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RESEARCH ARTICLE

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Respiration rates of *Beroe ovata* in the Black Sea

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Abstract Metabolic rates of the ctenophore *Beroe ovata* within the length range from 0.4 mm (newly hatched larvae) to 60 mm were investigated. At 20°C the respiration rates (Q, μg O_2 ind.$^{-1}$ h^{-1}) of individuals with wet weights (W, mg) less than or greater than 100 mg changed according to the equations $Q = 0.093W^{0.62}$ and $Q = 0.016W^{0.99}$, respectively. The weight-specific respiration rate of the juvenile ctenophores with wet body weights of 0.021–100 mg diminished approximately 20-fold (from 0.35 to 0.017 μg O_2 mg^{-1} h^{-1}, respectively), but did not change within the range from 100 to 30,000 mg. The difference in the slope of the regression lines seems to be attributable to the ontogenetic changes in *B. ovata* metabolism. For the tested temperature range of 10–28°C, the mean Q_{10} coefficient was equal to 2.17 ± 0.5. The basal metabolism of *B. ovata* narcotised by chloral hydrate was 4.5 ± 0.9 times lower than total metabolism. Such a metabolic range is considered to be characteristic of aquatic invertebrates with high levels of locomotory activity.

Introduction

In 1999, about 10 years after the introduction of the north-western Atlantic predator ctenophore *Mnemiopsis leidyi*, which significantly decreased the fodder zooplankton biomass as well as fishery catches and disturbed the entire pelagic ecosystem in an unprecedented manner (Vinogradov et al. 1992; Kideys 1994; Shiganova et al. 1998), mass development of a new gelatinous intruder to the Black Sea, *Beroe ovata*, occurred. This species is known to feed mainly on lobate ctenophores (Kamshilov 1960a, 1960b; Swanberg 1974), and therefore its diet in the Black Sea is almost exclusively limited to *M. leidyi* (Shiganova et al. 2000; Vinogradov et al. 2000; Finenko et al. 2001). As a result, the abundance of *M. leidyi* was sharply reduced and both the mesoplankton concentration and pelagic fish catches (mainly the anchovy *Engraulis encrasicolus* L.) began to increase (Zagorodnyaya and Kovalev 2001; Kideys 2002). Changes in the entire pelagic community structure occurred due to the trophic interactions of these two ctenophore species. Therefore, the positive events observed in the Black Sea, as a result of *B. ovata*'s arrival, presented a new dimension in dealing with the problems of invasive species in aquatic environments.

Vinogradov et al. (2000), Finenko et al. (2000, 2001, 2003), Shiganova et al. (2001) and Vostokov et al. (2001) estimated the ability of *B. ovata* to control the *M. leidyi* population in the Black Sea based on feeding rates. However, all of these authors analysed only the energy and food requirements of adult *B. ovata*, with body lengths exceeding 14 mm. The energetics of ctenophores of smaller size-classes has not yet been investigated. Studies on the changes in metabolic rates of the organism influenced by different environmental factors during ontogeny are necessary, not only for the analysis of energy transformation in the planktonic ecosystem, but also to assess the potential of these organisms for adaptation to the new environments. This is particularly important when one considers that *B. ovata* is the main candidate as a predator to eradicate the very high population levels and consequently adverse impact of *M. leidyi* (Kideys 2002; Kideys and Moghim 2003; Kideys et al. 2004) in

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the sensitive Caspian Sea, after the ballast-mediated transfer of *M. leidyi* into this sea in the late 1990s (Ivanov et al. 2000).

The aim of the present study was to investigate the relationship between the respiration rate and body weight of all developmental stages (including newly hatched ctenophores) of *B. ovata* at different temperatures and levels of activity.

Materials and methods

The experiments were carried out with *Beroe ovata* collected in Sevastopol Bay in September–November 2000 and in Sinop Harbour in August–September 2001, at the ambient temperatures of 21 ± 2°C and 26 ± 2°C, respectively.

Ctenophores with body lengths > 1.5 mm were sampled carefully near the sea surface using a wide-mouthed plastic bottle or hand net (500 μm mesh size) without damaging the delicate animals. After collection, the individuals were placed in aquaria containing 120-μm-filtered seawater for 1–2 h. Newly hatched *B. ovata* larvae were obtained from eggs and reared under laboratory conditions until the animals reached the length of 1 mm. For juvenile ctenophores of 0.4–3.0 mm, wet weight (W, mg) was calculated as: $W \cong M = V\rho$, where M is the wet body mass, $V = 1/6L3.14d^2$ is the volume of an ellipsoid in cubic millimetres (where L is the length and d is the diameter of the ellipsoid in millimetres and ρ is body density, which is close to that of seawater, i.e. 1.02 g cm^{-3}). The length, width and thickness of free-swimming ctenophores were determined using video images. For larvae immerged in water, a video camera connected with a dissecting microscope was used. The wet weights of animals in the size range of 4–60 mm were determined by direct weighing on an analytical balance.

Respiration rates (Q, μg O_2 ind.$^{-1}$ h^{-1}) of *B. ovata* within the size range of 0.4–3.0 mm (mainly juveniles) were measured using experimental and control respiration chambers (identical all-glass syringes) of 2.0, 5.0 and 20.0 ml, according to the size of tested animals. Flasks of 200 ml volume were used for determination of the respiration rates of *B. ovata* from 8 to 60 mm (mainly adults). One to five individuals of 1.5–60 mm and 60–200 newly hatched ctenophores of 0.4–0.5 mm and 2-day-old larvae (up to 1.0 mm) were gently (submerged in the water) transferred to each experimental chamber with 1-μm-filtered seawater.

Each experimental syringe was connected to a control syringe (without animals) with a fine plastic tube, allowing water exchange between the syringes. Afterwards, half the water volume from the experimental syringe was transferred through the tube to the control syringe, to achieve equal initial oxygen concentrations in both syringes. In order to preserve larvae in the experimental syringe, a 100-μm-mesh sieve was placed in front of the outlet of the syringe. The syringes were then separated, closed by the stoppers and incubated for 2–3 h at ambient temperatures. During incubation, larvae and adult ctenophores maintained the same level of locomotory activity as before the experiment. At the end of the experiment, the oxygen concentrations in the experimental and control syringes were determined.

Oxygen concentration was determined using a polarographic membrane oxygen sensor, joined with the measuring chamber (all-glass syringe) of 0.5 ml volume and containing a magnetic stirrer inside (Svetlichny and Umanskaya 1991). The water sample from the experimental syringe was transferred to the measuring chamber through the needle without contact with the surrounding air. After rinsing out the measuring chamber twice, the residual volume was sufficient for four replicate measurements of oxygen content.

Oxygen concentrations in flasks and in the water used to calibrate the oxygen sensor were determined by the Winkler technique (Strickland and Parsons 1972). The incubation period of the experimental and control flasks lasted up to 4–5 h.

Respiration rate (μg O_2 ind.$^{-1}$ h^{-1}) was calculated from the equation: $y = (x_c - x_e)V_c/n_s t$, where x_c is the oxygen concentration in the control chamber at the end of the experiment (mg l^{-1}), x_e is the oxygen concentration in the experimental chamber at the end of the experiment, V_c is the volume of the chamber (cm^3), n_s is the number of specimens and t is the duration of the experiment (h). During the incubation period, the total oxygen content consumed was never $> 30\%$ of the initial value.

The effect of temperature on *B. ovata* wet weight–specific respiration rate (μg O_2 mg^{-1} WW h^{-1}) was investigated at ambient temperatures of 18–23°C (Sevastopol Bay) and 26–28°C (Sinop Harbour) on the animals from two size-groups, 10–20 and 20–50 mm. In a separate series of experiments, the ctenophores were maintained for 2 days at 10°C. Ten replicates were run for each size-group at different temperatures. The results obtained with the polarographic method and the Winkler technique were analysed separately.

To study basal metabolism, the individuals of the 10–20 mm group were narcotised using 0.3% chloral hydrate at a temperature of 20 ± 1°C. Prior to the experiment, *B. ovata* were kept in the chloral hydrate solution (5–10 min) until cessation of beating of the ciliary comb plates. After incubation (2–3 h), the narcotised animals were transferred to aquaria, where they gradually regained motility. We analysed only the results of the experiments in which the ctenophores did not awaken during the incubation period, but completely recovered the initial level of respiration rate and swimming activity by the next day. The scope of activity was calculated from the difference between respiration rates of the same individuals before and after the chloral hydrate treatment.

Results

Morphometrics

During development, the body shape of *Beroe ovata* significantly changes. Due to the elasticity of body form, newly hatched larvae can markedly elongate or shorten their bodies when disturbed. However, during ordinary swimming the body form was close to ellipsoid, with a preliminary length:width ratio of 1.25 ± 0.11 ($n = 11$). In larvae, an increase in size and the development of ciliary combs are accompanied by flattening of the body. For juveniles of 1–2 cm, length:width and length:thickness ratios were 1.34 ± 0.06 and 2.63 ± 0.48 ($n = 20$), respectively. In adult ctenophores of 50–70 mm, length:width and length:thickness ratios amounted to 1.22 ± 0.12 and 3.31 ± 0.62 ($n = 20$), respectively. Therefore, the wet weight:length relation changes during *B. ovata* ontogeny (Fig. 1). In the size range of 0.4–3.2 mm, the relationship between calculated wet weight and length of larvae could preliminarily be expressed as $W = 0.31L^{2.92}$ ($n = 21$, $r^2 = 0.99$). For ctenophores of 5.0–55.0 mm, the relationship between wet weight obtained by direct weighing) and body length was described by the following equation: $W = 0.75L^{2.47}$ ($n = 102$, $r^2 = 0.96$).

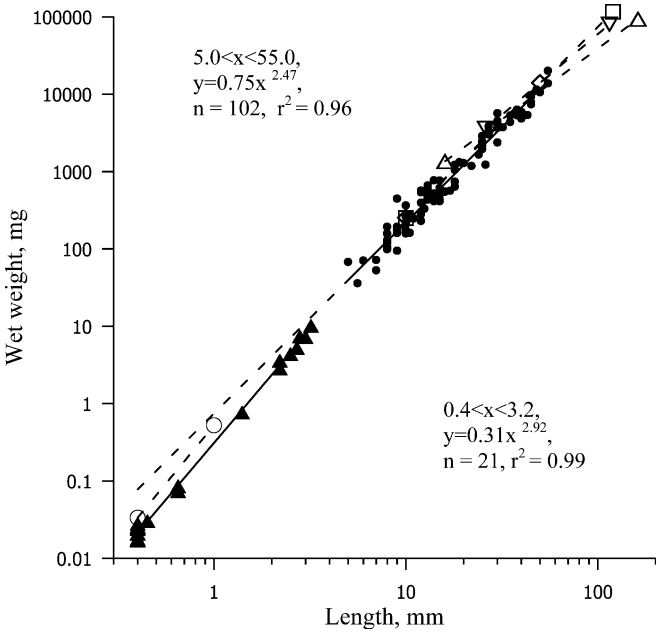

Fig. 1 *Beroe ovata*. Relationship between wet weight and length: the results of direct weighing (*solid circles*) and calculating (*solid triangles*). *Broken section* of the empirical regression line indicates extrapolated values of wet weight for preadult and adult individuals (*open symbols*: *circles* the weight of a sphere with a density of 1.018 g cm^{-1}; *diamonds* Kremer et al. 1986; *triangles* Shiganova et al. 2000; *inverted triangles* Vostokov et al. 2001; *squares* Finenko et al. 2000)

Respiration rate

The respiration rates of *B. ovata* obtained from separate experiments with ctenophores from Sevastopol Bay (S1) at 21 ± 2°C and from Sinop Harbour (S2) at 26 ± 2°C are presented in Fig. 2. In the wet weight range of 490–1,100 mg, weight-specific respiration rates of S1 individuals obtained by polarographic method and Winkler technique were 0.012 ± 0.01 and 0.017 ± 0.006 μg O_2 mg^{-1} WW h^{-1}, respectively. For S2 ctenophores of 104–500 mg, weight-specific respiration rates amounted to 0.030 ± 0.01 μg O_2 mg^{-1} WW h^{-1} (polarographic method) and 0.036 ± 0.007 μg O_2 mg^{-1} WW h^{-1} (Winkler technique), respectively. The difference between the results obtained by the two methods for S1 and S2 was insignificant (*t*-test; $P > 0.05$), which allowed us to combine these data.

Despite the pronounced temperature differences, trends in respiration rate during ontogeny were similar in S1 and S2. The respiration rate (Q, μg O_2 $ind.^{-1}$ h^{-1}) of *B. ovata* changed according to the following equations: $Q = 0.11W^{0.65}$ ($n = 25$, $r^2 = 0.93$) for S1 individuals with body wet weights of 0.021–700 mg and $Q = 0.14W^{0.58}$ ($n = 14$, $r^2 = 0.96$) for S2 individuals in the range of 0.03–100 mg. For larger specimens (700–55,000 mg for S1 and 100–50,000 mg for S2), the respiration rates changed following the equations: $Q = 0.0063W^{1.078}$ ($n = 51$, $r^2 = 0.83$) and $Q = 0.019W^{1.044}$ ($n = 73$, $r^2 = 0.93$), respectively.

The effect of temperature was investigated in *B. ovata* from two size-groups, with wet weights of 200–1,200 and 1,200–12,000 mg. At the same temperatures, no significant difference between the respiration rates of the ctenophores from these two groups was found. When the temperature rose from 10°C to 28°C, the weight-specific respiration rate of the ctenophores increased significantly ($P < 0.001$), from between 0.005 and 0.0072 to 0.032 mkg O_2 mg WW−1/h−1 according to the equation: $Q = 0.0021e^{0.096t}$ ($n = 24$, $r^2 = 0.76$; Fig. 3).

The chloral hydrate treatment of *B. ovata* individuals resulted, not only in complete cessation of beating of the macrocilia rows, but also in relaxation of the muscles used to maintain body shape and for prey capture. The bodies of ctenophores became softer and more amorphous. For narcotised *B. ovata* the relationship between the respiration rate and body wet weight was described as $Q = 0.0048W^{0.9}$ ($r^2 = 0.99$) at 20 ± 1°C (Fig. 4). The mean ratio between the respiration rate of active and immobilised individuals from five size-groups within the wet weight range from 100 to 3,200 mg amounted to 4.5 ± 0.9.

Discussion

Morphometrics

A problem encountered when studying gelatinous zooplankton is the difficulty in determining body weight.

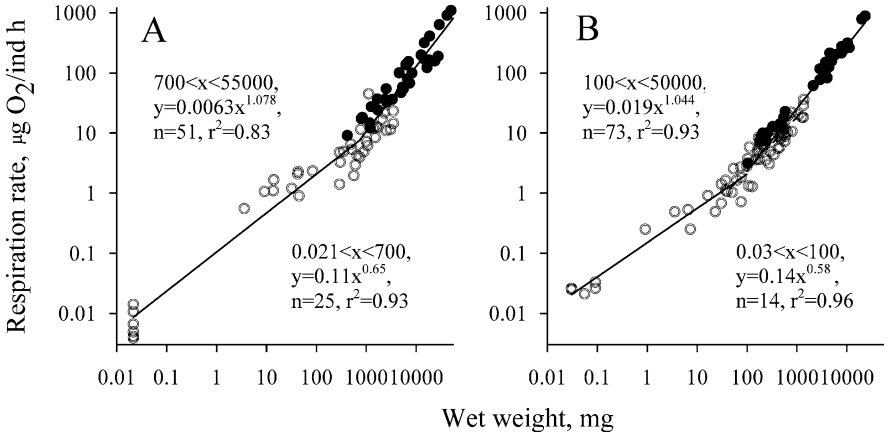

Fig. 2A, B *Beroe ovata*. Respiration rate of individuals collected in Sevastopol Bay (**A**) in September–November 2000 at 21 ± 2°C and in Sinop Harbour (**B**) in August–September 2001 at 26 ± 2°C. Data were obtained by the polarographic method (*open circles*) and by the Winkler technique (*solid circles*)

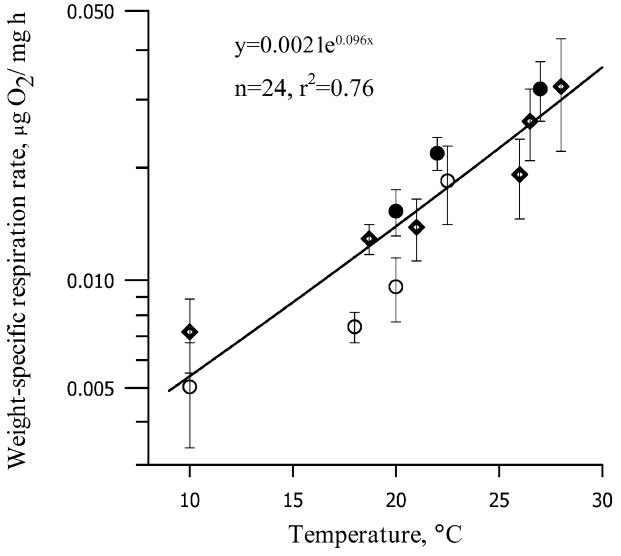

Fig. 3 *Beroe ovata*. Effect of temperature on weight-specific respiration rate: size range 10–20 mm (*open diamonds*) and 20–50 mm (*open circles*) studied by the polarographic method; size range 20–50 mm (*closed circles*) investigated by the Winkler technique. Values are means (± SD)

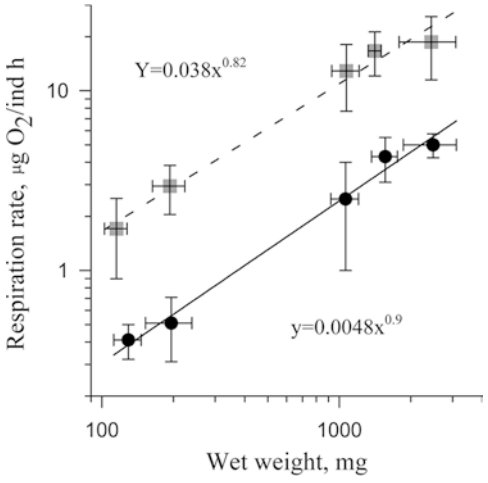

Fig. 4 *Beroe ovata*. Respiration rate before (*shaded squares*) and after (*closed circles*) narcotisation with 0.3% chloral hydrate. Values are means (± SD)

Direct weighing may damage the delicate animals used in long-term physiological experiments involving repeated measurements. Therefore, calculation of body wet weight on the basis of empirical weight:length relations is common experimental practice. The relationship between body weight and length is expressed as the allometric equation: $W = aL^b$, where b is equal to 3 when body shape does not change during ontogeny. During the course of development, the body of *Beroe ovata* flattens gradually, and body volume or weight per length unit decreases. Coefficient b also declines, which is confirmed by the empirical data (Table 1). In larvae of 0.4–4.0 mm, b amounted to 2.92, whilst for adult *B. ovata* of 16–162 mm, b decreased to 1.83 (Shiganova et al. 2001). The coefficients of the equation $W = 0.75L^{2.47}$ obtained using the results of direct weighing of ctenophores of 5–55 mm were close to those reported by Kremer et al. (1986) for *Beroe* of the same size (Table 1). However, this equation is not suitable for calculating the weight of small larvae, because the results are overestimated, even in comparison with the weight of individuals with a spherical body shape (Fig. 1). Direct weighing of jellyfish larvae may result in significant experimental error, associated with varying amounts of water retained on the surface of the body and the difficulties of evacuating water without overdrying the ctenophore. The geometrical method used in our study for preliminary estimation of body wet weight of *B. ovata* larvae allowed us to obtain magnitudes with an error margin of not more than 20–30% (Chislenko 1968).

Effect of temperature on respiration rate

To compare respiration rates of poikilothermal animals determined at different temperatures, data are usually normalised to the standard temperature of 20°C, using the following equation: $q = Q_{10}^{20-t/10}$, where q is the correction factor of metabolism for temperature (t) and Q_{10} is the Vant-Hoff coefficient (Suschenya 1972). After analysing numerous empirical and theoretical studies,

Table 1 Regressions of morphometric parameters and metabolic rates for freshly collected ctenophores of the genera *Beroe* and *Mnemiopsis*. Equation $Y = aX^b$ was used to derive the intercepts (*a*) and slopes (*b*) for the relationships between length (mm) and wet weight (mg) (*WW*) and between wet weight and respiration rate (μg O_2ind.$^{-1}$ h^{-1}) (*R*). Values of weight-specific respiration rate (μg O_2mg^{-1} h^{-1}) were normalised to 20°C (R_{20}/WW) (*DW* dry weight)

Species	Temperature (°C)	Salinity (‰)	Size range (mm)	DW range (mg)	DW (%WW)	WW		*R*		R_{20}/WW	Reference
						a	*b*	*a*	*b*		
Beroe cucumis	14.5–16.2	32.5	–	2.85–71.1	4[a]	–	–	0.28	0.61	0.081–0.023	Ikeda (1974)
Beroe ovata	25 ± 1	35.4	10–50	10.2–560.1	4	0.83	2.49	0.023	0.9	0.009–0.006	Kremer et al. (1986)
Beroe ovata	21 ± 1	18	14–120	10–1,680	2.4	1.77	2.23	0.0076	1.04	0.009–0.011	Finenko et al. (2001)
Beroe ovata	24.6–26.1	18	16–162	200–1,400	2.3	8.5	1.83	0.075	0.86	0.018–0.010	Shiganova et al. (2001)
Beroe ovata	19–21	18	26–115	90–2,000	2.5	–	–	0.104	0.8	0.020–0.011	Vostokov et al. (2001)
			26–50	–		–	–	0.25	0.72	–	
			50–115	–		–	–	0.012	1.0	–	
Beroe ovata	21 ± 2	18	0.40–16	–	2.4[b]	–	–	0.11	0.65	0.34–0.01	Present study
			16–90	–				0.006	1.08	0.010–0.014	
Beroe ovata	26 ± 1	18	0.4–4.0	–	2.4[b]	0.34	3	–	–	–	Present study
			4.0–66	–		0.75	2.47	–	–	–	
			0.45–7.0	–		–	–	0.14	0.58	0.43–0.013	
			7–66	–		–	–	0.019	1.04	0.014–0.018	
Mnemiopsis leidyi	20	31	8–80	13.6–1,290	3.4	–	–	–	–	0.0049	Kremer (1977)
Mnemiopsis leidyi	20	31	8–80	–	3.4	9	1.87	–	–	–	Kremer and Nixon (1976)
Mnemiopsis leidyi	22	18	–	0.99–34.8	2.2	–	–	0.031	0.83	0.014–0.007	Anninsky et al. (1998)
Mnemiopsis leidyi	24.5	18	–	0.2–310	2.2	–	–	0.011	0.91	0.006–0.003	Abolmasova (2001)
Mnemiopsis leidyi	19–21	18	10–90	3–2,000	2.0	–	–	0.0025	1.02	0.003	Vostokov et al. (2001)

[a]Kremer et al. (1986)
[b]Finenko et al. (2001)

Winberg (1983) suggested use of the coefficient $Q_{10} = 2.25$ for calculating the metabolic rates of aquatic ectotherms within the tolerance range of temperatures.

Data on the effect of temperature on the metabolism of gelatinous organisms are not numerous. Larson (1987) reported, for ten hydromedusan and two scyphomedusan species, a Q_{10} range of 1.4–5.3, with a mean of about 3. Values of Q_{10} for ctenophores, presented in Table 2, vary widely as well. According to Abolmasova (2001), the Q_{10} for *Mnemiopsis leidyi* was equal to 6.7 during autumn–winter (7–12°C) and 1.8 in spring and summer (12–23°C). In general, data on Q_{10} in ctenophores showed no relation to habitat temperature. In our study the weight-specific respiration rate of *B. ovata* gradually increased within the temperature range of 10–28°C (Fig. 3), independent of body size, suggesting the absence of a temperature preference zone. The mean Q_{10} was 2.17 ± 0.5. This value is close to the value of 2.25 reported by Winberg (1983).

Effect of size on respiration rate

All data on *B. ovata* respiration rates obtained in our experiments and the findings of other authors normalised to 20°C are presented in Fig. 5 and Table 1.

Our results for *B. ovata* with body wet weights >200 mg are in good agreement with the values given by Finenko et al. (2001), Shiganova et al. (2001) and Vostokov et al. (2001) for the Black Sea, Kremer et al. (1986) for the western Bahamas and Ikeda (1974) for Oshoro Bay. Only the weight-specific respiration rate in *B. cucumis* of 70 mg (Ikeda 1974) was five times higher. There were no significant differences between weight-specific respiration rates of adult *Beroe* and *Mnemiopsis* either (Table 1).

Vostokov et al. (2001) suggested that in adult ctenophores the slope value *b* of the regression line for respiration declined with decreasing body weight. For *B. ovata* of 25–50 and 50–115 mm, *b* was equal to 0.72 and 1.0, respectively. However, after examining the experimental data on the metabolism of all sizes of *Beroe*, we can conclude that the relationship between respiration rate and body wet weight changes only during early developmental stages. Regression equations were: $Q = 0.093W^{0.62}$ and $Q = 0.016W^{0.99}$, for *B. ovata* specimens with body wet weights less than and greater than 100 mg, respectively. Therefore, when the body weight increased from 0.021 to 100 mg, the weight-specific respiration rate of juvenile *Beroe* diminished nearly 20-fold (from 0.35 to 0.017 μg O_2 mg^{-1} WW h^{-1}), but did not change for the weight range from 100 to 30,000 mg.

Table 2 Temperature coefficient Q_{10} in Ctenophora. Our data were obtained by the polarographic method (*) and the Winkler technique (**)

Species	Size range (mm)	Temperature range (°C)	Q_{10}	Reference
Beroe ovata	10–20	10–18.7	1.94*	Present study
		10–21	1.95*	
		10–26	1.75*	
		10–26.5	2.19*	
		18.7–26	1.73*	
		18.7–26.5	1.94*	
		21–2621–28	2.03*	
			3.34*	
Beroe ovata	20–50	10–18	1.63*	Present study
		10–20	1.91*	
		10–22.5	2.85*	
		20–27	2.80**	
		22–27	2.13**	
Beroe gracilis	–	8–20	3.56	Gyllenberg and Greve (1979)
Bolinopsis infundibulum	–	8–20	3.73	Gyllenberg and Greve (1979)
Bolinopsis micado	21–50	16–27	1.9	Kasuya et al. (2000)
Mnemiopsis leidyi	—	7–1212–23	6.71.8	Abolmasova (2001)
Mnemiopsis leidyi	8–80	10.3–24.5	4.0	Kremer (1977)
Mertensia ovum	–	0–7	2.1	Percy (1988)
Pleurobrachia pileus	–	2–24	2.72	Gyllenberg and Greve (1979)

Zaika (2002) reported that isometric changes in individual metabolic rates of jellyfish were due to a constant ratio between the mesogloea and whole-body weight and the absence of skeleton. Larson (1987) found that the slope of the regression line for respiration ranged from 0.7 to 1.4 in 12 medusan species. However, most values were not significantly different from $b = 1$. For adult *Aurelia aurita*, values of coefficient b were equal to 0.86 (Frandsen and Riisgard 1997) and 1.0 (Olesen et al. 1994). Later Kinoshita et al. (1997) showed that only large *A. aurita*, with the bell diameters of 17–120 mm, had slopes close to isometric scaling ($b = 0.9$), whereas ephyra to young medusa, with bell diameters of 4.2–19 mm, had slopes of about 0.6. According to Schneider and Weisse (1985), the mean weight-specific respiration rates of the planulae larvae of *A. aurita* were approximately 30 times higher than the values reported for adults.

The decrease in organic content throughout ontogeny in jellyfish may be the reason for the changing relationship between respiration rate and wet weight. The carbon ratio for juvenile lobate ctenophores was found to be ten (Reeve et al. 1989) and seven times (Kasuya et al. 2000) higher than for adult animals. However, a 20-fold increase in the wet weight-specific respiration rate of *B. ovata* larvae in comparison with that of adults cannot be explained solely by changes in body organic content with size, because, in this case, carbon content would increase from 0.16% for adults (Finenko et al. 2003) to 3.2% of wet weight in newly hatched animals (an unrealistic value for ctenophores).

The sources of possible experimental error in the measurement of respiration rates must be carefully considered. When working with zooplankton larvae, one cannot avoid some experimental artefacts due to crowding. Because of their relatively low metabolism, it is necessary to use high densities of individuals in order to register measurable changes in respiration rate over a short period.

Lough and Gonor (1973) found no effect of crowding in *Adula californiensis*, when doubling the density of larvae from 16,000 to 30,000 larvae ml^{-1}. Experiments with five to ten *A. aurita*, with diameters of 4 and 10 mm, in 10-ml chambers did not lead to significant differences in respiration rates at low food concentrations (Olesen et al. 1994). In general, the lack of a concentration-dependent effect on respiration for embryos and larvae of the sea urchin *Strongylocentrotus purpuratus* and the seastar *Odontaster validus* within the range of 16–669 ind. ml^{-1} was reported by Marsh and Manahan (1999). However, Millar and Scott (1967) found that, while the density of *Ostrea edulis* larvae increased from about 25–250 larvae ml^{-1}, oxygen consumption decreased approximately 25-fold. During an incubation period of 24 h, the respiratory rate of larvae of the scallop *Patinopecten yessoensis* declined by 35%, when the density of animals increased from 5 to 25 ml^{-1} (MacDonald 1988). Probably, the oxygen consumption rate of larvae at high densities is diminished due to collisions between individuals or with the walls of experimental chamber, which would decrease swimming activity, or as a consequence of the accumulation of toxic excretory products.

In the present study, we determined the mean respiration rate of newly hatched *B. ovata* larvae during short-term incubation periods (2–3 h), using 60–200 individuals per respirometer of 2 ml. The mean body volume of the larvae was about 0.00002 cm^3. It is easy to calculate that one animal accounts for free space being equal to 500–1,700 larva body volumes, which corresponds to the density of one adult *Beroe* of 100 cm^3 per 50–170 l. Therefore, in the case of isometry of the metabolic rate, *Beroe* larvae should not be influenced by the effects of crowding. According to our data,

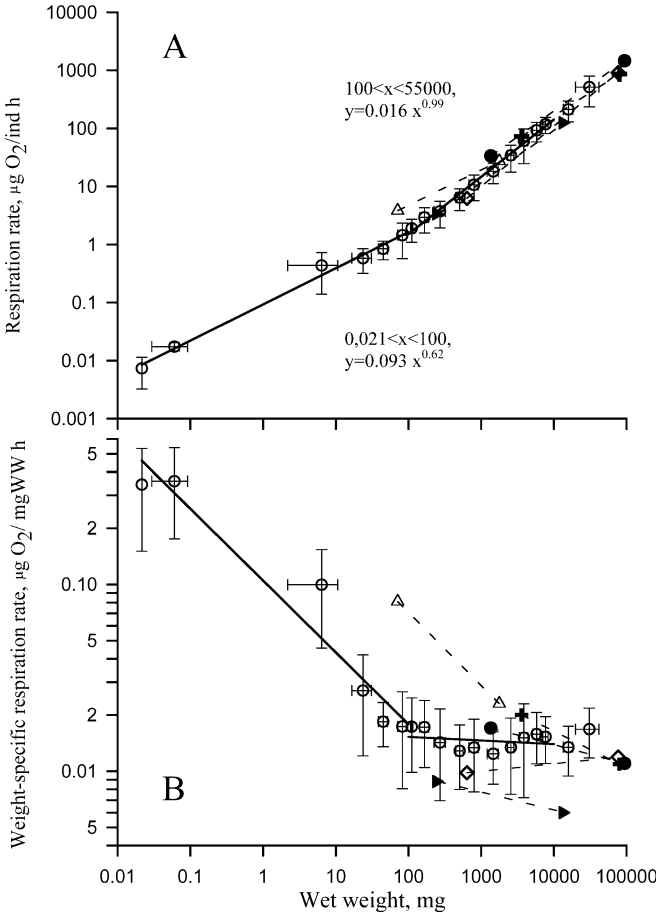

Fig. 5A, B *Beroe ovata*. Respiration rate (**A**) and weight-specific respiration rate (**B**) at 20°C [*open circles* our experimental data; *solid arrowheads* Kremer et al. 1986; *open diamonds* Finenko et al. 2000; *solid circles* Shiganova et al. 2000; *crosses* Vostokov et al. 2001; *open triangles* Ikeda 1974 (for *Beroe cucumis*)]. Values are means (±SD)

weight-specific respiration rates of larvae were significantly higher than those of adults. Thus, if errors due to crowding skewed the results of our experiments, they could only have decreased the expected energy requirements of *Beroe* larvae.

Scope of activity

In unfed animals the scope of activity is related to energy expenditure for swimming and can be determined from the difference between total and basal metabolism. During their search for prey, adult *B. ovata* are able to swim at a speed of 3.5 cm s^{-1} (Vostokov et al. 2001). Bailey et al. (1994) reported that the metabolism of ctenophores may change three- to sevenfold due to the differences in activity level. According to our estimation, the ratio between respiration rates of active and narcotised *B. ovata* amounted to 4.5. This value is considered to be rather high, because the metabolic range for planktonic copepods was found to be 6–7 (Pavlova 1987; Svetlichny et al. 2000) and 4 for cladocerans (Svetlichny and Hubareva 2002).

To compare the energy cost of swimming in ctenophores and in planktonic crustaceans, we expressed the scope of activity of *B. ovata* in terms of energy losses for moving per body carbon mass unit. Schneider (1992) found similar oxygen requirements per gram of carbon biomass in gelatinous (cnidarians, ctenophores and salps) and non-gelatinous (mainly crustaceans) zooplankton, whilst Bailey et al. (1995) showed that in pelagic ctenophores and medusae carbon-specific respiration rates were substantially higher than those in deep-sea benthic crustaceans and fishes.

Our previous results indicated that at 20°C females of the Black Sea copepod *Calanus euxinus*, with a wet weight of 1 mg and carbon content of 100 µg, could swim for a long time at a mean speed of 2.0 cm s^{-1}. The carbon-specific respiration rate of these animals was about 15.0 µg O_2 mg^{-1} C h^{-1} (Svetlichny et al. 2000). Taking into account that carbon constitutes approximately 0.16% of the wet weight of *B. ovata* (Finenko et al. 2003), ctenophores with the same body carbon mass as *C. euxinus* should have a length of 6 mm and a wet weight of 63 mg. The carbon-specific respiration rate in those individuals was equal to 12.0 µg O_2 mg^{-1} C h^{-1}. Using videotaping, we showed that *B. ovata* of 6 mm could swim constantly near the water surfaceat a speed of 1–2 cm s^{-1} (authors' unpublished data). Consequently, ctenophores and planktonic crustaceans with the same body carbon mass have similar energy losses and swimming speeds, but *Beroe* is able to move a volume that is 60-fold greater. On the one hand, these results suggest that *B. ovata* use the main part of their energy budget for swimming (especially taking into account the extremely high ratio between wet weight and the weight of biologically active tissues). On the other hand, the data may be evidence of the high energetic efficiency of locomotion in this ctenophore species.

Ecological energetics

Based on the respiration rate (Q) of *B. ovata*, we estimated their maximum specific rations (C, % of body energy content) using the equation: $C=(Q+P+F)100/m$, where P is the production, F is the energy of undigested food and m is the body energy content, assuming 1 mg WW = 0.64 cal (Finenko et al. 2001). According to Reeve et al. (1978), the maximum assimilation efficiency ($Q+P/C$) in ctenophores amounted to 0.72–0.75 at low food concentrations. We assumed a net growth efficiency coefficient of 0.6 (Vinogradov et al. 2000), with the calorific equivalent of oxygen consumed as 3.4 cal mg^{-1} O_2. The calculated daily rations of animals with wet weights exceeding 100 mg in our experiments (15–23%) were consistent with the maximal daily rations reported by Vinogradov et al. (2000) for adult *B. ovata* (Fig. 6). In contrast, in newly hatched larvae, C even reached 480%, suggesting high ecological valency of young size-classes

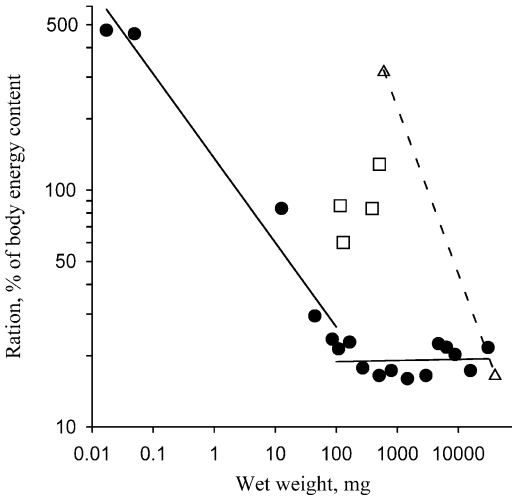

Fig. 6 *Beroe ovata*. Specific rations (C, % of body energy content) (*closed circles* maximum potential daily ration by our calculations; *open squares* Finenko et al. 2001; *open triangles* Finenko et al. 2003)

of the *Beroe* population. Probably, the food requirements of larvae are even higher. During their feeding experiments, Finenko et al. (2003) showed that the specific daily ration of *B. ovata* increased from 20% to 360% when body wet weight diminished from 40,000 to 500 mg. Such a high activity level in the young size-classes of *B. ovata* would be beneficial, not only in decimating the high abundance of very small *M. leidyi* individuals (Kideys and Moghim 2003), but also in controlling the number of adult *Mnemiopsis*, which may be attacked by *Beroe* larvae as well (authors' personal observations).

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