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Distribution of the alien ctenophore *Mnemiopsis leidyi* in the Caspian Sea in August 2001

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Abstract In this study, spatial and vertical distributions of the invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea were evaluated by using data collected at 41 stations during the August 2001 cruise. A comparison of data from different depths revealed that *M. leidyi* were generally confined to surface waters. The maximum size of the ctenophore was only 41–45 mm, and the bulk of individuals (85.5%) were <10 mm in length. The average and maximum biomasses of *M. leidyi* were calculated as 120 and 351 g wet weight m^{-2}, respectively. Whilst highest biomasses were observed in the western and central Middle Caspian Sea, hot spot areas of reproduction were present along the coasts of the western Caspian Sea, with abundance values of up to 2285 ind. m^{-2}. The impact of such high densities of *M. leidyi* is expected to be significant for the pelagic ecosystem of the Caspian Sea.

Introduction

In the 1980s, the introduction of a new species (a lobate ctenophore, *Mnemiopsis leidyi* or *M. mccradyi*) into the Black Sea radically affected the whole ecosystem (Vinogradov et al. 1989; Harbison 2001). By reaching enormous biomass levels (up to 1.5–2 kg m^{-2} in the summer of 1989), this ctenophore had a negative impact on the most dominant fish species of the Black Sea, the anchovy *Engraulis encrasicolus*, through competition for the edible zooplankton as well as through the consumption of anchovy eggs and larvae. The mass occurrence of *M. leidyi* was one of the most important reasons for the sharp decrease of anchovy and other pelagic fish stocks in the Black Sea (Kideys 1994). Due to the scale of the problem, the United Nations Environmental Programme became involved, in order to find a solution to the negative impact of *M. leidyi* on the Black Sea ecosystem (GESAMP 1997).

In the meantime, the possibility of its introduction into other sensitive, neighbouring ecosystems, notably the Caspian Sea, was mentioned (Dumont 1995; GESAMP 1997). And, as expected, this ctenophore has been reported in the Caspian Sea since November 1999 (Ivanov et al. 2000; Zaitsev and Öztürk 2001). Ivanov et al. (2000) suggested that this ctenophore was transported with ballast water taken aboard in the Black Sea or the Sea of Azov (where *M. leidyi* occurs in the warm months) and released after ballast-loaded ships had passed through the Volga Don Canal and the shallow, freshwater areas of the northern Caspian Sea into the saltier central or southern Caspian waters.

Since *M. leidyi* is a voracious predator on zooplankton, catches of the main zooplanktivorous fish, kilka (*Clupeonella* spp.), are reported to have already decreased significantly in some riparian countries since 2001 (Kideys et al. 2001a,b). For example, the kilka (*Clupeonella* spp.) catches of Iran initially dropped to 64-thousand tonnes in 2000 and to 45-thousand tonnes in 2001, from 82- and 83-thousand tonnes in 1998 and 1999, respectively (Kideys et al. 2001a). So within 2 years, an almost 50% decrease in the kilka catches of Iranian fishermen has occurred, with a minimum of 15-million US dollars in economic loss. Similarly, Azerbaijan kilka catches dropped to 9-thousand tonnes in 2001 from 20-thousand tonnes in 1999 and 18-thousand tonnes in 2000 (Kideys et al. 2001b). So, for Azeri fisheries, this too represents about a 50% decrease in the kilka catches between 1999 and 2001. Russian catches have also been reported to have decreased remarkably

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(Shiganova et al. 2001a). Therefore, some large predators feeding on these fishes, such as the white sturgeon (*Huso huso*) and the endemic Caspian seal (*Phoca caspica*), are also considered to be highly endangered in the Caspian Sea. There have already been reports of mass mortality events for the Caspian seal (Prof. H. Dumont, personal communication). Although seal mortality is often related to viral infections, we believe that such mortalities may have been contributed to by the decrease in the kilka populations. It has also been reported that the percentage of pregnant females among seal populations decreased significantly in 2001 (Shiganova et al. 2001a), which could be related to malnutrition.

Despite recognition of the problem, there is only one published study on the distribution of *M. leidyi* in the Caspian Sea. In that study, Shiganova et al. (2001b) reported the distribution of the ctenophore to be mainly in the North Caspian and eastern region of the Middle Caspian in 2000, for the summer–autumn period. It is important to understand whether the *M. leidyi* population has reached its peak level, as in the case of the Black Sea; therefore, data from basin-scale surveys in subsequent years are necessary. In this study, distribution related to the abundance and biomass of *M. leidyi* is presented from a survey undertaken in the Middle and South Caspian in August 2001.

Materials and methods

Mnemiopsis leidyi were collected from 41 stations during an acoustical survey (to estimate pelagic fish biomass) performed by the R.V. "Issledovatel Kaspiya", during 11–29 August 2001, over the entire Middle and Southern Caspian Sea (Fig. 1). The location and bottom depths of stations, as well as the lower limit of sampling depths, are given in Table 1. Samples were generally obtained from the bottom to the surface for the shallow stations (down to 79 m). However, at 12 of a total of 13 deep stations (>200 m) located in the Middle and South Caspian, samples from two different lower-limit depths (200–0 m and 35–0 m) were obtained to better understand the vertical distribution of ctenophores (Table 1). Unfortunately there was no flow meter (to evaluate net efficiency), nor any closing mechanism for the net used (i.e. the METU net, 500 μm mesh size and 50 cm mouth opening), so we could not obtain samples from completely different horizontal layers. At each station, temperature profiles (using a CTD) and the water clarity (using a Secchi disc) were measured. At a few stations, salinity, pH and dissolved oxygen (DO) from six to ten layers were also measured (salinity by CTD, pH by an electronic pH meter and DO by the Winkler method).

At the end of each tow, the net was washed from the exterior, and the cod end was passed into a container immediately to enumerate ctenophores by naked eye. The density (both per metre area and volume) of *M. leidyi* was calculated from the diameter of the net and the tow depth.

The ctenophores were sorted into length groups of 0–5 mm, 6–10 mm, 11–15 mm and so on, for size measurements (total length including lobes) in glass petri dishes using a ruler. A total of 7078 individuals were measured and grouped in this way. Individual weighing of these animals was not practical at sea. Weights of these animals were therefore calculated from size measurements using a conversion formula. Length groups were converted to weight (in g) by using the equation obtained for the southern Caspian in July 2001 (Kideys et al. 2001a): weight $=0.0011L^{2.34}$, $R^2=0.65$, $n=98$, where L is the median length (mm) of each size group.

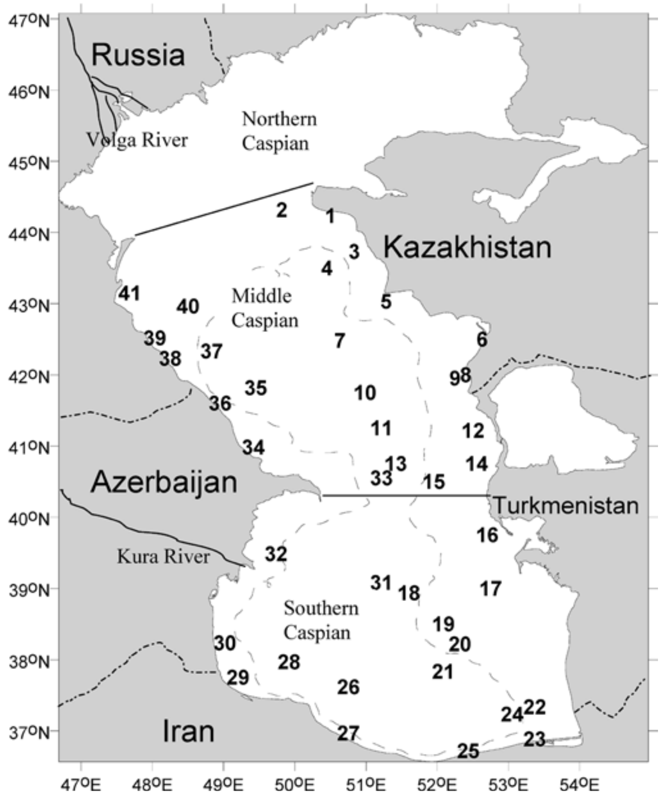


Fig. 1 Sampling stations for *Mnemiopsis leidyi* in the Caspian Sea in August 2001. *Broken line* shows the 100 m depth contour. *Solid lines* are conventional boundaries between three regions of the Caspian Sea

Results

The Secchi disk depth changed from 1 to 12.8 m during the cruise (Fig. 2). However, generally, except along eastern Iranian coasts, turbidity consistently increased from east to west. The sea-surface temperature distribution during the cruise is shown in Fig. 3. The sea-surface temperature ranged between 19.3°C and 29°C, higher values being measured in the southern Caspian. There was also a warm-water patch in the offshore region south of the Middle Caspian, with temperatures up to 28°C. There was a strong thermocline during the sampling period, its base being located at around 25–50 m depending on the station (stn) (Fig. 4). For example, whilst 22.0°C was measured at 25 m for stn 13, corresponding values for stns 35 and 10 were 16.8°C and 13.1°C, respectively (Fig. 4). The temperature decreased gradually down to 5.2°C below 400–500 m. Unfortunately the salinity could only be measured at 12 stations (all located in the eastern Caspian), where values ranged between 11.30‰ and 12.99‰ at the surface. A slight increase in salinity with depth (up to 13.67‰) was noticed (Fig. 4). The pH values from the sea surface were in the range of 8.4–8.8. Contrary to salinity, pH values decreased with depth down to 7.69. Dissolved oxygen values were generally high in the surface waters (up to

Table 1 Location, bottom depth and lower depths of stations sampled in August 2001 in the Caspian Sea. In all cases, samples were towed to the surface. At 12 stations (*bold print*), two different layers were sampled

Station no.	Sample no.	Latitude (N)	Longitude (E)	Bottom depth (m)	Lower sampling depth (m)
1	1	44.23	50.50	31	30
2	2	44.32	49.82	35	35
3	3	43.73	50.83	35	35
4	4	43.50	50.45	45	40
5	5	43.03	51.28	29	29
6	6	42.50	52.63	21	20
7	**7**	**42.48**	**50.63**	**465**	**35**
7	**8**	**42.48**	**50.63**	**465**	**200**
8	9	42.00	52.40	23	20
9	10	41.95	52.25	41	401
10	**11**	**41.75**	**50.98**	**509**	**35**
10	**12**	**41.75**	**50.98**	**509**	**200**
11	**13**	**41.25**	**51.22**	**410**	**35**
11	**14**	**41.25**	**51.22**	**410**	**200**
12	15	41.22	52.50	37	35
13	**16**	**40.75**	**51.42**	**209**	**35**
13	**17**	**40.75**	**51.42**	**209**	**200**
14	18	40.75	52.55	35	35
15	19	40.50	51.95	79	75
16	20	39.75	52.70	38	35
17	21	39.00	52.75	37	35
18	**22**	**38.93**	**51.60**	**424**	**35**
18	**23**	**38.93**	**51.60**	**424**	**200**
19	24	38.50	52.08	32	30
20	25	38.22	52.32	37	35
21	**26**	**37.83**	**52.08**	**602**	**35**
21	**27**	**37.83**	**52.08**	**602**	**200**
22	28	37.33	53.37	20	20
23	29	36.88	53.37	10	10
24	**30**	**37.23**	**53.05**	**306**	**35**
24	**31**	**37.23**	**53.05**	**306**	**200**
25	32	36.72	52.43	32	32
26	33	37.62	50.75	863	35
27	34	36.97	50.75	42	35
28	**35**	**37.97**	**49.92**	**845**	**35**
28	**36**	**37.97**	**49.92**	**845**	**200**
29	37	37.75	49.20	27	25
30	38	38.23	49.02	17	15
31	**39**	**39.08**	**51.22**	**623**	**35**
31	**40**	**39.08**	**51.22**	**623**	**200**
32	41	39.48	49.73	44	35
33	**42**	**40.55**	**51.22**	**250**	**35**
33	**43**	**40.55**	**51.22**	**250**	**200**
34	44	40.98	49.42	26	25
35	**45**	**41.82**	**49.45**	**700**	**35**
35	**46**	**41.82**	**49.45**	**700**	**200**
36	47	41.60	48.95	21	20
37	**48**	**42.33**	**48.83**	**350**	**35**
37	**49**	**42.33**	**48.83**	**350**	**200**
38	50	42.23	48.25	22	20
39	51	42.52	48.03	28	25
40	52	42.97	48.50	52	50
41	53	43.15	47.68	18	17

6.99 mg l^{-1}); however, there was a sharp decrease below 100 m to levels of <2 mg l^{-1} (Fig. 4).

Mnemiopsis leidyi was present at all 41 stations visited. Highest biomass values (up to 351 g m^{-2}) per unit area were seen all along the western Middle Caspian (including northern Azerbaijan coasts) and in the offshore region of the southern Middle Caspian, whilst

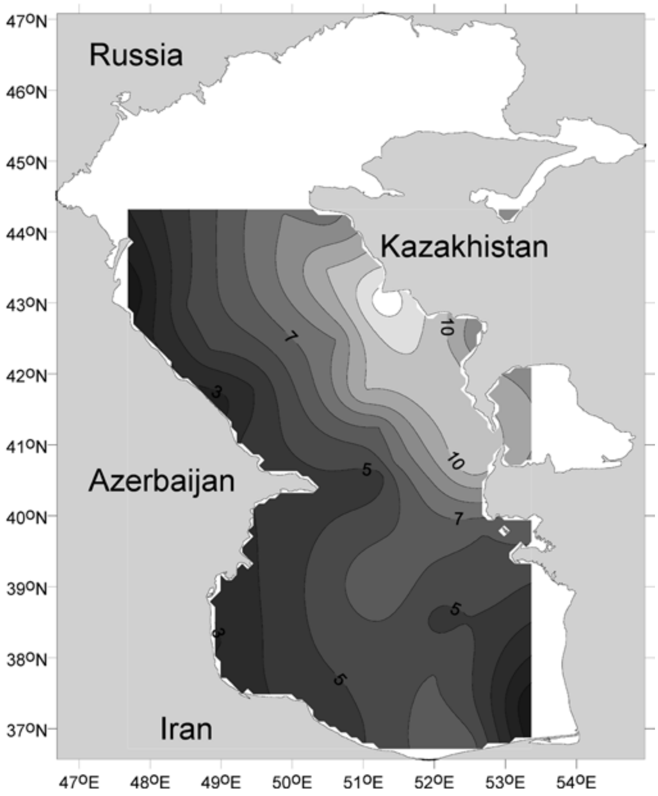


Fig. 2 Secchi disk depth (m) in the Caspian Sea in August 2001

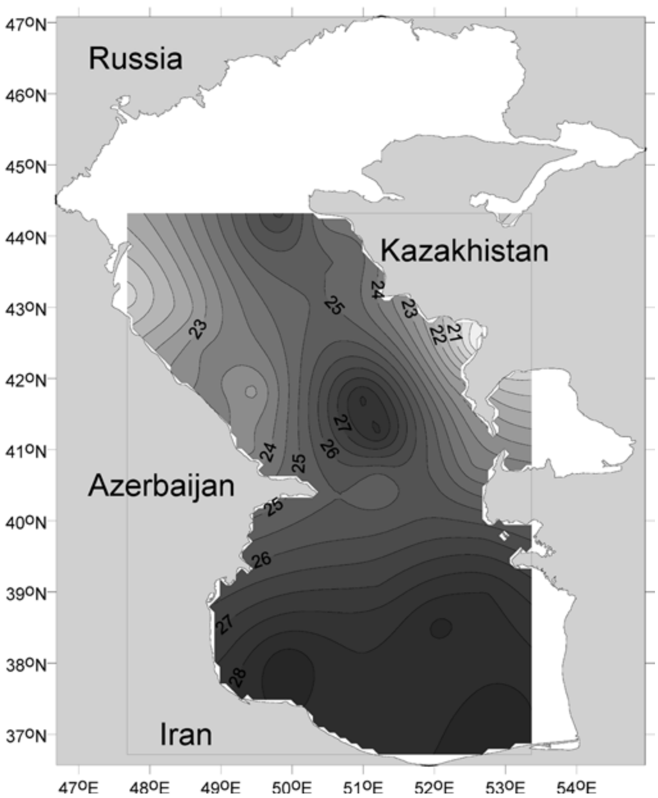


Fig. 3 Sea-surface temperature (°C) distribution in the Caspian Sea in August 2001

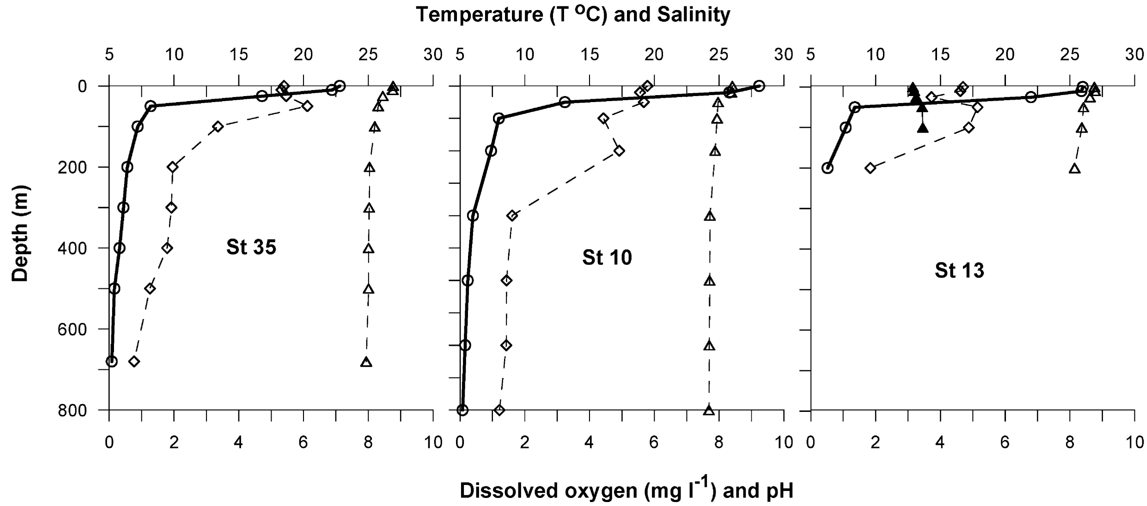
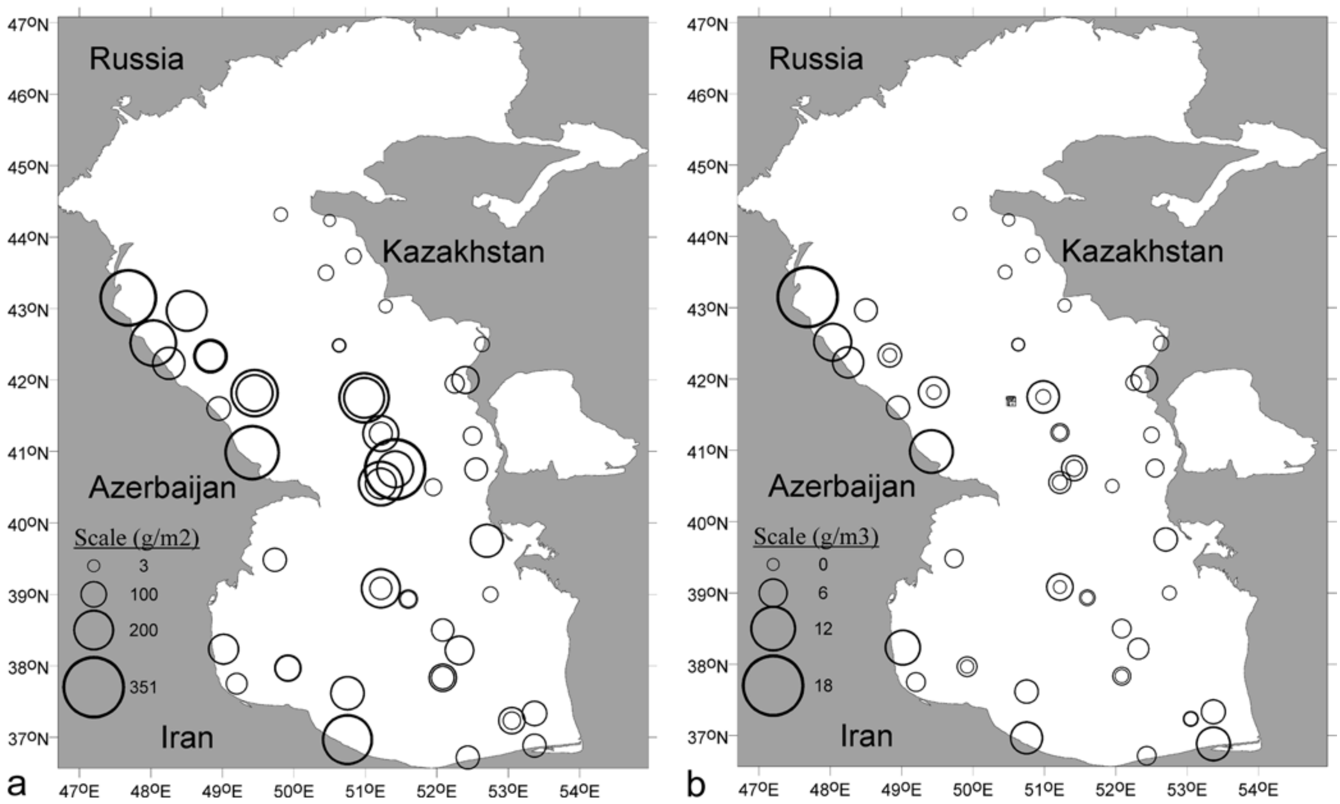


Fig. 4 Temperature (*open circles, solid lines*), salinity (*filled triangles*), dissolved oxygen (*open squares*) and pH (*open triangles*) profiles at selected stations in the Caspian Sea in August 2001

eastern coasts displayed low biomass values (down to 3.5 g m^{-2}, Fig. 5a). However, when the results were presented per unit volume, high values still occurred in the western Middle Caspian, but those for the offshore region were lower (Fig. 5b). The minimum and maximum values were calculated as 0.02 and 18.6 g m^{-3}, respectively, in this case.

Fig. 5a, b *Mnemiopsis leidyi*. Distribution of biomass in the Caspian Sea in August 2001: **a** by area (g m^{-2}) and **b** by volume (g m^{-3})

In terms of abundance, values ranged between 61 and 2285 ind. m^{-2} in the Caspian Sea (Fig. 6a). Higher abundances were observed in the west and also on the southern coasts, whilst the central and eastern regions displayed lower numbers. The two highest abundance values were observed in the coastal waters of northern Azerbaijan and of southern Russia and in the western Middle Caspian Sea. When the results were expressed per unit volume (by taking into account towing depth), it became clear that coastal areas in the west and south yielded the highest concentrations, indicating the main spawning areas (Fig. 6b). These abundance values ranged from 0.5 to 100 ind. m^{-3}.



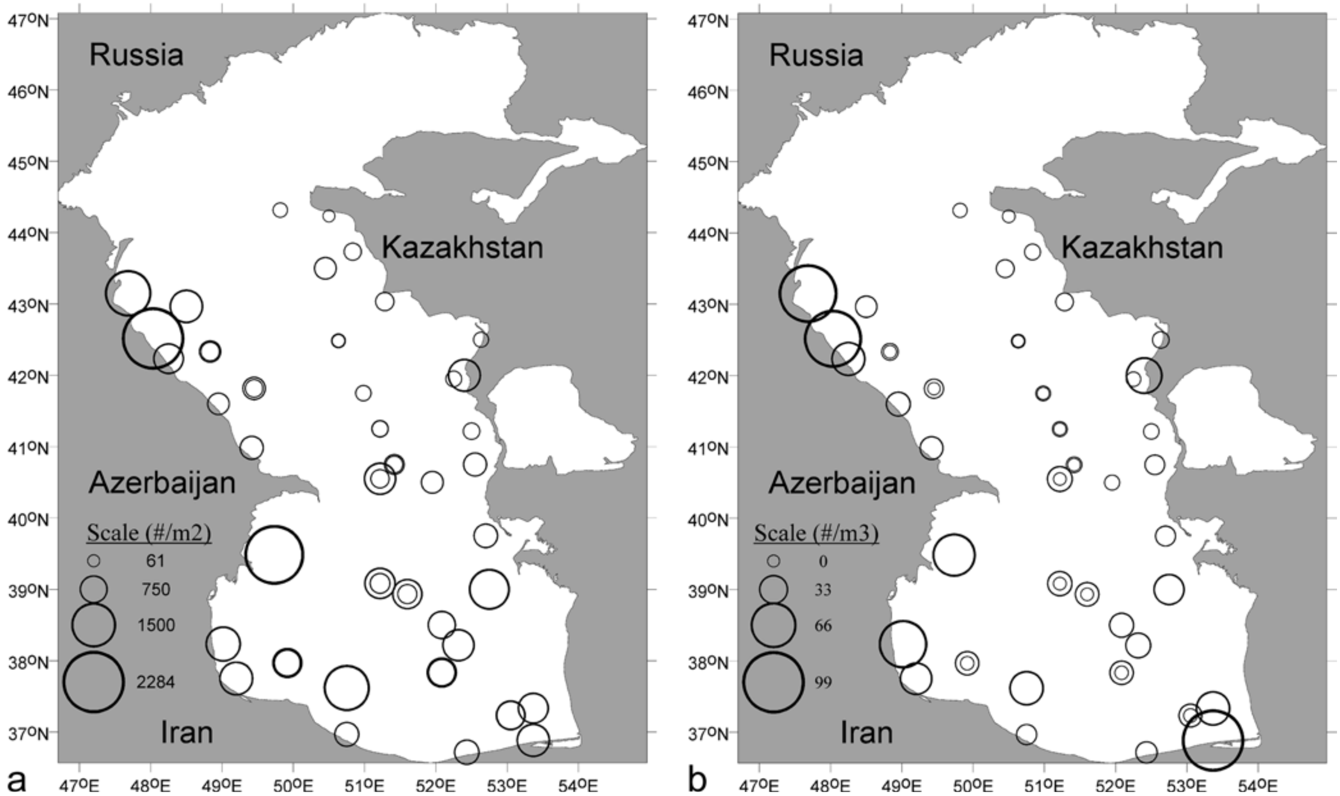


Fig. 6a, b *Mnemiopsis leidyi*. Distribution of abundance in the Caspian Sea in August 2001: **a a** by area (ind. m^{-2}) and **b** by volume (ind. m^{-3})

From a total of 7078 individuals measured, only 4 belonged to the largest length group of 41–45 mm. The length-frequency distribution displayed that 61.8% of the population belonged to the 0–5 mm group and 23.7% were from the 6–10 mm length group. Thus, these juveniles made up 85.5% of the total population.

The mean biomass distribution of *M. leidyi* from the survey confirmed that the high biomass (but low abundance) values from the offshore region of the southern Middle Caspian were due to larger animals as shown in Fig. 7. The individual mean weight of ctenophores in this region was 1.23 g compared to the overall mean weight of 0.24 g from the entire dataset.

The length-frequency distributions of *M. leidyi* from 0–35 m and 0–200 m layers are shown in Fig. 8. The ctenophores from the deeper layers displayed higher percentages of larger size groups compared to those from shallower depths. This indicates that mainly larger individuals penetrate through the thermocline to dwell in deeper waters. This was also confirmed by higher mean weight values of ctenophores from the deep tows (Table 2). However, tows from the deeper layers did not necessarily produce higher abundance values than the shallower tows (Table 2), as was confirmed by a one-tailed, paired-sample *t*-test ($t = 0.066$, $P > 0.05$). This shows that, despite the larger animals' ability to penetrate into deeper waters, the majority of ctenophores still remained at the surface waters (0–35 m).

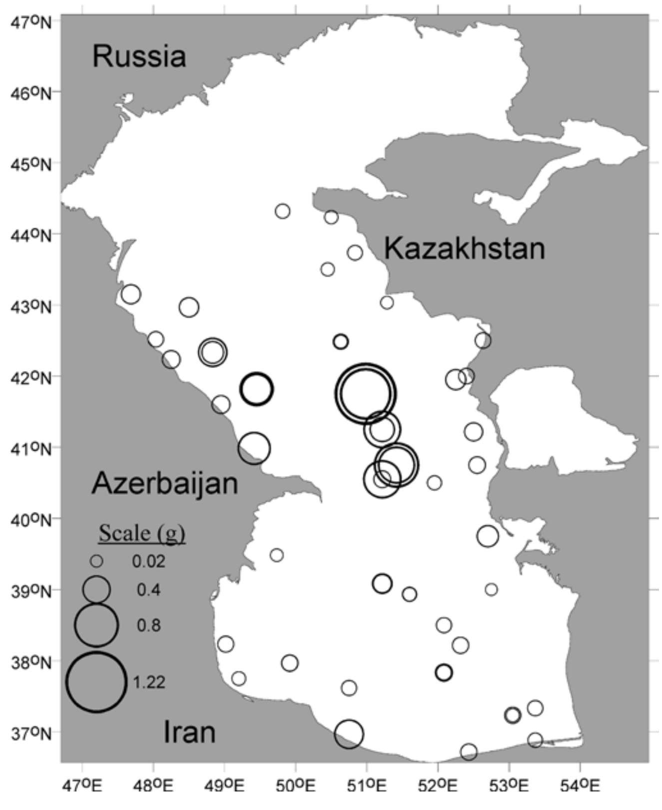


Fig. 7 *Mnemiopsis leidyi*. Distribution of the individual mean weight (g) of *M. leidyi* in the Caspian Sea in August 2001

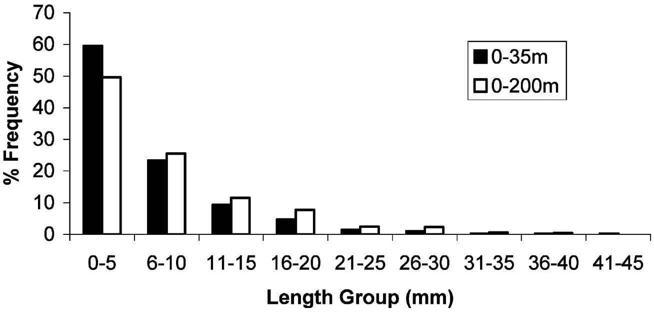


Fig. 8 *Mnemiopsis leidyi*. Comparison of size frequencies of the *M. leidyi* population from two depth layers in the Caspian Sea in August 2001. Total numbers of individuals are 1235 and 1035 for the 0–35 m and 0–200 m depth layers, respectively

Discussion

The minimum and maximum surface temperatures (19.3°C and 29°C) observed in our study are within the range of the general temperature distribution in the Caspian for the sampling month (i.e. August). Kosarev and Yablonskaya (1994) reported that in the northern Caspian, the maximum temperatures are 25–26°C in July. In August, temperatures in shallow regions of the Caspian, e.g. the northern Caspian, begin to fall, but in deeper regions they persist within the same range as for July, with values of up to 28–29°C. Despite shallow regions having a homogeneous vertical distribution for temperature, at the shelf edge, the temperature decreases sharply by 7–8°C at depths of 25 m, as was observed in our study. However, the depth of the mixed layer was not the same as in the basin, changing between 20 and 40 m (see Fig. 4), the higher values possibly indicating downwelling areas as was the case for stn 13 (located in the offshore region of the southern Middle Caspian, where the temperature at 25 m was still as high as 22°C) as opposed to stn 35 (where the temperature at 25 m was 16.8°C). Downwelling areas are known to concentrate plankton (Niermann et al. 1994); this must be the reason for the high ctenophore biomass obtained from this region as well as for the higher occurrence here in both number and biomass of organisms from the deeper layer (200–0 m) as compared to the other depths sampled.

The ability of *Mnemiopsis leidyi* to dwell in deep waters was not clear from the studies carried out in its native region (i.e. north-western Atlantic), where most studies were conducted in shallow areas, or in the Black Sea where the oxygen concentrations decrease very sharply at depth. *M. leidyi* is reported to be fairly evenly distributed vertically in the shallow, well-mixed Narragensett Bay (north-eastern American waters; Kremer and Nixon 1976). In the Black Sea, where the oxic layer may rarely extend below 200 m, *M. leidyi* was usually found in the upper mixed layer, or in and above the seasonal thermocline, with only a few individuals found in deeper layers with low oxygen concentrations (Vinogradov et al. 1989; Bogdanova and Konsulov 1993; Mutlu 1999). Kideys and Romanova (2001) also frequently observed *M. leidyi* in surface waters, as well as below the thermocline, down to the onset of the oxycline (< 20 μM or 0.5 mg l^{-2} DO). The reasons for the scarcity of ctenophores below the thermocline (of which the lower boundary is 25–50 m) in the Black Sea have been suggested to be low concentrations of food, temperature and oxygen (Kideys and Romanova 2001). Despite the fact that *M. leidyi* is known to display wide salinity and temperature tolerances (Kideys and Niermann 1994), its optimum temperature for spawning in the Black Sea is above 20°C (Zaika and Revkov 1994), correlating with the high annual biomass during the summer and autumn months (Finenko and Romanova 2000). *M. leidyi* also prefers warm and well-oxygenated surface waters. The results obtained in the present study imply that despite abundant levels of dissolved oxygen down to 100–200 m (Fig. 4), *M. leidyi* does not occur much below the thermocline (about 35 m; Table 2) in the Caspian Sea. Moreover, those penetrating below the thermocline are larger individuals, probably more resistant to the adverse conditions (such as lower food and temperature levels) at these depths. This study confirms that *M. leidyi* prefers surface waters (in or above the thermocline) with warmer temperatures.

In general, due to the virtual lack of permanent rivers, the eastern Caspian receives the least freshwater

Table 2 *Mnemiopsis leidyi*. Comparison of abundances and mean weights of *M. leidyi* from vertical tows from 0 to 35 m (*35*) and from 0 to 200 m (*200*), for 12 stations from the deep regions of the Caspian Sea in August 2001

Station	Total abundance (ind. m^{-2})			Mean wt (g)		
	35	200	Difference 35–200	35	200	Difference 35–200
7	153	91.8	61.2	0.10	0.05	0.05
10	224.4	214.2	10.2	1.23	0.97	0.26
11	244.8	275.4	–30.6	0.33	0.63	–0.30
13	290.7	428.4	–137.7	0.62	0.82	–0.20
18	861.9	392.7	469.2	0.06	0.08	–0.02
21	856.8	744.6	112.2	0.10	0.15	–0.06
24	816	841.5	–25.5	0.05	0.13	–0.08
28	851.7	724.2	127.5	0.13	0.13	–0.01
31	816	841.5	–25.5	0.05	0.13	–0.08
33	953.7	362.1	591.6	0.15	0.65	–0.50
35	545.7	326.4	219.3	0.46	0.55	–0.09
37	367.2	499.8	–132.6	0.43	0.27	0.16

input among the different regions. In shallow regions, the high riverine input decreases the salinity, as in the northern Caspian. The high riverine input and consequently higher primary production in the western and southern Caspian must be the reasons for the decreased visibility observed in these regions in our study. The eastern Caspian along the Turkmenistan coasts, with the highest visibility, displayed the lowest biomass and abundance values for *M. leidyi*. It is very well known that when predators are absent, as in the Caspian or the Black Sea, high food concentration and temperature are the two most important factors determining the levels of *M. leidyi* in surface waters (Kremer 1994; Zaika and Revkov 1994; Purcell et al. 2001). However, the main reason for the low levels of *M. leidyi* along the eastern coasts of the Middle Caspian (Figs. 5, 6) must be poorer food conditions as was revealed by turbidity distribution (Fig. 2). On the contrary, the western coasts of the Middle Caspian, which have similar temperatures to the east, had much higher levels of *M. leidyi*. The western coasts receive a higher riverine input (due to the Kura and several other small rivers, as well as being influenced by the Volga River due to dominant northerly winds); hence, higher primary production and, consequently, secondary production (i.e. zooplankton) are expected. Unfortunately no primary or secondary production measurements were carried out in the present study; however, Kosarev and Yablonskaya (1994) reported that eastern coasts are much poorer with respect to these parameters compared to the west or south. For example, in August 1976, whilst western coasts in the Middle and South Caspian yielded chlorophyll values of 2.00 and 2.27 μg l^{-1}, respectively, corresponding values for the east were only 1.08 and 0.80 μg l^{-1}. Primary production values for the western and eastern coasts of the South Caspian show almost one order of magnitude difference, from 0.3 g C m^{-2} in the east to 1.66–3.39 g C m^{-2} in the west for the summer and autumn months. Similar differences have also been reported for zooplankton biomass. Thus, it was not surprising that the hot spots in *M. leidyi* abundance, as an indication of reproduction, occurred in areas with higher food availability.

It is worth noting that values in this study regarding *M. leidyi* levels are uncorrected for net efficiency. Kideys and Romanova (2001) reported that although the average variation caused by patchy distribution of *M. leidyi* was only 50%, an average 2.7-fold difference occurred between the 112 μm Nansen and 300 μm Hensen nets, with the Hensen net consistently collecting more jellies in the Black Sea. 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 different nets used is attributed to clogging of the net material by gelatinous matter from the animals. Similar differences (three- to fourfold) in catchability for *M. leidyi* have been observed between the BR (mouth opening 80 cm, mesh size 500 μm) and Juday nets (mouth opening 50 cm, mesh size 200 μm) by Shushkina and Musayeva (1990). These studies clearly demonstrate the importance of mesh size of the nets used. Moreover, the latter authors obtained higher values for medusas and ctenophores from direct observation using a submersible than those obtained by either of these nets. Thus, they suggested that even a BR net with 500 μm mesh could catch, on average, only one-third or one-quarter of the organisms present in the sampled layer. Therefore, Russian data always included a correction factor of 2–3 for *M. leidyi* quantification. In this study the mesh size used was also large (500 μm); however, no correction factor was incorporated as we are unsure to what degree our results are an underestimation in the Caspian Sea conditions.

In our study the biomass of *M. leidyi* ranged between 3.5 and 351 g m^{-2}, with an average value of 120 g m^{-2}. Shiganova et al. (2001b) reported corrected mean values of 88 g m^{-2} for June, 372 g m^{-2} for July, 960 g m^{-2} for August and 556 g m^{-2} for October 2001 from the basin-wide surveys. However, assuming a correction factor of 3, August values obtained in the aforementioned work (320 g m^{-2}) would be very close to our results. The mean abundance value obtained in the summer of 2000 was around 170 ind. m^{-2}, with a biomass of 60 g m^{-2} (uncorrected value; Shiganova et al. 2001b). Thus, although there appears to be an increasing trend in the levels of *M. leidyi* in 2001 compared to the summer of 2000, even the values from the summer of 2001 are lower than the respective values for the Black Sea in the early 1990s. *M. leidyi* was reported to be as dense as 1.5–2 kg m^{-2} (corrected values for the net efficiency) during its peak period in the summer of 1989 in the open Black Sea (Vinogradov et al. 1989). After that peak, the biomass of *M. leidyi* became very low, with a mean value of 131 g m^{-2} in June 1991 for the southern Black Sea (uncorrected value; Kideys and Romanova 2001), which was shown to be caused by malnutrition (Anninsky et al. 1998). An increasing trend reappeared during the summers of 1992, 1993 and 1995, when the biomass of *M. leidyi* rose steadily to 465 g m^{-2} (uncorrected values). The levels in later years decreased to very low values due to arrival of predatory ctenophore *Beroe ovata* in the Black Sea (Finenko et al. 2001).

Despite the fact that the highest average biomass values for the Caspian Sea are, as yet, lower than those obtained in the Black Sea, the abundance of *M. leidyi* is much higher in the Caspian Sea due to the dominance of small-sized animals in the population. Whilst mean and maximum abundances of *M. leidyi* were 681 and 2285 ind. m^{-2} in our study, respective values were 11 and 47 ind. m^{-2} in June 1991 and 40 and 408 ind. m^{-2} in August 1993 in the Black Sea (Mutlu 1996). On the other hand, the mean weight of the ctenophores was 0.24 g in the Caspian Sea, whilst the respective figures for the Black Sea were 5.3 g in the same month (i.e. August) of 1993 and 4.2 g in July 1992. Based on the same sampling period, this denotes a 22-fold difference between the mean sizes of *M. leidyi* from the two seas. Similar low individual mean weight values were also obtained from monitoring studies in different coastal areas of the Caspian Sea (for the Azerbaijan coasts in the western Caspian, the south-western Caspian and the south-eastern Caspian, unpublished data of A.E. Kideys et al., S. Bagheri and A.E. Kideys and R. Abolghaseem et al., respectively). It is worth noting that compared to other regions in the Caspian Sea, the average weight of the ctenophores was slightly higher in the northern Caspian during September and October 2001 (2.94 and 1.3 g, respectively; Shiganova et al. 2001a). However, this difference may have been caused by the overlooking of small ctenophores in the sample in Shiganova et al.'s (2001a) study. The maximal size of *M. leidyi* obtained in this study (41–45 mm) is also much smaller than that obtained for the Black Sea, where *M. leidyi* reaches up to 180 cm (Shiganova 1997). However, the very high dominance (>85% under 11 mm in length) of smaller size groups in the population in this warm season indicates the high reproductive capacity of *M. leidyi* in the Caspian.

Kideys et al. (unpublished data) have observed that both the clearance rate and respiration rate of Caspian *M. leidyi* are higher by 2- and 1.5-fold, respectively, compared to that of the Black Sea population at a temperature of 22°C (Anninsky and Abolmasova 2000; Finenko and Romanova 2000; Abolmasova 2001). After analysing literature data, Purcell et al. (2001) showed that ctenophore metabolism is sensitive to temperature, both in its native region and in the Black Sea (which has similar maximum temperatures with the Caspian surface waters). These authors also reported that weight-specific metabolism is either the same or sometimes higher for the larger *M. leidyi*. However, L. Svetlichny et al. (unpublished data) has shown that for another ctenophore, *Beroe ovata*, very small specimens could have a much higher metabolism in the Black Sea. With a dry body weight ranging from 0.0004 to 2.0 mg, the weight-specific respiration rate of the juvenile *B. ovata* diminished approximately 25-fold (from 15–18 to 0.6–0.7 μg O_2 mg^{-1} h^{-1}, respectively), but did not change in specimens ranging from 2.0 to 1200 mg. A similar phenomenon could be valid for *M. leidyi* and could, therefore, lead to the population made up of small individuals in the Caspian displaying a higher metabolism level compared to that in the Black Sea. It has also been shown (Finenko et al. 1995) that the respiration rate of *M. leidyi* depends on prey abundance and can change by a factor of two from low to high food concentration. However, at the absence of data on natural feeding rates in the Caspian, we can not comment on this. Irrespective of the reason, it has been suggested by Kideys et al. (on the basis of personal observations) that, when assessed per unit weight, the impact of *M. leidyi* in the Caspian Sea will be higher than that in the Black Sea. Therefore, lower biomass levels observed in the Caspian Sea do not necessarily mean that their impact on the ecosystem will be lower compared to the Black Sea. As a matter of fact the existing data on zooplankton and fish catches confirm our conclusion. Comparison of our data on *M. leidyi* abundance (Fig. 6b) with the results of an acoustical survey on the distribution of pelagic fish (mainly kilka, *Clupeonella* spp.) during August–September 2001 (K.A. Johannesson, unpublished data) reveals that highest kilka biomasses occurred in areas where ctenophore abundances were low, such as the northern and eastern Middle Caspian. Although the survey did not cover the area, the northern Caspian is also expected to contain high biomasses of pelagic fish at those locations where *M. leidyi* levels are reported to be lower (Shiganova et al. 2001b); this distribution is probably due to suboptimal levels in salinity (between 10‰ and 0.1‰; Kosarev and Yablonskaya 1994) for the occurrence of the ctenophore.

Based on our results on *M. leidyi* levels, it can be suggested that Russian, Azerbaijan and Iranian coasts seem to be worst affected from the invasion of this ctenophore in the Caspian Sea. This has already become apparent from the fish landing statistics for these countries, and, if the ctenophore has not yet reached its peak levels in this new environment, further decreases in fish catches are inevitable. It is also worth noting that the decrease in fish landings is only the visible part of the iceberg within the context of an ecosystem.

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