Marine Ecology. ISSN 0173-9565

ORIGINAL ARTICLE

Impact of a new invasive ctenophore (*Mnemiopsis leidyi*) on the zooplankton community of the Southern Caspian sea

Abolghasem Roohi[1], Zulfigar Yasin[2], Ahmet E. Kideys[3,5], Aileen Tan Shau Hwai[2], Ali Ganjian Khanari[1] & Elif Eker-Develi[4]

1 Caspian Sea Research Institute of Ecology, Khazarabad Boolvar, Sari, Iran
2 School of Biological Science, Universiti Sains Malaysia, Penang, Malaysia
3 Institute of Marine Sciences, Middle East Technical University, Erdemli, Mersin, Turkey
4 European Commission, Joint Research Centre, Institute for Environment and Sustainability, Ispra, Italy
5 Present address: Dolmabahce Sarayi, 2 Hareket Kosku, 34353 Besiktas, Istanbul, Turkey

Keywords
Alien; Caspian Sea; exotic; holoplankton; invasion; Iranian coasts; merozooplankton; *Mnemiopsis leidyi*; seasonal zooplankton distribution.

Correspondence
Abolghasem Roohi, Caspian Sea Research Institute in Ecology, PO Box 961, Khazarabad Boolvar, Sari, Iran.
E-mail: roohi_ark@yahoo.com

Accepted: 27 May 2008

doi:10.1111/j.1439-0485.2008.00254.x

Abstract

The invasive ctenophore *Mnemiopsis leidyi* (Agassiz), which was transported from the Black Sea into the Caspian Sea at the end of the 1990s, has negatively affected the ecosystem of the Caspian Sea. Zooplankton abundance, biomass and species composition were evaluated on the Iranian coast of the Caspian Sea during 2001–2006. A total of 18 merozooplankton (13 species composed of larvae of benthic animals) and holozooplankton (four Copepoda and one Cladocera) species were identified. The total number of zooplankton species found here was 50% less than in a previous investigation performed in the same region in 1996 before the introduction of *Mnemiopsis leidyi* into the Caspian Sea. Cladocera species seemed to be highly affected by the invasion of *Mnemiopsis leidyi*; only one species, *Podon polyphemoides*, remained in the study area, whereas 24 Cladocera species were found in the study carried out in 1996. Whereas among the Copepoda *Eurytemora minor*, *Eurytemora grimmi*, *Calanipeda aquae dulcis* and *Acartia tonsa* that were abundant before the *Mnemiopsis leidyi* invasion, only *A. tonsa* (copepodites and adults) dominated the inshore and offshore waters after the invasion. The maximum in zooplankton abundance (22,088 ± 24,840 ind·m^{-3}) and biomass (64.1 ± 56.8 mg·m^{-3}) were recorded in December 2001 and August 2004, respectively. The annual mean zooplankton abundance during 2001–2006 was in the range of 3361–8940 ind·m^{-3}; this was two- to five-fold less than the zooplankton abundance in 1996. During 2001–2006, the highest abundance and biomass of *Mnemiopsis leidyi* were observed during summer-autumn months coincident with warm temperatures and generally when the abundance of other zooplankton organisms was low.

Problem

Mnemiopsis leidyi is an ecologically important lobate ctenophore inhabiting estuaries along the Atlantic coast of the USA, such as Narragansett Bay (Kremer & Nixon 1976; Deason & Smayda 1981), Barnegat Bay (Mountford 1980), Chesapeake Bay (Herman *et al.* 1968; Burrell & Van Engel 1976) and estuaries of North Carolina (Miller 1974). A decline in the standing stock of non-gelatinous zooplankton has often been associated with pulses of *M. leidyi* and other species of ctenophores in seas and oceans of the world (Bigelow 1915; Nelson 1925; Bigelow & Leslie 1930; Russell 1933, Russell 1935; Barlow 1955; Conover 1961; Fraser 1962, 1970; Cronin *et al.* 1962; Hopkins 1966; Herman *et al.* 1968; Sage & Herman 1972; Kideys 2002).

In the early 1980s, *Mnemiopsis leidyi*, already known as a voracious zooplankton feeder (Reeve *et al.* 1978), was introduced (likely via ballast waters) into the Black Sea from its native waters in the western Atlantic Ocean (GESAMP 1997; Mutlu *et al.* 1994; Mutlu & Bingel 1999). Since then it has spread all over the Black Sea and its introduction to other neighboring and sensitive ecosystems, notably the Caspian Sea, was an imminent threat (Dumont 1995; GESAMP 1997). This ctenophore was first reported in the Caspian Sea in November 1999 (Esmaeili *et al.* 1999; Ivanov *et al.* 2000). By the early 2000s, this species had spread all over the Caspian Sea (Roohi *et al.* 2001, 2003; Kideys & Moghim 2003). *Mnemiopsis leidyi* has been postulated to be important cause of the sharp decrease of the dominant fish group of the Caspian Sea, kilka fish (*Clupeonella* spp.), and of other pelagic fish stocks (Fazli & Roohi 2002; Daskalov & Mamedov 2007), through competition for the edible zooplankton and to a lesser degree by directly consuming kilka fish eggs and larvae (Mutlu 1999; Kasimov 2001). Normal levels of the anchovy kilka fecundity (8510 to 58,340 mature oocytes per fish) off Azerbaijan indicated that the recruitment failure of kilka in the years 2001–2004 was not related to a decrease in egg production (Mamedov 2004). In addition, the presence of only few juvenile kilka and their high level of post-larval mortality off Azerbaijan in 2004 were attributed to competition with or predation by *M. leidyi*, which is a voracious zooplankton predator (Daskalov & Mamedov 2007). *Mnemiopsis leidyi* impact on fodder zooptankton.

The explosion of *Mnemiopsis leidyi* in the Caspian Sea shortly after its introduction could be linked with the inability of kilka to compete with this ctenophore for zooplankton prey following intensive overfishing activities at the end of the 1991–2001 period (Bilio & Niermann 2004; Daskalov & Mamedov 2007).

The identification of the current composition and abundance of zooplankton in the Caspian Sea is of particular importance after the introduction of the invader comb jelly. At present, availability of such information is limited to the Caspian Sea Environment Program (CEP) materials, some reports and local publications mainly in Russian or Persian. As most representatives of zooplankton are thermophilous, summer data are especially important. In this investigation, we present 6 years (2001–2006) of monthly data documenting the variability of zooplankton, *Mnemiopsis leidyi* and other environmental variables in the southern Caspian Sea. This investigation is the longest time-series study in the Southern Caspian Sea with the most regular set of zooplankton collections to date. Previous studies have involved only short time periods and species identification was either not included or only performed at higher taxonomic levels (such as Copepoda) (Rezvani *et al.* 1991; Hossieni *et al.* 1996; Laloei *et al.* 1999; Roohi 2000; Roohi *et al.* 2001, 2003; Bagheri & Kideys 2003; Kideys & Moghim 2003).

Study Area, Material and Methods

The Caspian Sea, with a surface area of ~400,000 km^2, is the largest inland water body in the world. The average salinity of this brackish sea is 12.5 ppt. Among the three parts of the Caspian Sea – the Northern Caspian, Central Caspian and Southern Caspian, the Southern Caspian has the greatest volume (64% of the total). It is also the deepest, with a flat bottom inclining to the west, reaching depths of 1000 m in trenches, although the average depth is 325 m (Chaikin *et al.* 2001; Berkeliev *et al.* 2003).

Monthly samples of zooplankton were collected during 2003–2006 along six transects (Nowshar, Babolsar Amirabad, Lisar, Anzali and Sepidroud) perpendicular to the Iranian coast of the Caspian Sea (Fig. 1). Sampling onboard R/V *Guilan* was a result of collaboration between the Iranian Fisheries Research Organization and the Caspian Sea Research Institute in Ecology, Iran. During the period 2001–2002 only three transects (Nowshar, Babolsar, Amirabad) were sampled monthly. Each transect had four stations located at 5, 10, 20 and 50 m bottom depth. Two additional deep stations of 100 m were sampled off Anzali and Babolsar (Fig. 1). During the

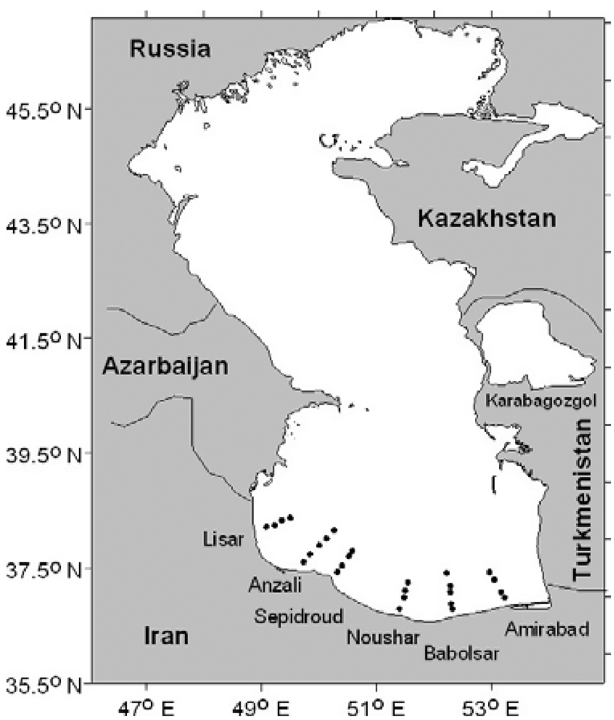

Fig. 1. Distribution of sampling stations in the southern Caspian Sea.

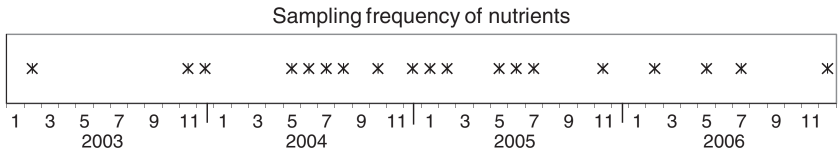

Fig. 2. Sampling frequency of nutrients in the Southern Caspian Sea from 2003 to 2006.

cruises, an Ocean Seven 316 multiparametric probe (Idronaut) and a Nansen water sampler were used. The horizontal and vertical distributions of temperature, salinity and pH were determined using the Idronaut probe. Temperature and salinity profiles were checked for the two stations with a depth of 100 m at Babolsar and Anzali to determine seasonal stratification patterns. Secchi disk measurements were performed at the stations of zooplankton sampling. The oxygen concentration was determined using the Winkler technique onboard, immediately after the water sampling, and the hydrochemical variables (phosphates, nitrates, ammonium, nitrites, silicate, total dissolved nitrogen and phosphorus were determined using standard methods (Sapozhnikov 1991). Sampling frequency is shown in Fig. 2.

Zooplankton samples were taken using a Juday net with a mouth opening of 0.1 m^2 and a screen cone with a mesh size of 100 μm. At the stations with a depth of <100 m, the zooplankton net was hauled from the bottom to the surface. Depth intervals of hauls at the stations 100 m deep were from bottom to 50, 50–20 and 20 m to the surface. Zooplankton samples were collected from the net and immediately preserved in neutral formaldehyde of a final concentration ~4–5% for further analyses in the laboratory. Samples were sub-sampled using a 1-ml Hensen–Stempel pipette and transferred to a Bogorov tray for counting. An inverted microscope was used for identification of non-gelatinous zooplankton. At least ~100–150 individuals were counted per sample (Postel *et al.* 2000 cited in Rezai *et al.* 2004) and the principal taxonomic groups and life cycle stages were identified. Biomasses, as wet weight, were estimated using respective conversion factors for each stage/species, obtained from the literature (Petipa 1957).

In parallel, ctenophores were collected with an METU net having a mouth opening of 0.2 m^2 and a screen with a mesh size of 500 μm, from the same depths as the Juday net (Vinogradov *et al.* 1989; Kideys *et al.* 2001). On completion of each tow, the cod end was immediately passed into a container and ctenophores counted by eye. The body length of each individual with lobes was measured lying flat (out of water) onboard, and the density of *Mnemiopsis leidyi* (per m^3) was calculated from the net diameter and tow depth. The ctenophores were sorted in length groups of 5-mm intervals to determine the abundance of different size groups. Length measurements were converted to wet weight using an appropriate equation (Kideys *et al.* 2001).

The sampling strategies applied in the present investigation are similar to those followed by Hossieni *et al.* (1996) in the same area. There were 18 transects in each season in the study of Hossieni *et al.* (1996), including the six transects of the present study. For comparison of zooplankton abundance and biomass data, the same stations of these six transects were used. In addition, the same methodology was used for the zooplankton sampling in both studies. The sampling by Hossieni *et al.* (1996) was performed during four months: March, August, November and February 1996.

Results

Hydrophysical characteristics of the Southern Caspian Sea

The highest surface water temperatures were observed during summer–autumn (max. ~30 °C) (Fig. 3). The summer temperatures during 2003–2005 were lower (~26–28 °C) than during 2001–2002 and 2006 (29–32 °C). The lowest water temperatures were recorded in winter (minimum ~8–12 °C) as consequence not only of air temperatures, but also of circulation of cold Volga River water from the western Caspian Sea and of other river flows (*e.g.* Tajan River in Amirabad, Sepidroud

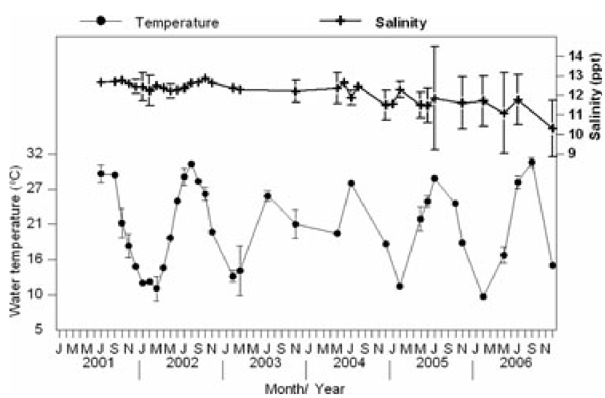

Fig. 3. Seasonal changes in surface temperatures (°C) and salinities in the Southern Caspian Sea during 2001–2006. Values are the averages of the stations and error bars show the standard deviations.

River), which carry winter melt water. There was a decreasing trend in average salinities of the surface water from 2001 (~12 ppt) to 2006 (~10–11 ppt). The spatial variability of salinity increased from 2001 to 2006, having higher standard deviations in the last 2 years. This could be related to fresh water input by rivers and different circulation characteristics in the last 2 years. For instance, during these years low salinity values (*e.g.* 5.6 ppt at the 10-m station off Anzali in February 2006, 7.21 ppt at the 5-m station off Anzali in July 2005, 8.29 ppt at the 20-m station off Amirabad) were measured. Seasonal stratification patterns at the two 100-m-deep stations were similar in all years and at both stations. Thus, 4 months were chosen as representative of different seasons between July 2001 and December 2006 (Fig. 4). The thermocline started to form in spring at ~20 m depth and deepened to 40–50 m during summer and autumn. The sharpest thermocline was observed in autumn. The halocline was observed at shallower depths (10–20 m) than the thermocline in the summer–autumn periods. The sharpest halocline was observed in winter–spring. The average salinity of all surface stations (11.9 ± 1.2 ppt) was lower than at 100 m depth (12.4 ± 1.6 ppt).

The Secchi disk depth fluctuated between 0.2 and 12.5 m with an average of 3.5 ± 2.2 m (not shown). The gradient of average dissolved oxygen concentration from ~8–9 $\mu g \cdot l^{-1}$ at the surface to ~7–8 $\mu g \cdot l^{-1}$ at 100 m indicated a top-down decreasing trend (Fig. 5).

The total dissolved inorganic nitrogen (TDIN = N-NO_2 + N-NO_3 + N-NH_4) concentrations were higher during autumn–winter (2.95–3.24 μM) than during spring–summer (2.10–2.15 μM, Table 1). Similarly, total dissolved inorganic phosphorus (TDIP = P-PO_4) concentrations were higher (0.65 μM) during autumn–winter than during spring–summer (0.5 μM). Seasonal changes

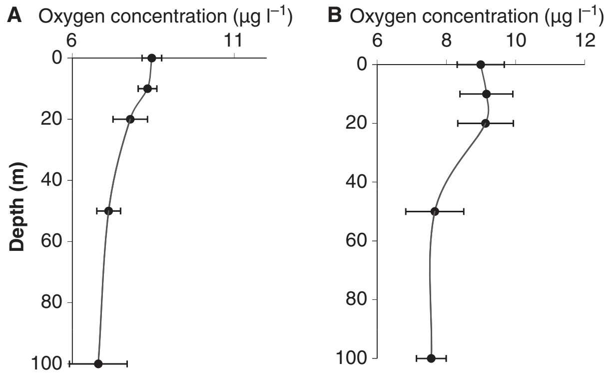

Fig. 5. Vertical profiles of average dissolved oxygen in the Southern Caspian Sea at Babolsar station. (A) Average of months June–July 2005, July 2006. (B) Averages of months November 2005, February and May 2006.

in silicate concentrations were not pronounced, varying between 8.2 and 9.5 μM. The molar dissolved inorganic silicate, nitrogen and phosphorus ratio was ~16:4:1. In contrast to the inorganic ratios, the N:P ratio of dissolved organic forms (as $\mu g \cdot l^{-1}$,) were high (32–52), exceeding the Redfield ratio (N:P = 16:1) (Table 1).

Species composition of zooplankton

A total of 18 zooplankton species (mero- and holozooplankton) were found. Among them there were 13 species of merozooplankton and only five species of holozooplankton. The latter belonged to Copepoda (four species) and Cladocera (one species) (Table 2). The only Cladocera species was *Podon polyphemoides*. Four copepod species were found, with the predominant calanoid *Acartia tonsa* present in all stations and every season. In 2006, a

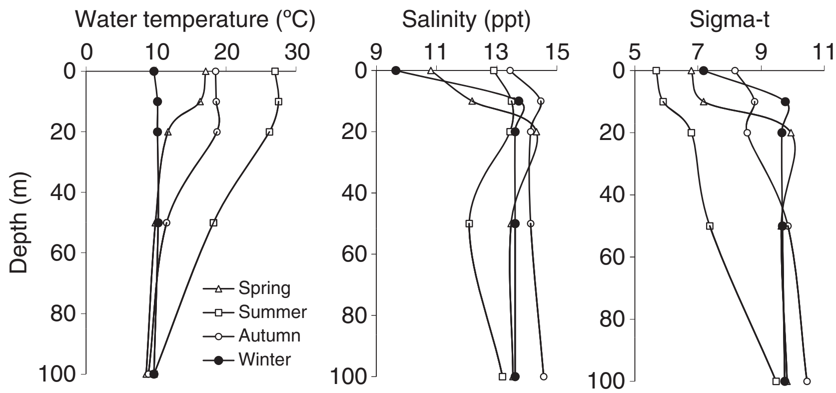

Fig. 4. Seasonal changes in temperature (°C). salinity and density profiles at the deepest station of Babolsar in the Southern Caspian Sea. Winter, spring, summer and autumn seasons were represented by the dates February 2006, May 2006, July 2006 and November 2005, respectively, for both temperature and salinity profiles.

Table 1. Average nutrient concentrations and elemental ratios of dissolved nutrients in different seasons in the Southern Caspian Sea during 2003–2006 (see Fig. 2 for sampling frequency).

	$\mu g \cdot l^{-1}$							μm					Inorganic	Organic
	$N\text{-}NO_2$	$N\text{-}NO_3$	$N\text{-}NH_4$	$P\text{-}PO_4$	$Si\text{-}SiO_2$	TDON	TDOP	NO_2	NO_3	NH_4	PO_4	SiO_2	Si:N:P	N:P
Wi	1.44 (0.82)	23.42 (5.57)	16.40 (10.78)	19.95 (4.69)	247.57 (58.49)	709.76 (240.73)	22.10 (11.42)	0.10 (0.06)	1.67 (0.40)	1.17 (0.77)	0.64 (0.15)	8.84 (2.09)	14:5:1	32
Sp	0.72 (0.27)	19.10 7.21	10.26 (3.02)	15.50 (2.45)	228.45 (73.18)	767.33 (192.75)	22.35 (10.07)	0.05 (0.02)	1.36 (0.52)	0.73 (0.22)	0.50 (0.08)	8.16 (2.61)	16:4:1	34
Su	0.85 (0.47)	14.19 3.56	14.24 (5.76)	15.27 (3.26)	240.82 (75.78)	867.95 (137.15)	16.76 (7.70)	0.06 (0.03)	1.01 (0.25)	1.02 (0.41)	0.49 (0.11)	8.60 (2.71)	18:4:1	52
Au	1.55 (1.34)	20.85 (9.12)	22.94 (18.90)	20.29 14.60	265.67 (92.96)	803.70 (209.01)	22.30 (11.18)	0.11 (0.10)	1.49 (0.65)	1.64 (1.35)	0.65 (0.47)	9.49 (3.32)	15:5:1	36

Numbers within parentheses are standard deviations.
Wi, winter; Sp, spring; Su, summer; Au, autumn.

Table 2. Species number of zooplankton before and after *Mnemiopsis leidyi* invasion in the Southern Caspian Sea.

Zooplankton group	Before *Mnemiopsis*	After *Mnemiopsis leidyi* invasion					
Year	Hossieni *et al.* (1996)	2001	2002	2003	2004	2005	2006
Copepoda	7	3	3	3	3	2	4
Cladocera	24	0	1	1	1	1	1
Merozooplankton	5	5	11	9	7	7	8
Total	36	8	15	13	11	10	13

slightly higher diversity of Copepoda was seen; *Eurytemora grimmi*, absent in 2001–2005, was then observed for the first time at 50 m depth of the 100-m-deep station off Anzali (49 °N and 37 °E) in 2006.

Abundance and biomass of zooplankton

In general, low zooplankton abundance and biomass (wet weight) were observed in summer months from 2001 to 2006. The highest abundance and biomass of zooplankton along the whole water column were not regularly found in the same season each year (Fig. 6). The maximum abundance recorded was 22,088 ± 24,840 ind·m^{-3} (average of stations and depths) in December 2001, whereas the highest biomass was 64.1 ± 56.8 mg·m^{-3} (average of stations and depths) in August 2004. Monthly variations of zooplankton biomass were similar to the fluctuations in abundance except in some summer–autumn periods when large-sized specimens dominated. The minimum zooplankton abundance and biomass were 397 ± 567 ind·m^{-3} and 1.8 ± 2.6 mg·m^{-3}, respectively, in September 2002. The annual mean zooplankton abundance varied between 3361 and 8940 ind·m^{-3} during 2001–2006. The average zooplankton abundance and biomass for all months and years were calculated as 7015 ± 11,959 ind·m^{-3} and 32.8 ± 57.6 mg·m^{-3}, respectively.

The maximum seasonal mean of zooplankton abundance was recorded in spring and the minimum in summer (Table 3, Fig. 7A–D). In spring, the greatest zooplankton abundance was observed at the Sepidrood River inlet (~9×10^4 ind·m^{-3}) (Fig. 7A). In summer, the abundance of zooplankton decreased compared with the values reported in spring, and an almost even distribution was found along the coastal regions (max. ~8–11×10^3 ind·m^{-3}) decreasing towards the open sea (Fig. 7B). In autumn, zooplankton concentration was slightly greater than in summer, again the highest abundance (~2×10^4 ind·m^{-3}) was reported at the Sepidrood River inlet of 5 m depth (Fig. 7C). In winter, abundance was greater than in autumn and the maximum was

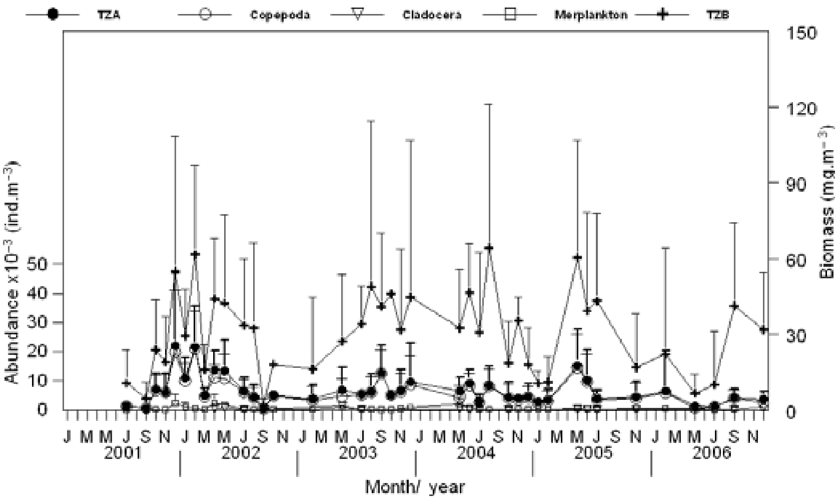

Fig. 6. Monthly variations in spatial and depth averages of Copepoda. Cladocera merozooplankton and total zooplankton abundance and biomass in the Southern Caspian Sea during 2001–2006. TZA, total zooplankton abundance; TZB, total zooplankton biomass.

Table 3. Seasonal variations in zooplankton abundance (ind·m^{-3}) during 2001–2006.

	2001–2006			
	Spring	Summer	Autumn	Winter
Average	13.605	4.157	5.227	7.728
SD	18.822	2.843	4.800	7.404

observed at the Babolsar stations (~3×10^4 ind·m^{-3}, Fig. 7D).

Comparison among different groups of zooplankton showed that Copepoda accounted for the maximum abundance and biomass every year from 2001 to 2006 (Fig. 6). Among Copepoda, different developmental stages of the calanoid species *A. tonsa* dominated during the study period. Copepoda, Cladocera and merozooplankton constituted 88%, 4% and 8% of total zooplankton abundance, respectively.

Abundance and biomass of *M. leidyi*

The ctenophore *Mnemiopsis leidyi* was found at all stations during 2001–2006. There was a seasonal succession of ctenophore densities every year, the maximum being observed in August and September, and the minimum density in the winter months. A significant correlation was found between the water temperature and the abundance of *Mnemiopsis leidyi* ($P < 0.005$). The highest summer–autumn average of *Mnemiopsis leidyi* abundance was observed in 2002 (760 ± 1148 ind·m^{-3}), although the biomass during this period (23.2 ± 23.3 g·m^{-3}) was lower than in 2001 (41.5 ± 44.3 g·m^{-3}) (Fig. 8). In terms of monthly averages, October 2001 was the month of the maximum abundance and biomass (1157 ± 1614 ind·m^{-3}

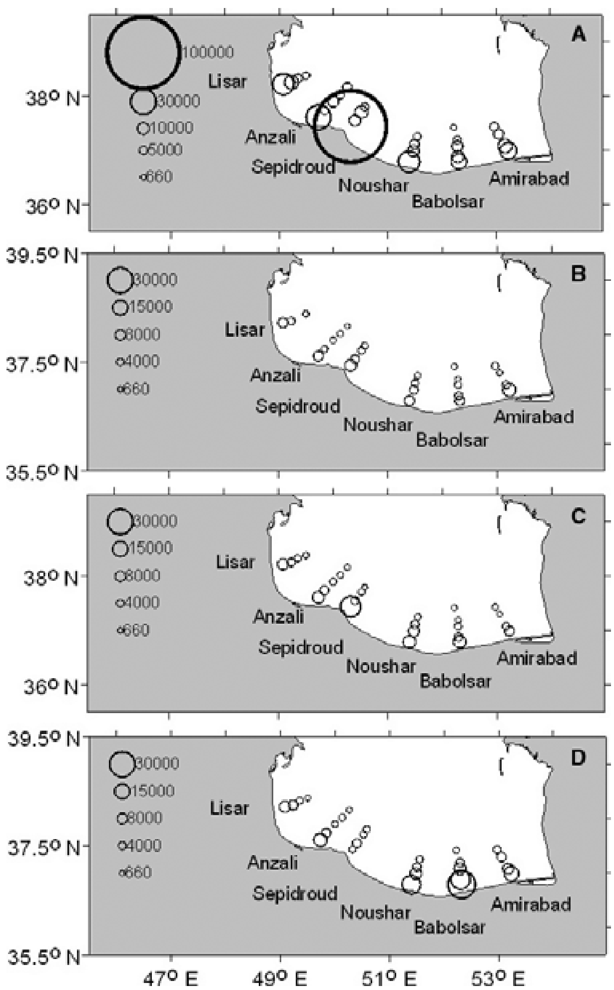

Fig. 7. Spatial distribution of zooplankton abundance in different seasons (depth averages of available months) in the Southern Caspian Sea during 2001–2006. (A) Spring. (B) Summer. (C) Autumn. (D) Winter.

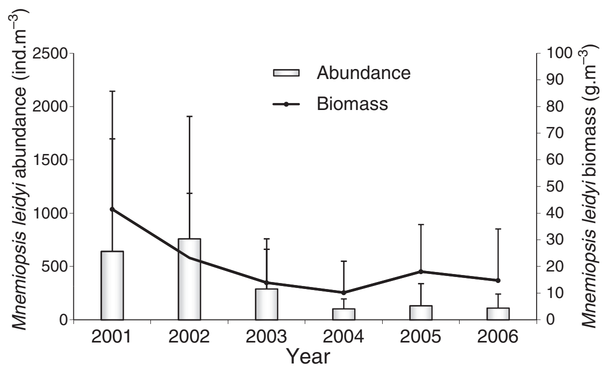

Fig. 8. Spatial and depth means of *Mnemiopsis leidyi* abundance and biomass in the Southern Caspian Sea during summer–autumn 2001–2006 (error bars are standard deviations).

and 58.9 ± 40.0 g·m^{-3}) (Fig. 9). Notably, after this abundance peak of *Mnemiopsis leidyi*, the abundance of other zooplankton organisms decreased the following year. Both yearly and seasonal values showed that this ctenophore reached the maximum abundances at the coastal stations (Fig. 10A–D).

In terms of spatial distribution, in spring (2001–2006) the maximum abundance of *Mnemiopsis leidyi* (141 ind·m^{-3}) was recorded in the coastal area of the southeastern Caspian Sea (Amirabad) and the minimum (3–14 ind·m^{-3}) in waters 100 m deep (Fig. 10A). In summer, the highest abundance was again noted in the southeastern Caspian Sea, with values 763 ind·m^{-3} (Fig. 10B). Likewise, in autumn, the maximum abundance was in the southeast at Babolsar (at the shallowest station of 5 m depth), with a value of 1235 ind·m^{-3} (Fig. 10C). In addition, abundance was high at a station with a depth <20 m (500–700 ind·m^{-3}). In winter the maximum abundance was recorded in the Anzali region, with a value of 653 ind·m^{-3} (Fig. 10D).

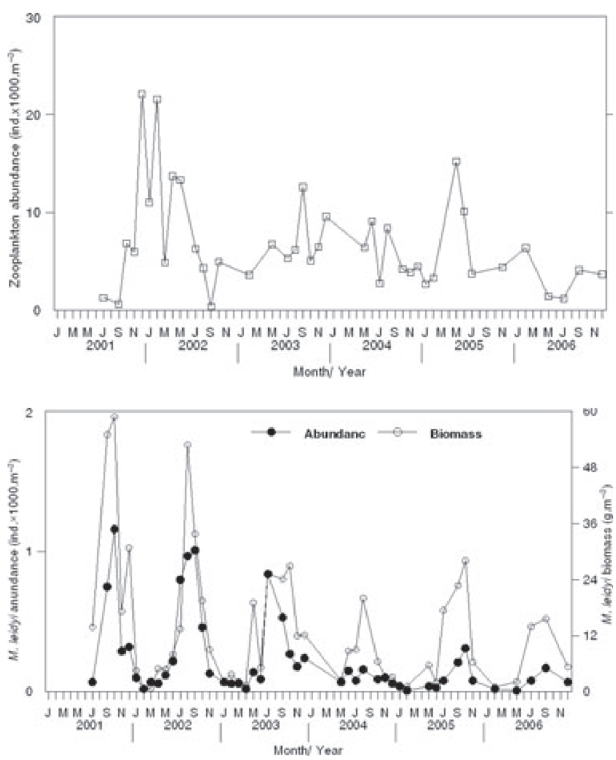

Fig. 9. Monthly variations in spatial and depth averages of *Mnemiopsis leidyi* abundance, biomass and zooplankton abundance in the southern Caspian Sea during 2001–2006.

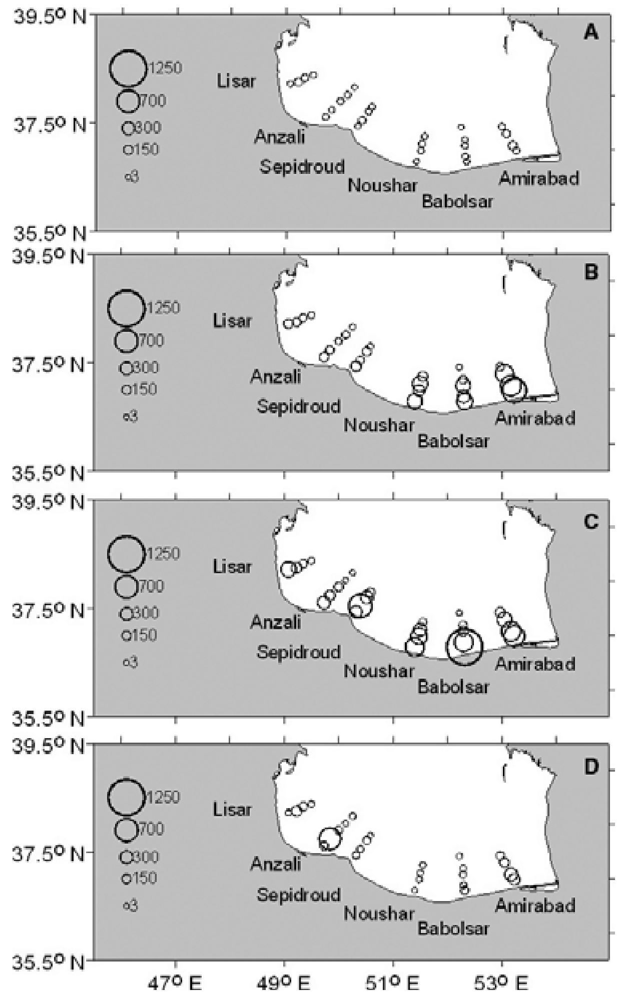

Fig. 10. Seasonal distribution of *Mnemiopsis leidyi* abundance (depth averages of available months) in the Southern Caspian Sea during 2001–2006. (A) Spring. (B) Summer. (C) Autumn. (D) Winter.

The means of abundance and biomass during the whole study period were 340 ind·m^{-3} and 20.3 g·m^{-3}, respectively. The total wet weight (biomass) of *Mnemiopsis leidyi* during the 6 years of the study was 3×10^6 kg in the Southern Caspian Sea (considering a surface area of 148,200 km^2). During the whole study

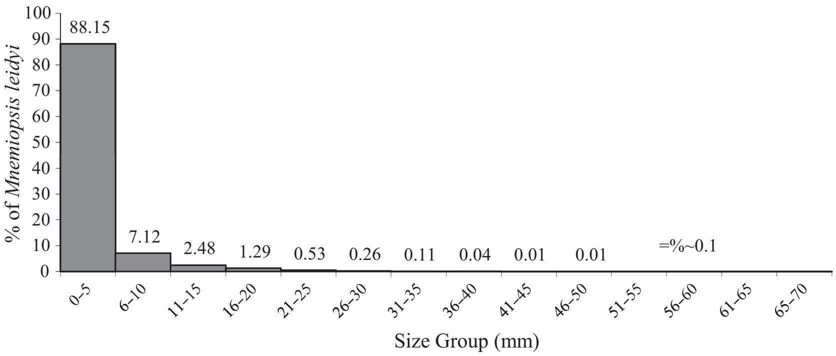

Fig. 11. *Mnemiopsis leidyi* size groups and their percentage within total number of individuals at all stations in the Southern Caspian Sea during 2001–2006.

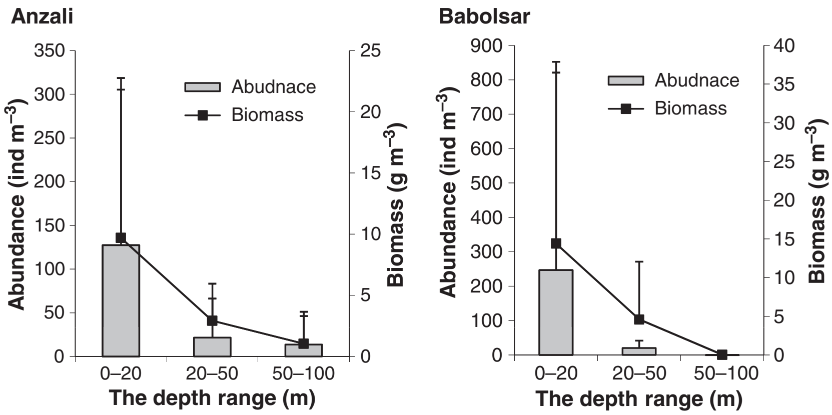

Fig. 12. The depth mean abundance and biomass of *Mnemiopsis leidyi* during 2001–2006 at the deep stations off Anzali and Babolsar.

period and at all stations, small individuals (<5 mm in length) and the ciddipid stage constituted 88% of all individuals, whereas 8% of the individuals were 6–10 mm in size. The largest individuals (30–70 mm) made up only 4% of the total abundance (Fig. 11). The highest abundances of *Mnemiopsis leidyi* were at the surface and at 20 m at the deepest stations off Anzali and Babolsar (Fig. 12).

Discussion

There are few publications on zooplankton of the Southern Caspian Sea, and most of these are either national reports on biodiversity or local literature (*e.g.* Rezvani *et al.* 1991; Hossieni *et al.* 1996; Laloei *et al.* 1999; Roohi 2000; Roohi *et al*. 2001, 2003; Bagheri & Kideys 2003; Kideys & Moghim 2003). We have compared our findings with the previous investigation by Hossieni *et al.* (1996), as this was the only study comparable with the present investigation in terms of sampling and methodology. Hossieni *et al.* (1996) reported 36 zooplankton species (86% holoplankton and 14% meroplankton) in the southern Caspian Sea, consisting of 24 species of Cladocera, seven species of Copepoda and meroplankton such as larvae of Bivalvia and Balanidae (Table 4). The species composition, abundance and biomass of zooplankton recorded in our investigation varied from those reported in Hossieni *et al.* (1996). Possible reasons for this change could include variations in hydrological and chemical properties of the Caspian Sea, climatic changes and invasion by the ctenophore *Mnemiopsis leidyi*. Unfortunately, nutrient data in the region for previous years are too limited to reveal changes in water chemistry, although there are some reports of increasing anthropogenic pollution of Iranian lagoons and coastal regions since the early 1980s (CEP 1998; Salmanov 1999; Stolberg *et al*. 2006). There are likewise no data on possible climate change, whereas data reported in the present study suggest possible relations between *Mnemiopsis leidyi* and zooplankton species composition, abundance and biomass.

After the invasion of *Mnemiopsis leidyi*, during our study 2001–2006, the total number of zooplankton species was 18, 50% less than in 1996. In 1996 the maximum number of species among the zooplankton belonged to Cladocera, but the representation of this group decreased drastically to only one species, *Podon polyphemoides*, following *Mnemiopsis leidyi* invasion. The number of Copepoda species was also lower (four species) during 2001–2006 (Table 4). Cladocera could be a preferred prey of *Mnemiopsis leidyi*. This zooplankton group has been observed in the gut of *Mnemiopsis leidyi* in the Black Sea

Table 4. Annual variations (A) in abundance (ind·m^{-3}) and (B) in biomass (wet weight, mg·m^{-3}) of total zooplankton, Copepoda, Cladocera and merozooplankton species in the Southern Caspian Sea (before and after *Mnemiopsis* invasion). (C) Seasonal variations in abundance and biomass of zooplankton species in 1996 from Hossieni *et al.* (1996). (D) Full list of Cladocera species reported by Hossieni *et al.* (1996).

	Hossieni *et al.* (1996)	After *Mnemiopsis leidyi* invasion												
		2001		2002		2003		2004		2005		2006		
Zooplankton	A	SD	A	SD	A	SD	A	SD	A	SD	A	SD	A	SD
A)														
Acartia tonsa	5766	4935	6999	12,544	10,360	8831	6176	6758	5370	4676	8144	8793	3975	8944
Limnocalanus grimaldii	5	11	0	0	0	0	0	0	0	0	0	0	0	0
Calanipeda aquae dulcis	85	115	1	0	0	0	1	0	0	0	0	0	0	0
Eurytemora grimmi and *Eurytemora minor*	2172	1774	0	0	0	0	0	0	0	0	0	0	5	0
Nauplii Calanoida	2763	3296	0	0	0	0	0	0	0	0	0	0	0	0
Halicyclops sarsi (Cyclopoida)	170	168	5	0	2	0	120	2	5	1	22	3	1	0
Ectinosoma consimum (Harpacticoida)	0	0	0	0	3	3	0	0	1	0	11	19	0.4	0
Total Copepoda	10,961	10,300	7005	12,544	10,364	8834	6296	6760	5375	4678	8177	8814	3981	8944
Podon polyphemoides	237	442	0	0	450	672	1205	822	228	342	328	398	367	415
Polyphemus exicus	83	129	0	0	0	0	0	0	0	0	0	0	0	0
Total Cladocera	320	571	0	0	450	672	1205	822	228	342	328	398	367	415
Lamellibranchia larvae	5459	13,156	0	0	282	642	33	23	365	777	55	75	430	934
Cirripedia larvae (*Balanus* spp.)	439	648	86	378	661	1446	387	708	723	1359	328	617	277	430
Arachnida larvae	0	0	14	25	170	488	3	1	8	11	0	0	0.3	0
Mysidaceae larvae	NQD	0	0	0	0	0	0	0	0	0	0	0	2	0
Nematidae	NQD	0	0	0	214	361	163	137	0	0	2	2	0.5	0
Nereididae larvae	0	0	573	1838	435	877	12	18	13	23	38	52	9	0
Ostracoda larvae	NQD	0	5	8	32	106	2	2	58	117	0	0	0	0
Chironomidae larvae	0	0	0	0	0	0	5	8	0	0	0	0	4	0
Oligochaeta larvae	0	0	0	0	13	1	133	284	208	241	150	281	75	244
Total Meroplankton	5898	13,804	677	2248	1806	3920	738	1181	1374	2527	572	1027	799	1608
Total Zooplankton	17,180	24,675	7682	14,792	12,620	13,426	8239	8763	6977	7547	9077	10,239	5147	10967
	Hossieni *et al.* (1996)	After *Mnemiopsis leidyi* invasion												
		2001		2002		2003		2004		2005		2006		
Zooplankton	B	SD	B	SD	B	SD	B	SD	B	SD	B	SD	B	SD
B)														
Acartia tonsa	37.2	36.5	23.0	32.0	35.4	26.6	30.1	33.6	36.9	34.2	42.0	38.6	22.9	33.4
Limnocalanus grimaldii	0.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calanipeda aquae dulcis	0.8	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eurytemora grimmi and *Eurytemora minor*	20.7	20.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Nauplii Calanoida	7.6	7.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicyclops sarsi (Cyclopoida)	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.004	0.0
Ectinosoma consimum (Harpacticoida)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.003	0.0
Total Copepoda	68	67	23	32	35.4	26.6	30.1	33.6	37.0	34.2	42.2	38.8	23.0	33.4
Podon polyphemoides	1.6	2.7	0.0	0.0	1.8	2.7	4.8	3.3	0.8	1.3	0.9	1.3	1.5	1.7
Polyphemus exicus	0.5	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total Cladocera	2.1	3.4	0.0	0.0	1.8	2.7	4.8	3.3	0.8	1.3	0.9	1.3	1.5	1.7
Lamellibranchia larvae	26.9	65.0	0.0	0.0	1.4	3.2	0.2	0.1	1.8	3.9	0.3	0.4	2.152	4.6704
Cirripedia larvae (*Balanus* spp.)	1.0	1.5	0.2	0.8	1.4	2.9	1.4	3.7	4.2	8.5	1.4	1.8	1.114	2.0674

Table 4. *(Continued)*

	Hossieni *et al.* (1996)	After *Mnemiopsis leidyi* invasion												
		2001		2002		2003		2004		2005		2006		
Zooplankton	B	SD	B	SD	B	SD	B	SD	B	SD	B	SD	B	SD
Arachnida larvae	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mysidaceae larvae	NQD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nematidae	NQD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nereididae larvae	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda larvae	NQD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae larvae	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oligochaeta larvae	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total Meroplankton	27.9	66.4	0.2	0.8	2.8	6.1	1.6	3.8	6.1	12.4	1.6	2.2	3.3	6.7
Total Zooplankton	97.7	137.0	23.2	32.7	40.0	35.4	36.5	40.7	43.8	47.9	44.8	42.3	27.7	41.8

	Spring				Summer				Autumn				Winter			
Zooplankton groups	ind·m^{-3}	SD	mg·m^{-3}	SD	ind·m^{-3}	SD	mg·m^{-3}	SD	Ind·m^{-3}	SD	mg m^{-3}	SD	Ind m^{-3}	SD	mg·m^{-3}	SD
C)																
Acartia tonsa	1093	1211	6.7	6.9	7484	1929	35.9	23.3	11717	4008	79.2	40.8	2456	1633	19.1	14.8
Limnocalanus grimaldii	18	17	1.3	0.8	0	1	0.1	0.3	0	1	0.2	0.2	0	1	0.1	0.2
Calanipeda aquae dulcis	82	90	0.9	1.1	32	39	0.3	0.3	215	362	1.8	2.7	176	151	1.3	1.0
Eurytemora grimmi and *Eurytemora minor*	3312	2266	34.9	23.9	705	488	4.6	3.4	1427	649	9.6	6.9	2433	1630	18.7	17.0
Nauplii Calanoida	1834	676	4.9	1.9	2559	1153	6.8	3.0	4600	6386	11.6	15.2	2191	1325	6.2	3.9
Total Calanoida	6347	3462	48.6	27.4	10780	2603	47.8	27.2	17960	8084	102.4	39.5	7256	3352	45.5	33.1
Cyclopoida	287	116	1.7	0.7	28	14	0.2	0.1	75	75	0.4	0.5	276	145	1.7	0.9
Harpacticoidae	0	1	0.0	0.0	0	0	0.0	0.0	0	0	0.0	0.0	0	0	0.0	0.0
Total Copepoda	6635	3371	50.4	26.9	10,808	2613	48.1	27.2	18,034	8077	102.9	39.3	7532	3367	47.2	33.1
Podon polyphemoides	693	700	4.2	4.2	13	29	0.1	0.2	87	72	0.9	1.0	139	203	1.0	1.4
Polyphemus exicus	0	1	0.0	0.0	58	69	0.4	0.5	48	33	0.3	0.2	192	217	1.2	1.3
Total Cladocera	1049	700	17.7	18.9	162	104	5.0	5.1	258	139	3.6	4.8	351	390	2.5	2.6
Lamellibranchia larvae	646	752	3.2	3.8	22,059	21,128	110.3	105.6	158	181	0.8	0.9	100	81	0.5	0.4
Cirripedia larvae	197	119	0.4	0.2	184	166	0.6	0.6	243	221	0.5	0.4	418	379	1.6	2.3
Total Zooplankton	8527	4943	71.7	49.8	33,213	24,012	163.9	138.6	18,694	8619	107.8	45.4	8402	4216	51.7	38.4

D)

1. *Podon polyphemoides*
2. *Polyphemus exicus*
3. *Podoevadne camptonyx typica*
4. *Podoevadne camptonyx orthonyx*
5. *Podoevadne camptonyx podonoides*
6. *Podoevadne camptonyx kajdakensis*
7. *Podoevadne camptonyx macronyx*
8. *Podoevadne camptonyx humulos*
9. *Podoevadne angusta*
10. *Podonevadne trigona trigonides*
11. *Podoevadne trigona typical*
12. *Podoevadne trigona intermedia*
13. *Cercopagis pengoi*
14. *Cercopagis socialis*
15. *Cercopagis cylindrata*
16. *Cercopagis longicaudata*
17. *Cercopagis ossiani*
18. *Cercopagis anonyx*
19. *Cercopagis robusta*
20. *Apagis longicaudata*
21. *Apagis ossiani*

Table 4. *(Continued)*

22. *Apagis cylindrata*
23. *Evadne anonyx producta*
24. *Evadne anonyx deflexa*

A, abundance; B, biomass;
SD, standard deviation;
NQD, qualitatively observed,
no quantitative data.

(Mutlu 1999). The diet of *Mnemiopsis leidyi* in the southwestern Caspian Sea was represented by copepods (*Acartia* and *Eurythemora* ~45%), cladocerans (*Pleopsis* 15%), larvae of *Balanus* (10%), Bivalvia (10%) and other species (Kasimov 2001).

In the present study, the annual mean zooplankton abundance during 2001–2006 was in the range 3361–8940 ind·m^{-3}. This is two to five times lower than the average 16,219 ind·m^{-3} for the months March, August, November and February in 1996 (Hossieni *et al.* 1996). The monthly averages of zooplankton abundance between 2001 and 2006 were also low (~400–22,000 ind·m^{-3}) compared to values in 1996 (~8400–~33,200 ind·m^{-3}) (Hossieni *et al.* 1996) before *Mnemiopsis leidyi* invaded the Caspian Sea. Similarly, the range of monthly mean zooplankton biomass during our study was 2–64 mg·m^{-3}, (Fig. 6), lower than the range, 51–164 mg·m^{-3}, recorded in 1996, (Table 4C). In addition, whereas the maximum abundance was observed in summer and autumn in 1996, during 2001–2006, after *Mnemiopsis leidyi* invasion, the maximum zooplankton abundance was generally recorded in winter–spring (Table 3). During the highest concentrations of *Mnemiopsis leidyi*, the abundance of zooplankton was low (*e.g.* ~0.7–10^{3} ind·m^{-3} in September 2001), which might indicate predation by *Mnemiopsis leidyi* on zooplankton (Fig. 9). *Mnemiopsis leidyi* has long been reported as an effective predator on zooplankton. Reeve *et al.* (1978) found that the ingestion rate of this ctenophore is proportional to the food concentration. Because of this, concomitant with the appearance of *Mnemiopsis leidyi*, a dramatic decrease in the number and/or biomass of copepods and other potential prey of *Mnemiopsis leidyi* is often observed in the native regions of this ctenophore. For example, Burrell (1968) suggested that predation by *Mnemiopsis leidyi* was responsible for 73% of total zooplankton mortality in the York River estuary of Chesapeake Bay (Virginia, USA). In addition, Finenko & Romanova (2000) calculated that, on a daily basis, about 20% of total fodder zooplankton was consumed by this ctenophore in summer 1995 in the Black Sea. They also reported a negative correlation between the abundances of *Mnemiopsis leidyi* and zooplankton ($r = -0.4$).

Previous studies have indicated overfishing, eutrophication and climatic changes (global warming) as possible factors triggering population explosions in both native and introduced comb jellies (Mills 2001; Bilio & Niermann 2004; Purcell 2005; Lynam *et al.* 2006). These factors might also have contributed to the explosion of *Mnemiopsis leidyi* in the Caspian Sea. In addition, higher salinities of the Southern Caspian Sea (~12.85 ppt) compared to the Northern and Central basins was another factor permitting fast development of *Mnemiopsis leidyi* in this area even in winter months in waters having a temperature of <8 °C (Shiganova *et al.* 2003). However, there was a seasonal pattern of *Mnemiopsis leidyi* related to water temperature. It reached the highest abundances in summer–autumn when the water temperature was high, similar to the pattern observed by Shiganova (1998) in the Black Sea. Annual variations in *Mnemiopsis leidyi* abundance also seem related to zooplankton food items. Following the highest abundances of zooplankton in the winter period of 2001–2002 (Fig. 9), high *Mnemiopsis leidyi* abundance was observed in summer of 2002. *Mnemiopsis leidyi* abundance was lower in summer 2003 than in previous summers, following low zooplankton abundance during winter–spring 2003. A minor increase in *Mnemiopsis leidyi* was observed in autumn 2005 following an increase in zooplankton during spring of the same year. Zooplankton abundances may have been affected by predation pressure of *Mnemiopsis leidyi* and other predators (*e.g.* fishes, larvae of benthic invertebrates) as well as concentrations of food items (phytoplankton) during the study period. Phytoplankton abundance was not measured in this study. However, seasonal changes in nutrients which influence phytoplankton concentration are presented here. The highest average inorganic nitrogen (nitrate, nitrite and ammonium together) concentration was observed in winter and autumn (Table 1). Nitrite and nitrate concentrations decreased somewhat during spring and summer, and the ammonium concentration increased in autumn. Kremer (1979) reported that *Mnemiopsis leidyi* excretion could result in a high turnover of nitrogen (in the form of ammonium) and phosphorus (daily 5–19% and 20–48% of body content, respectively). The increase in ammonium reported here could be linked with *Mnemiopsis leidyi* excretion, as well as phytoplankton degradation products. Phosphate concentrations were lower during spring and summer than in winter and autumn. In contrast to inorganic nitrogen, organic nitrogen concentrations were lowest in winter. The lowest organic and inorganic phosphorus concentrations were in summer. Previous studies showed that this ctenophore could not survive cold temperatures in the North Caspian Sea during winter (Ivanov *et al.* 2000; Kideys & Moghim 2003; Shiganova *et al.* 2003). However, the warmer temperature of the Southern Caspian Sea could allow *Mnemiopsis leidyi* to overwinter.

In the present investigation, the proportion of small individuals (<10 mm) and the total abundance of *Mnemiopsis leidyi* were high in summer when water temperature was >25 °C, whereas in winter, few large individuals were observed.

There seems to be an inverse relation between *Mnemiopsis leidyi* and zooplankton abundance by season (Figs 7 and 10). For instance, *Mnemiopsis leidyi* abundance was highest in summer and autumn (Fig. 10B,C), whereas zooplankton biomass was highest in spring and winter (Fig. 8A,D).

In the period 2001–2006, following the invasion by *Mnemiopsis leidyi*, the dominance of the calanoid copepod *Acartia tonsa* was striking, whereas the abundance of other large copepods such as *Eurytemora minor* and *Eurytemora grimmi* decreased compared to 1996 (Hossieni *et al.* 1996) or completely disappeared (Table 4), although in 2006 low numbers of *Earytemora grimmi* were observed at some stations. Among the cladocerans, only *Podon polyphemoides* survived the invasion of *Mnemiopsis leidyi*.

Conclusions

The present study records changes in the Caspian Sea pelagic ecosystem after the introduction of the ctenophore *Mnemiopsis leidyi* that can be reasonably attributed to the impact of this invader on this enclosed basin. In addition to *Mnemiopsis leidyi*, possible effects of other environmental factors on the ecosystem such as the climate and eutrophication can not be clearly detected. Even though zooplankton data before the invasion of this ctenophore are limited, we have observed that the range of zooplankton abundance and biomass values during our 6-year monthly monitoring study was well below that reported in 1996, before the introduction of *Mnemiopsis leidyi*. Changes in seasonal zooplankton abundance and biomass (summer–autumn maxima before the introduction of *Mnemiopsis leidyi* and winter–spring maxima afterwards) could be a result of *Mnemiopsis leidyi* predation on zooplankton. Changes in species composition of some zooplankton groups (*e.g.* a sharp decrease in the species number of Cladocera) were also observed. Although total *Mnemiopsis leidyi* abundance and biomass in the years after 2003 decreased in our study, the hypothetical and practical effects (*e.g.* the change in species and possibly size composition of zooplankton due to predation effects of *Mnemiopsis leidyi*, and possible change in the composition of predator organisms in the higher trophic level) might have remained for years without any direct control.

Acknowledgements

The authors are grateful to D.G. Reid for reading and improving the English of the draft manuscript and providing pertinent comments. The investigation was carried out with the support of the Iranian Fisheries Research Organization (IFRO) and Caspian Sea Research Institute of Ecology. We would like to thank F. Vahedi, A. Nasrollatabar for nutrient analyses, A. Hashemian, M. Rowshantabari, A. Keyhanisani, M. Nazaran, M. Rostamian, H. Khodaparast for their help in zooplankton sampling and also analyses, and the Captain and the crew of the R/V *Guilan* for their support during sampling and measurements.

References

Bagheri S., Kideys A.E. (2003) Distribution and abundance of *Mnemiopsis leidyi* in the western Iranian coasts of the Caspian Sea. In: Yilmaz A. (Ed.), *Proceedings of Second International Conference on Oceanography of the eastern Mediterranean and Black Sea: Similarities and differences of two interconnected basins*. TUBITAK Publishers, Ankara: 851–856.

Barlow J.P. (1955) Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biological Bulletin*, **109**, 211–225.

Berkeliev T., Mamedov R., Panian G., Ryanzhin S. (2003) *Scientific Report on Caspian Sea Environment*, Project Nr. ICA2-1999-10006 Contract Nr. ICA2-CT-2000-10054. Caspian Scientific Network Caspscience-Net, Kazakhstan.

Bigelow H.B. (1915) Exploration of the coastal water between Nova Scotia and Chesapeake Bay, July-August, 1913, by the U.S. Fisheries Schooner, Grampus, Oceanography and plankton. *Bulletin of the Museum of Comparative Zoology*, **59**, 149–359.

Bigelow H.B., Leslie M. (1930) Reconnaissance of the water and plankton of Monterey Bay, July 1928. *Bulletin of the Museum of Comparative Zoology*, **70**, 429–581.

Bilio M., Niermann U. (2004) Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Marine Ecology Progress Series*, **269**, 173–183.

Burrell V.G. (1968) *The ecological significance of a ctenophore, Mnemiopsis leidyi* (A. Agassiz) *in a fish nursery ground*. Master thesis, College of William and Mary, Virginia.

Burrell V.G., Van Engel W.A. (1976) Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River estuary. *Estuarine and Coastal Marine Science*, **4**, 235–242.

CEP (1998) *National Report, Iran*. Caspian Environment Programme, Baku, Azerbaijan.

Chaikin B., Rakhmatulina L., Sharapova L., Falomeeva A., Giszov A., Melnikov V., Ogar N., Stogova L., Kazenas V., Grachev Y. (2001) *Caspian Flora and Fauna Species Checklist*. Caspian Environment Programme, Available at: http://www.caspianenvironment.org/scripts/print.pl?word=report_technical.htm. (Accessed 20 June 2008).

Conover R.J. (1961) A study of Charlestown and Green Hill Ponds, Rhode Island. *Ecology*, **42**, 119–140.

Cronin L.E., Daiber J.C., Hulburt E.M. (1962) Qualitative seasonal aspects of zooplankton in the Delaware River Estuary. *Chesapeake Science*, **3**, 63–93.

Daskalov G.M., Mamedov E.V. (2007) Integrated fisheries assessment and possible causes for the collapse of anchovy kilka in the Caspian Sea. *ICES Journal of Marine Science*, **64**, 503–511.

Deason E., Smayda J. (1981) Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. *Journal of Plankton Research*, **4**, 203–217.

Dumont H. (1995) Ecocide in the Caspian. *Nature*, **377**, 673–674.

Esmaeili A., Abtahi B., Khoda Bandeh S., Talaeizadeh R., Darvishi F., Terershad H. (1999) First report on occurrence of a combjelly in the Caspian Sea. *Journal of Environmental Sciences and Technology, Islamic Azad University*, **3**, 63–69.

Fazli H., Roohi A. (2002) The impacts of *Mnemiopsis leidyi* on species composition, catch and CPUE of 'kilka' in Iranian commercial catch. *Caspian Floating University Research Bulletin*, **3**, 99–104 (in Russian).

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

Fraser J.H. (1962) The role of ctenophores and salps in zooplankton production and standing crop. *Rapports et Proces-Verbaux des Reunions, Conseil International pour L'Exploration scientifique de la Mer Mediterranee*, **153**, 121–123.

Fraser J.H. (1970) The ecology of the ctenophore *Pleurobrachia pileus* in Scottish waters. *ICES/CIEM International Council for the Exploration of the Sea/Conseil International pour l'Exploration de la Mer*, **33**, 149–168.

GESAMP (1997) *Opportunistic Settlers and the Problem of the Ctenophore Mnemiopsis leidyi Invasion in the Black Sea*. Reports and Studies No. 58, GESAMP (Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection), London.

Herman S.S., Mihursky J.A., McErlean A.J. (1968) Zooplankton and environmental characteristics of the Patuxent River estuary 1963–1965. *Chesapeake Science*, **9**, 67–82.

Hopkins T.L. (1966) The plankton of the St Andrew Bay System, Florida. *Publications of the Institute of Marine Science*, **11**, 12–64.

Hossieni A., Roohi A., Ganjian Khanari A., Roshantabari M., Hashemian A., Solimanroudi A., Nasroolazadeh H., Najafpour S., Varedi A., Vahedi F. (1996) *Hydrology and Hydrobiology of the Southern Caspian Sea*. Mazandaran Fisheries Research Center Report, Sari, Iran.

Ivanov P., Kamakim A., Ushivtzev V., Shiganova T., Zhukova O., Aladin N., Wilson S.I., Harbison G., Dumont H. (2000) Invasion of Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). *Biological Invasions*, **2**, 255–258.

Kasimov A.G. (2001) New introduced species in the Caspian Sea – *Mnemiopsis leidyi* (A. Agassiz). In: *The Invasion of the Caspian Sea by the Comb Jelly Mnemiopsis – Problems Perspectives, Need for Action*. Baku, Azerbaijan, April 2001 (Available at: http://www.caspianenvironment.org/mnemiopsis/mnem_attach11.htm).

Kideys A.E. (2002) Fall and rise of the Black Sea ecosystem. *Science*, **297**, 1482–1484.

Kideys A.E., Moghim M. (2003) Distribution of the alien ctenophore *Mnemiopsis leidyi* in the Caspian Sea in August 2001. *Marine Biology*, **142**, 163–171.

Kideys A.E., Ghasemi S., Ghninejad D., Roohi A., Bagheri S. (2001) *Strategy for Combatting Mnemiopsis in the Caspian Waters of Iran*. A report prepared for the Caspian Environment Programme, Baku, Azerbaijan, Final Report, July 2001.

Kremer P. (1979) Respiration and excretion of the ctenophore *Mnemiopsis leidyi*. *Marine Biology*, **44**, 43–50.

Kremer J.N., Nixon S.W. (1976) *A Coastal Marine Ecosystem*. Springer-Verlag, New York.

Laloei F., Roshantabari M., Roohi A., Ganjian khanari A., Hashemian A., Solimanroudi A., Nasroolazadeh H., Najafpour S., Varedi A., Vahedi F. (1999) *Hydrology and Hydrobiology of the Southern Caspian Sea with the Regard to Some Environmental Studies*. Mazandaran Fisheries Research Center, Sari, Iran (in Persian).

Lynam C.P., Gibbons M.J., Axelsen B.E., Sparks C.A.J., Coetzee J., Heywood B.G., Brierley A.S. (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology*, **16**, 492–493.

Mamedov E.V. (2004) *Morphobiological peculiarities of 'kilka' along the Azerbaijan coast of Caspian Sea in the modern ecological conditions*. PhD dissertation, Institute of Zoology, Academy of Sciences of Azerbaijan (in Russian), 166 pp.

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

Mills C.E. (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, **451**, 55–68.

Mountford K. (1980) Occurrence and predation by *Mnemiopsis leidyi* in Barnegat Bay, New Jersey Estuary. *Coastal Marine Science*, **10**, 393–402.

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

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

Mutlu E., Bingel F., Gucu A.C., Melnikov V.V., Niermann U., Ostr N.A., Zaika V.E. (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 Journal of Marine Science*, **51**, 407–421.

Nelson T.C. (1925) On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. *Biology Bulletin*, **48**, 92–111.

Petipa T.S. (1957) About average weight of main forms of the zooplankton in the Black Sea. *Proceedings of the USSR AS Sevastopol Biological Station*, **9**, 39–57 (in Russian).

Postel L., Fock H., Hagen W. (2000) Biomass and abundance. In: Harris R.P., Wieb P.H., Lenz J., Skjoldal H.R., Huntley M. (Eds), *ICES Zooplankton Methodology Manual*, Academic Press, London: 84–192.

Purcell J.E. (2005) Climate effects on formation of jellyfish and ctenophore blooms. *Journal of Marine Biological Association of the United Kingdom*, **85**, 461–476.

Reeve M.R., Walter M.A., Ikeda T. (1978) Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. *Limnology and Oceanography*, **23**(4), 740–751.

Rezai H., Yusoff H.M., Arshad A., Kawamura A., Nishida S., Othman H. (2004) Spatial and temporal distribution of Copepods in the Straits of Malacca. *Zoological Studies*, **43**(2), 486–497.

Rezvani S., Roohi A., Ganjian khanari A., Roshantabari M., Laloei F., Hashemian A., Solimanroudi A., Nasroolazadeh H., Najafpour S., Varedi A., Vahedi F., Takmilia K., Olomi Y. (1991) *Hydrology and Hydrobiology of the Southern Caspian Sea*. Mazandaran Fisheries Research Center, Sari, Iran (in Persian).

Roohi A. (2000) *An Introduction to the Some Ecological Aspects of the New Alien Ctenophore Mnemiopsis leidyi* in the Southern Caspian Sea. Caspian Sea Research Center in Ecology, Sari, Iran (in Persian).

Roohi A., Naderi M., Hasanzade K.B., Vahedi F., Ghasemi S., Afraei M.A., Bagheri S., Rostamian M.T. (2001) *Final Report of Mnemiopsis leidyi* Abundance and Biomass in the Caspian Sea. Caspian Sea Research Center in Ecology, Sari, Iran (in Persian).

Roohi A., Kideys A.E., Fazli H. (2003) Distribution and abundance of Mnemiopsis leidyi in the eastern Iranian coasts of the Caspian Sea. *Iranian Journal of Fisheries Scences*, **12**, 67–82.

Russell F.S. (1933) The study of copepods as a factor in oceanic economy. *Proceedings of 5th Pacific Scientific Congress, Vancouver, BC, Canada*, **3**, 2023–2032.

Russell F.S. (1935) The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring trawl in offshore waters in the Plymouth area. *Journal of the Marine Biological Association of the UK. Part II.*, **20**, 147–180.

Sage L.E., Herman S.S. (1972) Zooplankton of the Sandyhook Bay area, N.J. *Chesapeake Science*, **13**, 29–39.

Salmanov M.A. (1999) *Ecology and Biological Productivity of the Caspian Sea*. Institute of Zoology, Baku, Azerbaijan.

Sapozhnikov V. (1991) *Spravochnik gidrokhimika: rybnoe khozyaistvo (Geochemists RTef Book)*. Fishery, Moscow.

Shiganova T.A. (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fish Oceanography*, **7**, 305–310.

Shiganova T., Sapozhnikov V., Musaeva E., Domanov M., Bulgakova Y., Belov A., Zazulya N., Zernova V., Kuleshov A., Sokol'skii A., Imirbaeva R., Mikuiza A. (2003) Factors determining the conditions of distribution and quantitative characteristics of the ctenophore *Mnemiopsis leidyi* in the North Caspian. *Oceanology*, **43**, 676–693.

Stolberg F., Borysova O., Mitrofanov I., Barannik V., Eghtesadi P. (2006) *Caspian Sea GIWA Regional assessment report 23. Global International Waters Assessment*, Kalmar, Sweden. http://www.unep.org/dewa/giwa/areas/reports/r23/giwa_regional_assessment_23.pdf

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