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Seasonal change in acclimatised respiration rate of *Temora longicornis*

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ABSTRACT: We investigated the seasonal changes in the respiration rate (R) of adult *Temora longicornis* (Müller) acclimatised to *in situ* conditions over 1 yr. Mean (±1 SE) R varied from 50.5 ± 2.8 nl O_2 ind.$^{-1}$ h^{-1} in December to 73.2 ± 3.53 nl O_2 ind.$^{-1}$ h^{-1} in August for copepods of mean body dry weight (DW) of 33.5 ± 1.1 and 26.3 ± 0.95 µg, respectively. Males represented ~8% of the total measurements, and their respiration did not differ significantly from that of females. R scaled isometrically with dry weight (DW), i.e. the allometric exponent of the power function ($R = a\mathrm{DW}^b$) did not differ significantly from unity (b = 0.83 to 1.35). The relationship between *in situ* weight-specific respiration rate (R_{sp}) and temperature (T) was described by a sigmoid trend with Q_{10} ranging from 1 to 2.88 (mean 1.57 to 1.89). In contrast, the acclimated and acutely measured R_{sp} of copepods maintained under optimal feeding conditions in the laboratory increased exponentially with temperature and were characterised by higher mean Q_{10} of 2.05 and 2.41, respectively. Acclimatised ln R increased significantly with ln DW, T, ln chlorophyll *a* (ln Chl) and ln egg production rate (ln EPR). Our results indicate that seasonal changes in *T. longicornis* respiration rate are not simply determined by body mass and temperature but also reflect copepod nutritional and reproductive condition. We argue that predictive ecological models using fixed thermal coefficient values may overestimate copepod respiration, particularly under ambient conditions limiting growth and reproduction. Our findings have important implications for the calculation of carbon flow in marine food-webs and for understanding how zooplankton physiology responds to changes in global temperature.

KEY WORDS: *Temora longicornis* · Respiration · Acclimatisation · Acute rate · Temperature · Reproduction

INTRODUCTION

Respiration is a fundamental property of organisms and ultimately represents the main energy loss pathway within ecological systems. Thus, as the most abundant and diverse aquatic metazoan, marine copepods play an important role, through their respiration, in shaping the structure and dynamics of food-webs and the flow of carbon in the ocean. Therefore, knowledge of how copepod respiration changes with *in situ* conditions is central to understanding the mechanisms determining community diversity, secondary production and biogeochemical cycles in the ocean.

In temperate latitudes, copepods experience considerable fluctuation in ambient conditions over the seasonal cycle, which exerts a profound effect on their metabolism (e.g. Mauchline 1998). In copepods, as in poikilotherms in general, respiration rate is considered to vary mainly as a function of body mass and ambient temperature (Peters 1986, Ikeda et al. 2001, Brown et al. 2004). Published data, however, suggest that other factors, such as food quantity, food quality and temperature acclimatisation, are also important (Conover 1959, Conover & Corner 1968, Marshall & Orr 1958, 1966, Butler et al. 1970, Gaudy 1973). Respiration is also closely coupled with growth and reproduction (Mc Neill & Lawton 1970), both of

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which can represent a substantial energetic cost to an organism (Parry 1983, Kiørboe et al. 1985, Clarke 1993). Hence, several authors have argued that seasonal changes in the respiration rate of poikilotherms could be mainly a reflection of the effects of temperature on growth and reproduction rather than a direct effect of temperature on respiration (Parry 1983, Clarke 1993). Poikilotherms may also display species-specific physiological plasticity and genetic adaptation which enable them to cope with seasonal and latitudinal changes in temperature (Pretch 1958, Somero 2012, Dam 2013).

Despite previous studies, the relative importance of different environmental factors on copepod respiration remains unclear. Understanding how copepod metabolism varies with ambient conditions is also important for the correct parameterization of ecosystem models (Stock & Dunne 2010). Some models have proposed simple equations to describe the metabolic rate of all organisms from 'first principles', using a combination of body mass scaling and thermodynamic laws (Gillooly et al. 2001, Enquist et al. 2003, Brown et al. 2004). These predictive models generally use fixed body mass scaling, such as b = 0.75, and metabolic thermal coefficient values, such as the activation energy (E_a) = 0.63 eV derived from the Arrhenius formulation. Similarly, other modelling studies commonly use empirically derived values of the thermal coefficient Q_{10} between 2 and 4 (e.g. Olonscheck et al. 2013). However, these E_a and Q_{10} values are typically derived from acutely measured metabolism-temperature rates (i.e. M-T curves) of animals maintained under optimal feeding conditions (Peters 1986). In nature, however, copepods can often be food limited (Hirst & Bunker 2003), and under such circumstances, the respiration rate is reduced and does not respond to temperature changes in the same way of that of well-fed organisms (Mayzaud 1976, Thor 2003). Hence, Cossins & Bowler (1987) have argued that eco-physiological studies should measure acclimatised metabolic rates as these are ecologically meaningful. Acclimatised rates refer to the physiological rates of poikilotherms measured at *in situ* conditions. In contrast, acclimated rates refer to the rates of poikilotherms maintained in the laboratory at a given temperature, whereas 'acute' rates refer to measurements made on poikilotherms maintained in the laboratory and exposed to a sudden change in ambient conditions, generally temperature (Cossins & Bowler 1987).

Overall, published data on respiration rates of copepods acclimatised to *in situ* conditions are very scarce. One of the reasons for such scarcity is that the methods adopted by previous investigators to measure seasonal changes in respiration rate have been often inadequate; for instance, most studies have disregarded the effect of the nutritional condition and acute temperature exposure on metabolism by measuring copepods maintained under different feeding conditions at fixed arbitrary temperatures (Berner 1962, Conover 1962, Marshall & Orr 1966, Gaudy 1973, Gaudy & Thibault-Botha 2007). Thus, differences in methodological approaches used in the literature to measure copepod respiration rates make comparisons and synthesis of published data difficult and their use in predictive ecological models unreliable.

The small copepod *Temora longicornis* often dominates the spring and early summer zooplankton communities of coastal temperate waters of the North Atlantic (Peterson 1985, Fransz et al. 1991, Castellani & Lucas 2003). In its environment, this species experiences a wide fluctuation in temperature and feeding conditions over the seasonal cycle (Castellani & Altunbaş 2006). Because of its reduced ability to store body lipids, *T. longicornis* closely depends on its food supply to meet basal energy requirements, let alone to grow and reproduce (Clarke & Walsh 1993, Kreibich et al. 2008). Such physiological trait makes this species an ideal model organism to study how environmental change affects the respiration rate of small neritic copepods. Hence, the aim of the present study was to investigate how the acclimatised respiration rate of adult copepod *T. longicornis* varies in relation to seasonal changes in body mass, temperature, salinity, prey availability and reproduction. In addition, we explore whether temperature-acclimatised respiration rates differ from acclimated and acutely measured rates of copepods maintained in the laboratory under high food concentrations.

MATERIALS AND METHODS

Sampling

Zooplankton were collected weekly, between April 1996 and April 1997, with a 200 µm mesh WP-2 plankton net fitted with a non-filtering cod-end from the St. George Pier, Menai Strait (53° 13′ N, 4° 09′ W), eastern Irish Sea. After collection, the plankton was immediately re-suspended into an opalescent, polypropylene aspirator containing 20 l of natural seawater pre-screened through a 200 µm mesh filter to exclude predators. Salinity (S, ppt) and temperature (T, °C) were measured with a CTD (Braystoke, Series

600) at 2 m intervals from the surface to the seabed (i.e. maximum of 20 m water depth) during each sampling. Water samples for chlorophyll *a* concentration (Chl, µg l^{-1}) and microplankton community characterisation were collected with a 2 l Niskin bottle at ~2 m depth from the surface. Chl was determined from water samples of 100 to 750 ml, filtered onto GF/F filters, extracted in neutralised 90% acetone solution for 24 h at 4°C in the dark and measured using a Turner 10 fluorometer (Tett 1987). Microplankton samples were immediately fixed with Lugol's iodine to 2% final concentration (Kiørboe & Nielsen 1994), stored in 100 ml dark glass bottles in the dark at 4°C and analysed by the Utermöhl (1958) technique within 1 mo.

Copepod maintenance prior to respiration rate experiments

Adults *Temora longicornis* were sorted from the catch within 1 h of collection in a walk-in cold room set at *in situ* temperatures between 5 and 17.5°C. The copepods were used for 1 of the 3 following experiments: to investigate (1) seasonal changes in acclimatised respiration rate, (2) the respiration rate of copepods acclimated to temperature in the laboratory and (3) the respiration rate of copepods exposed to a sudden (i.e. acute) temperature change. Here, we refer to 'acclimatised' rates for the respiration rates of copepods measured at *in situ* conditions, to 'acclimated' rates for measurements on copepods maintained in the laboratory at a temperature different from *in situ* and to 'acute' rates for measurements made on copepods maintained in the laboratory and exposed to a sudden temperature change (Cossins & Bowler 1987). Thus, copepods were maintained under different conditions according to the type of experiment performed. The *T. longicornis* measured for (1) the seasonal respiration rate experiment were kept in batches of up to 10 ind. l^{-1} in 5 l glass jars filled with natural seawater pre-screened through a 250 µm mesh sieve and in temperature-controlled water baths for a maximum of 1 d at their original *in situ* temperature. The respiration rates of copepods that were (2) acclimated and (3) acutely exposed were measured over the temperature range of 4 to 20°C, and these copepods were maintained in the laboratory on an ad libitum diet of the cultured flagellate alga *Rhinomonas reticulata* (Novarino 1991) for 1 wk before measurements. The water in the jars was changed every other day by sieving the copepods in a submerged 200 µm sieve to avoid damage to the animals and gently re-suspended with some remaining water in a cleaned jar containing UV-treated filtered (0.2 µm) seawater (UFSW) and fresh cultured micro-algae. Jars were cleaned overnight with a 1% solution of sodium hypochlorite and thoroughly rinsed with hot tap water to remove chemical residues.

We also carried out a preliminary experiment to assess the time required by freshly caught copepods to attain a stable routine respiration rate once deprived of food to avoid the effect of the increase in oxygen consumption resulting from 'stress' after capture (Marshall & Orr 1966) and from feeding metabolism (viz. specific dynamic action [SDA]; Kiørboe et al. 1985, Secor 2009). Freshly caught copepods were placed in filtered seawater and their respiration rate measured continuously until the respiration rate stabilised. An inverse function fitted to the data set obtained from this time course experiment indicated that copepod respiration rate reached a stable routine rate ~10 h after capture and that such respiration rate remained stable at ~1.7 nl $µg^{-1}$ dry weight (DW) h^{-1} over at least the following 24 h (Fig. 1). Hence, a minimum time of 10 h since the start of fasting was allowed to elapse prior to all respiration rate measurements carried out in the 3 experiments outlined above.

Respiration rate measurements

Seasonal variation in copepod respiration rate in the field

We measure the seasonal variation in the respiration rate of adult *Temora longicornis* between April 1996 and April 1997. Here, respiration rate corresponds to routine rate, that is, the oxygen consumed

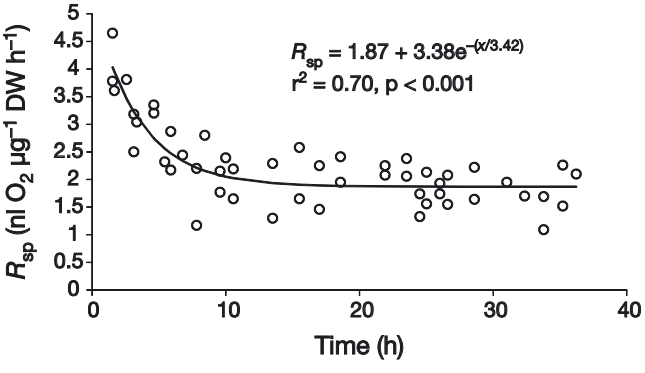

Fig. 1. *Temora longicornis*. Time course of changes in the weight-specific respiration rate (R_{sp}) of fasting *T. longicornis*. Time 0 h is the time at which copepods were deprived of food

over time by fasting copepods at minimum uncontrolled motor activity (Ikeda et al. 2001). The respiration rate of fasting copepods was measured individually using a polarographic oxygen electrode (pO_2-electrode, Strathkelvin model 1302) sensitive to changes in oxygen tension in a fluid media (Kanwisher 1959). The pO_2-electrode was fitted to the base of a closed transparent glass micro-respirometer chamber of 100 to 150 µl in volume to allow regular monitoring of animal activity and behaviour. The temperature inside the respirometer was kept constant within ± 0.2°C by a thermostat through a recirculating water bath system allowing a continuous water flow in the chamber water jacket. The pO_2-electrode was connected to an O_2 meter (Strathkelvin inst. model 781) to display the change in oxygen tension inside the respirometer and through this to a chart recorder to obtain a plot of the respiratory activity of the copepods over the time of observation. The pO_2-electrode was regularly calibrated with distilled water containing sodium dithionite to set the zero point on the O_2-meter, and then with air-saturated UFSW to set the 100% air saturation level. The electrode response was linear over the range 0 to 100% air saturation; hence, the amount of oxygen present in the chamber was calculated with the algorithm of Green & Carrit (1967). The 1302 microcathode oxygen electrode is a high precision electrode with a very small oxygen consumption rate (i.e. 0.5×10^{-10} to 3×10^{-10} mg O_2 min^{-1}). We used a low permeability polypropylene membrane so most of the resulting oxygen gradient is confined to the distance between the outside of the membrane and the cathode surface. Consequently, there is no need for vigorous physical movement of the solution to replenish the oxygen at the outer surface of the membrane. However, correction for electrode oxygen consumption was performed at regular intervals by running an oxygen respiration measurement without the animal (i.e. the blank). The blank was then subtracted from the oxygen rate measurement of the copepod. Copepods were measured under dim light conditions since bright light has been shown to increase the respiration rate in some species (Marshall et al. 1935). Respiration measurements were run for 1 h maximum.

Copepod DW vs. length relationship

At the end of each experiment, the prosome length (PL) of copepod was measured with an eye-piece graticule under a dissecting microscope (Wild M5). Lengths were converted to body mass from the regression ln DW = 2.79 ln PL − 15.9 ($r = 0.92$, $p < 0.001$, $df = 29$), constructed using copepods from the present study and published by Castellani & Altunbaş (2006), where PL is prosome length in µm, and DW is the dry weight in µg. The relationship was obtained by measuring 30 groups of adult copepods consisting of between 20 and 30 individuals of similar prosome length (±20 µm) over the full size range. The copepods were dried in pre-weighed aluminium cups in an oven at 50°C until the weight stabilised, and they were weighed to the nearest 1 µg with a microbalance (Cahan). Copepod DW was converted to carbon assuming a specific-C content of 40% (Omori & Ikeda 1984).

Copepod egg production rate

Measurements of egg production rates (EPR) of *Temora longicornis* were carried out at *in situ* conditions concomitantly to respiration rate measurements as described by Castellani & Altunbaş (2006). Briefly, between 25 and 30 intact active female *T. longicornis* randomly selected from the catch were incubated individually in 250 crystallising dishes filled with natural seawater pre-screened through a 53 µm mesh. The dishes were kept for 24 h in a temperature-controlled water bath at the ambient surface temperature ± 0.2°C (i.e. 1 m depth), under artificial lighting, with an ambient light/dark regime. After incubation, the females were gently removed from the crystallising dishes with a pipette, the content of each dish was filtered through a 53 µm sieve, and the eggs and nauplii were retained, stained with Lugol's iodine and counted in a Bogorov's tray under a dissecting microscope (Wild M5). The egg counts of copepods found dead or moribund at the end of the incubation time were discarded. EPR was calculated as the total number of eggs produced per female over the 24 h incubation period.

Calculation of the thermal coefficients Q_{10} and E_a

The relationship between the seasonal changes in the respiration rate of *Temora longicornis* with temperature was investigated determining the thermal coefficient Q_{10}, which is commonly used to describe the increase in physiological rates over a 10°C change (Schmidt-Nielsen 1990) (Eq. 1):

$$Q_{10} = \left(\frac{R_1}{R_2}\right)^{\frac{10}{(T_1 - T_2)}} \quad \text{(Eq. 1)}$$

where R_1 and R_2 are the respiration rates at the temperatures T_1 and T_2 respectively.

We also investigated the dependence of respiration on temperature using the Arrhenius equation (Eq. 2) by plotting the reciprocal of the absolute temperature, θ, expressed in kelvin (K) against the respiration rates:

$$R = Ae^{-E_a/\bar{R}\theta} \quad \text{(Eq. 2)}$$

where R is the rate constant, A is the frequency factor constant, e is the base of the natural logarithm (i.e. 2.718..), θ is the absolute temperature in K, $\bar{R}$ is the gas constant (i.e. 8.31 J mole^{-1} K^{-1}), and E_a (i.e. in J mol^{-1}) is the activation energy. The change in rate constant with temperature can be predicted from the proportionality constant E_a of an integrated form of the Arrhenius equation, that is:

$$\ln\left(\frac{R_2}{R_1}\right) = \frac{E_a}{\bar{R}\left(\frac{1}{\theta_1}-\frac{1}{\theta_2}\right)} \quad \text{(Eq. 3)}$$

where R_1 and R_2 are the rate constants at temperatures θ_1 and θ_2 in K. The Arrhenius plot of ln R against the reciprocal of the absolute temperature gives a straight line with a slope equal to $E_a/\bar{R}$ from which E_a can be calculated, as shown in Eq. 4:

$$E_a = \text{slope} \times 8.31\ (\text{J mol}^{-1}) \quad \text{(Eq. 4)}$$

RESULTS

Environmental conditions and microplankton composition

The sampling area is characterised by shallow water depth between 1 and 20 m, strong tidal currents and high tidal ranges between 3.4 m and 6.6 m, resulting in a well-mixed water column throughout the year. Table 1 and Fig. 2 summarise the seasonal changes in ambient variables at the sampling site already reported by Castellani & Altunbaş (2006). Briefly, *in situ* temperature (T, °C) recorded during the present study varied from a minimum of 5°C in February to a maximum of 17.5°C in August (Fig. 2a). Salinity changed little, reaching maximum values of 34.1 ppt in summer and a minima of 31.7 ppt in autumn (Table 1), during the highest local annual rainfall (i.e. 110 to 126 mm mo^{-1}; Eden 1997).

The early spring increase of Chl from low winter concentrations of 0.5–0.9 to ~3–8 µg l^{-1} (Fig. 2b) was almost exclusively diatomaceous and included species like *Ditylum brightwelli*, *Skeletonema costatum*, *Chaetoceros* sp., *Asterionella* sp. and *Thalassiosira* sp. Between April and June, the microplankton community was replaced by the mixed diatom-flagellates bloom of *Phaeocystis* sp. and *Rhizosolenia delicatula* during which Chl increased to ~16 to 26 µg l^{-1}. The spring bloom was followed by euglenoids and cryptomonad-like flagellates. A series of monospecific diatom blooms of *Leptocylindrus danicus*, *Rhizosolenia styliformis* and *Guinardia flaccida* developed in summer and autumn, with Chl ranging between ~3 and 8 µg l^{-1}. Ciliate biomass, mostly belonging to the genus *Strombidium*, also peaked between spring and early summer and was correlated with Chl ($r = 0.67$, $p < 0.05$, $df = 33$). Dinoflagellates, on the other hand, peaked in summer after the Chl maxima (Castellani & Altunbaş 2006).

Table 1. Sampling dates for *Temora longicornis* used for the respiration rate experiments and corresponding environmental variables. Dates given as dd/mm/yyyy

Sampling date	T (°C)	Salinity	Chl *a* (µg l^{-1})
17/05/1996	10.0	34	12.80
27/05/1996	10.0	34	25.92
02/06/1996	12.0	34	15.55
10/06/1996	13.0	34	8.99
12/06/1996	13.0	34	8.99
08/08/1996	17.5	33.8	4.84
11/08/1996	17.5	33.8	4.84
14/08/1996	17.5	33.8	2.76
14/09/1996	16.0	34	3.28
17/09/1996	16.0	34	3.28
06/10/1996	15.0	33.7	1.05
10/10/1996	15.0	33.7	1.52
30/10/1996	15.0	33.7	1.35
17/11/1996	10.1	33.6	0.48
28/11/1996	7.0	31.76	1.05
01/12/1996	7.0	33.1	0.62
12/12/1996	7.0	33.6	0.76
01/02/1997	5.0	33.04	0.33
05/02/1997	5.0	33.04	0.95
05/04/1997	8.0	33.8	2.11
12/04/1997	8.0	33.7	8.42
16/04/1997	9.0	33.7	8.42

Seasonal variation of copepod respiration with biotic and abiotic variables

Temora longicornis respiration rates began to increase between January and April, reached a maximum in August (R, mean ± SE, 83.2 ± 7.6 nl O_2 ind.$^{-1}$ h^{-1}) and a lower secondary peak in October–November before declining to the annual minimum

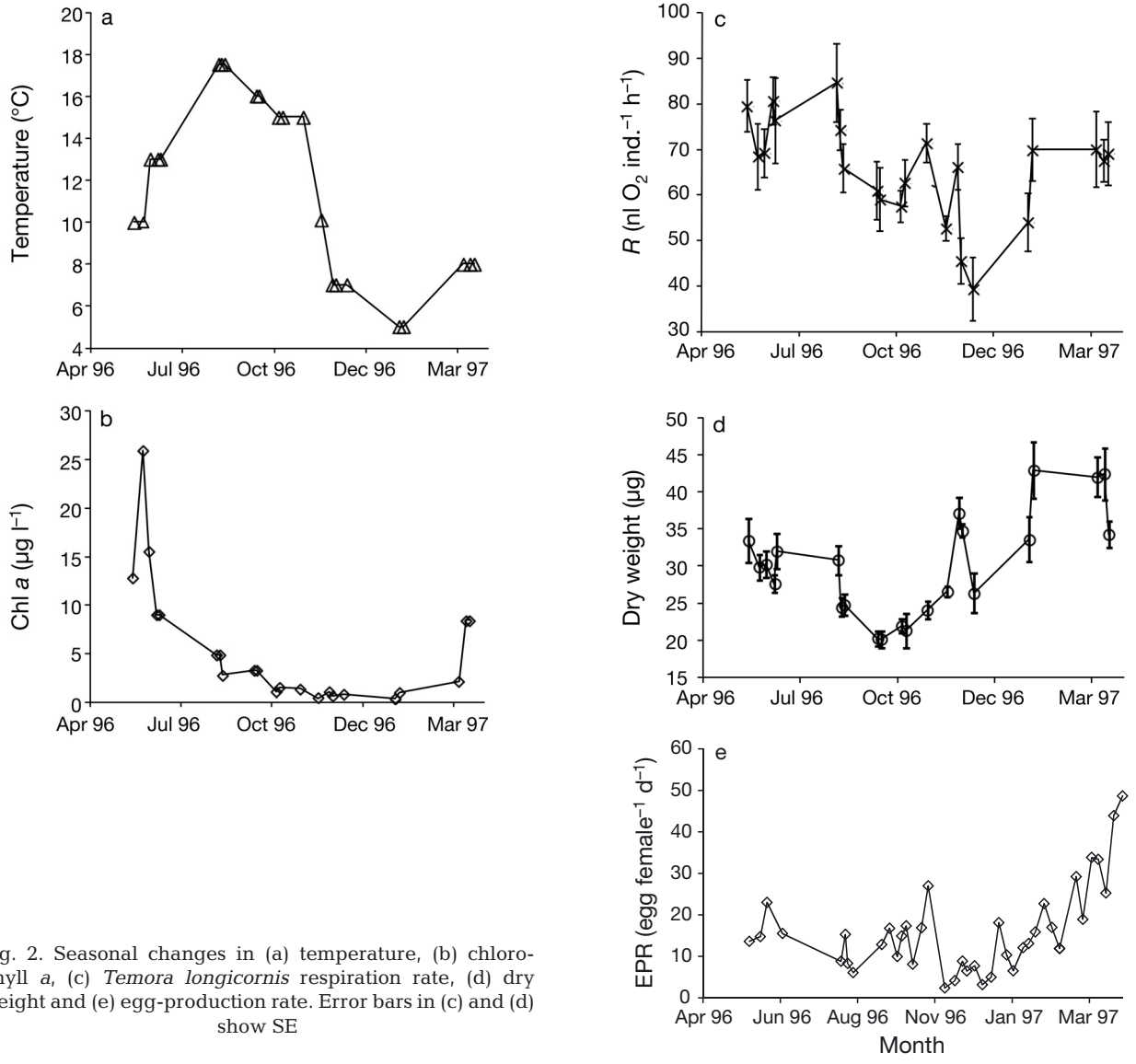

Fig. 2. Seasonal changes in (a) temperature, (b) chlorophyll *a*, (c) *Temora longicornis* respiration rate, (d) dry weight and (e) egg-production rate. Error bars in (c) and (d) show SE

in December (*R*, mean ± SE, 40.4 ± 5.7 nl O_2 ind.$^{-1}$ h^{-1}) (Fig. 2c). In contrast, copepod DW (mean ± SE) ranged between 19.6 ± 1.1 µg in September and 42.9 ± 3.7 µg in February (Fig. 2c,d).

The seasonal change in EPR at the study site has already been reported in detail by Castellani & Altunbaş (2006). Briefly, *Temora longicornis* produced eggs all year round. A mean (± SE) EPR maximum of 48 ± 7 eggs female^{-1} d^{-1} occurred in spring–early summer during the phytoplankton bloom, whereas a minimum of 1.3 ± 0.5 eggs female^{-1} d^{-1} was recorded in autumn–winter (Fig. 2e). *In situ* copepod respiration rate followed the variation in DW, chl *a*, EPR and *T* (Fig. 2). Logarithmically transformed respiration rate (ln *R*) was significantly correlated with ln DW ($r = 0.44$; $df = 297$; $p < 0.001$), ln Chl ($r = 0.33$; $df = 297$; $p < 0.001$), ln EPR ($r = 0.33$; $df = 186$; $p < 0.001$), *T* ($r = 0.23$; $df = 297$; $p < 0.001$) and salinity ($r = 0.19$; $df = 297$; $p < 0.001$). Table 2 shows the results of the multiple regression analysis between ln *R* and ln DW, *T*, ln Chl, and ln EPR for the temperature intervals 5 to 17.5 and 8 to 13°C (i.e. the temperature range within which respiration rate increased linearly with temperature, see Fig. 4). The normalised ß-coefficient from the multiple regression analysis, over both temperature intervals, indicated that ln DW (ß = 0.6 to 0.5) explained the largest proportion of variability in copepod *R* followed by *T* (ß = 0.4 to 0.5), ln Chl (ß = 0.2) and ln EPR (ß = 0.1), whereas salinity was not significant. Table 2 also shows that the goodness of fit of the regression is higher for the 8 to 13°C temperature interval where respiration rate increases linearly with temperature.

Table 2. Multiple regression analysis between ln-transformed *Temora longicornis* respiration rate (ln R, nl O_2 ind.$^{-1}$ h^{-1}) with copepod body dry weight (ln DW) *in situ* temperature (T), chlorophyll *a* (ln Chl) and egg-production rate (ln (EPR + 1), eggs female^{-1} d^{-1}). The thermal coefficient Q_{10} and the percentage of body carbon requirement calculated from the equation models are also shown. θ: absolute temperature (in kelvin, K); E_a: activation energy. Note that the F-test for all regression models is statistically significant at the 1% level. $^{*}p < 0.10$, $^{**}p < 0.05$, $^{***}p < 0.01$

Regression model **(a)**	ln DW (µg)	T (°C)	ln Chl (µg l^{-1})	ln (EPR+1)	Intercept	n	r^2	F-value	Q_{10}	% body-C 5°C	% body-C 10°C	% body-C 17.5°C
Temperature range: 5 to 17.5°C												
1) ln R = 1.00 ln DW + 0.06 T + 0.03	1.00*** (0.056)	0.06*** (0.005)			0.03 (0.218)	299	47.6	180.94	1.89	4.46	6.02	9.16
2) ln R = 0.96 ln DW + 0.06 T + 0.05 ln Chl + 0.21	0.96*** (0.058)	0.06*** (0.005)	0.05*** (0.014)		0.21 (0.225)	299	49.6	124.40	1.75	4.51	7.25	10.25
3) ln R = 0.87 ln DW + 0.05 T + 0.05 ln Chl + 0.04 ln (EPR + 1) + 0.56	0.87*** (0.099)	0.05*** (0.007)	0.05** (0.020)	0.04** (0.017)	0.56 (0.377)	188	43.9	36.79	1.57	4.75	7.62	9.90
Temperature range: 8 to 13°C												
4) ln R = 1.04 ln DW + 0.11 T − 0.50	1.04*** (0.067)	0.11*** (0.010)			−0.50* (0.272)	189	53.2	146.81	2.88		18.2	
5) ln R = 1.00 ln DW + 0.09 T + 0.05 ln Chl − 0.25	1.00*** (0.071)	0.09*** (0.011)	0.05*** (0.017)		−0.25 (0.290)	189	54.7	99.33	2.39		7.07	
6) ln R = 0.83 ln DW + 0.07 T + 0.06 ln Chl + 0.03 ln (EPR + 1) + 0.46	0.83*** (0.119)	0.07*** (0.014)	0.06** (0.025)	0.03 (0.021)	0.46 (0.474)	121	52.5	32.35	2.01		6.83	

(b)	ln DW (µg)	θ (1/K)	ln Chl (µg l^{-1})	ln (EPR + 1)	Intercept	n	r^2	F-value	E_a (KJ mol^{-1})	E_a (eV)
Temperature range: 5 to 17.5°C										
7) ln R = 0.99 ln DW − (5163/KT) + 18.9	0.99*** (0.055)	−5163*** (385.64)			18.9 1.28	299	47.8	180.16	42.93	0.45
8) ln R = 0.95 ln DW − (4585/KT) + 0.05 ln Chl + 16.9	0.95*** 0.058	−4585*** 395.83	0.045*** 0.014		16.89 1.31	299	49.5	122.25	38.12	0.39
9) ln R = 0.85 ln DW − (3670/KT) + 0.05 ln Chl + 0.03 ln (EPR + 1) + 14.01	0.85*** 0.099	−3670*** 570	0.046** 0.0198	0.034** 0.0169	14.01 1.83	188	35.8	43.7	30.51	0.31
Temperature range: 8 to 13°C										
10) ln R = 1.01 ln DW − (8627/KT) + 31.1	1.01*** 0.067	-8627*** 812			31.09 2.83	189	53.6	144.02	71.72	0.74
11) ln R = 0.99 ln DW − (7259/KT) + 0.04 ln Chl + 26.3	0.989*** 0.071	−7259*** 912	0.041** 0.0177		26.3 3.15	189	54.6	96.9	60.35	0.63
12) ln R = 0.81 ln DW − (5740/KT) + 0.05 ln Chl + 0.03 ln (EPR + 1) + 21.48	0.81*** 0.11	−5740*** 1182	0.054** 0.025	0.026 0.021	21.48 4.02	121	31.66	52.3	47.72	0.49

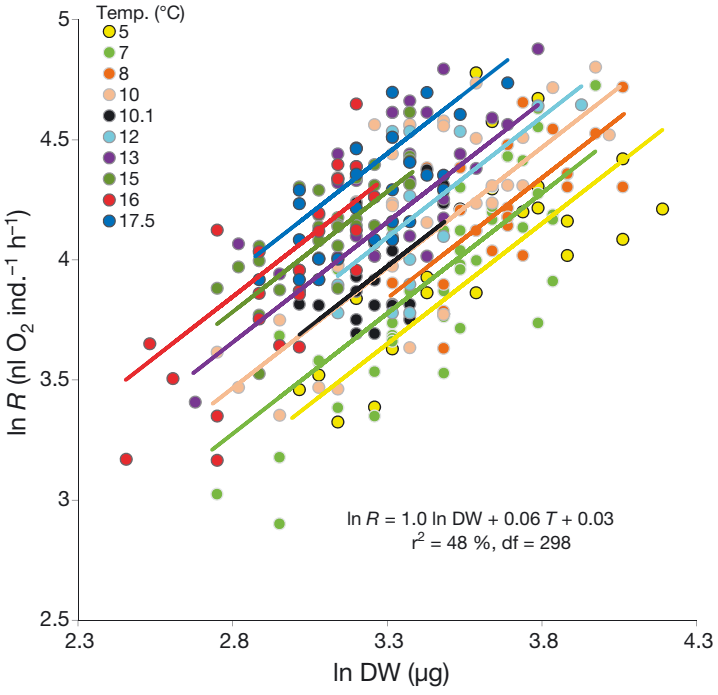

Fig. 3. *Temora longicornis.* ln-transformed respiration rate (ln *R*) of *T. longicornis* versus copepod dry weight (ln DW). Lines represent fitted values for each temperature obtained from the multiple regression between ln *R*, ln DW and temperature, which is used as a proxy to differentiate between the monthly experimental trials (Table 3)

Relationship between respiration and body DW

Copepod respiration rate increased with DW with the largest copepods showing the widest range in rates (Fig. 3). Table 3 summarises the relationship between respiration rate and body DW of *Temora longicornis* for different months and *in situ* temperatures. Following logarithmic transformation, the slopes (i.e. *b*) of the equations ranged from 0.83 to 1.35, and *t*-test analysis indicated that they were not significantly different from unity. Comparison of the slopes using analysis of covariance (ANCOVA) (generalized linear model [GLM], df = 9, $F = 0.44$, $p = 0.915$) also showed that they were not significantly different from each other. Overall, the total yearly variation in copepod respiration rates with DW was larger than the variation for each individual month, and a positive trend in respiration rate with temperature was evident (Fig. 3). Statistical analysis using ANCOVA (df = 9, $F = 25$, $p < 0.0001$) confirmed that the intercepts of the regression equations in Table 3 were significantly different from each other.

Relationship between respiration and *in situ* temperature

The variation in mean monthly weight-specific respiration rate (R_{sp}, nl O_2 µg^{-1} DW h^{-1}) with temperature was characterised by a sigmoid pattern (Fig. 4); R_{sp} remained at its lowest between 5 and 7°C from December to April, it increased between 8 and 13°C from April to May and reached a maximum plateau between 15 and 17.5°C from June to August. The pattern of *R* with temperature did not change for different DW, suggesting that the sigmoid trend was not caused by seasonal variation in copepod body mass. A logistic function model was fitted to the data set as such model fit statistically ($r^2 = 93$ %, see Fig. 4) better than the linear regression model ($r^2 = 86$ %). The multiple regression model shown in Table 2 predicts that the highest rate of increase in the acclimatised respiration of *Temora longicornis* occurs between 8 and 13°C (i.e. $Q_{10} = 2.01$ to 2.88). In contrast, above and below this temperature range, R_{sp} remains virtually constant (i.e. $Q_{10} = 1$). Overall, the change in R_{sp} over the whole *in situ* annual temperature range was characterised by Q_{10} varying from 1.57 to 1.89 depending on the variables included in the regression model (Table 2a).

Table 2b shows the E_a values calculated from the Arrhenius equation (i.e. Eq. 4). E_a varied from 30.5 to 42.9 KJ mol^{-1} (or 0.31 to 0.45 eV) over the whole *in situ* temperature range reaching the highest values

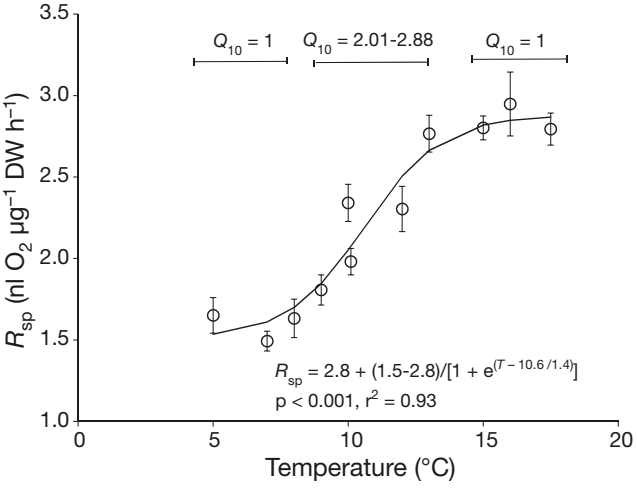

Fig. 4. *Temora longicornis.* Weight-specific respiration rate (R_{sp}) of *T. longicornis* versus temperature. The Q_{10} values calculated from the regressions in Table 2 for the temperature intervals 5 to 7, 8 to 13 and 15 to 17.5°C are also shown. Continuous line represents the logistic function fitted to the data. Error bars are SE

between 47.7 and 71.7 KJ mol^{-1} (or 0.49 to 0.74 eV) when calculated over the 8 to 13°C temperature range.

Relationship between respiration with chl *a* and EPR

Figs. 5 & 6 show the pattern of increase in *R* with Chl and EPR. Both relationships were characterised by an asymptotic trend with *R* rates reaching a maximum around 5 µg Chl l^{-1} and 15 egg female^{-1} d^{-1}. These results suggest that *R* reaches its maximum values during the phytoplankton bloom, i.e. when feeding conditions for copepods are most favourable (Fig. 2b). Moreover, the relatively constant *R* (i.e. energy consumption) for EPR increasing from ~15 to 50 eggs female^{-1} d^{-1} suggests higher reproduction efficiency possibly linked to higher food quality, such as the increase in nitrogen-rich ciliate diet during the spring bloom.

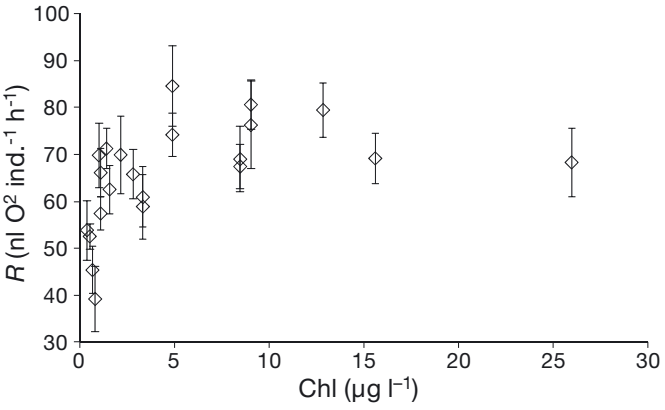

Fig. 5. *Temora longicornis.* Respiration rate (*R*) versus chlorophyll *a*. Error bars are SE

Changes in respiration rate with gender

Adult males represented ~8% of the total copepods in the population sampled during the present study, and they were smaller than females. As a result, the mean R_{sp} of *Temora longicornis* males (1.67 ± 0.12 nl O_2 µg^{-1} DW h^{-1}) was on average lower than that of females (2.27 ± 0.048 nl O_2 µg^{-1} DW h^{-1}). However, comparison of copepods of similar DW measured at the *in situ* temperature of 6.5°C showed that the respiration rate of the males did not differ significantly from that of the females (Table 4).

Table 3. Summary of regression analysis between *Temora longicornis* ln-transformed respiration rate (ln *R*, nl O_2 ind.$^{-1}$ h^{-1}) and body dry weight (ln DW, µg) (see Fig. 3). The temperature (*T*, °C) at which respiration rate was measured, the number of measurements (n), the mean (SD) copepod prosome length (PL, µm), DW and *R* are also shown. $^{*}p < 0.10$, $^{**}p < 0.05$, $^{***}p < 0.01$; coeff.: coefficient

Date	*T*	n	PL Mean (SD)	DW Mean (SD)	*R* Mean (SD)	Intercept Coeff. (SE)	Slope Coeff. (SE)	r^2 (%)	*F*-value
Feb 1997	5	24	1081.7 (126.1)	37.5 (12.3)	60.6 (23.8)	1.07* (0.581)	0.83*** (0.164)	46.86	25.46
Dec 1996	7	62	1043.6 (97.6)	33.5 (8.4)	50.5 (22.0)	0.02 (0.481)	1.09*** (0.139)	38.96	61.54
Apr 1997	8	25	1111.2 (82.9)	39.7 (8.5)	68.9 (19.2)	0.78 (0.750)	0.93*** (0.203)	47.21	21.29
May 1996	10	35	1016.0 (110.7)	31.4 (9.5)	73.2 (28.7)	0.75 (0.474)	1.02*** (0.137)	53.05	55.08
Nov 1996	10.1	20	966.0 (41.1)	26.6 (3.2)	52.6 (11.9)	0.96 (1.077)	0.91*** (0.333)	26.39	7.49
Jun 1996	12	17	1007.1 (80.0)	30.2 (7.3)	69.3 (21.9)	1.00* (0.537)	0.94*** (0.151)	39.67	39.32
Jun 1996	13	30	986.0 (82.9)	28.5 (6.5)	78.4 (23.3)	1.24** (0.570)	0.93*** (0.170)	49.42	29.72
Oct 1996	15	29	910.3 (56.0)	22.6 (3.9)	63.5 (14.3)	0.92* (0.539)	1.03*** (0.170)	60.11	36.81
Sep 1996	16	29	872.4 (65.6)	20.2 (4.0)	60.2 (25.0)	−0.01 (0.652)	1.35*** (0.213)	47.6	40.19
Aug 1996	17.5	28	960.0 (65.3)	26.3 (5.1)	73.2 (18.7)	1.40*** (0.463)	0.88*** (0.143)	46.16	38.21

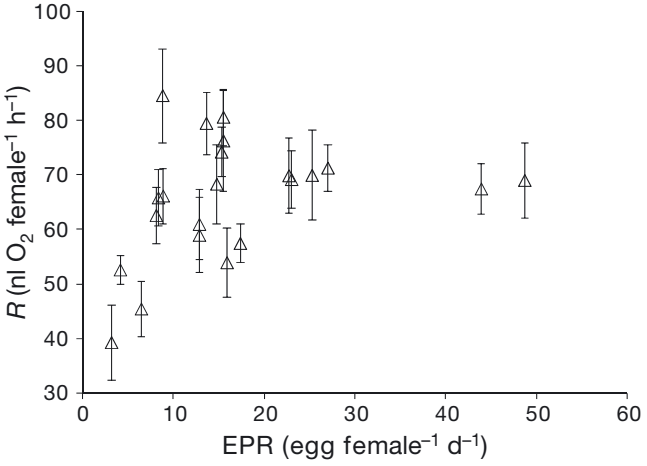

Fig. 6. *Temora longicornis.* Respiration rate (*R*) versus egg-production rate (EPR). Error bars are SE

DISCUSSION

Seasonal variation of copepod respiration rate

We investigated the seasonal variation in the respiration rate of *Temora longicornis* acclimatised to field conditions, during a 1yr study, by measuring individually 299 adults over the full range of copepod DW, EPR, *T*, salinity and chl *a* level as a proxy for prey availability. In our study, *T. longicornis* respiration increased from a minimum in December to a maximum during May and August (Fig. 2). Multiple regression analysis showed that seasonal changes in ln *R* were significantly related to ln DW, *T*, ln Chl and ln EPR (Table 1a). A spring increase in the respiration rate of *T. longicornis* has been reported before by Marshall & Orr (1966) in the Clyde Sea and by Conover (1959) in Southampton waters; whereas Marshall & Orr (1966) attributed the rise in the respiration rate of *T. longicornis* mainly to an increase in copepod body size, Conover (1959) argued that copepod metabolic rates may be 'geared to the phytoplankton bloom'. However, neither of these authors analysed their field data statistically or tested experimentally the factors that might have affected copepod respiration, rendering conclusions from their study speculative. Critically, all previous field investigations disregarded the effect of acute temperature exposure on copepod respiration rate by measuring *T. longicornis* at a fixed arbitrary temperature (Conover 1959, Raymont 1959, Berner 1962, Marshall & Orr 1966; see Table 5). In addition, these studies were mainly limited to between March and July. Thus, limited data sets and differences in methodology make the interpretation of published data on copepod respiration difficult and their use in predictive models questionable. In this respect, our investigation represents one of the largest and most comprehensive studies ever conducted on the seasonal changes in the respiration rate of a single copepod species acclimatised to *in situ* conditions.

Table 4. *Temora longicornis.* Result of the 2-sample *t*-test statistic comparing the mean (±1 SE) respiration rate (*R*, nl O_2 ind.$^{-1}$ h^{-1}) and weight-specific respiration rate (R_{sp}, nl O_2 µg^{-1} DW h^{-1}) of individual (n) female and male *T. longicornis* of similar prosome length (PL, µm) and dry weight (DW, µg) at 6.5°C

Gender	n	PL	DW	*R*	R_{sp}
Female	13	1060 (± 10.4)	34.4 (± 0.93)	65.9 (± 4.4)	1.91 (± 0.11)
Male	15	1048 (± 9.11)	33.32 (± 0.81)	56 (± 5.1)	1.68 (± 0.15)
t-value	1.48	1.23			
p-value	0.15	0.23			

Dependence of respiration on body size

In our study, copepod DW explained the largest proportion of variability in copepod respiration rate. This finding is not surprising since body mass is an important determinant of the metabolic rate of an organism (Peters 1986, Schmidt-Nielsen 1991). On the other hand, the weight exponent *b* of the power function (i.e. the slope of the ln function) between respiration rate and body weight has been reported to vary widely across taxa (Glazier 2006). In our study, *b* varied from 0.83 to 1.34 (Tables 2 & 3, Fig. 3), and it was not significantly different from unity, indicating direct proportionality (i.e. isometric scaling) between respiration rate and body mass. Conover (1959) reported a weight exponent of 0.76 for *Temora longicornis* from Southampton waters. Using the data published by Marshall & Orr (1966), we calculated a weight exponent (±1 SE) of 1.22 ± 0.23 (df = 6; $F = 27.9$; $r^2 = 81.8$ %; $p < 0.003$) for *T. longicornis* from the Clyde Sea. Thus, the weight exponent we estimated for *T. longicornis* in our study is similar to values reported by previous authors for this species and to the range of 0.5 and 1 generally reported for copepods (Mauchline 1998, Ikeda et al. 2000).

Although it is generally assumed that metabolic rate increases as the body mass increases to the power of ⅔ (i.e. 0.66, proportional to body surface) or ¾

Table 5. Summary of *Temora longicornis* respiration rates (*R*) measured during either field or laboratory experiments, given as ranges. PL: prosome length, DW: dry weight, FT: length of time copepods fasted prior to experiment, RV: respirometer volume, Cop: number of copepods incubated, ET: experimental temperature, and AT: acclimation temperature. Dry weight estimated from the equation ln DW= −15.9 + 2.79 ln PL for *T. longicornis* (Castellani & Altunbaş 2006). –: no data available

PL (µm)	DW (µg)	FT (h)	RV (ml)	Cop (n)	ET (°C)	AT (°C)	*R* (nl O_2 ind.$^{-1}$ h^{-1})	Method (incubation time)	Source
720–1340	12–66	9–12	0.15	1	5–17.5	5–17.5 (Jan to Dec)	13–150	Micro-electrode (1 h)	Present study, Menai Strait, UK[c]
973	27	24	0.07	1	16–17	16–17 (Jul)	87–186[b]	Clark-electrode (2–6 h)	Le Ruyet-Person et al. (1975), Roscoff, France[c]
594–968	7–27	24	7–35	1–10	10	– (Apr–Sep)	16–47	Winkler (1–5 d)	Berner (1962), Milliport, UK[c,d]
722–1139	12–42	Over-night	30–40	5–10	10	– (Mar to Jul)	24–143	Winkler (40–50 h)	Marshall & Orr (1966), Milliport, UK[c,d]
859–1040	19–33	Fed[a]	5	29–50	15	7–8 (Apr to May)	116–142	Barcroft-Dixon manometer (3 h)	Raymont (1959), Harvard, USA[c]
804–1082	16–36	Over-night?	5	50	20	5–10 (Feb to Jun)	98–183	Barcroft-Dixon manometer (3 h)	Conover (1959), Southampton, UK[c]
700–1030	11–32	–	5	30–62	10–20	–	62–253	Barcroft-Dixon manometer (3–4 h)	Gauld & Raymont (1953), Southampton, UK[e]

[a]Kept in lab overnight or up to 2 days feeding on cultured phytoplankton before experiment; [b]measurements standardised to copepod of 1 mm PL; [c]field experiment; [d]Use of antibiotics streptomycin (5 mg l^{-1}) and chloromycetin (5 mg l^{-1}); [e]laboratory experiment

(i.e. 0.75, intermediate proportionality between body weight and surface), there is still no broad consensus regarding the value of this coefficient (Kleiber 1961, Brown et al. 2004, Downs et al. 2008, Glazier 2010, Kolokotrones et al. 2010, Agutter & Tuszynski 2011). West et al. (1997) have argued that the ¾ metabolic scaling is the result of the fractal geometry of the internal network present in organisms (fractal network theory [FNT]), including the circulatory and respiratory systems. However, recent theoretical and empirical research has questioned the ¾-power law and the FNT model proposed to explain it by showing that such model is based on questionable or unsubstantiated assumptions (Glazier 2009, 2010, Kolokotrones et al. 2010, Agutter & Tuszynski 2011). Kolokotrones et al. (2010) have shown that the relationship between metabolic rate and body mass has a convex curvature on a logarithmic scale, suggesting that the metabolic coefficient is highly sensitive to the body mass range used. Moreover, Agutter & Tuszynski (2011) advocated that the quantum metabolism (QM) theory, which adopts a molecular-cellular perspective, can be used to predict the large variations in body scaling exponents and to predict the temperature dependence of the proportionality constant, issues that have eluded models such as the FNT. Interestingly, isometric scaling of metabolic rate appears to be common in planktonic animals, and Glazier (2006, 2009) argued that it probably represents an adaptation to the high-energy cost of continual swimming to stay afloat, rapid growth rates and high reproductive rates in response to high levels of mortality in open water.

Relationship between respiration rate and temperature

The respiration rate of *Temora longicornis* increased with temperature (Fig. 4), similar to the pattern generally reported for other poikilotherms (Schmidt-Nielsen 1991, Mauchline 1998, Castellani et al. 2005). Interestingly, respiration rates from our study overlap with rates reported by Berner (1962) and Marshall & Orr (1966) at 10°C and Le Ruyet-Person et al. (1975) at 16 to 17°C, but they are lower than rates reported by Raymont (1959) at 15°C and by Conover (1959) at 20°C for *T. longicornis* of comparable DW (Fig. 7) measured over a similar temperature range (Fig. 8). One of the reasons for such discrepancy may be attributed to methodological differences between studies; whereas we measured individually the respiration rate of fasting copepods acclimatised to environmental conditions, previous authors measured groups of copepods exposed to variable feeding conditions at a fixed arbitrary temperature (see Table 5). Berner (1962) and Marshall & Orr (1966) measured the respiration rate of fasting

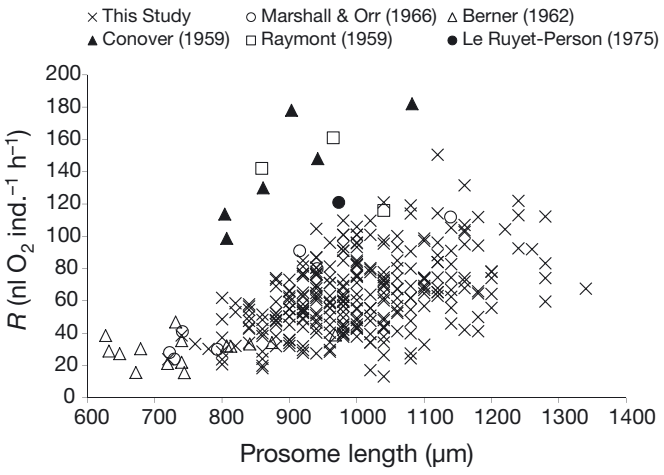

Fig. 7. *Temora longicornis.* Respiration rate (*R*) versus prosome length (PL) obtained by different field studies (see Table 5)

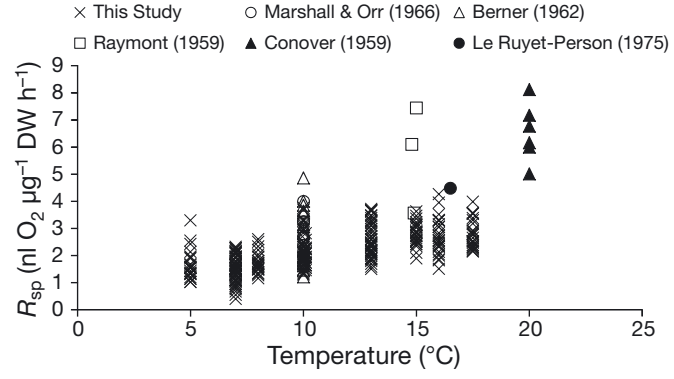

Fig. 8. *Temora longicornis.* Weight-specific respiration rate (R_{sp}) versus temperature obtained by different field studies (see Table 5)

T. longicornis at 10°C over 40 to 50 h incubations between the end of March and mid-July. Le Ruyet-Person et al. (1975) measured single fasting copepods acclimatised to 16 to 17°C during 3 to 6 h of incubation in July. In contrast, Raymont (1959) and Conover (1959) measured copepods maintained in the laboratory between 5 and 10°C on cultured phytoplankton at 15 and 20°C, respectively, over 3 h experiments between February and June (Table 5). Exposing a poikilotherm to a sudden temperature change results in a shift in the physiological rate lasting minutes to hours, known as the acute rate (Cossins & Bowler 1987). This rate, which is used to construct the acutely measured metabolism-temperature curve (Prosser & Brown 1961) is generally followed by a new, steady or acclimated state, which is gradually acquired some hours to days after the temperature change (Pretch 1958). In *T. longicornis*, a temperature shift of 5 and 15°C requires ~2 and 6 d, respectively, before respiration stabilises to the new rate, intermediate between the original and the acute rate (C. Castellani & Y. Altunbaş pers. comm.). Therefore, it is likely that the long incubation times used by Berner (1962) and by Marshall & Orr (1966) enabled copepod respiration to acclimate to their 10°C experimental temperature following a shift of at most 6°C, considering *in situ* temperatures ranging from 4 to 16°C for their study area. The copepods measured by Le Ruyet-Person et al. (1975) were also acclimatised, and therefore, their data coincide with our measurements. In contrast, the high respiration rates reported by Raymont (1959) and Conover (1959), who measured copepods over a short time (i.e. 3 h) following temperature increases of up to ~15°C, probably corresponded to acute respiration rates (Table 5).

In our study, the respiration rate of *Temora longicornis* acclimatised to field temperatures between 5 and 17.5°C followed a sigmoid pattern with Q_{10} values ranging between 1 and 2.88 depending on the temperature interval (mean Q_{10} ranging between 1.56 and 1.88; Table 2, Fig. 4). In contrast, the relationship we obtained from a compilation of published field data for *T. longicornis* was characterised by an exponential increase in respiration between 10 and 20°C and by a higher mean Q_{10} of 3.09 (Fig. 8). The Q_{10} reported for the respiration rates of marine copepod usually range between 2 and 4, although values above and below this range have also been reported (Hirche 1987, Mauchline 1998, Gaudy & Thibault-Botha 2007). It is noteworthy, however, that $Q_{10} > 2$ are generally estimated from acute measurements of copepods maintained in the laboratory on high microplankton concentrations (Cossins & Bowler 1987, Ikeda et al. 2001, Castellani et al. 2005). For instance, using data from Gauld & Raymont (1953) and our own data (Fig. 9a) on the acute respiration rates of fasting *T. longicornis* maintained on an ad libitum microalgal diet, we calculated mean Q_{10} values of 2.4 for the temperature interval 4 to 20°C. As mentioned above, the acutely measured respiration rate is a transient and short-lived shock response of an organism exposed to a sudden and often unrealistic change in temperature (e.g. the 15°C temperature shift applied by Raymont 1959 and Conover 1959), and as such, it represents a distortion of the 'natural' respiration rate. In contrast, the acclimatised respiration rate we measured in the present study displays the ecologically meaningful relationship between metabolism and the ambient conditions experienced

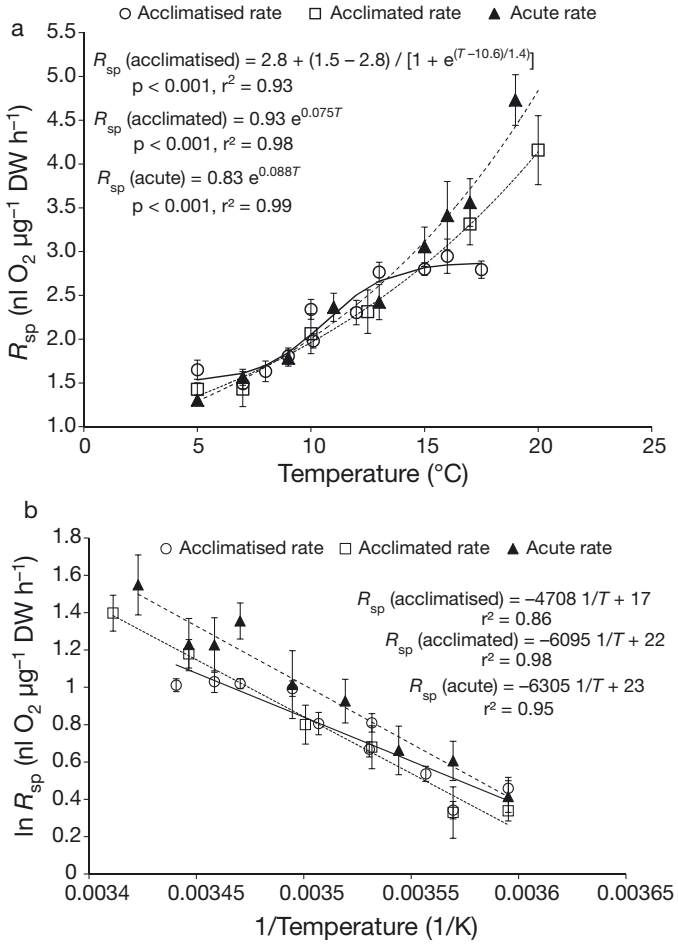

Fig. 9. *Temora longicornis.* Acclimatised, acclimated and acute mean (±1 SE) (a) weight-specific respiration rates (R_{sp}) versus temperature and (b) logarithmically transformed R_{sp} versus the inverse of the absolute temperature (1/K), i.e. the Arrhenius plot. Lines represent the fits from the regression models

by the organism (Cossins & Bowler 1987). Hence, the high Q_{10} we obtained pooling published field data on *T. longicornis* was probably the result of the acute measurements by Raymont (1959) and Conover (1959).

Respiration is typically measured on fasting copepods (Berner 1962, Marshall & Orr 1966, Ikeda et al. 2001, present study Table 5) to avoid the added effect of SDA (Kiørboe et al. 1985, Thor 2000, Secor 2009). However, the copepods measured by Raymont (1959) and Conover (1959) were maintained in the laboratory on cultured microalgae, and it is unclear whether they had been fasting prior to experiment. Since the respiration rate of *Temora longicornis* takes ~10 h to decrease to the routine rate after copepods are deprived of food (Fig. 1), it is possible that the higher respiration rates measured by Raymont (1959) and Conover (1959) were also partly due to the effect of SDA.

The low Q_{10} of 1 we measured in the present study during winter and late summer shows that over that time of the year, copepod metabolism did not change with temperature (Fig. 4). Values of Q_{10} < 2 have been generally interpreted as the result of homeostasis, resulting from seasonal adjustments in enzymes concentration and type (Somero & Hochachka 1971), and thought to confer a metabolic advantage to organisms living in an environment with fluctuating temperature (Gaudy 1973, Gaudy & Thibault-Botha 2007). However, Clarke (1993) has argued that attempting to explain seasonal variation in oxygen consumption as a direct response of metabolic rate to temperature is simplistic because respiration represents a cost to an organism, i.e. ATP demand for physiological processes such as growth, reproduction and locomotion besides the maintenance of basic bodily functions. Organisms are adapted to minimise energetic costs, and therefore, their cells will not synthesize ATP (i.e. will not increase R) unless it is required to produce work and unless they have sufficient energy to do so. Hence, Clarke (1993) has proposed that seasonal changes in the oxygen consumption of poikilotherms could reflect changes in their growth and reproductive rates. Interestingly, we obtained the lowest rate of increase in respiration (i.e. Q_{10} = 1) during winter and late summer when both prey concentration and copepod reproductive rates were lower (Fig. 2b,e). In contrast, we measured the highest Q_{10} (between 2.01 and 2.88) during spring–early summer at a time when *in situ* feeding conditions for the copepods were optimal and reproductive activity was maximal (Table 2, Figs. 2 & 4). Similarly, Ikeda et al. (2001) reported Q_{10} values between 1.8 and 2.1 for the respiration rate of fasting copepod species acclimatised between –1 and 30°C calculated only from measurements made during spring–summer when feeding conditions were most favourable.

A comparison of acclimatised respiration rates, from the present study, with acclimated and acute respiration rates suggests that the response of *Temora longicornis* metabolism to temperature depends on both exposure time and nutritional conditions (Fig. 9). The respiration of field-acclimatised copepods, which experience a lower and more variable availability/quality of prey, was the most variable (i.e. sigmoid trend) and the mean rate of change was the lowest (Q_{10} = 1.56 to 1.88). The acclimated respiration of laboratory maintained copepods increased exponentially, but the rate of change was

intermediate (Q_{10} = 2.1). In acutely measured copepods, the response was also exponential, but the rate of increase was the highest (Q_{10} = 2.4). However, Fig. 9a shows a substantial overlap between the 3 data sets, particularly in the middle of the temperature range. The logarithmic transformation did not linearise the sigmoidal pattern of the field-acclimatised respiration rates, and therefore, a statistical comparison between the slopes of the relationships was not possible. Nevertheless, we compared the data sets using a Two-sample *t*-test with equal variances at each of the common temperatures. Our results show that the respiration rates of field-acclimatised copepods was significantly higher at 5°C (df = 40, t = 2.54, p = 0.014) and significantly lower at 17.5°C (df = 35, t = −3.31, p = 0.0021) compared to that of acutely measured copepods. Similarly, field-acclimatised respiration rates were significantly lower than laboratory-acclimated rates at 17.5°C (df = 34, t = −2.33, p = 0.025), but at 5°C they were significantly higher than acclimated rates only at 10% (df = 37, t = 1.48, p = 0.0734). There were no significant differences between the respiration rates of acute and laboratory-acclimated rates. The higher respiration rates we measured for acclimatised copepods at 5°C may be the result of not only temperature acclimatisation but also of the favourable feeding conditions encountered by the copepods in the field at the beginning of February and the associated high reproductive rates; at this time, Chl had already increased above winter level to reach ~1 µg l^{-1} due to a mixed diatom bloom, and this promoted an increase in copepod EPR (mean ± SE: 16 ± 9.1 eggs $female^{-1}$ d^{-1}; range: 0 to 61 eggs $female^{-1}$ d^{-1}). Diatoms are known to support higher EPR in *T. longicornis* compared to other phytoplankton diets (Dam & Lopes 2003, Jónasdóttir et al. 2009), including the flagellate diets we fed to the copepods in our acclimated and acute respiration rates experiments. Similarly, the lower respiration rates we measured for the copepods from the field at 17.5°C may be the result of poorer feeding conditions (i.e. *Noctiluca* spp. bloom and the absence of diatoms) in the field, compared to copepods maintained on a high flagellate diet in the laboratory, and associated lower reproductive rates (see also next section). In support of our argument, Fig. 10 shows a sigmoid trend in the EPR_{sp} of *T. longicornis* (measured during the same study and published by Castellani & Altunbaş 2006) with temperature which is very similar to the acclimatised respiration rate trend presented in Fig. 4 and Fig. 9a. Furthermore, the logistic equation we fitted to the acclimatised respiration rate data in Figs. 4 & 9a is very often used to describe the growth of organisms, and hence, our results suggest that the seasonal trend in *in situ* respiration rate we measured largely reflects female copepod growth rate, i.e. their reproductive rate (Fig. 10). In summary, our findings suggest that respiration rates measurements carried out under acute temperature exposure are not representative of field-acclimatised copepod respiration rates, particularly at the extreme of the temperature range and depending on the nutritional conditions of the copepods. It is worth noting, however, that our findings may not apply to copepod species that store large body lipid reserves or those who experience large temperature changes over a short time scale through, for instance, diel vertical migration.

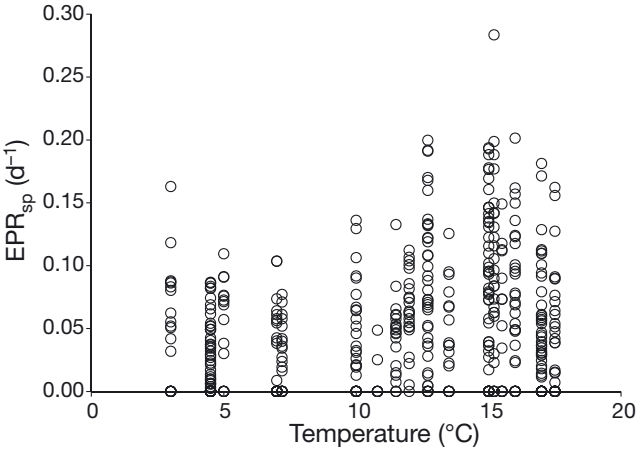

Fig. 10. *Temora longicornis.* Weight-specific egg-production rate (EPR_{sp}) versus *in situ* temperature

Effect of food sources and reproduction on respiration

The positive significant relationship we found between *Temora longicornis* respiration rates and ambient Chl levels suggests that seasonal changes in nutritional conditions were an important determinant of copepod metabolic rates (Table 2). Our results support the observation made by Conover (1959) that the spring increase in the respiration rate of *T. longicornis* might 'be geared in some way to its food supply'. Similarly, other studies have reported higher respiration rates for *Calanus finmarchicus*, *C. helgolandicus* and *C. hyperboreus* during the phytoplankton bloom in spring and summer compared to rates in winter (Marshall & Orr 1958, Conover & Corner 1968, Butler et al. 1970).

Aerobic metabolism is tightly coupled with feeding, particularly in small copepods such as *Temora longicornis* that do not store large lipid reserves (Clarke & Walsh 1993, Kreibich et al. 2008). For instance, citrate synthase, which is an important metabolic key enzyme of the tricarboxylic acid cycle, decreases after only 24 h in starving *T. longicornis* (Clarke & Walsh 1993). The increase in respiration rate of fed copepods, i.e. SDA, is largely related to protein biosynthesis (i.e. to growth and reproduction) and protein metabolism rather than to the mechanical filtering and ingestion of the food (Kiørboe et al. 1985, Thor 2000, Clarke & Fraser 2004, Secor 2009). However, protein synthesis is also a key component of basal metabolic rate (e.g. protein turnover, Clarke & Fraser 2004). Basal metabolic rate represents, in fact, the continuous cost the organism must meet to repair cell damage (e.g. protein turnover) and to conduct protein recycling (e.g. enzymes). However, the recycling of enzymes is probably not constant and is associated with the rate of growth, which depends on the type and quantity of substrate metabolised (Flynn 2005, Hochachka & Somero 2002). Thus, the 'basal rate' of a fasting poikilotherm can be expected to change according to the growth rate of the organism. The respiration rate of a starved copepod will also depend on the level and type of substrate metabolised (i.e. either protein or lipids) and its body reserves. The copepods we collected in the field were feeding on different concentrations and qualities of food sources, i.e. either lower or higher compared to the monospecific algal diet we fed to the copepods maintained in the laboratory. Since both the acclimatised and acclimated copepods in our study were fasted for the same length of time prior to measurement, the higher respiration rates we recorded in acclimated copepods at 17.5°C compared to those acclimatised in the field appear to be the result of a higher level of protein turnover and/or anabolism supported by the constant high prey supply in the laboratory (Fig. 9).

In our study, the seasonal change in *Temora longicornis* respiration rate was also significantly related to EPR. Coupling between egg production and respiration rate has been reported in *Acartia tonsa* (Kiørboe et al. 1985, Thor 2003), and Conover (1962) observed that ripe *Calanus hyperboreus* females had higher respiratory rates than immature or spent ones. In adult female copepods, anabolic processes are mainly linked to the cost of reproduction (e.g. in the copepod *A. tonsa*, Kiørboe et al. 1985). Several authors have also suggested that body size, food availability and temperature often indirectly influence metabolic rates through their effects on growth rates, rather than directly (Parry 1983; see Clarke 1993 for a critical review of this topic). For instance, Parry (1983) showed that the 'cost of growth' could account for up to 80% of ectotherm metabolism, and he interpreted seasonal changes in respiration rates of marine poikilotherms as a reflection of changes in synthetic activity rather than simply the result of a mechanistic response of metabolism to temperature changes. Indeed, the protein content (hence the synthetic activity) of *T. longicornis* fluctuates over the year as a result of changes in the nutritional conditions experienced by the copepods (Helland et al. 2003). In our study, however, EPR explained the lowest proportion of variability in respiration compared to other variables. This result is not surprising since copepod respiration combines different energetic costs in addition to that of producing eggs. It is also difficult to equate rapid changes in EPR with metabolism because of the lag time between the formation (i.e. demand for ATP) and the release of eggs (Tester & Turner 1990). In addition, in our study, we measured respiration on fasting copepods and EPR on copepods that had been feeding before incubation (see 'Materials and methods'). Furthermore, the asymptotic relationship between respiration and EPR (Fig. 6) indicates an increase in reproductive efficiency in spring that might have resulted from an increase in food quality (e.g. the increase in N-rich ciliates during the spring bloom). The results of a recent laboratory study (R. Nobili et al. pers. comm.) showing a decrease in the reproductive cost of *T. longicornis* with increase in the N:P ratio of the diet support our field observation. The similarity in the pattern of EPR and respiration rate with temperature shown in Fig. 4 and Fig. 10, as already discussed in the previous section, also supports our view that seasonal changes in metabolic rates were driven by seasonal changes in copepod growth rates. Overall, our results suggest that reproductive activity (i.e. anabolic processes) modulated by food availability and possibly quality also contributed to the observed seasonal changes in the respiration rate of *T. longicornis*.

Metabolic coefficients and the importance of acclimatised rates for predictive models

Using the correct metabolic coefficient values is critical to estimate energy flow and secondary production. Our study has shown that the body mass exponent of *Temora longicornis* scaled isometrically

(i.e. b = 1) with metabolism, similarly to the pattern commonly reported in planktonic animals (Glazier 2006). Such value is significantly different from the coefficient b = 0.75 predicted by the metabolic theory of ecology (MTE, Gillooly et al. 2001, Brown et al. 2004). Our work and past studies have also shown that under natural conditions, the Q_{10} of copepod physiological rates are often characterised by Q_{10} values < 2 (present study, Ikeda 1985, Ikeda et al. 2000, Hirst & Bunker 2003). In contrast, the physiological responses to temperature of zooplankton experiencing optimal feeding conditions either in the field or in the laboratory and measured over unrealistic and sudden temperature changes seem to be characterised by Q_{10} > 2 (i.e. acute measurements; Peters 1986, Cossins & Bowler 1987, Hirche 1987 present study). Moreover, our study has also shown that under acclimatised and acclimated conditions, the physiology of copepods is characterised by lower Q_{10} than that of copepods exposed acutely to temperature changes. It is not unreasonable to assume that in the marine environment, the metabolism of most copepods will have sufficient time to acclimatise to changes in ambient temperature since seasonal thermal fluctuations are relatively small, compared to the terrestrial environment, due to the higher heat capacity of seawater. Most copepod species experience food scarcity and variable prey quality over large part of the year, all of which could affect their metabolism and reproductive rates. In this respect, our results have shown that the goodness of fit of the regression improved when we included Chl and EPR in addition to DW and temperature (Table 2). Moreover, the value of the Q_{10} differed substantially depending not only on the temperature interval considered but also on the variables included in the regression analysis, whereas the body mass exponent was never significantly different from unity. Modelling studies generally use relatively high values of Q_{10} to estimate the effect of temperature change on metabolic rates of zooplankton. Interestingly, Stock & Dunne (2010) observed that the reports of high Q_{10} values by several high profile zooplankton studies (e.g. Huntley & Lopez 1992, report a Q_{10} of 3 for copepod generation times, and Rose & Caron [2007]report Q_{10} of 2.4 and 3.75 for bacterivorous and herbivorous protists, respectively) have prompted many modelers to adopt a Q_{10} of 3 despite substantial observational evidence that zooplankton rates (including growth) exhibit Q_{10} values of 2 or below (Hirst & Bunker 2003, Ikeda 1985, Ikeda et al. 2000). The E_a we calculated from the slopes of the Arrhenius equation for copepods acclimatised between 5 and 17.5°C ranged between 31 and 43 kJ mol^{-1}, or 0.31 to 0.45 eV (i.e. 1 eV = 96.49 kJ mol^{-1}) (Fig. 9b, Table 2b). These values are well below the E_a range of 0.60 to 0.70 eV and the mean E_a values of 0.63 eV (excluding endotherms) predicted by the MTE (Brown et al. 2004). We recorded the highest E_a (0.61 eV) only in the temperature interval 8 to 13°C, that is, during the phytoplankton bloom when copepods were exposed to good feeding conditions and actively reproducing (see 'Relationship between respiration rate and temperature'). Thus, our results indicate that during the largest part of the year, the respiration rate of *T. longicornis* would be well below the rates predicted by the MTE equation. This result has important implications for the interpretation of the response of plankton to environmental change and for predictive ecological modelling. In summary, the relationships between physiological rates and ecologically relevant parameters such as temperature and body size, upon which global predictive models rely, are incomplete and subject to significant methodological artefacts. Additional detailed studies of acclimatised *in situ* rates as a function not only of temperature and body size but also of other key parameters such as the nutritional conditions, reproductive and growth rates and the genetic 'make-up' of the organism are essential to improving these relationships and reducing uncertainties in predicted ecosystem responses to environmental change.

How much carbon is required by *T. longicornis* to support routine metabolism?

Our results provide information about individual variability of *Temora longicornis* respiratory response and energy demand. Metabolic studies based on the O:N ratio have indicated that the main substrate catabolized in small calanoid copepods, such as *T. longicornis*, is protein (Bamstedt 1988, Thor 2000) because these species usually do not store lipids and carbohydrates in large quantities (Evjemo & Olsen 1997, Helland et al. 2003). Thus, considering a respiratory quotient RQ = 0.8 for protein catabolism (Schmidt-Nielsen 1991) and that µg carbon catabolized = 0.8 × µl O_2 d^{-1} respired × (12 µg C $µmol^{-1}$/ 22.4 µl $µmol^{-1}$), the daily carbon requirement by a *T. longicornis* of 1000 µm in length, estimated from our multiple regression model (Table 2), would vary between ~5 and 10% of body carbon at 5 and 17°C, respectively. However, Table 2 also shows that using DW and T only results in an estimated copepod C consumption almost 3-fold higher than that esti-

mated taking into account chl and EPR. The discrepancy in energetic cost is stronger during the most productive time of the year when copepods are actively reproducing (Table 2).

CONCLUSIONS

Using one of the most comprehensive data sets on acclimatised copepod respiration rate, our study has shown that *in situ* seasonal changes in *Temora longicornis* metabolism are the result not only of body mass and temperature but also of copepod nutritional and reproductive conditions. Thus, the constancy of metabolic rate with temperature increase that we observed in winter and late summer appears to be the result of reduced anabolic processes due to food limitation rather than simply a seasonal physiological adjustment to temperature, i.e. homeostasis. The lower values of Q_{10} and E_a we measured in our studies compared to those reported in the literature also suggest that metabolic rates of acclimatised copepods may be less responsive to temperature changes than has been inferred so far from thermal coefficients calculated from acutely measured rates of copepods maintained in the laboratory on high food rations. The value of the thermal coefficient also differed according to the type of variable used in the regression model. Therefore, using high and fixed coefficient values may lead to overestimation or misrepresentation of copepod respiration, particularly under ambient conditions limiting growth and reproduction. Our results have important implications for ecological models aiming to predict energy flow in marine food-webs and to determine the impact of climate change on copepod metabolic rates.

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