1 **Limpet feeding rate and the consistency of physiological response to temperature**

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9 **Abstract**

10 Thermal reaction norms are fundamental relationships for geographic comparisons of organism

11 response to temperature. They are shaped by an organism's environmental history and provide

12 insights into both the global patterns of thermal sensitivity and the physiological mechanisms

13 underlying temperature response. In this study we conducted the first measure of the thermal

14 reaction norm for feeding, comparing the radula rasping rate of two tropical and one polar limpet

15 species. The consistency of thermal response was tested through comparisons with limpet duration

16 tenacity. Feeding and duration tenacity of limpets are ecologically important muscular mechanisms

17 that rely on very different aspects of muscle physiology, repeated concentric (shortening) and

18 isometric (fixed length) contraction of muscles, respectively. In these limpets the thermal reaction

19 norms of feeding limpets were best described by a single break point at a maximum temperature

20 with linear declines at higher (*S. atra*) or lower temperatures (*N. concinna* and *C. radiata*) rather

21 than a bell shaped curve. The thermal reaction norms for duration tenacity were similar in the two

22 tropical limpets. However, the rasping rate in Antarctic *Nacella concinna*, increased linearly with

23 temperature up to a maximum at 12.3°C (maximal range 8.5 to 12.3°C) when feeding stopped. In

24 contrast duration tenacity in *N. concinna*, was maximal at 1.0°C (-0.6 to 3.8°C), and linearly

25 decreased with increasing temperature. The thermal reaction norms of muscular activity were

26 therefore inconsistent within and between species, indicating that different mechanisms likely

27 underlie different aspects of species sensitivities to temperature.

28

29 **Key-words:** Thermal reaction norm; radula; rasping rate; tropical; Antarctic; *Nacella concinna*

30

31 **Introduction**

32 Understanding how species ranges are controlled by variation in their environment, and how these

33 ranges are likely to shift in response to future environmental conditions, is one of the major current

34 scientific challenges (Pennisi 2005). Whilst in the oceans a range of variables such as salinity, wave

exposure, primary productivity and competition are important controlling factors, temperature is arguably the most important for ectotherms as it controls the rates of all biochemical reactions within body tissues (Hochachka and Somero 2002). The magnitude and variation of temperature are important determinants of ectotherm physiological limits (Peck 2005; Gaston et al. 2009) which play a major role in limiting their distributions (e.g. Gaston et al. 2009). The predictability of temperature variation is, also, increasingly being recognised as a key factor determining both acclimatory capacity (Sinclair et al. 2006; Peck et al. 2006; Morley et al. 2012a) and thermal adaptation (Alto et al. 2013).

Unifying physiological principles such as oxygen and capacity limited thermal tolerance (Pörtner and Knust 2007; Pörtner and Farrell 2008) or the metabolic theory of ecology (Gillooly et al. 2001) provide mechanistic frameworks against which the generality of thermal response can be compared. These frameworks improve understanding of the physiological mechanisms underlying ectotherm response to temperature, which are, in turn, expected to improve predictions of future species ranges (e.g. Kearney et al. 2009; Calosi et al. 2010). However, rather than species sensitivity to temperature being caused by a single pervasive mechanism, it is increasingly argued that a combination of multiple physiological factors, which can have different thermal limits and can vary in importance through an organisms life history are likely to determine species vulnerability (Clark et al. 2013). This might explain why quite different predictions of the future range can be obtained using current realised and physiological niches based on single trait analyses (diving beetles, Sanchez-Fernandez et al. 2012). There is also evidence showing that the rate of temperature change has marked effects on measured thermal limits in both terrestrial and aquatic environments (Mora and Moya 2006; Terblanche et al. 2007; Chown et al. 2009; Peck et al. 2009; Richard et al. 2012; Nguyen et al. 2012) with indications that different mechanisms underlie temperature limits at different rates of change (Peck et al. 2009; Richard et al. 2012; Nguyen et al. 2012). Thermal limits may also vary hierarchically between different physiological measures, from high to low complexity, i.e. processes that rely on the integration of multiple organs, such as feeding and locomotion, are expected to have lower thermal limits than individual biochemical pathways (Prosser 1973; Pörtner et al. 2007). This might also be expected to vary between processes with different fitness consequences, with lethal limits being higher than those for escape responses or feeding.

Limpets and other gastropod molluscs feed using a chitinous ribbon with teeth that are hardened with iron and silicone oxides (Fig. 1, Liddiard et al 2004). The teeth of the radula rasp algae from hard substrata, which are then ingested (e.g. Boyden and Zeldis 1979). Whilst radula rasping rate is not the only factor affecting consumption rate, radula rasping is an easily quantifiable activity, which is expected to closely correlate with feeding rate. Most intertidal molluscs feed when they are awash or submerged and radula rasping rate in molluscs has generally been found to be sensitive to

69 both temperature and body size (Boyden and Zeldis 1979; Horn 1986; Petraitis 1992; although see

70 *Bembicium nanum*; Petraitis 1992). This study presents the first measure of the thermal reaction

71 norm for feeding in limpets from the Antarctic, *Nacella concinna* (recent synonym *N. polaris*) and

72 tropical Singapore, *Cellana radiata* and *Siphonaria atra*. Previous assessments of the thermal

73 reaction norm of duration tenacity of *N. concinna* found no difference between individuals collected

74 from the intertidal or subtidal (Morley et al. 2012a).

75 To investigate the mechanisms underlying thermal reaction norms, this new measure of the

76 thermal response of feeding in all three species and new data for the thermal response of tenacity

77 and mortality for *Siphonaria atra* were compared with previously published tenacity and mortality

78 data for *Nacella concinna* and *Cellana radiata* (Morley et al. 2012a). Current theory predicts that

79 thermal reaction norms will be consistent across different measures of muscular performance with

80 consistent optimal, upper and lower thermal limits which will correlate with experienced

81 microhabitat temperature (Angilletta 2009). This is increasingly being questioned as different

82 physiological processes are expected to rely on different mechanisms which are likely to have

83 different thermal responses (e.g. Morley et al. 2012; Clark et al. 2013). The study aimed to test, 1) if

84 differences in experienced thermal regime led to differences in the thermal reaction norm of feeding

85 in intertidal and subtidal *N. concinna*, 2) if the thermal reaction norm of rasping in one Antarctic and

86 two tropical limpets correlated with differences in their experienced environments and 3) if the

87 shape of the thermal reaction norm was consistent across these species and between rasping rate

88 and duration tenacity.

89

90 **Materials and methods**

91 *Cellana radiata* and *Siphonaria atra* were collected from the shore at the Tropical Marine Science

92 Institute, St John's Island, Singapore (1° 31.2'N, 103° 51.56'E) and *Nacella concinna* were collected

93 from both the shore and 6m depth (by SCUBA divers) at the British Antarctic Survey's Rothera

94 Research Station (67° 34.25'S, 68° 08.00'W). The temperature response of feeding was measured in

95 subtidal *N. concinna* in 2006/2007 and in both subtidal and intertidal *N. concinna* in 2012/13.

96 Singapore limpets were tested between November 2009 and March 2010.

97 In Rothera and Singapore, limpets were transferred after collection, in insulated seawater

98 containers, to flow-through aquaria for at least 24 hours. They were then transferred to jacketed

99 tanks which were heated by thermocirculators at a rate of $0.2 \pm 0.1°C$ hour^{-1} (after Morley et al.

100 2012a). Animals were maintained at test temperature for 24 hours (Table S1), to allow their

101 physiology to fully adjust, before the start of feeding experiments. Feeding rate was then measured

102 over 24 hours. Individuals were placed on a piece of overhead projector acetate sheet that had been

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103   incubated in the flow through seawater aquaria for over 2 weeks in Singapore and over 2 months in

104   the Antarctic. This was long enough to ensure that an algal biofilm had developed that was sufficient

105   to stimulate feeding. After 1 hour, any feeding individuals were filmed for three sequences of 6 to 10

106   radula rasps, with a Microsoft LifeCam Studio HD web camera, directly onto a computer hard drive.

107   Counts started after the completion of the forward stroke and closure of the mouth. After feeding

108   had been recorded the length of each limpet was measured and the limpet removed to the

109   aquarium so that each limpet was only used once. The duration of each radula rasp was analysed

110   from the time stamped videos. Trials were run at temperatures, evenly spaced over temperatures

111   they were predicted to survive (Peck et al. 2009; Nugyen et al. 2011), in a random order, until a

112   temperature was reached when less than 5 limpets fed within the 24 hour period (Table 1).

113   New data for the duration tenacity and survival of *S. atra* is also presented alongside

114   published data for *N. concinna* and *C. radiata* (Morley et al. 2012a). The detailed method for

115   duration tenacity is described in Morley et al. (2011, 2012), which utilised the same heating protocol

116   to measure feeding rates. Briefly, a fine soft stainless steel cradle (Leader wire, Bass Pro Shops) was

117   hooked underneath the shell edge, with contact at 4 points around the shell, (modified from Grenon

118   and Walker 1981), before temperatures were changed. Animals were then held in seawater at the

119   required experimental temperature for 24 hours before tenacity was measured following Morley et

120   al. (2011, 2012a). Individuals were tested at one trial temperature only. During all trials any

121   individual that did not have a measurable tenacity was tested by stimulation of the foot with a blunt

122   seeker. Failure of the foot muscle to respond was recorded as functional mortality. This was used to

123   determine upper 50% lethal (CT_{max}) and lower 50% lethal (CT_{min}) limits (following Peck et al. 2009).

124   To standardise measurements, limpet shells were tapped three times to stimulate a clamping

125   response (Grenon and Walker 1981), before the 200g (*N. concinna*) or 919g (*C. radiata* and *S. atra*)

126   weight was attached. 20 kg mono filament fishing wire was hooked to the stainless steel cradle or

127   cotton loop and passed over two 18KN pulleys (Petzl, France) supported by a retort stand frame. 20

128   seconds after the limpet shell was tapped, the weight was hooked to the line and gently lowered

129   until the full force was supported directly above the centre of each limpet. The subsequent time

130   taken for the limpet to be pulled from the substratum was recorded.

131   Microhabitat temperature for all three limpets was measured using biomimetic loggers (as

132   described in Morley et al. 2012a). Signatrol button loggers were silicon sealed into empty limpet

133   shells and glued onto the shore (using marine araldite) at the median height that each limpet species

134   was found. These loggers were set to record every 30 minutes and were deployed between

135   16/06/10 and 02/08/10 on break waters around St. John's Island, Singapore and between 29/12/12

136   and 15/02/13 on East Beach, Rothera Point. Previously published logger data were also available

137   (Singapore *C. radiata*, Morley et al. 2012a; Rothera, *N. concinna*, Waller et al. 2006). On spring low

138   waters foot temperatures of *N. concinna* were also recorded, using a thermocouple. As the loggers

139   were fixed in position and limpets are mobile, movement patterns of individuals were monitored

140   during successive low waters. The distance moved from the first recorded position was monitored

141   over 3 low tides for *N. concinna* and *S. atra* and 19 low waters for *C. radiata*.

142

143   Data analysis

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145   Temperatures recorded by biomimetic loggers were analysed by calculating the average

146   number of hours in each day that each temperature was experienced (collated into 1°C bins). The

147   temperature profiles of each replicate logger were not normally distributed and so differences

148   between the recorded temperature distributions were tested with multiple (bonferroni corrected)

149   Mann-Whitney tests.

150   The R-package strucchange (Zeileis et al. 2002) was used to find the most appropriate

151   piecewise linear breakpoints within the relationship between temperature and either rasping rate or

152   duration tenacity of individuals (TF_{max} and TT_{max}). After breakpoint selection, linear models were

153   fitted to the respective sections, incorporating the endpoints in all contiguous sections. Quadratic

154   functions were also fitted to the data. Akaike Information Criteria (AIC) were compared to determine

155   the best overall fit to the data sets and the significance of the parameters in each model compared

156   (modified from Angilletta 2009). 4 out 6 quadratic fits had lower AIC's (Table S2), but this was not

157   significantly different from a 1:1 ratio ($\chi^2 = 0.67$, P = 0.41). However, as half of the quadratic (T^2)

158   parameters were not significant (Table S2) and there were visible discontinuities in the thermal

159   profiles, the piecewise linear fits were chosen as the overall best fit and biological description of the

160   data. Post Hoc multiple Tukey test were then used to determine which temperatures were not

161   significantly different from this breakpoint value.

162

163   **Results**

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165   *Microhabitat temperatures*

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167   There were no significant differences in the temperature distributions recorded by the replicate

168   loggers (Mann-Whitney; *N. concinna*, U<122, p>0.79; *C. radiata*, U<86, P>0.07; *S. atra*, U=174,

169   p=0.94; Fig. 2). Median logger temperature for *N. concinna* was 1°C, with a summer minimum of -1°C

170   but also a few high temperatures to a maximum of 9°C. *S. atra* loggers also recorded a few high

temperatures with a maximum over 40°C. *S atra* experienced higher maximum temperatures than those recorded by *C. radiata* loggers (maximum of 35°C). The median temperature for *S. atra* (30°C) was 1°C higher than that for *C. radiata* (29°C). The minimum logger temperature for both tropical limpets was 24°C.

The two tropical limpets moved very little (median 10cm) between successive low waters, remaining on the same rock surface, and therefore experiencing the same level of exposure to the sun during each low water (Fig. 3). *N. concinna* moved much greater distances, up to 3.4m between tides. Individuals moved to different rock surfaces and might, therefore, have experienced a wider temperature range than that recorded by loggers fixed to the rocks. However, foot temperatures of *N. concinna* were similar to those recorded by loggers (Table 1); on 31/12/12 the logger temperature was 1 to 2°C higher than the limpet foot temperature, but 1 to 2°C lower on 16/1/12. The highest foot temperature was 13.2°C, recorded on 28/12/12.

Radula rasping rate

There was no relationship between feeding rate and limpet size, or the interaction of size and temperature for any of the 3 groups of limpets: *N. concinna* ($F_{1,265}$=3.8, p=0.052; $F_{1,265}$=0.88, p=0.35); *C. radiata* ($F_{1,69}$=1.7, p=0.20; $F_{1,69}$=1.9, p=0.18) or *S. atra* ($F_{1,63}$=0.00, p=0.99; $F_{1,63}$=0.01, p=0.94).

The rasping rate of *N. concinna* increased with temperature until the temperature was too high for them to feed (Fig 4A, Table S3). The highest temperature at which individuals fed in 2007 was 6.6°C, with no feeding at 8.4°C, but 4 intertidal and 3 subtidal individuals fed at 12.3°C in 2012. Most *N. concinna* were moribund at 12.3°C, none fed at 14.4°C and only 1 intertidal limpet survived at this temperature. Despite this interannual difference in temperature limit there was no significant difference in the relationship between rasping rate and temperature in the 3 *N. concinna* trials (ANCOVA; $F_{2,265}$=0.70, p=0.50) or the interaction with temperature ($F_{2,265}$=0.29, p=0.75), so the data were combined. Tukey *posthoc* multiple comparison tests showed that the temperature over which rasping rates of *N. concinna* were fastest occurred within the range 8.5 to 12.3°C. *Cellana radiata* had a maximum rasping rate at 30.6°C and *posthoc* tests showed the optimal range was between 26.6 and 34.6°C (Fig4B). *S. atra* had a maximum rasping rate at 24.6°C with an optimal range between 24.6 and 36.6°C (Fig 4C).

Tenacity

203   A lower Akaike Information Criteria was obtained for a polynomial fit for tenacity of Singapore *S.*

204   *atra*, rather than the breakpoint analysis (AIC= 3288 versus 3976). The polynomial fit had a

205   maximum tenacity at 24.9°C, but tenacity was relatively constant across the temperature range 18-

206   30°C. The individual variability in duration tenacity was high enough that *posthoc* tests could not

207   identify significant pairwise differences between temperatures (fig 5A). *N. concinna* had a break

208   point at 1.0°C with an optimal temperature range between -0.6 and 3.8°C (Fig S1; Morley et al.

209   2012a). *C. radiata* had a maximum temperature for tenacity of 27.6°C and there was a significant

210   linear reduction in tenacity above and below this temperature.

211

212   *Mortality data*

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214   The CT_{min} of *S.atra* was between 13.6 to 15.6°C and the CT_{max} between 36.6 to 37.6°C (fig 5B). The

215   CT_{max} of Rothera *N. concinna* was 12.0°C (Morley et al. 2012a). The CT_{min} for *C. radiata* was 2.6 to

216   4.6°C and the CT_{max} 33.6 to 34.6°C (Morley et al. 2012a).

217

218   **Discussion**

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220   *Thermal reaction norm*

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222   Despite the approximately 30°C difference in environmental temperature between the seas around

223   the Western Antarctic Peninsula and Singapore, average rasping rates of *N. concinna* and *S. atra*

224   were similar (0.2-0.3 rasps sec^{-1}). Instead there was a bigger difference between the two tropical

225   limpets, with *C. radiata* having three times faster average rasping rate (0.9 rasps sec^{-1}). Many factors,

226   such as previous feeding history (Boyden and Zeldis 1979), can affect the rasping rate but there are

227   also large differences between species (Petraitis 1992). Inter-specific comparisons were therefore

228   focussed on the shape of the thermal reaction norms and their relationship with experienced

229   temperature.

230   The concept that ectotherms will have an optimal physiological temperature range is a

231   fundamental paradigm within thermal physiology and has led to thermal reaction norms typically

232   being described by bell shaped curves, with an optimal range and a decline in performance either

233   side of this range (Huey and Kingsolver 1989; Pörtner and Knust 2007, Pörtner and Farrell 2008;

234   Angilletta 2009). These curves are useful for comparing the relative thermal response between

235   species as temperature ranges are expected to be wider in species that experience more variable

236   thermal environments and have optima that match their experienced environment (e.g. Huey and

237   Kingsolver 1989; Angilletta 2009). The thermal reaction norms for these three species were best

238   described by a single breakpoint at a temperature where feeding rate was at a maximum, with a

239   gradual linear reduction at temperatures below this in *N. concinna* and *C. radiata*, but a signficiant

240   linear reduction at temperatures above this in *S. atra*. For both species the optimal temperature

241   range over which the change in feeding rate was not significant had an upper boundary at a

242   temperature close to that of their upper lethal limit. Previous studies of rasping rate in molluscs

243   have also measured a linear increase with temperature, at least over a limited temperature range

244   (Boyden and Zeldis 1979; Horn 1986; Petraitis 1992). The generally poor fit of the quadratic term

245   meant that the expectation of a bell shaped rate temperature curve was not met. This was

246   particularly true in *N. concinna* whose rasping rate increased linearly with temperature to a

247   maximum that was also close to their upper lethal limit. Several recent studies have found a similar

248   thermal response with aerobic scope only collapsing at temperatures close to upper lethal limits,

249   contradicting one of the central tenets of the principle of oxygen and capacity limitation of thermal

250   tolerance (see Clark et al. 2013).

251   Whilst the reaction norms for duration tenacity and feeding in the two tropical limpets were

252   very similar the temperature responses were reversed, giving very different measures of thermal

253   sensitivity in *N. concinna* (figs 5 and S1). Duration tenacity measures the time to fatigue of constant

254   (tetanic), fixed length (isometric) contraction of muscles, as they resist a constant force (Morley et

255   al. 2012a). Feeding, however, relies on alternate shortening (concentric contraction) of atagonistic

256   muscles of the odontophore that scrape the radula back and forth. These are very different muscle

257   mechanisms and are likely to have different reliance on aerobic metabolism. Behavioural responses,

258   such as feeding, can also be governed by a hierarchical response to stimuli, where, for example, the

259   presence of food leads to a feeding bout which overrides the stimulus of a prosobranch mollusc to

260   right itself (Davis et al. 1974). It is therefore perhaps more surprising that the thermal reaction

261   norms for the two tropical limpets were so similar in shape.

262

263   *Microhabitat and thermal limits*

264

265   In the current study there was no difference in the thermal response of rasping in intertidal and

266   subtidal *N. concinna*, despite their vastly different experienced environments. This was the same

267   pattern as previously measured for duration tenacity in this species (Morley et al. 2012). Intertidal

268   temperatures in the Antarctic are highly variable and the cyclical pattern of temperature variation

269   and the unpredictability of temperature may preclude acclimatisation to the intertidal environment

270   (Morley et al. 2012). However, although subtidal Southern Ocean temperatures are amongst the

271 most stable there was a large difference in the maximum temperature for feeding of subtidal *N.*

272 *concinna* between 2007 (6.4°C) and 2012 (12.4°C). This corresponded to a difference in the

273 maximum summer seawater temperature between 2007, which was a cooler year (1.0°C) and 2012,

274 which was one of the warmest years on record (1.9°C). Differences in the upper temperature limits

275 of Antarctic species have previously been recorded between years; with the starfish *Odontaster*

276 *validus* and the clam *Laternula elliptica* having higher lethal limits in warmer years (Morley et al.

277 2012b).

278   Whilst there were no differences in the rasping rate of Rothera *N. concinna* between years,

279 there were differences between Rothera *N. concinna* measured in this study and rasping rate of

280 Signy Island *N. concinna* (60° 42.16'S, 45°35.45'W) measured over a reduced temperature range in

281 1986 (Fig. S1). Signy *N. concinna* measured in 1986, had a significantly faster rasping rate at all

282 temperatures than Rothera *N. concinna* (ANCOVA; $F_{1,286}=57.9$, $p<0.01$), but rasping rate had the

283 same slope with temperature ($F_{1,286}=1.1$, $p=0.29$). The consistent response of rasping rate to

284 temperature suggests that it is a robust measure of thermal response in *N. concinna*.

285   Within the tropics, *S. atra* experiences higher maximum and median environmental

286 temperatures than *C. radiata,* but approximately the same lower environmental temperature (Table

287 1). As predicted *S. atra* had higher upper lethal limits and a wider optimal temperature range for

288 feeding than *C. radiata* but these ranges were centred on the same midpoint. In global latitudinal

289 analyses, lower lethal limits of marine ectotherms are also generally correlated with latitudinal

290 temperature gradients (e.g. Sunday et al. 2012). However, in the current study, the lower lethal

291 limits of both tropical species were below the minimum environmental temperature experienced in

292 Singapore. The CT_{min} of *C. radiata* was extremely low (2.6 to 4.6°C), as was the previously measured

293 CT_{min} of the Singapore clam *Laternula truncata* (5.7°C, Lai et al. 2011) and three species of tropical

294 oyster (1.4 to 5.0°C; Davenport and Wong 1992). There are clearly factors, other than recent thermal

295 history, which affect the temperature tolerance of ectotherms, such as the predictability of

296 temperature variation (Morley et al. 2012a) and evolutionary history (Bozinovic et al. 2011; Richard

297 et al. 2012). This understanding is particularly important for intertidal species, where the complex

298 microhabitat structure on the shore means that even small differences in climate temperature

299 (0.75°C in 60 years) have had dramatic effects on the structure of Californian intertidal communities

300 (Barry et al. 1995; Sagarin et al. 1999).

301   The thermal reaction norm for these two very different muscular activities was consistent in

302 the two species of tropical limpet but was almost opposite in the one Antarctic species. Even

303 measurements from these three species indicate how very different estimates of species'

304 vulnerability to climate warming can be predicted from the thermal reaction norms measured for

9

305   different muscle activity. Acute thermal tolerance will be modified by species physiological flexibility

306   (acclimitisation capacity) and ultimately adaptation. Polar and tropical species are known to have

307   reduced acclimation capacity (Nguyen et al. 2011; Richard et al. 2011; Peck et al. 2013) and are

308   expected to have slower rates of adaptation (Peck 2011) than species from temperate regions.

309   Climate warming is also a non-linear process and extreme events are also expected to increase in

310   frequency (Karl et al. 1997). Understanding which physiological mechanisms underlie these different

311   measures, and which will be most important to future fitness, is an important step towards

312   improving our assessments of future vulnerability.

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419

420   Figure legends

421

422   Figure 1. Feeding *Nacella concinna*, showing the head and radula. Photo credit: Pete Bucktrout.

423

424   Figure 2. The average number of hours each temperature was experienced per 24 hour period was

425   measured by replicate biomimetic loggers (different coloured bars) recording every 30 minutes. A,

426   Rothera *Nacella concinna*, B, *Cellana radiata* and C, *Siphonaria atra*. Note logarithmic scales to

427   emphasise rare high and low temperatures.

428

429   Figure 3. Distance moved by individual limpets, A) Rothera *Nacella concinna* at air temperatures

430   between -1 to 9°C, B) *Cellana radiata* at air temperatures between 24 and 33°C , C) *Siphonaria atra*

431   at air temperatures between 25 and 37°C, between successive tides. *C. radiata*, movement was

432   averaged over 19 low tides. *S. atra* and *N.concinna*, averaged over 3 low tides. Median, 5 and 95%

433   percentiles. Solid circles indicate outliers.

434

435   Figure 4. The rate of radula rasping at different temperatures (mean ± 1SEM). A, *Nacella concinna*, B,

436   *Cellana radiata*, C, *Siphonaria atra*. Whilst *N. concinna* survived at 8.6°C in 2007 there was no

437   feeding at this temperature. Dotted lines indicate non-significant linear regressions (Table S2).

438

439   Figure 5. A, Duration tenacity and B, mortality of *Siphonaria atra*.

440

441   Tables

442

443   Table 1. Rothera *Nacella concinna* foot temperatures and the 4 logger temperatures at the time of
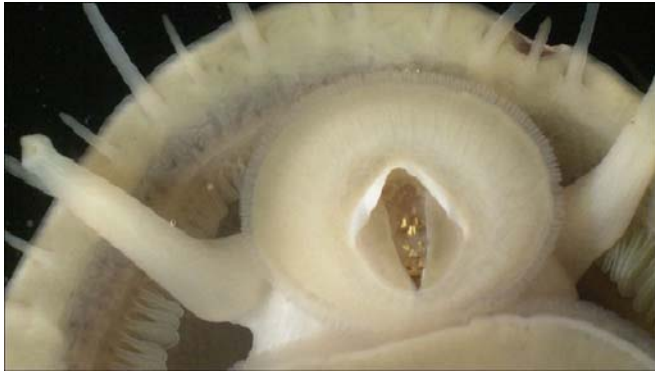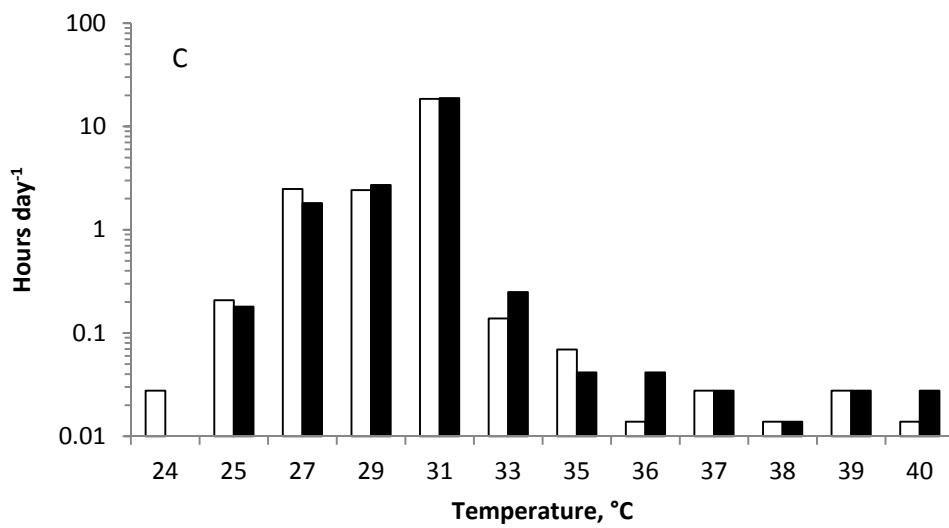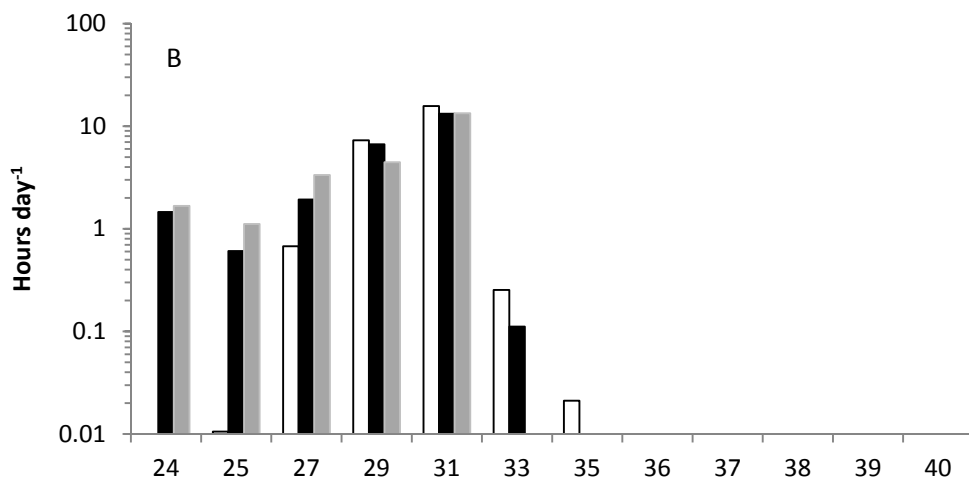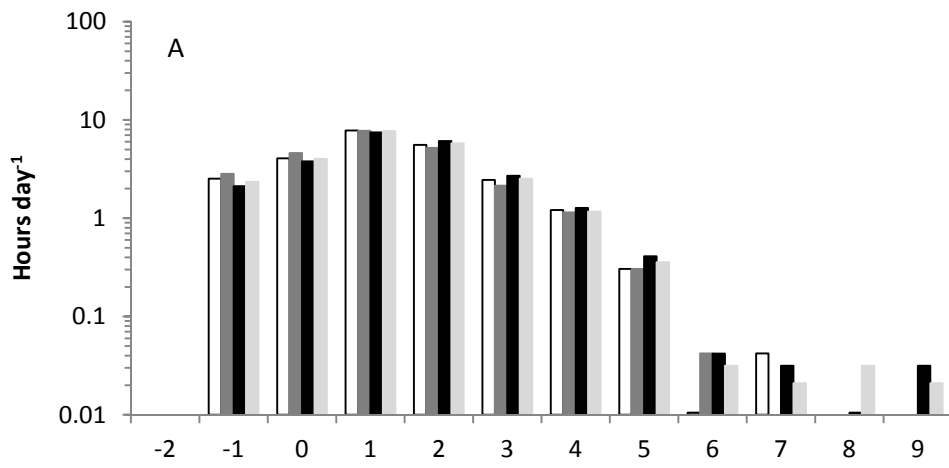
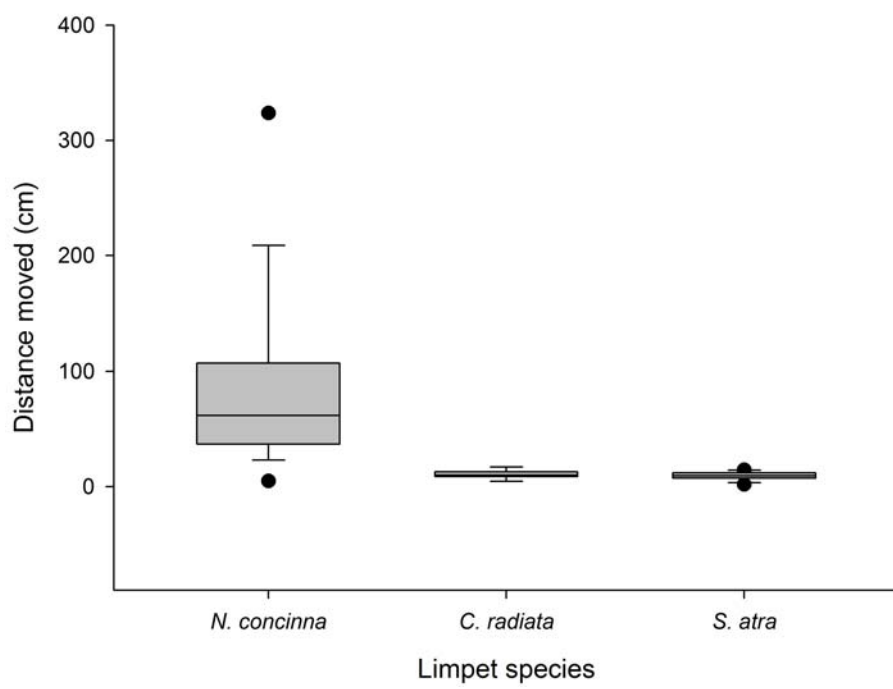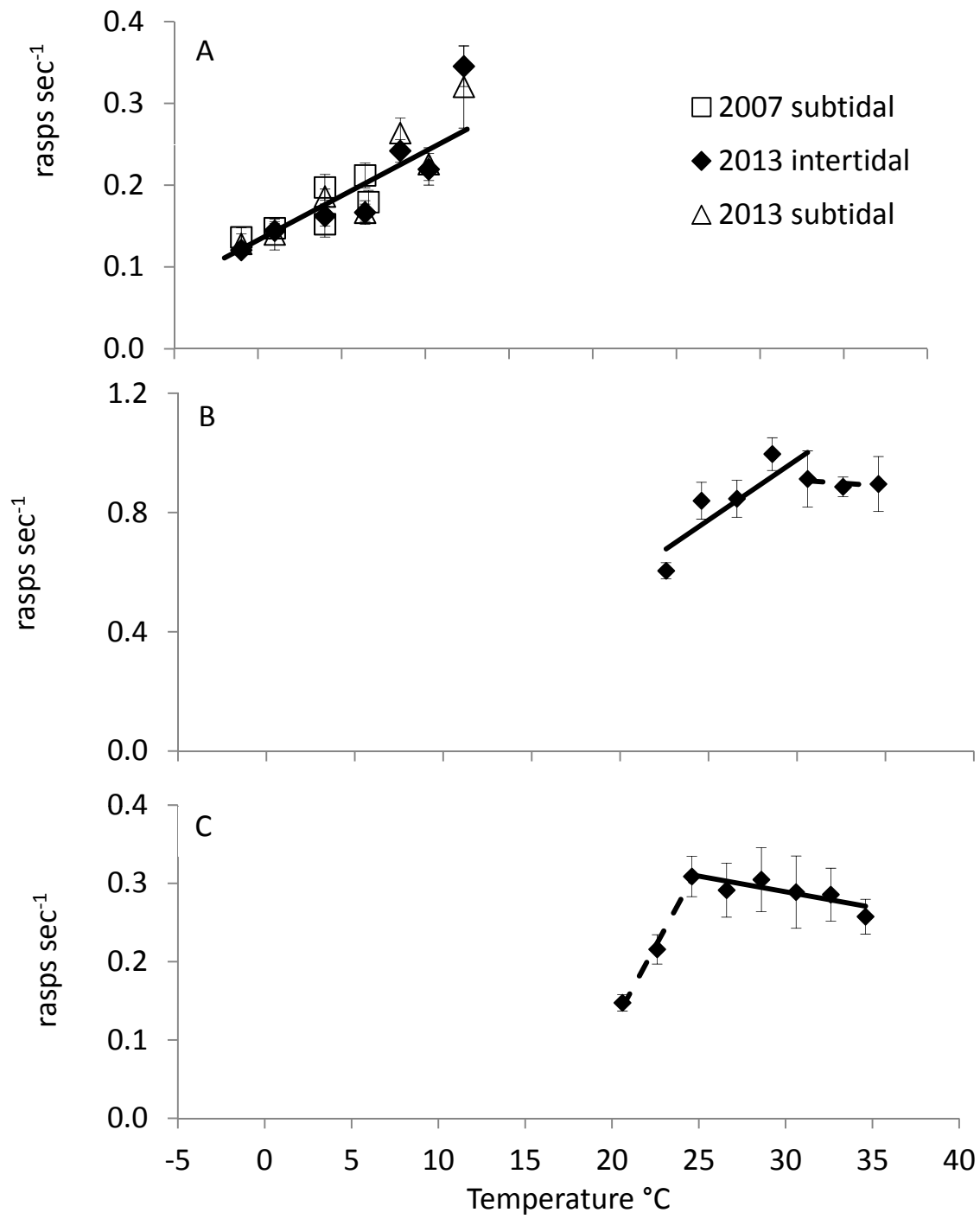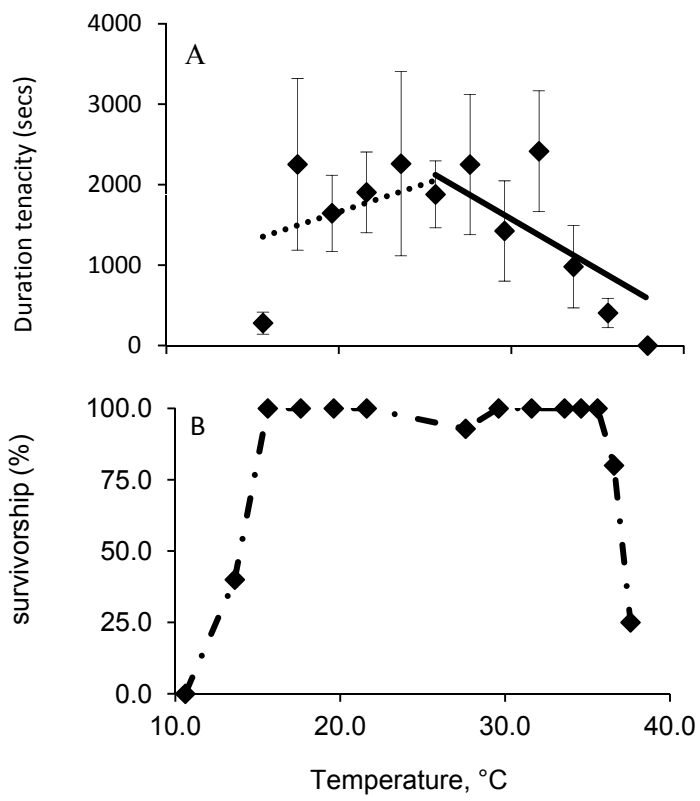444   foot measurement.

445

446

447

Fig. 1

Fig. 3

A

B

Table 1. Rothera *Nacella polaris* foot temperatures and the 4 logger temperatures at the time of foot measurement.

Date		Foot temperature °C Mean	SEM	N	Logger temperature °C
28/12/2012	emersed	9.68	0.34	32	-
	partially immersed	8.60	0.10	2	
	Immersed‡	9.45	0.40	26	
31/12/2012	emersed	2.45	0.11	10	3.31 ,4.26, 4.30, 4.04
	immersed	2.00	0.06	3	
16/01/2012	emersed	4.45	2.55	2	2.18, 2.40, 2.23, 2.09
	immersed	2.07	0.28	15	

‡ Immersed limpets were in semi-isolated rock pools in which water could have been heated by solar radiation.