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Chemical composition, respiration and feeding rates of the new alien ctenophore, *Beroe ovata*, in the Black Sea

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Abstract

Maximum daily rations of the ctenophore *Beroe ovata* Brugière and predatory impacts on the *Mnemiopsis leidyi* A. Agassiz population were estimated via digestion time, prey biomass and predator and prey density in Sevastopol Bay and adjacent water regions. Digestion times ranged from 0.5 to 5.2 h and depended on the prey/predator weight ratio. Overall, the mean daily ration was 45% of *B. ovata* wet weight. Preliminary conclusions are given on the *B. ovata* population as an effective control of the *M. leidyi* population and on the dynamics and structure of the planktonic community as a whole.

Introduction

The massive population explosion of the invading ctenophore, *Mnemiopsis leidyi* at the end of the 1980s led to tremendous changes in the Black Sea ecosystem, which was already suffering due to eutrophication. Feeding voraciously on zooplankton as well as on fish eggs and larvae, *Mnemiopsis* was one of the most important reasons for the adverse changes in the planktonic community structure (Vinogradov et al., 1989; Gordina & Klimova, 1996; Zaitsev, 1998; Kovalev et al., 1998; Shiganova et al., 1998; Kideys et al., 2000; Purcell et al., 2001) and pelagic fish stocks of the Black Sea and adjacent seas (Volovik et al., 1991; Kideys, 1994; Niermann et al., 1994; Kideys et al., 1999). The lack of natural predators feeding on *M. leidyi* resulted in temperature and food conditions being the only factors apparently controlling its population in the Black Sea (Purcell et al., 2001). Such an unprecedented impact caused this alien species to attract great attention from the scientific community, so much so that UNEP intervened to develop a strategy and to recommend measures to overcome the ctenophore and prevent similar invasions in other parts of the world, using the Black Sea region as a key example (GESAMP, 1997). One of the strategies recommended was the introduction of a predator to the Black Sea; along with the American butterfish, *Peprilus triacanthus*, ctenophores in the genus *Beroe* emerged as the best candidates for reducing the high biomass levels of *Mnemiopsis*.

Interestingly, by October 1997, the ctenophore, *Beroe ovata*, had already appeared in shallow waters of the Black Sea (Konsulov & Kamburska, 1998; Zaitsev, 1998), in September 1998 in the Sea of Marmara (A. E. Kideys, unpublished data) and in August–September 1999 in Sevastopol Bay and adjacent water regions as well as in the northeastern Black Sea (Finenko et al., 2000, Shiganova et al., 2000, Vostokov et al., 2000, Vinogradov et al., 2000). As in the genus *Mnemiopsis* (Order Lobata), species of *Beroe* spp. (Order Beroida) are difficult to differentiate (see Mills et al., 1996 for review), and *Beroe* in the Black Sea was identified either as *B. ovata* (in Konsulov & Kamburska, 1998; Shiganova et al., 2000, 2001), or as *B. cucumis* Fabricius (in Zaitsev, 1998). Although here it is cited as *B. ovata*, it could just as well be *B. cucumis*. The main criterion for distinguishing the two species is the presence of connection (i.e. anastomosing) of the meridional channels; whilst they are not joined in *B. cucumis, B. ovata* have anastomosing meridional channels (Gosner, 1971; Mianzan, 1999).

Apparently both structures are observed in the Black Sea. It is worth noting that *Beroe ovata* already had been reported from the Sea of Marmara by October, 1992 (Shiganova et al. 1994).

All previous studies suggest that species of *Beroe* almost exclusively feed on other ctenophores (Kamshilov, 1960; Greve, 1970; Swanberg, 1974; Harbison et al., 1978; Matsumoto & Harbison, 1993; Mianzan, 1999). In studies of predator–prey relationships of beroid and lobate ctenophore species, both Greve (1970) for *B. cucumis* vs *Bolinopsis infundibulum* (O. F. Müller, 1776) and Swanberg (1974) for *Beroe ovata* vs *Bolinopsis vitrea* (L. Agassiz, 1860) claimed that the feeding interactions among ctenophores form an ecological feed-back system that also affects other compartments of the planktonic community. Within each feed-back system, quantitative predator–prey relations are direct; both members of the system affect each other immediately. While these primary effects are more obvious and immediate, evaluation of secondary, tertiary etc. effects on other compartments of the ecosystem will take a longer time and effort to assess. By analyzing the long-term distribution of *M. leidyi*, it has already been observed that the biomass of this ctenophore has been decreasing since the appearance of its predator *B. ovata* in the southern Black Sea (Kideys & Romanova, 2001).

Here, we attempt to quantify the predation impact of the new alien ctenophore *B. ovata* on the earlier invading *M. leidyi* population by studying digestion and respiration rates of *B. ovata* in the laboratory along with abundance, biomass and population structure of both ctenophores from the shallow waters of the Black Sea.

Methods

Abundance, biomass and population structure

Ctenophores (*M. leidyi* and *B. ovata*) were collected by vertical tows (10–0 m) with a Bogorov-Rass net (500 μm mesh size and 80 cm diameter) at 11 stations in Sevastopol Bay and adjacent water regions during September–November 1999 (Fig. 1). Simultaneously, with the same net, horizontal tows were performed from the surface (0–0.5 m). The net filtered 77.2 m^3 of seawater in each 5 min horizontal tow. Immediately upon retrieval, samples were examined, ctenophores were counted and their lengths (total length of *B. ovata* and oral-aboral length of *M. leidyi*) were measured to the nearest 1 mm without removing them from the water-filled jars. For the estimation of length-weight equations, 22 *B. ovata* and 230 *M. leidyi* were weighed individually on a balance to the nearest 0.01 g and simultaneously length measurements were taken.

Chemical analysis

For the analysis of chemical composition as well as respiration and feeding experiments, ctenophores were collected gently with hand-held jars from the bay shore. Only undamaged and active animals were used for the experiments. In order to determine the dry weight of *B. ovata* 17 newly caught ctenophores were individually weighed to the nearest 0.01 g and then dried at 60 °C to a constant weight. Individually homogenized dry tissue of nine *B. ovata* were stored at −20 °C for further analysis of organic matter, protein, lipid and carbohydrate contents to calculate calorific value of *B. ovata*. The body length and wet weight of these specimens ranged from 35 to 103 mm, and from 5.9 to 65.3 g, respectively.

The biochemical assays, which are routine colourimetric techniques (Anninsky, 1994), were made within 10 days following the sample collection. Protein was measured by the Lowry method with an HSA (human serum albumin) standard; free amino acids were measured by the Pochinok method with a D,L-α - alanine standard; carbohydrate was measured by the Dubois method with a D-glucose standard. Lipid was determined according to the Amenta method, following the Folch chloroform/methanol (2:1) extraction. The standard was triolein/cholesterol (1:1). The energy content of *B. ovata* specimens was calculated by dry weight and the calorific value of each main biochemical compound determined (i.e. 5.65 cal mg^{-1} for protein, 9.45 cal mg^{-1} for lipid and 4.10 cal mg^{-1} for carbohydrate; Winberg, 1971).

Respiration

Sixteen *B. ovata* specimens were incubated at 21±1 °C after minimal delay (<2 h) to determine the freshly collected metabolic rate. The individual ctenophores were kept in the dark in respiration chambers (0.25–3.27 l capacity according to specimen size) filled with 120 μm filtered sea water for 17–19 h. Calculations of the metabolic rates were made from the measured difference in oxygen concentration between bottles with and without ctenophores. At the end of the incubation period, oxygen concentrations were measured in subsamples of seawater transferred into 60 ml

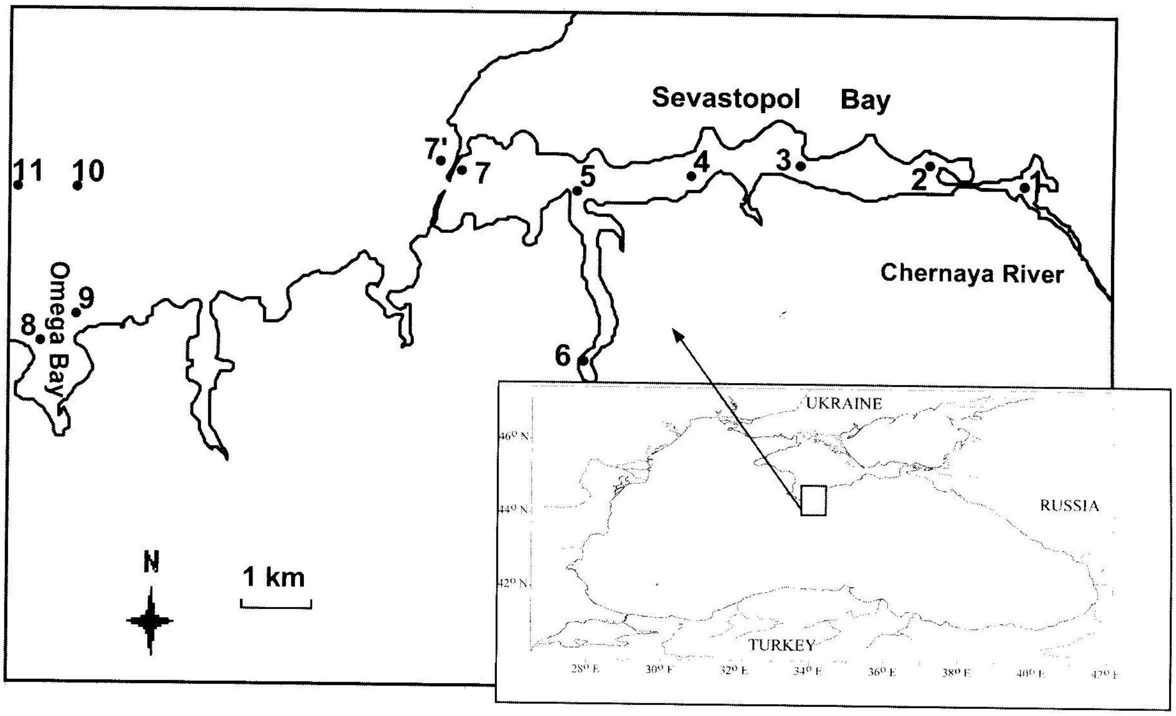

Figure 1. Sampling stations in Sevastopol Bay and adjacent regions in the Black Sea, during September–November 1999.

biochemical-oxygen demand bottles. Oxygen concentrations were determined by titration (Omori & Ikeda, 1984). For the conversion of respiration rate into energy values, the coefficient value of 4.86 cal ml O_2^{-1} was used (Omori & Ikeda, 1984).

Estimation of digestion time and rate of consumption

Feeding experiments were conducted during 23 September–18 October using two series of experiments. All experiments were carried out in the dark at 21±1 °C (close to the ambient temperature for Sevastopol Bay for this time) using containers of 5 l capacity.

Two independent methods were used to determine the consumption rate of *B. ovata*. In the first series of experiments, maximum feeding rate was measured under experimental conditions. These experiments were run over a relatively longer period (duration varied from 2 to 4 days) with a single *B. ovata* and 3–5 *M. leidyi* being held in the same container. In this condition, *B. ovata* had many prey available and could feed ad lib over the whole period. The number of *M. leidyi* in the containers was counted daily and new prey animals were added to ensure that prey items were never exhausted. The wet weight of *B. ovata* in these experiments (total 19) ranged from 4.85 to 21.31 g and *M. leidyi* from 0.93 to 25.0 g. The consumption rates were calculated from the measured differences in concentration and total weight of the prey at the beginning and at the end of observations.

The second series of feeding experiments were designed to determine the digestion time with respect to the size ratio of prey and predator. Then, knowing the size distribution of ctenophores from field sampling, this relationship could be used to calculate the maximum potential consumption rate in field. In these experiments, one specimen each of *B. ovata* and *M. leidyi* were placed in each container after starving the predator for 24 h. There were 4 containers present in each observation during 8–10 h. The wet weight of *B. ovata* ranged from 1.4 to 58.6 g and *M. leidyi* ranged from 0.25 to 13.69 g during 19 estimations of digestion time. The duration between the start of the experiment and commencement of ingestion was also noted. Once ingestion occured, the *B. ovata* specimens were monitored every 15 min until defecation was complete and the gut was empty. Daily consumption rates were calculated from such digestion time and wet weight of the prey.

In both series of experiments, *B. ovata* mainly preferred prey smaller than itself. Only once was a larger prey swallowed whole. Although there were no partial feeding during the experiments, in aquariums we observed partial predation of *B. ovata* on *M. leidyi* as reported by Swanberg (1974). On some occasions, *B. ovata* refused to feed during the entire experimental period. Unfed ctenophores were discounted during the calculation of miscellaneous experimental values, however, an allowance was made for unfed animals in the calculation of field consumption rates. The potential impact of predation by *B. ovata* was estimated from ctenophore densities in the field and the daily ration.

Results

Abundance, biomass and population structure of ctenophores

Biomasses of two ctenophore species were estimated from their numerical abundance and mean wet weight. The wet weight was calculated from the following relationships between wet weight (WW, mg) and body length (L, mm) for three groups of ctenophores:

B. ovata (14–120 mm): $WW = 1.77L^{2.23}$

$(n = 22; r^2 = 0.982)$

M. leidyi (2–10 mm): $WW = 1.074L^{2.76}$

$(n = 135; r^2 = 0.986)$

M. leidyi (11–65 mm): $WW = 1.31L^{2.49}$

$(n = 95; r^2 = 0.956)$

The mean values of abundance and biomass of *B. ovata* and *M. leidyi* for all 11 stations are shown in Table 1. In September–October, *B. ovata* was present in 10–25% of vertical tows and 60–70% of horizontal tows. In November, it was observed in 2% of horizontal tows only. *B. ovata* length ranged from 14 to 120 mm, weight was 0.5–70.0 g. Ctenophores of between 20 and 40 mm long were the most abundant (51%) in September, and this range was 30–60 mm in October (57%). In November some large *B. ovata* (about 100 mm) were found in the horizontal tows. There were eggs and juvenile ctenophores (0.4–1.5 mm length) found in several stations of the bay in September–October.

M. leidyi was more abundant (0.2 m^{-3}) than *B. ovata* (0.022–0.075 m^{-3}). The lengths for *M. leidyi* were 0.5–65.0 mm, and weights were 0.16–43.0 g, respectively. Possible reproduction of *M. leidyi* occurred during the study period, because the majority of the population consisted of juvenile ctenophores (with lengths of 10–20 mm) in September (52%) and 5–15 mm in October (72%).

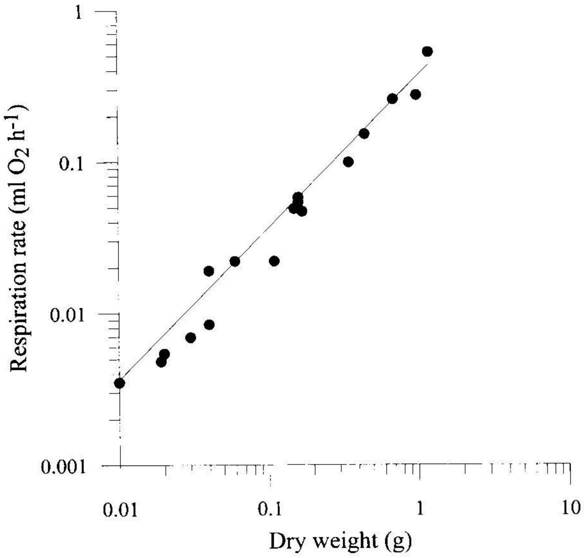

Figure 2. Relationship of *Beroe ovata* body weight and its oxygen consumption rate at 21 °C.

Chemical composition

Data on the chemical composition of *B. ovata* are shown in Table 2. Dry weight was equal to 2.40 ± 0.13% of wet weight. The main component of organic matter was protein (80%). The mean calorific value of *B. ovata* tissue was determined from the known energetic standards of protein, lipid and carbohydrate as 16.0±2.4 cal g^{-1} WW, or 640±96 cal g^{-1} DW.

Respiration rate

The relationship between oxygen consumption rate (Q) and dry weight (DW) of *B. ovata* was expressed by the allometric equation (Fig. 2):

$$Q = 0.341DW^{1.04},$$
$$(r^2 = 0.98; n = 17; \text{ at } 21 \pm 1\ ^\circ C);$$

where Q is respiration rate (ml O$_2$ g^{-1} h^{-1}), and DW is dry weight (g). The slope of 1.04 indicated that the weight-specific respiration rate was independent of weight over the measured weight range (0.01–0.9 g

Table 1. Abundance, biomass and average individual wet weight (WW) of ctenophores *Beroe ovata* and *Mnemiopsis leidyi* at 11 stations in Sevastopol Bay and adjacent water regions in 1999 estimated from vertical sampling

Species	Date	Temperature (°C)	Abundance (ind m^{-3})	Biomass (g WW m^{-3})	Mean WW* (g)
B. ovata	23 Sep.	22.5±1.2	0.02±0.07	0.11±0.33	14.87±14.76
B. ovata	25 Oct.	16.2±0.6	0.08±0.14	1.74±3.66	23.24±25.09
B. ovata	10 Nov.	13.8±1.2	0	0	51.50±0
M. leidyi	23 Sep.	22.5±1.2	0.21±0.20	0.53±0.60	2.79±4.87
M. leidyi	25 Oct.	16.2±0.6	0.20±0.19	0.43±0.68	2.85±6.47
M. leidyi	10 Nov.	13.8±1.2	0.34±0.60	1.55±3.79	3.66±4.384

*From horizontal tows.

Table 2. The proximate chemical composition of the ctenophore *Beroe ovata* in the Black Sea (mean ± 1 SD from 9 individuals)

Chemical components	Concentration (mg g^{-1} WW)	As % of organic matter
Organic matter	2.72±0.43	100.0
Protein	2.17±0.36	79.8
Lipid	0.26±0.04	9.6
Free amino acids	0.15±0.06	5.5
Carbohydrate	0.14±0.04	5.2

DW). The cost of respiration was calculated to be equal to 10% d^{-1} of *B. ovata* DW.

Digestion time and daily ration

In the laboratory, *B. ovata* was not very active. It either remained motionless or swam slowly. Individuals did not immediately locate prey that had been newly placed in the tank. In our experiments, the duration between the start of the experiment and commencement of ingestion was on average 2.3±1.2 h and did not depend on prey or predator size. Similarly, the ctenophores did not engulf new prey just after recent digestion. *M. leidyi* was generally completely engulfed, except on a few occasions when the prey was larger than *B. ovata* and was partly eaten. There was no cannibalism behaviour by *B. ovata*, however, once one individual engulfed another *B. ovata*, but after 30-40 min, it was regurgitated alive and healthy.

In long-term experiments, the daily rations of *B. ovata* specimens of 4.85–21.31 g WW varied from 3.4 to 27.4 g WW ind^{-1} day^{-1} or from 60 to 128% of its own WW (Table 3) and were close to the rations calculated from digestion time in the first series of experiments (see below). *B. ovata* fed in only 8 out of 19 long-term experiments; therefore, if we assume that half of the ctenophores in population feeds daily, the average ration of *B. ovata* in the field amounts to about 45% of its wet weight daily. Because the dry: wet weight ratios and calorific values of *B. ovata* and *M. leidyi* are similar (Finenko & Romanova, 2000), the daily ration in terms of energy content would be 45% of body energy content.

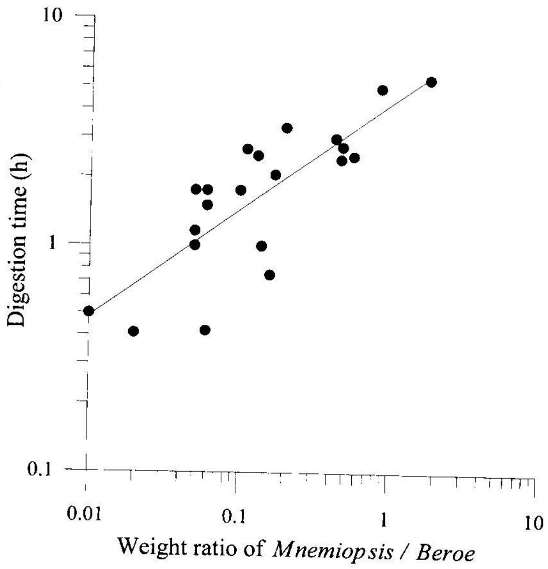

Figure 3. Relationship of the prey/predator weight ratio and the time required for *Beroe ovata* to digest *Mnemiopsis leidyi* ctenophores at 21 °C.

Digestion time of *B. ovata* feeding on *M. leidyi* at 21±1 °C varied from 0.5 to 5.5 h in the studied weight range of both ctenophores. *B. ovata* of every size consumed both small and large *M. leidyi*, and the ratio between prey and predator weight (*P′*, range 0.01–

Table 3. The daily ration of *Beroe ovata* in long-term laboratory experiments with unlimited prey (*Mnemiopsis leidyi*)

B. ovata weight (g)	Duration of feeding (d)	Total consumed food (g WW ind^{-1})	Ration (g WW ind^{-1} d^{-1})	Ration as % *B. ovata* WW
4.85	3.0	12.51	4.17	85.9
5.57	4.0	13.40	3.35	60.1
16.00	3.0	40.20	13.40	83.7
21.31	2.0	54.80	27.40	128.6
			Mean	89.6

Table 4. Estimated maximum daily predation rate of the *Beroe ovata* population on *Mnemiopsis leidyi* biomass for Sevastopol Bay in autumn 1999. Biomasses of ctenophores are in Table 1. The digestion time (*D*) and ration (*R*) of *B. ovata* were estimated from the regression of digestion time and wet weight ratio of ctenophores from the second series of feeding experiments

Date	WW ratios of ctenophores W_M/W_B (P)	Digestion time (h) (D)	Ration (g WW ind^{-1}d^{-1}) (R)	Ration as % *B. ovata* WW	Ration in field (g m^{-3} d^{-1})	Daily predation as % of *M. leidyi* biomass
23 Sep.	0.188	1.92	15.87	106.7	0.05	9.3
29 Sep.	0.125	1.57	11.35	77.5	–	–
12 Oct.	0.024	0.72	2.15	19.5	–	–
25 Oct.	0.123	1.56	17.72	76.4	0.57[a]	132.1

[a] With temperature correction Q_{10}= 2.2.

<2.0) affected digestion time (*D*). The relationship between these values was expressed by the allometric equation (Fig. 3):

$$D = 4.26P^{0.478}, (n = 19; r^2 = 0.65).$$

The maximum potential daily ration of *B. ovata* for the field in September–October in Sevastopol Bay was calculated using digestion time from this equation and the *M. leidyi/B. ovata* weight ratio and the mean weight of *M. leidyi* from these data. Since the duration between the completion of digestion and commencement of new feeding was on average 2.3 h in the experiments, the number of meals would be $24/(2.3 + D)$ in a day. In our experiments, *B. ovata* was never observed to consume more than one prey at a time and the period between the completion of digestion and commencement of new feeding did not depend on how many prey were available. We suggest that the same situation exists in the sea. Then daily rations (C in g WW ind^{-1} d^{-1}) of *B. ovata* calculated as $C = 24W/(2.3+D)$, where W and D represent the most weight (g) of *M. leidyi* consumed and digestion time (h), respectively, ranged from 2.2 to 17.7 g ind^{-1} d^{-1} or from 20 to 107% of its own WW (Table 4). The wide range in daily ration was due to wide range of *M. leidyi/B. ovata* wet weight ratio as well as *M. leidyi* weight that varied over about one order of magnitude. The maximum daily ration occurred at maximum P (the W_M/W_B ratio) and the minimum ration when this ratio was low.

The potential predatory impact of B. ovata *on the* M. leidyi *population*

On the basis of data on abundance and maximum daily ration, we estimated the predatory impact of *B. ovata* on the *M. leidyi* population in Sevastopol Bay. Data on the abundance of *B. ovata* and *M. leidyi* were taken from Table 1. The daily ration of *B. ovata* at 22 °C amounted to 45% of its biomass if we assume only half of the *B. ovata* population feeds daily (Table 3).

We estimate that in September, the *B. ovata* population consumed 9.3% and in October 132% of the *M. leidyi* biomass (Table 4). It should be pointed out that in October, *B. ovata* biomass was one order of magnitude higher than that in September. The grazing values determined here should be considered as maximum ones with continuous feeding of *B. ovata* when food is constantly available. In the field, the proportion of *B. ovata* with *M. leidyi* in the stomadeum could be more or less than a half as we suggested (12–20%, Shiganova et al., 2000; Vostokov et al., 2000). In these cases, our values calculated would decrease to 2–53%.

A comparison of mean daily specific growth rate of the *M. leidyi* population for the year in Sevastopol Bay (3.9% of population biomass; Finenko & Romanova, 2000) with predatory impact of *B. ovata* population on *M. leidyi* (2–53%) showed that in inshore waters of the Black Sea, despite their low numbers, the *B. ovata* population may control abundances of their prey population in certain periods.

Discussion

Abundance, biomass and population structure of ctenophores

B. ovata was found in the Black Sea in October 1997 for the first time in the inshore waters of Bulgaria (Konsulov & Kamburska, 1998). Later it appeared during May–August 1998 in a coastal zone of the northwestern Black Sea stretching from Odessa to the mouth of the Danube (Nastenko & Polishchuk, 1999). Numerical abundance of *B.ovata* determined from zooplankton samples in this region varied from 0.2 to 0.4 ind m^{-3} in May and from 35 to 392 ind m^{-3} in August. The population was comprised of young ctenophores ranging from 0.2 to 9 mm long, and as a result the population biomass was low (0.00001–0.097 g m^{-3}). In August–October 1999, *B. ovata* occurred in the northeastern Black Sea near Gelendzhik (Anokhina et al., 2000; Shiganova et al., 2000, 2001), where numbers were 0.06–0.13 ind m^{-3} and biomass was from 18.6 to 42.8 g m^{-3}. The ctenophores ranged in size between 20 and 120 mm in length in the population.

This is the first report about the occurrence of *B. ovata* in the inshore waters near Sevastopol based on samples obtained in September–October 1999. Here, the abundance in Sevastopol Bay and adjacent waters ranged from 0.02 to 0.07 ind m^{-3} and biomass from 0.11 to 1.74 g m^{-3}. The ctenophores measuring 20–60 mm in length were most numerous. *B. ovata* biomass in Sevastopol Bay was an order of magnitude lower than in coastal waters of the northeastern Black Sea near Gelendzhik.

The numerical abundance of *M. leidyi* in September–October 1999 was greatly reduced as compared with that in previous years. In September–October 1995, abundance and biomass of *M. leidyi* were 125 ind m^{-3} and 33 g WW m^{-3}, respectively (Finenko & Romanova, 2000) in September–October 1999, *M. leidyi* abundance and biomass were only 0.2 ind m^{-3} and 0.5 g WW m^{-3}. This marked decrease was probably caused by grazing of *M. leidyi* by *B. ovata*. Similarly, since the summer of 1997 when *B. ovata* was first noted, a clear decreasing trend in *M. leidyi* biomass from the southern Black Sea was also noticed (Kideys & Romanova, 2001).

Respiration rate

To compare the respiration rate of *B. ovata* with the data of other authors under similar temperature conditions, we have calculated oxygen consumption in ml O_2 $g^{-1}h^{-1}$ and recalculated for standard temperature 20 °C by introducing the temperature correction Q_{10} = 2.2 (Winberg, 1983). In our case, it corresponded to 0.34 ml O_2 g^{-1} h^{-1}, whereas in Kremer et al. (1986) and Shiganova et al. (2000), these estimates were 0.14 and 0.35 ml O_2 g^{-1} h^{-1}, respectively. Our value is quite similar compared with that of Shiganova et al. (2000a), but higher than is obtained by Kremer et al. (1986).

Chemical composition

Our data on the chemical composition of *B. ovata* are in good agreement with the literature for many other species of epipelagic ctenophores. This is true not only for the total organic content, which usually amounts in these animals to 1–8 mg g^{-1} WW (Kremer et al., 1986; Clarke et al., 1992; Bailey et al., 1994, 1995), but also for relative values, where the organic matter typically contains 60–80% protein (Hoeger, 1983; Schneider, 1989; Anninsky, 1994). By contrast, some Arctic or deep sea specimens sometimes accumulate lipids in their bodies (Larson & Harbison, 1989).

At the same time, with respect to the amount of organic matter, a wide range of values have been reported within the species of Beroida. According to Kremer et al. (1986), the organic content of *B. ovata* calculated by carbon (C × 1.9) usually varied from 1.33 to 3.99 mg g^{-1} WW, while the values obtained for *B. cucumis* (Hoeger, 1983) and *B. gracilis* Künne (Bailey et al., 1994) amounted to 6.56 and 4.99 mg g^{-1} WW, respectively. Besides, there are other values, being equal to 5.8–7.3 mg g^{-1} WW of organic matter for *Beroe* sp. (Clarke et al., 1992; Bailey et al., 1994).

Evidently, the organic content in *B. ovata* is the lowest among the Beroida.

On the whole, *B. ovata* ctenophores have a greater organic content (2.4–3.1 mg g^{-1} WW) and caloric values (14.0–18.7 cal g^{-1} of wet weight), compared with other ctenophore species of the Black Sea. For instance, the organic content of *Pleurobrachia rhodopis* Chun, 1880 (synonym *P. pileus* (O. F. Müller, 1776)) is 2.0–2.9 mg g^{-1} WW, and of *M. leidyi* is 1.0–1.5 mg g^{-1} (Anninsky, 1994). Energetic value of their tissues ranged from 12.6 to 17.6 cal g^{-1} WW and from 7.4 to 13.4 cal g^{-1} WW, respectively. The highest values for *B. ovata* could be caused by the specific carnivorous life style of this species.

Digestion time, consumption rate and the potential predatory impact of B. ovata *on the* M. leidyi *population*

Digestion times and rations of *B. ovata* in the Black Sea determined in our experiments and by other authors, are very close. According to Shiganova et al. (2000) digestion time varied from 3 to 5 h at 24–26 °C and the daily minimum ration calculated from respiratory demands was 30% of wet weight. In September 1999 in the northeastern Black Sea, they estimated that the *B. ovata* population grazed 0.7–5.7% of *M. leidyi* biomass daily.

The food ingestion rate in our experiments far exceeded respiratory demands (average 5.72±1.35% of *B. ovata* energy content) of the ctenophore for the studied weight range. The food rations of *B. ovata* observed in the experiments would be considered as maximal under abundant food conditions. It was shown that in a homogenous environment, *B. ovata* could find 1 prey item approximately every 17 h (Swanberg, 1974). Kamshilov (1960) claimed that a *B. cucumis* requires a 10 mm *Bolinopsis infundibulum* to support a 1.6% growth increment every 18.3 h. In nature, *B. ovata* probably are able to realize their high feeding activity only rarely and over short periods. Moreover, in nature, partial predation, lower prey densities, and escape of *M. leidyi* (in Kreps et al., 1997) would result in lower consumption rates. Probably the ingestion rate of ctenophores in the Black Sea was limited mainly by the rate at which the predators captured prey rather than by the rate at which they digested it. The large capacity of the predator's stomach enables them to consume the large prey items and thus to receive at once sufficient food to meet their respiratory demands for a long time. This ability is an adaptation tool to take advantage of episodic periods of high prey density.

It is obvious that ctenophores of the genus *Beroe* form an important link in pelagic food chains, however, little is known of their general feeding biology. The species of order Beroida feed mainly on other ctenophores (Kamshilov, 1960; Swanberg, 1974; Matsumoto and Harbison, 1993; Shiganova et al., 2000). In the Black Sea, *B. ovata* seems to be restricted to the surface waters and therefore their food would mainly consist of *M. leidyi* because the other ctenophore species, *Pleurobrachia pileus*, is mainly distributed in deeper waters with low oxygen concentrations (Mutlu, 1999; Kideys & Romanova, 2001). The high concentrations of *B. ovata* were found in areas of high *M. leidyi* abundance (Shiganova et al., 2000). *Beroe* spp. can have a substantial impact on the population structure of planktivorous ctenophore communities. *B. ovata* reduced *M. leidyi* populations in the autumn in Narragansett Bay (Kremer et al. 1986). Greve & Reiners (1980) showed that predation by the ctenophore *B. gracilis* may be a factor in controlling the *P. pileus* population in the southeastern North Sea and Van Der Veer & Sadee (1984) reported similarly for the Dutch Wadden Sea.

Kamshilov (1960) claimed that *B. cucumis* indirectly modified the composition of other zooplankton by feeding on the zooplanktivorous *Bolinopsis infundibulum*. Purcell & Cowan (1995) also suggested that feeding by the cnidarian *Chrysaora quinquecirrha* (Desor), on *M. leidyi* populations may reduce mortality of zooplankton and ichthyoplankton. We suppose that due to its intensive feeding on *M. leidyi*, *B. ovata* could cause an increase in the concentration of edible zooplankton in the Black Sea. If this holds true, schooling zooplanktivorous fishes, which are the main food competitors of *M. leidyi*, will greatly benefit from the consequences of this new arrival to the Black Sea.

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