

Factors Influencing the Invasion of the Alien Ctenophore *Mnemiopsis leidy* Development in the Southern Caspian Sea

Aboulghasem Roohi^{1*}, Reza Pourgholam¹, Ali Ganjian Khenari¹, Ahmet Erkan Kideys²,
Ameneh Sajjadi³ and Ramin Abdollahzade Kalantari⁴

¹ Assistant Professor, Caspian Sea Research Institute of Ecology, Sari, Iran

² Professor, Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey

³ Assistant Professor, Islamic Azad University, Rasht Branch, Rasht, Iran

⁴ MSc. Student, Islamic Azad University, North Tehran Branch, Tehran, Iran

Received: 25 March 2012 / Accepted: 11 May 2013 / Published Online: 24 November 2013

ABSTRACT *Mnemiopsis leidy* population activities first were recorded during the coastal observations in 2001 in which its population considerably increased afterward and now sustained the southern Caspian Sea. Maximum summer-autumn *M. leidy* abundance was recorded in euphotic layer in 2002 (851 ± 85 ind. m^{-3}) and maximum biomass was in 2001 with 48.1 ± 14.4 g. m^{-3}) while minimum were in aphotic layer. In years 2003 to 2011, *M. leidy* abundance and biomass sharply declined to $1-843$ ind. m^{-3} and $0.07-37.7$ g. m^{-3} , respectively. The length-frequency distribution of *Mnemiopsis* showed larval, juveniles and transitional stages that made up 98.6% of the total population. In the southern Caspian Sea, *Acartia tonsa* was the highest number of mesozooplankton species (36 species) which decreased tenfold after *Mnemiopsis* invasion during 2001-2010. Fecundity experiments of *Mnemiopsis* showed the average of 8 eggs. day⁻¹, with a maximum of 35 eggs.day⁻¹ which increased with increasing body length. The main food was larger amounts of zooplankton prey such as copepodites and adult of *A. tonsa*. It seems the sharp decreased of *Mnemiopsis* abundance could be related the decreasing of ova reproduction; and food ability is the main reasons of *M. leidy* sustained in the southern Caspian Sea. The objective of present study was to provide information about parameters influencing the *M. leidy* decreased after initial bloom invasion in the southern Caspian Sea.

Key words: Caspian Sea, Diet, *Mnemiopsis leidy*, Ova reproduction, Zooplankton.

1 INTRODUCTION

The introduction and spread of non-indigenous species (NIS) beyond their native range accelerated during the second half of the twentieth century due to a variety of human activities (e.g., Streftaris *et al.*, 2005; Wonham and Carlton 2005; Ricciardi 2006; Leuven *et al.*,

2009). The planktonic predator, *Mnemiopsis leidy* (Figure 1) is a cosmopolitan lobate ctenophore native to near-shore marine pelagic communities along the Atlantic coasts of North and South America (Kremer, 1979). As a highly versatile predator, *M. leidy* has become a notorious invader, first appearing in the Black

* Corresponding author: Caspian Sea Research Institute of Ecology, B.O.Box 961, Khazarabad Boolvar, Sari, Iran, Tel: +98 151 3462498, E-mail: roohi_ark@yahoo.com

Sea in the early 1980s (Vinogradov *et al.*, 1989), and shortly thereafter in the Sea of Azov (Studenikina *et al.*, 1991), the Sea of Marmara, and the eastern Mediterranean (Shiganova *et al.*, 2001). It is now widely distributed in the Caspian Sea (reported in 1999) and Adriatic Sea (reported in 2005) (Shiganova and Malej, 2009), and has most recently established itself in the Baltic Sea (reported in 2006) (Javidpour *et al.*, 2006) and parts of the North Sea (Hansson, 2006). As Ghabooli *et al.* (2011) expressed population genetic analyses showed the invasion of Eurasia from at least two different pathways, the first from the Gulf of Mexico (e.g., Tampa Bay) to the Black Sea and thence to the Caspian Sea, the second from the northern part of the native distribution range (e.g., Narragansett Bay) to the Baltic Sea. However, its arrival in each of these regions has led to decreased zooplankton abundances and diversity (Kideys, 2002; Kideys *et al.*, 2005; Oguz *et al.*, 2008; Roohi *et al.*, 2008 and 2010), often with trophic cascades that increase phytoplankton standing stocks (Kideys *et al.*, 2008; Roohi *et al.*, 2010).

In contrast to higher metazoans such as copepods and fish, ctenophores are a basal metazoan lineage possessing a relatively narrow set of sensory-motor capabilities. Lobate ctenophores can capture prey at rates comparable to sophisticated predatory copepods and fish, and they are capable of altering the composition of coastal planktonic communities (Colin *et al.*, 2010). However, *M. leidyi* is self-fertilizer and a voracious feeder on small fish larvae and mesozooplankton, and competes with zooplanktivorous fishes for food (Niermann *et al.*, 1994). The high fecundity (an average of 8000 eggs within 23 days in native waters; about 12000 eggs in 10 days in the Black Sea) and the huge growth rates (up to a daily doubling of individual biomass) observed in this ctenophore can only be sustained by high feeding rates (Reeve *et al.*, 1978; Purcell *et al.*, 2001). A series of feeding experiments were undertaken to

measure *M. leidyi* diet in the southern Caspian Sea (Bagheri *et al.*, 2008; Karpyuk *et al.*, 2004), and an additional experiments were performed in order to monitor jelly comb feeding rate at the same regions (Roohi *et al.*, 2011). The main aim of the present study was focused on *M. leidyi* stomach contents and reproduction decreased after initial population explosion in the southern Caspian Sea. In addition, it was hypothesized that the feed spectra (zooplankton) of *M. leidyi* should be decreased after 10 years of invasion in the southern Caspian Sea.

2 MATERIALS AND METHODS

2.1 *M. leidyi* and zooplankton Data (Cruises analysis)

Biological and environmental data used in this study were collected by the R/V Guilan cruises conducted in 1996 (Hossieni *et al.*, 2011) and 2001-2011. Monthly temporal and spatial data were collected along six transects (1=Lisar, 2=Anzali, 3=Sepidroud, 4=Nowshar, 5=Babolsar and 6=Amirabad) in the Iranian coast of the southern Caspian Sea. Each transect had four stations located at 5, 10, 20 and 50 m bottom depth contours with two deep stations having 100 m total depth off Anzali and Babolsar (Figure 2).



Figure 1 Side view of *Mnemiopsis leidyi* in position with oral lobes semi-closed (Photo; A. Roohi)



Figure 2 Distribution of sampling stations in the southern Caspian Sea

Comb jelly (*M. leidyi*) were collected with the METU net having a mouth opening of 0.2 m² (mesh size of 500 μm) same as the Juday net from the same depths (Vinogradov *et al.*, 1989; Kideys *et al.*, 2001a). The body length of each individual with lobes were counted and measured immediately upon collection on board of the ship to calculate the density of *M. leidyi* (per m³). The ctenophores were sorted in length groups with 5 mm intervals such as 0-5 mm, 6-10 mm up to the maximum length of 70 mm for determining the abundance of different size groups. For appropriate analysis, lengths were categorized into three groups cidipid and juvenile (<5mm), transitional (6-15mm) and adult (>16mm) stages due to start of reproduction size (Dumont *et al.*, 2004; Salihoglu *et al.*, 2011). Length measurements were converted to the weight for biomass (wet

weight per m³, $W = 0.0013 \times L^{2.34}$, where, W= Wet weight, g and L= Length, mm, n= 90 and R²= 0.65) measurement by using the appropriate equation (Kideys *et al.*, 2001a).

Zooplankton were taken using a Juday net with a mouth opening of 0.1 m² (mesh size of 100 μm) hauled from the different layers. Zooplankton samples were enumerated by method of Postel *et al.* (2000) cited in Rezai *et al.* (2004) photic stratification in some cases was analyzed based on pelagic (< 20 m) and offshore (> 50 m).

2.2 *M. leidyi* reproduction rate data

Egg production was studied in the laboratory at the Caspian Sea Research Institute of Ecology, Sari, Iran (at 5=Babolsar and 6=Amirabad). After an hour acclimation, freshly collected ctenophores were put in two liter containers

(one ctenophore per container) and kept there overnight at a temperature of 24°C. In the morning, the ctenophore were removed, the water was filtered, and the numbers of ova spawned were counted under inverted microscope. Experimental studies of egg production were conducted in forty-seven replications with ranged size of 5-42 mm and a salinity of 12.6‰ in 2001 (Shiganova *et al.*, 2004). Also, in another same methodology repeated experiments, 92 replications with 14-46 mm of freshly *M. leidy* individuals were established at the temperature of 25±1°C and a salinity of 12 ±0.5‰ in 2010.

2.3 *M. leidy* diet data

According to previous observations in the southern Caspian Sea, *M. leidy* samples were collected by plankton net hauls and preserved in formalin (4%) to be transported for laboratory microscopic analysis. While in this study, (in 2010) specimens individually attempt was made to find *M. leidy* by hand picked from snorkeling and diving and put into jars in different layers (e.g. surface, 5 and 10 M at 5=Babolsar and 6=Amirabad), hence fixed on board to carry into laboratory for microscopic zooplankton determination analysis. In 2011, however, a total of 84 samples of *Mnemiopsis* were gathered for feeding survey at the southern parts of the Caspian Sea.

In the laboratory, some available Caspian Sea zooplankton such as *Acartia tonsa* with nauplii, copepodites and adult stages, *Balanus* sp., *Branchionus* sp. were offered to 27-40 mm *M. leidy*. Relative Index of Importance (RII) was calculated as $RII = (F \times B) / \sum (F \times B)$ (Pinkas *et al.*, 1971), where F is the exposure food item to the *M. leidy*, B is the food remain ness in aquarium. Feeding habit determination was estimated from RII with indices values higher than of 15%, which considered as jelly diet

predominant. Electivity index was estimated with $E = (r_i - p_i) / (r_i + p_i)$ (Ivlev, 1961), where E = electivity index; r_i = percentage of each item in the stomach content (RII %); p_i = percentage of each item in the aquarium (relative abundance). The electivity index ranges from - 1 to + 1, being considered positive selectivity when > 0, absence of selectivity when equal to zero, negative selectivity when < 0 (Zavala-Camin, 1996).

3 RESULTS

3.1 Development of *M. leidy* in 2001-2011

M. leidy population first was recorded during the coastal observations in 2001 in the southern Caspian Sea which its population considerably increased afterward; it spread widely in the coastal waters but was not common in deep-sea areas. The highest summer–autumn average of *M. leidy* abundance was observed in 2002 (851 ± 85 ind. m⁻³), although the biomass during this period (25.3 ± 13.1 g. m⁻³) was lower than in 2001 (48.1 ± 14.4 g. m⁻³). In years 2003 to 2011, *M. leidy* population did not increase to initial peak (1338±1058 ind. m⁻³, in August 2002) and even its abundance and biomass sharply declined to 1-843 ind. m⁻³ and 0.07-37.7 g. m⁻³, respectively (Figure 3).

Results of spatial distribution pattern have shown that *M. leidy* abundance and biomass in the southern Caspian Sea significantly different in euphotic compared to aphotic layer which was lower than during years 2001-2011 (P<0.05). Maximum *M. leidy* abundance was recorded in euphotic layer in 2001 (674±831 ind. m⁻³ and 48.1±111.6 g. m⁻³) while was 0 ind. m⁻³ in aphotic layer, *M. leidy* biomass was vice versa (Figure 4). Collectively, a difference among *M. leidy* abundance was much pronounced concerning to photic zone, which increased 3-14 folds in euphotic layers in the southern Caspian Sea.

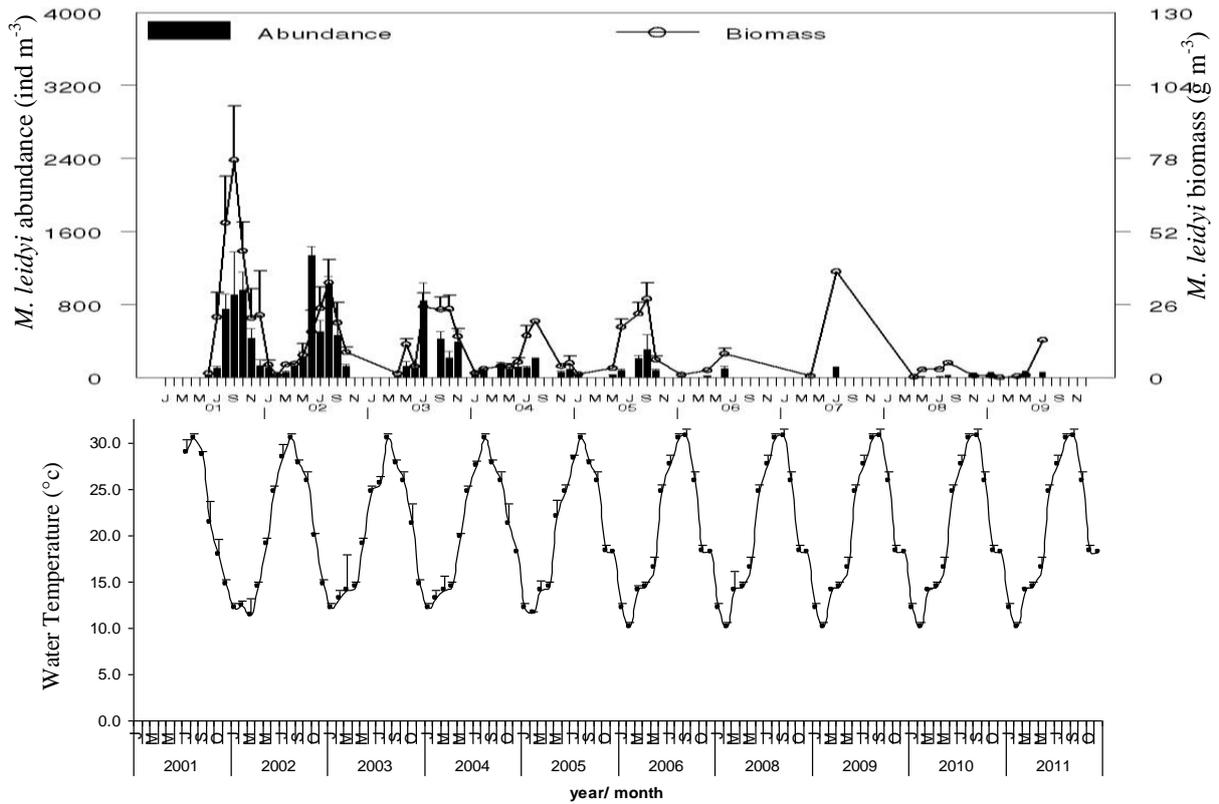


Figure 3 Annual variations in the abundance and biomass *Mnemiopsis leidyi* and water temperature in the southern Caspian Sea during 2001-2011 (values are depth and station averages)

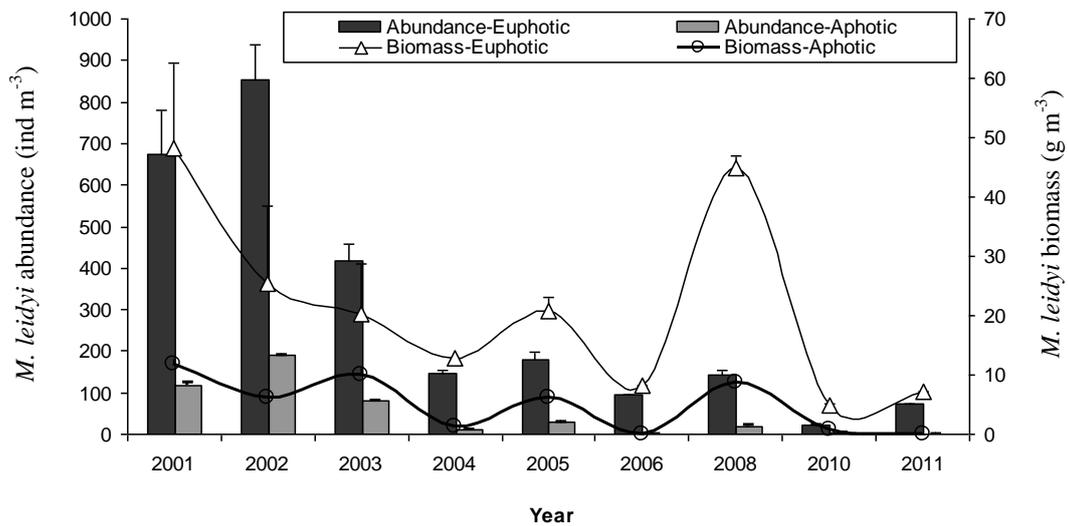


Figure 4 Summer-Autumn Photic zone distribution pattern of *Mnemiopsis leidyi* abundance and biomass in the southern Caspian Sea

The length-frequency distribution of Caspian *Mnemiopsis* with lobes, displayed that whilst 90.8% of the population belonged to the cidipid and juveniles (0-5 mm) group, only 7.8% were from transitional (6-15 mm), and the adults (>16 mm) were 1.4% length group. Thus, these larvae and juveniles made up 98.6% of the total population. In euphotic layer, 92.9% of the population belonged to the eggs and juveniles, 6.2% and 1.0% were transitional and adults, respectively (Figure 5-A), while in aphotic layer it was 83.1, 14.0 and 2.9%,

respectively. Predominated small -sized individuals (<5 mm total length) predominated, particularly in the euphotic zone, and ctenophores from the deeper layers had larger size compared to those from the shallower depths (Figure 5-B). The maximum size and wet weight were measured in May with 70 mm with lobes and 7.2 mg, respectively; and small sized specimens were recorded in summer-autumn at the southern Caspian Sea (Figure 5-A, B).

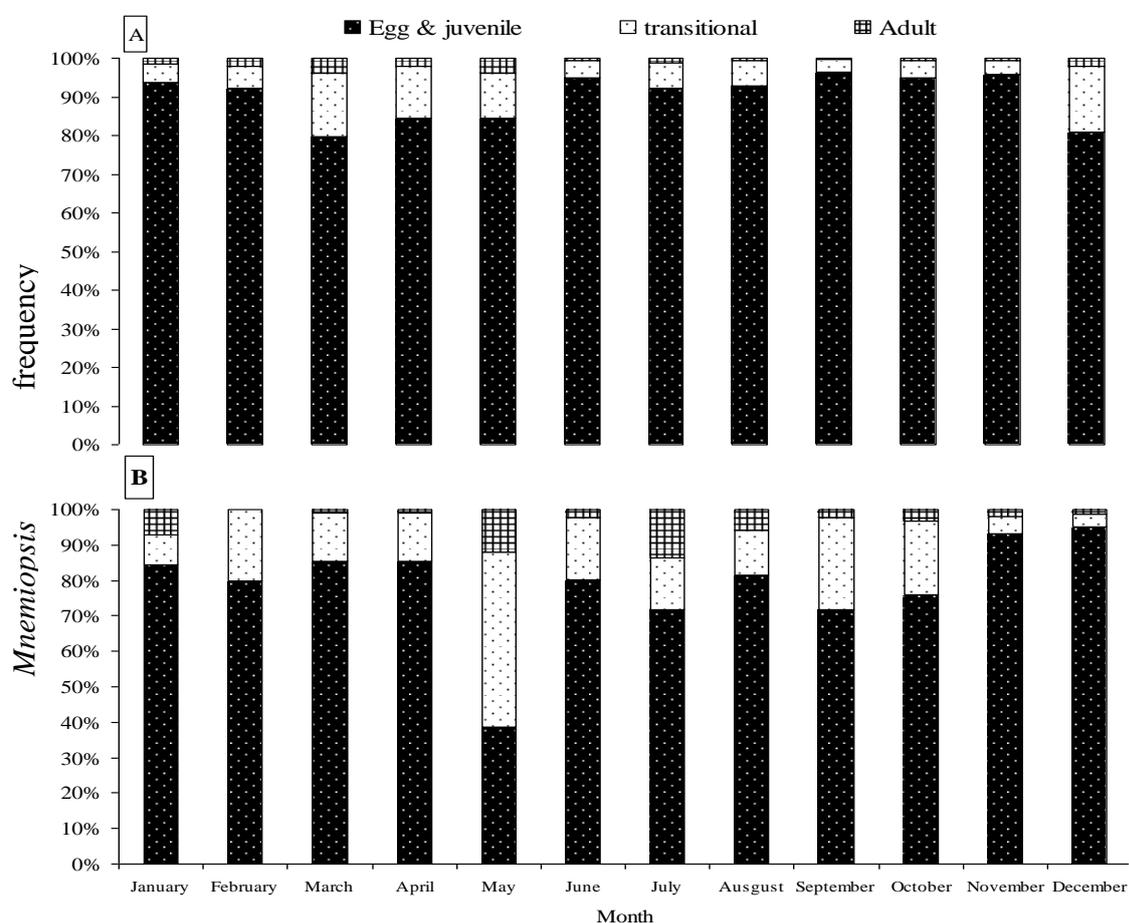


Figure 5 Percentage of *Mnemiopsis* size (mm) frequency of A) euphotic and B) aphotic at different months in the southern Caspian Sea

3.2 Long-term dynamics of zooplankton

After comparing the long-term fluctuations of zooplankton of the southern Caspian Sea, the maximum recorded abundance was $54579 \pm 11831 \text{ ind. m}^{-3}$ (average of stations and depths) in autumn, while the highest biomass was $381.2 \pm 177.3 \text{ mg. m}^{-3}$ (average of stations and depths) in spring 1996 (before *Mnemiopsis* invasion). The zooplankton population decreased tenfold after the invasion as this value of zooplankton has never been found after *Mnemiopsis* invasion (Figure 6).

3.3 *M. leidyi* reproduction rate analysis

These experiments showed that freshly collected *Mnemiopsis* had average fecundity of 12 eggs. day⁻¹, with a maximum of 115 eggs. ind⁻¹ day⁻¹ for specimens of 15-46 mm in length and weighing about 0.7-9.7 g in the Caspian Sea water (Figure 7A). Fecundity increased with increasing body length (Figure 7B).

3.4 *M. leidyi* diet analysis

Diet spectra compositions of *Mnemiopsis* in the Caspian Sea water were zooplankton, which mainly feed on copepoda. In spite of 83.3% *Mnemiopsis* stomachs were empty of food, copepodites stage (IV) was the principal item in *M. leidyi* stomach in all hand-picked from snorkeling and diving. Data on jelly specimens up to 26-30 mm long showed the tendency of more and big sized prey in 2010 (zooplankton) (Figure 8A, B).

Among a few food spectrum offered to *Mnemiopsis*, the jelly showed significant ($P < 0.05$) relative indices of importance (RII) and positive electivity on higher sized of copepodites (IV, V- male and VI-female stages) (Table 1).

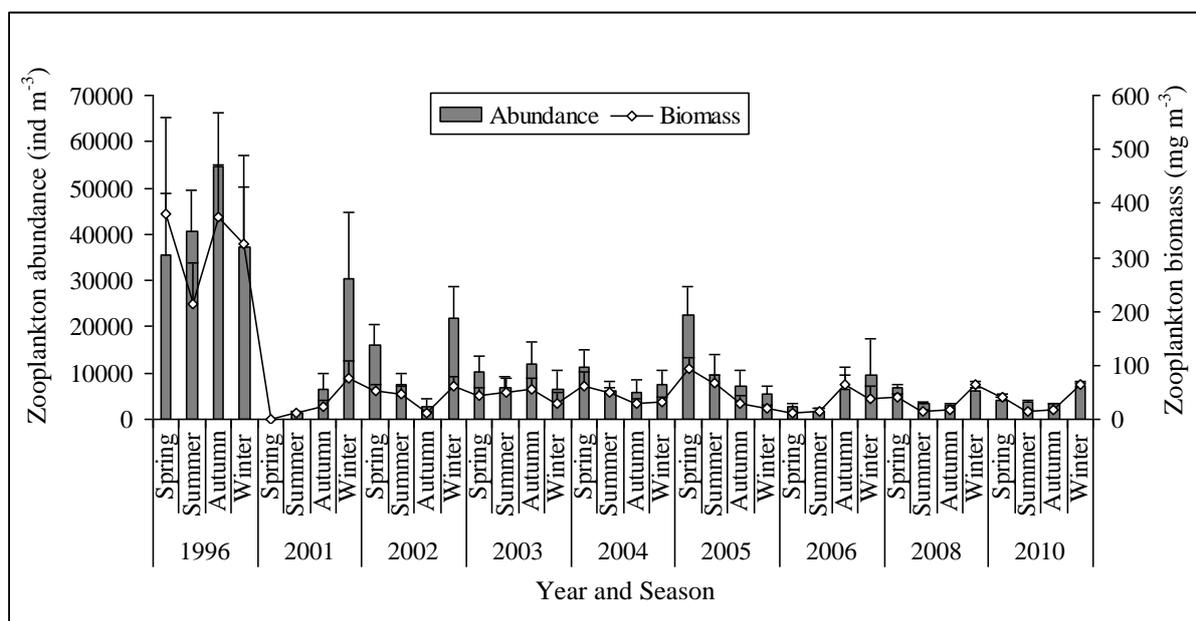


Figure 6 Long-term seasonally variation in the abundance and biomass of zooplankton in the southern Caspian Sea

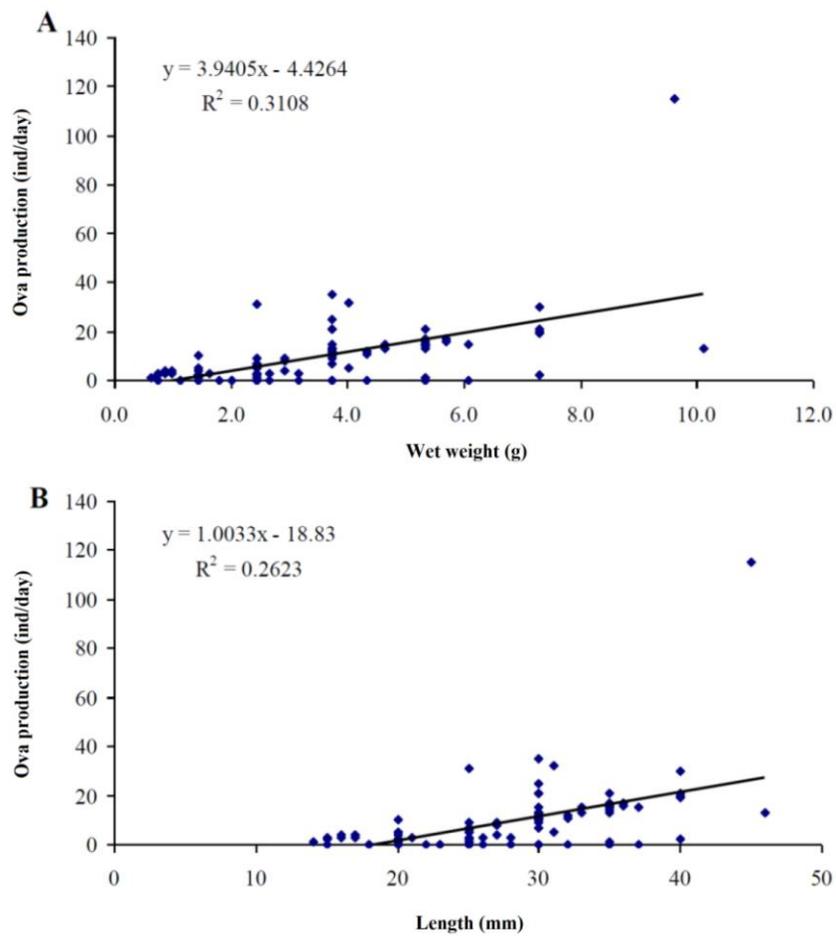


Figure 7 Reproduction rate of *Mnemiopsis* in the southern Caspian Sea. A- wet weight; B- Length

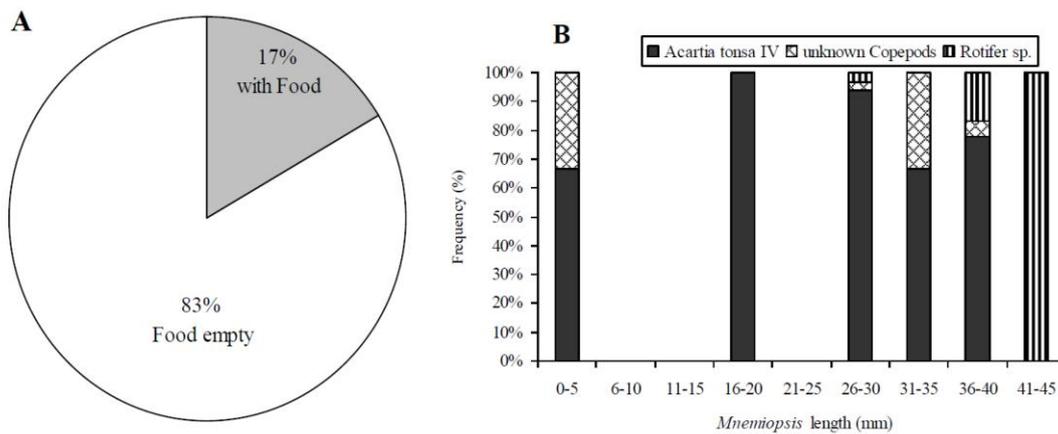


Figure 8 A) Stomach fullness and B) *Mnemiopsis* diet spectrum in the southern Caspian Sea

Table 1 Laboratory studies of the dominant zooplankton species abundance (ind.l⁻¹) in *Mnemiopsis* diet

Zooplankton item	Stage	F	ri	B	pi	RII	E
<i>Acartia tonsa</i>	I	93	1.1	13	0.2	0.0002	-0.652
	II	420	5.0	138	2.5	0.0086	-0.341
	III	491	5.9	261	4.7	0.0190	-0.115
	IV	1772	21.2	1237	22.1	0.3237	0.020
	V- male	1982	23.8	1350	24.2	0.3952	0.008
	V- female	392	4.7	266	4.8	0.0154	0.005
	VI- male	545	6.5	366	6.5	0.0295	0.000
	VI- female	1369	16.4	718	12.8	0.1452	0.122
<i>Hypania</i> sp.		603	7.2	505	9.0	0.0450	0.110
Nauplii <i>Acartia tonsa</i>	I	167	2.0	206	3.7	0.0051	0.298
	II	180	2.2	215	3.8	0.0057	0.281
	III	140	1.7	151	2.7	0.0031	0.235
<i>Nereis</i> sp.		186	2.2	164	2.9	0.0045	0.135

F= food item (ind l⁻¹) B= remain food in aquarium (ind l⁻¹) RII= Relative Index of Importance E= electivity index; ri= percentage of each item in the stomach content, Pi= percentage of each item in the aquarium (relative abundance).

4 DISCUSSION

One of the factors that provoked the enormous development of *M. leidyi* in the Black Sea, never observed in its natural estuarial waters of North America, was the absence of a predator controlling its population size (Purcell *et al.*, 2001). Long-term monitoring of gelatinous plankton revealed no other jelly beside *M. leidyi* in the Caspian Sea (Karpyuk *et al.*, 2004; Roohi *et al.*, 2008 and 2010; CEP, 2005). Other biological factors that contribute to the colonization success are the often omnivorous feeding mode, relatively short life span and generation time and high fecundity of the invaders (Bij de Vaate *et al.*, 2002). Recent studies in the southern Caspian Sea showed that *M. leidyi* abundance increased towards the end of the summer especially the early year's invasion and however remains with lower concentration (Figure 3). Long-term summer-autumn data (2001-2011) of *M. leidyi* in photic zone showed that its abundance and biomass recently were decreased 66% in the southern

Caspian Sea (851±85 ind m⁻³ in 2002 and 48.1±14.4 g m⁻³, in 2001 to 73±16 ind m⁻³, 7.2±2.3 g m⁻³, in 2011, Figure 4).

During the entire study period, a total of 5797 specimens were sampled and individually measured for their body length. The length-frequency distribution displayed that whilst 95% of the population belonged to the ctenophore, juvenile and transitional groups in euphotic zone, only less than 5% were from adult length group (Figure 5). Thus, these larvae and juveniles made up 97% of the total population. The largest size that the ctenophore could attain in southwestern Caspian Sea was 70 mm, which was measured in September 2001 (Roohi *et al.*, 2008). The length-frequency distributions of *M. leidyi* from photic zonation are presented to understand the vertical distribution of ctenophores with respect to their size. In both layers small ctenophores (<5 mm) dominated the *M. leidyi* population (Figure 5A, B), they comprised 90% (at euphotic) and 80% (at aphotic) of total abundance. However,

ctenophores from the deeper layers had larger size compared to those from the shallower depths. This indicates that mainly larger individuals penetrate through the thermocline to dwell in deeper waters. Despite the larger animals' ability to penetrate into deeper waters, the majority of ctenophores still remained at the surface waters. The larger specimens were observed more often during May to October (mid spring-late autumn) compared to other months (Figure 5). It seems that the ctenophore who were capable to reproduce, doing rearing in aphotic zone and reached to surface layers for feeding and surviving.

According to Roohi et al. (2010) and figures 3, 4 and 6 of present study, it seems that the principal parameters to resistance of *M. leidy* would be the favorite water temperature especially in summer (22-30 °C) and food availability in the southern Caspian Sea. Laboratory experiments and in situ studies on the predation potential of *Mnemiopsis* had shown that this ctenophore is an important predator of zooplankton which mainly fed on copepods. After *M. leidy* arrived, not only the zooplankton abundance and biomass were decreased (41995±11797 ind m⁻³ and 323.6±128.2 mg m⁻³, in 1996 to 4568±482 ind m⁻³ and 34.8±3.6 mg m⁻³, in 2010, Figure 6), but also the zooplankton species diversity decreased from 36 to 15 (Roohi et al., 2010).

It seems that the main reasons of *M. leidy* sustained in spite of sharp decreased could be the decreasing of food ability and ova reproduction (fecundity) in the southern Caspian Sea.

Experimental studies of egg production were conducted by Shiganova et al. (2004) showed that *Mnemiopsis* begins to produce eggs when it reaches a length of about 16 mm, and the average fecundity in the Caspian Sea experiments was 1174 eggs day⁻¹, with a maximum of 2824 eggs day⁻¹ for specimens of 30-39 mm in length and weighing about 2.0-

2.7g. In our experiments, average fecundity was 8±8 eggs day⁻¹, with a maximum of 35 eggs day⁻¹ for specimens of 15-46 mm in length and weighing about 0.7-9.7 g in (Figure 7A and B). Mean fecundity of *Mnemiopsis* showed 88% decreased from 2004 to 2011 in the Caspian Sea water, which could be the lack of food accessible decline by the ctenophore - concerned more on copepods- which shrink *Mnemiopsis* in unfavorable conditions. As Zaika and Revkov (1994) expressed, *M. leidy* fecundity in the Aegean Sea was much lower (400-448 eggs day⁻¹) than that in the Black Sea (average 2000-3000 eggs day⁻¹). They also mentioned to this fact that low fecundity of the ctenophore could be reflect to low ambient food concentration. Shiganova et al. (2004) also determined fecundity reduction characteristic for ctenophores were related to low prey availability. Another work on the reproduction rate of *Bolinopsis vitrea* revealed a very weak fecundity (12-96 eggs day⁻¹), probably due to the low ambient prey availability (Shiganova et al., 2004).

In the southern Caspian Sea, the highest number of mesozooplankton species was also observed in 2001-2010 period (Roohi et al., 2010; Roushantabari et al., 2011) with the occurrence of the copepod species *A. tonsa* which were absent in the past (Kurashova and Abdullaeva, 1984). *Mnemiopsis* prefers copepods and cladocera as a more energy-rich food (Reeve et al., 1989). Also studies, of Karpyuk et al. (2004) and Bagheri et al. (2008) expressed the principal diet of *M. leidy* was nauplii, copepodites and adult stages of copepod *A. tonsa* (66%) and bivalve larvae (13%) in the southern Caspian Sea. In recent study, mostly ctenophore samples which collected with hand-picked from snorkeling and diving had empty stomach that indicate the starvation (Figure 8), but copepodites and adults of copepod *A. tonsa* (IV stage) and rotifer had the highest feeding frequency

comprising 90% and 10% of food items taken by the organism, respectively. The ctenophore *M. leidyi* can consume large amounts of zooplankton prey. Albeit, quantitative measurements of feeding rates, based on field data, are scarce. However, it is indeed characteristic for ctenophores to reduce fecundity in conditions of low prey availability (Shiganova *et al.*, 2004). Laboratory *Mnemiopsis* diet experiments also showed in a mixed spectrum of zooplankton exposure, larger sized of prey can be consumed and in this regards it seems *M. leidyi* acts a selective behavior animal not really passive (Figure 8), and also *Mnemiopsis* is an actively hunting carnivore in which often feeds superfluously, regurgitating excess ingested food, and it can consume up to ten times its own weight per day (Kremer, 1979). Low fecundity of *Mnemiopsis* which was due to decreasing of edible zooplankton and the shrink it in unfavorable conditions was the main and important reason of the jelly declined. The result from the present study and the results of Finenko *et al.* (2006) shows such a high pressure on zooplankton especially on adult copepods exerted by *Mnemiopsis* would not permit zooplankton population to rise, and as a consequence, no recovery can be expected and/or predicted until the jelly abundance decrease substantially. Resulted in changes of the trophic chain (phytoplankton → zooplankton → planktivorous fish) happened in the Caspian Sea and also when the scyphozoan *Aurelia aurita* became a progressively more dominant member of the planktonic community, in which *Aurelia* during the 1970s and 1980s, and next *Mnemiopsis* in the 1990s become the jelly organisms directly tap the secondary production instead of fish (Gücü, 2002).

5 ACKNOWLEDGMENT

The authors are grateful to the Iranian Fisheries Research Organization (IFRO) and Caspian Sea

Research Institute of Ecology for their technical and financial support. Hereby, we would like to thank M. Roushantabari, A. Keyhanisani, M. Nazaran, M. Rostamian and H. Khodaparast for their help in zooplankton sampling and analyses and the captain and crew of R/V Guilan for their support in cruises sampling.

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عوامل مؤثر بر رشد و توسعه مهاجم شانه‌دار *Mnemiopsis leidyi* در حوضه جنوبی دریای خزر

ابوالقاسم روحی^۱، رضا پورغلام^۱، علی گنجیان خناری^۱، احمد ارکان کدیش^۲، آمنه سجادی^۳ و رامین عبدالله زاده کلانتری^۴

- ۱- استادیار، پژوهشکده اکولوژی دریای خزر، ساری، ایران
- ۲- استاد، پژوهشکده علوم دریایی، دانشگاه تکنولوژی خاورمیانه، مرسین، ترکیه
- ۳- استادیار، دانشگاه آزاد اسلامی واحد رشت، رشت، ایران
- ۴- دانشجوی کارشناسی ارشد، دانشگاه آزاد اسلامی واحد تهران شمال، تهران، ایران

تاریخ دریافت: ۶ فروردین ۱۳۹۱ / تاریخ پذیرش: ۲۱ اردیبهشت ۱۳۹۲ / تاریخ چاپ: ۳ آذر ۱۳۹۲

چکیده اولین فعالیت‌های تحقیقاتی در خصوص جمعیت شانه‌دار مهاجم دریای خزر *Mnemiopsis leidyi* با انجام گشت‌های دریایی در سال ۱۳۸۰ صورت گرفت که جمعیت آن به‌طور قابل ملاحظه‌ای در حال افزایش بوده به‌طوری که هم‌اکنون به‌صورت پایدار در این دریا ماندگار شده است. بیش‌ترین میزان تراکم این گونه در فصول تابستان- پائیز در لایه نوری سال ۱۳۸۱ با 85 ± 85 عدد در متر مکعب و بیش‌ترین میزان زی‌توده آن در سال ۱۳۸۰ با $48/1 \pm 14/4$ گرم در متر مکعب به ثبت رسید. در طی سال‌های ۸۳-۱۳۸۲، تراکم و زی‌توده این شانه‌دار به‌شدت کاهش یافت و به‌ترتیب به ۱-۸۴۳ عدد در متر مکعب و $0/07 - 37/7$ گرم در متر مکعب رسید. پراکنش فراوانی طولی شانه‌دار *Mnemiopsis* نشان داد که سه مرحله در طول زندگی شانه‌دار شامل مراحل لاروی، جوانی و انتقالی وجود داشت که بیش از $98/6$ درصد جمعیت آن را تشکیل داد. در حوضه جنوبی دریای خزر، هم‌اکنون زئوپلانکتون پاروپای *Acartia tonsa* بیش‌ترین میزان تراکم به‌عنوان غذای زنده دریایی از بین ۳۶ گونه زئوپلانکتون پیش از ورود شانه‌دار مهاجم را تشکیل می‌دهد که در طی سال‌های ۱۳۹۰-۱۳۸۰ حدود ۱۰ برابر کاهش یافت. هم‌چنین، آزمایش‌های باروری شانه‌دار *Mnemiopsis* نشان داد که متوسط تخم‌ریزی آن ۸ عدد در روز بوده و حداکثر میزان تخم‌ریزی ۳۵ عدد در روز بوده که با اندازه طول جانور میزان تخم‌ریزی نیز افزایش نشان داد. غذای عمده شانه‌دار در حوضه جنوبی دریای خزر از زئوپلانکتون‌های بزرگ نظیر پاروپایان خصوصاً گونه *A. tonsa* بوده است. به‌نظر می‌رسد که کاهش سریع تراکم شانه‌دار *Mnemiopsis* در حوضه جنوبی دریای خزر مربوط به کاهش تولید مثل بوده که این امر به‌دلیل کاهش غذای زنده زئوپلانکتونی باشد، از طرفی دلیل اصلی ماندگاری این شانه‌دار در این حوضه، نیز وجود هم‌مین زئوپلانکتون‌ها می‌باشند. هدف از انجام مطالعه حاضر، ارائه اطلاعات در خصوص فاکتورهایی است که سبب کاهش جمعیت شانه‌دار بعد از افزایش ناگهانی و بلوم آن در سال‌های اولیه مهاجم این جانور به حوضه جنوبی دریای خزر می‌باشد.

کلمات کلیدی: تولیدمثل، دریای خزر، رژیم غذایی، زئوپلانکتون، *Mnemiopsis leidyi*