

THE ECOLOGICAL AND PHYSIOLOGICAL STATE OF THE CTENOPHORE
MNEMIOPSIS LEIDYI (AGASSIZ) IN THE BLACK SEA IN AUTUMN 1996

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Abstract. The survey was made in off-shore waters of the Black Sea near the Anatolian coast of Turkey during a research cruise of the R/V Bilim (24 Sept - 4 Oct 1996). The biomass of gelatinous macroplankton and the glycogen content in the body of the ctenophore *Mnemiopsis leidyi* were studied at 14 stations. Though the ctenophore still dominated the plankton in terms of biomass (average biomass $\pm$ standard deviation $276 \pm 115 \text{ g/m}^2$), this estimate was significantly lower than corresponding estimates obtained for the same months in recent years. A simultaneous reduction in the stock of small-sized fodder zooplankton and the large copepod *Calanus euxinus* indicates this case may be due to a general aggravation of trophic conditions for ctenophores. Data on the ctenophore's body glycogen content varied from 21 to 44 $\mu\text{g/g}$ fresh weight and accounted for $52.5 \pm 14.2\%$ of total polysaccharide content on average, the condition of *M. leidyi* observed during the conducted survey corresponded to that expected after a two-day fasting period. Tentative experiments have shown that metabolic rates of the examined ctenophores were notably reduced. The rate of oxygen consumption (R , $\mu\text{l O}_2 \cdot \text{ind}^{-1} \cdot \text{h}^{-1}$) was 1.7-1.8 less than that which would indicate a sufficient food supply; depending on the estimate of fresh body weight (W , g) at 12-14°C, it may be described by the following equation: $R = 2.50 W^{0.83}$.

Minimum metabolic demands of the entire population are evaluated as $91 \text{ cal} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, that is 40% of the energy which would normally be assimilated from small-sized fodder mesozooplankton. However, in autumn the mesozooplankton production sustains only half of the food requirements of the ctenophores.

1. Introduction

The recent introduction and subsequent explosion of the ctenophore *Mnemiopsis leidyi* caused drastic changes in the ecosystem of the Black Sea which were seen most clearly amongst planktonic communities [1,2]. In particular, the abundance of fodder

zooplankton was seen to decrease several fold. Some species which were common formerly such as *Oithona nana* vanished completely, whilst others, for example *Paracalanus parvus* appeared only in certain regions rather than throughout the Black Sea. Even the abundance of medusae which had earlier dominated pelagic waters decreased as a result of competition with the new ctenophore [3]. These and many other events which have recently developed in the pelagic area of the Black Sea [4,5] are indicative of the strikingly high impact of *Mnemiopsis leidyi*. Therefore the monitoring of the stock and the condition of *M. leidyi* along with its physiological state is very important to understand the impact of this species on pelagic communities. We endeavoured to do this using data of hydrological surveys conducted in autumn 1996. Among the main goals of this study was to look at the state of this ctenophore by employing such parameters as the body glycogen content.

2. Materials and methods

The data for the present study were obtained from both field and laboratory experiments. The field data were collected at 14 stations in off-shore waters along the Anatolian coast of Turkey (see Fig. 1 and Table 2 for the locations) during a research cruise of the R/V Bilim, between 24th September and 4th Oct 1996. At each station, sampling was performed via vertical hauls from the depth corresponding to the upper boundary of the hydrogen sulfide zone ($\sigma_t = 16.20$) to the surface; for gelatinous macrozooplankton using a Hensen net (mouth diameter 70 cm, mesh size 300 μm) was used and for mesozooplankton a Nansen net (mouth diameter 70 cm, mesh size 112 μm). The salinity and temperature of the water column were measured using a CTD probe (Seabird Electronics).

Mesozooplankton samples were fixed with a 4% buffer solution of formaldehyde and later analysed at the laboratory for species composition under a microscope with the routine technique [6].

The numbers of three gelatinous organisms (i.e. *Mnemiopsis leidyi*, *Aurelia aurita* and *Pleurobrachia rhodopsis*) were assessed following sampling. Their lengths were also measured to the nearest mm on board. The wet weight of the ctenophore was calculated using the equation proposed by Finenko et al. [7];

$$W = 1.074 L^{2.76},$$

where W is the wet weight in mg and L is the aboral length in mm.

For the carbohydrate content determination of *Mnemiopsis*, 4-6 individuals of similar length and biomass ($L = 13\text{--}16$ mm, $W = 1.3\text{--}2.3$ g) were combined into one sample. After freezing at -20°C and homogenisation, subsamples were taken from the integrated sample in order to determine the glycogen content (subsamples fixed with 30% KOH solution) as well as mono- and polysaccharides (fixed with 80% ethanol). For glycogen determinations the Shomody technique [8] was used and for carbohydrate evaluation the Dubois technique [9] was employed utilising D-glucose as a standard.

In order to understand the changes in the carbohydrate content and respiration rate of ctenophores exposed to varying food supplies, fasting experiments were carried out at the laboratory of the Institute of Biology for the Southern Seas (Ukraine) with freshly caught ctenophores (from Sevastopol Bay) comparable in size ($L = 12\text{--}13$ mm, $W \approx 1$ g) during October–November of 1994 and 1995. They were first placed in laboratory aquaria for a day where they were fed on natural zooplankton. Then they were transferred into filtered seawater for the onset of fasting. The carbohydrate content and respiration rates of 15 ctenophores were measured at 1-3 days intervals. The rate of oxygen uptake was obtained using closed respirometers and the subsequent estimation of oxygen content was achieved by the Winkler method [10].

3. Results and discussion

Three species of gelatinous macrozooplankton occurred in the samples (Table 1). *M. leidyi* was the dominant species amongst the predatory macrozooplankton in terms of both abundance and biomass: Its average biomass value was 3.6 times greater than that of *P. rhodopsis* and 8.6 times that of *A. aurita* biomass.

TABLE 1. Average abundance and biomass of gelatinous macrozooplankton in the Black Sea during September–October 1996. Standard deviations are given in parenthesis.

Species	Numbers (ind. m^{-2})	Biomass (g m^{-2})
<i>Mnemiopsis leidyi</i>	722 (± 200)	276 (± 255)
<i>Pleurobrachia rhodopsis</i>	138 (± 94)	75 (± 37)
<i>Aurelia aurita</i>	6 (± 1)	32 (± 7)

The spatial distribution of *Mnemiopsis* biomass is shown in Fig. 1 (and also in Table 2) where the greatest estimates were obtained at sts. 13 and 14 in the eastern ($382\text{--}506$ g m^{-2}) and at st. 7 in the central Black Sea (439 g m^{-2}). The lowest values ($146\text{--}152$ g m^{-2}) were found at the two nearshore stations (sts. 1 and 9) in the west off the Bosphorus (Istanbul) and east of Samsun (st. 9).

On the whole, the variation in the biomass of *M. leidyi* ($146\text{--}506$ g m^{-2}) was of moderate range and no significant differences were seen among the different sea regions namely the western, central and eastern areas, or between coastal and off-shore waters.

Moreover, biomass estimates did not differ significantly ($p > 0.05$) between cyclonic (sts. 4-7 and 12 average biomass 296 ± 107 g m^{-2}) and anticyclonic regions (sts. 1, 9, 13 and 14 average biomass 296 ± 178 g m^{-2}), or in the eddies and convergence zones (sts. 2, 3, 8, 10 and 11 average biomass 239 ± 74 g m^{-2}).

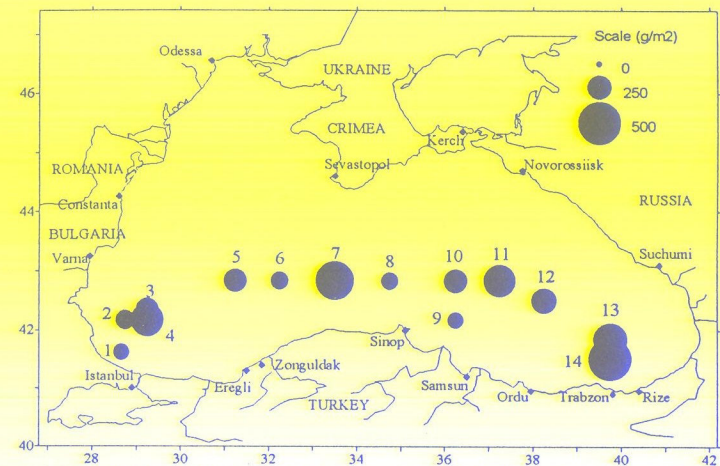


Figure 1. Distribution of *Mnemiopsis* biomass in the Black Sea in autumn 1996. Numbers denote stations.

TABLE 2. The biomass (g m^{-2}) and glycogen content ($\mu\text{g g}^{-1}$ wet weight [WW]) of *Mnemiopsis leidyi* in the southern Black Sea in Sept-Oct 1996. Glycogen content is also given as a percentage of total carbohydrates (TC) and polysaccharides (Ps).

Station	Position	Biomass (g m^{-2})	Glycogen content		
			$\mu\text{g g}^{-1}$ WW	%TC	%Ps
1	41 37N 28 40E	146	36.8 ± 10.3	38.4	45.7
2	42 10N 28 45E	192	28.8 ± 4.9	43.8	55.9
3	42 20N 29 15E	242	38.8 ± 3.6	28.5	31.5
4	42 10N 29 15E	370	24.1 ± 4.0	40.6	54.8
5	42 50N 31 15E	239	33.3 ± 3.4	31.0	37.1
6	42 50N 32 15E	170	32.4 ± 4.2	40.4	50.8
7	42 50N 33 30E	439	37.9 ± 5.1	61.8	85.7
8	42 50N 34 45E	159	43.6 ± 2.8	38.4	42.8
9	42 10N 36 15E	152	32.0 ± 5.4	42.4	55.2
10	42 50N 36 50E	250	20.8 ± 1.3	36.9	44.8
11	42 50N 37 15E	353	31.9 ± 5.6	55.1	74.7
12	42 30N 38 15E	264	29.8 ± 9.2	39.2	52.8
13	42 50N 39 45E	382	32.8 ± 3.4	37.1	43.4
14	41 30N 39 45E	506	34.0 ± 3.3	49.8	60.0

The overall average biomass value of *M. leidyi* ($256 \pm 115 \text{ g m}^{-2}$) evaluated during this investigation is close to the summer estimates obtained for the southern Black Sea during 1992-1993 [4], but is considerably lower than autumn estimates for the same period (Fig. 2). Decreases in the biomass of both small-sized fodder zooplankton and the

large copepod species *Calanus euxinus* since the early 1990's must have affected the food supply of the ctenophore *Mnemiopsis* over the entire Black Sea. It is difficult to point out the causes provoking such fluctuations in the planktonic community. Possible factors may be annual variations in hydrological and biotic conditions [1,2]. However, the drastic drop in the biomass of zooplankton that has been evident since the mass development of *M. leidyi* in 1989 allows the hypothesis to be proposed that the changes in the plankton are to a considerable extent due to the ctenophore pressure (predator-prey relationship). The data cited above suggest that in autumn 1996 the food base of *M. leidyi* was constrained within narrow limits. Besides predation, gelatinous organisms affect their environment by excreting mucus and nutrients (which may trigger the growth of bacteria and mixotrophic algae).

By grazing zooplankton abundantly, ctenophores conspicuously impoverish the environment. In turn, the chemical composition of ctenophores also display changes depending on the quantity of food intake. When there is sufficient food supply the metabolic rate of ctenophores increases as well as the activity of digestive enzymes [15]. The storage of lipids and glycogen is also increased [16]. Under conditions of starvation, although the chemical composition remains relatively stable, the content of low molecular compounds, such as free aminoacids and monosaccharides, is reduced more notably while the portion of protein in organic substances increases [17]. Glycogen, which is a polysaccharide, often provides the main source of accumulated energy in ctenophores [18]. In *M. leidyi* the content of proteins is within the range $800\text{-}1125 \mu\text{g g}^{-1}$, lipids $70\text{-}230 \mu\text{g g}^{-1}$ and carbohydrates $60\text{-}115 \mu\text{g/g}^{-1}$ wet weight, while the store of glycogen (up to $50 \mu\text{g g}^{-1}$) is four times larger than all lipid reserves, correlating positively with their total content and with the rate of protein metabolism too [19]. Earlier [20] it has been shown that glycogen content reliably characterises seasonal dynamics of the food supply of *M. leidyi* in the Black Sea. Recent studies confirm this. It was found that during the first day of fasting at $12\text{-}14^\circ\text{C}$ the relative glycogen content in the ctenophore's body de-creased by 20-30%, during a two-day fasting period the decrease amounted to 50%, and over a 10-day starvation trial the glycogen content has reduced by 3 fold (Fig.3A)

In autumn 1996 glycogen content in the body of *M. leidyi* varied from 21 to $44 \mu\text{g g}^{-1}$ wet weight or, using relative values which describe the state of ctenophores more accurately, glycogen accounted for 32-86% of total polysaccharides. Usually glycogen estimates were higher at stations where biomass estimates obtained for *M. leidyi* were also high ($r = 0.53$, $p < 0.05$; Table 2, Fig. 4). This may indicate a conformity between the somatic growth and formation of reserve compounds in examined animals, and, besides, a better food supply of ctenophores at greater biomass and high glycogen store in the body. Comparing biomass and glycogen content, the latter appears to be a finer indicator of food supply, describing changes in food conditions for shorter periods of time.

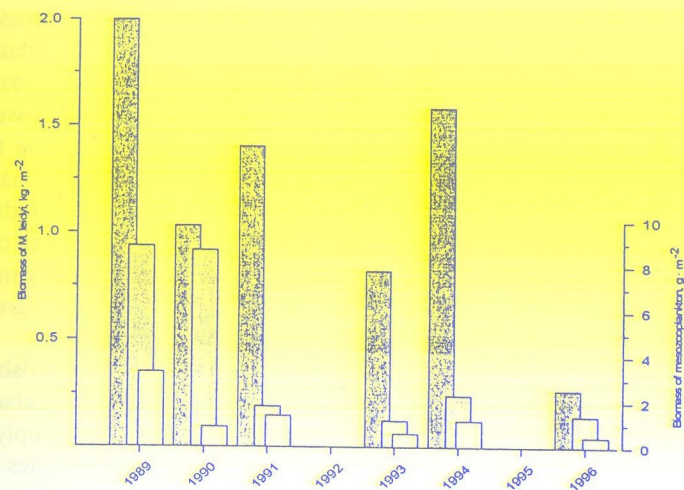


Figure 2. Long-term dynamics of the biomass of *Mnemiopsis leidyi* (shaded bars), *Calanus euxinus* (spot bars) and small-size food mesoplankton (empty bars) in autumn months in the Black Sea. References: data from 1989 and 1991, Vinogradov et al. [1]; data from 1990, Kovalev [11]; mesoplankton from 1993, Zagorodnyaya and Skryabin [12]; *M. leidyi* from 1993, Shiganova and Khoroshilov [13]; data from 1994, Kovalev et al. [14]; data from 1996, our data.

As for biomass, it is difficult to point out a specific location in which the glycogen content of *M. leidyi* would be markedly higher than average. No significant difference ($p > 0.05$) manifested itself between the glycogen content of ctenophores taken from near the Bosphorus, central or the eastern Black Sea and likewise of organisms sampled from the cyclonic and anticyclonic gyres and convergence zone. In addition ctenophores from coastal stations were similar to those from open sea waters ($p > 0.05$). Stations in which the glycogen content of the sampled ctenophores varied erratically provided evidence of considerable changes in the trophic conditions of *M. leidyi* during the study period. The only exception was st. 7 where the maximum glycogen content occurred (86%) and where plankton were in abundance [21]. The cruise report also states that at this location a surprisingly high biomass (up to 3 g m^{-2}) of mesozooplankton including *Cladocera* (0.5 g m^{-2}) was present.

Earlier, in 1991-1992, a greater expanse of the Black Sea had been providing the ctenophores with a good food supply. *M. leidyi* sampled from near the Caucasus coast in June 1991 (R/V Prof. Vodyanitsky, 33rd research cruise) and the Kerch Peninsula and near the southern coast of the Crimea in July 1992 (R/V Prof. Vodyanitsky, 37th research cruise) were seen to be in good condition. On average, the content of glycogen

(as a % of total carbohydrates) in the ctenophore *M. leidyi* was $50.1 \pm 6.0\%$ in 1991, $46.2 \pm 7.9\%$ in 1992 and $41.7 \pm 8.8\%$ in 1996. Data obtained in 1996 considerably differ from those for 1991 ($p < 0.01$), while distinctions between 1996 and 1992 data sets can not be deemed significant ($p > 0.05$). As the studies were conducted in different areas and during different months, we may assume only with caution that the gradual reduction of the glycogen content of *M. leidyi* seen in recent years is coupled with the increasing variability of ctenophore glycogen content over the entire Black Sea. The latter can be deduced from a comparison of average estimates with the dispersion values 36.0, 62.4 and 77.4%, respectively [22].

Converted to polysaccharides, the average glycogen content of *M. leidyi* in autumn 1996 was $52.5 \pm 14.2\%$. Compared with data obtained from our experiments in autumn 1994 (Fig. 3A), this value is characteristic of ctenophores which have undergone a 2-day fasting period. According to this, the condition of *M. leidyi* conformed to the food supply available during the present investigation at two stations only, namely sts. 7 and 11. Outwith these examples the ctenophores apparently did not receive the amount of food required to maintain normal metabolism. The store of glycogen in their bodies was equivalent to that expected after 1-8 days of fasting. These results should not be treated as unexpected. According to direct evaluation of the nutrition of *M. leidyi*, as many as 90 % of the ctenophore population may be surviving in food conditions causing stress [23].

In such cases the metabolic rates of *M. leidyi* are considerably reduced (Fig. 5).

If in freshly captured well-fed ctenophores (the index of fullness corresponding to the small mesozooplankton concentration $50\text{--}60 \text{ ind. l}^{-1}$ [6]) the rate of oxygen consumption (R , $\text{mcl O}_2 \cdot \text{ind}^{-1} \cdot \text{h}^{-1}$) dependent on raw weight (W , g) is described by the equation

$$R = 6.73 W^{0.83} \quad (r = 0.988; p < 0.001; t^\circ = 22^\circ\text{C}), \quad (1)$$

then for ctenophores surviving a 3-day fasting period, the equation is

$$R = 4.57 W^{0.83} \quad (r = 0.957; p < 0.001; t^\circ = 22^\circ\text{C}). \quad (2)$$

Hence, values of slopes of both equation are the same, the rate of metabolism of *M. leidyi* decreases 1.5 fold at a given temperature. More details have been learnt about the dynamics of oxygen uptake in ctenophores fasting for 10 days at $12\text{--}14^\circ\text{C}$ (Fig. 3B). In that case the rate of oxygen consumption in individuals with a fresh weight of about 1 g reduced eventually to a third of the initial rate, and decreased by nearly two-fold after three days of starvation. It is easy to see that the latter estimate ($2.29 \mu\text{l O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) agrees well with that computed for the fasting ctenophores applying the above equation and taking into account $Q_{10} = 2.2$ ($2.25 \mu\text{l O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$). Then, given the tendency towards a lower metabolic rate developed by fasting ctenophores,

$$R_1 = 2.89 D^{-0.21} \quad (r = 0.967; p < 0.001; t^\circ = 12\text{--}14^\circ\text{C}), \quad (3)$$

where R_1 is oxygen consumption intensity ($\mu\text{l O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) and D the duration of fasting (d), for a 2-day fasting for *M. leidyi* at $12\text{--}14^\circ\text{C}$ the equation is as follows:

$$R = 2.50 W^{0.83} \quad (4)$$

Metabolism evaluated using equation (4) is 1.7-1.8 fold less than that of well-fed ctenophores. Similar data ($2.5\text{--}2.7 \mu\text{l O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) related to oxygen uptake in *M. leidyi* have earlier been reported, in particular, for 1-2 day fasting periods at $10.3\text{--}15.8^\circ\text{C}$ [24].

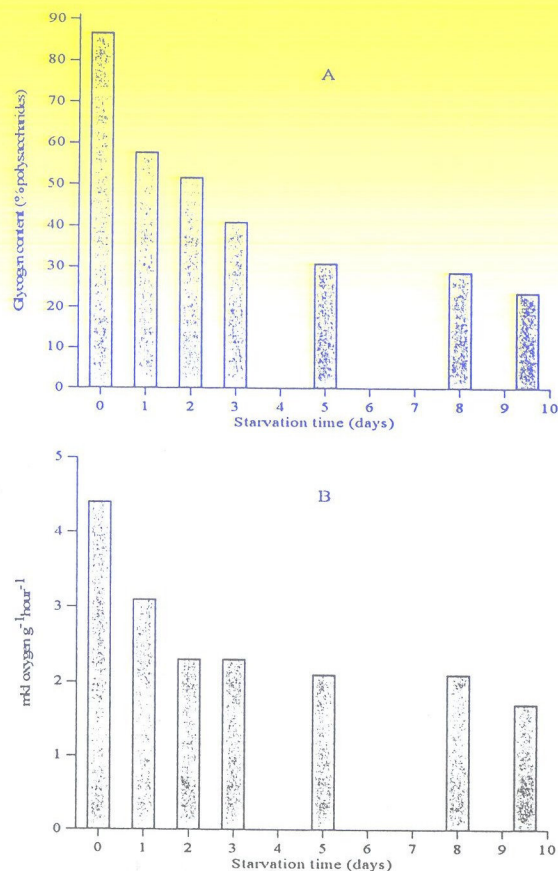


Figure 3. Dynamics of the glycogen content (A) and the oxygen consumption intensity (B) in ctenophores *Mnemiopsis leidyi* under the starvation experiment (autumn 1994).

Occurring in the warm water layer and thermocline, at an ambient temperature as moderate as $12\text{--}14^\circ\text{C}$ ctenophores display metabolic rates very close to those in autumn. During our studies, the population of *M. leidyi* comprised ctenophores of between 1 to 60 mm long, young individuals (1 to 5 mm in length) contributed up to 50% of the total numbers. At $12\text{--}14^\circ\text{C}$, at the cited size range (average body weight 0.496 g), the biomass amounting to 276 g m^{-2} and metabolism corresponding to that expected after a 2-day

fasting period, (see equation 4) the metabolic requirements of this population were estimated as $18.7 \text{ ml O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. Or, given the generally accepted value of the calorific equivalent of consumed O₂ as being equal to 4.86 cal per ml O₂ [10] the estimate is $91 \text{ cal} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. In ctenophores inhabiting near-surface waters, metabolic demands may approximate $150\text{--}160 \text{ cal} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ at a temperature of about 20°C .

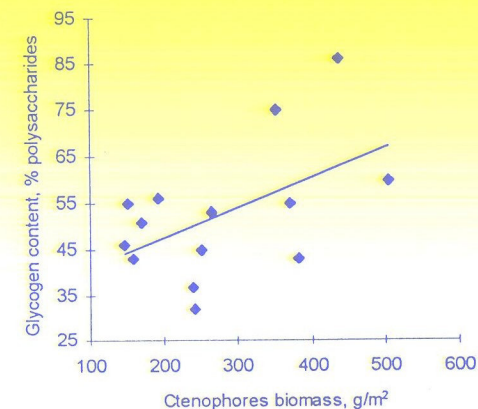


Figure 4. Relationship between glycogen content (% polysaccharides) and biomass (g m^{-2}) in the ctenophore *M. leidyi* in the Black Sea in Sept-Oct 1996.

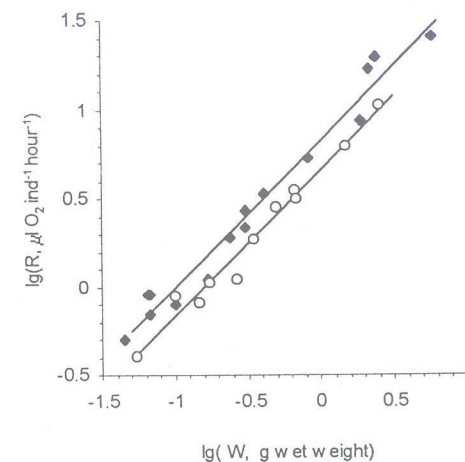


Figure 5. Weight-specific respiration rates in fed *M. leidyi* at the good trophic condition (1) and after 3-days fasting (2). $T^\circ = 22^\circ\text{C}$. Autumn 1995.

It is interesting to compare those food requirements with the food supply actually available in the sea.

In autumn 1996, mesozooplankton composition was typical for the season, showing prevalence of the copepod *C. euxinus* and the luminous protozoan *Noctiluca miliaris*. Among the small copepods, *Pseudocalanus elongatus* and *Acartia spp.* prevailed (Table 3).

M. leidy is known to feed on a wide range of food items which include zooplankton as the main food component [23, 25], followed by detritus and phytoplankton [26] and dissolved organic matter [3]. However, if their diet was restricted solely to phytoplankton and detritus this would lead to extinction of the ctenophores [1, 26]. Besides, it is still unknown as to what extent *M. leidy* shows selectivity in its diet, in particular, for different varieties of mesozooplankton. It has been stated that ctenophores do not eat *N. miliaris* [3] or eat but negligibly [2]. Another food supplement may be the copepod *C. euxinus* of which some spatially isolated from the ctenophore population [1]. *Calanus* is consumed less than small copepods [25]. Thus, we may conclude tentatively that the main food item for *M. leidy* is small mesozooplankton which is a prey item usually found in the gastric cavities of feeding ctenophores [23, 25]. It is the small mesozooplankton which have been consumed most dramatically by the developing ctenophore population [1, 27].

A suggested relationship between the condition of ctenophores and the availability of food has revealed a tendency towards the food preference for small forage mesozooplankton. Of all tested combinations (Table 4), the correlation between the glycogen content of *M. leidy* and the concentration (abundance) of potential food was the strongest ($r = 0.46$) if the food items consisted of small copepods (excluding stages V-VI of *C. euxinus*) combined with Cladocera. When the food supply comprised of only copepods or Cladocera alone, the correlation was not as strong ($r = 0.13$ and 0.44 , respectively). The addition of stage VI of *C. euxinus* to the main fodder (consisting of small copepods and Cladocera) also reduced the correlation to $r = 0.41$. Certainly, the given relationships are not rigid ($p > 0.05$), given that spatial distribution of zooplankton is patchy, the migrating part of the *C. euxinus* population varies in composition as well as other species dependent on the area of the sea. It could be suggested that impact of the *M. leidy* predation is stronger on younger (I-IV) stages of *C. euxinus*. That might explain the fact that in 1989-1990 when the outbreak of *M. leidy* took place, the biomass of the copepod *C. euxinus*, unlike that of small mesozooplankton, was remained at its usual level and later began to fall in 1991 [1, 27].

The biomass of small mesozooplankton averaged for all stations was estimated as 460 mg m^{-2} , or given the average calorific content of 0.65 cal mg^{-1} wet weight [28], the value was 299 cal m^{-2} . With the food assimilation estimate being 0.8 for ctenophores [29], the food efficiency of mesozooplankton is 239 cal m^{-2} . Correspondingly, the daily energy demand of the *M. leidy* population accounts for 40% of total energy which may be potentially assimilated from consumed small mesozooplankton. In other terms, given the current metabolic demands, the ctenophores would consume the available stock of fodder zooplankton in no more than 3 days. If 30% of the *C. euxinus* stock were added

TABLE 3. The composition of mesoplankton of the Black Sea in autumn 1996.

Species	Biomass, (g m^{-2})	Numbers, (ind. m^{-2})
<i>Calanus euxinus</i> *	1.380	11049
<i>Pseudocalanus elongatus</i> *	0.120	10683
<i>Acartia genus</i> *	0.099	13498
<i>Oithona similis</i>	0.028	8114
<i>Noctiluca miliaris</i>	0.655	7735
<i>Sagitta setosa</i>	0.063	269
<i>Oicopleura dioica</i>	0.012	639
Others	0.013	1217
Total	2.494	58878

* including eggs and nauplii

TABLE 4. Potential food concentration for the ctenophore *M. leidy* in the water column from the lower depth of the thermocline up to the sea surface

Station	Food concentration* (mg m^{-3})			
	I	II	III	IV
1	-	-	-	-
2	-	-	-	-
3	5.2	3.8	9.0	10.4
4	8.0	3.7	11.7	12.3
5	7.6	4.2	11.8	13.7
6	13.0	2.5	15.5	18.1
7	6.1	11.6	17.7	19.5
8	5.9	1.8	7.7	9.6
9	9.7	2.7	12.4	13.6
10	3.8	0.5	4.3	4.7
11	9.2	0.5	9.7	11.2
12	9.6	1.0	10.6	12.1
13	8.3	0.5	8.8	10.2
14	5.5	0.8	6.3	6.8

* I- small-size Copepoda; II- Cladocera; III- small-size Copepoda and Cladocera; IV- small-size Copepoda and Cladocera, and 10% of the *C. euxinus* female biomass

to the food ration [4], the situation would improve a little bringing a total of 469 cal m^{-2} but would not solve the problem of food provision for the ctenophores as in this case the food supply would be depleted in 5 days.

Assuming that the average coefficient for the specific daily production of mass mesozooplankton species of the Black Sea is 0.15 [30] and the estimate of small-sized food mesoplankton equals 299 cal m^{-2} , their production in autumn would approximate $45 \text{ cal} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. Bearing in mind that the above value is calculated disregarding predators pressure from other components of the plankton, that amount of production would provide only half the minimum food requirement of the *M. leidyi* population. If so, the ctenophore biomass would be expected to reduce as is usually observed during the autumn months. By early winter the drop is even more pronounced [31].

Our calculations (see Equation 1) show that the food requirement of the ctenophore population with a biomass of about 276 g m^{-2} would be no less than $250 \text{ cal} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, at $t^\circ = 22^\circ\text{C}$, given a better food supply (positive estimates of the efficiency of food assimilation for growth). The resulting estimate is comparable with the total and efficient (uptaken) energy values of total small-sized food zooplankton (239 and $299 \text{ cal} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, correspondingly). Considering the energy value calculated for the biomass of the ctenophores, 1.8 kcal m^{-2} (the calorific content of raw matter 6.5 cal g^{-1} [19], it is easy to deduce that small-sized food zooplankton alone cannot satisfy the metabolic demands of the *M. leidyi* population. Possibly, our computations underestimate the numbers of zooplankton and overestimate the metabolic/energy expenditure of ctenophores which may in fact be less, due to vertical migration to the thermocline. However, a very probable hypothesis is that computation techniques presently available do not provide actual evaluation of the share contributed by alternative food sources like microzooplankton, dissolved organic matter and detritus. In particular it has been reported [32] that many planktonic coelenterates, which are morphologically close to ctenophores, develop a tendency to feed on plant debris for survival in fasting conditions.

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A BIOCHEMICAL PROVISION FOR

Abstract. Some food provision (September 1996. To *Calanus euxinus* phyll-a of the $r=0.79$, $P<0.1$) glycogen content

Comparison of ces used was of pycnocline is lo content than the is located at 160 trients (phosph and thereby the

Long-term *sprattus* revealed species. As a re of this fish had dices may be su heterotrophic sp