

1 Seasonality of oxygen consumption in five common Antarctic benthic marine invertebrates

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12 Abstract

13 The waters of the Southern Ocean exhibit extreme seasonality in primary production, with marine life

14 living below 0°C for much of the year. The metabolic cold adaptation (MCA) hypothesis suggests that

15 polar species need elevated basal metabolic rates to enable activity in such cold resulting in higher

16 metabolic rates, or at least rates similar to temperate species. This study aimed to test whether any of

17 the five common marine invertebrates around Adelaide Island (Western Antarctic Peninsula) displayed

18 MCA: the suspension-feeding holothurian *Heterocucumis steineni*, the grazing limpet *Nacella*

19 *concinna*, the omnivorous brittle star, cushion star and sea-urchin *Ophionotus victoriae*, *Odontaster*

20 *validus* and *Sterechinus neumayeri* respectively. We also tested a second hypothesis that secondary

21 consumers will exhibit less seasonal variation of metabolic rate than primary consumers. Routine

22 oxygen consumption was measured in both the austral summer and winter using closed circuit

23 respirometry techniques. Metabolic rates for all the species studied were low compared with temperate

24 species, in a fashion consistent with expected temperature effects on biological systems, and therefore

25 the data do not support MCA. All the species studied showed significant seasonal differences for a

26 standard mass animal except *N. concinna*. In two species *N. concinna* and *H. steineni*, size affected the

27 seasonality of metabolism. There was no difference in seasonality of metabolism between primary and

28 secondary consumers. Thus for secondary consumers seasonal factors, most likely food availability and

29 quality, vary enough to impact metabolic rates, and produce seasonal metabolic signals at all trophic

30 levels. Other factors such as reproductive statuses that are linked to seasonal signals may also have  
31 contributed to the metabolic variation across trophic levels.

32 Keywords

33 Metabolism; Polar Benthos, secondary consumer, primary consumer, MCA

34

35 **Introduction**

36 Routine metabolic rate is measured as the rate of oxygen consumption based on an unfed animal  
37 carrying out routine activity. Routine metabolic rate in marine ectotherms increases with temperature  
38 (Clarke and Fraser 2004; Clarke and Johnston 1999; Watson et al. 2013). Krogh (1916) noted that polar  
39 species are active at low temperatures and that temperate species are inactive when cooled, so  
40 hypothesised that polar species must have raised metabolic rates to support the observed activity. Early  
41 Antarctic studies in the 1950s and 1960s produced data to support this (e.g. Wohlschlag 1964) and the  
42 hypothesis of metabolic cold adaptation (MCA) was proposed (Mileikovsky 1971). There have been  
43 many investigations of rates of oxygen consumption by polar marine ectotherms since. The vast  
44 majority of these have shown metabolic rates in high latitude species to be much lower than  
45 taxonomically related temperate species (Clarke and Peck 1991, Clarke and Johnston 1999, Peck and  
46 Conway 2000, Peck 2016). The lowered metabolic rate of these species has been suggested to be a  
47 consequence of reduced basal costs at low environmental temperatures, of which protein turnover  
48 appears to be a major component (Clarke 1998, Fraser, Clarke et al. 2007, Peck et al. 2016). Studies on  
49 Perciform fish (Clarke and Johnston 1999), bivalve molluscs (Peck and Conway 2000), polar fish  
50 (Steffensen 2002) and the invasive snail *Cornu aspersum* (Gaitan-Espitia and Nespolo 2014) all  
51 showed no MCA in comparison across latitude. Clarke (1993) argued against MCA as a higher  
52 metabolic rate would have a significant fitness cost to marine organisms and also many studies have  
53 used poor techniques such as inadequate holding time of species prior to oxygen consumption  
54 measurement, or there were methodological issues. Support for MCA has been found in other  
55 ectotherms, such as, in a global scale analysis of insects (Addo-Bediako et al. 2002), latitudinal  
56 analyses of the common woodlouse (Lardies et al. 2004) and the common bivalve mollusc *Mytilus*  
57 *edulis* (Thyrring et al. 2015), while four fresh water minnow from the United states *Fundulus notatus*  
58 species showed mixed support (Schaefer and Walters 2010). In addition, mitochondria and enzyme  
59 analyses in fish across latitudes supported the concept of MCA (White et al. 2011). Uliano et al. (2010)

60 showed that when metabolic rate was corrected for temperature using Boltzmann's factor and average  
61 base composition of genes then polar teleost fish have a higher metabolic rate than temperate species  
62 with tropical species showing the lowest metabolic rate, therefore supporting MCA. Antarctic marine  
63 benthic invertebrates live at low but stable temperatures with an annual temperature range of between -  
64 1.8 and + 2.0 °C (Venables et al. 2013 Fig. 1), and exhibit low basal metabolic rates. Despite its  
65 significance from both life history and physiological perspectives, MCA in polar marine species  
66 remains debated and is one of the most controversial hypotheses in physiological ecology (White et al.  
67 2011).

68  
69 Although temperatures are stable in Antarctic marine environments other factors including photoperiod  
70 and food availability vary markedly, and more than at lower latitudes (Clarke 1988; Clarke and  
71 Brockington 2001; Clarke et al. 2008; Groeneveld et al. 2015). Many Antarctic benthic marine  
72 invertebrates exhibit seasonal cycles in activities such as feeding (Barnes and Clarke 1995), growth  
73 (Barnes 1995; Fraser et al. 2002; Kock and Everson 1998; Peck et al. 2000), storage of reserves (Clarke  
74 and Peck 1991), and reproduction (Bowden 2005; Grange et al. 2004; Norrbin 1991; Pearse et al. 1991;  
75 Stanwell-Smith et al. 1999). Metabolic rates would therefore be expected to vary with season.  
76 Metabolic rates vary with temperature as well as with the availability of food and these two variables  
77 may not necessarily vary synchronously. On the Antarctic Peninsula sea temperature begins to warm in  
78 November during the austral spring but the arrival of the phytoplankton bloom may vary by a few  
79 months depending on the previous winter fast ice break out (Venables et al. 2013). The seasonality of  
80 food supply seems to drive growth and reproduction, which will have an effect on metabolic rates  
81 (Barnes 1995, Grange et al. 2004). On this basis some authors have suggested that seasonality of  
82 metabolism should differ between trophic groups, with scavengers and predators having less seasonal  
83 variation than primary consumers because their food supplies are more constant through the year  
84 (Clarke 1988, Pearse et al. 1991, Obermüller et al. 2010).

85  
86 Few studies of seasonality of metabolic rate in Antarctic marine species involving more than a single  
87 species have been conducted and these have found a mixture of seasonal strategies (Obermüller et al.  
88 2010; Peck and Barnes 2004). The Antarctic demosponges had the largest seasonal variation in  
89 metabolic rate so far reported for any group (Morley et al. 2016).

90

91 This study investigated the seasonality of metabolism in five abundant pioneer benthic invertebrate  
92 species using measurements of oxygen consumption as a proxy for routine metabolic rate. These  
93 species comprise a large percentage of the biomass in near-shore Antarctic shallow rocky habitats and  
94 therefore are important components of the Antarctic ecosystem. The species under study comprised:  
95 the suspension feeding holothurian *Heterocucumis steineni*, the grazing limpet *Nacella concinna*, an  
96 omnivorous benthic pioneer species, the brittle star *Ophionotus victoriae* the cushion star *Odontaster*  
97 *validus* which is an opportunistic feeder with a varied diet and the omnivorous echinoid *Sterechinus*  
98 *neumayeri*.

99

100 The aim was to identify if the metabolic rates of these species provide support for the MCA hypothesis.  
101 In addition we aimed to identify if these species showed metabolic seasonality and whether primary  
102 consumers displayed greater seasonality of metabolism than secondary consumers.

103

#### 104 **Materials and Methods**

105 Specimens of all species were hand collected by scuba divers during the austral summer (January –  
106 March) of 2015 and the austral winter (June – October) of 2015 from depths between 6m and 20m  
107 between Cheshire Island and South Cove just south of Rothera Research Station, Adelaide Island  
108 Western Antarctic Peninsula 67°35'8''S, 68°7'59''W (Fig.2). A wide size range (Fig.3) from juveniles  
109 to fully reproductive adults was collected for each species to give a good representation of the routine  
110 metabolic rate across the population size range. After collection specimens were transferred to a flow  
111 through aquarium system, with care being taken to ensure they remained submerged at all times. They  
112 were carefully sorted, any epibionts removed, and then held in the aquarium for 48 hours, to allow for  
113 recovery from any collection and handling stress. Respirometry was performed as described in  
114 Obermüller et al. (2010). Briefly, animals were placed in open chambers (scaled to animal size using  
115 data from preliminary experiments in this study) with mesh lids, submerged in flow through aquarium  
116 tanks for a minimum of eight hours prior to measuring oxygen consumption to allow specimens to  
117 adjust to experimental conditions (Peck and Conway 2000). Thereafter the water inside the chamber  
118 was gently exchanged with clean seawater, any bubbles removed and the chamber sealed. Thirty  
119 specimens of each species were placed individually in chambers scaled to animal size (using data from

120 preliminary trials) so that oxygen concentration dropped by approximately 15% over a 6 - 12 hour  
 121 period. The species studied were all determined to be oxyregulators down to an oxygen concentration  
 122 of 50% (*S. neumayeri*, from Brockington and Clarke (2001) and *O. victoriae*, *H. steineni*, *N. concinna*  
 123 and *O. validus* from preliminary trials in this study. The oxygen saturation in experimental chambers at  
 124 the end of the experiments was not allowed to fall below 60% of the initial concentration. Dissolved  
 125 oxygen concentration in the chamber was recorded using a FIBOX-3 optode system.

126

127 In all experiments, respirometer volume was corrected for the volume of water displaced by the animal  
 128 and oxygen consumption [ $\mu\text{mol O}_2 \text{ g AFDM}^{-1} \text{ hr}^{-1}$ ] was adjusted by comparison with control chambers  
 129 (blanks without animals). Whole-animal dry mass (DM) was measured after drying to a constant mass  
 130 at 60°C and ash mass (AM) was obtained following incineration in a muffle furnace at 475°C for 12  
 131 hours (juveniles) and 24 hours (adults.) AM was subtracted from DM to obtain ash free dry mass  
 132 (AFDM) for each specimen. To compare between species the metabolic rate was adjusted to that of a  
 133 0.3g AFDM standard sized animal using logarithmic regressions for all metabolic data from both  
 134 seasons. A standard animal size of 0.3g AFDM was used as this mass was within the adult size range  
 135 of all five species studied. Standard animal oxygen consumption was calculated for a species using the  
 136 following equation:

137

$$138 \quad \text{O}_2 \text{ hr}^{-1} 0.3\text{g AFDM}^{-1} = e^{A \ln(0.3) + \ln(\text{O}_2 \mu\text{molhr}^{-1}) - A \ln(\text{AFDM})}$$

139

140 Where exponent A is: 0.84 for *N. concinna*; 0.88 for *O. validus*; 1.05 for *S. neumayeri*, 0.78 for  
 141 *O. victoriae* and 0.90 for *H. steineni*.

142

### 143 **Statistics**

144 Routine oxygen consumption data for each species were tested for normality (Anderson-Darling test)  
 145 and non-normal data were transformed logarithmically. The normalized data were analysed using the  
 146 GLM package in MINITAB version 17 for Windows, including season as a fixed effect and size  
 147 (AFDM) as a covariate. Comparisons of oxygen consumption between species were based on a  
 148 standard animal mass (0.3g AFDM) using a one way ANOVA separately in both summer and winter,  
 149 to test for differences between the mass standardized oxygen consumption of the different species. If

150 the ANOVA showed a significant difference a post hoc Fishers pairwise comparison was conducted to  
151 determine which species were different. Statistical results from the post hoc Fishers pairwise were  
152 displayed with the lowest T value. To identify differences in metabolic rate between seasons within the  
153 same species a Two Sample T Test was used.

154

## 155 **Results**

156 Seasonal oxygen consumption

### 157 *Sterechinus neumayeri*

158 In *S. neumayeri*, the slope of the relationship between Ln oxygen consumption and urchin size (Ln  
159 AFDM) was not significantly different between summer and winter ( $Slope = 0.89 \pm 0.03$ ;  $F_{(1,58)} =$   
160  $0.01$ ,  $P = 0.93$ ). *S. neumayeri* did, however, consume significantly more oxygen in summer than winter  
161 across the size range studied as the elevation of the regression lines differed ( $F_{(1,58)} = 6.12$ ,  $P = 0.02$   
162 Table 1). The oxygen consumption in *S. neumayeri* in summer was 39% higher than the winter (Figure  
163 3A).

164

### 165 *Odontaster validus*

166 The slopes of the oxygen consumption relationship with size (Ln O<sub>2</sub> consumption vs Ln AFDM) for *O.*  
167 *validus* were not significantly different between summer and winter ( $Slope = 0.89 \pm 0.02$   $F_{(1,56)} =$   
168  $1.99$ ,  $P = 0.16$ ). *O. validus* consumed significantly more oxygen in summer than winter across the size  
169 range studied ( $Intercept F_{(1,56)} = 15.03$ ,  $P < 0.001$ , Table 1). The rate of oxygen consumption in *O.*  
170 *validus* in summer was 44% higher than in winter (Figure 3B).

171

### 172 *Nacella concinna*

173 In *N. concinna* the slope of the relationship between Ln oxygen consumption and Ln AFDM was  
174 significantly different in summer compared with winter ( $GLM F_{(1,55)} = 5.50$ ,  $P = 0.02$  Table 1). The  
175 seasonal effect on oxygen consumption was the opposite in large *N. concinna* compared to small *N.*  
176 *concinna* (Figure 3C). Small animals (size 0.002 - 0.05g) consumed less oxygen in summer than winter  
177 and vice versa for large individuals (0.05 - 1.00g). For seasonal comparison using a standard animal of  
178 0.3g AFDM there was no seasonal difference and the rate of oxygen consumption was  
179  $1.3 \mu\text{mol O}_2 \text{ hr}^{-1}$  in both seasons.

180

181 *Ophionotus victoriae*

182 In *O. victoriae*, the slope of the relationship between Ln oxygen consumption and Ln AFDM was not  
183 significantly different in summer compared with winter ( $Slope = 0.78 \pm 0.06$   $F_{(1,55)} = 0.37$ ,  $P = 0.55$ ,  
184 Table 1) and there was also no significant seasonal difference in the intercepts ( $Intercept = 0.66 \pm 0.1$   
185  $F_{(1,55)} = 2.14$ ,  $P = 0.15$ ), therefore a single regression line was fitted (Figure 3D.). The residuals for  
186 each season were not significantly different from each other (*Paired t test*,  $P = 0.37$ ,  $n = 56$ ).

187

188 *Heterocucumis steineni*

189 In *H. steineni* the relationship between Ln oxygen consumption and Ln AFDM was significantly  
190 different in summer compared with winter (GLM  $F_{(1,55)} = 7.00$ ,  $P = 0.01$ ; Figure 3E). This indicates  
191 that seasonal differences exist for large, but not small individuals. Small animals ( $\pm 0.17$ g) consumed  
192 more oxygen in summer than winter and vice versa for large individuals (size 0.3g – 15g). For seasonal  
193 comparison using a standard animal of 0.3g AFDM there was a seasonal difference in metabolic rate  
194 and the rate of oxygen consumption in summer was  $0.67 \mu\text{mol O}_2 \text{ hr}^{-1}$  compared with  $0.45 \mu\text{mol O}_2 \text{ hr}^{-1}$   
195 in winter, giving a factorial increase of 1.5.

196

197 Comparisons of mass standardized metabolic rate

198 To allow comparisons of metabolic rate between species metabolic rate was mass standardised to an  
199 animal of 0.3g AFDM. All the species studied showed significant seasonal differences *O. victoriae*  
200 (*Paired t test*,  $T = 4.68$ ,  $P < 0.001$ ), *H. steineni* (*Paired t test*,  $T = 6.39$ ,  $P < 0.001$ ), *O. validus* (*Paired t*  
201 *test*,  $T = 4.38$ ,  $P < 0.001$ ) and *S. neumayeri* (*Paired t test*,  $T = 3.04$ ,  $P < 0.05$ ) except *N. concinna*,  
202 which showed no significant seasonal difference in metabolic rate (*Paired t test*,  $T = -0.36$ ,  $P = 0.72$   
203 Figure 4).

204

205 Summer rates of mass standardised oxygen consumption were significantly different between species  
206 (*ANOVA*  $F_{(1,128)} = 16.05$ ,  $P < 0.001$ ). Summer metabolic rates of *H. steineni* ( $0.67 \mu\text{mol O}_2 \text{ hr}^{-1}$ ) were  
207 significantly lower than those of *N. concinna*, *S. neumayeri*, *O. victoriae* and *O. validus* (*Post hoc T*  
208  $> 1.99$ ,  $P < 0.05$ ). *O. validus* oxygen consumption was significantly lower than *S. neumayeri* and

209 *N. concinna* (Post hoc  $T > 3.22$ ,  $P = 0.002$ ). *S. neumayeri* and *N. concinna* had significantly higher  
210 metabolic rates than *O. victoriae* (Post hoc  $T = -4.86$ ,  $P < 0.001$ , Post hoc  $T = -3.12$ ,  $P < 0.001$   
211 respectively; Figure 4). *S. neumayeri* also had the highest oxygen consumption in the summer (1.57  
212  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ), followed by *N. concinna* (1.35  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ) then both *O. victoriae* (0.93  $\mu\text{mol O}_2 \text{ hr}^{-1}$ )  
213 and *O. validus* (0.93  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ), which were not significantly different.

214

215 Comparisons of winter rates of mass standardised oxygen consumption were significantly different  
216 between species (ANOVA  $F_{(1,54)} = 71.63$ ,  $P < 0.001$ ). *N. concinna* had the highest oxygen consumption  
217 in winter (1.39  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ; Post hoc  $T > 4.83$ ,  $P < 0.001$ ). The oxygen consumption of *O. victoriae*  
218 (0.67  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ) and *O. validus* (0.63  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ), was significantly less than that of *N. concinna*  
219 and *S. neumayeri* (1.08  $\mu\text{mol O}_2 \text{ hr}^{-1}$ ; all post hoc  $T > 7.81$ ,  $P < 0.001$ ) but were not significantly  
220 different to each other. *H. steineni* had the lowest rate of oxygen consumption in winter (0.45  $\mu\text{mol O}_2$   
221  $\text{hr}^{-1}$ ; Post hoc  $T > 2.81$ ,  $P < 0.05$ ).

222

## 223 Discussion

### 224 Metabolic Cold Adaptation

225 In this study, *S. neumayeri*, *H. steineni*, *N. concinna* and *O. victoriae* had oxygen consumption rates  
226 similar to previous reported values (Brockington and Peck 2001; Fraser et al. 2002; Fraser et al. 2004;  
227 Obermüller et al. 2010; Obermüller et al. 2011). These rates are low compared to species from  
228 temperate localities (Belman and Giese 1974; Fang et al. 2014; Fraser et al. 2004; Watson et al. 2013)  
229 Table 2. The metabolic cold adaptation (MCA) hypothesis, states ectotherms living at low temperatures  
230 should show elevated metabolic rates to overcome the problems of performing activities at low  
231 temperatures (Milleikovsky 1971). This has not been supported by the data from this study. If there  
232 was MCA then the polar animals should show higher metabolic rates, or at least rates similar to  
233 temperate species when measured at ambient sea temperature, which is not the case. The data in this  
234 study are in line with several previous studies. Fraser et al. (2004) collated rates of oxygen  
235 consumption in a range of holothurian species from tropical, temperate and polar habitats and *H*  
236 *steineni* had the lowest metabolic rate of the holothurians investigated. The rate reported here for *H.*  
237 *steineni* is similar to that reported by Fraser et al. (2004). Comparing the metabolic rate for *H. steineni*  
238 with two tropical holothurians (Table 2), *H. steineni* had a metabolic rate 11 – 12 times lower than that



239 of tropical holothurians *Pearsonothuria graeffi* and *Holothuria edulis* measured in seawater of 28°C  
240 (Wheeling et al. 2007) which is in line with the expected Q<sub>10</sub> of 2.5 and 2.7 respectively (Q<sub>10</sub>  
241 calculated using the equation from Seebacher et al. (2014)). The metabolic rate of *O. victoriae* was 22  
242 times lower than the temperate species *Ophiopholis mirabilis* at 15°C (Table 2) resulting in a Q<sub>10</sub> of 10.  
243 The polar species either had a lower metabolic rate than expected or the temperate species had a higher  
244 metabolic rate than expected. In either case *O. victoriae* had a markedly lower rate of metabolism  
245 (Fang et al. 2014). Watson et al. (2013) looked at the difference in metabolic rate across a latitudinal  
246 gradient of 17 species of calcified marine invertebrates including *S. neumayeri*. The rate reported here  
247 for *S. neumayeri* is similar to that found by Watson et al. (2013) and the metabolic rate of *S. neumayeri*  
248 was 4 times lower than the temperate urchin *Psammechinus miliaris* with a Q<sub>10</sub> of 2.3 (Table 2).  
249 Belman and Giese (1974) found the metabolic rate of *S. neumayeri* to be 3.5 µl g<sup>-1</sup> hr<sup>-1</sup> which using the  
250 conversion in Peck and Uglow (1990) equates to 0.16 µmol O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup> for a 1g WM animal. Converting  
251 these data for comparison, the metabolic rate in this study for *S. neumayeri* was 0.26 µmol O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup>  
252 which is similarly low. Belman and Giese (1974) also showed that *S. neumayeri* had a much lower  
253 metabolic rate than the tropical urchins *Lytechinus anamesus* and *Echinometra mathaei* therefore not  
254 supporting the MCA theory. Belman and Giese (1974) also showed the metabolic rate for 1g WM *O.*  
255 *validus* in their study was 0.22 µmol O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup> (conversion from Peck and Uglow (1990)) which was  
256 lower than those of temperate and tropical species. The rate for *O. validus* from this study for a 1g WM  
257 animal was 0.29 µmol O<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup> and therefore the data do not support MCA. The metabolic rate for  
258 *N. concinna* was 4 times lower than the temperate species *Patella vulgata* with a Q<sub>10</sub> of 2.9 (Table 2).  
259 These data like those for *S. neumayeri* are in line with the expected Q<sub>10</sub> range (Ralph and Maxwell  
260 1977) and therefore none of the species in this study showed MCA. Furthermore, Peck (2016), in a  
261 comparison of oxygen consumption in bivalve molluscs from the tropics to the poles, showed that the  
262 rate of polar species matched those predicted for lower latitude species from the Arrhenius relationship.  
263 All the data in this study compliment the findings of that paper.

264

265 Some studies reporting MCA have been criticised on methodological grounds (Chapelle and Peck  
266 1999; Rakusa-Suszczewski 1982) but some studies show MCA for biochemical and mitochondrial  
267 processes e.g White et al. (2011) and within species latitudinal studies often report MCA e.g Houlihan  
268 and Allan (1982). Other studies comparing metabolic rates in Antarctic marine animals with those from

269 lower latitudes have however, like this study usually found no evidence of MCA including; Fraser et al  
270 (2004) for holothurians, Luxmoore (1984) for Isopods, Ralph and Maxwell (1977a) for the bivalve  
271 *Gaimardia*, Clarke and Johnston (1999) for Perciform fish, and Peck and Conway (2000) for bivalve  
272 molluscs. The data suggest that comparisons of metabolic rates of animals at their normal habitat range  
273 vary as would be expected from standard temperature effects, with Q10 values in the range 1 – 4, not  
274 supporting MCA. However, when polar species are compared with lower latitude species at the same  
275 temperature the polar species usually have higher metabolic rates (Peck 2016). These two outcomes  
276 conflict with each other and need further explanation. It is possible that species held at the edges of  
277 their temperature ranges do not follow expected thermal relationships.

### 278 **Seasonal changes in metabolic rate**

279 Antarctic shallow water habitats are characterised by extreme seasonal environmental variation such as  
280 photoperiod, presence of winter fast ice and food availability. There have been few seasonal studies on  
281 physiological rates of Antarctic marine species due to the logistical challenges of carrying out marine  
282 research during the Antarctic winter periods. The data here show that there was a significant difference  
283 between seasons in metabolic rates for *S. neumayeri* and *O. validus* (Figures 3A and 3B respectively)  
284 and this was evident across the whole size range studied. There was no similar consistent metabolic  
285 seasonality across the size range in *N. concinna*, *O. victoriae* and *H. steineni* (Figures 3C, 3D and 3E  
286 respectively) although there were different seasonal signals in small and large individuals of  
287 *N. concinna* and *H. steineni* (Figure 3C and 3E).

288  
289 Seasonal factorial change is the rate of metabolic increase from winter to summer (Figure 5). The data  
290 here are within the previously observed range for seasonal factorial changes in oxygen consumption for  
291 polar marine species (Morley et al. 2016). Of the primary consumers previously studied there was a  
292 range of seasonal factorial change in oxygen consumption between 0.8 for the Porifera *Clathra*  
293 *nidificata* and 5.5 for *Suberites sp* both of which are sponges, which demonstrates the diversity possible  
294 within just one trophic level and one taxonomic group (Morley et al. 2016). It was expected that  
295 *H. steineni* as a primary consumer would have the largest factorial change in this study due to the high  
296 seasonality of food supply from the summer phytoplankton bloom compared with secondary  
297 consumers, some of which can continue to feed during winter (Barnes and Clarke 1995). This was,  
298 however, not the case as the factorial change for *H. steineni* was the same as for *S. neumayeri* and *O.*

299 *validus*, which are both opportunistic scavengers, despite the fact that *H. steineni* stops feeding for 4-6  
300 months in a typical winter (Fraser et al. 2004). The factorial change for *H. steineni* from this study (1.5)  
301 was similar to previous data for the same species reported by Fraser et al. (2004) who recorded a value  
302 of 2.0. It is therefore unlikely this was an unusual year for this primary consumer. The Antarctic clam  
303 *Laternula elliptica* another suspension feeding primary consumer, like *H. steineni* also ceases to feed  
304 during the winter, but its seasonal change in metabolism is x3.7 (Morley et al. 2007). There is  
305 flexibility in feeding for secondary consumers and primary consumers, for example, the  
306 grazer/scavenger urchin *S. neumayeri* ceases feeding for 4-7 months of the year (Brockington et al.  
307 2001), equally not all primary consumers cease feeding during the winter, for example the Bryozoan  
308 *Arachnopusia inchoata* feeds all year round (Barnes and Clarke 1995). While food availability is the  
309 obvious main driver in the effect of season on metabolic rates within species there are other variables to  
310 consider that could explain the diversity of results within the different trophic levels.

311

## 312 **Conclusions**

313 The hypothesis that seasonal change in metabolic rates will vary differently between animals of  
314 different trophic levels and that secondary consumers would be less affected by seasonality than  
315 primary consumers is not supported by the data presented here. This adds to the growing evidence from  
316 other studies (Obermüller et al. 2010) showing variation in the seasonality of species within and  
317 between trophic levels. This variation between species of the same trophic level could be caused by  
318 seasonal physical factors or seasonal biological factors. Physical factors affecting the physiology and  
319 metabolism of Antarctic benthic marine invertebrates include photoperiod, temperature (Clarke and  
320 Brockington 2001), sea ice cover (Arrigo et al. 2008), salinity (Gyllenberg and Lundqvist 1979),  
321 acidification (Seibel et al. 2012) and sedimentation from nearby glaciers (Torre et al. 2012). Biological  
322 factors affecting physiological mechanisms and metabolism are phytoplankton bloom (Peck et al.  
323 1997), predation pressure (Seibel and Drazen 2007), competition (Seibel and Drazen 2007), activity  
324 (Whitney et al. 2016), feeding (Chapelle et al. 1994), reproduction (Blackmer 2005; Grange et al. 2007;  
325 Grange et al. 2004).

326

327 The data in previous studies do, however, increase the level of confidence in our assessments of  
328 changes in metabolic rates between seasons as, the level of change is similar between years and studies

329 (Figure 5; (Brockington and Peck 2001; Fraser et al. 2002; Fraser et al. 2004; Obermüller et al. 2010).  
330 The variability of seasonality of metabolism within this study was typical of the small but growing  
331 body of data on this subject for Antarctic marine benthic invertebrates. The timing of different  
332 physiological and ecological requirements may override purely seasonal patterns. For example  
333 reproductive activity is carried out at different times of the year for different species, the gonad index  
334 of *O. validus* peaked in April/May at Signy (Stanwell-Smith and Clarke 1998) whereas *N. concinna*  
335 spawn in the summer around January/February (Peck 2016). Reproductive cycles in certain species  
336 such as *O. validus* and *O. victoriae* have multi-year periodicities and therefore in some years certain  
337 adults will spawn and others may not, or levels of spawning will vary greatly (Grange et al. 2007;  
338 Grange et al. 2004). The timing of metabolic rate measurements within the season could also affect the  
339 variability of the measurements made, due to food availability, the phytoplankton bloom peaks at  
340 different times during the summer which is influenced by the previous winter fast ice duration. For  
341 scavengers and carnivores the amount of carrion available will change dependant on iceberg scour  
342 which is low in winter when icebergs are locked by ice, but much greater in summer when there is  
343 open water. Differences in metabolic rates could also be caused by interannual variation as well as  
344 seasonal, both from internal cycles such as those seen in the growth of the Antarctic bivalves *Yoldia*  
345 *eightsi* and *Laternula elliptica* (Román-González et al. 2017). This study also shows Antarctic  
346 secondary consumers have much more seasonally variable metabolic rates than would be expected  
347 given a year round food supply. This may be an effect of food quality varying seasonally, or the  
348 requirement for food being seasonal due to some other factor than a direct impact of food availability.  
349 Irrespective of the causes there is strong seasonality in the metabolism of the vast majority of Antarctic  
350 species investigated whether primary or secondary consumers.

351

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362

363 Compliance with ethical standards

364 To the authors knowledge there is no conflict of interest in the production of this manuscript

365

366 References

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 508

509 Figure Legends

510 **Fig.1** Seasonal trends in temperature and chlorophyll a between 1998 and 2015 at 15m in Marguerite  
 511 Bay 4km from Rothera Research Station

512

513 **Fig.2** Location of Adelaide Island on the Western Antarctic Peninsula and Rothera Research station on  
 514 Adelaide Island showing the sample collection site

515

516 **Fig.3** A regression analysis of seasonal metabolic rates of (A) the Antarctic urchin *S. neumayeri* austral  
 517 summer (N = 29) and austral winter (N= 30), B the cushion star *O. validus* austral summer (N = 25)  
 518 and austral winter (N= 32), C the limpet *N. concinna* austral summer (N = 27) and austral winter (N=

519 29), **D** the brittle star *O. victoriae* austral summer (N = 23) and austral winter (N= 33) and **E** the  
520 holothurian *H. steineni* Austral summer (N = 25) and austral winter (N= 31) using oxygen consumption  
521 and size (AFDM) ◆ summer January – March 2015, ● winter June – October 2015, solid line =  
522 summer regression, dotted line = winter regression

523

524 **Fig.4** Comparison of the mean metabolic rates between species for a standard mass animal of AFDM  
525 0.3g . Summer (Jan – March 2015) and Winter (June – October 2015) with 95% confidence bars.  
526 Species with the same capital letter above have no significant difference in summer metabolic rates.  
527 Species with the same small red letter below have no significant difference in their winter metabolic  
528 rates. \* indicates a significant seasonal difference within species

529

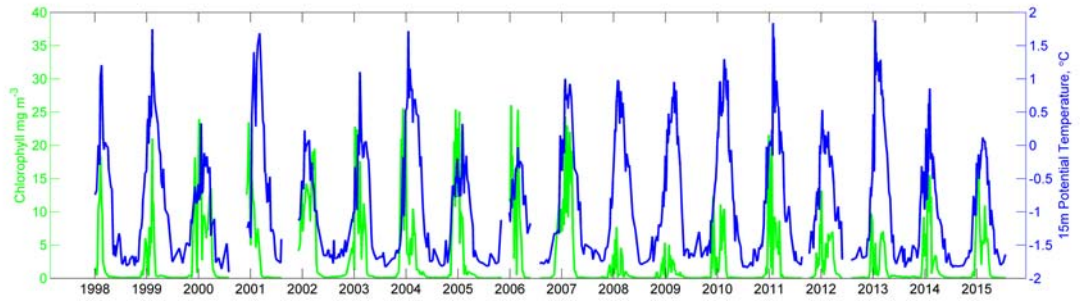
530 **Fig.5** Comparison of seasonal factorial rise in oxygen consumption from winter to summer in a range  
531 of polar marine species. Open symbols represent data from previous studies, diamonds denote  
532 herbivores and circles denote scavengers/carnivores. Symbols filled in represent data from the present  
533 study (*Heterocucumis steineni*, *Nacella concinna*, *Sterechinus neumayeri*, *Ophionotus victoriae* and  
534 *Odontaster validus*). Previous data from *Laternula elliptica* (Brockington 2001), *Camptoplites*  
535 *bicornis*, *Isoseculiflustra tenuis* and *Kymella polaris* (Barnes & Peck 2005), *Doris kerguelenensis*  
536 (Obermüller et al. 2010), *Heterocucumis steineni* (Fraser et al. 2004) *Nacella concinna* (Fraser et  
537 al.2002), *Nacella concinna (Intertidal)* (Obermüller et al. 2010), *Sterechinus neumayeri* (Brockington  
538 2001), *Clathria nidificata*, *Sphaerotylus antarcticus*, *Suberites* sp and *Dendrilla antarctica* (Morley et  
539 al. 2016) *Glyptonotus antarcticus* (Janecki 2006), *Harpagifer antarcticus*, *Paraceradocus miersii*,  
540 *Parborlasia corrugatus* and *Ophionotus victoriae* (Obermüller et al. 2010)

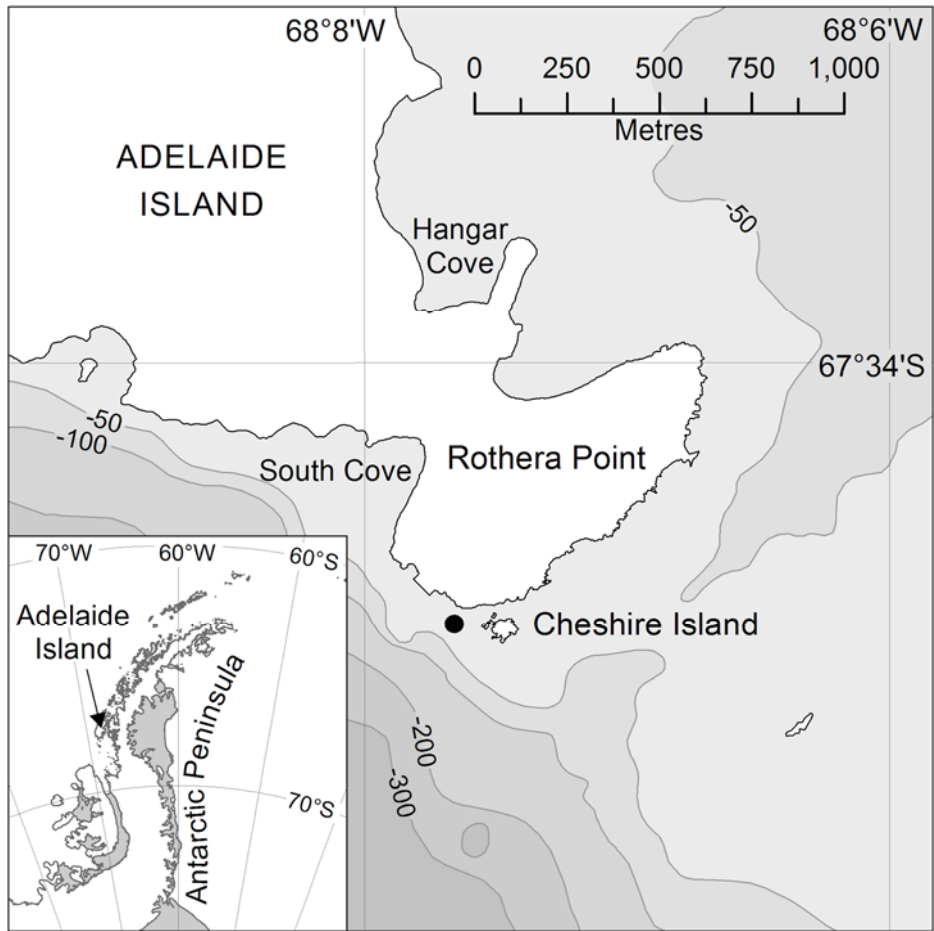
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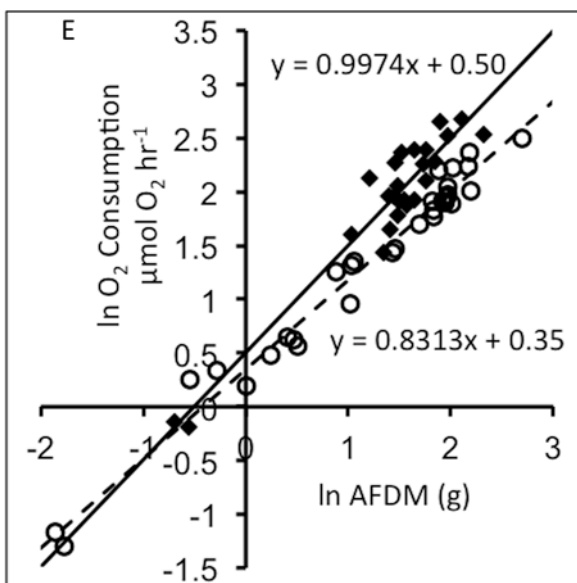
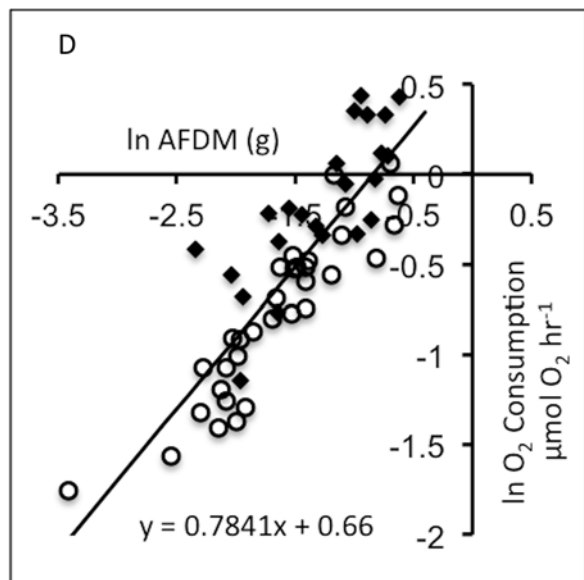
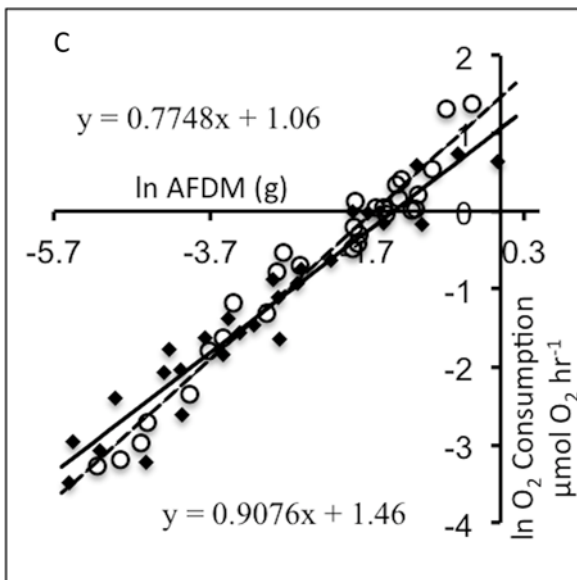
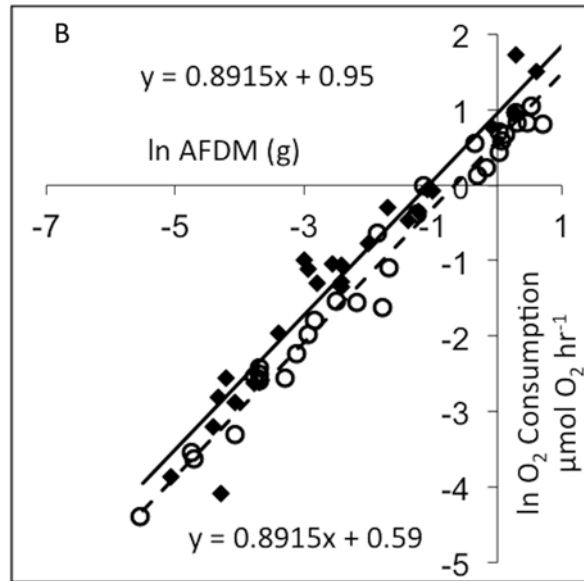
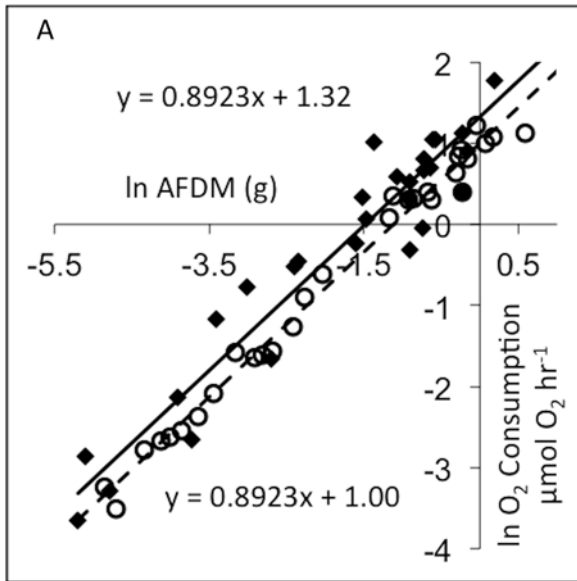
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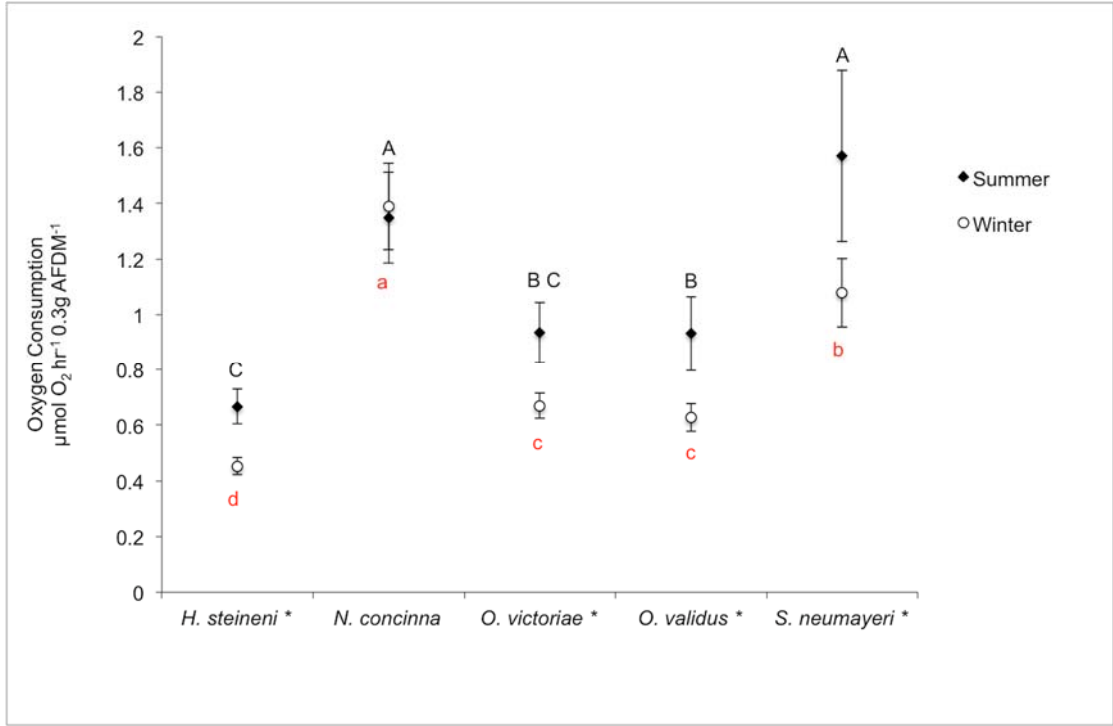
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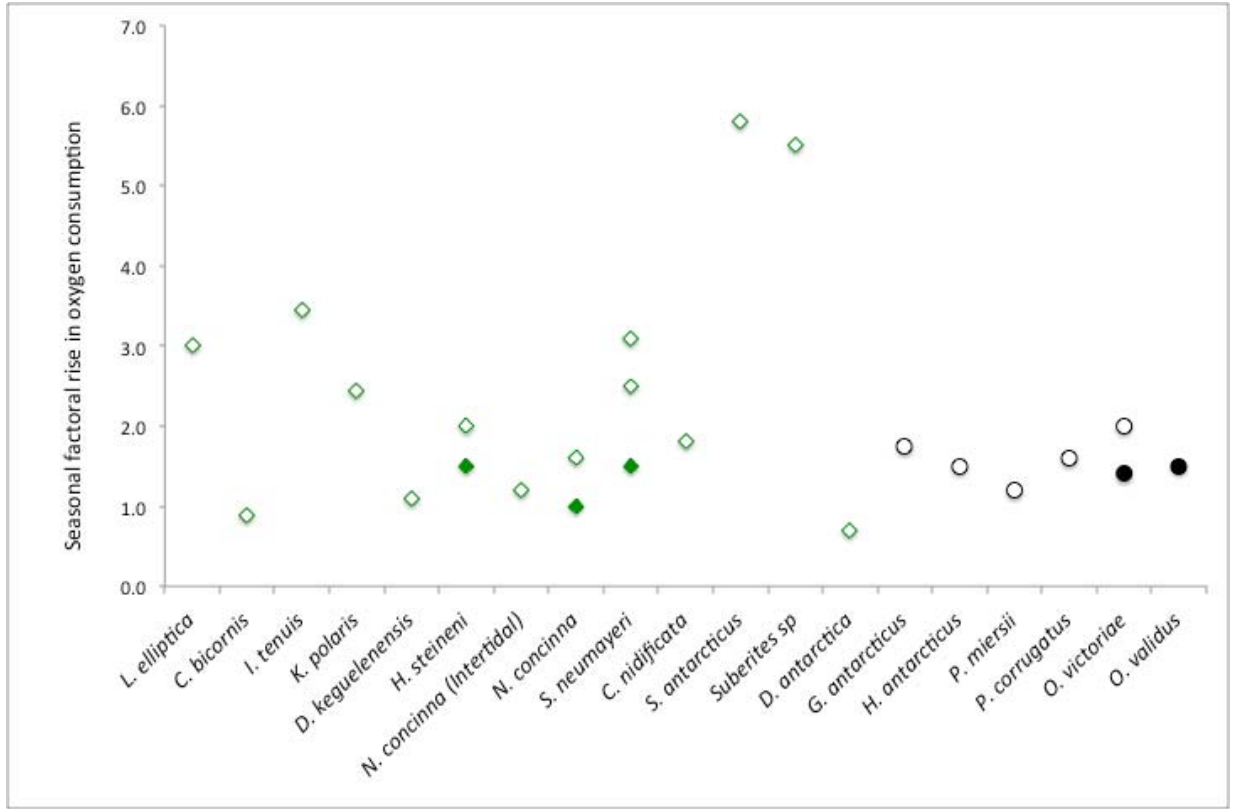












**Table 1** GLM statistical model output of metabolic data

<b>Species</b>	<b>Covariate</b>	<b>Intercept</b>	<b>Slope</b>
<i>S. neumayeri</i>	$F_{(1,58)} = 1151.93, P < 0.001$	$F_{(1,58)} = 6.12, P = 0.017$	$F_{(1,58)} = 0.01, P = 0.930$
<i>O. validus</i>	$F_{(1,56)} = 1458.58, P < 0.001$	$F_{(1,56)} = 15.03, P < 0.001$	$F_{(1,56)} = 1.99, P = 0.16$
<i>N. concinna</i>	$F_{(1,55)} = 882.18, P < 0.001$	$F_{(1,55)} = 5.33, P = 0.025$	$F_{(1,55)} = 5.50, P = 0.023$
<i>O. victoriae</i>	$F_{(1,55)} = 136.50, P < 0.001$	$F_{(1,55)} = 2.14, P = 0.15$	$F_{(1,55)} = 0.37, P = 0.55$
<i>H. steineni</i>	$F_{(1,55)} = 847.42, P < 0.001$	$F_{(1,55)} = 2.47, P = 0.122$	$F_{(1,55)} = 7.00, P = 0.011$

**Table 1** Results of GLM, two factors: season and size (AFDM), Slope – rate of metabolic change with respect to mass (AFDM), Intercept – Effect of season on metabolic rates, Covariate – effect of mass (AFDM) on metabolic rate

**Table 2** Latitudinal metabolic rate comparisons

Species	<b>Polar</b> <i>Heterocucumis steineni</i>	<b>Tropical</b> <i>Pearsonothuria graeffi</i>
Metabolic Rate $\mu\text{mol O}_2 \text{ g}^{-1} \text{ hr}^{-1}$	0.14	1.61
Collection temperature $^{\circ}\text{C}$	1.5	28.1
Collection location	67° 34' S, 68° 08' W	9°20'30" N, 123°18'31" E
Collection depth m	10 - 20	10 - 20
Collection period	January – March 2015	April – July 2005
Q10		2.5
References		Wheeling et al. 2007
Species	<b>Polar</b> <i>Heterocucumis steineni</i>	<b>Tropical</b> <i>Holothuria edulis</i>
Metabolic Rate $\mu\text{mol O}_2 \text{ g}^{-1} \text{ hr}^{-1}$	0.14	1.96
Collection temperature $^{\circ}\text{C}$	1.5	28.1
Collection location	67° 34' S, 68° 08' W	9°20'30" N, 123°18'31" E
Collection depth m	10 – 20	10 – 20
Collection period	January – March 2015	April – July 2005
Q10		2.7
References		Wheeling et al. 2007
Species	<b>Polar</b> <i>Ophionotus victoriae</i>	<b>Temperate</b> <i>Ophiopholis mirabilis</i>
Metabolic Rate $\mu\text{mol O}_2 \text{ g}^{-1} \text{ hr}^{-1}$	0.23	5.14
Collection temperature $^{\circ}\text{C}$	1.5	15
Collection location	67° 34' S, 68° 08' W	39° 02.514' N, 122°44.089' E
Collection depth m	10 - 20	
Collection period	January – March 2015	November – December 2012
Q10		10
References		Fang et al. 2014
Species	<b>Polar</b> <i>Nacella concinna</i>	<b>Temperate</b> <i>Patella vulgata</i>
Metabolic Rate $\mu\text{mol O}_2 \text{ hr}^{-1}$	2.57 (5g WM)	10.63 (5g WM)
Collection temperature $^{\circ}\text{C}$	1.5	15
Collection location	67° 34' S, 68° 08' W	European
Collection depth	10 - 20	
Collection period	January – March 2015	
Q10		2.9
References		Ralph and Maxwell 1977
Species	<b>Polar</b> <i>Sterechinus neumayeri</i>	<b>Temperate</b> <i>Psammechinus miliaris</i>
Metabolic Rate $\mu\text{mol O}_2 \text{ hr}^{-1}$	1.57 (0.3g AFDM)	6.48 (0.3g AFDM)
Collection temperature $^{\circ}\text{C}$	1.5	18.9
Collection location	67° 34' S, 68° 08' W	Torquay, UK
Collection depth	10 - 20	
Collection period	January – March 2015	
Q10		2.3
References		Watson et al. 2013

**Table 2** Comparisons of metabolic rates for Polar species within this study to metabolic rates of those species from temperate and tropical areas. Latitudinal comparisons were carried out between species which were ecologically and taxonomically similar. Q10 calculations from Seebacher et al. 2014