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Long-term changes in gelatinous zooplankton, mesozooplankton and kilka fish in the Southern Caspian Sea: Environmental controls and trophic webs interactions

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Gelatinous zooplankton (GZ) populations are sensitive to climate change such as environmental perturbations, and spatial changes in their abundance and biomass may be associated with degraded environmental and biota conditions. Big data time series of GZ abundances and biomass were used to analyze the annual population dynamics of gelatinous zooplankton as well as mesozooplankton in the southern Caspian Sea, Iran from 1996, 2001-2006, 2008-2013 to 2018-2019. The ctenophore, *Mnemiopsis leidyi* population control by environmental factors was primarily a result of decreasing the concentration of zooplankton resulted to lower reproduction as well as temperature which was highest in August-September and lowest in winter time. On the other hand, the maximum catch of Kilka on the whole coast of Iran was equivalent to 95,000 tons in the year of 1996, and after that it was severely reduced to 15,000 tons in the year 2003 and afterward.

Key words: Gelatinous zooplankton, abundance and biomass, temperature, Caspian Sea.

INTRODUCTION

The Caspian Sea is the world's largest inland body of water, variously classed as the world's largest lake or a full-fledged sea. The sea has a surface area of 371,000 km^2 and its surface is about 27 m (89 ft) below sea level. The sea bed in the southern part reaches as low as 1,023 m. The Caspian Sea is one of the world's largest brackish ecosystems, a habitat for many species of planktonic organism and pelagic and benthic fish. When the Gelatinous Zooplankton (GZ) or comb jelly (*Mnemiopsis leidyi* Agassiz, 1865) was introduced into the Caspian, played a key role in the dynamics of the food web of the sea (Roohi et al., 2010, 2016). The success of invasive aquatic organisms is aided by a variety ofattributes such as high genetic variability, wide environmental tolerance, short generation time, high reproductive capacity, early sexual maturity and a broad

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diet. Normally, following some period of time after its introduction, invasive species show an exponential population increase and expansion. Eventually, the immigrant population may decline, for instance due to increased predation pressure, parasite infestation or loss of genetic vigour (Essink and Dekker, 2002; Neideman et al., 2003). Since the ctenophore feeds on a wide range of crustaceans, and exerts significant top-down control during blooming periods (GZ bloom) (Purcell et al., 1994, 2001; Purcell and Decker, 2005; Condon and Steinberg, 2008). In addition, it may also consume fish larvae and mussels that are important commercial and ecological species (Govoni and Olney, 1991; Bagheri et al., 2008).

The lack of long-term data on the response of aquatic systems to water-level and climatic changes is seen as an impediment to the assessment of the vulnerability and risks that large water-bodies face with respect to ongoing and future global changes. It is essential to understand the mechanisms driving these changes; but so far, they have remained rather unclear. Very few of the quaternary species establishing outside their natural range, negatively impacting local ecosystems, are of increasing global concern. Biological invasions can have large ecological and economic impacts (Butchart et al., 2010; Walsha et al., 2016), especially in aquatic systems (Sommer and Lewandowska, 2011) and species translocations are steadily increasing worldwide (Butchart et al., 2010; Seebens et al., 2017). Within the nonindigenous species that are moved around the world, only a minute fraction become invasive and form self-sustained populations (Mack et al., 2000; Williamson and Fitter, 1996). A long-standing issue in ecology has been to characterize potent invasive species (Baker, 1974; Tingley et al., 2016) through traits that promote invasion success (McKnight et al., 2017; Pysek et al., 2009). It is important problem as ecological, invasion of the marine systems by the gelatinous organism that distributed natural balance. Caspian Sea ecosystem has changed critical level by some causes such as marine pollution, eutrophication, climate change, overfishing, invasive gelatinous organisms (Roohi et al., 2008, 2010, 2013, 2016; Bagheri et al., 2008; Kideys and Moghim, 2003; Shiganova et al., 2003, 2004; Kideys et al., 2008; Ghabooliet al., 2013;Lattuada et al., 2019). Effect in the ecosystem of gelatinous organisms occurred especially with collapsed of Caspian Sea Kilka (*Clupeonella* spp.) stock and fishery production (Fazli, 2011). In the study, gelatinous zooplankton species, important for Caspian Sea, and its effects in the Caspian Sea ecosystem were presented.

MATERIALS AND METHODS

GZ (*M. leidyi*) and mesozooplankton were collected by zooplankton net of 100 and 500 µm mesh from 2001-2006, 2008-2013 to 2018-2019 where annual and inter-annual changes in population size and distribution of the ctenophore was compared with changing environmental conditions and zooplankton density fluctuations in 1996 in the southern Caspian Sea with 36-39°27-52´N and 48-53°22-57´E (Roohi et al., 2008, 2010). The GZ samples and mesozooplankton (Postel et al., 2000) were gathered in vertical layers of 0-5, 0-10 and 10-20, 20-50 and 50-100 m. The body length of each ctenophores 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. Length measurements were converted to weight/biomass (wet weight per m^3) using the equation (Roohi et al., 2008; $W=0.0011\times L^{2.34}$; where W is wet weight of *M. leidyi* in mg and L is the length in mm. Identification of mesozooplankton was established based on Boltovskoy (2000), Kuticova (1970), Manolova (1964) and Birshtein et al. (1968) and sample counts were performed according to the method of Postel et al. (2000).

RESULTS

There were considerable annual changes in total GZ abundance and biomass, which the highest mean value of biovolume abundance were recorded in 2002 with 463.0±101.8 ind.m^3 while the maximum biomass were in 2001 of 25.4.0±4.2 g.m^3 with a sharp decreased after 2003 to 1/20 initial concentration in the southern Caspian Sea. The mean GZ abundance and biomass also showed a constant concentration decreased reach to 32-42 ind.m^3 and 2-2.5 g.m^3 in 2018-2019 (Figure 1).Size frequency structure of GZ showed population of less than 5 mm was consisted of 75.3%, 6-15 mm of 18.8% and the ctenophore with >16 mm comprised approximately 5.8%, the GZ maximum size was recorded of 70 mm in October 2001 (Figure 2).

Comparison of monthly changes in mean Total GZ abundance, mesozooplankton and water temperature of long time data showed that GZ highest abundance was in August-September of 349.2±72.7 ind.m^3 and the lowest in winter time, while the lowest mesozooplankton abundance was recorded in August-September with 179-210 ind.m^3 with highest in winter time with a range of1000-1400 ind.m^3. These long-term changes in biovolume were correlated with changes in environmental conditions. There was a negative correlation between the total GZ abundance and mesozooplankton in which the analysis of water temperature showed a significant positive relationship with temperature. Therefore with increasing water temperature in summer, total GZ abundance increased rapidly, it is associated with the decrease of mesozooplankton abundance with the highest water temperature in summer at 25-30 °C and the lowest at 8-10°C (Figure 3).

Long time data comparison of GZ and mesozooplankton biomasses showed 10 folds decreased of plankton after its invasion in 2001 (from 22.2±0.8 mg.m^3 in 1996 to 2.7±0.2 mg.m^3 in the early 2000s, respectively (Figure 4). Evaluation of mesozooplankton copepods data during the years 2001-2006, 2008-2013 and 2018-2019, comparison with the year of 1996 (consisted 60% of mesozooplankton) showed a sharp

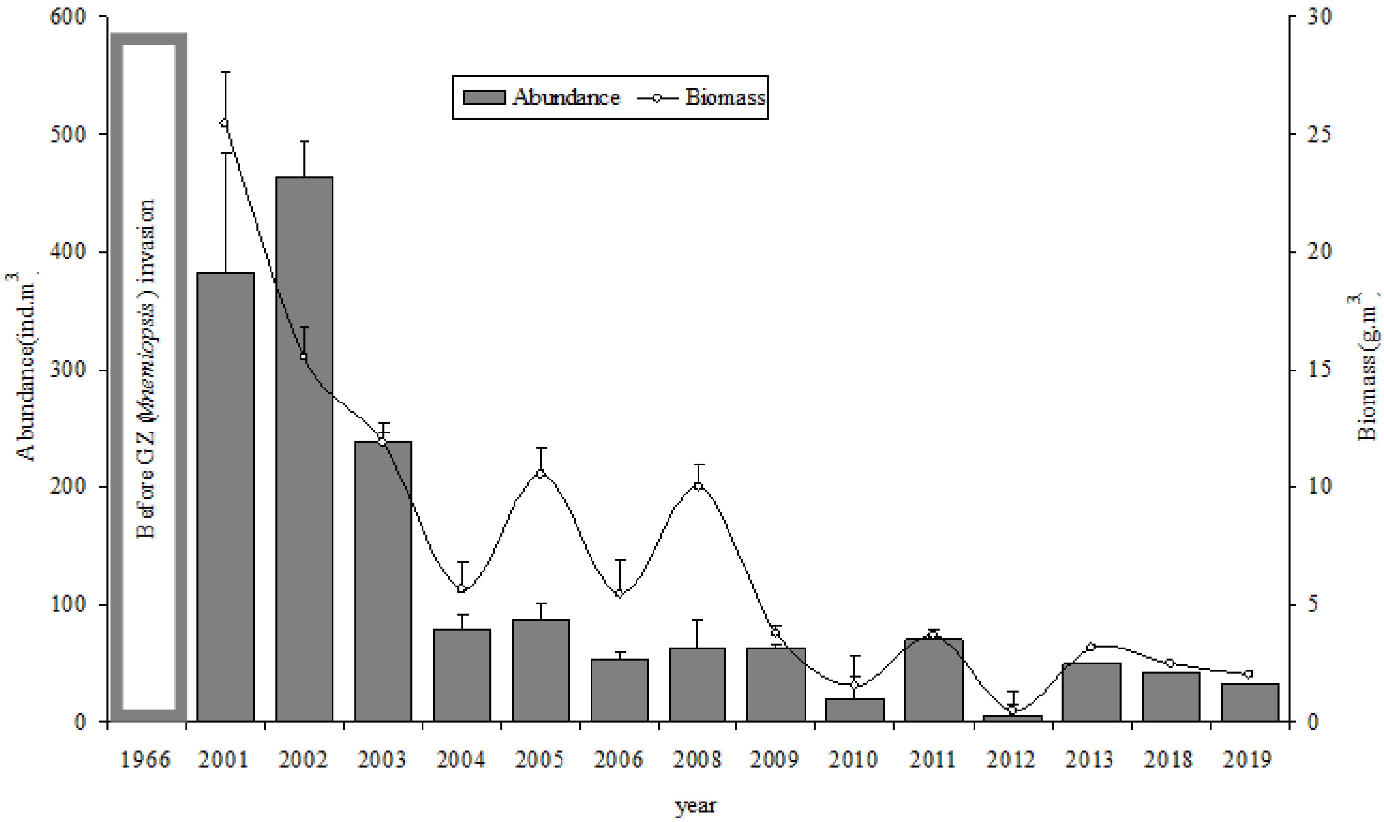

Figure 1. Long-term annual mean GZ abundance and biomass changes distribution in the southern Caspian Sea during the years of 2001-2006, in 2008-2013 and 2018-2019.

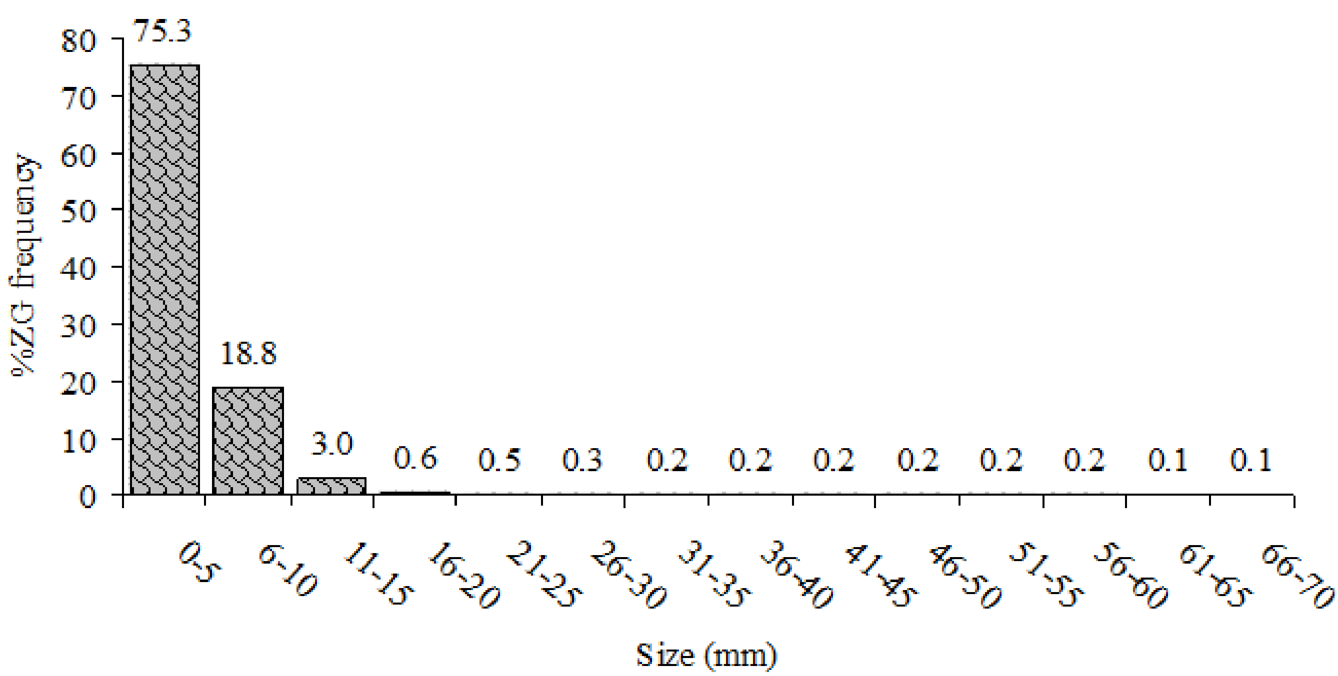

Figure 2. Frequency percentage (%) contributions of different size ranges of GZ to the total abundance in the southern Caspian Sea from 2001-2006, 2008-2013 and 2018-2019.

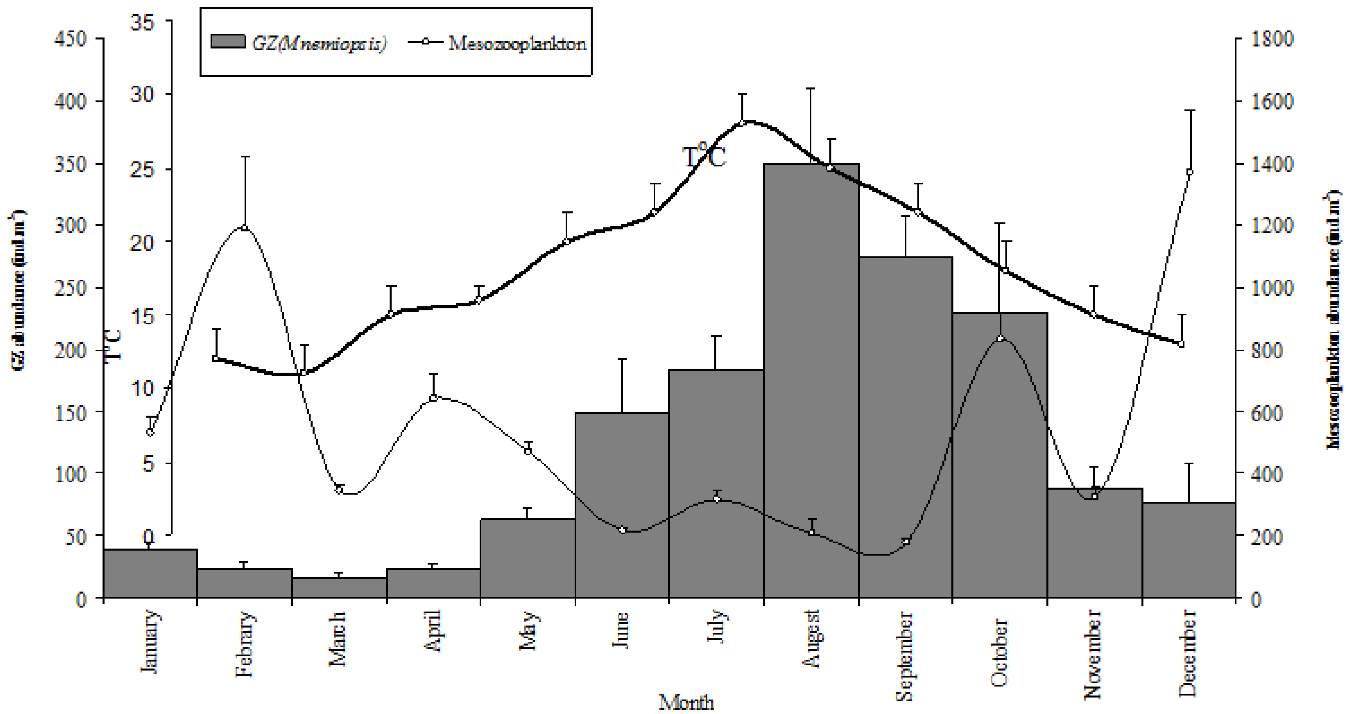

Figure 3. Comparison of monthly abundance of total GZ, mesozooplankton and water temperature in the southern Caspian Sea.

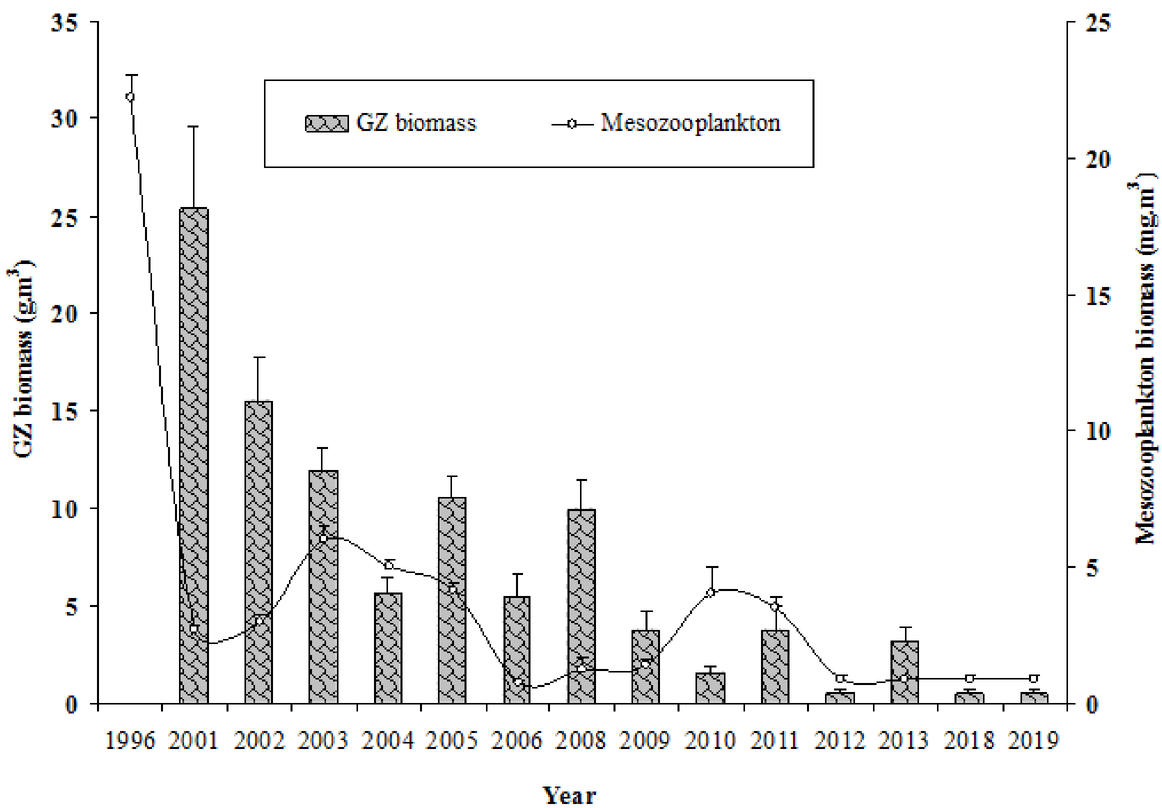

Figure 4. Comparison of GZ and mesozooplankton biomasses from 2001-2006, 2008-13 and 2018-2019 in the Caspian Sea.

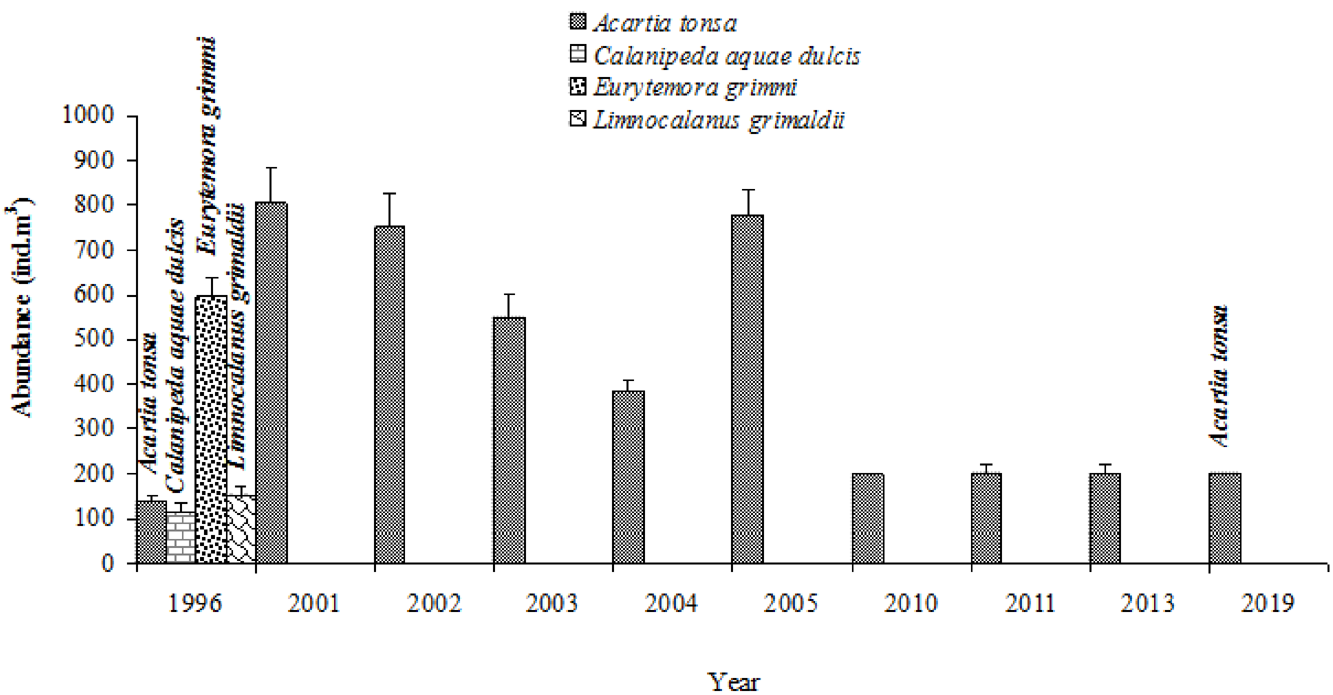

Figure 5. Abundance copepod Calanoida fluctuation during the years of 2001-2006, in 2008-2013 and 2018-2019 and comparison with 1996 in the southern sea.

decreased in Copepoda species which identified as *Acartia tonsa*, *Calanipeda aquaedulcis*, *Eurytemora grimmi*, *Limnocalanus grimaldii*, *Halicyclops sarsi*, and *Ectinosoma concinnum* lived prior to GZ invasion in the southern Caspian Sea, remaining only three species of *A. tonsa* (consisted 90% of mesozooplankton), *H. sarsi* and *E. concinnum* after invasion (Figure 5).

On the other hand, comparing the Kilka catch in 1996 with 2001-2019 showed a maximum in 1996 with 95000 tons and after that it decreased dramatically, reaching 15000 tons in 2001 so far in the southern Caspian Sea. There are three species of Kilka in which Anchovy *Clupeonellaen grauliformis* was catch maximum in 1996 and 2001; Common *Clupeonella cultriventris* was consisted second at the same time while Big-eye *Clupeonella grimii* was lowest in the southern Caspian. After the GZ invasion Anchovy accounted for more than half of the catches with 69.5 and 50.5 tons in 2002-2003, respectively.

But at one point in 2004, it reached nearly half of last year, and then went down strongly, with only 3.5% of total catch in 2008 afterwards. In other words, the catch of Anchovy Kilka sharply decreased from 67450 in 1996 to 791 tons in 2008 so far. As a whole an average of about 21,000 tons of the three species of Kilka were catch from 2004 to 2019 (Figure 6A). Also, with the arrival of the GZ into the Caspian Sea in 2001, mesozooplankton biomass drastically reduced the food available to Kilka fish (Figure 6B).

DISCUSSION

The Caspian Sea is a unique ecosystem that has not connected to the oceans but has more or less all the characteristics of the seas. In this sea, an invasive comb jelly *M. leidyi* was introduced through the ballast water in 1998 (Esmaili et al., 1999). This species posed a serious threat to the Caspian Sea because of its planktonic diet as a competitor to pelagic aquatic animals. Due to the destructive effect of GZ on some planktonic organisms such as mesozooplankton, in recent years, their population has decreased. The comb jelly is a predatory animal that feeds significantly on mesozooplankton and thus became a large impact on the ecosystem and its extent depends on the abundance of nutrients and suitable environmental conditions (Reeve et al., 1978). Among the factors that led to the formation of large GZ colonies early in any new ecosystem, there is an omnivorous diet system as well as a smaller reproductive life cycle with high fertility (Bij de Vaate et al., 2002; Roohi et al., 2010; Finenko et al., 2006).

Data of GZ in 2001-2019 showed the maximum population during the early entry of invasion into the Caspian Sea in the years 2001-2002 between 380-463 ind.m^3 and since the GZ biomass has been decreasing and increasing intermittently since years 2002-06 and the trend has been declining steadily since the years 2008-2013 (Figure 1). Combined with the decline of the mesozooplankton community and the release of nutrients,

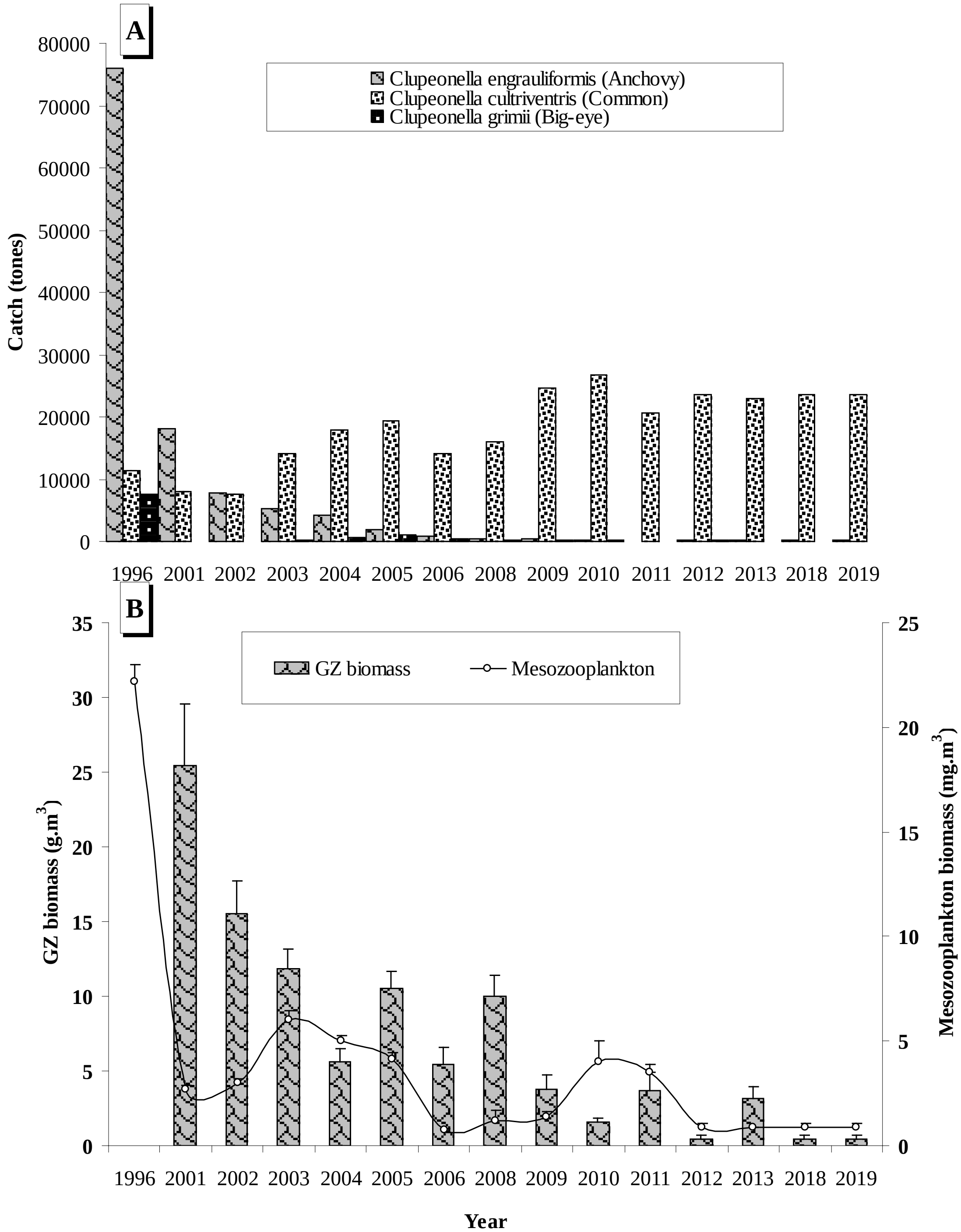

Figure 6. Comparison of (A) three species of Kilka catch (B) GZ and mesozooplankton biomass in 1996 and the years 2001-2019 in the southern Caspian Sea.

GZ cause many changes in the southern Caspian ecosystem (Roohi et al., 2010). The abundance and biomass of mesozooplankton were decreased from 4143 ind.m^3 and 22.2 mg.m^3 in 1996 to 600-800 in.m^3 and 0.2-2.6 mg.m^3, in early 80s respectively (Figure 4). In addition, in terms of species diversity, mesozooplankton had a variation coefficient of 58.3% declined (Roohi et al., 2008;Bagheri et al., 2013).

Although *M. leidyi* abundance decreased in the southern Caspian Sea after 2003, due to its competitive advantage, global warming, no limiting factor in susceptibility to overfishing, the low Caspian biodiversity but its abundance remains effective over the years to come. One of the factors that led to the rapid population and rapid expansion of the comb jelly even in the early invasion in the Black Sea was the absence of a controlling predator such as *Beroeovata* as a specialized predator, which is also true in the Caspian Sea (Shiganova et al., 2003, 2004; Roohi et al., 2008).

On the other hand, length frequency of the GZ showed three life stages; larval (Cydipid) with less than 5 mm, transition stage between 10-15 mm and finally adult stage exceeds 15 mm in size in order to complete its life cycle (Salihoglu et al., 2011). At the present study, the percentage of GZ length frequency with less than 5 mm (larval stage) was 56-93%, transitional stage 5-22% and only 2% of adult population with the largest size of 70 mm (Figure2). However, the GZ life cycle in the Caspian Sea is such a way that the creatures that were survived in winter begin to spring up in the spring and in summer with adequate water temperatures (25-30°C) and food supply (especially Copepods and Cladocera mesozooplankton) are rapidly proliferating, and because of this, it was found small groups of these GZ in these seasons that will continue until mid-autumn. Then, in winter, the abundance decreases again with the decrease in water temperature (8-15°C) (Figure3). It seems the reasons for the decline of the GZ population in the Caspian Sea is due to reduced of species diversity and the shortage of edible mesozooplankton (Figures 4 and 5). Therefore, the long-term zooplankton data in the southern Caspian showed that zooplankton species diversity decreased from 36 species in 1996 to 15 species after the GZ invasion. Since before the GZ invasion into the Caspian Sea, there were three sub-orders of Calanoida, Harpacticoida and Cyclopoida (Copepods), with two species *Eurytemora minor* and *Acartiatonsa* forming the dominant population of sub-order Calanoida in 1996 (Roohi et al., 2010), while after the invasion only *Acartiatonsa* became the dominant mesozooplankton consisted of 90% mesozooplankton abundance and biomass.

The major pelagic fish in the southern Caspian Sea are the Kilka fish, which have three species of Anchovy, *Clupeonellaen grauliformis*, Big eye, *C. grimmi* and Common *C. cultriventris* that play very important role in total catch and feeding other aquatic species such as sturgeon and *Pusacaspica* of the Caspian Sea. During the 1960s and 1970s, the Kilka catch was reported to be over 300,000 and the amount of anchovy Kilka consumption was reported to be around 400,000 (Fazli, 2011). In Iran during the 1980s, the Kilka catch, including Kilka Anchovies, was widespread. Due to the importance of this fish in the feeding of Caspian animals and its economy importance for the people of the Caspian Sea, extensive studies have been done in Iran. The results showed that in commercial fishing of Iranian waters in three ports of Amirabad, Babolsar and Anzali before the GZ invasion, all three species of Kilka were observed (Fazli et al., 2007a). The long- term data showed that the abundance of Anchovy Kilka in 2002 and 2003 was more than half of the catch with 69.5 and 50.5, respectively. But at one point in 2004, it reached nearly half of last year, and then went down strongly, with only 3.5% of total catch in 2016. Concurrent with the overfishing, the Caspian Sea's ecosystem has changed due to the *M.leidyi* invasion, and due to the food competition of this non-native species with Kilka Anchovy, the fish stocks of Kilka have declined sharply, while the Anchovy decreased from 67450 tons in 1999 to 791 tons in 2016 (Figure 6A).

In recent years, Caspian Sea water levels have risen and fall and the distribution of the three Kilka species has changed, making the situation unsuitable for Anchovy species. In addition, the shock to the Caspian Sea ecosystem with the GZ invasion and affecting the food chain linkages, changes in meso- and macroplankton in the southern Caspian Sea (Bagheri et al., 2008) and subsequent depletion of zooplankton reserves. Specifically, *Eurytemora minor* (which supplied the main food of Kilka Anchovy) and its replacement with *Acartia tonsa* (Figure 5) caused severe destruction of the two main species of Kilka anchovy and big eye. On the other hand, the maximum catch of Kilka on the whole coast of Iran was equivalent to 95,000 tons in the year 1996, and after that it was severely reduced to 15,000 tons in the year 2003 and afterward. The decrease in the main species of Kilka catch, especially at offshore, has led to the change of fishing position and its shift to coastal areas with the predominant catch being the common Kilka species. From 2004 to 2013, an average of 21800 tons of the three Kilka species have been caught, and the catch and stocks of the Kilka species have been hunted due to the combined effects of fishing activities and the removal of access to zooplankton species such as *Limnocalanus grimaldii*. The GZ feeding has been reduced and degraded, but the catch and reserves of the common Kilka species have been favorable over the same period, and even increase because the common Kilka has a wider nutritional range than the other two Kilka species (Karpyuk et al., 2004). It was mentioned above that the dominant Caspian zooplankton (especially in the inshore) was *Acartia tonsa* constitute the habitat can provide the right nutrition for the fish. Common Kilka seems to be more dependent on this species, given the decline in the abundance of other zooplankton species, and is probably one of the major preys for this species (Roohi et al., 2013; Karpyuk et al., 2004). The result seems to be a decrease in GZ population in the southern Caspian compared to the early years of its invasion due to a decrease in edible zooplankton. The high pressure of GZ on the zooplankton, especially the copepods, has led to the inadequate nutrition of the pelagic animals, resulting a decline in fertility and reproduction. On the other hand, despite the specific and fragile conditions of the Caspian Sea due to the introduction of various contaminants, it seems unlikely that re-growth of plankton and consequently a return to a favorable nutritional period in the southern Caspian Sea unless *M. leidyi* remove the sea by the biological control with its specific predator *Beroe ovata*.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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