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Effect of temperature on clearance rate, daily ration and digestion time of *Mnemiopsis leidyi* from the southern Caspian Sea

M. Rowshantabari^{1*}, G.A. Finenko², A. E. Kideys³ and B. Kiabi⁴

1- The Caspian Sea Ecology Research Center Sari, Iran .

2- Institute of Biology of the Southern Seas, Sevastopol, Ukraine.

3- Commission on the Protection of the Black Sea Against Pollution, Dolmabahce Palace, II Harekat Kosku, Besiktas, Turkey

4- Shahid Beheshti University, Tehran, Iran

* Corresponding author's E-mail: rowshantabari@yahoo.com

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ABSTRACT

The effect of temperature on the main feeding parameters of *Mnemiopsis leidyi* from the southern Caspian Sea was studied in 2002. The clearance rates and daily rations were estimated from laboratory experiments in a wide range of temperatures from 12 to 27 °C for *M. leidyi* of 12–17 mm in length. Clearance rate values changed from 52.5 to 107.3 ml ind⁻¹ h⁻¹. The coefficient Q₁₀ in temperature 12 - 20 °C was higher than that in 20 - 27 °C (3.81 and 1.91, respectively). The specific daily ration changed from 1.56±0.19 to 0.24±0.05 mg C mg C⁻¹ day⁻¹ when temperature decreased from 27 °C to 12 °C. The direct relationship occurred between daily ration and temperature (R²=0.99). The digestion time decreased with temperature rise and did not display any clear relation to quantity of digested food.

Keywords: *Ctenophora*, *Mnemiopsis leidyi*, clearance rate, daily ration, digestion time

INTRODUCTION

M. leidyi is believed to have entered the Caspian Sea from the Black Sea with ballast waters through Volga-Don channel in the late 1990s (Ivanov *et al.*, 2000). In August *M. leidyi* was found in the northern Caspian near the Volga delta with salinity of 2-4‰. It is expected that the central and southern Caspian Sea with salinities of 12-13.0‰ and higher temperature would be more favorable for *Mnemiopsis* than the northern shallow part with lower salinity and low temperature in winter (Ivanov *et al.*, 2000).

M. leidyi is an active predator that feeds on zooplankton, meroplankton, fish eggs and larvae and can cause their rapid decrease, resulting in a change in species composition and biodiversity in the ecosystems (Bishop, 1967; Vinogradov *et al.*, 1989; Purcell, 1992; Tzikhon-Lukanina *et al.*, 1993; Purcell *et al.*, 1994; Shiganova, 1997; Kovalev *et al.*, 1998; Finenko *et al.*, 2003).

The study of zooplankton composition in Iranian coastal waters showed that two

species of copepoda *Acartia* and *Eurytemora* were dominant in the Caspian Sea before the *M. leidyi* appearance (Rowshantabari *et al.*, 2001). In 2000-2001 and 2005 *Eurytemora* was not observed at all (Rowshantabari *et al.*, 2003, 2007).

The modern climate changes have had significant impacts on the ecosystem structure, biodiversity, productivity and function. Thus the temperature effect study on ecological and physiological characteristics of marine inhabitants becomes very important to understand and predict this impact. Although the ecological physiological features of *M. leidyi* were studied in numerous research studies in different regions (Kremer, 1976; Reeve *et al.*, 1978; Finenko *et al.*, 1995; Finenko and Romanova, 2000; Finenko *et al.*, 2005; Finenko *et al.*, 2006 a, b), almost nothing is known about temperature effects on any of the energetic parameters in *M. Leidyi* – and especially not on feeding related parameters.

The aim of this paper is to determine the effect of temperature on the main

feeding parameters of *M. leidyi*: clearance rate, daily ration, digestion time.

MATERIALS AND METHODS

Mnemiopsis was collected in summer 2002 (from August to September) by a 500 µm mesh net in region of Khazarabad in the southern Caspian Sea, where salinity was 12.3 - 12.8‰. Total length of each *Mnemiopsis* was measured just after capture and the wet weight was determined using an analytical balance (accuracy up to 1×10^{-2} g) after preliminary blotting the animals on a nylon mesh to remove excess water (Finenko et al, 2006 b). The relationship between length and weight was calculated using measurements from 384 individuals.

For studying the clearance rate and daily ration, *M. leidyi* were put into an aquarium (20 l volume), and were kept there until at least 1-2 hours before the experiments.

Zooplankton was collected daily with horizontal sampling by net (100 µm mesh). The zooplankton samples included nauplii, copepodits and adult *Acartia tonsa*. Before experiments the number of Copepoda was counted in 3 replicate 10 ml subsamples of this sample. Filtered Caspian Sea water (from 30 µm mesh) with the salinity of 12.3-12.8 ‰ was poured into six 5 l jars.

Two jars served as controls and four jars were used for the experimental groups. All experiments were performed in the dark and lasted for six hours. The container volume, density of predators and duration of the experiments were chosen to get a feeding response. As it was shown with calanoid copepods, a decrease of the final prey abundance by 30-40% is optimal (Gifford, 1993). Experiments for studying the effect of temperature on feeding rate were carried out at 12, 22 and 27 °C with small *Mnemiopsis* of 12, 15 and 17 mm oral-aboral length (0.42 ± 0.17 ; 0.47 ± 0.15 and 0.83 ± 0.08 g of wet weight, respectively). The temperature was about 27 °C in the sea at that time and the ctenophores were kept at the experimental temperatures for 24 h to acclimate.

Additional experiments on relationship between feeding rate and *Mnemiopsis* size were conducted at 21°C using specimens of 5, 9.5 and 17.5mm. After the experiments, *Mnemiopsis* specimens were removed from experimental jars and water with zooplankton was filtered through 30µm

mesh to have the total volume of 200-250 ml. The number of different stages of *Acartia tonsa* was counted in each jar. The average biomass of food was calculated from number and individual weight of each stage in the control jar. The average food concentration in the jars was 20 ind l⁻¹. The clearance rate was computed on difference of prey number in the control and experimental jars (Finenko & Romanova, 2000).

$$CR = V (\lg C_c - \lg C_e) / 0.4343 nt$$

$$CR = \text{clearance rate, ml ind}^{-1} \text{ h}^{-1}$$

$$V = \text{volume of experimental jar (ml)}$$

$$C_c = \text{concentration of prey in control (ind ml}^{-1}\text{)}$$

$$C_e = \text{concentration of prey in experiment (ind ml}^{-1}\text{)}$$

$$n = \text{number of } Mnemiopsis$$

$$t = \text{time (hour)}$$

To study digestion time the ctenophores of different size from 5 to 35 mm, without any visible food in their guts after catching, were placed in the dish with *Acartia* (200 ind l⁻¹) at 27 °C. After 10 minutes, when *Mnemiopsis* captured some prey, the number of prey was counted in *M. leidyi* gut and then the start time of digestion was recorded. Then these animals were continuously observed to record complete digestion time. The digestion time was also determined for *Mnemiopsis* of 5 mm length at different temperatures. The quantity of digested food was estimated by number of captured prey (different stages of *Acartia*) and their weight (Petipa, 1957).

RESULTS

The relationship between wet weight and *M. leidyi* length in the wide size range from 4 to 50 mm was as follows:

$$WW = 0.0037 L^{1.900}$$

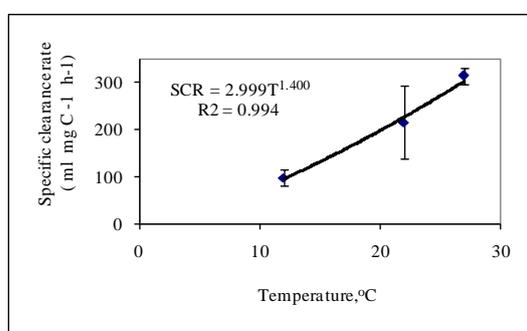
$$WW = \text{wet weight (g)} \quad L = \text{length (mm)}$$

The relationship between wet weight (WW) and oral-aboral length (L) of *M. leidyi* of three size groups (<10, 10-20 and >20 mm) were analyzed separately. The exponent in the equation was the highest (2.12) for the largest ctenophores with a length of >20 mm and was smallest (1.38) for the small ones (Table 1). The relation between dry and wet weight on an average amounted to 1.6% of wet weight, being 1.5 and 1.8% for different size groups (Table 1).

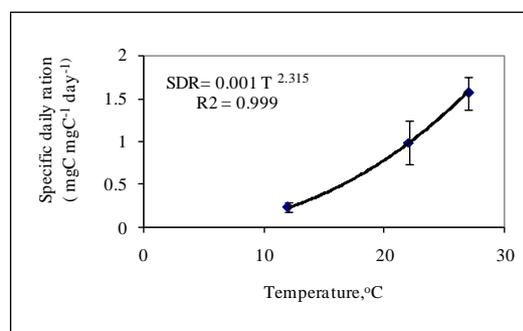
Table 1. Morphometric characteristics (L mm, WW and DW mg) of *Mnemiopsis leidyi* from the southern shores of the Caspian Sea

Size range, mm	4-50	< 10	10-20	>20
Equation(WW-L)	WW=0.0037 L ^{1.901}	WW = 0.0096 L ^{1.380}	WW =0.0032 L ^{1.899}	WW= 0.0021 L ^{2.117}
R2	0.871	0.811	0.801	0.811
Samples	384	73	124	102
Equation(DW-WW)	DW=0.0151 WW ^{1.015}	DW=0.0179 WW ^{1.091}	DW=0.0175 WW ^{1.113}	DW=0.0182 WW ^{0.909}
R2	0.876	0.805	0.837	0.851
Samples	390	85	131	113
% DW/WW	1.536	1.638	1.737	1.615

The clearance rate of 12 - 17 mm *M. leidyi* increased from 52.48 to 107.33 ml ind⁻¹ h⁻¹ and the specific clearance rate from 98.53 to 314.42 ml mgC⁻¹ h⁻¹ when temperature rose from 12 to 27 °C (Figure 1).

**Fig 1.** The relationship between the specific clearance rate and temperature (Mean ± SD)

The coefficient Q₁₀ in the temperature range from 12 to 20 °C was higher than that between 20 and 27 °C (3.81 and 1.91, respectively) In the whole studied temperature range Q₁₀ is 2.16.

**Fig 2.** The correlation between specific daily ration of *Mnemiopsis leidyi* and different temperatures in the Caspian Sea (Mean±SD)

The feeding rate increased from 0.24 to 1.56 mgC mgC⁻¹ day⁻¹ when temperature rose from 12 to 27 °C (Table 2). There was a direct correlation between specific daily ration (SDR, mgC mgC⁻¹ day⁻¹) and

temperature (T) which could be described in the following equation (Figure 2):

$$\text{SDR} = 0.001 T^{2.315} \quad R^2 = 0.999$$

Table 2. The daily ration and the specific daily ration of *Mnemiopsis leidyi* fed on *Acartia* (Mean±SD)

N	T °C	<i>Mnemiopsis</i> Length, mm	<i>Mnemiopsis</i> Carbon content (mgC)	Daily ration (mgC day ⁻¹)	Specific daily ration (mgC mgC ⁻¹ day ⁻¹)	Daily ration %C
1	27	12	0.31 ± 0.08	0.48 ± 0.06	1.56 ± 0.19	156.00 ± 18.72
2	22	15	0.41 ± 0.05	0.41 ± 0.07	0.99 ± 0.26	98.76 ± 25.94
3	12	17	0.53 ± 0.05	0.13 ± 0.04	0.24 ± 0.05	24.77 ± 4.93

The specific daily ration of *Mnemiopsis* at 21 °C decreased with increase in body carbon content. The correlation between the specific daily ration and carbon content is as follows (Figure 3):

$$\text{SDR} = 0.210 C^{-0.234} \quad R^2 = 0.853$$

The correlation between specific clearance rate (ml mgC⁻¹ h⁻¹) and carbon content of *M. leidyi* at 21°C is described in the following power function (Figure 4):

$$\text{SCR} = 160.38 C^{-0.332} \quad R^2 = 0.820$$

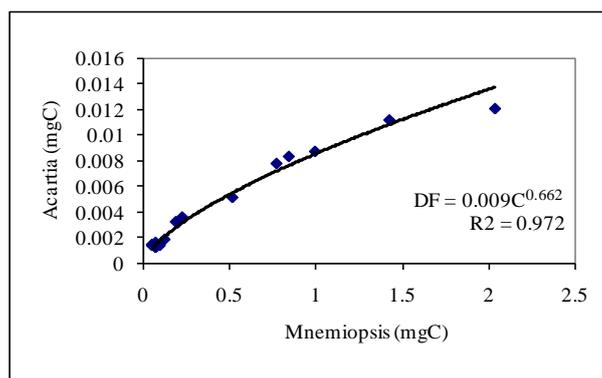


Fig 5. The correlation between the digested food (DF) in experiment and weight (mg C) of *Mnemiopsis* at 27 °C

Quantity of consumed (digested) food increased with increase in ctenophore weight, so larger ctenophores could catch and digest more food in the same time as small ones (Figure 5).

DISCUSSION

The relationship between length (L, mm) and wet weight (WW, g) in *M. leidyi* in the south Caspian Sea differed among the size groups. The exponent in the equations varied from 1.38 to 2.11 and was the largest in the large ctenophores (20–50 mm). This variability is a result of changing of morphometric proportions in this species with development and growth. Morphometric characteristics (WW, C and N mg) of *M. leidyi* from the different regions are given in Table 4. The weights of small *M. leidyi* (<30mm) calculated from the equations for *M. leidyi* in the northern Caspian Sea (Kideys *et al.*, 2001, Shiganova *et al.*, 2001) are in good agreement with our data while the weights of large ctenophores (30–50mm) differ by about 20% from ours (in Kideys *et al.* they are higher and in Shiganova *et al.* they are lower than ours).

In Finenko *et al.* (2003) as well as in some other studies (Deason, 1982, Sullivan and Gifford, 2004) the oral – aboral length of ctenophores was measured while other authors cited, used total length with lobes. If oral–aboral length is 75% of total length (Finenko and Romanova unpublished data) the weights of *M. leidyi* from the different regions are very close (Table 5).

It is worth noting that the relationships between the wet weight and length for separate size groups are more accurate

than that for the whole length range of ctenophores and they can be recommended for computation of population biomass.

M. leidyi dry weight in the south Caspian Sea (with the salinity of 13 ‰) averaged 1.6% of wet weight, ranging between 1.5 and 1.8% for different size groups. In the north Caspian Sea at the salinity of 5.7‰ these values varied from 0.61 to 0.97% (averaging 0.78%) in the ctenophores of 2.5–4.6 mm (Shiganova *et al.*, 2001). The ratios in the present study are significantly lower than those in the other regions due to low salinity of the Caspian Sea. In *M. leidyi* from the Black Sea it is 2.2% and in ctenophores from the Atlantic Ocean with salinity of 32–34 ‰, it is equal to 3.4% (Finenko *et al.*, 1995, Reeve *et al.*, 1978).

In the present study, effects of temperature (12–27 °C) were studied on clearance rate of three size groups of *M. leidyi*. As mentioned above 5 litre jars were used for the feeding experiments. It is known that clearance rate in the laboratory experiments is affected by experimental container volume: there is a “wall effect” in small volumes when ctenophores tighten their lobes making contact with bottle walls and stop feeding (Reeve *et al.*, 1978, Finenko *et al.*, 2005). Finenko *et al.* (1995) revealed the ingestion and clearance rates of 20 mm *Mnemiopsis* increased three times when container volume changed from 1 to 5 liters. We believe the experimental volumes of 4–5 l are optimum for small *M. leidyi* and our data represent more realistic values of clearance rates occurring in the sea.

It is well known that the important characteristics of Lobate ctenophores is the proportionality between the consumption rate and the food concentration over an extremely wide range of prey concentrations (Bishop, 1968, Gibbison and Painting, 1992, Reeve *et al.*, 1978). When copepods were used as food, the food saturation was not observed at concentrations as high as 3000 specimens per liter (Reeve *et al.*, 1978). Under this type of functional response to the increase of the prey concentration the clearance rate does not depend on the prey density (Kremer, 1976, Monteleone and Duguay, 1988, Finenko and Romanova, 2000) so we can analyze clearance rate values but not daily rations that are affected by prey concentration in the experiments.

Data from literature and in this study on the clearance rate of *M. leidyi* at various temperature and food items is difficult to compare because the experiments differed by experimental volumes (from 1 to 20-40 l) and food items (nauplii, copepodits, adult Copepoda, nauplii *Acartia*, *Bivalvia*, nauplii *Balanus* sp., fish eggs). However, in our experiments the clearance rate values are in a good agreement with the results of the most experiments where Copepoda were used as a food and volume of experimental jars was close to ours. At temperature 8-15 °C in *M. leidyi* of 20 – 60 mm feeding on Copepods clearance rate values were about 0.75 – 3.94 l gDW⁻¹ h⁻¹, at 15 – 20 °C *Mnemiopsis* of the same size cleared 1.7 – 8.75 l gDW⁻¹ h⁻¹; at 20- 25 °C maximum clearance volume was as high as 16.85 l gDW⁻¹ h⁻¹ and reached 18.5 l gDW⁻¹ h⁻¹ at temperature >25 °C (Table 6). There is clear tendency of clearance rate to increase with temperature. According to our results Q₁₀ values of clearance rate in the temperature range of 12 -20 °C were 3.81 and within the range of 20 -27 °C were 1.91. In the whole studied temperature range of 12 -27 °C Q₁₀ was 2.16. As mentioned above data on the effect of temperature on feeding characteristics of gelatinous organisms are very scarce but there are some data on effect of temperature on the metabolism that were analyzed in Svetlichny *et al.*

(2004) and Purcell (2009). In *M. leidyi* Q₁₀ of respiration rate measured at ambient temperature of 7 – 12 °C were high (6.7) and in the range from 12 to 23 °C were much lower (1.8). In the whole temperature range of 7 – 23 °C it was 2.1 (Svetlichny *et al.*, 2004) In Kremer (1977) Q₁₀ was 4.0 in the temperature range of 10.3 - 24.5 °C. In the study by Svetlichny *et al.* (2004), weight specific respiration rate of another ctenophore *Beroe ovata* gradually increased within temperature a range of 10–28 °C, independent of body size. Mean Q₁₀ was 2.17±0.5. Meantime Purcell (2009) revealed that respiration rates of scyphomedusae and *Mnemiopsis leidyi* ctenophores measured at or near ambient temperatures did not change with temperature in accordance with experimentally measured Q₁₀s respiration rates. She considers that the respiration rates of *Aurelia* spp., *Chrysaora* spp., and *Cyanea* spp. Scyphomedusae, and *M. leidyi* ctenophores can be predicted from most habitats with regressions using mass, and that adjustment for temperature by Q₁₀ determined from experimentally changed temperatures may misestimate metabolic rates. If it is true for feeding rates, it is difficult to estimate now because of lack of data on feeding of medusa and ctenophores in different temperature conditions, but we agree with her recommendations to measure these values at ambient temperatures but not with short-term acclimation.

Digestion time of *M. leidyi* observed in our experiments is amongst the lowest for ctenophores from different studies where it varied from 20 to 400 min and was affected by temperature (Larson, 1987, Reeve *et al.*, 1978, Tzikhon- Lukanina *et al.*, 1995 Finenko *et al.*, 2005). The digestion time also depends on prey and predator sizes. To digest small prey (<1 mm – *Oithona*, nauplii Copepoda, *Balanus* larvae) 50mm *M. leidyi* spent only 20–40 min (Larson, 1987). Large copepoda are digested much slower than small ones. Ctenophore of all sizes digested *Acartia* of 1-2 mm length in 60–100 min that is half the time taken for *Pontellidae* and *Calanus* (length of 3-3.5 mm).

Table 5. Morphometric characteristics (WW, C and N mg) of *Mnemiopsis leidyi* from different regions

Size range, mm	Region	Equation	Reference
3-22	Caspian Sea	WW=0.0011 L ^{2.34}	Kideys <i>et al.</i> , 2001
2.5 - 4.6	Caspian Sea	WW = 0.0094 L ^{1.67}	Shiganova <i>et al.</i> , 2001
4-50	Caspian Sea	WW =0.0037 L ^{1.90}	Our data
< 10	Narrangansett Bay	WW= 0.0007 L ^{2.636}	Deason, 1982
0.5 - 16	Narrangansett Bay	C= 0.0017 L ^{2.014}	Sullivan and Gifford, 2004
0.5 - 5	Narrangansett Bay	C= 0.0017 L ^{1.925}	Sullivan and Gifford, 2004
6-16	Narrangansett Bay	C= 0.0113 L ^{1.227}	Sullivan and Gifford, 2004
0.5 - 16	Narrangansett Bay	N = 0.0003 L ^{2.119}	Sullivan and Gifford, 2004
0.5 -5	Narrangansett Bay	N = 0.0003 L ^{2.095}	Sullivan and Gifford, 2004
6-16	Narrangansett Bay	N = 0.0033 L ^{1.057}	Sullivan and Gifford, 2004
2-10	Black Sea	WW = 0.0011L ^{2.76}	Finenko <i>et al.</i> , 2003
11-65	Black Sea	WW = 0.0013 L ^{2.49}	Finenko <i>et al.</i> , 2003

Table 6. Clearance rate (CR, l g⁻¹ DW h⁻¹) in *Mnemiopsis leidyi* at different temperature and food conditions [All of them have been obtained at natural salinity of this region (32- 34 ‰), except Finenko *et al.*, 2006 and this paper,(12 -13‰), Finenko *et al.*, 2005 (18 ‰)]*

<i>Mnemiopsis</i> length (mm)	T (°C)	Volume (l)	Food	CR (l g ⁻¹ DW h ⁻¹)	Reference
20-50	8	6	Copepoda	1.1	Miller, 1970
17	12	5	Copepoda	3.94	This paper
24-58	10-15	20-40	Copepoda	0.75-3.6	Kremer, 1979
0.5-1	15	1	microzoo	0.6 -1.8	Stocker <i>et al.</i> 1987
20-50	16	6	Copepoda	4.17	Miller, 1970
< 10mm	20	1	Copepoda	1.46-2.71	Lonsdale, 1981
< 10mm	20	1	Nauplii Copepoda	2.27	Deason, 1982
< 10mm	20	1	Copepoda	3.54-6.82	Miller, 1970
5-20	21	5	<i>Acartia sp.</i>	5.9 - 10.5	Finenko <i>et al.</i> , 2006
15	22	5	Copepoda	8.75	This paper
24-58	20-25	20-40	Copepoda	1.7-5.68	Kremer, 1979
10-50	22-24	4	Copepoda	3.59-10.6 (6.43)	Quaglietta, 1987
20-50	24	6	Copepoda	7.95	Miller, 1970
9-67	21-24	15	fish eggs	2.27-16.85	Monteleone & Duguay, 1988
20-25	21-24	15	fish eggs	3.98-16.85	Monteleone & Duguay, 1988
20-30	26	5	nauplii <i>Artemia</i>	10.9	Finenko <i>et al.</i> , 2005
40 - 50	26	5	nauplii <i>Artemia</i>	4.5 - 9.09	Finenko <i>et al.</i> , 2005
12	27	5	Copepoda	6.08	This paper
50	27-30	sea	zooplankton	0.35 -3.65.8	Larson, 1987

*-Average values are in parenthesis

At the same time, digestion rate increased with *M. leidyi* size (Tzikhon-Lukanina *et al.*, 1995, Finenko *et al.*, 2005). A 10 mm *Mnemiopsis* digested *Pontellidae* in 400 min while 70 mm ctenophores spent half as much time under same conditions. Average digestion time at 26 °C was 50±20

min in 20-30 mm *M. leidyi* and 77±23 min in 40-50 mm ctenophores in the experiments with *Artemia* nauplii >1 mm (Finenko *et al.*, 2005).

Digestion time decreased with increase of temperature in the whole range of temperature studied in our experiments

with Q_{10} being 1.67 in temperature range of 12 --27 °C. These values are lower than that of clearance rate: between 12 – 20 °C it equal 3.81 and between 20 and 27 °C 1.91 respectively. Along with decrease of digestion time, number of prey caught increased: at 12 °C, a 5- mm *Mnemiopsis* can catch on average 1.4 *Acartia* within 10 min while at 27 °C this increased to 3.5 *Acartia*. Probably this difference in number of prey caught especially for such small ctenophores can explain lower Q_{10} values of digestion time in compare to Q_{10} of clearance rate values. Purcell (2009) also found a significant effect of temperature with digestion by jellyfish of similar size (12.6–28.6 g WW) ranging between 0.71 h at 30 °C and 3.85 h at 4 °C. This is equivalent to a Q_{10} of 2.08. She supposes that such rapid digestion at warm temperatures may have been exacerbated by small prey sizes at those locations.

The present study is the first where *M. leidyi* feeding characteristics have been examined at low salinity in wide range of temperature. Our data are important to assess trophic impact of the ctenophore on the Caspian Sea planktonic community and ecosystem as a whole all the year round can be used for modeling purposes.

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اثر درجه حرارت روی **Daily ratio, Clearance rate**، نرخ تغذیه و زمان هضم *Mnemiopsis leidy* در حوضه جنوبی دریای خزر

م. روشن طبری*، جی. فیننکو، ا.ای. کیدیز، ب. کیابی

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چکیده

اثر درجه حرارت روی تغذیه *Mnemiopsis leidy* در حوضه جنوبی دریای خزر در سال ۲۰۰۲ مطالعه شد. نرخ چرا **clearance rates** و نرخ تغذیه **daily ration** در شرایط آزمایشگاهی برای *M. leidy* با طول ۱۷-۱۲ میلی متر در دمای ۱۲ تا ۲۷ درجه سانتی گراد اندازه گیری شد. نرخ چرا از ۵۲/۵ تا ۱۰۷/۳ میلی لیتر/عدد/ساعت در دماهای مختلف تغییر کرد. ضریب **Q10** در درجه حرارت بین ۱۲ تا ۲۰ درجه سانتی گراد بیش تر از دمای بین ۲۰ تا ۲۷ درجه سانتی گراد (به ترتیب ۳/۸۱ و ۱/۹۱) بود. نرخ تغذیه ویژه از ۱/۵۶±۰/۱۹ تا ۰/۲۴±۰/۰۵ میلی گرم کربن/میلی گرم کربن/روز وقتی که درجه حرارت از ۲۷ درجه سانتی گراد به ۱۲ درجه سانتی گراد کاهش داشت، تغییر کرد. ارتباط مستقیم بین درجه حرارت و نرخ تغذیه وجود داشت (R²=۰/۹۹). زمان هضم با افزایش درجه حرارت کاهش داشت و ارتباط واضحی با مقدار غذای هضم شده، نشان نداد.

*مؤلف مسئول