

1 Title: Diel vertical migration of the Southern Ocean euphausiid, *Euphausia triacantha*, and  
2 its metabolic response to consequent short-term temperature changes.

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13

14 Abstract

15 We investigated the effect of short-term temperature change on the respiration rate of  
16 *Euphausia triacantha*, a common component of the Southern Ocean zooplankton and a  
17 prominent vertical migrator. We found respiration to vary in response to size, with a value of  
18 0.84 for the scaling coefficient,  $b$ . When scaled to  $b$ , respiration varied strongly in response to  
19 transitory temperature change, ranging from 0.37 to 1.65  $\mu\text{l O}_2 \text{ mg DW}^{-b} \text{ h}^{-1}$  between 0.17 and  
20 4.74 °C, resulting in a  $Q_{10}$  of 3.6. This  $Q_{10}$  is higher than found by other studies examining the  
21 short term respiration response of euphausiids, including those taking a multi-species  
22 perspective. This indicates that *E. triacantha* shows little compensation during short-term

## Respiration of *Euphausia triacantha* during DVM

1 exposure to temperatures normally encountered during their migration. Furthermore, it shows  
2 that there is a distinct metabolic cost to diel vertical migration (DVM) when substantive  
3 changes in temperature are encountered over the course of the transit. This temporal variability  
4 in respiration rate has important implications for how community respiration is estimated, and  
5 for our understanding of the behaviour of DVM. Our results also have particular relevance to  
6 estimating the flux and sequestration of respiratory products, such as dissolved carbon dioxide  
7 ( $\text{CO}_2$ ), to and within the ocean interior.

8 Keywords: Respiration, temperature coefficient ( $Q_{10}$ ), Diel Vertical Migration (DVM),  
9 *Euphausia triacantha*, Southern Ocean, Scotia Sea, elemental composition

1 1. Introduction

2 Diel migrant zooplankton have been considered agents of active carbon flux for well over four  
3 decades, although early attention was focussed solely on the contribution made from faecal  
4 pellets (Angel 1986). Longhurst (1990) additionally considered the role of respiration,  
5 suggesting that the respiratory carbon flux from diel migrants could be considerable, and range  
6 from 13-53% of estimated particulate carbon flux sinking across the pycnocline. This process  
7 becomes particularly important when it is assumed that the majority of carbon being respired  
8 is consumed at the surface, thus expediting the transport of respired CO<sub>2</sub> into the comparatively  
9 unmixed waters of the deeper ocean. The question has remained an important one with Ariza  
10 et al. (2015) estimating that respiratory flux from migrators alone could account for the  
11 equivalent of 23-71% of the gravitational flux of carbon measured at 150 m depth. This is  
12 underscored by the suggestion that the mesopelagic migrant pump may be the greatest  
13 contributor to carbon sequestration of all biological and physical carbon pumps (Boyd et al.  
14 2019).

15 The question of how metabolism varies as a response to changing physical and chemical  
16 conditions as zooplankton migrate within the water column remains poorly parameterised. For  
17 organisms where aerobic respiration is the primary means of supplying the oxygen required for  
18 cellular metabolism, its measurement is most commonly achieved by quantifying oxygen  
19 consumption (Lampert 1984). Certain relationships are commonly upheld when considering  
20 rates of metabolism, the first being that respiration rate increases as a function of size, described  
21 by the relationship  $R = aW^b$ , where the scaling exponent  $b$  is generally between 0.7-0.9  
22 (Hernández-León & Ikeda 2005a). The second is that respiration rate is strongly regulated by  
23 temperature. Activation energy ( $E_a$ ) is fundamental to defining the thermodynamic relationship  
24 between temperature and reaction rate (Clarke 2017) and is described according to the  
25 Arrhenius relationship,  $k = Ae^{-E_a/RT}$  where  $k$  is the rate constant,  $E_a$  is the activation energy,  $R$

1 is the ideal gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ) and  $T$  is the temperature in Kelvin. In physiological  
2 studies, this is often described as the van't Hoff rule, with reference to the  $Q_{10}$  coefficient, a  
3 measure used to describe the sensitivity to temperature of a species' respiration rate, defined  
4 as the increase in rate with a  $10 \text{ }^\circ\text{C}$  rise in temperature.

5 Many studies have addressed the role of temperature on zooplankton respiration through global  
6 or interspecific relationships (e.g. Teal & Carey 1967, Ikeda 1970, Ivleva 1980, Ikeda 2013).  
7 However, with some notable exceptions such as *Euphausia superba*, *E. pacifica* and  
8 *Meganyctiphanes norvegica* (e.g. Small & Hebard 1967, Hirche 1983, Torres & Childress  
9 1983, Ikeda & Kirkwood 1989, Opalinski 1991, Saborowski et al. 2000), detailed studies of  
10 individual species, and particularly their response in relation to DVM, are still relatively few.

11 *Euphausia triacantha* (Holt & Tattersall 1906) is a common, predominantly sub-Antarctic,  
12 constituent of the Southern Ocean zooplankton with a circumpolar distribution. It generally  
13 ranges from south of the Antarctic Convergence to the northerly limits of the East Wind and  
14 Weddell Drifts (Mauchline & Fisher 1969, Kirkwood 1982), although it has been found as far  
15 south as  $66^\circ 08' \text{ S}$  in the waters off the Antarctic Peninsula (Piatkowski 1985). It is a large  
16 species of euphausiid, with adults ranging from 24 to 41 mm, and has a lifespan of up to three  
17 years (Baker 1959, Siegel 1987). *Euphausia triacantha* does not swarm, yet it is the most  
18 abundant euphausiid on the north-west shelf of South Georgia, contributing 6% to overall  
19 nekton biomass (Piatkowski et al. 1994). It is also one of the most important contributors to  
20 abundance and biomass in the Polar Frontal Zone and replaces *E. superba* as the dominant  
21 euphausiid in that region (Pakhomov & McQuaid 1996). In addition, *E. triacantha* displays a  
22 pronounced diel vertical migration (DVM). It has been recorded at depths of up to 750 m during  
23 the day and in surface waters at night (Baker 1959), thus experiencing temperatures across the  
24 most thermally variable parts of the water column within its natural habitat.

1 Due to its extensive migratory behaviour and high levels of abundance, *E. triacantha* has the  
2 potential to be a significant contributor to the active flux of carbon. Whilst clearly able to cross  
3 sharp thermal gradients, the effect of temperature on the respiration rate of *E. triacantha*  
4 remains unknown. The purpose of this study is twofold: first, to describe the distribution and  
5 diel migratory behaviour of *E. triacantha* in the Scotia Sea using abundance data obtained from  
6 cruises as part of the DISCOVERY 2010 programme. Second, to investigate the respiration  
7 rate of *E. triacantha* over the range of temperatures it is likely to experience *in situ*, determining  
8 its variation in response to the time-course of temperature changes experienced during DVM,  
9 based on experiments conducted on two experimental cruises.

## 10 2. Materials and methods

### 11 2.1. Distribution, abundance and environmental conditions of *Euphausia triacantha*

12 Day and night time MOCNESS (Multiple Opening and Closing Net with Environmental  
13 Sensing System, 1 m<sup>2</sup> mouth opening, 330 µm mesh) net samples were collected at four stations  
14 encompassing Antarctic and Polar Frontal zones in the Scotia Sea, Southern Ocean, on one  
15 summer (JR177) and one autumn (JR200) cruise (see Table S1). Day and night were defined  
16 as before and after apparent sunset respectively. These cruises took place in December to  
17 February 2007/08 and March to April 2009 respectively, on the RRS James Clark Ross. They  
18 were part of the multidisciplinary DISCOVERY 2010 sampling programme, an objective of  
19 which was the collection of depth-discrete zooplankton abundance data at repeat locations  
20 during different seasons, across three consecutive years, therefore having excellent  
21 geographical, vertical and seasonal coverage. The campaign is described in detail in Tarling et  
22 al. (2012). Hereafter, the summer and autumn DISCOVERY cruises will be referred to as  
23 JR177 (2008) and JR200 (2009), respectively. Nets were sequentially closed at 125 m depth  
24 intervals from 1000 m to the surface: 1000 - 875 m, 875 - 750 m, 750 - 625 m, 625 - 500 m,  
25 500 - 375 m, 375 - 250 m, 250 - 125 m and 125 - 0 m. The stations sampled were R1 (an ice-

1 influenced station), C3 (an open water, oligotrophic region), P2 (a putative oligotrophic region,  
2 upstream of the South Georgia & South Sandwich Island (SGSSI) archipelago) and P3 (a  
3 naturally iron-fertilised and highly productive region, downstream of the archipelago) (Figure  
4 1). Samples were preserved in buffered formalin and were subsequently sorted and analysed  
5 for species counts at the home laboratory.

6 [Insert Figure 1]

7 Where counts were obtained from a split, they were multiplied by the split to give a count for  
8 the whole sample. The whole sample count was converted to abundance  $m^{-2}$  by dividing by the  
9 volume of water filtered by the net ( $m^3$ ) and multiplying by the sampled depth interval (125  
10 m). Flow rate data were taken from the flowmeter attached to the MOCNESS where possible.  
11 Where this failed (<25% nets), the volume filtered was calculated by plotting duration of  
12 individual net haul against volume filtered from the observed flowmeter readings.

13 The vertical movement of *Euphausia triacantha* between day and night, based on the  
14 abundance data obtained on JR177 (2008) and JR200 (2009), was assessed by calculating the  
15 weighted mean depth (WMD, m) of individuals during the day and at night, according to  
16 Equation 1:

17 
$$WMD (m) = \frac{\sum(n_i \times z_i)}{N} \quad \text{Equation 1}$$

18 where  $n_i$  is the number of the concentration of individuals (inds.  $m^{-2}$ ) in each net horizon  $i$ ,  $z_i$  is  
19 the mid-depth (m) of each net horizon  $i$ , and  $N$  is the total number of depth horizons sampled.

20 The significance of the change in WMD, between day and night, was tested statistically using  
21 a paired Wilcoxon signed-rank test.

22 Temperature data for the same cruises were obtained by deploying a Sea-Bird Scientific SBE  
23 9Plus Conductivity Temperature Depth (CTD) profiler with a dual SBE 3Plus temperature

1 sensor (Sea-Bird Scientific, Bellevue, Washington). Data were averaged for every 2 m from  
2 the surface to 1000 m.

### 3 2.2. On-board respiration experiments

4 Oxygen consumption experiments were conducted on board RRS James Clark Ross during two  
5 Southern Ocean research cruises which took place 5-7 years later in the austral spring: JR304,  
6 in November to December 2014; and JR15002, in November to December 2015. Hereafter,  
7 these cruises will be referred to as JR304 (2014) and JR15002 (2015) (see Table S2).

8 Oxygen measurements were taken using a PreSens (Regensburg, Germany) Fibox 4 fibre-optic  
9 oxygen optode with temperature sensor Pt100 and PSt3 sensor spots (Presens GmbH 2014), a  
10 device based on the principle of dynamic luminescence quenching by molecular oxygen.  
11 During JR304 (2014), experiments were carried out on manufacturer calibrated (to 0% and  
12 100% saturated water) sensor spots. Prior to JR15002 (2015), all sensor spots were user  
13 calibrated following manufacturer's instructions. Briefly, the 0% saturation point was achieved  
14 by adding a sodium sulphite and cobalt nitrate mixture to 0.22  $\mu\text{m}$  filtered seawater (FSW) and  
15 shaking the bottles vigorously. 100% oxygen saturated water was produced by half filling  
16 bottles with 0.22  $\mu\text{m}$  FSW, shaking the bottles vigorously, removing the stoppers and allowing  
17 them to equilibrate to temperature and atmospheric  $\text{O}_2$  concentrations. Calibration was carried  
18 out at  $\sim 3.5$ . Bottles were prepared at least 48 hours prior to calibration using the prescribed  
19 routine on the PreSens device. The 100% saturation calibrations were repeated on board prior  
20 to first use, as per the manufacturer's recommendation. Subsequent on-board recalibration was  
21 not necessary as the number of measurement points did not exceed the re-calibration threshold.  
22 To account for differences in calibration procedure and to allow both years to be compared,  
23 raw phase data from JR304 (2014) were retrospectively calibrated with the calibration  
24 constants from JR15002 (2015). This followed advice from the manufacturer and employed

1 the PreSens Oxygen Calculator v3.0.0.0 and PreSens Oxygen Calculator Software Instruction  
2 Manual V3.0.0 designed for this purpose (Presens GmbH 2016).

### 3 2.3. Incubator set-up

4 Incubations for the oxygen consumption experiments were conducted in the cold room (set to  
5  $\sim 4$  °C) on the RRS James Clark Ross, in tanks designed to simulate the temperature range (0.2  
6  $-4.7$  °C) experienced by *E. triacantha* during their DVM within the area of study. Experiments  
7 involved the incubation of euphausiids concurrently at two temperatures. The low temperature  
8 experiments (T1) were conducted at temperatures of  $1.26 \pm 0.70$  °C (JR304 (2014)) and  $1.58$   
9  $\pm 0.17$  °C (JR15002 (2015)) and the high temperature experiments (T2) at  $3.08 \pm 0.29$  °C  
10 (JR304 (2014)) and  $4.66 \pm 0.07$  °C (JR15002 (2015)) (Table 1). Incubations took place in the  
11 dark with the exception of the few minutes when measurements were taken. The incubator  
12 setup was modified between JR304 (2014) and JR15002 (2015) to provide improved  
13 temperature control. Specifically, this meant that, in JR15002 (2015), the two temperatures  
14 were achieved in separate tanks as opposed to a graded tank in JR304 (2014).

15 During JR304 (2014), a purpose-built incubator (Spartel Temperature Gradient Incubator) was  
16 used. This had a C-400 circulator unit at the warm end and an FC-500 in-line cooler unit and  
17 C-85D circulator unit at the cold end, with temperature at each end controlled by ethylene-  
18 glycol anti-freeze being circulated through the end blocks of the incubator.

19 In JR15002 (2015), two separate thermostatically-controlled incubation tanks were used. This  
20 comprised a chiller unit (Julabo FL300 chiller) and a thermocirculator heating unit with cooling  
21 coil for each tank (ED Heating Immersion Circulator and Julabo Cooling Coil). The chiller unit  
22 worked against the heater unit to achieve the desired temperatures. The chiller unit was filled  
23 with ethylene-glycol anti-freeze, which was circulated through tubing sequentially connected  
24 to the cooling coils fitted to each thermocirculator.



1 The experimental setup is illustrated in Figure 2.

## 2 2.4. Animal capture and experiment set-up

3 Healthy specimens of *E. triacantha* were selected from three RMT8 (8 m<sup>2</sup> mouth opening, 5  
4 mm mesh) and five MOCNESS (1 m<sup>2</sup> mouth opening, 330 µm mesh) net catches during JR304  
5 (2014) and two RMT8 (specification as above) net catches during JR15002 (2015), all of which  
6 were in the northern Scotia Sea (see Figure 1). Temperature data were obtained from  
7 deployment of the CTD (details given in Section 2.1). All animals in a given incubation  
8 originated from the same net catch. Details of the nets that animals were obtained from are  
9 given in Supplementary Table S2. Animals were deemed to be healthy if they were translucent,  
10 swimming actively and had no visible signs of damage. Animals were gently rinsed twice in  
11 0.22 µm FSW and transferred to incubation bottles.

12 On JR304 (2014), one animal was incubated in each 60 ml bottle. On JR15002 (2015), four or  
13 five animals were incubated in 250 ml bottles, depending on the numbers of healthy animals at  
14 the time of the experiment. The change in vessel size was due to the change in design of  
15 experimental incubators, whilst maintaining approximately the same volume of water per  
16 animal between years. In an experiment on *E. superba*, the size of experimental vessel was  
17 found not to impact the measured metabolic rate, thus rates obtained in different sized vessels  
18 were considered comparable (Opalinski 1991). A drop of unfiltered seawater, equivalent to  
19 between 2-5 ml, from the same container as the euphausiids, was placed into control bottles to  
20 model the amount of unfiltered seawater added to the incubation bottles while transferring the  
21 animals.

22 Details of experiments are given in Table 1.

23 [Insert Figure 2]

1 Experimental bottles were topped up with FSW, maintained at experimental temperatures for  
2 at least an hour before incubations and stoppered, taking care to remove all air bubbles. At least  
3 2 hours elapsed between capture and introduction to the experimental bottles, during which  
4 time animals were maintained in water at the temperature of the experiment. Approximately a  
5 further 30 minutes elapsed between experiment set-up and the first measurement. Readings  
6 were taken every one to four hours throughout the incubation period, with between three and  
7 seven measurements made during the ~2 to 28 hour duration of the eight experiments.

8 Whilst taking readings, the animals were inspected for general health and activity i.e., that the  
9 animals responded to the gentle rotation of bottles with active swimming and were displaying  
10 the same colour, shape and translucency as at the start of the incubation, or had visible signs of  
11 deterioration. Bottles were subject to the natural movement of the ship and gently rotated before  
12 measurement to ensure water was well mixed. The oxygen saturation of the water in the bottles  
13 was also carefully monitored. The critical concentration of oxygen, below which respiration  
14 rates of marine animals markedly decline, is considered to be ~50% (Ikeda 1970) although this  
15 varies between species. In this study, measured oxygen saturation (% air saturation (a.s.)) at  
16 the end of incubations was always >70%.

17 Bottles containing dead or deteriorating animals were discarded. Incubations of bottles  
18 containing healthy animals were completed after at least three readings. At the end of the  
19 incubation, the animals were removed from the incubation bottles and frozen immediately at -  
20 80 °C. The length of incubations (generally between 2 and 6 hours) was a compromise between  
21 being long enough to obtain at least three reliable readings following a period of acclimation,  
22 and the space and time requirements to prepare for the next net haul and experiment setup.  
23 INC3 was the exception since there was no immediate pressure on equipment.

24 [Insert Table 1]

1        2.5. Determination of length, weight and elemental content

2        Frozen experimental specimens were thawed and length (L, mm) was measured, taken from  
3        the front of the rostrum to the tip of the telson. Wet weight (WW, g) was determined  
4        immediately after the measurement of body length, within two minutes of thawing, in pre-  
5        weighed weighing boats. Animals were quickly dabbed on absorbent paper to remove excess  
6        water. Animals were dried at 65 °C for 48 hours and re-weighed for dry weight (DW, g).

7        After dry weight measurements, animals from JR15002 (2015) were homogenised using a  
8        ceramic pestle and mortar and transferred to tin capsules for elemental (C and N) analysis and  
9        weighed. Analysis was carried out with a CE440 Elemental Analyser (Exeter Analytical (UK)  
10       Limited, Coventry, United Kingdom). Malfunction of the elemental analyser prevented the  
11       same analysis being carried out on animals from JR304 (2014).

12       2.6. Respiration data treatment and statistical analysis

13       Oxygen (O<sub>2</sub>) consumption per bottle (μmol l<sup>-1</sup>) was calculated by subtracting the mean O<sub>2</sub>  
14       consumption of control bottles from that of experimental bottles. Values were converted from  
15       μmol l<sup>-1</sup> to μl l<sup>-1</sup> by multiplying by 22.391 (ICES, 2018). Oxygen consumption (μl O<sub>2</sub>) ind<sup>-1</sup> h<sup>-1</sup>  
16       was calculated by dividing by duration (h) of experiment and number of individuals per bottle,  
17       and adjusting for bottle volume.

18       To examine the effect of body size and temperature on the respiration rate of *E. triacantha*,  
19       body weight (in mg dry weight (DW), carbon (C) and nitrogen (N)) and temperature were  
20       included as variables in a multiple regression, following the model described by (Ikeda 1985).  
21       Since C and N were only experimentally determined for JR15002 (2015) animals, the  
22       regressions between DW, and C/N given in Figure 4 were applied to the DW for animals  
23       incubated during JR304 (2014) to obtain a full set of C and N values for the multiple regression.

1 In the multiple regression we performed, three coefficients resulted:  $a_0 = \text{constant}$ ,  $a_1 = \text{body}$   
2  $\text{weight}$ , and  $a_2 = \text{temperature}$  (Table 3). Since respiration rate tends to scale with body size  
3 according to the relationship  $R = a * W^b$ , the body weight constant,  $a_1$ , thus determined the  
4 scaling exponent,  $b$ . Similarly, the sensitivity of an animal's respiration rate to increases in  
5 temperature can be assessed by calculation of the  $Q_{10}$ , following the van't Hoff rule (Equation  
6 2).

$$7 \quad Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2-T_1}\right)} \quad \text{Equation 2}$$

8 where  $T_1$  is the lower temperature,  $T_2$  is the higher temperature and  $R_1$  and  $R_2$  are the respiration  
9 rates at  $T_1$  and  $T_2$  respectively.

10 Using a rearrangement of the formula as set out in Equation 3 (see Ikeda 1985), the temperature  
11 constant,  $a_2$ , can be used to calculate the  $Q_{10}$  for *E. triacantha*.

12

$$13 \quad a_2 = \frac{\ln Q_{10}}{10} \quad \text{Equation 3}$$

14 Length-weight coefficients were determined by log transforming all data and regressing WW,  
15 DW, C and N against length with a linear fit according to the relationship  $y = a + b*x$ . The  
16 relationship between DW and C or N content; and DW and the C:N ratio was examined by  
17 fitting the data (from JR15002 (2015) alone, see section 3.2) to the same linear model.

18 Statistics were carried out in SigmaPlot V.13.0.0.83 (Systat Software Inc.) and RStudio  
19 (V.3.6.2 (R Core R Development Core Team 2019)).

### 20 3. Results

#### 21 3.1. Distribution and environment of *Euphausia triacantha*

1 Specimens of *Euphausia triacantha* were found throughout the water column at three stations  
2 across the Scotia Sea from the sub-Antarctic to Antarctic zones, both in the summer (JR177  
3 (2008)) and autumn (JR200 (2009)) abundance cruises, where surface temperatures varied  
4 from <1 to 5 °C (Figure 3). This included C3 (the open water oligotrophic region south of the  
5 Sub-Antarctic Circumpolar Current Front (SACCF)), P2 (upstream of SGSSI and putatively  
6 oligotrophic), and P3 (the naturally iron fertilised area downstream of SGSSI). None were  
7 found at the ice-influenced station, R1. Across the 1000 m water column, summer abundances  
8 ranged from 3 inds. m<sup>-2</sup> at C3 to 18 inds. m<sup>-2</sup> at P3, and autumn abundances ranged from 1 ind.  
9 m<sup>-2</sup> at C3 to 46 inds. m<sup>-2</sup> at P3. The animals occurred throughout the water column, from the  
10 surface to as deep as 1,000 m, at all stations in both seasons. They also displayed clear evidence  
11 of diurnal vertical migration, with a total absence of animals in the top 250 to 375 m at C3 and  
12 P2 during the day, but occupation of these layers during the night in both seasons. At P3,  
13 animals were found between 125 and 250 m during the day in summer, followed by an ascent  
14 by the majority of the population to the surface at night. In autumn, a bimodal distribution was  
15 apparent and, although a small number of animals were found in the surface during the day,  
16 this markedly increased at night. The weighted mean depth (WMD) of animals during day and  
17 night (Table 2) illustrated the consistency of DVM by *E. triacantha*, with shallower night-time  
18 compared to daytime depths in every sample. During daytime, the WMD of *E. triacantha*  
19 ranged from 232 to 500 m in summer and 438 to 531 m in autumn, whilst at night, WMDs were  
20 80 to 349 m in summer, and 81 to 339 m in autumn. A Wilcoxon signed-rank test confirmed  
21 the WMD (m) between paired day and night-time samples to be significantly different ( $p <$   
22 0.05). Across their vertical migratory ranges, the temperatures experienced by *E. triacantha*  
23 during JR177 (2008) and JR200 (2009) ranged from -1.5 to 2.1 °C at the most southerly station,  
24 and from 0.4 to 5.0 °C at the most northerly, representing a temperature range of 6.5 °C. The  
25 strongest temperature gradient experienced during a typical DVM was across the thermocline,

1 between ~60 to 100 m, where the mean temperature change was 3.5 °C (range 2.5 °C to 4.5  
2 °C). Temperatures during experimental years, JR304 (2014) and JR15002 (2015), were similar,  
3 ranging from -1.4 to >3 °C over the same geographical area, representing a range of >4.4 °C.

4 [Insert Table 2]

5 [Insert Figure 3]

### 6 3.2. Morphometric and elemental analysis

7 A total of 159 animals obtained from the experimental cruises, JR304 (2014) and JR15002  
8 (2015) in austral spring, were measured and weighed. Animals ranged in length (L) from 20.0  
9 to 39.4 mm. This likely represents animals from at least two age cohorts, the sub-adult  
10 population (<24 mm) and the adult population (>24 mm) (Baker 1959, Siegel 1987). Wet  
11 weights (WW) ranged from 60.31 to 427.32 mg and dry weights (DW) ranged from 12.49 to  
12 96.01 mg. A significant relationship between L and weight was found ( $P < 0.0001$ ) (see Figure  
13 4, panel A and Supplementary Table S3).

14 A total of 90 animals were analysed for elemental composition, in addition to length and weight  
15 measurement. The plots are shown in Figure 4, panels B and C, and regression results are given  
16 in Supplementary Table S4. C content ranged from 37.9% to 45.0% and N content ranged from  
17 8.8% to 10.1%. The mean C:N ratio was 4.39 (ranging from 3.93 to 4.90). Significant  
18 relationships between C and N were found for both measures of weight. The relative  
19 proportions and hence the C:N ratio varied positively, weakly but significantly ( $P < 0.0001$ )  
20 with DW.

21 [Insert Figure 4]

### 22 3.3. Effect of size and temperature on respiration

1 Over our experimental temperature range of 0.17 to 4.74 °C, individual respiration rates ranged  
2 from 5.83 to 38.06  $\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}$ . Multiple regression confirmed a significant effect of all  
3 measures of weight (mg DW, C or N), and temperature, on individual respiration (Table 3).  
4 The body weight coefficient, or scaling exponent,  $b$ , was 0.84 for mg DW, ranging from 0.81  
5 (mg C) to 0.87 (mg N). The temperature coefficient yielded a  $Q_{10}$  of 3.6 for all measures of  
6 weight (Table 3). Body weight contributed most to the variance in individual respiration rate,  
7 and temperature contributed a significant additional component (Figure 5). [Insert Figure 5].

8 When standardised to body weight using the  $b$  value of 0.84, respiration rates over the same  
9 temperatures ranged from 0.37 to 1.65  $\mu\text{l O}_2 \text{ mg DW}^{-b} \text{ h}^{-1}$ , decreasing with increasing DW and  
10 increasing with temperature.

11 [Insert Table 3]

## 12 4. Discussion

### 13 4.1. Distribution and abundance of *Euphausia triacantha*

14 Analysis of depth-discrete zooplankton samples taken from across the Scotia Sea during the  
15 abundance cruises, JR177 (2008) and JR200 (2009), showed *Euphausia triacantha* to be  
16 abundant (up to 46 individuals  $\text{m}^{-2}$ ) and distributed over a wide latitudinal gradient in both  
17 summer and autumn. This included the colder waters south of the Southern Antarctic  
18 Circumpolar Current Front (SACCF) to the warmer, more productive region of the north  
19 Scotia Sea, north of the front. Abundances were substantially greater north of the SACCF in  
20 both summer and autumn, ranging from 1 to 3 inds.  $\text{m}^{-2}$  south of the SACCF, to between 8  
21 and 46 inds.  $\text{m}^{-2}$  in the north. *Euphausia triacantha* also displayed a prominent diel vertical  
22 migration (DVM), with deeper weighted mean depths in daytime compared to night-time  
23 demonstrative of a clear movement of the population towards the surface at all stations and in  
24 both seasons. This confirms previous observations of the species exhibiting a wide vertical

1 and latitudinal distribution, and a consistent absence of *E. triacantha* in surface waters during  
2 the day compared with their presence at night (Baker 1959). Temperatures experienced by the  
3 animals over this DVM varied with location and season, reaching up to 6.5 °C, with the most  
4 rapid and substantial changes occurring in the 50 to 100 m layer and corresponding to the  
5 depth the euphausiids would likely cross during their upward and downward migrations. This  
6 justified our study into the effect of short-term temperature change on the respiration rate of  
7 *E. triacantha*, and the temperature range examined during this study.

#### 8 4.2. Response of respiration rate to size and temperature

9 To consider the effect of temperature on *E. triacantha*, we used a multiple regression model  
10 that incorporated both body size and temperature variables concurrently. The respiration of *E.*  
11 *triacantha* was found to be significantly dependent on both variables. The majority of the  
12 variance was explained by body mass, with a scaling exponent of 0.84, and a significant  
13 additional component was explained by temperature, with a  $Q_{10}$  of 3.6. Despite the suggestion  
14 that pelagic animals may be more likely to scale isometrically i.e. with ratio of 1 (Small &  
15 Hebard 1967, Glazier 2006), the scaling coefficient obtained confirmed that the respiration of  
16 *E. triacantha* scales allometrically with size. Nevertheless, the value of 0.84 was greater than  
17 the three quarter power rule commonly used to describe the relationship between respiration  
18 and body weight (Kleiber 1932), and greater than the coefficient obtained in a global analysis  
19 of 24 species of euphausiid (Ikeda 2013). It was, however, closer to the value of 0.81 obtained  
20 for adult and juvenile *E. pacifica* (Ross 1982) where an increase in the value of the coefficient  
21 with age was observed. Considering that the present study on *E. triacantha* also incorporated  
22 both adults and juveniles, our result may support the suggestion of Ross (1982) that an  
23 increasing slope could reflect a metabolic change that occurs at maturation.



1 When considering the response of biological rate processes to temperature, a  $Q_{10}$  of between 2  
2 and 3 is typical (Schmidt-Nielsen 1997) essentially producing an exponential curve. This  
3 relationship has been found to hold across a wide spectrum of marine zooplankton, including  
4 euphausiids (e.g. Paranjape 1967, Small & Hebard 1967, Teal & Carey 1967, Ivleva 1980,  
5 Ikeda 2013). It is also consistent with previous studies that have found the respiration rate of  
6 northern krill, *M. norvegica* (Saborowski et al. 2002), and mixed Arctic zooplankton (Alcaraz  
7 et al. 2013), to rise exponentially as experimental temperature increased, and appears  
8 independent of experimental technique. In Saborowski et al. (2002), the same pattern was  
9 observed from measurements made with both a Clark-type electrode and the Winkler method,  
10 the only difference being a lower rate in the Winkler experiments due to reduced swimming  
11 activity; whilst Alcaraz et al. (2013) used optodes from the same manufacturer as in the present  
12 study.

13 Although a  $Q_{10}$  of between 1 and 4 may be considered within the ‘normal’ range within the  
14 geographical region of our study (Clarke & Peck 1991), higher values may be indicative of  
15 some sort of stress (Hirche 1984), too short an acclimation period (Ivleva 1973) or active rather  
16 than routine metabolism being measured (Conover 1978). In our study, the majority of  
17 experimental animals were taken from the northern Scotia Sea where the average ambient  
18 temperature below the thermocline was 1.8 °C, in contrast to 0.06 °C in the southern Scotia  
19 Sea. Saborowski et al. (2002) found different populations of *M. norvegica* to compensate for  
20 the temperature of their habitat, displaying the same respiration rate whether residing at 4, 8 or  
21 12 °C. Given the acute nature of our experiments, it may be that rates measured at the lowest  
22 end of the temperature spectrum are lower than might be expected of animals taken directly  
23 from that environment and that, with time, they may have compensated for this by elevating  
24 their metabolism (Clarke 1983). Another feature of the  $Q_{10}$ , is that it is inversely related to the  
25 temperature range over which it is calculated, and to temperature itself (Clarke 2017), with

1 lower temperatures and smaller ranges yielding higher values. Indeed, in his study of seven  
2 polar pelagic zooplankton species, Hirche (1984) found the  $Q_{10}$  to be systematically lower  
3 when calculated over 5-10 °C ( $Q_{10}$  of 2.6 to 5.2) compared to 0-5 °C (2.8 to 5.6).  
4 Nevertheless, our  $Q_{10}$  of 3.6 is higher than the average of 2.8 obtained during intraspecific  
5 studies on euphausiids (Paranjape 1967, Small & Hebard 1967, Teal & Carey 1967, Hirche  
6 1984, Iguchi & Ikeda 1995), and substantially higher than the  $Q_{10}$  of 1.7 determined by Ikeda  
7 (2013) in his global, interspecific compilation of 24 euphausiid species. This suggests that *E.*  
8 *triacantha* has not developed a mechanism to compensate for short-term temperature changes  
9 such as it was exposed to in this study, and that over the course of its migration it does not  
10 adjust its rate of respiration. This therefore represents a metabolic cost to the animal which we  
11 hypothesise is balanced by food intake upon reaching surface waters. We further hypothesise  
12 that this lack of compensation may be attributable to the migratory regime of *E. triacantha*.  
13 Specifically, the vertical distribution profiles of *E. triacantha* in Fig. 2 consistently show a  
14 relatively deep spread of animals throughout the water column at night, even though the bulk  
15 population moves upwards. Additionally, a bimodal distribution is apparent in at least three of  
16 the profiles (P2 in summer; C3 and P3 in autumn). This suggests that migration of the  
17 population is asynchronous (Pearre 1979) and that the whole population does not carry out full  
18 DVM every day. The implication of this for our study is that, if DVM is not as ubiquitous as  
19 currently assumed, and the animals do not cross a sharp thermal boundary every day, the cost  
20 to the animal is lower, and there is consequently little advantage to the development of a  
21 temperature compensation mechanism. The combination of elevated  $Q_{10}$  and insight into  
22 vertical distribution may therefore shed new light on the migratory behaviour of *E. triacantha*,  
23 with potential implications for biogeochemical fluxes.

24 4.3. High variability in respiration rate across the temperature spectrum

1 Notwithstanding the general trend of increasing respiration rate with temperature, we also  
2 observed individual-level variability across the temperature spectrum measured. This may be  
3 influenced by a number of factors, including locomotive activity, feeding, developmental stage,  
4 sex, injury or container crowding, and chemical or physical factors (e.g. Hernández-León &  
5 Ikeda 2005b). A small amount of variability may also be attributable to measurement at slightly  
6 different temperatures to that which the instrument was calibrated at. In our study, oxygen  
7 saturation was not found to be limiting, and the effect of pressure has been found to be low or  
8 negligible, especially at low temperatures (Teal & Carey 1967, King & Packard 1975, Torres  
9 & Childress 1983, Childress & Thuesen 1993, Thuesen et al. 1998). Thus, the determination  
10 of respiration rates of deeper-dwelling zooplankton at surface pressures is deemed  
11 experimentally sound (Childress & Thuesen 1993, Hernández-León & Ikeda 2005a). No  
12 obvious effect of injury was observed on any of the animals that were alive at the end of the  
13 experiment, and there was no evidence of a container effect in either year. Regarding activity,  
14 the distinction between basal, routine and active metabolism is important (Harris et al. 2000).  
15 Whilst not possible to quantify the effects of activity in the current study, activity levels of  
16 individuals were qualitatively noted throughout experiments, and most exhibited a mixture of  
17 periods of inactivity interspersed with bouts of active swimming. This likely represents routine  
18 metabolism, thus is consistent and comparable with most studies on euphausiid respiration  
19 where measurement in containers constrains full movement (Clarke & Morris 1983, Ikeda  
20 2013, Tarling 2020). As a result, the rates presented here are likely conservative estimates and  
21 do not take into account the full range of locomotive activity an animal is likely to exhibit in  
22 the environment.

23 Another consideration is light, which may exert an influence on respiration rate through its  
24 control on circadian rhythm (e.g. Mortola 2004, Teschke et al. 2011). Light was largely  
25 controlled for in this study, with all animals subjected to the same experimental conditions, so

1 it was assumed that any variability observed in a given experiment was individual rather than  
2 due to variability in circadian phase. However, since the timing of individual experiments  
3 varied (see Table S2), differences in phase of photoperiod may have led to variability in  
4 respiration rate between experiments. Feeding, or Specific Dynamic Action (SDA) (Secor  
5 2009), may also affect respiration rates, with polar ectotherms compensating for a lower post-  
6 prandial peak with a longer period of metabolic elevation (Peck 1998, Whiteley et al. 2001).  
7 Whilst we cannot exclude the possibility that some animals had fed more recently than others,  
8 the influence of SDA was minimised with a period of acclimation, and any risk of feeding in  
9 the net is likely to be outweighed by capture stress expediting gut passage. Unfortunately, the  
10 effects of SDA in epipelagic crustaceans, particularly euphausiids, are poorly understood,  
11 although one study did conclude that increases in post-prandial oxygen consumption were the  
12 effect of SDA, with the authors suggesting that the metabolism of wild krill may be 1.6 times  
13 that of their non-feeding counterparts (Ikeda & Dixon 1984).

14 Finally, variability between individuals may be introduced as a result of differences in  
15 developmental or reproductive state. Elevated rates have been observed in moulting specimens  
16 of *E. pacifica* (Paranjape 1967) and *E. triacantha* (Ikeda & Mitchell 1982), and are associated  
17 with gametogenesis (Lasker 1966, Clarke 1980). Since spawning in *E. triacantha* is thought to  
18 occur between October and November (Dzik & Jazdzewski 1978), it was considered that any  
19 females would have been spent before our period of study, and no moulting specimens were  
20 observed. However, we observed an increasing C:N ratio with size which may indicate greater  
21 lipid stores of larger animals (e.g. Post et al. 2007, Logan et al. 2008), or ovarian maturation in  
22 females. In a study on *E. superba*, Ikeda and Mitchell (1982) found the lowest weight-specific  
23 respiration rates for gravid krill, so values at the lowest extreme of our ranges could represent  
24 those of females with maturing ovaries.

#### 25 4.4. Comparison of respiration rate with other euphausiids

1 To contextualise our findings, we compared rates presented in this study with literature values  
2 from euphausiids of a similar size and lifestyle, normalised to the scaling coefficient  $b = 0.84$   
3 (Figure 6). The relationship we obtained is almost identical to that obtained for *M. norvegica*  
4 (Saborowski et al. 2002), and close to rates observed for *E. crystallorophias* (Ikeda & Fay  
5 1981) and *E. triacantha* (Ikeda & Mitchell 1982, Torres et al. 1994). *Meganyctiphanes*  
6 *norvegica* and *E. crystallorophias* are omnivorous species of a comparable size so may  
7 represent a good analogue for *E. triacantha*. *Meganyctiphanes norvegica* performs DVM and  
8 has been found to exhibit elevated rates of respiration during migration (Saborowski et al.  
9 2000), and recent work suggests *E. crystallorophias* may also perform shallow DVM (Conroy  
10 et al. 2020). We also compared our results to the global-bathymetric model proposed by Ikeda  
11 (2013) in which body mass, temperature and depth of occurrence were used in an attempt to  
12 describe the global respiration of euphausiids (Figure 6). We assumed an average size for *E.*  
13 *triacantha* of 34.2 mg DW and a median depth of occurrence of 370 m based on our own data,  
14 and calculated rates across a 5 °C temperature range using the Ikeda (2013) empirical model.  
15 The modelled curve was flatter and predicted a smaller increase in respiration rate with  
16 temperature than the regression we obtained. Torres et al. (1994) also considered depth,  
17 estimating that the metabolism of Antarctic micronekton at 1000 m is a third of that at the  
18 surface. However, our comparison of rates suggests that seasonality may be of greater influence  
19 than depth, and this may be especially true for a migrating organism such as *E. triacantha*,  
20 whose depth of occurrence at the time of sampling may not be representative of the depth at  
21 which it most commonly resides (e.g. Teal & Carey 1967). In copepods, higher rates in spring  
22 compared to winter have been linked to food availability, nutritional condition and metabolic  
23 slowdown during diapause (Conover 1959, Marshall & Orr 1966, Båmstedt 1979, Castellani  
24 & Altunbas, 2014). The effects of seasonality on euphausiids are less well-studied, although  
25 Torres et al. (1994) confirmed lower metabolic rates in *E. superba* over winter. More recent

1 work suggests that reduced feeding (Meyer et al. 2010) and changes to the local light regime  
2 (Meyer 2012, Tremblay et al. 2014, Piccolin et al. 2018) may drive seasonal metabolic cycles  
3 in *E. superba*. Although *E. triacantha* exhibits less seasonality in growth than *E. superba*  
4 (Siegel 1987), a study by Donnelly et al. (2004) obtained substantially higher respiration rates  
5 during a summer ice-edge bloom than similar experiments conducted during winter (Torres et  
6 al. 1994), although data were insufficient to enable a statistical comparison. The rates obtained  
7 in the present study, which was carried out in spring, were more comparable to the winter-time  
8 rates of Torres et al. (1994) but still substantially lower than those of Donnelly et al. (2004),  
9 suggesting that there may be a seasonal component to the metabolism of *E. triacantha* that  
10 merits further investigation. However, our experiments took place in late-spring in the northern  
11 Scotia Sea, where day lengths were long (~17 hours) and diatom blooms were encountered in  
12 both years. Since this was not associated with a rate as high as that observed by Donnelly et al.  
13 (2004), factors such as population structure, availability of alternative food sources, timing of  
14 the bloom and nutritional state at bloom onset may also be important. It is also worth noting  
15 that the average seasonal temperature change (~2 °C in the vicinity of South Georgia,  
16 Whitehouse et al. (2008)) is low in comparison to the gradient experienced during DVM (up  
17 to 4.5 °C), a factor that may also contribute to the steeper curve that we observed (Figure 6).

18 Finally, the difference between the steeper slope obtained in the present study and that  
19 predicted from Ikeda (2013)'s model may be attributable to intra- versus inter-specific  
20 responses. It is common for a lower  $Q_{10}$  to be obtained when comparing between species that  
21 have *adapted* to a temperature over evolutionary time, than for individuals within a species  
22 where the response being measured is *acclimation* to a short-term temperature change (Ikeda  
23 2013). We therefore suggest that the value of such a global model lies in describing general  
24 relationships across contrasting temperatures and habitats but it is not able to predict the full

1 physiological response elicited by an organism such as *E. triacantha* which is subject to  
2 substantial depth and temperature changes over the course of a diel vertical migration.

3 As we suggest, the strong response of *E. triacantha* to temperature indicates a lack of  
4 compensation, or adjustment, for substantive temperature changes experienced over its  
5 migration, which we propose may represent a metabolic cost to migration. This may reflect  
6 asynchronous or partial DVM, with the implication being that a compensatory response has  
7 not been developed due to animals not being engaged in extensive DVM on a daily basis. This  
8 not only challenges our assumptions of the ubiquity of DVM, but also has important  
9 implications for biogeochemical cycling in the Southern Ocean. Animals that undertake deep  
10 DVMs, such as euphausiids, have significant potential to pump carbon into deeper layers of  
11 the ocean, bypassing the mixed layer and isolating carbon from the atmosphere over  
12 climatically significant timescales (Longhurst & Harrison 1988, Steinberg & Landry 2017,  
13 Cavan et al. 2019). How much time migrators spend above or below the thermocline is  
14 therefore an important quantity to resolve if we are to generate reliable estimations of active  
15 CO<sub>2</sub> flux (Conroy et al. 2020), and a better understanding of DVM in euphausiids is  
16 fundamental to this (Cavan et al. 2019). For example, a high respiration rate in warmer surface  
17 waters may result in increased amounts of dissolved carbon dioxide (CO<sub>2</sub>) being respired  
18 during periodic excursions into the mixed layer. This may however, be more than offset by  
19 substantially longer durations spent at depth, where carbon consumed at the surface is respired  
20 below the thermocline, under a scenario whereby an animal only migrates a fraction of the  
21 time. A clearer understanding of the behaviour and ubiquity of DVM in *E. triacantha* is  
22 therefore of critical importance in estimating its contribution to the active flux of carbon.

23 [Insert Figure 6]

24 4.5. Concluding remarks

1 This analysis of the distribution, migration and metabolic rate of *E. triacantha* is the most  
2 comprehensive such study to date. It is also the first to consider the potential effect of  
3 temperature changes experienced during DVM on the respiration of this important euphausiid.  
4 Over our experimental temperature range of 0.17 to 4.74 °C, respiration ranged from 0.37 to  
5 1.65  $\mu\text{l O}_2 \text{ mg DW}^{-b} \text{ h}^{-1}$ . Despite *E. triacantha* being found in environments with wider ranging  
6 temperatures than the ~4.5 °C range they were exposed to in this study, our results suggest that  
7 it does not compensate for the short-term exposure to such temperature change, perhaps  
8 indicating that DVM is not so ubiquitous a behaviour as commonly assumed. We hypothesise  
9 that diel vertical migration in *E. triacantha* represents a metabolic cost that is offset by exposure  
10 to prey. Comparison with literature-derived rates suggest that *E. triacantha* has a wide  
11 metabolic scope, which may be seasonally-influenced, thus our results represent a conservative  
12 estimate of average spring-time rates. We conclude that global relationships of respiration to  
13 body size and temperature may not be sufficient to understand the full range of physiological  
14 and interspecific variability in how organisms respond to temperature changes over short time  
15 scales such as occurs during DVM. Such interspecific variations in behaviour and physiology  
16 may have important implications for how community respiration is estimated, with associated  
17 implications for our understanding of biogeochemical cycling. Our results are of particular  
18 relevance for constructing accurate estimates of the flux and sequestration of respiratory carbon  
19 to the ocean interior.

20

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5

6

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49

Respiration of *Euphausia triacantha* during DVM

1 Tables

2 Table 1: Details of the experiments carried out on *Euphausia triacantha* during JR304 (2014) and JR15002 (2015). T1 and T2 refer respectively  
 3 to the mean and standard deviations of the low and high temperatures experienced by animals during each experiment. Animals were exposed  
 4 either to T1 or to T2 for the duration of the experiment. ‘Animals at start’ refers to the number of animals exposed to each temperature. ‘Animals  
 5 at end’ refers to the number of healthy animals remaining at the end of each experiment. INC and EXP refer to the names experiments were given  
 6 in respective cruises.

Cruise	Month/ Year	Exp #	Duration (h)	T1 (°C)	T2 (°C)	Animals per bottle	Animals at start	Animals at end	Mean animal length (mm)
JR304 (2014)	11/14	INC3	27.9	0.80 ± 0.12	3.28 ± 0.15	1	6	3	24.7 ± 0.5
JR304 (2014)	12/14	INC4	4	1.20 ± 0.13	2.92 ± 0.06	1	12	10	25.4 ± 1.3
JR304 (2014)	12/14	INC5	6.4	0.20 ± 0.68	3.35 ± 0.16	1	12	11	24.5 ± 1.2
JR304 (2014)	12/14	INC6	3.7	1.81 ± 0.04	3.14 ± 0.01	1	12	11	31.5 ± 3.1
JR304 (2014)	12/14	INC7	6.2	1.56 ± 0.10	2.57 ± 0.05	1	12	9	30.4 ± 3.3
JR304 (2014)	12/14	INC8	4	2.20 ± 0.05	3.19 ± 0.12	1	12	12	28.8 ± 4.3
JR15002 (2015)	12/15	EXP1	2.1	1.43 ± 0.00	4.66 ± 0.00	5	50	50	27.0 ± 3.1
JR15002 (2015)	12/15	EXP2	2.2	1.74 ± 0.11	4.73 ± 0.08	4	40	40	27.7 ± 2.6

7

1 Table 2: Weighted mean depth (WMD, m) of *Euphausia triacantha* for pairs of nets deployed  
 2 during summer, JR177 (2008) and autumn, JR200 (2009) abundance cruises. Nets were  
 3 deployed at stations C3, P2 and P3, during the DISCOVERY 2010 programme. Calculations  
 4 are based on abundances (inds. m<sup>-2</sup>) and depth profiles presented in Figure 3 following  
 5 Equation 1. For each pair of nets, the shallower depth is highlighted by bold text.

DISCOVERY 2010 sampling station	Summer: JR177 (2008)		Autumn: JR200 (2009)	
	Day	Night	Day	Night
C3	500	<b>173</b>	438	<b>339</b>
P2	404	<b>349</b>	531	<b>81</b>
P3	232	<b>80</b>	460	<b>172</b>

6

7

8 Table 3: Multiple regression statistics for *Euphausia triacantha* O<sub>2</sub> consumption ( $y = \text{O}_2 \text{ ind}^{-1}$   
 9  $\text{h}^{-1}$ ) as a function of log weight ( $\ln X_1$ , mg DW, C and N) and temperature ( $X_2$ , °C), following  
 10 Ikeda (1985). The coefficients are:  $a_0 = \text{constant}$ ,  $a_1 = \text{DW}$  and  $a_2 = \text{temperature}$ .  $R^2_{\text{adj}} =$   
 11 adjusted  $R^2$ , SE = standard error and DF = degrees of freedom.

$\ln Y$ ( $\mu\text{l O}_2$ consumption)	Mass (mg)	$a_0$	$a_1$	$a_2$	$R^2_{\text{adj}}$	Q <sub>10</sub>	SE	DF
R ind <sup>-1</sup> h <sup>-1</sup>	DW	-0.64226 *	0.84255 ***	0.12846 ***	0.677	3.6	0.271	73
R ind <sup>-1</sup> h <sup>-1</sup>	C	0.17957	0.80857 ***	0.12776 ***	0.678	3.6	0.271	73
R ind <sup>-1</sup> h <sup>-1</sup>	N	1.31137 ***	0.86891 ***	0.12773 ***	0.679	3.6	0.270	73

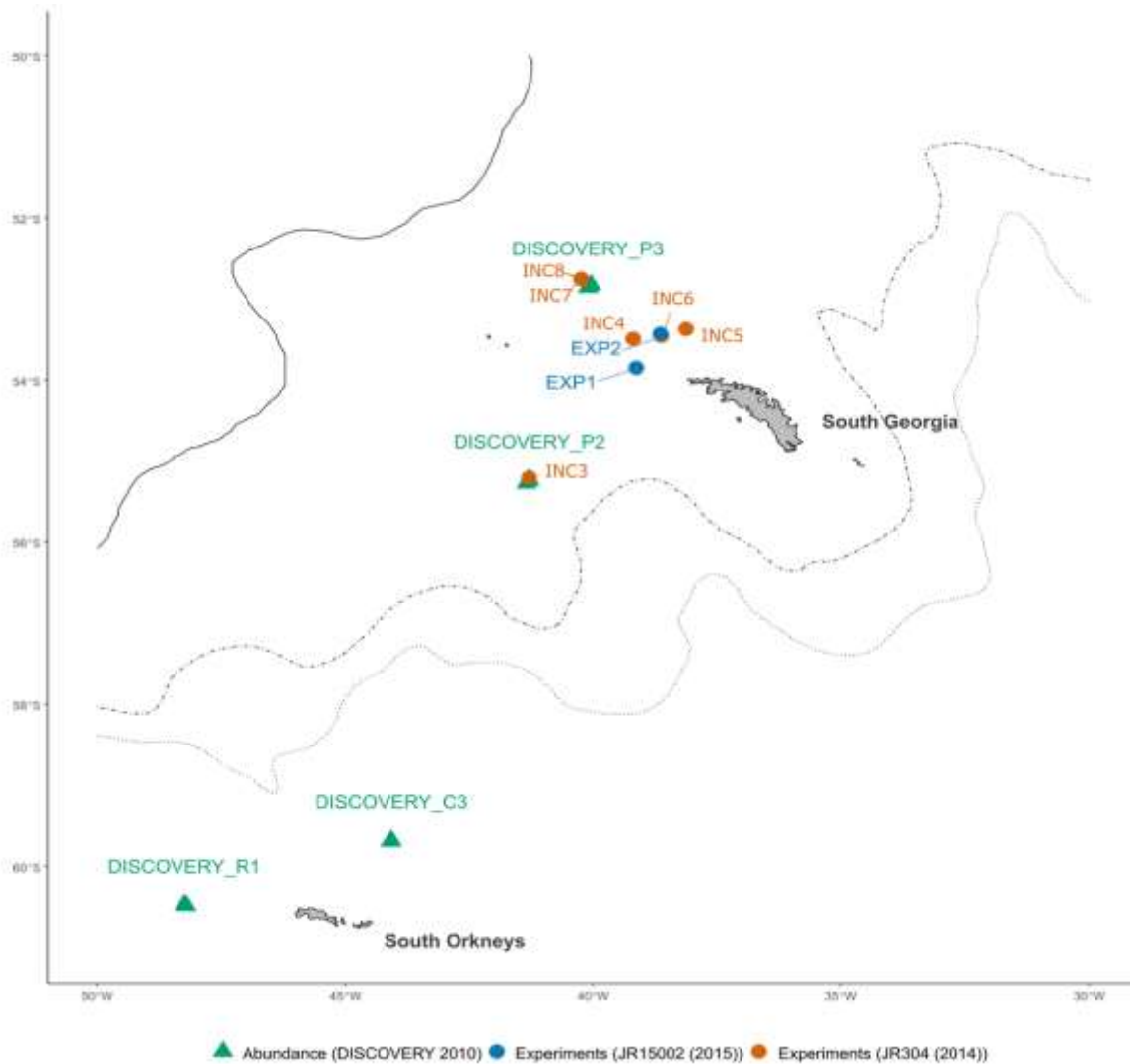
Model form  $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2$

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$

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14 Figures

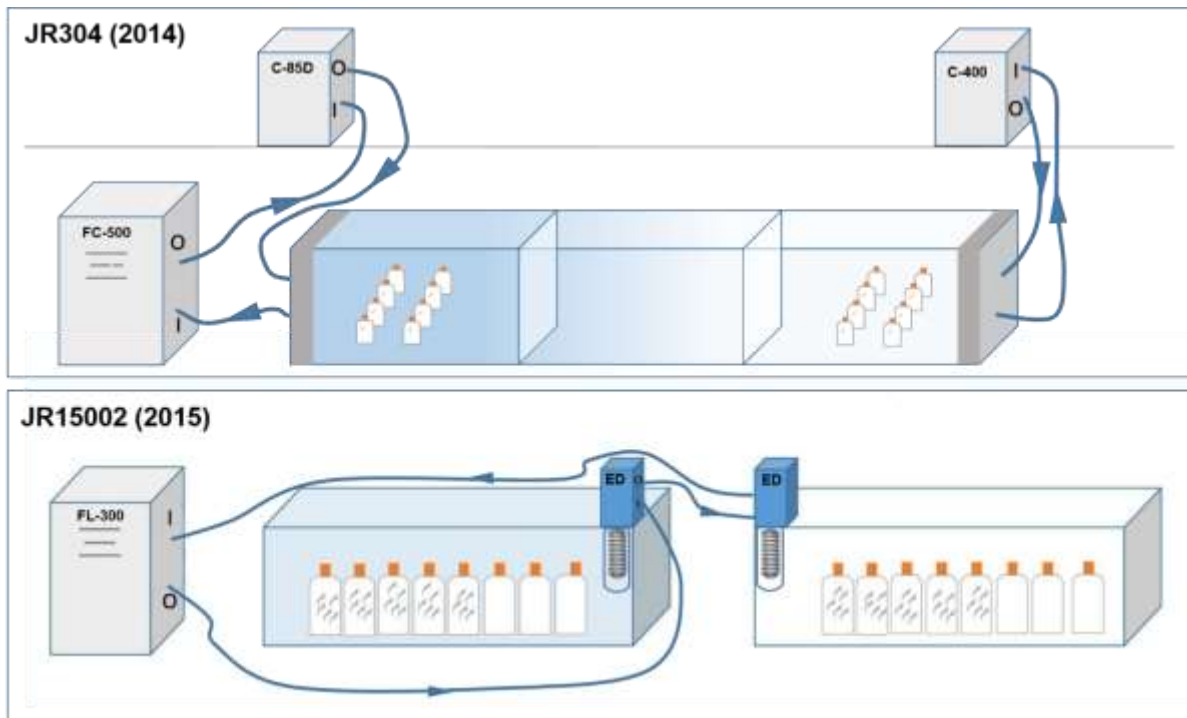


1

2 Figure 1: Map showing the sampling locations for the distribution and abundance of  
3 *Euphausia triacantha*, based on the DISCOVERY 2010 abundance cruises: JR177 (2008)  
4 and JR200 (2009); and for the collection of animals for respiration experiments: JR304  
5 (2014), prefixed with INC- and JR15002 (2015), prefaced with EXP-. The position of the  
6 fronts are, from north: Polar Front (solid), Sub-Antarctic Circumpolar Current Front (dashed)  
7 and Southern Boundary (dotted) based on Park and Durand (2019).

8

9



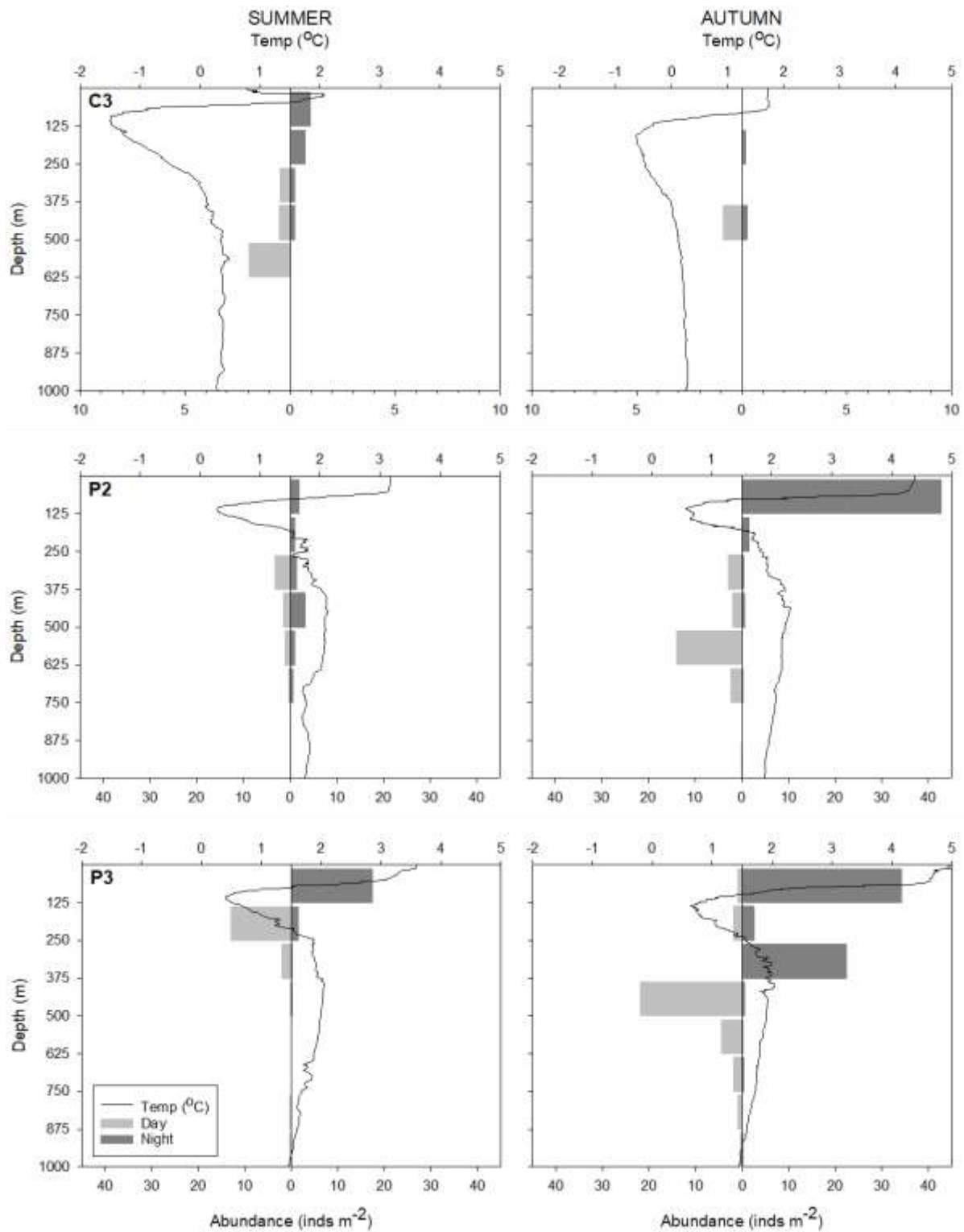
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2 Figure 2: Schematic showing the setup of the *Euphausia triacantha* incubation experiments in  
3 Cruise 1 (JR304) and Cruise 2 (JR15002) (not to scale). The main blocks depict the incubation  
4 units containing incubation bottles. The boxes on the left of each image (FC-500 and FL-300)  
5 depict the chiller units. The smaller boxes (C-85D and C-400 in JR304 (2014); and ED in  
6 JR15002 (2015)) depict the thermocirculators. The chillers and circulators are connected to one  
7 another via the blue tubing containing ethylene glycol antifreeze, with arrows showing the  
8 direction of flow. I = In; O = Out.

9



Respiration of *Euphausia triacantha* during DVM

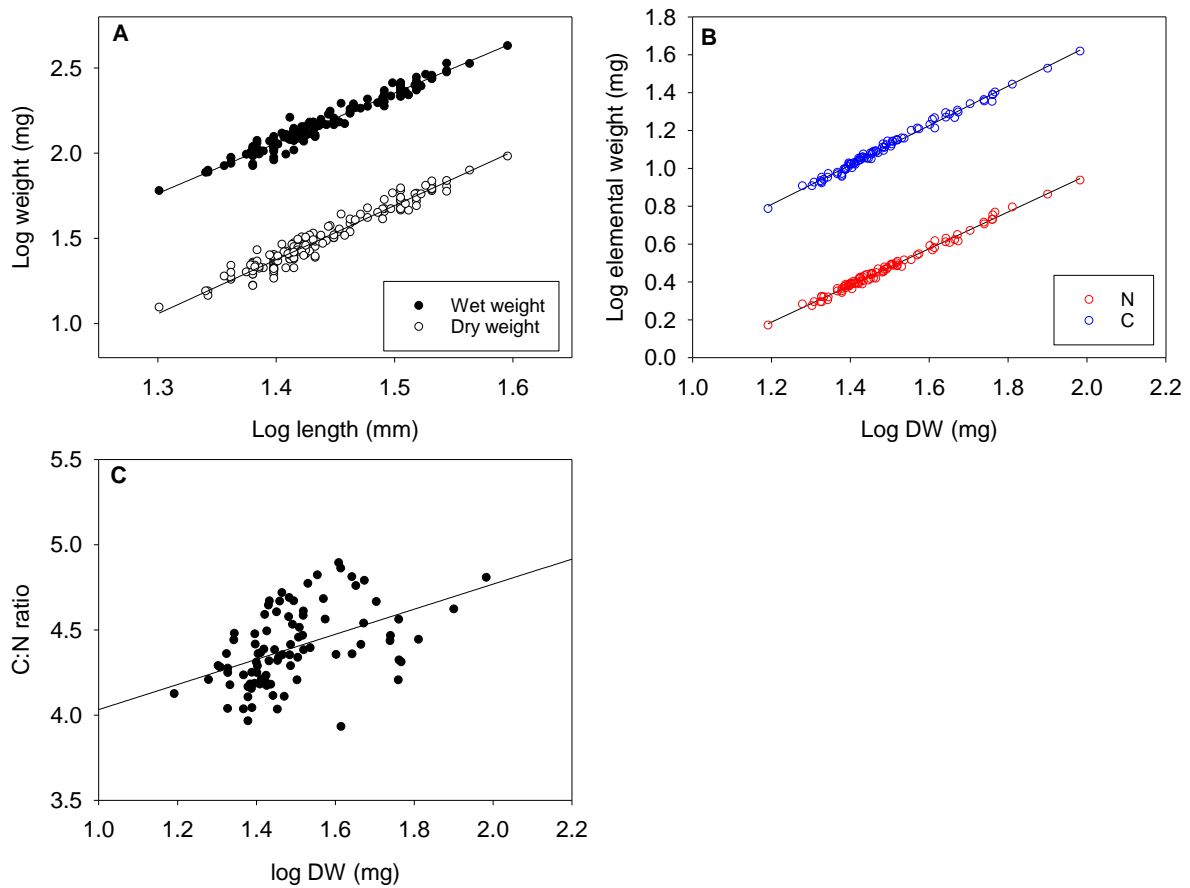


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2 Figure 3: Plots showing the day and night time abundances (individuals m<sup>-2</sup>, bottom axis) of  
 3 *Euphausia triacantha* from the DISCOVERY 2010 sampling programme during summer  
 4 (JR177 (2008)) and autumn (JR200 (2009)) at C3 (top), P2 (middle) and P3 (bottom). No *E.*  
 5 *triacantha* were recorded at R1 in the years sampled. Temperature data recorded from the CTD

1 at each station at the same time are overlain (top axis). Note the different scale for the  
 2 abundance axis at C3.

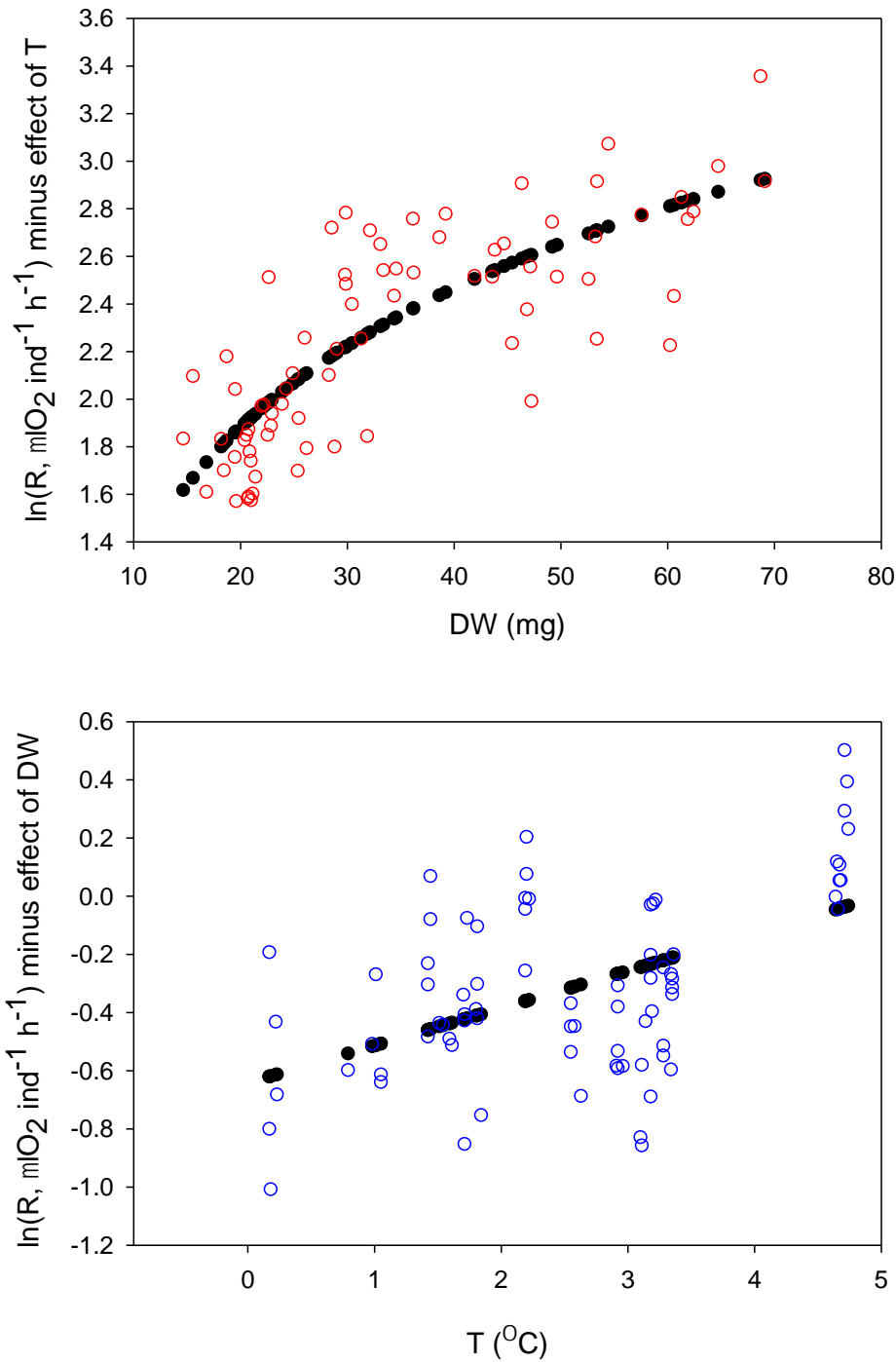
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5 Figure 4: Plots showing the relationships between A) log length (L) and log wet/ dry weight  
 6 (WW/DW) ( $DW = 3.1723 * L - 3.0656$ ,  $WW = 2.9432 * L - 2.0619$ ), B) log dry weight (DW)  
 7 and log carbon (C)/ nitrogen (N) content ( $C = 1.0424 * DW - 0.4416$ ;  $N = 0.9703 * DW -$   
 8  $0.9763$ ), and C) log DW and C:N ratio ( $C:N = 0.7364 * DW + 3.2960$ ) for *Euphausia*  
 9 *triacantha*. All significant at  $P < 0.001$ .

10



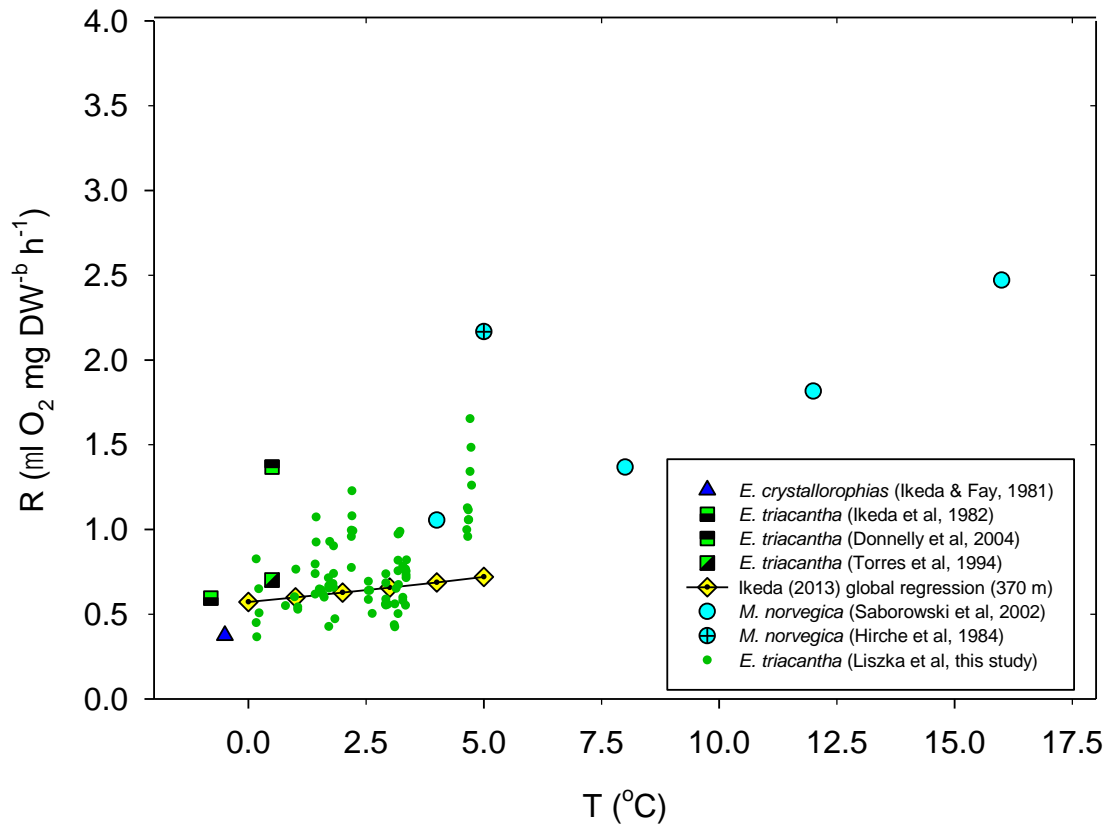
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2 Figure 5: Plot showing the predicted and measured respiration rate (lnR,  $\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}$ ) of  
3 *Euphausia triacantha* in response to dry weight (DW, mg), minus the effect of temperature  
4 (top panel); and in response to temperature (T, °C), minus the effect of DW (bottom panel).

5 Predicted values (black dots) were calculated from the regression coefficients in Table 3  
6 following a rearrangement of the regression equation. Measured values (red, top; and blue,

1 bottom) were calculated by subtracting the predicted values of temperature or DW,  
 2 respectively, from the measured respiration rate ( $\text{ind}^{-1} \text{h}^{-1}$ ).

3



4

5 Figure 6: Published respiration rates (converted to  $\mu\text{l O}_2 \text{ mg DW}^{-b} \text{ h}^{-1}$  using the  $b$  coefficient  
 6 determined in this study) for *Euphausia triacantha* and comparable species of euphausiid,  
 7 across temperatures ranging from -0.8 to 16 °C. Where rates for a range of body weight were  
 8 provided, the rate plotted is the mean. The line joining the yellow diamonds is calculated  
 9 following Ikeda (2013)'s global regression,  $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 \ln X_3$ , where  $X_1$  was  
 10 DW (mg),  $X_2$  was temperature (°C) and  $X_3$  was depth (m). Values used from this study were  
 11 average dry mass for euphausiids (34.21 mg DW), with temperatures ranging from 0 °C to 5  
 12 °C, and a median depth of 370 m.