

Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community

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ABSTRACT: The impact of the invasive ctenophore *Mnemiopsis leidyi* on the zooplankton community of the Caspian Sea was quantified according to food consumption and other major physiological activities (i.e. respiration and reproduction), coupled with field data on population structure. The adverse effects of *M. leidyi* on the zooplankton community during the first years of the invasion were tremendous for the Caspian Sea compared to other regions affected by this ctenophore. The impact was highest in summer, due to high water temperatures and a population size structure in which juvenile ctenophores with mean lengths of 2 to 5 mm accounted for most of the population. During winter/spring, these ctenophores could consume the available stock of zooplankton in 3 to 8 d, whereas in summer consumption took only 1 d. The computed critical ctenophore biomass that does not affect (decrease) the abundance of mesozooplankton in the Caspian Sea is about 4 g m^{-3} (or 120 g m^{-2} , assuming most of the ctenophores occur in the upper 30 m layer). As is clear from the monitoring data, the *M. leidyi* biomass in summer in different regions of the Caspian Sea is far in excess of this value. Such a high abundance of ctenophores, if maintained, would constantly keep the non-gelatinous zooplankton biomass at very low levels, and, as a consequence, no recovery could be expected in the pelagic fishery.

KEY WORDS: *Mnemiopsis leidyi* · Feeding · Respiration · Reproduction · Predatory impact

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INTRODUCTION

The invasion of the Caspian Sea by the western Atlantic ctenophore *Mnemiopsis leidyi* (Agassiz) since the late 1990s is a demonstrative phenomenon of the threat of an alien species on the biodiversity and functioning of marine environments. This invasion has already caused enormous economic and environmental impacts on the Caspian ecosystem (Kideys 2002).

The Black Sea was the first impressive example of the damaging impact of this invasive species upon an ecosystem in general and upon the pelagic community in

particular. The accidental introduction and subsequent explosion of the ctenophore *Mnemiopsis leidyi* in the late 1980s resulted in not only a dramatic decrease in the abundance of almost all species preyed on by pelagic fish, but also in disappearance of some species (the copepod *Oithona nana*, the chaetognath *Sagitta setosa*) from the zooplankton community (Vinogradov et al. 1992, Kovalev et al. 1998, Shiganova et al. 1998, Kideys et al. 2000). *M. leidyi* competition with planktonic fish for zooplankton as a food resulted in a remarkable decline in the pelagic fishery during those years (i.e. 1988 to 1992; Kideys 1994, 2002).

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The possibility of this ctenophore invading other neighboring ecosystems, notably the Caspian Sea, was mentioned (Dumont 1995, GESAMP 1997). And, as expected, this species was reported to be in the Caspian Sea by November 1999 (Ivanov et al. 2000). Most probably *Mnemiopsis leidyi* was transported into the central or southern Caspian from the Black Sea or the Sea of Azov in the ballast waters of ships through the Volga-Don Canal (Ivanov et al. 2000).

Investigations of the new invader to the Caspian Sea in 2000 to 2001 showed that it was found almost everywhere, including the northwestern Caspian, where salinity exceeded 4 ppt (Shiganova et al. 2003). There was an increasing trend in the abundance of *Mnemiopsis leidyi* in 2001 compared to 2000. In August 2001, the average and maximum biomasses of *M. leidyi* over the entire middle and southern Caspian Sea were as high as 120 and 351 g wet weight (WW) m⁻², respectively, compared to a mean value of 60 g m⁻² in the summer of 2000 (Shiganova et al. 2001, Kideys & Moghim 2003).

Non-gelatinous mesozooplankton in the northern Caspian showed a 5-fold density decrease and a 6-fold biomass decrease in October 2001, compared with July when *Mnemiopsis leidyi* was absent; the most considerable decline was in the density of copepods (Shiganova et al. 2001). The most drastic decrease in the zooplankton biomass appeared to be in the southern Caspian, where the highest biomasses of *M. leidyi* have been observed.

The impact of *Mnemiopsis leidyi* on the Caspian Sea ecosystem is expected to be greater than in the semi-enclosed Black Sea, as the former is a completely enclosed basin and, hence, has a greater sensitivity to invasion stresses (Dumont 1995). Since *M. leidyi* is a voracious predator and a competitor with planktivorous fish for zooplankton, a significant decline in catches of the main small pelagic fish (i.e. the kilka *Clupeonella* spp.) has already been reported for some riparian countries (Kideys et al. 2001a,b). Within 2 yr (2000 and 2001) an almost 50% decrease in the kilka catches of Iranian fishermen has occurred, with a minimum of 15 million US dollars financial revenue loss (Kideys & Moghim 2003).

Determination of the food consumption and major physiological rates (i.e. reproduction and respiration) of *Mnemiopsis leidyi*, along with monitoring the population and its condition *in situ*, are very important in assessing the impact of this predator on the pelagic community. Here, we attempt to quantify the predatory impact of the alien ctenophore *M. leidyi* on the zooplankton community by studying its feeding and respiration rates in the laboratory, as well as its abundance, biomass and population structure in different regions of the Caspian Sea. In our calculations we

examined the case in which mesozooplankton is considered the main food source for *M. leidyi*, as this species has traditionally been considered to be a carnivore (Baker & Reeve 1974, Kremer 1979, Mutlu 1999, Finenko & Romanova 2000). Although there have been a number of experimental studies on the consumption of microplankton prey items by adult and, especially, by larval and post-larval *M. leidyi* (Stanlow et al. 1981, Stoecker et al. 1987, Costello & Coverdale 1998, Sullivan & Gifford 2004), their trophic impact on microplankton in the sea has not yet been estimated. An attempt was made recently by Sullivan & Gifford (2004), on the basis of their experimental values for the clearance rate of early stages of *M. leidyi* and Deason's (1982) ctenophore abundance of <10 mm length. This estimation showed the high clearing potential of *M. leidyi* larvae, which, at their maximum abundance, could potentially clear up to 60% of the water column per day. In addition, we attempted some preliminary calculations to estimate the predatory impact of small *M. leidyi* on the microplankton of the southern Caspian Sea.

MATERIALS AND METHODS

Chemical composition. Measurements of ctenophore chemical composition were carried out from September to October 2001 using samples from the inshore waters of the southern Caspian Sea (Khazerebad region in the Mazandaran province of Iran). Ctenophores were collected daily with a net (mesh size: 500 µm) and put in large aquaria (20 l volume). All the collected animals were visually checked to be undamaged and maintaining activity typical for their natural behavior. The specimens were delivered to the laboratory within 1 h, where they were sorted using sieves and hand-selection in accordance with their sizes. As a result, the ctenophores were divided into 10 size groups: 1, 2, 5, 10, 15, 20, 25, 30, 35 and 40 mm. Pooled samples of about 300 specimens from the small-sized ctenophores (1 to 2 mm), 10 to 40 specimens from the middle groups (5 to 30 mm) and 4 to 5 specimens from the large-sized ctenophores (35 to 40 mm) were taken in triplicate from each individual size group. After carefully removing the adhering water (on nylon mesh with absorbent paper below), the ctenophores were placed into hermetically closed vials and frozen at -20°C. The samples were stored in a freezer for up to 10 d and thawed at ambient temperatures before chemical fixation. From 1 replicate of 0.2 to 0.5 ml volume (0.2 to 0.5 g WW) separate subsamples were taken from freshly thawed homogenate for protein, lipids, carbohydrates and free amino acids (see Table 1). Protein was fixed by 3% TCA solution, lipids by 2:1 (v/v)

chloroform/methanol (Folch et al. 1957) and carbohydrates and free amino acids by 80% ethanol (Zaslavsky 1980).

Protein was measured with the Lowry method modified by Hartree using HSA as a standard (Hartree 1972). Amino acids (ninhydrine-positive substances) were measured by the Pochinok method with D,L- α -alanine as a standard (Kuzmenko 1975). Carbohydrates were determined by the Dubois method with D-glucose as a standard (Dubois et al. 1956). Total lipids were estimated by the method of Amenta (Amenta 1964, Clarke et al. 1992); the standard was triolein/cholesterol (1:1).

Organic matter content in the ctenophores was determined by summing all the organic constituents. Calorific value of the ctenophore tissues was calculated, using standard energy equivalents, to be 5.65 cal mg⁻¹ for protein, 9.45 cal mg⁻¹ for lipids and 4.10 cal mg⁻¹ for carbohydrates (Omori & Ikeda 1984).

These techniques of biochemical measurements have previously been evaluated (Clarke et al. 1992) and assessed to be reliable for determination of the proximate biochemical composition of gelatinous zooplankton.

Feeding experiments. The ctenophores utilized for feeding experiments were collected in the same region (i.e. Khazarabad) and using the same collection methods as those for chemical analyses; they were subsequently placed in 20 l aquaria. Within 1 to 2 h after sampling undamaged specimens were very carefully selected from the aquaria for use in the experiments.

The zooplankton prey specimens were collected daily by horizontal tows (3 tows each of 10 min duration) using a 100 μ m net, followed by filtration through a coarse mesh, basically to remove *Mnemiopsis leidyi*. Prey items consisted mostly of nauplii, copepodites and adults of the copepod *Acartia* sp. (mixture of *A. clausi* and *A. tonsa*). Seawater filtered through a 30 μ m mesh was added to the samples to bring the total volume of containers with zooplankton stock to 1000 ml. Prior to the experiments, the number of *Acartia* was counted 3 times in 10 ml subsamples from the stock container. To ensure an initial concentration of about 100 adult and copepodite *Acartia* per liter in each experimental container (volume of 5 l), we added a specific volume (ranging from 85 to 140 ml for the various experiments) that was calculated from the average concentration of *Acartia* in the stock container. The food concentration ranged from 0.8 to 2.1 mg l⁻¹ of *Acartia* (adults and copepodites) and from 0.07 to 0.45 mg l⁻¹ of nauplii (see Table 2). These concentrations were within the range of zooplankton biomasses in the Caspian Sea, which, in the summer of 2001, varied between 60 and 700 mg m⁻³, depending on the region (Shiganova et al. 2004). Experiments with the 3 size groups of *M. leidyi* (lengths of 4–5, 9–10 and 15–20 mm and average

wet weights of 0.04, 0.22 and 0.92 g, respectively) in individual containers, were carried out on 4 replicates at 21°C during a 6 h period (between 12:00 and 18:00 h in most of the experiments) in the dark, to avoid local aggregation of prey and predators. Because there are some diel variations in the *in situ* feeding rate of *M. leidyi* (Sergeeva et al. 1990), the timing of our experiments was chosen to obtain the mean daily consumption rate. For experiments, 10 ctenophores from the first size group and 5 ctenophores each from the second and third size groups were added to each container. Two containers with the same initial concentration of zooplankton, but without ctenophores, were used as controls. The container volume, density of predators and duration of the experiments were chosen to obtain a statistically significant feeding response. As has been shown for calanoid copepods, a decrease in the final prey abundance by 30 to 40% is optimal (Gifford 1993). The abundance of food items in our experimental containers decreased by about 40 to 45%, which is not much more than 40%, and we therefore do not believe that feeding activity changed in response to lowered food concentrations. No change occurred in the control vessels up to the end of the experiment.

After each experiment, ctenophores were removed from the experimental containers and water with zooplankton was filtered through a 30 μ m mesh to reduce the total volume to 200–250 ml. The numbers of different stages of *Acartia* (nauplii, copepodites and adults) were counted in every container. The average prey biomass (mg l⁻¹) was calculated from numbers and individual weights of each stage in the container. The clearance rate was computed by the difference between the control and the experimental containers at the end of the experiment using the equation:

$$CR = V \times (\log C_c - \log C_e) / 0.4343 \times N \times T$$

where CR is the clearance rate (ml ind.⁻¹ h⁻¹), V is the volume of the experimental container (ml), C_c and C_e are the prey concentrations in the control and experimental containers (ind. ml⁻¹), respectively, N is the number of *Mnemiopsis leidyi*, T is time (in hours) and 0.4343 is a coefficient used to change a natural logarithm into a base 10 logarithm. Regression analysis was performed to evaluate clearance rate as a function of body weight using the Microsoft Excel 98 software package.

The consumption rates of *Acartia* by *Mnemiopsis leidyi* were calculated from the clearance rate and mean abundance and from the individual weights of different stages (Stage I to V copepodites, males and females; Petipa 1957) in each container. The ration of copepod nauplii consumed was computed by taking into account their total number and mean wet weight (0.002 mg; Petipa 1957).

Upon completion of the experiment, *Mnemiopsis leidyi* specimens from each experimental container were measured and their weight was calculated from the equation $W = 0.0011L^{2.34}$, where W is wet weight in grams and L is length in millimeters (Kideys & Moghim 2003).

Respiration rate. The respiration rate of *Mnemiopsis leidyi* was measured at an ambient temperature of 24°C in the dark in 250 ml volume bottles having 1 to 240 specimens each depending on the ctenophore's size. *M. leidyi* length ranged from 1.2 to 38 mm and wet weight ranged from 0.0015 to 2.46 g. The experimental and control (without animals) respirometers were incubated for 14 to 15 h; the oxygen concentration decreased 10% of initial values.

Calculations of the metabolic rates were made from the measured difference in oxygen concentrations in the experimental and control bottles. At the end of the incubation period, oxygen concentrations were measured in subsamples of seawater transferred into 30 ml bottles of biochemical oxygen demand (BOD). Oxygen concentrations were determined by titration using the Winkler method (Omori & Ikeda 1984).

Reproduction. Forty-seven experiments were performed to study the reproduction rate of *Mnemiopsis leidyi*. Freshly collected adult specimens of different sizes were placed in the 2 l filtered seawater containers and kept in the dark for spawning at 22 to 25°C. Because spawning in *M. leidyi* takes place at night (Pianka 1974, Zaika & Revkov 1994), we examined and counted the number of fertilized eggs and early embryos after 24 h, to be sure that spawning was complete. After examination, eggs and embryos were put into incubators (containing filtered water) for hatching at the same temperature 22 to 25°C, and, after another 24 h, the number of hatched eggs was estimated.

Abundance, biomass and population dynamics. To obtain data on temporal distribution, the ctenophores were collected monthly from shallow waters near Khaz-erabad, Iran (southern Caspian Sea), during the period from July 2001 to September 2002 (A. E. Kideys & A. Roohi unpubl. data). The sampling was done using a net (500 mm mesh size, with a 50 cm wide mouth opening) during daytime by vertical hauls from a depth of 5 m to the surface. Upon retrieval, samples were immediately examined, the ctenophores were counted and their total lengths were measured to the nearest 1 mm; the size-specific abundance of ctenophores (in intervals of 10 mm) was estimated. Wet weight was calculated using the regression equation provided earlier in this section. The total biomass was computed as the sum of biomasses of all size groups.

In order to study the spatial distribution of the *Mnemiopsis leidyi* population in the northern, middle and southern Caspian, samples were taken during a cruise

in August 2001. The shallow northern region had a maximum depth of 24 m at its boundary with the middle Caspian and a minimum depth of 5 m close to the mouth of the Volga River. The surface-water temperatures varied from 26.6 to 30.9°C; salinity was 10‰ at the southernmost stations and 6‰ at the northernmost stations in the northern Caspian.

Hauls were obtained from 23 stations (Fig. 1). The sampling of *Mnemiopsis leidyi* was carried out using an ichthyoplankton net, with a 50 cm diameter mouth opening and a 500 mm mesh size. Samples were collected from near the bottom (5 to 24 m) to the surface in the northern Caspian and from 20 m depth (thermocline layer) to the surface in other regions. Simultaneously, mesozooplankton was sampled at 9 stations from 50 m depth to the surface: at 2 stations in the northern Caspian with Apshtein net (25 cm diameter, 95 µm mesh size), at 4 stations in the middle and at 3 stations in the southern Caspian with a Juday net (36 cm diameter, mesh size 112 mm). Samples were immediately fixed using 4% formaldehyde solution and analyzed using standard methods (Kiselev 1969).

Ctenophore biomass was calculated from the abundance and from the mean wet weight of each group. Wet weight was calculated using the regression equation given previously in this section. Total biomass was computed as the sum of the biomasses of all size groups.

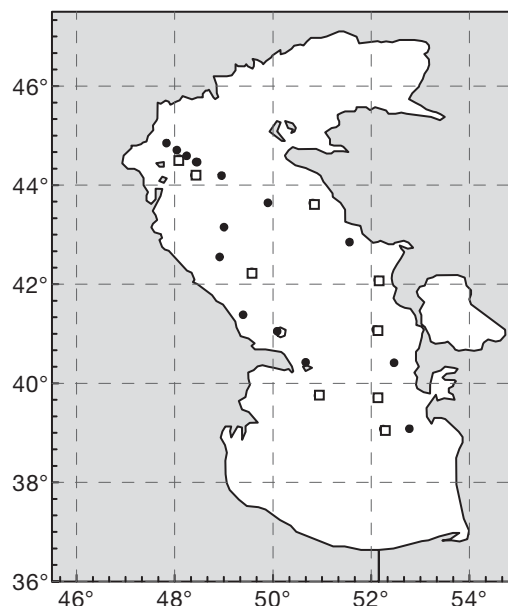


Fig. 1. Sampling stations in the Caspian Sea in August 2001 (□, zooplankton and *Mnemiopsis leidyi* sampling; ●, *M. leidyi* sampling only). The deepest stations were situated in the middle and southwestern areas, where depths varied from 35 to 735 m. Salinity in the middle and southern Caspian varied from 12.6 to 13.0‰; temperature varied from 23.1 to 27.1°C in the eastern part and from 23.0 to 27.5°C in the western part

Table 1. *Mnemiopsis leidyi*. Proximate biochemical composition in the Caspian Sea. N: number of samples analyzed

Component	Wet weight (mg g ⁻¹) (±SD)	Organic matter (%) (±SD)	N
Organic matter	1.31 ± 0.29	–	30
Protein	1.04 ± 0.21	79.6 ± 2.0	30
Lipids	0.14 ± 0.06	9.9 ± 2.2	30
Carbohydrates	0.09 ± 0.02	6.7 ± 1.1	30
Amino acids	0.05 ± 0.01	3.8 ± 0.5	30

Estimation of the predation rate by the ctenophore population was based on *Mnemiopsis leidyi* abundance, individual weights of the ctenophores in the population and the clearance rate measured in the laboratory for animals of various weights. The correction factor $Q_{10} = 2.2$ was used to compute the clearance rate at ambient temperature during the entire year (Winberg 1983).

The daily rations of the ctenophore population in energy units were calculated from the clearance rate and zooplankton biomass values, assuming 1 mg of zoo-

plankton wet weight to be equivalent to 1 cal (Vinoogradova 1964). To estimate the population biomass of *Mnemiopsis leidyi* in energy units, the monthly average biomass (in wet weight) for each size group in the population was multiplied by size-specific caloric value of *Mnemiopsis* (see Fig. 2f). The daily minimum food requirements were computed by taking into account respiration rate measured in the laboratory and total numerical abundance of ctenophores from the field data.

RESULTS

Chemical composition

The organic matter content of *Mnemiopsis leidyi* in the Caspian Sea ranged from 0.1 to 0.2% WW. The predominant biochemical constituent of the whole body tissue of the ctenophore was protein (76 to 82%), followed by lipids (7 to 13%), carbohydrates (5 to 8%) and free amino acids (3 to 5%) (Table 1). Variability in specific organic content and its constituents was mainly due to the size spectrum of the individuals analyzed (Fig. 2a–e). Over the whole size spectrum of ctenophores (1 to 40 mm), all organic substances in *M. leidyi* changed per gram wet weight by approximately 1/2. The components decreased especially sharply from 1 to 10–15 mm length specimens. In ctenophores with lengths of 10 to 40 mm, the specific organic content remained relatively stable.

The energy content of *Mnemiopsis leidyi* also changed with body size, decreasing almost 2-fold with increasing individual length in the range from 1 to 15 mm. Between 10 and 40 mm, the value (mean ± SD) was 6.80 ± 0.40 cal g⁻¹ WW.

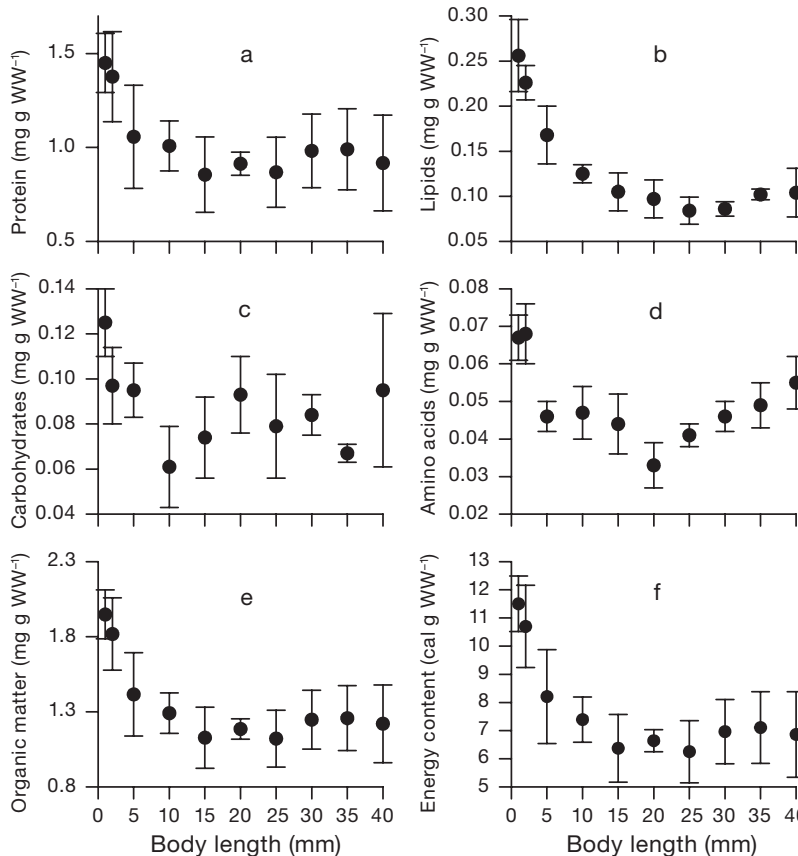


Fig. 2. *Mnemiopsis leidyi*. Proximate biochemical composition (per gram wet weight, WW): (a) protein, (b) lipids, (c) carbohydrates and (d) amino acids, as well as organic (e) and energy (f) contents in ctenophores of different sizes from the Caspian Sea (means ± SD)

Feeding rate

In our experiments, the clearance rate (±SD) of this species (the volume that *Mnemiopsis leidyi* have to sweep in order to consume a specific number of prey items) ranged from 32.5 ± 13.6 to 112.2 ± 59.0 ml ind.⁻¹ h⁻¹ when consuming adults and copepodites of *Acartia* sp.; the rate increased with increasing predator weight (Fig. 3). The relationship between the clearance rate (CR, ml ind.⁻¹ h⁻¹) and *M. leidyi* wet weight (g) can best be described by the following

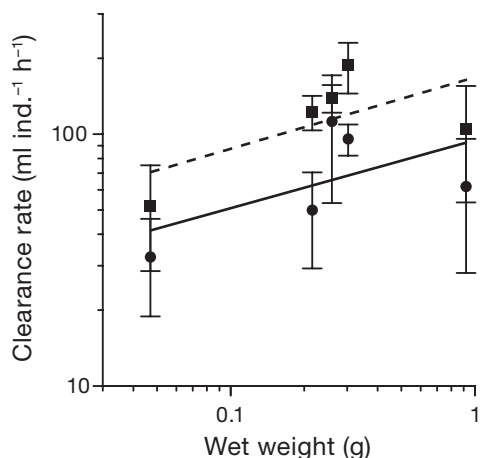


Fig. 3. *Mnemiopsis leidyi*. Relationship between clearance rate and wet weight (means \pm SD). Ctenophores were fed *Acartia* sp. copepodites and adults (●) or nauplii (■)

power function (Kremer 1976, Finenko & Romanova 2000), which displays a higher coefficient of determination compared to the linear function (Båmstedt et al. 2000):

$$CR_A = 94.55 W^{0.270} \quad r^2 = 0.670 \quad (1)$$

The clearance rate of ctenophores was about 2-fold higher when they fed on copepod nauplii:

$$CR_n = 168.08 W^{0.284} \quad r^2 = 0.397 \quad (2)$$

The clearance rates on copepodites/adults and nauplii of *Acartia* sp. in terms of per unit wet weight were 2.27 and 4.03 l g⁻¹ ctenophore WW d⁻¹. By using the wet weight (W , g) and volume (V , ml) equation of Kideys & Romanova (2001), $W = -0.249 + V \times 0.886$, these values corresponded to 2.49 and 4.45 l ml⁻¹ ctenophore d⁻¹, in terms of per unit volume of ctenophore (for comparative purposes with the literature).

Power coefficients of these 2 equations (0.270 and 0.284) were close to each other. Since we did not have data on zooplankton composition, Eq. (1) (with the higher correlation value) was used to calculate

the population clearance rate and estimate the predatory pressure of *Mnemiopsis leidyi* on mesozooplankton.

The weight-specific daily rations in the tested weight range of *Mnemiopsis leidyi* changed from 0.31 to 1.0% WW when they were fed on *Acartia* copepodites and adults at concentrations of 0.8 to 2.1 mg l⁻¹, but were only 0.08 to 0.33% WW at low nauplii concentrations of 0.07 to 0.45 mg l⁻¹. In terms of energy units, the difference between the 2 groups were even more notable: 32.7 to 122.3% in the group fed *Acartia* copepodites and adults and 9.9 to 38.6% of the body energy content in the nauplii-fed group (Table 2).

Respiration rate

The relationship between the oxygen consumption rate (Q , ml O₂ ind.⁻¹ h⁻¹) and the wet weight of *Mnemiopsis leidyi* (g) at 24°C (Fig. 4) is expressed by the equation:

$$Q = 0.0042 W^{0.776} \quad r^2 = 0.952 \quad (3)$$

The specific respiration rates of *Mnemiopsis leidyi* were weight dependent and decreased with increasing weight. Metabolic demands for ctenophores expressed as a percentage of body energy content ranged from 35 to 4% in the weight range from 0.001 to 10 g WW.

Reproduction

Mnemiopsis leidyi started to produce eggs in the Caspian Sea when it reached about 15 mm in total length, although in rare cases eggs were obtained from smaller ctenophores, even from a specimen of 12 mm length and 0.5 g WW.

There was a tendency for fecundity to increase with ctenophore size, though the most abundant size of reproducing *Mnemiopsis leidyi* was 20 to 30 mm in the Caspian Sea. The relationship between egg number in

Table 2. *Mnemiopsis leidyi*. Daily rations of ctenophores feeding on different stages of *Acartia* sp. Means \pm SD were calculated from 4 measurements

<i>M. leidyi</i> wet weight (g)	Copepodites and adults			Nauplii		
	Food concentration (mg l ⁻¹)	Specific daily ration (% WW)	Specific daily ration (% cal)	Food concentration (mg l ⁻¹)	Specific daily ration (% WW)	Specific daily ration (% cal)
0.303 \pm 0.053	2.0 \pm 0.5	1.04 \pm 0.30	122.3 \pm 31.9	0.08 \pm 0.02	0.08 \pm 0.02	9.9 \pm 2.8
0.216 \pm 0.018	2.1 \pm 0.4	0.36 \pm 0.12	42.5 \pm 12.9	0.32 \pm 0.04	0.33 \pm 0.01	38.6 \pm 1.4
0.920 \pm 0.345	1.0 \pm 0.2	0.31 \pm 0.17	32.7 \pm 29.1	0.45 \pm 0.1	0.09 \pm 0.04	11.1 \pm 5.1

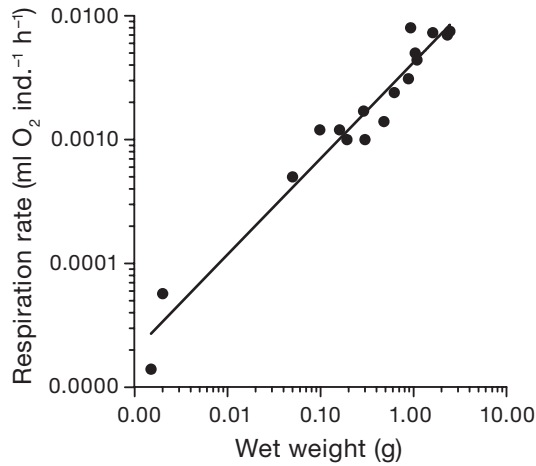


Fig. 4. *Mnemiopsis leidyi*. Relationship between respiration rate and wet weight at 24°C

a clutch (E) and *M. leidyi* length (L , mm) could be expressed by the power function: $E = 1.77 \times L^{1.96}$ ($r^2 = 0.46$; Fig. 5). The average fecundity of *M. leidyi* in the Caspian Sea was 906 ± 470 eggs (mean \pm SD) for freshly collected ctenophores from the examined length range.

Population dynamics and the predatory impact of *Mnemiopsis leidyi* on the zooplankton community

In the shallow waters of the southern Caspian, the abundance and biomass values of ctenophores were low (18 to 100 ind. m^{-2} and 0.8 to 4.5 $g\ m^{-2}$) during the winter and early spring (January to April), gradually increasing during summer and autumn; maximum

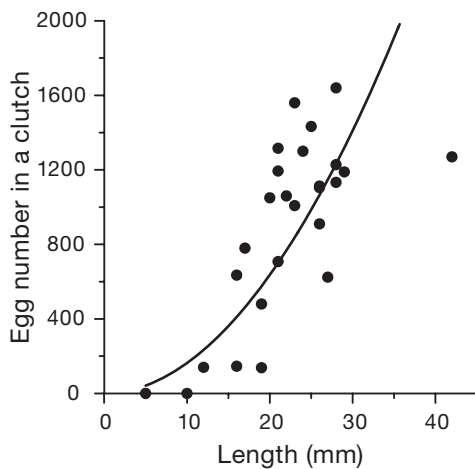


Fig. 5. *Mnemiopsis leidyi*. Effect of body length on egg number in a clutch in ctenophores from the Caspian Sea

abundances and biomasses were observed from August to October (Fig. 6a,b). Reproduction mainly occurred in the warmer period, reaching its maximum in July or August. Minimum mean weight of specimens (which could be due to either spawning or probably shrinking) in the population was observed in March (Fig. 6c). However, there was a notable biomass increase after this period. Somatic growth appeared to take place from July to August/September and from October to December (Fig. 6c), when maximum weights of specimens were recorded. The mean

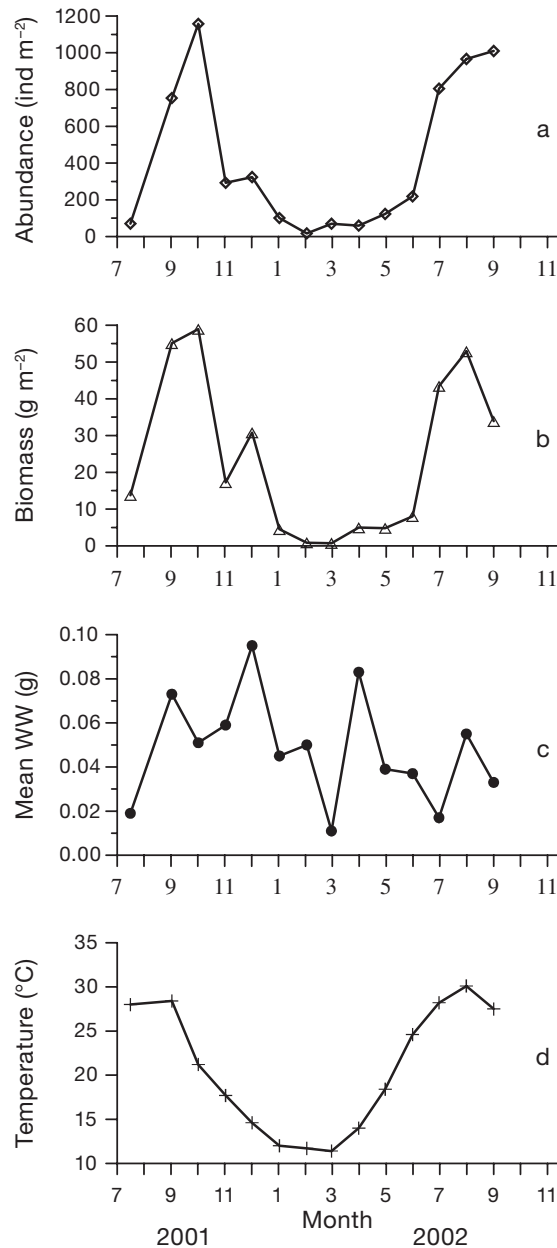


Fig. 6. *Mnemiopsis leidyi*. (a) Abundance, (b) biomass, (c) mean wet weight and (d) water temperature in southern Caspian waters in 2001 and 2002

weights of specimens from March to April increased almost 8-fold. If ctenophore growth took place at a constant relative rate and was exponentially related to time (Reeve & Walter 1978), the specific daily growth rate was 0.07 at temperatures between 11 and 14°C. After this intensive growth period, ctenophores began reproduction that was maintained until July. So periods of somatic growth alternate with propagation periods in *M. leidy* population dynamics in the southern Caspian Sea.

The largest size that the ctenophore could attain in the Caspian Sea was 65 mm. However, it is striking to see that the year round population was mostly composed of small individuals, with an average weight of 0.011 to 0.095 g and an average length of 2 to 7 mm. This size composition resulted in the very high predatory impact of the *Mnemiopsis leidy* population on zooplankton, exceeding 100% of the daily zooplankton biomass in the summer/autumn months, when the maximum development of the ctenophore population occurred (Fig. 7). In winter and spring, the predatory effect decreased due to the decline in ctenophore abundance, but it still remained high (29 to 12% daily) (Table 3).

Minimum food requirements (or maintenance rations) were calculated as the respiration rates of the *Mnemiopsis leidy* population. These were as high as 16% of the population biomass in summer at temperatures of 27 to 30°C and decreased to 4.6% in the winter months (Table 3). So, to grow in the summer months, *M. leidy* must consume daily rations of 16% of its own biomass.

As for the spatial ctenophore distribution in summer (August 2001), minimum abundance was observed in the northern Caspian, but biomass was high, due to the large sizes of *Mnemiopsis leidy* in that area (Fig. 1, Table 4). Probably, reproduction in that population had not yet started, in contrast to the populations in the

middle and southern Caspian, where maximum abundance but low biomass occurred. The mean individual weight of specimens in the middle and southern populations was 1 order of magnitude lower than that in the north. In the middle eastern and western Caspian, the individual weight of ctenophores was almost the same, but abundance and biomass were 1.5 times higher in the middle western.

The predatory impact of the *Mnemiopsis leidy* population was as high as 62% of the total mesozooplankton biomass daily in the middle western and southern Caspian; however, this effect was only half as strong in the northern and middle eastern Caspian (Table 4). Food provision of the *M. leidy* population was better in the middle eastern and southern Caspian (compared to the other regions), where the minimum specific food requirements of the population (Q/B , %) were close to the population daily rations (R/B , %), while in northern and western areas they were much higher than the rations.

DISCUSSION

Chemical composition

The proximate biochemical composition of the ctenophore *Mnemiopsis leidy* was studied earlier for the Black Sea (Anninsky 1994) and for the Caspian Sea populations (Yousefian & Kideys 2003). According to the Black Sea data, the organic matter content (mean \pm SD) for this species was $1.15 \pm 0.15 \text{ mg g}^{-1}$ WW and ranged from 0.98 to 1.55 mg g^{-1} within the ctenophore size spectrum from 3 to 68 mm. Within a similar size range (3 to 40 mm), an organic matter content of the Black Sea population was obtained of $1.12 \pm 0.16 \text{ mg g}^{-1}$ WW and did not differ ($p > 0.05$) from the values for the Caspian Sea population ($1.18 \pm 0.19 \text{ mg g}^{-1}$ WW). In Yousefian & Kideys' (2003) study for 10 to 20 mm ctenophores from the Caspian Sea, a very similar organic matter content was determined (1.09 mg g^{-1} WW). Thus, despite both different conditions in the seas (salinity, food availability, etc.) and different size spectra of *M. leidy* in the Black and the Caspian Seas, there are no strong biochemical differences between these ctenophores.

It is of interest to compare these data with the results of carbon, hydrogen and nitrogen (CHN) analyses of ctenophore tissues from Biscayne Bay (Florida, USA). The carbon content expressed as a percentage dry weight (DW) in *Mnemiopsis leidy* from this region changed between 1 and 13% in the size range of 1 to >40 mm (Reeve et al. 1989). If we assume ctenophore dry weight to be nearly 3.4% of wet weight at the typical oceanic salinity (34‰) (Kremer

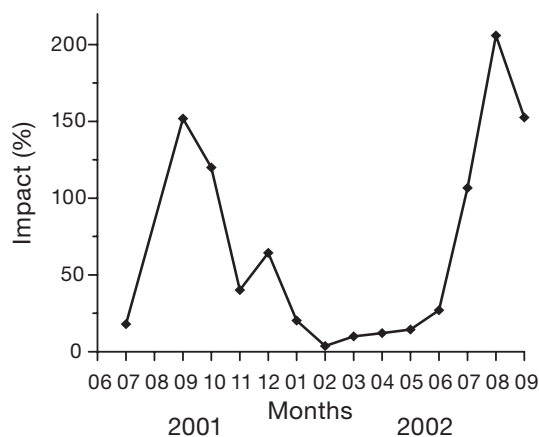


Fig. 7. *Mnemiopsis leidy*. Predatory impact of the population on mesozooplankton in the southern Caspian Sea in 2001 and 2002

Table 3. *Mnemiopsis leidyi*

		(g m ⁻³)	consumed daily	biomass
Autumn (Sep–Nov 2001)	22.5 ± 5.5	43.76 ± 23.05	103.9 ± 57.5	10.1 ± 4.3
Winter (Dec 2001–Feb 2002)	12.7 ± 1.3	12.08 ± 16.33	29.5 ± 31.4	4.6 ± 0.3
Spring (Mar–May 2002)	12.2 ± 2.2	3.52 ± 2.39	12.1 ± 2.2	5.8 ± 1.5
Summer (Jun–Aug 2002)	27.6 ± 2.8	24.79 ± 24.48	113.2 ± 89.6	16.1 ± 3.4

& Nixon 1976), *M. leidyi* carbon content would be in the range of 0.35 to 4.55 mg g⁻¹ WW. This means that the organic matter content (carbon × 1.9, Omori & Ikeda 1984) for the Biscayne Bay population would be equal to 0.67–7.58 mg g⁻¹ WW. So, for the body length range from 5 to 40 mm, organic matter content (0.67 to 1.33 mg g⁻¹) was very similar to that of the Caspian Sea population (1.07 to 1.37 mg g⁻¹). At the same time, values for the smallest specimens (1 to 4 mm) tend to be 3- to 4-fold higher in Biscayne Bay (~1.60 to 7.58 mg g⁻¹) than in the Caspian Sea (1.37 to 1.90 mg g⁻¹). Because of the lack of material for each size group, the data could not be tested statistically. But, to some extent, the discrepancies could be due to the exceptionally delicate structure of the smallest specimens and a food supply effect on the organic content of the ctenophore. Even for similar-sized *M. leidyi* specimens, the organic content could vary by at least 2-fold, depending on an individual's nutritional state (Reeve et al. 1989). On the whole, the similarity in organic content for *M. leidyi* of the Caspian and the Black Seas and of Biscayne Bay indicated that the metabolic rates of these ctenophores are not substantially different under the same conditions.

The general trend of a decrease in specific organic content and its constituents with size is a common feature in ctenophore species (Kremer et al. 1986, Reeve et al. 1989, Anninsky 1994). This is due to the non-homogeneous distribution of organic matter among the different tissues constituting the ctenophores' body bulk. Their body consists of regions of carbon-rich structures, such as ctenes, tentacles, muscles and gut wall, that are embedded in a very low carbon matrix (Reeve et al. 1989). The decrease observed in specific organic content with increasing *Mnemiopsis leidyi* size indicates that the ratio of low carbon matrix to wet weight increases gradually during somatic growth of the ctenophore. In fact, organic growth of *M. leidyi* occurs more slowly than it appears from the ctenophore wet weight increase.

Respiration, reproduction and feeding

The respiration rate of Caspian Sea *Mnemiopsis leidyi* is 1.5-fold higher than that of the Black Sea population (Anninsky & Abolmasova 2000, Finenko & Romanova 2000, Abolmasova 2001), which is probably a result of different food conditions (biomass of zoo-

Table 4. *Mnemiopsis leidyi*. Abundance, biomass, predatory impact, respiration and feeding rates of population in different regions of the Caspian Sea in August 2001 (Temp.: surface temperature; n: number of stations; N: abundance; B: biomass; W: mean wet weight of *M. leidyi* in the population; ZB: zooplankton biomass; PI: predatory impact; Q: respiration rate; R: daily ration). Values are mean ± SE

Region	Temp. (°C)	Depth (m)	n	N (ind. m ⁻³)	B (g m ⁻³)	W (g)	ZB (g m ⁻³)	PI (%)	Q (cal d ⁻¹)	R (cal d ⁻¹)	Q/B (%)	R/B (%)
Northern Caspian	26.9±0.6	5–24	7	106.1±38.7	42.9±10.1	0.592±0.150	31.95	28.1±8.2	25.3±6.0	9.0±2.6	4.9±1.3	1.9±0.6
Eastern middle	25.3±0.50	35–89	6	221.8±89.6	10.7±4.1	0.182±0.094	27.50	31.1±15.7	10.1±4.2	9.9±5.0	3.5±1.5	3.7±1.9
Western middle	25.1±0.5	35–725	6	364.4±93.1	45.7±13.4	0.187±0.079	27.50	61.5±15.1	34.0±8.3	19.6±4.8	8.9±2.1	5.8±1.6
Southern middle	26.4±0.4	35–735	4	389.7±67.4	21.0±2.0	0.056±0.005	31.73	61.9±10.2	20.4±2.2	19.8±3.2	7.0±1.8	6.8±1.3

plankton) and nutritional states of the ctenophores. A marked effect of food availability on the respiration rate of ctenophores has been shown (Kremer 1982, Finenko et al. 1995, Anninsky et al. 1998); the respiration rate of *M. leidyi* can change by a factor of 2, from low to high food concentration.

Mean fecundity of *Mnemiopsis leidyi* is lower in the Caspian Sea than in the Black Sea (906 ± 470 compared to 3350 ± 1385 eggs in a clutch, respectively, with a maximum of about 6200 eggs ind.⁻¹ d⁻¹; T. Shiganova unpubl. data). The maximal size of *M. leidyi* in the Caspian Sea (45 mm in Kideys & Moghim 2003, 65 mm in the present study) is also smaller than that recorded for the Black Sea, where this ctenophore could attain a length of 180 mm (Shiganova 1997).

A characteristic feature of the size composition of the *Mnemiopsis leidyi* population in shallow waters in the Caspian Sea (especially in the south) is the predominance of small ctenophores of <10 mm, similar to the results of Kideys & Moghim (2003). These small ctenophores made up 86% of the total abundance in August 2001. The low salinity of the Caspian Sea might be the reason for the smaller size of ctenophores, as well as their low fecundity.

The aim of feeding experiments was to calculate the *Mnemiopsis leidyi* clearance rate in order to estimate its impact on the zooplankton community in different regions of the Caspian Sea. It is known that one of the most important characteristics of lobate ctenophores is the proportionality between the consumption rate and food concentration over an extremely wide range of prey concentrations (Bishop 1968, Reeve et al. 1978, Gibbson & Painting 1992). In this case, the clearance rate does not depend on the prey density (Frost 1975, Kremer 1976, Monteleone & Duguay 1988, Finenko & Romanova 2000). In our feeding experiments of 6 h duration, the difference between initial and final concentrations was about 45%, but, in accordance with the above conclusion, the clearance rate was not affected by lowered food concentrations. In the range of food concentrations from 0.7 to 2.1 mg l⁻¹, the clearance rate was affected slightly by ctenophore weight and prey items: it was nearly twice as high on copepod nauplii as on copepodites and adults of *Acartia* sp. This difference was probably determined by the 2 different mechanisms of prey encounter demonstrated by *M. leidyi*, which function simultaneously. *M. leidyi* utilize 3 prey-catching mechanisms during the course of development from larvae to adult stages (Sullivan & Gifford 2004). From hatching until they reach ~4 mm in length, they feed using their tentacles trailing passively. At a body length of ~5 mm, *M. leidyi* larvae begin to develop small oral lobes and feed using a combination of tentaculate and lobate mechanisms to

capture prey. At ~6 mm, *M. leidyi* larvae are exclusively lobate and use the same prey-capture mechanism as adults, which allows predation on both macrozooplankton using primarily the oral lobes and on microzooplankton using the tentacles (Costello & Coverdale 1998, Waggett & Costello 1999). Using these 2 different mechanisms of prey encounter allows ctenophores to obtain food from 2 nutrition sources (meso- and microzooplankton).

The main factors affecting the ctenophore clearance rates are temperature, body weight and prey item. In the experiments, container size and probably consumer density or the ratio between resource and consumer abundances also seemed to be important factors (Hansson et al. 2001); many authors have noted that feeding of ctenophores in the laboratory is depressed in small-sized containers. Hence, when the laboratory measurements are compared to the field results, the consumption rate seems to be underestimated. However, it is important to evaluate the magnitude of this underestimation. The grazing rates of *Pleurobrachia pileus* were measured from the stomach content of ctenophores kept in containers of 1300 m³, and in controlled laboratory experiments in smaller containers adopting a wide range of ctenophore sizes and food concentrations. Comparison of these values revealed that, in spite of large variability, both methods resulted in a mean difference factor of 2 (Sullivan & Reeve 1982). The clearance rate of medium-sized *Mnemiopsis leidyi* in water volumes of 200 l increased by a factor of 3, as compared with 4 and 35 l containers (Gibbson & Painting 1992). So our calculations on *M. leidyi* consumption of the mesozooplankton community do not seem to be overestimated.

The estimated clearance rate for Caspian *Mnemiopsis leidyi* (2.49 to 4.45 l ml⁻¹ of ctenophore d⁻¹) feeding on copepods at similar temperatures is at the higher end of the range reported for this species from different regions of native waters (4.2 l ml⁻¹ of ctenophore d⁻¹ [Miller 1970] and 1.9 to 5.6 l ml⁻¹ of ctenophore d⁻¹ [Quaglietta 1987]; 0.9 to 3.0 l ml⁻¹ of ctenophore d⁻¹ [Kremer 1979] and 1.4 to 3.8 l ml⁻¹ of ctenophore d⁻¹ from the Black Sea [Finenko & Romanova 2000]). In a recent study of effects of low dissolved oxygen on zooplankton predation by the ctenophore *M. leidyi*, the values of 1.2 to 2.64 l ml⁻¹ d⁻¹ were found in air-saturated conditions (Decker et al. 2004). Average per capita clearance rate for the 11 size classes of *M. leidyi* larvae and post-larvae <10 mm feeding on assemblages of microplankton prey ranged from 0.216 to 5.5 l ind.⁻¹ d⁻¹ (Sullivan & Gifford 2004). Unfortunately, no ctenophore volumes were mentioned in the cited paper, and we have not been able to calculate the volume-specific clearance rate.

Population dynamics and predatory impact

There was a strong seasonality in the abundance of *Mnemiopsis leidyi* throughout the year (A. E. Kideys & A. Roohi unpubl. data). Whilst up to 1200 specimens m^{-2} were present during the summer months, the population fell to very low levels of about 50 specimens m^{-2} during several months in the colder period. This means that there is what could be called mass mortality and, then, renewal of the population in the following summer. Similar phenomena have also been observed in the Black Sea (Finenko et al. 2003). So, the ctenophore population shrinks and expands again every year from small number of specimens. In this case, the genetic diversity of the species should become constrained by a bottleneck (depending on the few specimens that remain). This is, indeed, confirmed by substantial similarity in the genetics of *M. leidyi* (both from the nuclear and mitochondrial sequence data) collected from different regions of the world (Bayha & Gaffney 2005).

Some previous studies showed an inverse correlation between the densities of crustaceans and gelatinous zooplankton, which led the authors to conclude that ctenophores control copepod biomass (Mountford 1980, Deason 1982, Vinogradov et al. 1992, Kovalev et al. 1998, Shiganova et al. 1998, Kideys et al. 2000, Hubareva et al. 2004). However, gelatinous predators ingesting <10% of the zooplankton biomass daily cannot cause a substantial decrease in its abundance and biomass (Burrell & Van Engel 1976, Kremer 1979, Larson 1987, Purcell & Nemazie 1992, Purcell et al. 1994). Higher ingestion values (>20%) will result in a sharp drop in prey abundance (Deason 1982, Matsakis & Conover 1991, Purcell 1992). In its native waters of Chesapeake and Narragansett Bays, the maximum predation potential of the *Mnemiopsis leidyi* population could be as high as 31% of the total zooplankton biomass daily, with average values of 5 to 10% (Bishop 1968, Kremer 1979). The daily predation rate was about 20% of the zooplankton standing stock in Narragansett Bay when larvae and juveniles were taken into account, and up to 56–91% of the total grazing was due to predation by the <1 cm size class of *M. leidyi*. Larval stages of *M. leidyi* had a disproportionate influence on predation relative to their biomass, because of their higher weight-specific clearance rate: it was 7-fold lower in adults ($0.052 \text{ l mg}^{-1} \text{ DW d}^{-1}$) compared to larval stages ($0.36 \text{ l mg}^{-1} \text{ DW d}^{-1}$) at 20 to 25°C (Deason 1982, Kremer 1979).

In Sevastopol Bay (northern Black Sea) from July to August 1995 and in open waters of the Black Sea during September 1996, 6 to 7 yr after the main *Mnemiopsis leidyi* bloom, daily grazing values by this ctenophore were still as high as 30 to 40% of the zoo-

plankton biomass (Anninsky et al. 1998, Finenko & Romanova 2000). In August/September 2000 and August 2001, after appearance of the invasive predator *Beroe ovata*, the *M. leidyi* population could only remove daily 4 to 6% and about 16% of the zooplankton biomass, respectively. During other periods of the year, the grazing effect on zooplankton was very low (<1% d^{-1}) due to the effectiveness of the top-down control of *M. leidyi* by *B. ovata* (Finenko et al. 2003, Kideys et al. 2004).

In the Caspian Sea, the effect of ctenophores on the zooplankton community during the first years of invasion was more destructive than in all other regions affected by *Mnemiopsis leidyi*. In the southern Caspian (i.e. Iranian waters), the effect was highest in summer, due to high water temperatures and to a population size structure in which juvenile ctenophores with mean lengths of 2 to 5 mm accounted for most of population. These ctenophores consumed the available stock of zooplankton during 3 to 8 d in the winter and spring months, but practically during 1 d in summer. In other regions (northern and middle Caspian), the *M. leidyi* pressure on the zooplankton community in August 2001 was also huge, and the food supply could be consumed in 1.5 to 3 d. The great predatory impact of *M. leidyi* is supported by zooplankton abundance and biomass values, which decreased in the Caspian Sea after *M. leidyi* appeared. In the northern Caspian, zooplankton abundance dropped by a factor of 5.3 and biomass declined 6-fold in October 2000, as compared to July of that year. Most of this change occurred in the Copepoda. In the middle and southern Caspian, the annual values of zooplankton biomass dropped by factors of 4 (middle Caspian) and 9 (southern Caspian), in comparison to those from 1998. In 2001, the effect on the zooplankton became much more decisive, and it was paralleled by a huge increase in the population size of *M. leidyi* (Shiganova et al. 2004).

Our calculations of the ingestion rate (daily rations) of the *Mnemiopsis leidyi* population were based on clearance rates from laboratory experiments and mean *in situ* zooplankton concentrations. A comparison of these calculations with the measured metabolic requirements revealed that ctenophores did not have sufficient food to sustain growth in any of the regions. Only in the middle eastern and southern Caspian, where respiration and ingestion rates were similar and displayed a high assimilation efficiency (0.8; Reeve et al. 1978), could the population possibly meet its minimum food requirements. In other regions, for example, in the middle western and especially in the northern Caspian, the ctenophores lack food. Miller & Williams (1972), interpreting published data for the Patuxent River Estuary, also showed that the zooplankton stock could only maintain the *M. leidyi* population for a very

short period (in most cases <1 d), so the main outcome of their study was to pose the question as to what ctenophores eat in the sea. It should be mentioned, however, that a number of factors affect the feeding rates *in situ*, e.g. prey selection, different digestion times of prey items, prey behavior (especially swimming speed and direction), prey vulnerability (ability to escape) and relative prey availability (prey density and distribution) (Ivlev 1961, Reeve & Walter 1978, Underwood et al. 2004). *In situ* prey densities are difficult or impossible to accurately measure when prey are patchy over small spatial scales. It appears that patches of *Acartia* sp. may reach densities up to 15 times greater than mean values (Larson 1987), and thus using mean zooplankton densities for ration calculations would result in distortions. However, no general principles exist yet to assess the effect of such factors, and their significance for ctenophores must still be determined.

It is of interest to compare the laboratory and *in situ* feeding rates, since laboratory-measured clearance rates have been extrapolated to field populations to predict predatory impact. *In situ* investigations of *Mnemiopsis leidyi* gut content, digestive time and ctenophore number were carried out by Larson (1987) in Link Port (Florida, USA) and by Zaika & Revkov (1998) in the Black Sea. These studies showed that copepods (both nauplii and adults) were the most important prey items, along with cladocerans (in the Black Sea), barnacle nauplii and bivalve veligers. In Larson's study, clearance rates of 5 cm *M. leidyi* specimens ranged from 0.1 to 1.3 l ind.⁻¹ h⁻¹, depending on prey taxon. These values were lower than those from laboratory experiments, but the difference was not statistically significant. We calculated clearance rates from Zaika & Revkov's (1998) data on *M. leidyi* gut content in the Black Sea in July 1992, by taking into account our data on digestion period (Finenko et al. 2005) and data on *M. leidyi* abundance during that time from Mutlu et al. (1994). The clearance rates of *M. leidyi* (190 g WW) varied from 2.08 to 9.17 l ind.⁻¹ h⁻¹ for different prey items (bivalve veligers, cladoceran *Pleopis polyphemoides* and copepods) and amounted to 0.5–2.2 g⁻¹ DW h⁻¹. These values were close to those obtained from laboratory experiments elsewhere (Kremer 1979, Miller 1970, Quaglietta 1987).

Predatory pressure of *Mnemiopsis leidyi* on *Pleopis polyphemoides* which was the main component of the zooplankton, varied from 8 to 63% (mean ± SD: 32 ± 26%) of their stock in different regions. Based on these data, we consider that results of laboratory experiments can be used to extrapolate for field populations. The weakness of such an extrapolation is that prey preference is not taken into account; however, food selectivity in *M. leidyi* is questionable. According

to our calculations based on Zaika & Revkov's findings, consumption of different prey items was proportional to their relative densities in the total zooplankton abundance.

Prey food (*Acartia tonsa* and/or *A. clausi*) used in our study consisted of nearly the only mesozooplankton species surviving in coastal waters of the southern Caspian Sea, especially after the endemic cladoceran species disappeared (Kideys et al. 2005). So, at present, these copepod species, whether preferred or not, are the main food source for *Mnemiopsis leidyi*. Thus, we are not sure if *Acartia* sp. is a preferred food of ctenophores; this quandary requires further and specially designed experiments (Underwood et al. 2004). Such studies would be very useful both for understanding why other mesozooplankton species (mainly cladocerans, but also some other copepod species) disappeared from the ecosystem and for better quantification of predation impact. Such an approach could also aid in explaining the decreased levels (and hence) impact of *M. leidyi* observed over the years, both in the Black Sea and the Caspian Sea. Similar trends in other cases of invasion tempt us to suggest that both impacted prey and competitors 'learn' (as suggested by Underwood et al. 2004), in this case, how to deal with the invasive species.

Besides zooplankton, *Mnemiopsis leidyi* probably has additional food sources. Stoecker et al. (1987) and Sullivan & Gifford (2004) discovered that phytoplankton, planktonic ciliates and other species of microplankton could be an important component of the diet of *M. leidyi*, especially for larvae and post-larvae with lengths <10 mm. In our study *M. leidyi* of <10 mm comprised 86 to 90% of the total ctenophore abundance during the periods of maximum ctenophore populations, i.e. 670 to 1040 ind. m⁻³ in September and October 2001 and 830 to 870 ind. m⁻³ in August and September 2002. To calculate the potential trophic impact of these small ctenophores on microzooplankton, we applied Sullivan & Gifford's (2004) equation (CR = 9.316 L + 4.541, where CR is clearance rate [ml ind.⁻¹ h⁻¹] and L is *M. leidyi* length [mm]) to our abundance data, supposing that the mean length of ctenophores is 5 mm. Our calculations showed that *M. leidyi* larvae can potentially clear daily from 83 to 128% of the water column in September and October 2001 and from 102 to 107% in August and September 2002. Thus, predation on microplankton can be so significant that predation pressure on mesozooplankton decreases.

Our hypothesis is supported by the estimations of potential daily grazing of microzooplankton and daily rations of ctenophore populations in Sevastopol Bay (the Black Sea) in August 2003. The calculations revealed that the daily grazing of microzooplankton was

as high as 23 to 25 % of its biomass, and daily rations of *Mnemiopsis leidyi* larvae on microzooplankton were close to those on mesozooplankton (0.7 to 29.3 % and 0.7 to 13.1 % of the energy content, respectively) (Finenko et al. in press). Possibly, using mesozooplankton and microplankton together as 2 food sources, the ctenophores were not only able to meet their metabolic requirements, but had excess energy for growth.

Assuming a daily body loss of 1 % of body caloric value, the starvation period that caused the largest specimen (65 mm, or 19.2 g) to shrink to 12 mm (or 0.37 g, being the onset of adult size found in the present study) could also be calculated as 394 d (by using the exponential decrease equation: $0.37 = 19.2 (1 - 0.001)^n$, where n is the number of days (Krebs 1972) at winter temperatures of 12.7°C (see Table 3). However, gradually increasing temperature and decreasing body weights will greatly shorten this theoretical maximum starvation period. Finding occasional food items during these periods will, however, extend the starvation period. This must be the strategy employed by *Mnemiopsis leidyi* to overcome the low food availability period in colder months.

Our overall results indicate that the warnings of several investigators that 'the impact of *Mnemiopsis leidyi* on the Caspian Sea ecosystem could be much worse than in the Black Sea' appear to be true. Assuming that the daily consumption rate of the *M. leidyi* population does not exceed 10 % of the zooplankton biomass and the mean clearance rate calculated from our feeding experiments is about $1.5 \text{ l ind.}^{-1} \text{ d}^{-1}$, the computed critical ctenophore biomass that would not affect (decrease) the abundance of mesozooplankton in the Caspian Sea is about 4 g m^{-3} , or 120 g m^{-2} if the majority of ctenophores occur in the upper 30 m layer (Kideys & Moghim 2003). As is clear from the monitoring data, the *M. leidyi* biomass in summer in different regions of the Caspian Sea is far in excess of this value. Such a high pressure exerted by this ctenophore would not allow zooplankton biomass levels to rise, and, as a consequence, no recovery can be foreseen with respect to the catch of planktivorous pelagic fishes until *M. leidyi* levels decrease substantially.

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