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ORIGINAL PAPER

Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the Southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis Leidyi*

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Abstract Monitoring for 6 years (2001–2006) showed that the population explosion of the alien ctenophore *Mnemiopsis leidyi* in the southern Caspian Sea coincided with a decline in the abundance and species number of mesozooplankton. While this decline appeared to have reduced the nourishment of sprat (also known as kilka), it seemed to have affected phytoplankton favorably mainly due to the decrease in grazing pressure. During 2001–2002, when *M. leidyi* abundance and biomass were at their highest levels, abundance of dinoflagellates and cyanophytes exceeded that of diatoms. Before the invasion (1996) and in some years after the invasion (2003, 2004 and 2006) diatom abundance was higher than the abundance of other groups. In September 2005, an unprecedented bloom of the toxic cyanophyte *Nodularia* sp. was observed in the southern Caspian Sea. Disappearance of edible zooplankton such as *Eurytemora* spp. was among the first changes observed after the expansion of *M. leidyi* in the area. Some changes in the macrobenthic fauna were also conspicuous after the increase of this ctenophore. While the biomass of some deposit feeders, such as the polychaete *Nereis diversicolor* and oligochaete species increased, benthic crustaceans decreased sharply in abundance during 2001–2003 and completely disappeared during 2004–2006. Iranian catches of kilka, the most abundant and widespread zooplanktivorous fish, decreased significantly in the southern Caspian Sea after 1999. Iranian landings of kilka dropped ∼70% from 69,070 ± 20,270 t during 1995–2000 to 23,430 ± 12,240 t during 2001–2006, resulting in a loss of at least 125 million US dollars to the economy. There were also changes in the total catches of large predators such as the kutum and mullet, which mainly feed on kilka, between 1991 and 2006.

Keywords Caspian Sea · Zooplankton · Phytoplankton · Macrobenthos · *Mnemiopsis leidyi* · Fishes

Introduction

The ctenophore *Mnemiopsis leidyi* was first introduced into the Black Sea in the 1980s from its native waters in North America, possibly via ballast water of

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ships (Vinogradov et al. 1989). From the Black Sea it was transported to the Caspian Sea in the late 1990s, probably in the same way (Ivanov et al. 2000; Roohi 2000). It was first seen in November 1999 in the Middle Caspian Sea (Ivanov et al. 2000), expanded over all regions in 2000 (Shiganova et al. 2004) and exploded in the southern Caspian Sea in autumn 2001. This alien species flourished in its new ecosystem in the Caspian Sea and caused tremendous damage in this region. Competing for food with the main zooplanktivorous fish of the Caspian Sea, kilka (*Clupeonella* spp.), *M. leidyi* caused a dramatic recruitment failure of kilka from 2001 to 2004 (Daskalov and Mamedov 2007; Fazli and Roohi 2002; Shiganova et al. 2004). Kilka stocks in the Caspian Sea are now in a critical condition and decline further each year. The collapse of the kilka fishery has damaged the local and regional economy, and the social conditions of the fishermen (Bilio 2004). Total biomass of the anchovy kilka catch, which used to make up 80–90% of total kilka catch (bigeye kilka, common kilka and anchovy kilka) (Fazli and Besharat 1998), declined from ~186,000 t in 1996 to 12,000 t in 2004 in Iranian waters (Fazli et al. 2007). After the invasion of this ctenophore, both abundance and species number of edible zooplankton also changed (Roohi et al. 2008a). Some copepods such as *Eurytemora minor*, *Eurytemora grimmi* and *Calanipeda aquaedulcis*, decreased in abundance or even were not observed at all in the majority of samples (Roohi et al. 2008a). While 24 cladoceran species were recorded in 1996 alone before the invasion (Hossieni et al. 1996), only one cladoceran, *Podon polyphemoides*, was observed during 2001–2006 after the invasion. The decrease in the abundance of edible zooplankton, especially during summer-autumn, concomitant with the high *M. leidyi* abundance (Roohi et al. 2008a; Kideys et al. 2008), coincided with an increase in phytoplankton biomass (inferred from monthly composite satellite chlorophyll *a*) in the southern Caspian Sea (Kideys et al. 2008). In addition, after the invasion the abundance of some benthic animals, such as the polychaete *Nereis diversicolor* and oligochaete species increased, while abundance of benthic crustaceans decreased.

Sudden outbursts of *M. leidyi* when food densities are high (Reeve et al. 1978), in both introduced regions and in native waters, can be attributed to high fecundity, rapid generation time and the capacity for self-fertilization (Baker and Reeve 1974). Under optimal conditions this comb jelly was able to produce 8,000 eggs from its maturation time (13 days) until 23 days from hatching (Baker and Reeve 1974). Over fishing, eutrophication and global warming have also been suggested as triggering factors for explosions in both native and introduced waters (Mills 2001; Lynam et al. 2006; Bilio and Niermann 2004; Purcell 2005). According to long-term data, the highest density of *M. leidyi* is observed during warm months in both introduced regions (Black Sea, Caspian Sea, Baltic Sea) and native waters (e.g. Narragansett Bay and Chesapeake Bay in NW Atlantic) (Shiganova 1998; Purcell et al. 2001; Sullivan et al. 2001; Kideys et al. 2005a, b, 2008; Roohi et al. 2003, 2008a, b; Javidpour et al. 2009). This shows the importance of warm temperature for population explosions. It has also been reported that this ctenophore has a competitive advantage at high food densities compared to predators such as chaetognaths (Reeve et al. 1978), which suggests that *M. leidyi* abundance could increase further in eutrophied ecosystems.

This study documents the changes in phytoplankton, zooplankton, macrobenthos and fish communities after the introduction of the invasive ctenophore *M. leidyi* to the southern Caspian Sea. Large changes in these plant and animal populations, which closely interact with each other, have been observed in the past two decades due to the combination of several anthrophogenic impacts such as over fishing, pollution and the introduction of *M. leidyi*. Possible reasons for these changes were investigated in the present research.

Materials and methods

Biological and environmental data used in this study were collected by the R/V *Guilan* cruises conducted in 1996 (Hossieni et al. 1996) and 2001–2006. Monthly data were collected along six transects (Nowshar, Babolsar Amirabad, Lisar, Anzali and Sepidroud) off the Iranian coast of the southern Caspian Sea. Each transect had four stations located at the points off the shore where the bottom depth was 5, 10, 20 and 50 m, respectively, and two transects (Anzali and Babolsar) had an additional

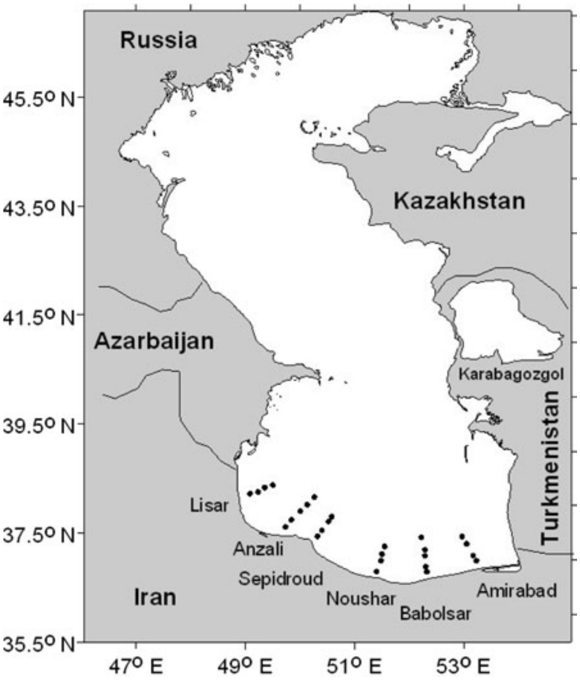


Fig. 1 Distribution of sampling stations in the southern Caspian Sea

station further offshore at the point at which the bottom depth was 100 m (Fig. 1).

During the cruises an Ocean Seven 316 multi-parametric probe (Idronaut) and a Nansen water sampler were used. The horizontal and vertical distributions of temperature were determined using the Idronaut probe. Temperature profiles were recorded for the two stations with a water depth of 100 m at Babolsar and Anzali, in order to determine seasonal stratification patterns.

Non-gelatinous zooplankton samples were taken by vertical hauls using a Juday net, having a mesh size of 100 μm and a mouth opening of 0.1 m^2, from different layers. At the three shallowest stations, hauls were taken from the bottom to the surface at each (i.e. from 5–0 m, 10–0 m and 20–0 m). At the fourth station offshore hauls were taken from the bottom at 50–20 m, and from 20 m to the surface. At the most offshore station (two transects only) the hauls were from 100–50 m, 50–20 m and 20–0 m. Samples were preserved with neutral formaldehyde at a 4–5% final concentration for analyses in the laboratory. They 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).

Mnemiopsis leidyi was collected with a METU net having a mouth opening of 0.2 m^2 and mesh size of 500 μm, from the same depth intervals as the Juday net (Vinogradov et al. 1989; Kideys et al. 2001). The body length of each individual with lobes was measured onboard and the density of *M. leidyi* (per m^3) was calculated from the net diameter and the tow depth. The ctenophores were sorted in length groups at 5 mm intervals up to 70 mm, to determine the abundance of different size groups. In order to define reproductive individuals, lengths were categorized into two groups, >15 mm and 16–70 mm (Dumont et al. 2004). Length measurements were converted to weight/biomass (wet weight per m^3) using the following equation (Kideys et al. 2001):

$$W = 0.0011 \times L^{2.34},$$

where W is wet weight of *M. ledyi* in mg and L is the length in mm.

Macrobenthos data were collected with a Vanveen Don grab having a mouth opening of 0.1 m^2. Three replicates from each station were taken and sieved with a 500-μm mesh size net using sea water, and immediately fixed in a neutral formaldehyde solution with a final concentration of ~10% for taxonomic identification (to genus or species level) and counting under binocular microscope (Mcintyre and Holmes 1984).

Phytoplankton samples were collected in 0.5-L dark bottles from the surface waters and preserved using buffered formaldehyde at a final concentration of 2.5%. Samples were concentrated to a volume of ~20 ml by the sedimentation method, after keeping the samples stagnant for at least two weeks. The microphytoplankton present in a subsample of 1 ml, taken from the ~20 ml sample, was counted using a Sedgewick–Rafter cell under a phase-contrast binocular microscope. For nanoplankton analysis, 0.01-ml subsamples were scanned on a slide. The volume of each cell was calculated by measuring its diameter, length and width (Senichkina 1986; Hillebrand et al. 1999). Volumes were converted to biomass assuming 1 μm^3 to be equivalent to 1 pg.

Fishery data were obtained from the Iranian Fishery Research Organization (IFRO) (http://www.ifro.ir/portal.aspx) and Caspian Sea Research Institute of

Ecology (CSRIE), which retrieved the data from commercial catches at three fisheries ports, Anzali, Noushar and Amirabad.

Results

Water temperature

Water temperature data from 2001 to 2006 showed that there were seasonal fluctuations in vertical stratification pattern from spring to winter. In summer–autumn, it was relatively warm and the water temperatures reached ~18–31 °C at the surface, while in winter–spring it declined to ~9–22 °C due to cold weather and the transport of Volga River water via currents from the North Caspian and through some adjacent rivers (e.g. Tajan, Sepidroud) carrying melted snow to the southern Caspian Sea. Temperature profiles at the deepest station off Babolsar sampled during July 2001 to December 2006 showed that the thermocline started to form in spring, sharpened in summer, began to degrade or completely degraded in autumn, and was not observed at all in winter (Fig. 2).

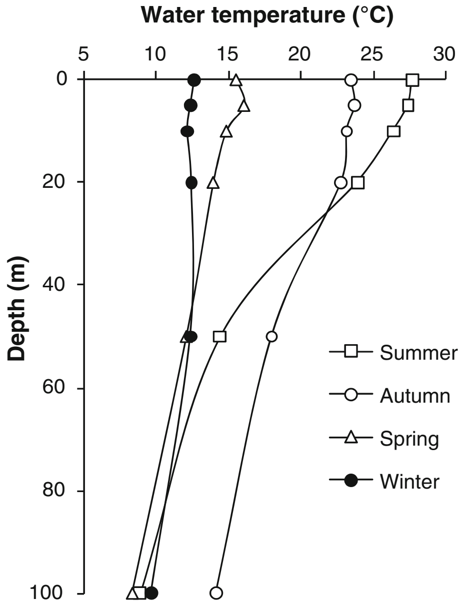


Fig. 2 Seasonal temperature (°C) profiles at the deepest station off Babolsar in the southern Caspian Sea (values are means of 2001–2006)

Mnemiopsis leidyi distribution pattern

Mnemiopsis leidyi was observed at all stations all over the sampling periods during July 2001 to December 2006. There was a seasonal pattern of ctenophore density each year, the maximum being observed in August and September, and the minimum in the winter months. The highest abundance and biomass of *M. leidyi* were observed in 2001 and 2002 (Fig. 3). In the summer and autumn of the following 3 years the total biomass of *M. leidyi* decreased by almost 50% although the abundance was still high in 2003. The mean and maximum lengths of *M. leidyi* with lobes during 2001–2006 were 14.9 ± 3.1 and 70 mm, while the mean and maximum wet weights were 0.97 ± 0.32 and 7.2 mg. In terms of abundance, about 93–98% of the *M. leidyi* sampled consisted of small individuals (cydippid and post-larvae) of less than 15 mm length. (Figs. 4, 5a). However, in terms of biomass large-sized adults (>16 mm, Dumont et al. 2004) made up about 68–85% of annual samples (Fig. 5b).

Records of vertical and spatial distribution of *M. leidyi* revealed that the bulk of individuals (both 0–15 mm and 16–70 mm size groups) predominated at a depth shallower than 20 m during all months (Table 1). The ctenophore was found in the deepest layer of the most offshore stations, at 50–100 m, only in summer months (June, July) (Table 1). While the abundance of *M. leidyi* was higher in 0–20 m depth layer of deep stations than in the 0–5 m depth of first coastal stations during January–April, after May, abundance in the 0–5 m depth layer generally exceeded abundances in deeper layers (Table 1). Only in August was abundance at 0–20 m higher than at shallower stations. The highest abundance and biomass of *M. leidyi* was observed in autumn (Table 2a).

Phytoplankton population

In the present study, a total of 226 phytoplankton species were identified. While diatoms constituted 45% of the total species number, chlorophytes, cyanophytes, dinoflagellates and euglenophytes formed 20, 17, 11 and 8% of phytoplankton species, respectively (Fig. 6).

Number of species in spring (91 species) and summer (101 species) were higher than in autumn (86 species) and winter (77 species).

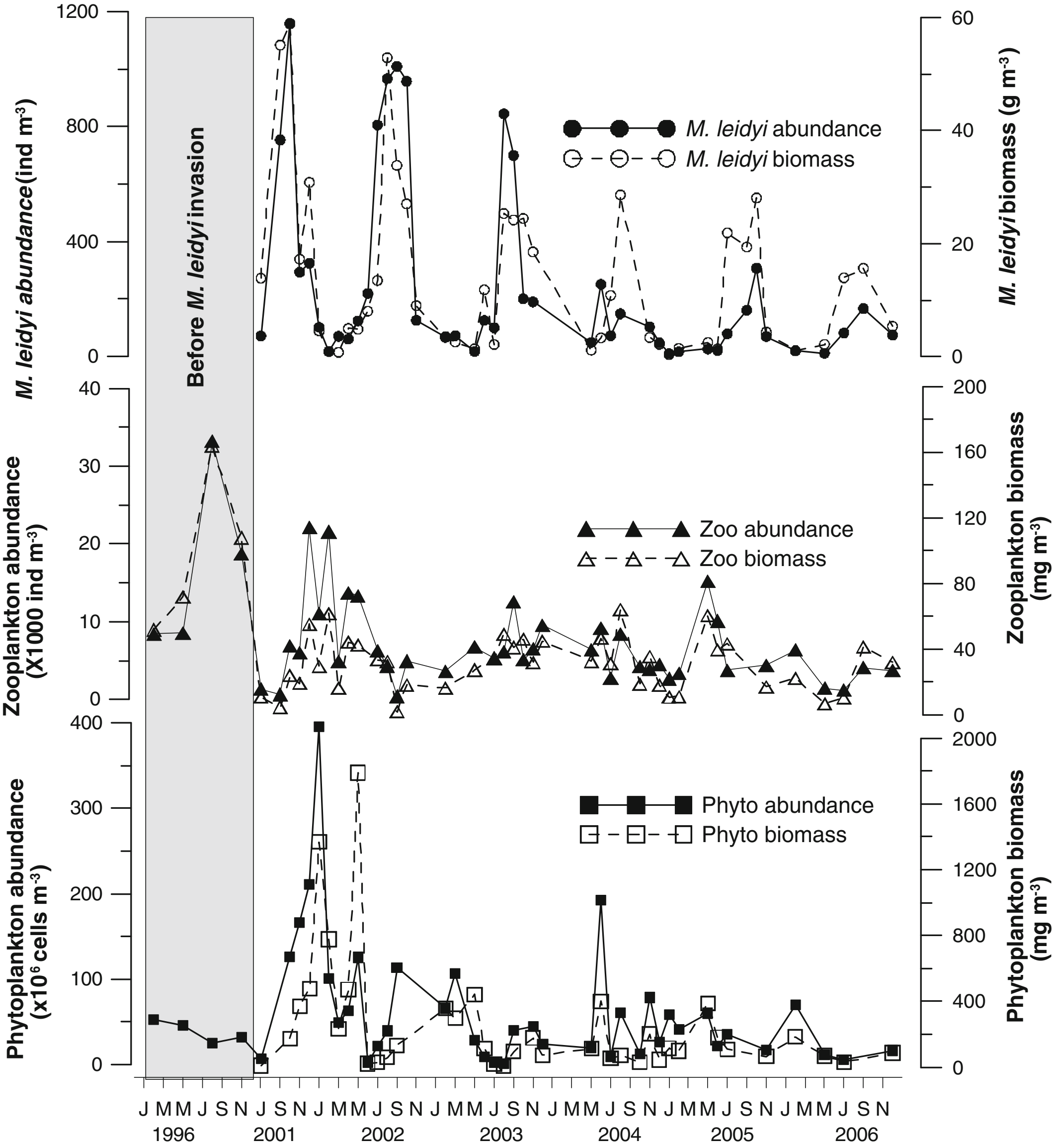


Fig. 3 Annual variations in the abundance and biomass of phytoplankton, zooplankton and *Mnemiopsis leidyi* in the southern Caspian Sea during 2001–2006 (values are depth and station averages). 1996 values are from Hossieni et al. (1996), spring 2001 values are from Kideys et al. (2001)

The highest monthly mean phytoplankton abundance and biomass were 396 × 10^6 ± 299 × 10^6 cells m^{-3} in January 2002 and 1,789 ± 1,761 mg m^{-3} in May 2002 (Fig. 3). Minimum abundance and biomass values were observed in August 2003 (1 × 10^6 ± 1 × 10^6 cells m^{-3} and 7 ± 5 mg m^{-3}) (Fig. 3). The overall average cell abundance and biomass of phytoplankton during 2001–2006 were 64 × 10^6 ± 76 × 10^6 cells m^{-3} and 250 ± 360 mg m^{-3}, respectively. While diatoms were the most abundant phytoplankton group during 1996, after the introduction of *M. leidyi* the abundances of cyanophytes (in autumn) and dinoflagellates (in winter) exceeded diatom abundance in 2001 and 2002 (Fig. 7). Excluding 2005, diatom abundance was again high during 2003–2006. An unprecedented bloom of the toxic cyanophyte *Nodularia* sp. was observed between the second half of August and the end of September in 2005. The bloom area covered ~20,000 km^2 (CEP 2006a). According to the sampling on 20 September 2005, in addition to *Nodularia* sp.,

Fig. 4 Percentage (%) contributions of different size ranges of *Mnemiopsis leidyi* to the total abundance in the southern Caspian Sea from 2001 to 2006

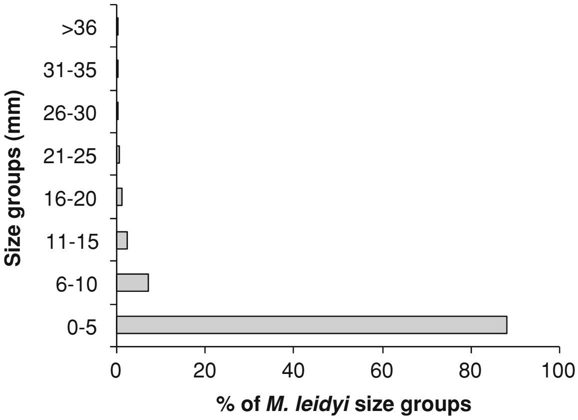


Fig. 5 Annual variations in the a abundance and b biomass of *Mnemiopsis leidyi* of two different size ranges, and percentage contributions of these size ranges to total abundance and biomass in the southern Caspian Sea during 2001–2006

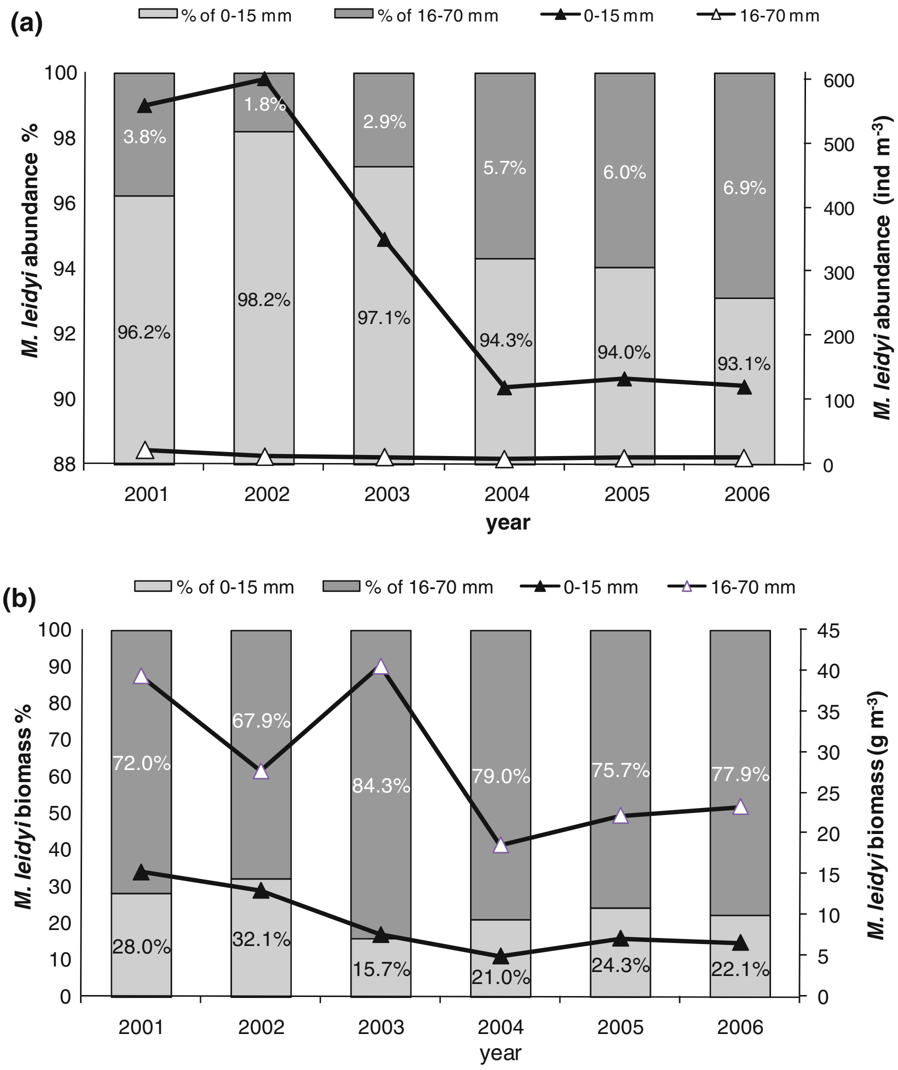


Table 1 Monthly variations in abundance and biomass of two different size classes of *Mnemiopsis leidyi* at different depth intervals in the southern Caspian Sea during 2001–2006

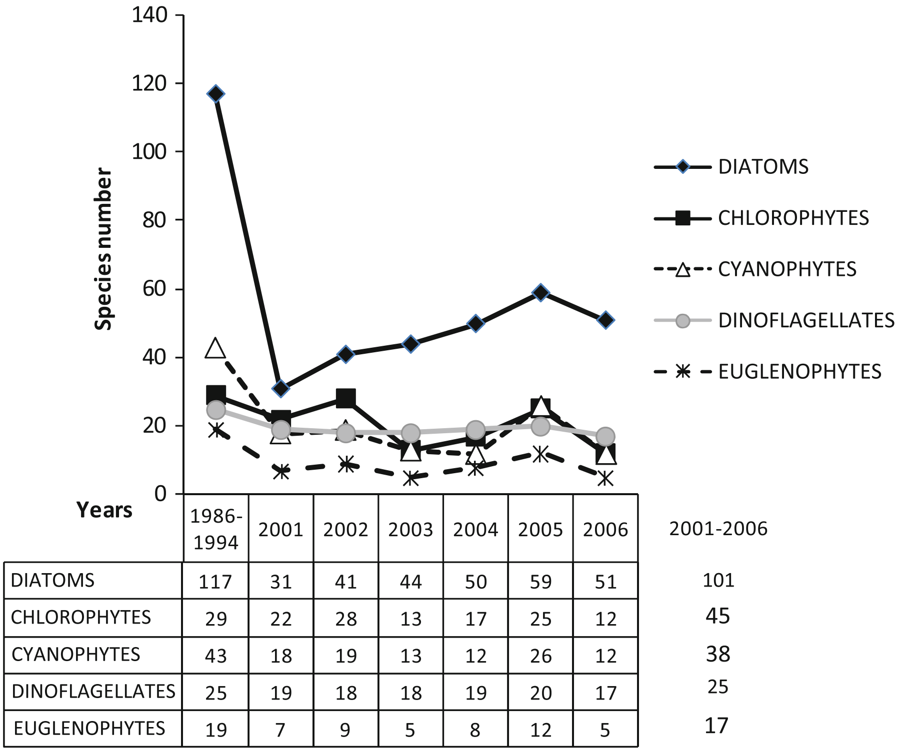
Abundance (ind m^{-3})	*Mnemiopsis leidyi* (0–15 mm)					*Mnemiopsis leidyi* (16–70 mm)				
Depth layers (m)	0–5	0–10	0–20[a]	20–50[a]	50–100	0–5	0–10	0–20[a]	20–50[a]	50–100
January	36	171	64	13	0	2	4	2	2	0
February	11	21	34	5	0	1	2	1	1	0
March	25	47	35	5	0	0	1	2	0	0
April	16	77	78	64	0	3	0	4	2	0
May	64	65	52	22	0	4	3	2	1	0
June	183	129	66	1	2	8	4	7	0	0
July	508	194	111	18	7	17	9	7	3	0
August	588	756	1,060	0	0	18	17	11	0	0
September	606	738	301	29	0	18	22	13	1	0
October	1,196	377	243	21	0	23	25	10	4	0
November	291	232	115	32	0	15	7	6	5	0
December	210	245	151	32	48	23	8	6	5	3
Biomass ($g\ m^{-3}$)										
February	0.7	0.8	1.0	0.2	0.0	1.0	3.3	1.9	1.6	0.0
March	0.3	1.9	1.1	0.3	0.0	0.0	1.0	4.4	0.4	0.0
April	1.3	3.2	5.3	0.0	0.0	2.6	0.0	4.6	0.0	0.0
May	3.2	3.3	3.2	1.0	0.0	4.1	3.7	3.2	0.8	0.0
June	6.6	5.5	3.8	0.1	0.2	14.7	5.6	11.0	0.0	0.0
July	14.4	4.9	4.3	1.7	0.9	31.6	31.6	18.2	7.5	0.1
August	17.4	19.5	20.5	0.0	0.0	30.7	32.7	15.1	0.0	0.0
September	19.9	21.1	9.2	1.0	0.0	33.6	49.4	36.8	3.9	0.0
October	25.3	13.5	6.7	2.8	0.0	70.5	38.8	20.4	9.2	0.0
November	9.5	5.9	3.2	1.9	0.0	29.9	17.1	17.3	21.6	0.0
December	19.1	5.3	3.9	1.5	1.4	32.2	13.2	15.4	10.7	5.2

[a] 0–20 m depth layer was sampled at the third, forth and fifth offshore stations from the coast and the 20–50 m depth layer was sampled at the forth and fifth stations from the coast

Table 2 Seasonal changes in (a) *Mnemiopsis leidyi* abundance and biomass (b) phytoplankton abundance and biomass

	2001–2006 Abundance (Ind m^{-3})	2001–2006 Biomass (g m^{-3})
(*a*)		
Spring	54	3
Summer	291	16
Autumn	442	24
Winter	75	6

	1996 Abundance ($\times 10^6$ cells m^{-3})	2001–2006 Abundance ($\times 10^6$ cells m^{-3})	2001–2006 Biomass (mg m^{-3})	Abundance increase (fold)
(*b*)				
Spring	46	94	768	2.0
Summer	25	60	459	2.4
Autumn	33	141	561	4.3
Winter	52	180	880	3.4



Years	1986-1994	2001	2002	2003	2004	2005	2006	2001-2006
DIATOMS	117	31	41	44	50	59	51	101
CHLOROPHYTES	29	22	28	13	17	25	12	45
CYANOPHYTES	43	18	19	13	12	26	12	38
DINOFLAGELLATES	25	19	18	18	19	20	17	25
EUGLENOPHYTES	19	7	9	5	8	12	5	17

Fig. 6 Variations in species number of different phytoplankton groups in the southern Caspian Sea during 2001–2006 and 1986–1994

another cyanophyte *Oscillatoria* sp. was also high in abundance. Abundance of *Nodularia* sp. was 18×10^6 cells m^{-3} at 7 m depth and $1{,}006 \times 10^6$ cells m^{-3} at 20 m depth. Average cyanophyte abundance and biomass at 7 and 20 m depths were 582×10^6 cells m^{-3} (of which 512 cells m^{-3} was *Nodularia* sp.) and 1,655 mg m^{-3}. The highest seasonal means of phytoplankton abundance and biomass were 179 ×

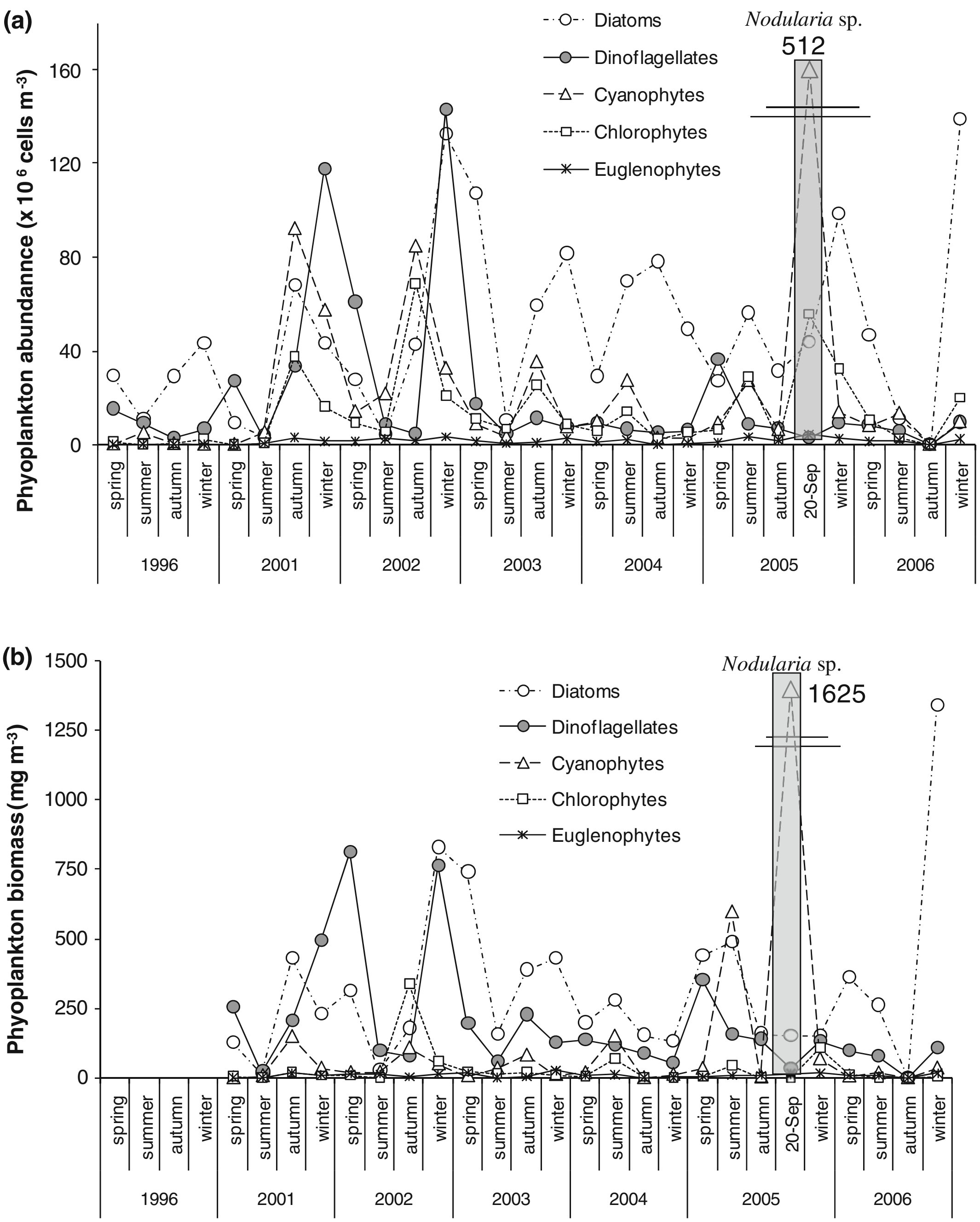


Fig. 7 Seasonal changes **a** in abundance and **b** in biomass of different phytoplankton groups before (Hossieni et al. 1996) and after *Mnemiopsis leidyi* invasion in the southern Caspian Sea (values are depth and station averages)

10^6 cells m^{-3} and 880 mg m^{-3} in winter during 2001–2006. The maximum abundance before *M. leidyi* invasion was also in winter (Fig. 7; Table 2b).

Average abundance of phytoplankton during 2001–2006 was higher in the uppermost 5 m than at lower depths (Fig. 8).

Zooplankton population

During the study, a total of 18 zooplankton species were identified, of which 13 were meroplankton and the rest were holoplankton. The holoplanktonic species were four copepods and one cladoceran species.

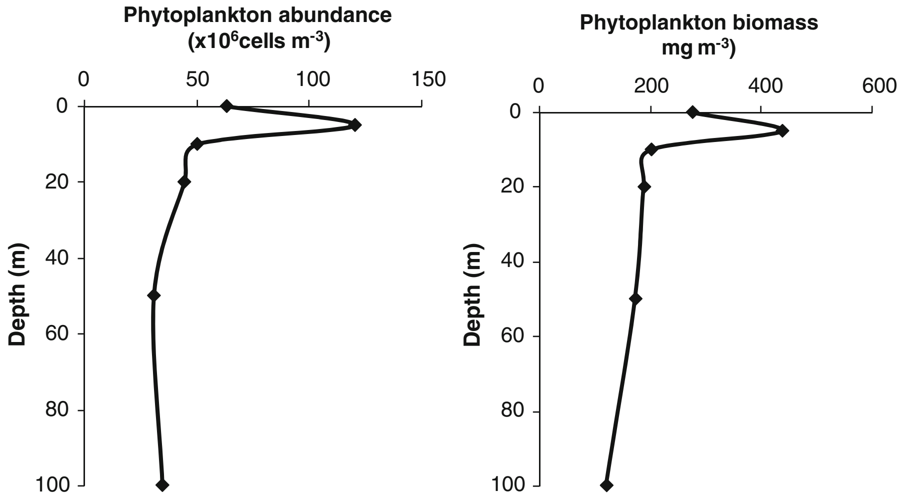


Fig. 8 Depth distribution of phytoplankton abundance and biomass at the deepest station in the southern Caspian Sea during 2001–2006

In 2001, when the spread of *M. leidyi* began, only three copepod and five meroplankton species were recorded. Number of zooplankton species gradually decreased from 11 species in 2002 to 8 species in 2005. During 2001–2006, only one cladoceran, *Podon polyphemoides*, was found. In 2006, one of the copepods, *Eurytemora grimmi*, which was not observed during 2001–2005, appeared again at some stations, but in low abundance (Table 3).

During the 6-year study, the maximum monthly zooplankton abundance was 22,088 ± 24,840 ind m^{-3} (average of stations and depths) in December 2001, while the highest biomass was 64 ± 156.8 mg m^{-3} (average of stations and depths) in August 2004. Monthly variations of zooplankton biomass were similar to the fluctuations in abundance (Fig. 3). The minimum zooplankton abundance and biomass were 397 ± 567 ind m^{-3} and 1.8 ± 2.6 mg m^{-3} in September 2002 (Fig. 3). Copepods were the major non-gelatinous zooplankton in terms of abundance and biomass, and were present at every station and season during 2001–2006 (Fig. 9). Among these, different developmental stages of the calanoid species *Acartia tonsa* dominated during the study period.

The annual mean zooplankton abundance varied between 3,361 and 8,940 ind m^{-3} during 2001–2006. The mean zooplankton abundance for the months March, August, November and February ranged from 8,402 to 33,213 ind m^{-3} in 1996 (Hossieni et al. 1996), while monthly average values were in the range of 397–22,088 ind m^{-3} during 2001–2006. Overall, there was a 2–5-fold decrease in abundance from 1996 to 2001–2006 after the invasion of *M. leidyi*. Similarly, zooplankton biomass in 1996 (51–164 mg m-389.9 mg m^{-3}) was also higher than that recorded during 2001–2006 (2–64 mg m^{-3}) (Fig. 9).

Macrobenthic animals

A total of 21 macrobenthic species were identified of which 57% were crustaceans, 28% were annelids and 14% were bivalves during 2001–2006 (Table 4).

During 2001-2006, annelids contributed most to the total macrobenthic abundance (250 ± 109 ind m^{-2}), followed by bivalves (40 ± 35 g m^{-2}) and crustaceans (14 ± 5 ind m^{-2}) (Fig. 10). Macrobenthos composition was different before the invasion of *M. leidyi*. Hossieni et al. (1996) reported that crustaceans (Corophiidae, *Corophium robustum*) were the most abundant group in 1996 (1,000 ± 418 ind m^{-2}). After the invasion of *M. leidyi*, crustacean abundance decreased by 98%, while the abundance and biomass of bivalves increased two-fold and 15-fold, respectively (Fig. 10). The macrobenthic community therefore shifted from the dominant filter-feeding group of crustaceans (Gammaridae) in 1996 to deposit-feeding annelids (*Nereis diversicolor* and oligochaetes) during 2001–2006.

Depthwise distribution (0–100 m) of macrobenthic species also showed that the abundance and biomasses of annelids (maximum 1,478 ± 1,027 ind m^{-2} at 100 m) and molluscs (maximum 80.7 ± 70.8 g m^{-2} at 20 m) were higher than of crustaceans during 2001–2006 (Fig. 11).

Table 3 Zooplankton species in the southern Caspian Sea (1996 data are from Hossieni et al. 1996)

Before *M. leidyi* invasion		After *M. leidyi* invasion						
Zooplankton/year	1996	2001	2002	2003	2004	2005	2006	2001–2006
Hossieni et al. (1996)								
Acartia tonsa	+	+	+	+	+	+	+	+
Calanipeda aquae dulcis	+	+	–	+	–	–	–	+
Eurytemora grimmi	+	–	–	–	–	–	+	+
Eurytemora minor	+	–	–	–	–	–	–	–
Limnocalanus grimaldii	+	–	–	–	–	–	–	–
Halicyclops sarsi (Cyclopoida)	+	+	+	+	+	–	+	+
Ectinosoma consimum (Harpacticoida)	+	–	+	–	+	+	+	+
# Copepoda	7	3	3	3	3	2	4	5
Podon polyphemoides	+	+	+	+	+	+	+	+
Polyphemus exiguus	+	–	–	–	–	–	–	–
Other species	+	–	–	–	–	–	–	–
# Cladocera	24	0	1	1	1	1	1	1
Arachnida larvae	–	+	+	+	+	–	+	+
Cirripedia larvae *(Balanus spp.)*	+	+	+	+	+	+	+	+
Lamellibranchia larvae	+	–	+	+	+	+	+	+
Mysidaceae larvae	+	–	+	–	–	–	+	+
Nematidae	+	–	+	+	–	+	+	+
Nereididae larvae	–	+	+	+	+	+	+	+
Ostracoda larvae	+	+	+	+	+	–	–	+
Chironomidae larvae	–	–	–	+	–	–	–	+
Oligochaeta larvae	–	–	–	–	–	+	+	+
# Meroplankton	5	4	7	7	5	5	7	9
# Σ Zooplankton	36	7	11	11	9	8	12	15

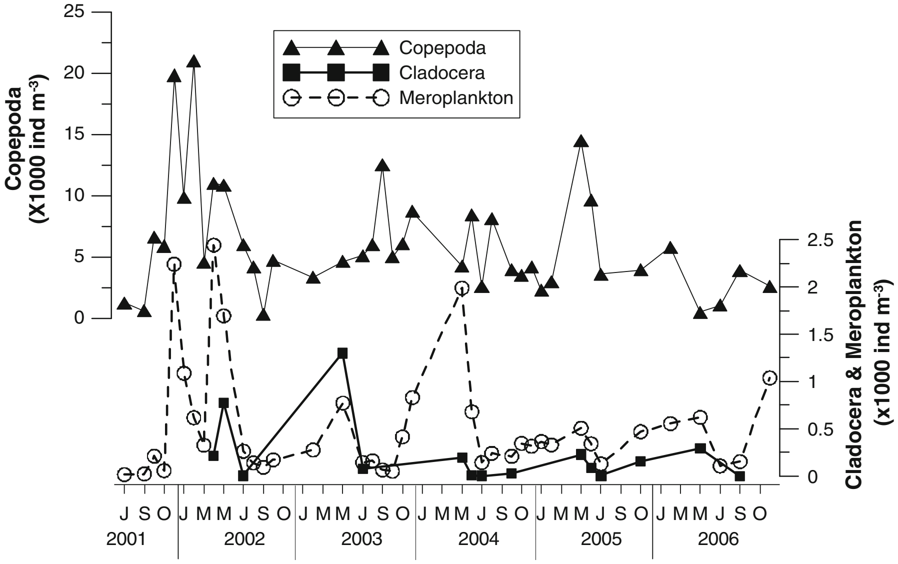


Fig. 9 Monthly variations in abundance of Copepoda, Cladocera and merozooplankton in the South Caspian Sea during 2001–2006 (values are station averages)

Table 4 Macrobenthic fauna species of the southern Caspian Sea during 2001–2006

Phylum	Class	Family	Species
Mollusca	Bivalvia	Scrobicularidae	*Abra ovata*
		Cardidae	*Cerastoderma lamarcki*
		Mytilidae	
Annelida	Polychaeta	Amphartidae	*Hypania invalida*
			Hypaniola kowalewskii
			Parahypania brevispinis
		Nereididae	*Nereis diversicolor*
		Herpobdellidae	*Archeobdella* sp
	Oligochaeta		
Arthropoda	Crustacea	Balanidae	*Balanus* sp
		Gammaridae	*Cardiophilus baeri*
			Niphargoides carausi
			Niphargoides compactus
			Niphargoides sp
		Xantidae	*Rhithropanopeus harrisii*
		Pseudocumidae	*Pterocuma pectinata*
			Schizorhynchus eudorelloides
			Stenocuma diastyloides
			Stenocuma gracilis
			Stenocuma graciloides
	Insecta	Chironomidae	

Fishes

The main widespread pelagic and benthopelagic fishes of the Caspian Sea are kilka (anchovy kilka *Clupeonella engrauliformis*, big-eye kilka *C. grimmi* and common kilka *C. cultriventris*), kutum, also called white fish (*Rutilus frisii kutum*, Cyprinidae) and mullet (*Liza* spp., Mugilidae). The total annual kilka catch in Iran dropped from 41,000–95,020 t during 1995–2000 to 7,672–45,181 t during 2001–

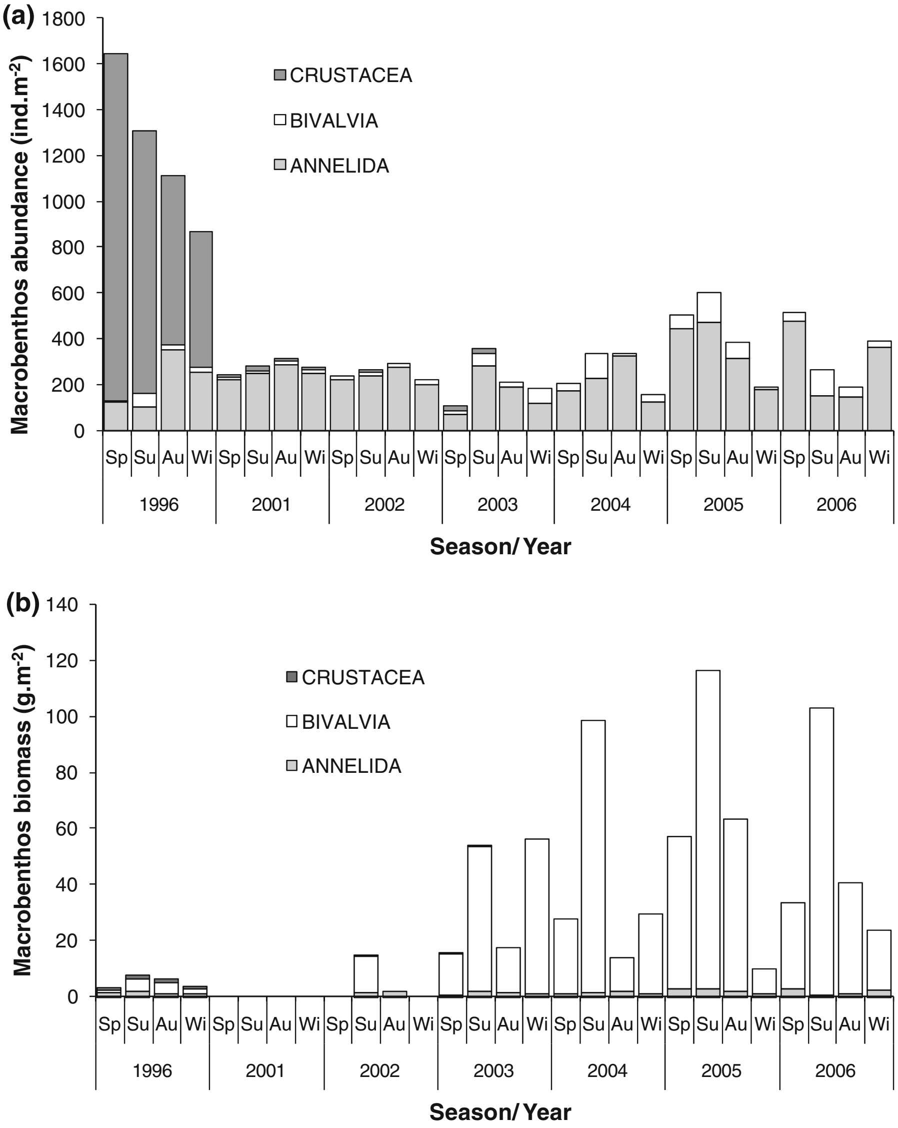


Fig. 10 a Abundance b biomass of macrobenthic groups in the southern Caspian Sea during 2001–2006 (1996 data from Hossieni et al. 1996), *Sp* spring, *Su* summer, *Au* autumn, *Wi* winter

2006 (Fig. 12a). Recruitment failure of kilka after the outburst of *M. leidyi* in the Caspian Sea is indicated by consistently low catches after the year 2000, when *M. leidyi* started its spread. On average, total kilka catch decreased threefold from 69,068 ± 20,271 t during 1995–2000 to 23,432 ± 12,237 t during 2001–2006. Anchovy kilka was historically the most abundant fish species in the Caspian Sea, constituting 70–99% of the total kilka catch between 1995 and 2003 (Fig. 12b). However, its contribution to the total kilka catch suddenly dropped after 2003, when the highest percentage of anchovy kilka was caught at the same time as the minimum total kilka catch. After this year, anchovy kilka formed only 9–27% of the total kilka catch for 2004–2006 (Fig. 12b).

There has also been fluctuation in some other commercial fish catches, such as kutum (*Rutilus frisii kutum*) and mullet (*Liza* spp.), since 1991. These changes could be due to overfishing or other anthrophogenic and environmental impacts, as well as the invasion of *M. leidyi* after the year 2000. The total catch of kutum decreased from the levels of ~12,000–12,700 t during 1991–1993 to ~6,400–10,100 t during 1994–2005 (Fig. 13). In 2006, kutum

Fig. 11 Depthwise abundance and biomass of macrobenthic groups in the southern Caspian Sea during 2001–2006

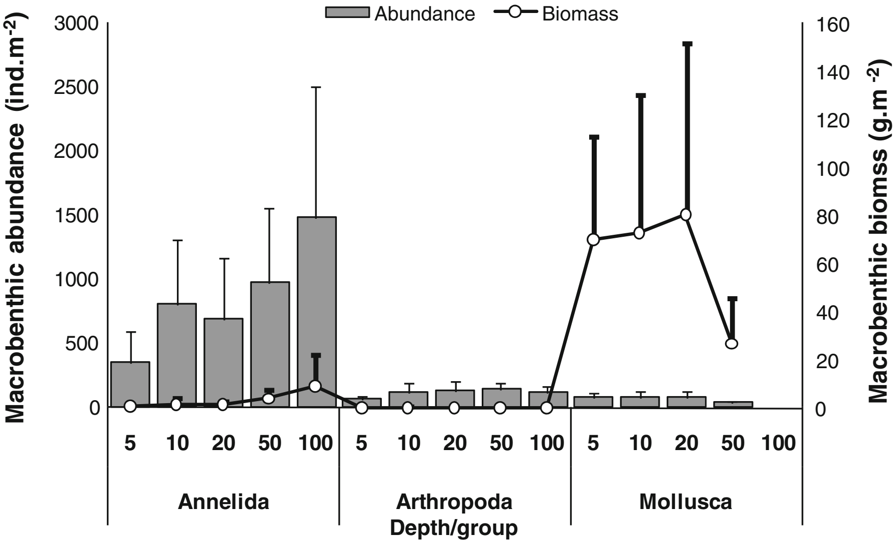
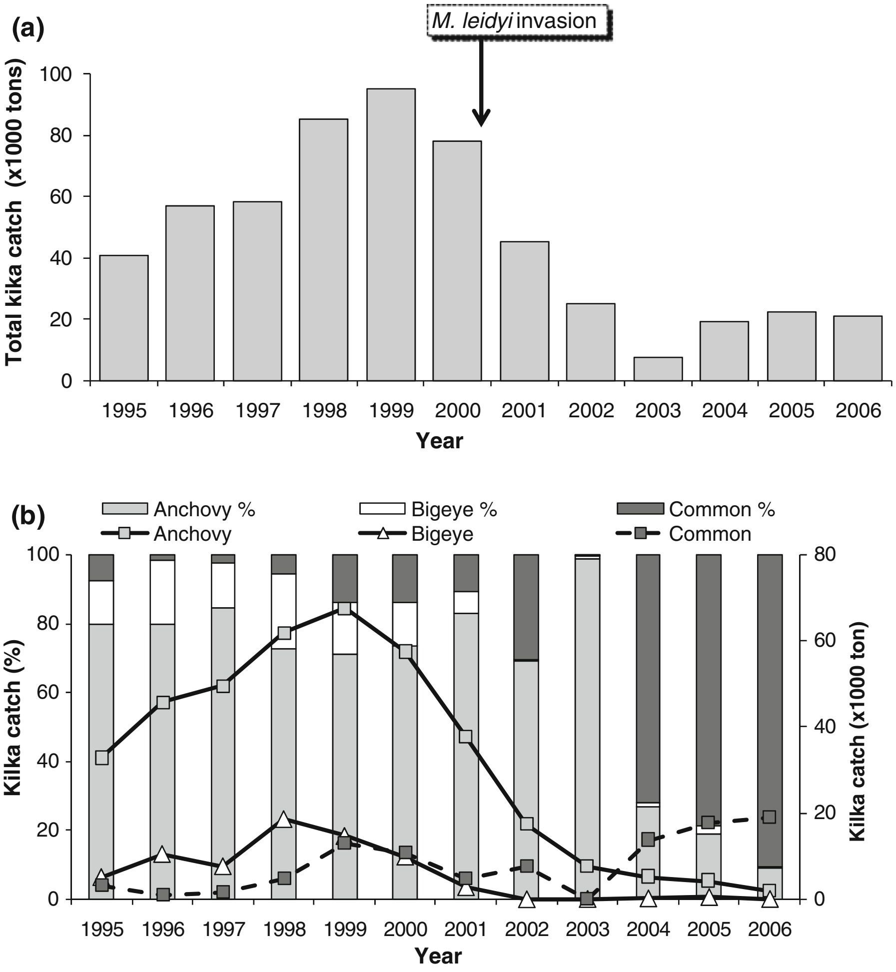


Fig. 12 aTotal kilka catch, b percentage contributions of different kilka species to the total kilka catch as weight in the southern Caspian Sea during 1995–2006



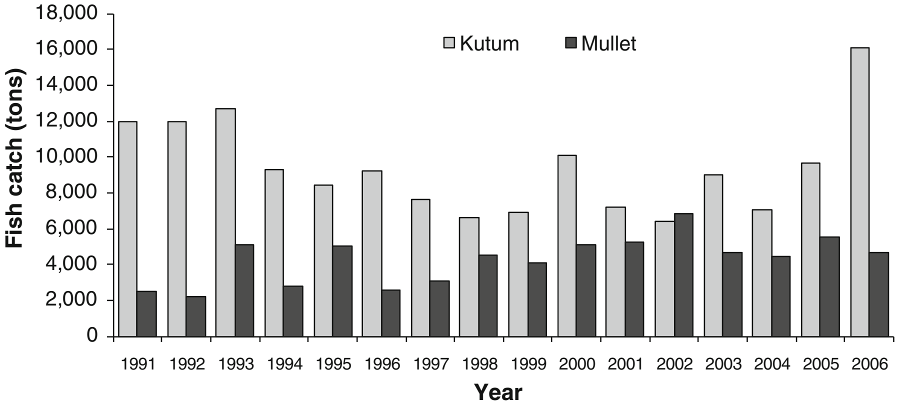


Fig. 13 Variations in total catch of kutum and mullet in the southern Caspian Sea during 1991–2006

catch, ~16,100 t, increased to a level higher than 1991–1993 levels. There was an increasing trend in mullet catches from 1991 to 2006 (Fig. 13).

Discussion

Numerous changes in the biodiversity of organisms have been observed in the Caspian Sea following the invasion of the ctenophore *Mnemiopsis leidyi* (Roohi et al. 2008a; Kideys et al. 2005a, b). A decrease in total zooplankton abundance and an increase in total phytoplankton abundance were among the most obvious changes recorded after the introduction of *M. leidyi* (Fig. 3). Not only abundance, but also species number of zooplankton decreased after the invasion. While a total of 36 zooplankton species (24 Cladocera, 7 copepods, 5 meroplankton) were recorded during 1996 (Hossieni et al. 1996), only 15 zooplankton species (1 Cladocera, 5 copepods, 9 meroplankton species) were found during 2001–2006, after the invasion (Table 3). Phytoplankton composition was also different in the period coinciding with the *M. leidyi* explosion. High abundances of cyanophytes (*Oscillatoria* spp.) and dinoflagellates (*Prorocentrum cordatum*) were observed in 2001 and 2002 (Fig. 7). Collapse of the kilka fishery after 2000 also corresponded to the period after invasion of *M. leidyi*. In addition, there were changes in the benthic macrofauna. Certainly other factors such as overfishing, climate change and anthropogenic pollution might also have played a role in the variations of the Caspian Sea ecosystem, in addition to the impact of *M. leidyi* (Kideys et al. 2008). Levels of these impacts can be estimated to some degree by examining the long term data. For instance, the total kilka catch started to decrease in 2001, indicating low kilka stocks during the period of the initial outburst of *M. leidyi*. This suggests that the decrease in edible zooplankton abundance was mainly due to predation by *M. leidyi*, rather than predation by kilka. Satellite-derived sea surface temperature did not show significant change that might have affected zooplankton abundance in the period before and after *M. leidyi* invasion (Kideys et al. 2008). Subsequently, low edible zooplankton abundance may have caused starvation of kilka larvae, further reducing kilka stocks (Daskalov and Mamedov 2007).

Mnemiopsis leidyi has successfully reproduced and overwintered (at minimum temperatures of 8–12°C and within a salinity range of 8–13 psu) in the southern Caspian Sea (present study), whereas in the northern Caspian Sea it has been limited by water of salinity <4.3 psu in summer when the temperature was ~24°C (Shiganova et al. 2004). Both in its native waters of Chesapeake Bay and in the introduced region of the Black Sea, *M. leidyi* was restricted by the low water temperatures of 2°C (Purcell et al. 2001). Abundance values in the warm South Caspian Sea (16,000 ind m^{-2}) were higher than in the Middle (6,000 ind m^{-2}) and in the North (2,000 ind m^{-2}) Caspian Sea in August 2001 (Shiganova et al. 2004). Mean length of *M. leidyi* was higher in the North Caspian (21.5 mm) than in the Middle (15 mm) and South (11.4 mm) Caspian in August 2001 (Shiganova et al. 2004). This may indicate higher reproductive rates in the South Caspian Sea. Such a successful adaptation of *M. leidyi* to the Caspian Sea ecosystem could be related to an environment made more vulnerable through overfishing (Daskalov and Mamedov 2007) and pollution from multiple sources (Salmanov 1999; Ivanov et al. 2000).

The thermocline is most pronounced in August and it is usually located within the 30–40 m depth layer in the southern Caspian Sea. In autumn, the thermocline degrades with the cooling of water and disappears by the end of November (Fig. 2). *Mnemiopsis leidyi* dominated within the upper water layers. The low abundance of *M. leidyi* at lower depths (20–100 m) were likely due to low temperatures, which constrain the reproductive potential of this ctenophore (Purcell et al. 2001). While the abundance of *M. leidyi* was higher at the offshore stations (where sampling was done at 0–10 m and 0–20 m) during winter–spring, during summer–autumn abundances were generally higher in shallowest onshore waters (0–5 m) than at other stations and depth intervals (Table 1). Only in August was abundance at a deeper station (where the vertical hauling was between 0 and 20 m) higher than at shallower stations during 2001–2006. Remaining in deeper waters during cooler periods (February–April) may help *M. leidyi* to avoid flushing in shallow coastal waters. It has been reported that during winter months when population density was low *M. leidyi* congregated in shallow bays that serve as a refuge (Costello et al. 2006). If there are no such shallow bays the ctenophore might remain in deeper layers to avoid flushing. In the central Baltic Sea *M leidyi* overwintered below the halocline layer where temperature does not drop below 4°C (Kube et al. 2007). No ctenophores were found below 20 m in August, probably due to the shallow thermocline in this month during 2001–2006 (Table 1).

Mnemiopsis leidyi is quite effective in consuming mesozooplankton prey organisms in both native waters (Burrell and Van Engel 1976; Deason and Smayda 1982; Sullivan et al. 2007) and in introduced regions (Kideys et al. 2005a, b; Shiganova 1998; Finenko et al. 2006). Based on a feeding experiment, it was calculated that *M. leidyi* can suppress available stocks of zooplankton within 1 day in summer and within 3–8 days in winter in the Caspian Sea (Finenko et al. 2006). The seasonal impact of *M. leidyi* on zooplankton was the highest in summer-autumn due to increasing feeding rates at higher water temperatures (Kremer 1979) and the small size structure of the population in this season (*M. leidyi* larvae with mean lengths of 2–5 mm accounted for most of the population) (Finenko et al. 2006). Larval stages of *M. leidyi* had sevenfold higher weight-specific clearance rates than adults, in Narragansett Bay, USA (Deason 1982). In native habitats of *M. leidyi* zooplankton abundance was observed to be high and the copepod *Acartia tonsa* predominated (Purcell et al. 2001), similar to the present study.

The abundance of zooplankton reported in the present study was 2–5 times lower than the values reported in 1996 (Hossieni et al. 1996), before the *M. leidyi* invasion (Roohi et al. 2008a). There was also a change in the seasonal maxima of zooplankton abundance. While the maximum zooplankton abundance was recorded in summer in 1996, after the invasion it shifted to a cooler period (winter–spring) (Fig. 3).

Dominant phytoplankton groups changed from diatoms to dinoflagellates and cyanophytes when *M. leidyi* abundance was at a maximum level during summer-autumn of 2001–2002 in the southern Caspian Sea (Fig. 7). There was ∼2–4-fold increase in phytoplankton abundance in all seasons (Fig. 7; Table 2b) from 1996 to 2001–2006. Summer increase of phytoplankton abundance was attributed to *M. leidyi* predation on herbivorous zooplankton and the nutrient excretion accompanying such grazing in Narragansett Bay during 1972–1977 (Deason and Smayda 1982). Increase in phytoplankton abundance might also be related to *M. leidyi* in the present study. The highest increase in phytoplankton abundance (4.3-fold) from 1996 to 2001–2006 was observed in autumn when *M. leidyi* reached its highest abundance and biomass (Table 2a, b). It is also worth noting that the toxic cyanophyte, *Nodularia* sp., bloomed in 2005, which could be linked to the slight decrease of silicon (data not shown, CEP 2006b).

High fishing rates of the main pelagic zooplanktivorous fish, kilka *Clupeonella* spp., especially during 1998–2000, were not sustainable after the invasion of *M. leidyi* in the southern Caspian Sea (Fazli and Roohi 2002; Fazli et al. 2007). The introduction of *M. leidyi* resulted in a reduced abundance and biomass of zooplankton, the main food source of kilka. As a result, kilka stocks, which were already vulnerable due to overfishing, diminished and average kilka catches dropped by a factor of ∼3 from 1995–2000 to 2001–2006 in the South Caspian (Fig. 12a, b). A decrease in fish catch between 2001 (18,500 t) and 2004 (5,500 t) was also observed in Azerbaijan waters (Mamedov 2006). Although the total allowable kilka catch was 300,000 t, catch by Russia, Azerbaijan and Iran dropped from 182,700 t in 2000 to 74,700 t in 2001 (Mamedov 2006).

The diet of *M. leidyi* in the southern Caspian includes Cladocera (*Podon polyphemoides*), copepods (mainly *Acartia tonsa*), bivalve larvae, crab larvae and *Balanus* larvae. *Acartia tonsa* and bivalve larvae dominated the diet of *M. leidyi*, while other species account for about 10% of total food (Bagheri et al. 2004). Anchovy kilka is planktophagous and its main food (>90% annually) was copepods before the invasion of *M. leidyi*. *Eurytemora* spp. alone used to constitute 70% of the annual food source of anchovy kilka (Prikhodko 1975; Sedov and Paritskiy 2001). Anchovy kilka, which was traditionally the most abundant fish species in the Caspian, constituted ∼70–99% of the total kilka catch between 1995 and 2003. Its catch dropped suddenly to <30% of total kilka catch after 2004 (Fig. 12b). Anchovy kilka lives mostly in the shallow coastal zone where the copepod *A. tonsa* was dominant. *Mnemiopsis leidyi* also inhabits the same region and thus it potentially competes with the anchovy kilka for zooplankton prey. When the high reproduction rate of *M. leidyi* was considered, recruitment failure of kilka as a result of competition was anticipated (Finenko et al. 2006).

Macrobenthic diversity also changed dramatically from domination by crustaceans (Corophidae, *Corophium robustum*) in 1996 to annelids (*Nereis diversicolor*) and bivalves (*Cerastoderma lamarcki*) after the invasion of *M. leidyi* (Table 4; Figs. 10, 11). There was a 99–100% decrease in annual crustacean abundance from 1996 to 2001–2006. Annual bivalve abundance decreased 36–52% from 1996 to 2001–2002 and increased 28–58% from 1996 to 2003–2006. Annelid abundance increased 11–41% from 1996 to 2001–2006, excluding the year 2003 when there was a 20% decrease (Fig. 10). Increase in annelid abundance after the *M. leidyi* invasion could be related to marine snow which must have occurred during summer–autumn peak of *M. leidyi* as a result of mass flux of dead ctenophores to the bottom, nourishing deposit feeders. It was observed that increase in marine snow corresponded with an increase in benthic mussel feeding activity and maximum rates of pseudofaeces production by mussels along the coast of Maine, USA (Newell et al. 2005). It can be predicted that increasing abundance of annelids and bivalves may lead to an increase in some benthopelagic fishes that feed on these benthic organisms.

There were changes in the fish catch data of commercially important, benthopelagic bony fishes, kutum and mullet, between 1991 and 2006 in the southern Caspian Sea (Fig. 13). These changes seemed to be related more to overfishing than to *M. leidyi* invasion. Kutum catches decreased about 30% from 12,242 ± 419 t during 1991–1993 to 8,125 ± 1,298 t during 1994–2005 (Fig. 13). In 2006, annual kutum catch suddenly increased to 16,117 t, which is ∼25% higher than the yield obtained during 1991–1993. This may show a slight recovery in kutum stocks in 2006. There was an increasing trend in mullet catches from 1991 to 2006. Low catches of mullet (2,200–3,000 t) recorded some years during 1991–1997 were not observed during 1998–2006 (Fig. 13). Based on a study related to population ecology parameters and biomass of golden grey mullet it was reported that this fish was not overfished during 2004–2005 in Iranian waters of the Caspian Sea (Fazli et al. 2008).

Anthropogenic impacts may affect ecosystems differently in distinct geographical regions due to the differences in biota (e.g. species composition of prey and predators), climate and physico-chemical properties of the habitats. Alterations in the structure of food webs might be unpredictable due to different responses of populations to the changes in environmental conditions. Our results showed that the introduction of *M. leidyi* to the Caspian Sea resulted in some changes that were similar to those observed in the Black Sea after the invasion of this comb jelly. Abundance and species number of zooplankton decreased in both seas (Shiganova 1998; Shiganova et al. 2001; Roohi et al. 2008a) and the main pelagic fish of both seas (anchovy in the Black Sea and kilka in the Caspian Sea) collapsed, also due to the impact of overfishing (Shiganova 1998). However, a similar decrease in zooplankton abundance and species number was not observed in Chesapeake Bay, in the native waters of *M. leidyi* (Purcell et al. 2001). Reduction in zooplankton abundance appeared to lead to an increase in phytoplankton abundance in the southern Caspian Sea. There were also changes in macrobenthic fauna (increased bivalve and annelid abundance, but decreased benthic crustacean abundance) after the invasion of the *M. leidyi* in the southern Caspian, which could be related to predation of their larvae by *M. leidyi*, to decrease in predators of macrobenthos and/or to increase in their food source by settling of dead ctenophores.

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