea had been providing the ctenophores with a good food supply (Anninsky 1995).

Although the trend in the biomass of *M. leidyi* observed in the early to mid-1990s appears to be related to malnutrition, the decreasing trend since then has also been affected by predation. The ctenophore *Beroe ovata* is the most recent invader in the Black Sea. All previous studies suggested that *Beroe* spp. almost exclusively feed on other ctenophores (Harbison et al. 1978; Mianzan 1999), and, therefore, this species was one of the best candidates proposed for reducing the impact of *M. leidyi* in the Black Sea (GESAMP 1997). Since its arrival in the Black Sea, several studies have already been performed to understand the feeding relationship between the two ctenophores (i.e. *B. ovata* vs. *M. leidyi*: ; Vostokov et al. 2000; Finenko et al., 2001; Shiganova et al., in press). All these new studies report almost exclusive predation on *M. leidyi* by *B. ovata* in the Black Sea. Moreover, Finenko et al. (2001), comparing mean daily specific growth rate (3.9% of population biomass: Finenko and Romanova 2000) of the *M. leidyi* population with the predatory impact of *B. ovata* (2–53% of *M. leidyi* population), suggested that particularly in the inshore waters of the Black Sea the *B. ovata* population, despite their low numbers, may control the abundance of their prey. In the present study, this was reflected in 1999 in the lowest biomass value obtained (12 g m^{-2}) since the mass development of *M. leidyi* in the Black Sea. It is worth noting that this value was obtained during the warm season, which is usually the main growth period for *M. leidyi* in the Black Sea (Zaika and Revkov 1994).

We suggest that the low biomass values of *M. leidyi* obtained from the last cruise will be maintained due to its efficient predator *B. ovata*. Given the impact of *M. leidyi* on the pelagic food web, the implications of such a relationship on the distribution and quantity of other gelatinous zooplankton, as well as on prey zooplankton and consequently on fish, will be of potential significance in the Black Sea.

Acknowledgements The present investigation was carried out with the support of a NATO Linkage Grant (ENVIR.LG.974491) and of the Turkish Scientific and Technical Research Council (TUBITAK: YDABÇAG100Y017). We would like to thank Mr. E. Dipli and Miss E. Eker for their help during the cruises, and Mrs. A. Kideys for correcting the English. We are grateful to Dr. P. Kremer and an anonymous referee for their significant contributions and constructive criticism.

References

Anninsky BE (1995) Seasonal dynamics of the chemical composition of organic matter in the ctenophore *Mnemiopsis leidyi* A. Agassiz in the Black Sea. Oceanology 35:395–399

Anninsky BE, Romanova ZA, Abolmasova GI, Gucu AC, Kideys AE (1998) Ecological and physiological state of the ctenophore *Mnemiopsis leidyi* (Agassiz) in the Black Sea in autumn 1996. In: Ivanov L, Oguz T (eds) NATO TU-Black Sea project: ecosystem modeling as a management tool for the Black Sea, symposium on scientific results. Kluwer, Dordrecht, pp 249–262

Arai MN (1997) A functional biology of Scyphozoa. Chapman and Hall, London

Besiktepe S (2001) Diel vertical distribution, and herbivory of copepods in the south-western part of the Black Sea. J Mar Syst 28:281–301

Besiktepe S, Kideys AE, Ünsal M (1998) In situ grazing rate and diel vertical migration of female *Calanus euxinus* in the Black Sea. Hydrobiologia 363:323–332

Bingel F, Kideys AE, Ozsoy E, Tugrul S, Oguz T (1993) Stock assessment studies for the Turkish Black Sea coast. NATO-TU fisheries final report, October 1993, Middle East Technical University, Institute of Marine Sciences, Erdemli, Turkey. (prepared for NATO Scientific Affairs Division, Science for Stability Program)

Bogdanova DP, Konsulov AS (1993) On the distribution of the new ctenophora species *Mnemia mccradyi* in the Black Sea along the Bulgarian coastline in the summer of 1990. Dokl Akad Nauk Bulg 46:71–74

Breitburg DL (2000) Does low oxygen favor gelatinous zooplankton in eutrophic estuaries. In: Abstracts of the international conference on jellyfish blooms held January 2000 in Gulf Shores, Ala., USA

Cassie RM (1963) Microdistribution of plankton. Oceanogr Mar Biol Annu Rev 1:223–252

Deason EE, Smayda TJ (1982) Ctenophore–zooplankton–phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. J Plankton Res 4:203–216

Finenko GA, Romanova ZA (2000) The population dynamics and energetics of ctenophore *Mnemiopsis leidyi* in Sevastopol Bay. Oceanology 40:677–685

Finenko GA, Anninsky BE, Romanova ZA, Abolmasova GI, Kideys AE (2001) Chemical composition, respiration and feeding rates of the new alien ctenophore, *Beroe ovata*, in the Black Sea. Hydrobiologia 451:177–186

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection) (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. Rep Stud GESAMP 58:1–84

Greve W (1994) The 1889 German Bight invasion of *Muggiaea atlantica*. ICES J Mar Sci 51:355–358

Harbison GR, Madin LP, Swanberg NR (1978) On the natural history and distribution of oceanic ctenophores. Deep-Sea Res 25:233–256

Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. Mar Ecol Prog Ser 205:43–59

Kideys AE (1994) Recent dramatic changes in the Black Sea ecosystem: the reason for the sharp decline in Turkish anchovy fisheries. J Mar Syst 5:171–181

Kideys AE, Niermann U (1994) Occurrence of *Mnemiopsis* along the Turkish coast. ICES J Mar Sci 51:423–427

Kideys AE, Gordina AD, Niermann U, Uysal Z, Shiganova TA, Bingel F (1998) Distribution of eggs and larvae of anchovy with respect to ambient conditions in the southern Black Sea during 1993 and 1996. In: Ivanov L, Oguz T (eds) NATO TU-Black Sea project: ecosystem modeling as a management tool for the Black Sea, symposium on scientific results. Kluwer, Dordrecht, pp 189–198

Kideys AE, Gordina AD, Bingel F, Niermann U (1999) The effect of environmental conditions on the distribution of eggs and larvae of anchovy (*Engraulis encrasicolus* L.) in the Black Sea. ICES J Mar Sci 56:58–64

Kideys AE, Kovalev AV, Shulman G, Gordina AD, Bingel F (2000) A review of zooplankton investigations of the Black Sea over the last decade. J Mar Syst 24:355–371

Konsulov AS, Kamburska LT (1998) Ecological determination of the new ctenophora–*Beroe ovata* invasion in the Black Sea. Tr Inst Okeanol BAN, Varna, Bulgaria 2:195–198

Kovalev AV, Gubanova AD, Kideys AE, Melnikov VV, Niermann U, Ostrovskaya NA, Prusova IYu, Skryabin VA, Uysal Z, Zagarodnyaya JuA (1998a) Long-term changes in the biomass and composition of fodder zooplankton in a coastal regions of the Black Sea during the period 1957–1996. In: Ivanov L, Oguz T (eds) NATO TU-Black Sea project: ecosystem modeling as a management tool for the Black Sea, symposium on scientific results. Kluwer, Dordrecht, pp 209–220

Kovalev AV, Niermann U, Melnikov VV, Belokopytov V, Uysal Z, Kideys AE, Ünsal M, Altukhov D (1998b) Long-term changes in the Black Sea zooplankton: the role of natural and anthropogenic factors. In: Ivanov L, Oguz T. (eds) NATO TU-Black Sea project: ecosystem modeling as a management tool for the Black Sea, symposium on scientific results. Kluwer, Dordrecht, pp 221–234

Kremer P, Nixon S (1976) Distribution and abundance of the ctenophore, *Mnemiopsis leidyi* in Narragansett Bay. Estuar Coast Mar Sci 4:627–639

Lazareva LP (1961) The effect of temperature and salinity on oxygen consumption by different sized ctenophores *Pleurobrachia pileus* O.F. Müller. Tr Khar'k Biol Stn Kiev 17:85–96

Mianzan HW (1999) Ctenophora. In: Boltovskoy D (ed) South Atlantic zooplankton. Backhuys, Leiden, The Netherlands, pp 561–573

Miller RJ (1974) Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). Chesapeake Sci 15:1–8

Mountford K (1980) Occurrence and predation by *Mnemiopsis leidyi* in Barnegat Bay, New Jersey. Estuar Coast Shelf Sci 10:393–402

Mutlu E (1996) Distribution of *Mnemiopsis leidyi, Pleurobrachia pileus* (Ctenophora) and *Aurelia aurita* (Scyphomedusae) in the western and southern Black Sea during 1991–1995 period: net sampling and acoustical application. PhD thesis, Middle East Technical University, Erdemli, Turkey

Mutlu (1999) Distribution and abundance of ctenophores, and their zooplankton food in the Black Sea. II. *Mnemiopsis leidyi*. Mar Biol 135:603–613

Mutlu E, Bingel F (1999) Distribution and abundance of ctenophores, and their zooplankton food in the Black Sea. I. *Pleurobrachia pileus*. Mar Biol 135:589–601

Mutlu E, Bingel F, Gucu 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 51:407–422

Niermann U, Bingel F, Gorban A, Gordina AD, Gücü AC, Kideys AE, Konsulov A, Radu G, Subbotin AA, Zaika VE (1994) Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991–1992. ICES J Mar Sci 51:395–406

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

Purcell JE (1988) Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. Mar Ecol Prog Ser 45:197–200

Saydam C, Tugrul S, Basturk O, Oguz T (1993) Identification of the oxic/anoxic interface by isopycnal surfaces in the Black Sea. Deep-Sea Res 40:1405–1412

Shiganova TA, Kideys AE, Gucu AC, Niermann U, Khoroshilov VS (1998) Changes in species diversity and abundance of the main components of the Black Sea pelagic community during the last decade. In: Ivanov L, Oguz T (eds) NATO TU-Black Sea project: ecosystem modeling as a management tool for the Black Sea, symposium on scientific results. Kluwer, Dordrecht, pp 171–188

Shiganova TA, Bulgakova YuV, Volovik SP, Mirzoyan ZA, Dudkin SI (in press) The new invader *Beroe ovata* Esch and its effect on the ecosystem in the northeastern Black Sea in August–September 1999. Hydrobiologia

Shulman GE (1972) Physiological–biochemical characteristics of annual cycles of fish (in Russian). Pishcheprom, Moscow

Shulman GE, Yuneva TV, Yunev OA, Svetlichny LS, Anninsky BE, Romanova ZA, Arashkevich EG, Kideys AE, Bingel F, Uysal Z, Yilmaz A (1998) A biochemical approach for the estimation of food provision for heterotrophic organisms of the Black Sea. In: Ivanov L, Oguz T (eds) NATO TU-Black Sea project: ecosystem modeling as a management tool for the Black Sea, symposium on scientific results. Kluwer, Dordrecht, pp 263–280

Shushkina EA, Arnautov GN (1985) Quantitative distribution of the medusa *Aurelia* and its role in the Black Sea ecosystem. Oceanology 25:102–106

Shushkina EA, Musayeva EI (1983) Role of medusae in plankton community energetics. Oceanology 23:125–130

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

Tsikhon-Lukashina YeA, Reznichenko OG (1991) Diet of the ctenophore *Mnemiopsis* in the Black Sea as a function of size. Oceanology 31:320–323

Tsikhon-Lukashina YeA, Reznichenko OG, Lukasheva TA (1991) Quantitative patterns of feeding of the Black Sea ctenophore *Mnemiopsis leidyi*. Oceanology 31:196–199

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

Vinogradov ME, Flint MV, Shushkina EA (1985) Vertical distribution of mesozooplankton in the open area of the Black Sea. Mar Biol 107:89–75

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

Vinogradov ME, Arashkevitch EG, Ilchenko SV (1992) The ecology of the *Calanus ponticus* population in the deeper layer of its concentration in the Black Sea. J Plankton Res 14:447–458

Vostokov SV, Arashkevich EG, Drits AV, Lukasheva TA, Tolomeev AN (2000) The investigations of the peculiarities of biology of the ctenophores *Beroe ovata* and *Mnemiopsis leidyi*, invaders into the Black Sea (in Russian). In: Matishov GG (ed) Species-invaders in the European seas in Russia. Abstracts of the presentations of the scientific seminar held 27–28 January 2000) in Murmansk

Yilmaz A, Tugrul S, Polat C, Ediger D, Coban Y, Morkoc E (1998) On the production, elemental composition (C, N, P) and distribution of photosynthetic organic matter in the southern Black Sea. Hydrobiologia 363:141–156

Yuneva TV, Svetlichny LS, Yunev OA, Romanova ZA, Kideys AE, Bingel F, Uysal Z, Yilmaz A, Shulman GE (1999) Nutritional condition of female *Calanus euxinus* from cyclonic and anticyclonic regions of the Black Sea. Mar Ecol Prog Ser 189:185–204

Zaika VE, Revkov NK (1994) Anatomy of gonads and spawning regime of ctenophore *Mnemiopsis* sp. in the Black Sea (in Russian). Zool J 73:5–10