

Latest Diversity Trend and Seasonal Abundance of Population of Zooplankton (Holoplankton) Communities in the South Caspian Sea, Iran

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Abstract

Seasonal variations of zooplankton communities were studied in the southern Caspian Sea for 4 successive seasons and 8 transects with 5 stations from 5 to 100 m depths which sampled during 2009. The zooplankton population constituted of 73.33% copepods, 24.21% rotifers, 2.23% cladocerans and 0.23% protozoans. Copepods were dominant at all stations with a density between 1456 ± 531 ind. m^{-3} (Transect 8) to 4524 ± 1215 ind. m^{-3} (transect 2). The predominant species of copepods was *Acartia tonsa* constituting 99.50% of all copepod populations. They were most abundant during warm months of summer in the upper layers (surface to 20 m depth) while rotifers replaced them during cold season. The maximum density of zooplankton was observed in the west decreasing towards the eastern parts of the sea.

Keywords: Zooplankton, Caspian Sea, Copepods, Rotifers, *Acartia tonsa*

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Introduction

Caspian Sea is the largest enclosed water body in the world (Dumont, 1998) with brackish water with an average salinity of about 13 parts per thousand in the south. Its faunal composition has changed a great deal during last decades because of its water level fluctuations, human manipulation and the entrance of an alien invasive species of a Ctenophore jellyfish, *Mnemiopsis leidyi* during 80s origination from the north Atlantic waters transferred to the Black Sea, Azof, Marmara and east Mediterranean Seas and then to Caspian (Vinogradov et al., 1989; Studenikina et al., 1991; Zaitsev, 1992; Shiganova, 1993; Dumont, 1995; Shiganova et al., 2001; Fuentes et al., 2010).

Several studies have been done regarding the zooplankton communities and their structures alongside the Iranian coasts in the southern parts of the Caspian in recent years including RowshanTabari, 2000; Laloei et al., 2004; Hashemian et al., 2006 and Hosseini et al., 2011. The results of these studies showed that copepods were the dominant groups of zooplankton which is similar to other findings by other authors in different parts of the world (Mayer, 1912; Nelson, 1915; Main, 1928; Herman et al., 1968; Kermer, 1975 and 1976).

There are different origins for the Caspian zooplankton faunal composition. Calanoids Cyclops and Harpacticoids had been first reported from the Caspian Sea in 1375 (RowshanTabari, 2000). Calanoids have four groups and constituted the main population of copepods. *Eurytemora grimmeri* and *E. minor* are native species to the Caspian and exist mostly in deeper layers from 50-100 m,

Acartia tonsa and *Calanipeda aquae-dulcis* are found mostly in surface waters and have their origin from the Black Sea, while *Limnocalanus grimmeri* is an arctic origin species and exists deeper than 100 m depth (RowshanTabari, 2000).

As it was mentioned earlier, *M. leidyi* appearance in the Caspian has affected greatly the zooplankton populations regarding their species composition, sharp decrease in abundance, distribution and biomass. As to *Acartia tonsa* constitutes main population of zooplankton at present while *Eurytemora grimmeri*, *E. minor* and *Limnocalanus grimmeri* which have had dominated the zooplankton community had been disappeared from the Caspian waters and are no longer exist (Bagheri et al. 2010; RowshanTabari et al., 2012). This has been the case in the Black Sea as well (Shiganova et al., 1998). These changes in the ecological food chain were the basis for this study to examine the latest zooplanktonic structures in the south of Caspian Sea.

Materials and methods

Alongside the Iranian coastline, eight transects were sampled during four successive seasons including spring (May) summer (August), autumn (November) and Winter (February) on a board of R/V Guilanian 2009. At each site (transect) 5 stations (5m, 10m, 20m, 50m and 100m depths) at each transect (Fig. 1).

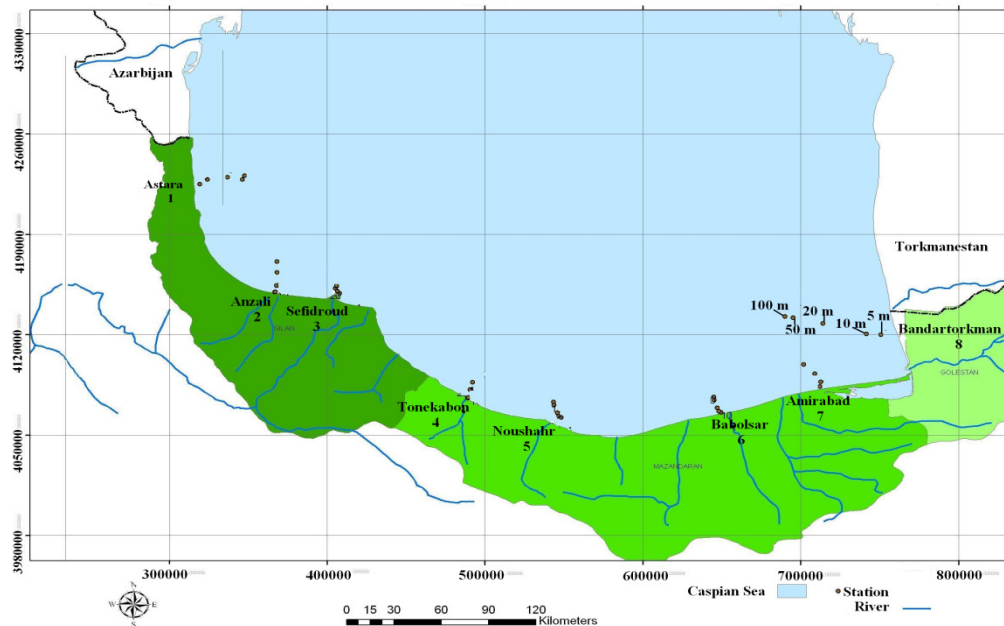


Figure 1: Sampling stations along the Southern Caspian Sea

Samples were collected by a zooplankton net (0.36 m in mouth diameter and 100 μ m mesh) by vertical hauling at each depth. All specimens were preserved in a 4% formaldehyde seawater solution and then studied in a Bogarov tray containing 0.5 ml of each sample (Postel et al., 2000). Biomass was estimated from the shape of each zooplankton (Petipa 1957) and an inverted microscope was used for identification using works of Manolova (1964), Brishtein et al. (1968), and Kuticova (1970). Data on biomass and abundance were calculated per cubic meter. During the sampling on board water temperature was measured.

Kruskal-Wallis non-parametric test was used for any temporal and spatial significant differences in density. Spearman rank correlation was also used to examine relationships between environmental parameters and zooplankton changes.

Results

Temperature changes at surface waters were measured between 10°C at winter to 27°C at summer with a sharp thermocline at the depth of 20-50 m during summer period. The range of temperature was 18.6°C in summer and it reached less than 1°C in winter from surface to bottom. Comparing the total density of zooplankton with depth shows a strong relation between them indicating a decrease towards the depth. *Acartia tonsa* as the dominant species follows the same pattern (Fig. 2).

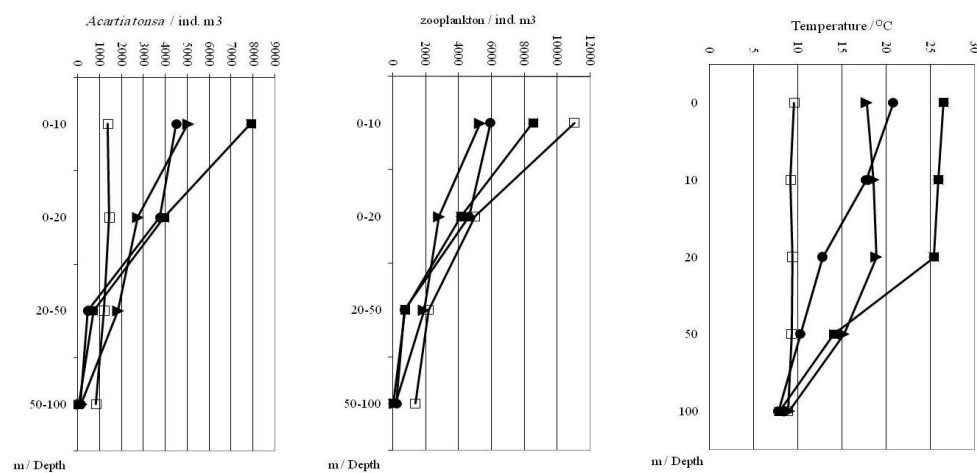


Figure 2: Seasonal temperature (°C) and zooplankton in different depth in the southern Caspian Sea, 2009.

Spring —●— Summer —■— Autumn —▲— Winter —□—

Altogether, 22 species of zooplankton (holoplankton) belonging to four major groups were identified through this study including four copepod species, seven cladocerans, nine rotifers and two protozoans (Table 1). The results show that copepods dominate the zooplankton community with 73.33% of the

total abundance (2884 ± 247 ind. m^{-3}) and biomass (22.27 ± 1.86 mgm^{-3}) (Table 2), then followed by rotifers (24.21%), cladocerans (2.23%) and protozoa (0.23%) (Table 1 and Fig. 3a). The maximum average abundance was observed in summer. Copepods increased with increasing temperature.

Table 1: List of major identified zooplankton groups and species along the southern Caspian Sea in 2009.

Taxon	Abundance(ind.m ⁻³)	% within group	% overall
1) Protozoa	8.93	-	0.23
<i>Tintinopsistobulosa</i>	7.49	83.87	0.19
<i>Foraminifera sp</i>	1.44	16.13	0.04
2) Rotifera	952.2	-	24.21
<i>Asplanchnapriodonta</i>	875.99	92.00	22.28
<i>Brachionuscalyciflorus</i>	7.4	0.78	0.19
<i>Brachionusplicatilis</i>	0.97	0.01	0.02
<i>Syncheatavorax</i>	51.83	5.44	1.32
<i>Keratellatropica</i>	15.94	1.67	0.41

Continue table1:			
<i>Keratellaquadrata</i>	0.03	<0.01	<0.01
<i>Keratellacochlearis</i>	0.02	<0.01	<0.01
<i>Monostylacornuta</i>	0.02	<0.01	<0.01
<i>Lecanesp</i>	0.01	<0.01	<0.01
3) Cladocerans	87.55	-	2.23
<i>Podonpolyphemoides</i>	85.43	97.58	2.17
<i>Podonintermedius</i>	0.22	0.25	0.01
<i>Podonevadnetrigonatypica</i>	1.77	2.02	0.04
<i>Evadneanonyx</i>	0.01	0.01	<0.01
<i>Bosminalongirostris</i>	0.01	0.01	<0.01
<i>Daphnia sp</i>	0.09	0.11	<0.01
<i>Cercopagispengoi</i>	0.02	0.02	<0.01
4) Copepods	2883.57	-	73.33
<i>Acartiatonsa</i>	2869.28	99.50	72.97
<i>Calanipedaquaedulcis</i>	1.62	0.06	0.04
<i>Halicyclopssarsi</i>	12.42	0.43	0.31
<i>Ectinozomaconcinnum</i>	0.25	0.01	0.01

Table 2: Seasonal changes in abundance and biomass (mean±SE) of the zooplankton groups in the southern of Caspian Sea 2009.

season	Copepods	Cladocerans	Rotifera	Protozoa
Abundance ind. m ⁻³				
Spring	3102±495	300±48	117±57	1.00
Summer	3612±605	4±2	1.00	<1
Autumn	3089±457	<1	1.00	32±19
Winter	1695±354	42±9	3775±1096	2±1
Average	2884±247	88±15	952±285	9±5
Biomass mg m ⁻³				
Spring	17.91±2.28	1.84±0.29	1.10±0.28	<0.01

Continue table 2:

Summer	35.75±5.35	0.03±0.01	0.01	<0.01
Autumn	22.97±3.12	<0.01	<0.01	<0.01
Winter	12.12±2.72	0.26±0.06	71.07±21.48	<0.01
Average	22.27±1.86	0.54±0.09	17.63±5.55	<0.01

Seasonal trend of density shows an increasing trend from spring to winter with a sharp difference (Fig. 3b). Comparing to yearly average, only winter time figure is above average showing a bloom of zooplankton in this time of the year. Copepods are dominant group for most of the year especially during the spring with water temperature of about 21 °C but for winter

period when water temperature drops below 10 °C, rotifers become dominant with a density of 3775±1096 ind. m⁻³). Other groups show a very low density throughout the year. Kruskal-Wallis test shows a significant difference between density of copepods, rotifers and cladocerans with regard to the season ($p<.05$).

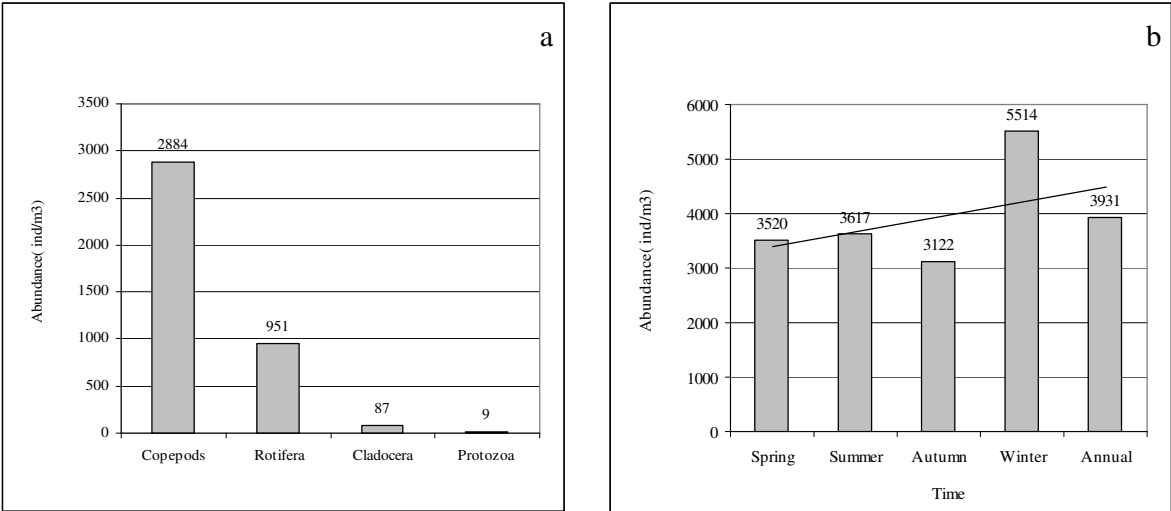


Figure 3: Abundance (a) and seasonal variations of major zooplanktonic groups (b) in the southern Caspian waters, 2012

Regarding the dominant species groups, *Acartia tonsa* were the dominant species in all samples constituting 99.50% of the total copepods density and showing amoderate

significant correlation with temperature ($r=0.549$, $p<.01$). On the other hand, *Podon polyphemoides* was dominant species of cladocerans increasing in number in spring

constituting 97.58% of the total cladocerans density. Population of *Podon polyphemoides* began to increase in winter, reaching the highest density in spring (Fig. 4). Rotifers were most abundant during winter time and

Asplanchna priodonta with a density of 3535 ± 1073 ind. m^{-3} was predominant in this group with 92.00% of the total rotifers population (Table 1 and Fig. 4).

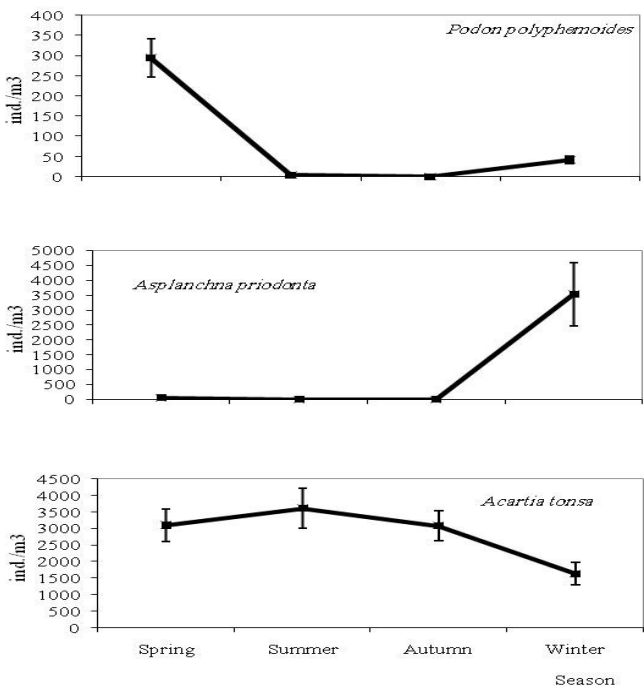


Figure 4: Seasonal occurrence of the predominant zooplankton groups in the southern of Caspian Sea during 2009

According to transects, from west to the east of Caspian, density changes and the maximum values occur in transect 1 (Astara) at the west coasts and then towards the eastern stations (transects 4 and 5) gradual decrease occurs while it reaches the minimum values at the last transects 8 (Fig. 5). Copepods had shown maximum abundance in all transects fluctuating between 1456 ± 531 ind. m^{-3} (Transect 8) to 4524 ± 1215 ind. m^{-3} (transect

2). Cladocerans presented in all transects but their population was very low. The abundance of rotifers was more than cladocerans and the maximum density occurred in transect 1 at the west. The density of copepods was 3 times more than rotifers. Kruskal-Wallis test showed a significant difference between the density of zooplankton with regard to the stations ($p < .05$).

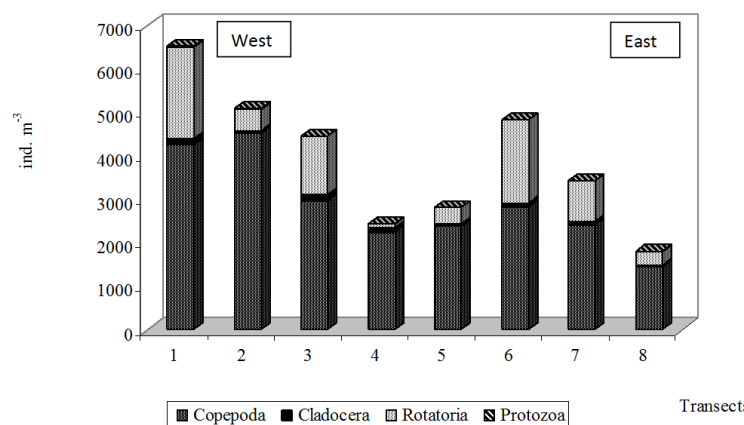


Figure 5: The changes of zooplankton in different transects (southern of Caspian Sea) 2009

Discussion

The results of this comprehensive survey reveals that there were twenty-two species of zooplankton in the southern of Caspian Sea in 2009, including 4 copepods, 9 rotifers, 2 protozoans and 7 cladocerans. The most diverse groups were rotifers followed by cladocerans with 9 and 7 species respectively. RowshanTabari et al. (2012) did a similar work and found only 14 species in the same area. This difference could be due to variation of temperature in spring and winter (Vahedi et al., 2011; Nasrollahzadeh et al., 2012). Bagheri et al. (2010) identified 12 species of holoplankton in the south-western area of the Caspian Sea.

Comparing these diversity figures to the past, RowshanTabari et al. (2003) had founded 55 species about 10 years ago including 9 copepods, 6 rotifers, 5 protozoans and 29 cladocerans, before *Mnemiopsis leidyi* invaded the Caspian Sea. Similar works (RowshanTabari et al., 2007; Roohi et al., 2010; Hosseini et al., 2011; RowshanTabari et

al., 2012) in the south Caspian Sea. They clearly reveals that zooplankton diversity had declined considerably after the invasion of *M. leidyi* into the Caspian Sea from late 80s. *M. leidyi* is an active predator of zooplankton and fish larvae to an extent that could deplete zooplankton biomass if their populations increase abnormally (Mayer, 1912; Herman et al., 1968; RowshanTabari et al., 2007). These could also have an effect on the appearance or disappearance of some zooplankton species. For example, *Halicyclops sarsi* and *Calanipeda aquae-dulcis* have again appeared in water column when *M. leidyi* population decreased in recent years. In Black Sea the same situation happened and some species of zooplanktons, especially *Calanus euxinus* which have had declined recovered again and the populations of other copepods species were also increased. Shiganova et al. (2001) had stated that the presence of some species had greatly been affected by the biomass and abundance fluctuations of this invasive

Ctenophore. In 1996, *Acartia tonsa* was dominant in summer and autumn but *Eurytemora grimmeri* and *E. minor* were dominant in copepod population in spring and winter (RowshanTabari, 2000).

Since 1982, *Acartia tonsa* has been transferred to Caspian Sea and since then its population has grown sharply after 1985 so that it is now the major and dominant zooplankton species in the sea which before that *Acartia clausi* (Kurashova and Abdullaeva, 1984) was the dominant species. Before entrance of *Acartia* In the south Caspian, it was *Calanipeda aquae-dulcis* which was dominant (Yelizarenko, 1992). This species lives at the surface layers and its abundance was 1329 ind.m⁻³ in winter 1996 (RowshanTabari, 2000). After introduction of *M. leidy*, their population disappeared in south Caspian and now again they were found in our samples (maximum 13 ind. m⁻³ in western area in winter).

In this survey, copepods constituted the dominant population of zooplankton in summer, autumn and spring, the same pattern as previous works (Omori and Ikeda, 1984; Mauchline, 1998; RowshanTabari, 2000). They constituted about 88% in spring, 99% in summer and autumn and 31 % in winter of the whole zooplankton population. *Acartia tonsa*, the dominant species of copepods, dominated other species and reached its maximum value in summer. From the west of north USA Pacific, *Acartia tonsa* has been reported to constitute more than 90% of copepods population in summer and autumn (Conover et al., 1956).

Within rotifers, higher densities were shown by *Asplanchna priodonta* and it

constituted more than 90% of rotifers population. *A. priodonta* is a cosmopolitan rotifer and is one of the biggest planktonic predators and it feeds on Cyanobacteria, diatoms, dinoflagellates and protozoa and is both grazer and predator (Pociecha and Wilk-Woźniak 2008). Also it feeds on other rotifers, such as *Keratella* and cladocerans (Kappes et al., 2000). Among cladocerans, *Podon polyphemoides* was the most abundant and its highest density was observed in spring with a decrease in summer and autumn (1 ind.m⁻³) and again increased towards the winter. *P. polyphemoides* exist in surface layers (Manolova, 1964). In this study was observed in surface layers above 20 m.

As conclusion, the zooplankton diversity structures and densities in the south Caspian have gone under great changes after the invasion of comb jelly *M. leidy* since 80s. *Acartia* at present dominates more than 90% of the whole copepods population while *Eurytemora* was not seen again after the invasion and seems to have been vanished from the ecosystem.

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Reference

- Bagheri, S., Mashhor, M., Wan Maznah, W. O. and Negarestan, H., 2010.** Distribution of *Mnemiopsis leidyi* and zooplankton in the South – Western Caspian Sea, 2008. International of offshore and polar engineering Conference. Beijing, China, June 20-25, 2010.
- Birshtein, Y. A., Vinogradov, L. G., Kondakova, N. N., Koun, M. S., Astakhva, T. V. and Ramanova, N. N., 1968.** Atlas of invertebrates in the Caspian Sea. Mosko. 413P (InRussian).
- Conovern, R. J., 1956.** Oceanography of Long Island Sound, 1952-1954. VI. Biology of *Acartiaclausi* and *Acartia tonsa*. *Bulletin of Bingham Oceanographic Collection*. 15, 156-233.
- Dumont, H. J., 1995.** Ecocide in the Caspian. *Nature*. pp.673-674.
- Dumont, H. J., 1998.** The Caspian Lake: History, biota, structure and function. *Limnology Oceanography*. 43, 44-52.
- Fuentes, V. L., Angel, D. L., Bayha, K. M., Atienza, D., Edelist, D., Bordehore, C., Gili, J. M. and Purcell, J. E., 2010.** Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiology*, 645(1), 23-37.
- Herman, S. S., Mihursky, J. A. and McErlean, A. J., 1968.** Zooplankton and environmental characteristics of the Patuxent estuary. *Chesapeake Science*, 9, 67-82.
- Hashemian, A., RowshanTabari, M., Roohi, A., Makhlogh, A., Ganjyan, A., Tahami, F. And Rostamian M. T. 2006.** Hydrology, hydrobiology and pollution in 10 m depth and less in the southern of Caspian Sea. Pub. IFRO. 185P. (In Persian).
- Hosseini, S. A., Ganjyan, A., Makhlogh, A., Keyhansani, A., Tahami, F., Mohamadjani, T., Makaremi, M. and RowshanTabari, M. 2011.** Hydrology and hydrobiology of southern of Caspian Sea (1375-1376). Pub. IFRO. 296P. (In persian).
- Kappes, H., Mechenich, C. and Sinsch, U., 2000.** Long-term dynamics of *Asplanchna priodonta* in Lake Windsborn with comments on the diet. *Hydrobiology*, 432, 91-100.
- Kermer, P., 1975.** The ecology of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay. Ph.D Thesis, University of Rhode Island. 311P.
- Kermer, P., 1976.** Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. In: Wiley, M. (ed), Estuarine processes. Academic Press, New York.1: pp.197-215.
- Kurashova, E. K. and N. M Abdollaev., 1984.** *Acartia clause* Giesbrecht (Calanoidae, Acartiidae) in Caspian Sea. *Zoological*. 63(6), 931-933.
- Kuticova, L. A., 1970.** Rotatoria. Mosco: Leningrad. 744P. (InRussian).
- Laloei, F., RowshanTabari, M., Roohi, A., Takmilian, K., Ganjyan, A., Makhlogh, A. and Rostamian M. T., 2004.** Hydrology, hydrobiology and pollution in 10 m depth and less in the southern of Caspian Sea. Pub. IFRO. 394P. (In persian).
- Main, R. J., 1928.** Observations of the feeding mechanism of a ctenophore *Mnemiopsis leidyi*. *Biological Bulletin*, 55, 69-78.
- Mauchline, J., 1998.** The biology of calanoid copepods. *Advance in Marine Biology*. 33, 710.
- Manolova, E. Q., 1964.** Cladocerans. Mosco: Leningrad. 326P. (In Russian).
- Mayer, A. G., 1912.** Ctenophores of the Atlantic Coast of North America. Carnegie Institution of Washington (publ. 162), Washington. 58P.

- Nasrollahzadeh, H. S., Younesipour, H., Olomi, Y., Nasrollatabar, A., Elyasi, F., Noroozian, M., Delinad, G. H., Mokarami, A., Makhloogh, A., Golaghaei, M. and Kardar, M., 2012. Study on physico-chemical Characteristics of water in the southern Caspian Sea., Final Report. Caspian Sea Ecology Research Center, Mazandaran, 98P. (In Persian).
- Nelson, T. C., 1915. On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. *Biological Bulletin*, 48, 92-111.
- Omori, M. and Ikeda, T., 1984. Methods in Marine Zooplankton Ecology. New York : Wiley-Interscience publication. 331P.
- Petipa, T. S., 1957. On average weight of the main zooplankton forms in the Black Sea. Proc. Sevastopol. *Biological Station*. 9, 39-57.
- Pociecha, A. and Wilk-Woźniak, E., 2008. Comments on the diet of *Asplanchna priodonta* (Gosse, 1850) in the Dobczycki dam reservoir on the basis of field sample observations. *Oceanography and Hydrobiology*, 37(3), 63-69.
- Postel, L., Fock, H. and Hagen, W., 2000. Biomass and abundance. In: Harris, R., Wiebe, P., Lenz, J., Skjoldal, H. R. and Huntley, M. (Eds), ICES Zooplankton Methodology Manual. Academic Press, London. pp.83-192.
- Roohi, A., Kideys, A. E., Sajjadi, A., Hashemian, A. Pourgholam, R., Fazli, H., Khanari, A. G. and Eker, E., 2010. Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the Southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis leidyi*. *Biological Invasions*, 12, 2343-2361.
- RowshanTabari, M. R., 2000. Distribution of zooplankton in the southern of Caspian Sea (Copepods: order). B. C thesis. Tarbiat Modaress University. Iran. 102P. (In Persian).
- RowshanTabari, M. R., Takmilian, K., Sabkara, J., Roohi, A. and Rostamian, M. T., 2003. Distribution of zooplankton in the southern of Caspian Sea. *Iranian Scientific Fisheries Journal*, 12(3), 83-96. (In Persian).
- RowshanTabari, M. R., Nejatkhah, P., Hoseini, S. A., Khodaparast, N. and Rostamian, M. T., 2007. Diversity, abundance and distribution of zooplankton in the southern of Caspian Sea in winter 1384 and comparis on with previous years. *Journal of Environmental Sciences and Technology*, 9(4), 129-137. (In Persian).
- RowshanTabari, M. R., Rahmati, Khodaparast, N., R., Rezvani, Gh, Eslami. F., Soleimaniroudi, A., Keyhansani, A., Kanani, M. R. and Amani, Gh., 2012. The survey of diversity, distribution and abundance of zooplankton in the southern of Caspian Sea. Final Report. Caspian Sea Ecology Research Center, Mazandaran. 99P. (In Persian).
- Shiganova, T. A., 1993. Ctenophore *Mnemiopsisleidyi* and ichthyoplankton in the Sea of Marmara in October of 1992. *Oceanology*, 33, 900-903.
- Shiganova, T. A., 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsisleidyi* and recent changes in pelagic community structure. In: Coombs Steeve (ed). *Fish Oceanography*.7 – GLOBEC Special Issue. pp.305-310.
- Shiganova, T. A., Mirzoyan, X. A., Studenikina, Volvik, S. P., Siokou-Frangou, I., Zervoudaki, S., Christou, E. D., Shirta, A. Y. and Dumont, H. D., 2001. Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. *Marine Biology*, 139, 431-445.
- Studenikina, E. I., Volovik, S. R., Mirzoyan, Z. A. and Luts, G. I., 1991. Ctenophore

Mnemiopsis leidyi in the Azov Sea. *Oceanology*. 31(5), 722-725.

Vahedi, F., Younesipour, H., Olomi, Y., Nasrollatabar, A., Elyasi, F., Noroozian, M. and Delinad, G. H., 2011. Study on physico-chemical Characteristics of water in the southern Caspian Sea., Final Report. Caspian Sea Ecology Research Center, Mazandaran, 72P. (In Persian).

Vinogradov, M. E., Shushkina, E. A., Musaeva, E. I. And Sorokin, P. Y., 1989. A new acclimated species in the Black Sea: The

ctenophore *Mnemiopsis leidyi* (Ctenophora: Lobata). *Oceanology*, 29(2), 293-298.

Yelizarenko, M. M., 1992. Feeding of kilka in the Middle Caspian during the summer season. In: *Biological resources of the Caspian Sea. Abstracts of the 1st International Conference*, September 1992, Astrakhan. pp.111-113. (in Russian).

Zaitsev, Yu. P. 1992., Recent changes in the trophic structure of the Black Sea. *Fish. Oceanography*, 1, 180–189.