

Temperature affects respiration rate of *Oithona similis*

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ABSTRACT: *Oithona* spp. is considered the most abundant and ubiquitous copepod genus in the marine environment, often outnumbering calanoid copepods throughout the year. Previous studies have argued that one of the reasons for such success is that the respiration rate of *Oithona* spp. is insensitive to temperature changes and lower than in calanoids. However, comprehensive data on the thermal biology of this important copepod genus is lacking. In this study, the respiration rate of adult female *O. similis* from the English Channel, was measured over the temperature range 4 to 25°C. The respiration rate of *O. similis* changed exponentially with temperature ($\ln O_2\text{-rate} = -3.59 + 0.114 T$, $df = 35$, $r^2 = 0.85$, $p < 0.001$, $Q_{10} = 3.1$) similar to that of other poikilotherms. Over the temperature range examined, *O. similis* basic metabolic cost varied from a minimum of ~1.4 % body-C d⁻¹ at 4°C to a maximum of 23 % body-C d⁻¹ at 25°C, corresponding to an energy demand of ~3 % and 32 % body-C d⁻¹ respectively. The respiration rate of *O. similis*, from the present study, is ~8 times lower than that of a calanoid copepod of equivalent body weight estimated from published empirical metabolism–temperature data. We suggest that these differences in metabolic rates may account for the year-round persistence and higher abundances of *Oithona* spp. over calanoid copepods, particularly in oceanic and oligotrophic environments where food resources may be limiting for calanoid copepods.

KEY WORDS: *Oithona similis* · Respiration rate · Temperature · Cyclopoid · Calanoid · Energy demand

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INTRODUCTION

Paffenhöfer (1993) has argued that low respiratory rates may be one of the explanations for the high abundance and ubiquity of *Oithona* spp. (Bigelow 1926, Nishida 1985, Gallienne & Robins 2001). Nevertheless, there has been no comprehensive study on the respiration rate of this widespread copepod group. Previous investigations have concluded that the respiration rate of *Oithona* spp. is temperature-insensitive (Marshall & Orr 1966, Lampitt & Gamble 1982, Hiromi et al. 1988, Nakamura & Turner 1997). Temperature, however, is one of the most important factors affecting the respiration rate of poikilotherms (Schmidt-Nielsen 1991) and zooplankton in general (Ikeda 1974, Ikeda & Motoda 1978, Vidal 1980, Ikeda et al. 2001). On the other hand,

the ability to maintain constant metabolic rates (homeostasis) in spite of temperature changes has been reported for a range of invertebrate species, including copepods (Gaudy et al. 2000, Parra et al. 2003), as an adaptation to rapid temperature fluctuations (eurythermy). With the exception of Hiromi et al. (1988), who measured the respiration rate of *O. davisae* over a wide temperature range, other investigators have studied the respiration of *Oithona* spp. over narrow ranges (Klekowski et al. 1977, Lampitt & Gamble 1982, Nakamura & Turner 1997) or at a single temperature (Marshall & Orr 1966). Thus, the reported lack of metabolic response to temperature changes in *Oithona* spp. remains to be verified.

Knowledge of an organism's respiration rate at different temperatures is important, as it provides a basic

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indication of its metabolic requirements in different environments. Estimates of *Oithona* spp. energy demand in recent field studies have relied on the assumption that *Oithona* spp. metabolism is either constant with temperature (McKinnon & Klumpp 1998) or similar to that of calanoid copepods (Atkinson 1996, Lonsdale et al. 2000). The problem with such assumptions is that currently there is still no general consensus on whether the respiration rate of *Oithona* spp. is lower (Lampitt & Gamble 1982) or similar (Sabatini & Kiørboe 1994) to that of calanoid copepods.

Among all cyclopoid species, *Oithona similis* probably experiences the largest latitudinal and seasonal temperature variation because it has the widest distributional range (Nishida 1985, Nielsen & Sabatini 1996, Atkinson 1998). Thus, the present study focuses on this species to investigate the relationship between respiration rate and temperature and compare it with published metabolism–temperature relationships for calanoid copepods. The questions we asked are: (1) Does the respiration rate of *O. similis* respond to temperature changes as observed for calanoid copepods and poikilotherms in general? (2) Is the weight-specific respiration rate of *O. similis* similar to that of calanoid copepods?

MATERIALS AND METHODS

Plankton was collected by gentle vertical hauls from 50 m depth with a 200 μm WP-2 net at Stn L4 (50° 15' N, 04° 13' W) in the English Channel between July and December 2003, and the catch was returned to the laboratory within 2 h of collection in thermally insulated containers. Adult *Oithona similis* females were isolated with a Pasteur pipette under a dissecting microscope, placed in GF/F–filtered seawater and pre-conditioned overnight in the dark (Nakamura & Turner 1997) to temperatures between 4 and 25°C ($\pm 0.1^\circ\text{C}$). The incubation temperatures of pre-conditioned copepods were within $\pm 10^\circ\text{C}$ of the *in situ* temperatures (i.e. 15°C). On 3 occasions the experiment was undertaken at the *in situ* temperatures of 10.5, 15 and 18°C. The respiration rate of *O. similis* females was determined from *in vitro* changes in dissolved oxygen. Pre-filtered seawater from Stn L4 was cartridge filtered to 0.2 μm (Criticap-100 sterile capsule) into a 10 l autoclaved polycarbonate aspirator and siphoned into 60 ml borosilicate glass bottles. We prepared 4 zero time (*t*-zero), 4 control and 2 to 4 replicate bottles containing between 25 and 200 *O. similis* at each temperature. High numbers of *O. similis* (>70 to 80 copepods per bottle) were only used at temperatures lower than 7°C when respiration rates became too low to be distinguished from the control.

The *t*-zero replicates were fixed at the start of the experiment. The controls and the experimental bottles were incubated for 24 h in the dark in temperature-controlled incubators in static conditions, as preliminary observations indicated that healthy *Oithona similis* swims throughout the bottle without the need for artificial re-suspension. The respiration rate of potential bacteria was calculated from the difference in dissolved oxygen between the *t*-zero replicates and the incubated control replicates. The respiration rate of *O. similis* was calculated from the difference in dissolved O_2 between the mean of the controls and the experimental bottles at the end of the incubation. Measurements of dissolved oxygen were made with an automated Winkler titration system with a photometric endpoint (Williams & Jenkinson 1982). Chemical reagents were based on Carrit & Carpenter (1966) and the oxygen saturation was calculated from the equations for the solubility of oxygen in seawater of Benson & Krause (1984).

The *Oithona similis* used in the experiments were sized using an ocular micrometer to the nearest 20 μm and the copepod's carbon content was derived from the length–weight relationship of Sabatini & Kiørboe (1994). The weight-specific respiration rate of *O. similis* was then calculated from the ratio between the respiration rate of the copepods and their estimated body carbon (body-C). The metabolic response of *O. similis* to temperature was determined as a Q_{10} estimated from the relationship: $Q_{10} = e^{(10 \times \text{slope})}$, where e is the base of the natural log and the slope is the gradient obtained from the regression analysis between respiration rate and temperature.

The salinity of the seawater used in the incubation was also measured with a portable salinometer (Model WTW LF-197) fitted with a salinity/temperature sensor (TetraCon 325) to enable oxygen saturation to be calculated.

RESULTS

There was no evidence of density-dependence of respiration over the range of copepod concentrations used, as respiration rates (standardised to 15°C using a Q_{10} of 3.1 found in the present study) were not significantly correlated ($r = -0.25$, $df = 35$, $p = 0.160$) with the number of individuals per bottle (Fig. 1).

The weight-specific respiration rate of *Oithona similis* increased exponentially with increasing temperature ranging from 0.026 $\mu\text{lO}_2 \mu\text{gC}^{-1} \text{d}^{-1}$ at 4.6°C to 0.423 $\mu\text{lO}_2 \mu\text{gC}^{-1} \text{d}^{-1}$ at 25°C for body weights ranging from 0.5 to 0.6 μgC (Fig. 2). Regression analysis after semi-logarithmic transformation of the data was used to establish the relationship between weight-specific

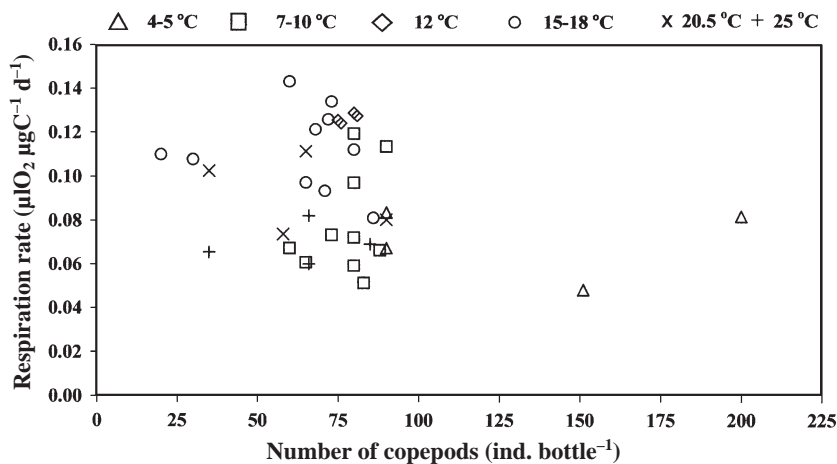


Fig. 1. *Oithona similis*. Weight-specific respiration rate ($\mu\text{lO}_2 \mu\text{gC}^{-1} \text{d}^{-1}$) versus copepod number per bottle for different temperatures ($^{\circ}\text{C}$). Rates standardised to 15°C using a Q_{10} of 3.1 found in the present study. Please note the pairs of diamond symbols overlapping each other

respiration rate and temperature. The rise in respiration rate of *O. similis* with increasing temperature calculated from the fitted equation corresponded to a Q_{10} of 3.1.

Fig. 2 shows that the respiration rates of *Oithona similis* acclimated at the field temperature fits the pattern of the metabolism–temperature ($M-T$) curve for copepods incubated at set laboratory temperatures.

The percentage in oxygen saturation of the seawater at the end of the experiments was between 80 and 100%. Bacterial respiration was low, representing a change of between 0 and 0.5% of total dissolved oxygen. The standard deviation of the respiration in the control bottles varied from 0.00208 to 0.0066 $\mu\text{l O}_2$ copepod $^{-1} \text{d}^{-1}$.

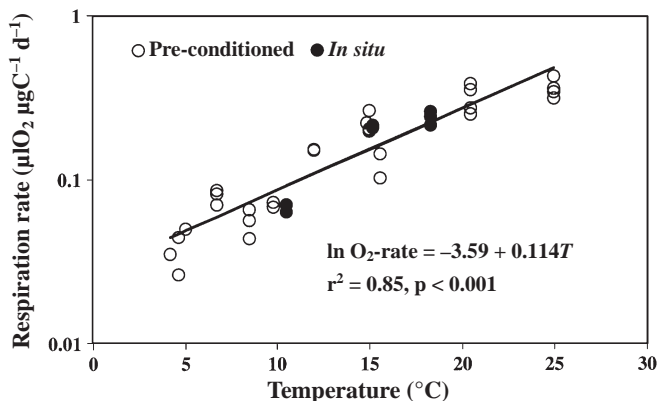


Fig. 2. *Oithona similis*. Weight-specific respiration rate ($\mu\text{lO}_2 \mu\text{gC}^{-1} \text{d}^{-1}$) versus temperature (T , $^{\circ}\text{C}$) measured at *in situ* temperature (\bullet) or after pre-conditioning at experimental temperature (\circ). Note logarithmic scaling

DISCUSSION

Respiration rates of *Oithona* spp. and temperature

The present study measured the respiration rate of *Oithona similis* over the temperature range 4 to 25°C and at *in situ* acclimation temperatures of 10.5, 15 and 18°C . To our knowledge this is the first study in which the respiration rate of *O. similis* has been measured over a wide temperature range. Our results show that the respiration rate of *O. similis* varies as a function of temperature ($Q_{10} = 3.1$), as reported for other poikilotherm organisms including zooplankton (Ikeda & Motoda 1978, Schmidt-Nielsen 1991, Ikeda et al. 2001).

The overlapping between *Oithona similis* respiration rates measured at similar temperatures for *in situ* and pre-conditioned copepods rules out the possibility that the temperature response measured (Fig. 2) was an artifact of laboratory conditions. Similarly, Robinson & Williams (1993) found that experimental manipulation and temperature acclimation did not bias the respiration rates of plankton community respiration. The present finding contrasts with those of previous studies suggesting that the respiration rate of Oithonidae is temperature-insensitive. Hiromi et al. (1988) could not detect any significant change in the respiration rate of *O. davisae* over the temperature range 5 to 30°C , whereas, in their seasonal study, Lampitt & Gamble (1982) could not find any relationship between the respiration rate of *O. nana* and environmental temperatures between 7 and 12°C (R. Lampitt pers. comm.). More recently, Nakamura & Turner (1997), measuring the respiration rate of *O. similis* at 19 and 20.5°C , found comparable rates to those reported by Marshall & Orr (1966) for *O. similis* at 10°C and concluded that the effect of temperature on the respiration rate of oithonids may be minimal. However, the respiration rates from 0.14 to 0.21 μlO_2 copepods ($\text{cop})^{-1} \text{d}^{-1}$ measured in the present study for *O. similis* at 20°C in laboratory conditions overlap with the 0.20 to 0.23 μlO_2 $\text{cop}^{-1} \text{d}^{-1}$ reported by Nakamura & Turner (1997) at 19 and 20.5°C for the same species. In addition, observations that *O. similis* could survive for >10 d without food led Marshall & Orr (1966) to conclude that the respiration rates they measured for this cyclopoid species were probably too high.

Copepod body weight and nutritional condition are all factors known to alter the relationship between metabolic rates and temperature (Vidal 1980, Kiørboe

et al. 1985, Ikeda et al. 2000). In the present study the majority of the respiration rate measurements (i.e. pre-conditioned *Oithona similis*) were made over a relatively short time span (i.e. 1 mo) during which *in situ* temperature, copepod size and the concentration/composition of potential food sources remained approximately constant (C. Castellani pers. obs.). Thus, it is possible that the lack of correlation between *O. nana* respiration rate and temperature reported by Lampitt & Gamble (1982) in their seasonal study resulted from measuring copepods of very different body weights and nutritional states over a narrow temperature range (i.e. 7 to 12°C).

Table 1 summarises the respiration rates reported for different *Oithona* spp. in the literature. The rates measured with the bottle incubation for *Oithona similis* (i.e. 1.4 to 28% body-C d⁻¹) of similar body weight and temperature range (present study and Nakamura & Turner 1997) are less variable than rates derived from the diver-/micro-respirometer method for *Oithona* spp. (i.e. 8 to 88% body-C d⁻¹, Klekowski et al. 1977). In larger *Oithona* species this variation appears even wider, with metabolic rates ranging between ~6 and 265% body-C d⁻¹ (Klekowski et al. 1977). In contrast, the maximum % body-C respired per day by calanoid copepods weighing between 3 µgC and 4 mgC measured at between -1 and 29°C (Vidal 1980, Kiørboe et al. 1985, Ikeda et al. 2001) and most cyclopoids (Table 1) is at most ~31% body-C d⁻¹. Comparisons of

the similarly sized *O. nana* (Lampitt & Gamble 1982) and *O. davisae* (Nakata & Nakane 1987, Hiromi et al. 1988) also suggest that the respiration measured for this latter species represent maximum rates.

The chances of a copepod encountering the wall of the experimental vessel is higher in the micro-respirometer (1 to 10 µl) than in the bottle (60 ml) and this may result in the copepod being more stressed and having a higher metabolic rate when the former method is used. Although incubation of multiple individuals may also present a drawback of the bottle incubation technique through a crowding effect, in the present study, *Oithona similis* respiration rate was unrelated to copepod concentration, indicating that the number of individuals incubated did not affect our results (Fig. 1). In addition, higher metabolic rates reported for the micro-respirometer might have also arisen from high bacterial growth due to coarsely filtered (i.e. >0.2 µm) seawater (Hiromi et al. 1988). Thus, it is possible that the method used by Klekowski et al. (1977) and Hiromi et al. (1988) was responsible for the higher and more variable *Oithona* spp. respiration rates they reported.

Respiration rate of *Oithona* spp. versus calanoid copepods

Paffenhöfer (1993) argued that lower metabolic requirements may give an 'edge' to *Oithona* spp. over

Table 1. *Oithona* spp. Summary of respiration rates (range) reported in the literature at different locations. *T*: temperature (°C); *WT*: copepod carbon weight (µgC); *cop*: copepods; *R*: respiration rate (µlO₂ copepod⁻¹ d⁻¹); *R_{sp}*: weight-specific respiration rate (µlO₂ µgC⁻¹ d⁻¹), *Body-C* d⁻¹: body carbon respired daily (%)

Species	<i>T</i> (°C)	<i>WT</i> (µgC)	<i>R</i> (µlO ₂ cop ⁻¹ d ⁻¹)	<i>R_{sp}</i> (µlO ₂ µgC ⁻¹ d ⁻¹)	<i>Body-C</i> d ⁻¹ (%)	Method	Location	Source
<i>O. similis</i>	4–25	0.5–0.6 ^a	0.019–0.25	0.026–0.42	1.4–22.6	Winkler	Stn L4, English Channel, UK	This study
<i>O. similis</i>	19–20.7	0.44 ^a	0.20–0.23	0.45–0.52	24.4–28	Winkler	Buzzards Bay, MA, USA	Nakamura & Turner (1997)
<i>O. similis</i>	10	0.54–1.13 ^b	0.28–0.36	0.47–0.56	12–31.5	Fox–Wingfield	Clyde Sea, UK	Marshall & Orr (1966)
<i>O. nana</i>	7–12	0.20 ^c	0.02–0.078	0.1–0.38	5.3–20.8	Winkler	Loch Thurnaig, Scotland, UK	Lampitt & Gamble (1982)
<i>O. davisae</i>	5–30	0.23 ^c	0.11–0.14	0.51–0.68	25.6–31.4	Diver–respirometer	Shibaura, Tokyo Bay, Japan	Hiromi et al. (1988)
<i>O. davisae</i>	25	0.23 ^c	0.13	0.56	30.3	Diver–respirometer	Shibaura, Tokyo Bay, Japan	Nakata & Nakane (1987)
<i>Oithona</i> spp.	19.4–22.5	0.46–0.6 ^{b,c}	0.13–0.62	0.25–1.22	7.9–88.8	Micro–respirometer	Pacific Ocean ^d	Klekowski et al. (1977)
<i>O. plumifera</i>	22.5–25.5	0.3–1.52 ^{b,c}	0.12–0.79	0.10–1.65	5.5–88	Micro–respirometer	Pacific Ocean ^d	Klekowski et al. (1977)
<i>O. setigera</i>	22.5–25.5	0.28–1.52 ^{b,c}	0.34–1.02	0.22–3.62	12.1–194	Micro–respirometer	Pacific Ocean ^d	Klekowski et al. (1977)
<i>O. tenuis</i>	22.5–24.5	0.19–1.37 ^{b,c}	0.31–0.94	0.23–4.95	12.3–265	Micro–respirometer	Pacific Ocean ^d	Klekowski et al. (1977)

^aCalculated from body length versus carbon equation of Sabatini & Kiørboe (1994); ^bconverted to carbon from dry weight assuming body carbon as 40% of dry weight (Mauchline 1998); ^cconverted to dry weight from wet weight assuming 81% water content (Mauchline 1998); ^dmeasurements made during Cruise 17 of RV 'Akademic Kurchatov' between 05° 21' N, 88° 05' W and 00° 01' S, 139° 41' W

Table 2. One-sample *t*-test between ln-transformed mean respiration rate (R , μO_2 copepod $^{-1}$ d $^{-1}$) standardised to 15°C using Q_{10} for *Oithona similis* (present study) and calanoid copepod of equivalent body mass (i.e. weight [WT] = 0.56 $\mu\text{g C}$) estimated from regression line of Ikeda et al. (2001) in Fig. 3. n: number of observations; 95 % CI: confidence intervals of means; R-ratio: ratio between respiration rate estimated for *O. similis* and a calanoid copepod

Group	n	ln WT	ln R	95 % CI	<i>t</i> -value	<i>p</i> -value	R-ratio
Calanoid	43	-0.571	-0.3423 (± 0.0011)	-0.364, -0.321	-42.88	<0.001	8.33
<i>O. similis</i>	36	-0.571	-2.4619 (± 0.0494)	-2.562, -2.362			

calanoid copepods (e.g. in situations where food sources are low) and could be one of the reasons why *Oithona* spp. are so ubiquitous and abundant. Although several investigations have noted that the respiration rate of *Oithona* spp. is lower than that of calanoids (Lampitt & Gamble 1982, Nakamura & Turner 1997), this hypothesis has not been thoroughly tested. In addition, other studies have challenged this idea, attributing the success of *Oithona* spp. more to its ability to feed on a wider size range and diversity of prey (Lampitt 1978, Uchima 1988, Gonzalez & Smetacek 1994, Roff et al. 1995, Lonsdale et al. 2000) rather than to real differences in the metabolic rates between *Oithona* spp. and calanoids (Sabatini & Kjørboe 1994, Nielsen & Sabatini 1996).

We compared the data of *Oithona similis* from this study with those of calanoid copepods from Table 2 in Ikeda et al. (2001), since the respiration rates were measured using similar methods (Fig. 3). To make the comparison possible, the 2 sets of data were first standardised to 15°C using the Q_{10} found by Ikeda et al. (2001) and by the present study for calanoids and *O. similis* respectively. Fig. 3 shows that the regression line relating respiration rate and body mass of calanoids lies above the data of the cyclopoids. A 1-sample *t*-test (Table 2) indicated that the mean respiration rate of an *O. similis* female is significantly lower (i.e. ~8 times) than that of a calanoid copepod of similar body mass estimated from the regression analysis of Ikeda's (2001) data.

The lower respiration rate of *Oithona similis* may reflect different physiological, behavioural and ecological adaptations from those of calanoid copepods to life in the pelagial. *Oithona* spp. are ambush and coprophagous feeders, mostly drifting passively without generating a feeding current (Svensen & Kjørboe 2000, Paffenhöfer & Mazzocchi 2002). Thus, whereas calanoids spend on average 80 % of their time swimming, *Oithona* spp. copepodites only move 0.9 % or less of the time (Paffenhöfer 1993, Hwang & Turner 1995, Paffenhöfer & Mazzocchi 2002). However, energy is

expended not only in swimming speed, but also in the movement of mouth-parts. Thus, the lower metabolic rates of *O. similis* could also be attributable to the absence of a feeding current.

Their smaller size, transparency and reduced motion probably make *Oithona* spp. less conspicuous than calanoids to both tactile and visual predators (Paffenhöfer 1993, Atkinson & Snyder 1997). Recently, Eiane & Ohman (2004) have shown that overall *O. similis* suffers lower mortality rates

than *Calanus finmarchicus* and *Pseudocalanus elongatus*. Thus, the high abundance often reported for *Oithona* spp. (Gallienne & Robins 2001 and references therein) could be equally accounted for by both lower metabolic and mortality rates, as these are directly related to reduced swimming activity.

The relationship between respiration and temperature (Fig. 2) allows calculation of the basic metabolic costs and energetic requirements that must be met by an adult female *Oithona similis* to survive over a wide temperature range. Such information is very important, particularly for an organism such as *O. similis*, whose distribution extends from polar to tropical oceans. Thus, our study predicts that the cost of respiration for *O. similis* varies from a minimum of ~1.4 % body-C d $^{-1}$ at 4°C to a maximum of 23 % body-C d $^{-1}$ at 25°C, corresponding to an energy demand of ~3 % and 32 % body-C d $^{-1}$ (i.e. assuming a respiratory quotient, RQ, of 0.8 [for protein metabolism] and assimilation efficiency, A, of 0.7 [Ikeda & Motoda 1978]) respectively.

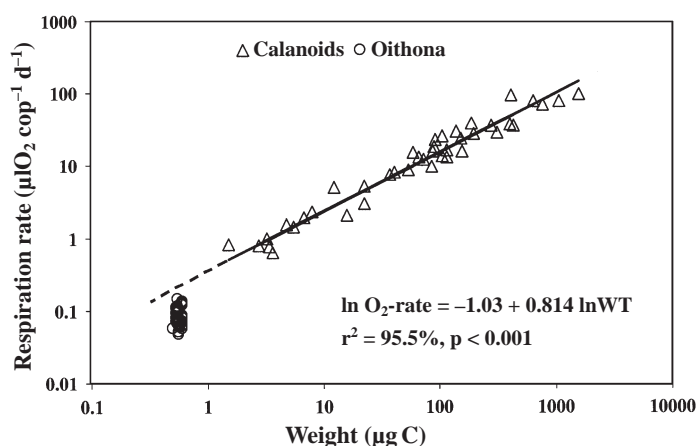


Fig. 3. Respiration rate (μO_2 copepod $^{-1}$ d $^{-1}$) of *Oithona similis* (present study) and of calanoid copepods (Ikeda et al. 2001) versus body mass (WT in $\mu\text{g C}$). All values standardised to 15°C using appropriate Q_{10}

Reported *in situ* ingested carbon for *Oithona similis* of 5 to 327 % body-C d⁻¹ at temperatures between -1 and 6.5°C in the sub-antarctic respectively (Atkinson & Shreeve 1995, Atkinson 1996, Swadling et al. 1997, Lonsdale et al. 2000) and up to ~40% in temperate areas (Lampitt & Gamble 1982, Nakamura & Turner 1997) are in excess of the energy demand for respiration estimated by the present study. In addition, the coprophagous feeding of *O. similis* spp. (Gonzalez & Smetacek 1994) signifies that published feeding rates probably represent underestimates, as ingestion of faecal pellets in feeding experiments is rarely taken into account. These observations suggest that *Oithona* spp. is less dependent on microplankton blooms and thus less likely to suffer mortality rates due to starvation than calanoids.

The success of *Oithona* spp. is probably dependent on more than one factor. We argue, however, that lower metabolic needs may increase the chances of survival and reproduction of *O. similis* and contribute to explaining its higher abundance in oceanic oligotrophic environments, and in winter, when food resources may become limiting for the majority of calanoid copepods.

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