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1 **Microhabitats choice in intertidal gastropods is species-, temperature- and**
2 **habitat-specific**

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26 **ABSTRACT**

27 Understanding how behavioural adaptations can limit thermal stress for intertidal gastropods
28 will be crucial for climate models. Some behavioural adaptations are already known to limit
29 desiccation and thermal stresses as shell-lifting, shell-standing, towering, aggregation of
30 conspecifics or habitat selection. Here we used the IRT (*i.e.* infrared thermography) to
31 investigate the thermal heterogeneity of a rocky platform at different spatial scales, with four
32 different macrohabitats (*i.e.* bare rock, rock with barnacles, mussels and mussels incrustated by
33 barnacles) during four seasons. We investigated the body temperature of *Littorina littorea* and
34 *Patella vulgata* found on this platform and the temperature of their microhabitat (*i.e.* the
35 substratum within one body length around of each individual). We also considered the
36 aggregation behaviour of each species and assessed the percentage of thermal microhabitat
37 choice (*i.e.* choice for a microhabitat with a temperature different than the surrounding
38 substrate). We did not find any aggregation of *L. littorea* on the rocky platform during the
39 four studied months. In contrast, *P. vulgata* were found in aggregates in all the studied periods
40 and within each habitat, but there was no difference in body temperature between aggregated
41 and solitary individuals. We noted that these two gastropods species were preferentially found
42 on rock covered by barnacles in the four studied months. The presence of a thermal
43 microhabitat choice in *L. littorea* and *P. vulgata* is habitat-dependent and also season-
44 dependent. In June, July and November the choice was for a microhabitat with temperatures
45 lower than the temperatures of the surrounding substrate whereas in December, individuals
46 choose microhabitats with higher temperatures than the temperatures of their substratum. All
47 together, these results suggest that gastropods species are able to explore their environment to
48 find sustainable thermal macrohabitats and microhabitats and adapt this behaviour in function
49 of the conditions of temperatures.

51 **Key words:** Gastropods – behaviour – temperature – temperature – microhabitat choice –

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70 1. INTRODUCTION

71 For both terrestrial and aquatic animals, habitat selection is a way to attract mates, raise
72 offspring, avoid both predation and extreme climatic conditions, and may be influenced by
73 biotic (competition, predation) and abiotic (temperature, relative humidity) factors. Among
74 marine systems, rocky intertidal shores are considered as one of the most thermally variable
75 and stressful environments (Harley, 2008). In these environments, intertidal species have to
76 cope with physical and chemical stresses which intensity depends on the interaction of four
77 major environmental gradients: the vertical gradient (*i.e.* "tidal" gradient), the horizontal
78 gradient (*i.e.* exposure to waves), the sediment particle size gradient, and the marine-
79 freshwater gradient of salinity (Raffaelli and Hawkins, 1999). These gradients, together with
80 species interactions, lead to a zonation in the distribution of intertidal rocky shores species
81 (Little et al., 2009; Raffaelli and Hawkins, 1999). Within this meso-scale zonation, mobile
82 species can select different microhabitats, such as boulders, crevices or pools. The thermal
83 stress has been shown to be triggering this microhabitat choice. Indeed, intertidal species can
84 typically face temperatures variations up to ca. 20°C during a tidal cycle (Helmuth, 2002) and
85 most intertidal invertebrates live close to the upper limit of their thermal tolerance window
86 (Somero, 2002) that lead them to choose the most favourable environment for their survival.
87 The body temperature of intertidal invertebrates can vary by 8-12°C depending on the
88 microhabitat they occupy (Seabra et al., 2011); for instance, the gastropod *Nerita atramentosa*
89 is found on rock platforms and boulder fields with different topographic complexity and thus
90 different substratum temperatures (*i.e.* up to 4.18 °C of mean temperature difference in
91 autumn; Chapperon and Seuront, 2011a). On the other hand, it has been shown that other
92 littorinid snails, such as *Cenchritis muricatus*, rarely inhabit open areas and are preferentially
93 found in crevices or in depressions (Judge et al., 2011). The orientation of the microhabitat
94 towards sunlight can also influence the distribution of intertidal species; for example, the snail

95 *Littoraria scabra*, is consistently found on the shaded part of its habitat and thus actively
96 chose a microhabitat with lower temperatures than microhabitats directly exposed to solar
97 radiations (Chapperon and Seuront, 2011b).

98 In a context of global climate change, rare events such as storms, floods, droughts or heat
99 waves are likely to become the norm (Meehl and Tebaldi, 2004; Oswald and Rood, 2014;
100 Rahmstorf and Coumou, 2011). In particular, heat waves may have dramatic consequences on
101 intertidal species as massive mortality in juvenile barnacles, limpets and mussels (Harley,
102 2008; Seuront et al., 2019). Intertidal ectotherms developed some physiological adaptations as
103 heat-shock protein expression, modifications in heart function or in mitochondrial respiration
104 (Somero, 2002) and behavioural adaptations as habitat selection, aggregation, retraction of the
105 foot into the shell or orientation of the shell (Chapperon and Seuront, 2011a, 2011b; Miller
106 and Denny, 2011) to face these heat waves. These adaptations may become the norm under
107 future climatic scenarios and their understanding in thus critical to assess the diversity and
108 functioning of intertidal communities for the next decades.

109 Temperatures of rocky intertidal substrates are highly variable between shaded and
110 exposed areas (Bertness and Leonard, 1997), vertical and horizontal surfaces (Helmuth, 1998;
111 Miller et al., 2009), north-and south-facing substrates (Denny et al., 2006; Harley, 2008;
112 Seabra et al., 2011), and between crevices and emergent rock (Jackson, 2010). The presence
113 of ecosystem engineers also contributes to the natural variability in temperatures (Bertness
114 and Leonard, 1997) and modify the biotic and abiotic properties of the rocky shores (Jones et
115 al., 1994). Mussels are the dominant ecosystem engineers in the intertidal zone of temperate
116 rocky shores through the formation of multi-layered beds that create microhabitats.
117 Particularly, mussel beds generate interstitial space where water is trapped and thus reduce the
118 effect of desiccation and heat stress (Gutiérrez et al., 2003; Sousa et al., 2009; Suchanek,
119 1985). Their presence also offers protection against wave action during high tides (Choat,

120 1977; Lewis and Bowman, 1975). Mussel beds also increase the reflection of solar radiation,
121 which leads to a reduction of substratum temperature (Little et al., 2009). Other ecosystem
122 engineers, such as barnacles, have also been shown to increase the fine-scale topographic
123 complexity of the substratum, reduce the temperature (by up to 8°C compared to bare rock or
124 to rock with low cover of barnacles) of the surrounding substratum by shading and increase
125 interstitial humidity within patches (Lathlean et al., 2012). Barnacles have also been shown to
126 reduce interspecific competition between the limpets *Cellana tramoserica* and *Patelloida*
127 *latistrigata*, reduce heat stress and wave exposure that facilitated settlement of *P. latistrigata*
128 (Lathlean, 2014).

129 In these environments, the use of thermal imaging has drastically increased over the last 10
130 years, in particular to investigate the role of thermal stress at scale pertinent for individual
131 organisms (Lathlean et al., 2017; Lathlean and Seuront, 2014; Seuront et al., 2018). Infrared
132 thermography (IRT) is a non-invasive tool for simultaneously measuring the temperature of
133 multiple organisms and their environment. IRT thus allows assessing the thermal
134 heterogeneity of complex environments such as intertidal rocky shores (Lathlean and Seuront,
135 2014; Seuront et al., 2018). This methodology was previously applied on mussel beds, in
136 which observed peak temperatures were 10-15°C lower than on the adjacent bedrock (Jurgens
137 and Gaylord, 2016), and on barnacle-covered bedrocks, an increasing barnacle density
138 reducing the heat stress for inhabiting gastropods (the limpet *Patelloida latistrigata*; Lathlean,
139 2014). For intertidal mollusks, the body temperature is significantly correlated with the
140 substrate temperature but not with the air temperature (Chapperon et al, 2013; Seuront et al.,
141 2019) and the aggregation behaviour of some gastropod species is suspected to favour a
142 decrease in individual body temperature (e.g. *Nerita atramentosa*; Chapperon et al., 2013).
143 Overall, these results stress the fact that climate change models should integrate both abiotic

144 variables, such as substratum temperature (rather than air temperature: Seuront et al., 2019),
145 and biotic parameters, such as behavioural adaptations (Ng et al., 2017).

146 Noticeably, the previous studies that dealt with both habitat and microhabitat choice in
147 intertidal organisms, in particular gastropods (Chapperon et al., 2013, 2017; Chapperon and
148 Seuront, 2011a, 2011b; Lathlean, 2014), essentially focused on one season, one species and/or
149 one habitat. In this context, the present study aimed at assessing microhabitat choice in two
150 common temperate gastropod species, *Littorina littorea* and *Patella vulgata*, within four
151 distinct habitats (*i.e.* bare rock, rock covered by barnacles or mussels, and rock covered by
152 mussels encrusted by barnacles) occurring on a topographically homogenous intertidal rock
153 platform extending over the whole intertidal zone during four distinct months. Specifically,
154 we first assessed where these habitats occur on the rocky platform and in which habitat *L.*
155 *littorea* and *P. vulgata* occur on the platform under different meteorological conditions (*i.e.*
156 different months). We also assessed the presence and intensity of aggregation behaviour of
157 these two species often reported as gregarious (Little et al., 2009). We subsequently inferred
158 the presence of a habitat preference for *P. vulgata* and *L. littorea*, and if this choice was
159 species-specific/month-specific. Finally, we described the thermal properties of the four
160 habitats, assessed potential differences between the body temperature of each species and
161 substratum temperature, and inferred the presence of a choice for a thermal microhabitat.

162

163 **2. METHODS**

164 *2.1 Study site*

165 This work was conducted on a temperate intertidal rocky platform, typical of the rocky
166 habitats found along the French coast of the Eastern English Channel, located in Wimereux,
167 France (50°45'09.94"N, 1°35'44.01"E). This platform ranges over the whole intertidal zone

168 and is directly exposed to the dominant South-South West swell direction and submitted to a
169 semi diurnal megatidal regime with a tidal range ranging between 3 and 9 m. We specifically
170 chose this study site for its topographic homogeneity and the presence of four distinct
171 macrohabitats from the supralittoral zone to the low intertidal zone. These habitats were (i)
172 bare rock (Fig. 1A), (ii) rock covered by barnacles *Semibalanus balanoides* and *Austrominus*
173 *modestus*, respectively native and introduced (Fig. 1B), (iii) rock covered by the blue mussels
174 *Mytilus edulis* (Fig. 1C) and (iv) rock covered by mussels with barnacles (Fig. 1D). The
175 location is submitted to a large range of temperatures over a seasonal cycle (*i.e.* from -2°C to
176 32°C in 2019). Thus, four periods of sampling were chosen for the present study, to
177 encompass typical temperature variations of the location: June, November and December
178 2018 and in July 2019. The common periwinkle *Littorina littorea* and the common limpet
179 *Patella vulgata* were observed on this platform and were chosen as target species for the
180 study. These two species can face large variations of temperatures during a year; typically, *L.*
181 *littorea* can be exposed to air temperature as low as -15°C (Murphy, 1979) and its lethal
182 temperature is 46°C (Evans, 1948), whereas the lethal temperature of *P. vulgata* is 42.8°C
183 (Evans, 1948).

184 2.2 Thermal imaging

185 In order to characterize the thermal properties of these four different habitats, thermal imaging
186 was used as a non-invasive temperature measurement (Lathlean and Seuront, 2014; Seuront et
187 al., 2018). We used a Fluke Ti25 camera (Fluke Corporation, Everett, Washington, USA),
188 which sensitivity is $\leq 0.1^\circ\text{C}$ at 30°C and the temperature measurement accuracy is $\pm 2^\circ\text{C}$ for
189 the temperature range measured in the present study (*i.e.* temperatures $< 100^\circ\text{C}$; Fluke
190 Corporation). The emissivity (*i.e.* ability of an object to emit thermal radiation; Lathlean and
191 Seuront, 2014) value of substrata was set at 0.95 as previous studies show that emissivity
192 values of rocky shores typically vary between 0.95 and 1 (Chapperon and Seuront, 2011a;

193 Cox and Smith, 2011; Denny and Harley, 2006; Helmuth, 1998; Miller et al., 2009). All
194 thermal images were analysed using the software SmartView 4.1 (Fluke Corporation). For
195 each thermal picture, a closed curve marker was drawn around each photographed individual
196 to calculate the mean value of body temperature (*BT*) and line were drawn to determine the
197 surrounding substrate temperature.

198

199 2.2.1 Thermal properties of the four habitats

200 The experiments were conducted on one day per studied month. Three replicate IR images of
201 25 cm × 25 cm quadrats were haphazardly taken every 10 meters along a transect on the
202 platform from the low intertidal zone to the supralittoral zone. The photo-quadrats were not
203 fixed but varied in their relative position along the shore for each month. Specifically, 26
204 stations were sampled in June ($n = 78$), 27 in July ($n = 81$), 19 in November ($n = 57$) and 30 in
205 December ($n = 90$). The difference in the number of stations sampled is due to differences in
206 the tidal range at the different sampling occasions. We recorded the presence of each habitat
207 along each transect and we calculated the percentage of occurrence of each habitat on the
208 rocky platform as N_{hab} / n , where N_{hab} is the number of sampling stations where the habitat
209 was observed and n is the total number of sampling stations for each month. This allowed the
210 estimation of the vertical distribution of the different habitats at each sampling date. The
211 abundance of *L. littorea* and *P. vulgata* on each habitat were based on the photo-quadrats;
212 specifically, we choose the photo-quadrats where only one habitat was found to calculate the
213 maximal abundance of each species.

214 To minimise the potential sources of bias in the measurements of intertidal habitat and
215 species temperatures, IR images were consistently taken on days when low tide fell between
216 11 am and 1 pm (*i.e.* midday \pm 1h) and cloud cover was minimal or absent. Air and water
217 temperature and wind speed were considered as environmental variables that were most likely

218 to affect substrate temperature and the behaviour and distribution of both *L. littorea* and *P.*
219 *vulgata* (Seuront et al., 2018). Hourly air temperature and wind speed were obtained from
220 Météo France (www.donneespubliques.meteofrance.fr) weather station of Boulogne-Sur-Mer
221 (50°43'54N, 1°35'53E). Water temperature was measured using temperature loggers
222 (DSL1922L iButtons; resolution 0.1 °C) that were installed throughout the rocky platform.
223 iButtons were wrapped in parafilm, epoxied into shallow depressions chiseled into the rock,
224 and covered by a 1–2 mm layer of epoxy, which was flush with the rock surface.

225 To determine the temperature of each habitat found on each quadrat sampled, 3 horizontal
226 or vertical lines were haphazardly drawn in SmartView 4.1 to measure the range of
227 temperature of the substratum (*ST*). The temperature of each pixel found on each line was
228 subsequently extracted with SmartView 4.1.

229

230 2.2.2 Body temperatures (*BT*) and microhabitat substrate temperatures ($ST_{\mu hab}$)

231 To determine the presence of a thermal microhabitat choice (*i.e.* choice for a microhabitat
232 with a temperature significantly different from the temperature of the habitat *ST*) in the
233 intertidal gastropods *Littorina littorea* and *Patella vulgata*, we measured the body temperature
234 (*BT*) of individual organisms and the temperature of their microhabitat ($ST_{\mu hab}$), *i.e.* the
235 substratum within one body length of each individual, from infrared images with SmartView
236 4.1 (Chappon and Seuront, 2011a, 2012). A thermal microhabitat choice can either be
237 defined as positive (*i.e.* choice for a microhabitat with a temperature significantly warmer
238 than the temperature of the habitat, *i.e.* $ST_{\mu hab} > ST$) or negative (*i.e.* choice for a microhabitat
239 with temperature significantly cooler than the temperature of the habitat, *i.e.* $ST_{\mu hab} < ST$). The
240 percentage of positive choice was defined as n_1/N , where N is the total number of
241 observations, n_1 the number of observations with $ST_{\mu hab} > ST$, and the percentage of negative
242 choice was defined as n_2/N where n_2 is the number of observations with $ST_{\mu hab} < ST$.

243 2.3 Aggregation status

244 *Patella vulgata* and *Littorina littorea* individuals were considered as being aggregated when
245 there was a direct shell contact with the shell of at least one conspecific (Chapperon and
246 Seuront, 2011a, 2011b; Chapperon et al., 2013).

247

248 2.4 Statistical analysis

249 Depending on the normality of the data, body temperature of solitary and aggregated
250 individuals were compared using either a Mann-Whitney test or a t-test, within each habitat
251 for each month. ST were compared between habitats within each month using a Kruskal-
252 Wallis test (hereafter referred to as K-W test) and when necessary a subsequent post-hoc test
253 was performed using a Dunn test (Zar, 2010). BT and $ST_{\mu hab}$ were compared using a Mann-
254 Whitney test for all habitats and months for both species. The Spearman's coefficient of
255 correlation ρ between BT and $ST_{\mu hab}$ was calculated for the two species. The mean temperature
256 of the microhabitat ($ST_{\mu hab}$) of *L. littorea* and *P. vulgata* individuals was compared with the
257 habitat temperature (ST) for each habitat at each tidal level using a Mann-Whitney test.

258

259 **3. RESULTS**

260 3.1 Environmental conditions

261 Recorded air temperature (Meteo France data) ranged between 15 and 16°C in June, 23 and
262 27°C in July, 10 and 13°C in November and 2 and 3°C in December. These temperatures
263 were characteristic of the studied months except in July, where the experiment was performed
264 during what could be considered as a heat wave period
265 (www.donneespubliques.meteofrance.fr). Wind speed (Meteo France data) was $5.1 \pm 1 \text{ m.s}^{-1}$
266 in June, November and December, but decreased to $2.1 \pm 0.5 \text{ m.s}^{-1}$ in July. Mean sea surface

267 temperature (iButtons recordings) during the periods of experiment was $16.4^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$ in
268 June, $19.1^{\circ}\text{C} \pm 0.7^{\circ}\text{C}$ in July, $11.9^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ in November and $7.5^{\circ}\text{C} \pm 0.8^{\circ}\text{C}$ in December.

269

270 *3.2 Habitat distribution*

271 The four habitats were encountered at all tidal levels along the rocky platform, except on the
272 very high shore where only bare rock was found. However, there were variations in the
273 habitats' distribution and overlap during the four months (Fig. 2). Specifically, in June,
274 November and December, all four habitats were present on the platform (Fig. 2A, C, D). In
275 contrast, in July mussels covered by barnacles were absent (Fig. 2B). In June, the habitats the
276 most represented were the rock covered by barnacles found on 80.8% of the platform and the
277 rock covered by mussels with barnacles found on 69.2% of the platform. In contrast, in July,
278 November and December, the habitats the most represented were the rock covered by
279 barnacles, respectively found on 88.9%, 84.2% and 73.3% of the platform, and the bare rock,
280 respectively found on 85.2%, 57.9% and 70% of the platform.

281

282 *3.3 Abundance and occurrence of Patella vulgata and Littorina littorea*

283 *Patella vulgata* was totally absent from mussel beds during the four studied months and also
284 from mussel beds encrusted by barnacles in November and December. The maximal
285 abundances of *Patella vulgata* and *Littorina littorea* were found on the rock incrustated by
286 barnacles for the four studied months excepted in July for *P. vulgata* which was more
287 abundant on bare rock (Table. 1).

288 Aggregation was never observed in *L. littorea* in any habitat, at any sampling date. On the
289 contrary, for *P. vulgata*, some patches were found in all habitats at each sampling occasion
290 (Table. 1). The size of the patches varied between 2 and 5 individuals, except in June on
291 mussels with barnacles where a patch of 8 individuals was observed.

292 3.4 Substrate temperature (*ST*)

293 The substrate temperature of the four habitats exhibited a clear seasonality (Fig. 3), with
294 significant differences consistently observed between months (K-W test, $p < 0.001$). For each
295 habitat, *ST* ranked from high to low temperatures as July > June > November > December
296 (Dunn test, $p < 0.001$). Within each month, there was significant difference in *ST* between the
297 different habitats (K-W test, $p < 0.001$). In July, November and December, *ST* of the four
298 habitats were significantly different (Dunn test, $p < 0.001$). In June, *ST* on bare rock was
299 significantly hotter than the three others habitats (Dunn test, $p < 0.001$). *ST* was not
300 significantly different between the habitats mussels with barnacles and mussels (Dunn test, p
301 > 0.05). There was no significant difference in *ST* between the habitats rock covered by
302 barnacles, mussels and mussels with barnacles (Dunn test, $p > 0.05$).

303

304 3.5 Body temperature (*BT*) and microhabitat temperature ($ST_{\mu hab}$)

305 For *P. vulgata*, a significant positive correlation ($\rho > 0.805$, $p < 0.001$) was consistently
306 found between *BT* and $ST_{\mu hab}$ for the three habitats where the species was found, *i.e.* bare
307 rock, substratum with barnacles and mussels with barnacles (Fig. 4). *BT* was significantly
308 higher than $ST_{\mu hab}$ in July and November for all the habitats, and only for bare rock and rock
309 with barnacles in June (Mann-Whitney test, $p < 0.05$). No significant difference was found
310 between *BT* and $ST_{\mu hab}$ in mussels encrusted with barnacles in June, and in all habitats in
311 December (Mann-Whitney test, $p > 0.05$). Finally, no significant difference ($p > 0.05$) was
312 found between the body temperature of solitary and aggregated individuals.

313 For *L. littorea*, a significant positive correlation was found between *BT* and $ST_{\mu hab}$ in the
314 four habitats ($\rho > 0.978$, $p < 0.001$; Fig. 5). In July and November on bare rock and on rock
315 with barnacles, *BT* was significantly higher than $ST_{\mu hab}$ (Mann-Whitney test, $p < 0.05$). For

316 the others months and habitats there was no significant difference between BT and $ST_{\mu hab}$
317 (Mann-Whitney test, $p > 0.05$).

318

319 *3.6 Frequency of thermal microhabitat choice*

320 Thermal microhabitat choice was observed for *Patella vulgata* in all the habitats and for all
321 the studied months. Specifically, the proportion of individuals performing choice ranged from
322 16.7% (on rock incrustated by barnacles in November and on mussels incrustated by barnacles in
323 June) to 57.1% (on bare rock in June; Fig. 6A). Both positive and negative choice were
324 observed; on bare rock and on rock with barnacles in November and on mussels with
325 barnacles in June, there was only negative choice, whereas on bare rock in December, only
326 positive choice was detected. For the other habitats and seasons there was a co-occurrence of
327 both negative and positive choice (Fig. 6A) with a predominance of negative choice in June,
328 July and November and a predominance of positive choice in December.

329 For *Littorina littorea*, there was no thermal microhabitat choice in June and November on
330 bare rock, and in November on mussels incrustated by barnacles. The maximum proportion of
331 individuals displaying a choice was observed in June on rock incrustated by barnacles (47.4%;
332 Fig. 6B). As for *P. vulgata*, both positive and negative were observed: there was only negative
333 choice in July on the three habitats where the species was found, as well as on mussels with
334 barnacles in June whereas in December, we only found positive choice on rock with
335 barnacles, mussels and mussels with barnacles. For the other habitats and months, both
336 negative and positive choice were found (Fig. 6B) with a predominance of negative choice in
337 June, July and November and a predominance of positive choice in December, as for *P.*
338 *vulgata*.

339

340

341 **4. DISCUSSION**

342 *4.1 Aggregation*

343 The aggregation behaviour of intertidal snails was reported in numerous studies (Chapman
344 and Underwood, 1996; Chapperon et al., 2013; Chapperon and Seuront, 2009, 2012). These
345 studies suggested that aggregation behaviour was controlled by local climatic conditions
346 (Bertness, 1989; Chapman and Underwood, 1996; Chapperon et al., 2013; Chapperon and
347 Seuront, 2012; Rojas et al., 2000) or by substrate topography (Rickards and Boulding, 2015;
348 Stafford et al., 2008). However, in the present study, aggregation of *Littorina littorea* was not
349 observed on the topographically homogeneous rocky reef. On nearby rocky platform with a
350 highly complex topography, many *L. littorea* aggregates were previously observed
351 (Chapperon and Seuront, 2009). These results suggest that, in the study area, the aggregation
352 behaviour of *L. littorea* was not governed by climatic conditions (*i.e.* temperature) but mainly
353 by substrate topography. Our observations are also consistent with the hypothesis that
354 aggregation behaviour is selected to cope with thermal and desiccation stresses only on shores
355 with a high crevice density (Stafford et al., 2008).

356 Some aggregates of *Patella vulgata* were however found. Benefit from living in
357 aggregation for *P. vulgata* is likely to be a reduction in physical or biological stresses
358 (Coleman et al., 2004). Living in group may allow to retain moisture on rock surface and
359 modify air flow over the individuals and thus reduce evaporation. However, there is only
360 relatively weak evidence of the effect of aggregation on desiccation stress in limpets
361 (Coleman et al., 2004). Here, we found no difference on body temperature between solitary
362 and aggregated individuals. This result suggests that aggregation behaviour was not used as a
363 response against thermal and desiccation stresses but was driven by others factors. As
364 suggested by Coleman (2010), aggregation in limpets may more likely be a behavioural
365 response against predation risks than a way to reduce desiccation stress (Coleman, 2010).

366 4.2 The selection of a macrohabitat as refuge

367 The four habitats described here were encountered at all tidal levels during the study and thus
368 often overlapped (Fig. 2). Both species were consistently observed in these habitats, whatever
369 the tidal level, except for the limpet *P. vulgata* which was absent from mussel beds whatever
370 the distribution of this habitat along the shore. These two results testify for a meso-habitat
371 choice rather than a distribution of the species related to tidal height of the shore.

372 The four habitats previously described on the rocky platform (*i.e.* bare rock, rock covered by
373 barnacles, rock covered by mussels and rock covered by mussels with barnacles) were found
374 in June, November and December. In contrast, in July the habitat “mussels covered by
375 barnacles” was absent and there were only a few mussels present. This absence of mussels is
376 most probably related to the massive mortality of the blue mussel *Mytilus edulis* observed on
377 the Opal Coast in summer 2018 (Seuront et al., 2019). Limpets are usually absent from
378 mussel beds, unless boulders are present, as described for this habitat in the EUNIS
379 classification (Connor et al., 2004) and previously observed on temperate intertidal mussel
380 beds (Saier, 2002; Norling and Kautsky, 2007). On our study site, *Littorina littorea* and
381 *Patella vulgata* were mostly found on substrate covered by barnacles at all sampling months.
382 This result suggests that, at the scale of the platform, the rock covered by barnacles is the
383 most favourable habitat for *P. vulgata* and *L. littorea*. This is in accordance with the results of
384 Lathlean, (2014), who showed that the abundance of the limpet *Patelloida latistrigata*
385 decreased with the diminution of barnacles cover associated to an increase of heat stress
386 which increases with the free space due to the diminution of barnacle cover (Lathlean, 2014).
387 Barnacles create biogenic structures and provide refuges from desiccation and predation,
388 increase the surface for attachment for mobile gastropods species (Barnes, 2000) and also
389 create topographically complex microhabitats which greatly reduce flow velocity and allow
390 snails to persist against wave-swept (Denny and Wetthey, 2001; Silva et al., 2015). Thus, the

391 biogenic structures formed by barnacles can act as thermal refuges for gastropod species.
392 Regarding littorinids, the body temperature of the temperate snail *Littorina saxatilis* in
393 summer is on average 1°C cooler than their surrounding substrate when found on substrate
394 with barnacles than on bare rock (Chapperon et al., 2017). Furthermore, Cartwright and
395 Williams, (2012) showed that *Echinolittorina malaccana* and *E. vidua* used the barnacles as
396 refuges during times of the year where the environmental conditions, and in particular
397 temperature, were stressful. They also showed that these two species did not used barnacles as
398 refuges all along the year; when environmental conditions became cooler *E. malaccana* and
399 *E. vidua* were found on other areas without the need of thermal refuges.

400

401 *4.3 Microhabitat selection: a way to escape from unfavourable temperatures?*

402 The habitat selection is a consistent behavioural feature in molluscs. This behavioural
403 adaptation allows molluscs to reduce or avoid desiccation stress or predators. For examples
404 *Littorina saxatilis* hide in crevices to reduce water loss (Little et al., 2009) or the high shore
405 snails *Cenchritis muricatus* climb on terrestrial vegetation to avoid extremes temperature of
406 the rocks surface (Emson et al., 2002). Limpets usually select their habitat through their
407 homing behaviour, thus reducing desiccation stress and also predation risks (Little et al.,
408 2009). In the present study, food availability was not estimated in the different habitats and
409 we assume that all resting positions in air recorded are based on temperature. Controlled
410 laboratory experiments or controlled field observations would be needed to tease out this
411 potential effect. The rationale behind the thermal microhabitat choice behaviour relies on the
412 fact that gastropods body temperature is primarily determined by the substrate temperature,
413 due to conductance between the foot and the substratum (Chapperon and Seuront, 2011a,
414 2011b; Garrity, 1984); in a thermally heterogeneous environment, gastropods would then be
415 able to actively chose the most favourable thermal habitat, to either favour or limit heat

416 exchange with the substrate. Our results showed that the body temperatures (*BT*) of *Littorina*
417 *littorea* and *Patella vulgata* were always significantly and positively correlated with the
418 microhabitat temperatures ($ST_{\mu hab}$) in each habitat for each season which supports the thermal
419 microhabitat choice hypothesis. However, for both species, this choice was both habitat-
420 dependent and season-dependent. In December, individuals predominantly choose
421 microhabitats with higher temperatures than the temperatures of their substratum (*i.e.* positive
422 thermal microhabitat choice). Under cold conditions of temperature, *L. littorea* individuals
423 drastically reduced their metabolic rate (down to 20% of the regular metabolic rate; Jackson,
424 2008); the choice for a microhabitat with higher temperature during cold seasons allows
425 individuals to maintain their metabolic rate or at least to limit the reduction of metabolic rate.
426 On the contrary, in June, July and November the choice was principally for a microhabitat
427 with temperatures lower than the temperatures of the surrounding substrate (*i.e.* negative
428 thermal microhabitat choice) which suggests a selection of a cool substrate to reduce the
429 increase of body temperature by conduction between gastropod's foot and the substratum.
430 Individuals, were thus able to navigate in their thermally heterogeneous environment to find
431 the most sustainable temperatures, in particular during the heat wave of July when this choice
432 was predominantly positive for *P. vulgata* and always positive for *L. littorea*. *P. vulgata* and
433 *L. littorea* ceased their spontaneous movement around 32°C and their lethal temperature are
434 42°C and 46°C, respectively (Evans, 1948). Thus, the choice of microhabitat with lower
435 temperature, allows individuals to maintain their body temperature under lethal or sub-lethal
436 temperature as previously observed in tropical littorinids (*Littoraria scabra*; Chapperon and
437 Seuront, 2011b) and limpets (*Cellana tramoserica*; Sinclair et al., 2006; *Cellana grata*;
438 Williams and Morritt, 1995). In addition to microhabitat choice, others behavioural
439 adaptations have previously been described, such as shell-lifting, shell-standing and towering
440 that reduce conduction from the substrate in littorinids (Seuront and Ng, 2016; Ng et al.,

441 2017) and "mushrooming" in limpets which raise their shell to allow evaporative cooling
442 (Garrity, 1984). These behaviours were, however, never observed in the present study, not
443 even, to our knowledge, in the study area. This suggests that microhabitat choice is the
444 predominant behaviour and that, under particularly harsh thermal conditions, other
445 behavioural adaptations may be involved. With the expected rise in both mean temperatures
446 and frequency of extreme high temperature events (IPCC, 2018), behavioural adaptations
447 remain highly important for intertidal gastropods to maintain their body temperature under
448 thermal stress and to avoid lethal temperature, and we may observe in the near future in
449 temperate areas (such as the present study site) behaviours that are usually seen in tropical
450 environments (e.g. shell-towering) where the thermal stress level is already high. The critical
451 importance of the survival of herbivores such as limpets and littorinids goes beyond the
452 individual and population interest, since their presence has been shown to dampen the impact
453 of warming on the overall intertidal community composition and functioning (Kordas et al.,
454 2017).

455

456 **5. CONCLUSION**

457 This study suggests that the two intertidal gastropods species, *Littorina littorea* and *Patella*
458 *vulgata* showed a clear preference for the thermally favourable biogenic habitat created by
459 barnacles. Moreover, these two gastropods species, at the individual scale, also showed a
460 choice for thermally favourable microhabitats. In winter, both species showed a clear
461 behavioural preference for microhabitats with temperatures higher than the temperature of the
462 substratum, whereas during other seasons, they showed a preference for microhabitats with
463 temperatures lower than the ones measured on the substratum. These differences between
464 temperature of their microhabitats and their substrate may lead to a difference in the way they
465 face thermal stresses such as frost or heat wave. It also means that, temperature variations et

466 very small scales are really important to understand how intertidal gastropods, and intertidal
467 ectotherms in general, can survive in a context of global change. Specially, climate change
468 scenarios do not integrate variations in temperature at pertinent scales for the individuals.
469 Furthermore, these scenarios do not considerate that the body temperature of gastropods is
470 strongly correlated to the temperature of the substrate and never to the air temperature. These
471 results showed that climate models probably underestimate the effect of climate change in the
472 body temperature of intertidal gastropods. This study also reveals that gastropods species are
473 able to explore their environment to find thermal refuge and thus may find refuges under new
474 environmental conditions and possibly adopt locally new adaptive behaviours.

475

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488 **REFERENCES**

- 489 Barnes, M., 2000. The use of intertidal barnacle shells. *Oceanogr. Mar. Biol.* 38, 157–187.
- 490 Bertness, M.D., 1989. Intraspecific competition and facilitation in a northern acorn barnacle
491 population. *Ecology* 70, 257–268.
- 492 Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions in communities :
493 lessons from intertidal habitats. *Ecology* 78, 1976–1989.
- 494 Cartwright, S.R., Williams, G.A., 2012. Seasonal variation in utilization of biogenic
495 microhabitats by littorinid snails on tropical rocky shores. *Mar. Biol.* 159, 2323–2332.
496 <https://doi.org/10.1007/s00227-012-2017-3>
- 497 Chapman, M.G., Underwood, A.J., 1996. Influences of tidal conditions, temperature and
498 desiccation on patterns of aggregation of the high-shore periwinkle, *Littorina*
499 *unifasciata*, in New South Wales, Australia. *J. Exp. Mar. Bio. Ecol.* 196, 213–237.
500 [https://doi.org/10.1016/0022-0981\(95\)00131-X](https://doi.org/10.1016/0022-0981(95)00131-X)
- 501 Chapperon, C., Le Bris, C., Seuront, L., 2013. Thermally mediated body temperature , water
502 content and aggregation behaviour in the intertidal gastropod *Nerita atramentosa*. *Ecol.*
503 *Res.* 28, 407–416. <https://doi.org/10.1007/s11284-013-1030-4>
- 504 Chapperon, C., Seuront, L., 2012. Keeping warm in the cold : on the thermal benefits of
505 aggregation behaviour in an intertidal ectotherm. *J. Therm. Biol.* 37, 640–647.
506 <https://doi.org/10.1016/j.jtherbio.2012.08.001>
- 507 Chapperon, C., Seuront, L., 2011a. Space-time variability in environmental thermal properties
508 and snail thermoregulatory behaviour. *Funct. Ecol.* 25, 1040–1050.
509 <https://doi.org/10.1111/j.1365-2435.2011.01859.x>

510 Chapperon, C., Seuront, L., 2011b. Behavioral thermoregulation in a tropical gastropod: links
511 to climate change scenarios. *Glob. Chang. Biol.* 17, 1740–1749.
512 <https://doi.org/10.1111/j.1365-2486.2010.02356.x>

513 Chapperon, C., Seuront, L., 2009. Cue synergy in *Littorina littorea* navigation following
514 wave dislodgement. *J. Mar. Biol. Assoc. United Kingdom* 89, 1133–1136.
515 <https://doi.org/10.1017/S0025315409000150>

516 Chapperon, C., Studerus, K., Clavier, J., 2017. Mitigating thermal effect of behaviour and
517 microhabitat on the intertidal snail *Littorina saxatilis* (Olivi) over summer. *J. Therm.*
518 *Biol.* 67, 40–48. <https://doi.org/10.1016/j.jtherbio.2017.03.017>

519 Choat, J.H., 1977. The influence of sessile organisms on the population biology of three
520 species of Acmaeid limpets. *J. Exp. Mar. Bio. Ecol.* 26, 1–26.
521 <https://doi.org/10.1017/CBO9781107415324.004>

522 Coleman, R.A., 2010. Limpet aggregation does not alter desiccation in the limpet *Cellana*
523 *tramoserica*. *J. Exp. Mar. Bio. Ecol.* 386, 113–118.
524 <https://doi.org/10.1016/j.jembe.2010.02.011>

525 Coleman, R.A., Browne, M., Theobalds, T., 2004. Aggregation as a defense: limpet tenacity
526 changes in response to simulated predator attack. *Ecology* 85, 1153–1159.
527 <https://doi.org/10.1890/03-0253>

528 Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lierberknecht, L.M., Northen, K.O.,
529 Reker, J.B., 2004. The marine habitat classification for Britain and Ireland. Version
530 04.05. Joint Nature Conservation Committee, Peterborough.

531 Cox, T.E., Smith, C.M., 2011. Thermal ecology on an exposed algal reef: infrared imagery a
532 rapid tool to survey temperature at local spatial scales. *Coral Reefs* 30, 1109–1120.

- 533 <https://doi.org/10.1007/s00338-011-0799-2>
- 534 Denny, M.W., Wethey, D., 2001. Physical processes that generate patterns in marine
535 communities, in: Bertness M. D., G.S.M. and H.M.E. (Ed.), *Marine Community Ecology*.
536 Sinauer Associates, Sunderland, Massachusetts, pp. 3. – 37.
- 537 Denny, M.W., Harley, C.D.G., 2006. Hot limpets: predicting body temperature in a
538 conductance-mediated thermal system. *J. Exp. Biol.* 209, 2409–2419.
539 <https://doi.org/10.1242/jeb.02257>
- 540 Denny, M.W., Miller, L.P., Harley, C.D.G., 2006. Thermal stress on intertidal limpets: long-
541 term hindcasts and lethal limits. *J. Exp. Biol.* 209, 2420–2431.
542 <https://doi.org/10.1242/jeb.02258>
- 543 Emson, R.H., Morritt, D., Andrews, E.B., Young, C.M., 2002. Life on a hot dry beach:
544 behavioural, physiological, and ultrastructural adaptations of the littorinid gastropod
545 *Cenchritis (Tectarius) muricatus*. *Mar. Biol.* 140, 723–732.
546 <https://doi.org/10.1007/s00227-001-0738-9>
- 547 Evans, R.G., 1948. The lethal temperatures of some common British littoral molluscs. *J.*
548 *Anim. Ecol.* 17, 165–173.
- 549 Garrity, S.D., 1984. Some adaptations of gastropods to physical stress on a tropical rocky
550 shore. *Ecology* 65, 559–574.
- 551 Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem
552 engineers: the role of shell production in aquatic habitats. *Oikos* 101, 79–90.
553 <https://doi.org/10.1034/j.1600-0706.2003.12322.x>
- 554 Harley, C.D.G., 2008. Tidal dynamics, topographic orientation, and temperature-mediated

555 mass mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* 371, 37–46.
556 <https://doi.org/10.3354/meps07711>

557 Helmuth, B.S.T., 2002. How do we measure the environment? Linking intertidal thermal
558 physiology and ecology through biophysics. *Integr. Comp. Biol.* 42, 837–845.
559 <https://doi.org/10.1093/icb/42.4.837>

560 Helmuth, B.S.T., 1998. Intertidal mussels microclimates: predicting the body temperature of a
561 sessile invertebrate. *Ecol. Monogr.* 68, 51–74.

562 Jackson, A., 2008. Common periwinkle, *Littorina littorea*, In Tyler-Walters H. and Hiscock
563 K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information*
564 *Reviews*.

565 Jackson, A.C., 2010. Effects of topography on the environment. *J. Mar. Biol. Assoc. United*
566 *Kingdom* 90, 169. <https://doi.org/10.1017/S0025315409991123>

567 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69,
568 373. <https://doi.org/10.2307/3545850>

569 Judge, M.L., Botton, M.L., Hamilton, M.G., 2011. Physiological consequences of the
570 supralittoral fringe: microhabitat temperature profiles and stress protein levels in the
571 tropical periwinkle *Cenchritis muricatus* (Linnaeus, 1758). *Hydrobiologia* 675, 143–156.
572 <https://doi.org/10.1007/s10750-011-0812-3>

573 Jurgens, L.J., Gaylord, B., 2016. Edge effects reverse facilitation by a widespread foundation
574 species. *Sci. Rep.* 6, 1–10. <https://doi.org/10.1038/srep37573>

575 Kordas, R.L., Donohue, I., Harley, C.D.G., 2017. Herbivory enables marine communities to
576 resist warming. *Sci. Adv.* 3. <https://doi.org/10.1126/sciadv.1701349>

577 Lathlean, J.A., 2014. Not all space is created equal: distribution of free space and its influence
578 on heat-stress and the limpet *Patelloida latistrigata*. *J. Therm. Biol.* 46, 16–23.
579 <https://doi.org/10.1016/j.jtherbio.2014.09.005>

580 Lathlean, J.A., Ayre, D.J., Minchinton, T.E., 2012. Using infrared imagery to test for quadrat-
581 level temperature variation and effects on the early life history of a rocky-shore barnacle.
582 *Limnol. Oceanogr.* 57, 1279–1291. <https://doi.org/10.4319/lo.2012.57.5.1279>

583 Lathlean, J.A., Seuront, L., 2014. Infrared thermography in marine ecology : methods,
584 previous applications and future challenges. *Mar. Ecol. Prog. Ser.* 514, 263–277.
585 <https://doi.org/10.3354/meps10995>

586 Lathlean, J.A., Seuront, L., Ng, T.P.T., 2017. On the edge: the use of infrared thermography
587 in monitoring responses of intertidal organisms to heat stress. *Ecol. Indic.* 81, 567–577.
588 <https://doi.org/10.1016/j.ecolind.2017.04.057>

589 Lewis, J.R., Bowman, R.S., 1975. Local habitat-induced variations in the population
590 dynamics of *Patella vulgata* L. *J. Exp. Mar. Bio. Ecol.* 17, 165–203.
591 [https://doi.org/10.1016/0022-0981\(75\)90029-5](https://doi.org/10.1016/0022-0981(75)90029-5)

592 Little, C., Williams, G.A., Trowbridge, C.D., 2009. *The biology of rocky shores*, Oxford Uni.
593 ed.

594 Meehl, G.A., Tebaldi, C., 2004. More intense, more frequent, and longer lasting heat waves in
595 the 21st century. *Science* (80-.). 305, 994–997. <https://doi.org/10.1126/science.1098704>

596 Miller, L.P., Denny, M.W., 2011. Importance of behavior and morphological traits for
597 controlling body temperature in littorinid snails. *Biol. Bull.* 220, 209–223.
598 <https://doi.org/10.1086/BBLv220n3p209>

- 599 Miller, L.P., Harley, C.D.G., Denny, M.W., 2009. The role of temperature and desiccation
600 stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. *Funct.*
601 *Ecol.* 23, 756–767. <https://doi.org/10.1111/j.1365-2435.2009.01567.x>
- 602 Murphy, D.J., 1979. A comparative study of the freezing tolerances of the marine snails
603 *Littorina littorea* (L .) and *Nassarius obsoletus* (Say). *Physiol. Zool.* 52, 219–230.
- 604 Ng, T.P.T., Lau, S.L.Y., Seuront, L., Davies, M.S., Stafford, R., Marshall, D.J., Williams,
605 G.A., 2017. Linking behaviour and climate change in intertidal ectotherms: insights from
606 littorinid snails. *J. Exp. Mar. Bio. Ecol.* 492, 121–131.
607 <https://doi.org/10.1016/j.jembe.2017.01.023>
- 608 Norling, P., Kautsky, N., 2007. Structural and functional effects of *Mytilus edulis* on diversity
609 of associated species and ecosystem functioning. *Mar. Ecol. Prog. Ser.* 351, 163–175.
610 <https://doi.org/10.3354/meps07033>
- 611 Oswald, E.M., Rood, R.B., 2014. A trend analysis of the 1930-2010 extreme heat events in
612 the continental United States. *J. Appl. Meteorol. Climatol.* 53, 565–582.
613 <https://doi.org/10.1175/JAMC-D-13-071.1>
- 614 Raffaelli, D., Hawkins, S.J., 1999. *Intertidal Ecology*. Chapman & Hall, London. 365 pp.
- 615 Rahmstorf, S., Coumou, D., 2011. Increase of extreme events in a warming world. *Proc. Natl.*
616 *Acad. Sci. U. S. A.* 108, 17905–17909. <https://doi.org/10.1073/pnas.1101766108>
- 617 Rickards, K.J.C., Boulding, E.G., 2015. Effects of temperature and humidity on activity and
618 microhabitat selection by *Littorina subrotundata*. *Mar. Ecol. Prog. Ser.* 537, 163–173.
619 <https://doi.org/10.3354/meps11427>
- 620 Rojas, J. M., Fariña, J. M., Soto, R. E., Bozinovic, F., 2000. Geographic variability in thermal

621 tolerance and water economy of the intertidal gastropod *Nodilittorina peruviana*. Rev.
622 Chil. Hist. Nat. 73, 543–552.

623 Saier, B., 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea:
624 Diversity differences of associated epifauna. Helgol. Mar. Res. 56, 44–50.
625 <https://doi.org/10.1007/s10152-001-0097-4>

626 Seabra, R., Wetthey, D.S., Santos, A.M., Lima, F.P., 2011. Side matters: microhabitat
627 influence on intertidal heat stress over a large geographical scale. J. Exp. Mar. Bio. Ecol.
628 400, 200–208. <https://doi.org/10.1016/j.jembe.2011.02.010>

629 Seuront, L., Ng, T.P.T., 2016. Standing in the sun: infrared thermography reveals distinct
630 thermal regulatory behaviours in two tropical high-shore littorinid snails. J. Molluscan
631 Stud. 82, 336–340. <https://doi.org/10.1093/mollus/eyv058>

632 Seuront, L., Ng, T.P.T., Lathlean, J.A., 2018. A review of the thermal biology and ecology of
633 molluscs, and of the use of infrared thermography in molluscan research. J. Molluscan
634 Stud. 84, 203–232. <https://doi.org/10.1093/mollus/eyy023>

635 Seuront, L., Nicastro, K.R., Zardi, G.I., Goberville, E., 2019. Decreased thermal tolerance
636 under recurrent heat stress conditions explains summer mass mortality of the blue mussel
637 *Mytilus edulis*. Sci. Rep. 9, 1–14. <https://doi.org/10.1038/s41598-019-53580-w>

638 Silva, A.C.F., Mendonça, V., Paquete, R., Barreiras, N., Vinagre, C., 2015. Habitat provision
639 of barnacle tests for overcrowded periwinkles. Mar. Ecol. 36, 530–540.
640 <https://doi.org/10.1111/maec.12161>

641 Sinclair, E.L.E., Thompson, M.B., Seebacher, F., 2006. Phenotypic flexibility in the
642 metabolic response of the limpet *Cellana tramoserica* to thermally different
643 microhabitats. J. Exp. Mar. Bio. Ecol. 335, 131–141.

644 <https://doi.org/10.1016/j.jembe.2006.03.010>

645 Somero, G.N., 2002. Thermal physiology and vertical zonation of intertidal animals: optima,
646 limits, and costs of living. *Integr. Comp. Biol.* 42, 780–789.
647 <https://doi.org/10.1093/Icb/42.4.780>

648 Sousa, R., Gutiérrez, J.L., Aldridge, D.C., 2009. Non-indigenous invasive bivalves as
649 ecosystem engineers. *Biol. Invasions* 11, 2367–2385. [https://doi.org/10.1007/s10530-](https://doi.org/10.1007/s10530-009-9422-7)
650 [009-9422-7](https://doi.org/10.1007/s10530-009-9422-7)

651 Stafford, R., Davies, M.S., Williams, G.A., 2008. Self-organization of intertidal snails
652 facilitates evolution of aggregation behavior. *Artif. Life* 14, 409–423.
653 <https://doi.org/10.1162/artl.2008.14.4.14401>

654 Suchanek, T.H., 1985. Mussels and their role in structuring rocky shore communities. *Ecol.*
655 *Rocky Coasts* 70–96.

656 Williams, G.A., Morritt, D., 1995. Habitat partitioning and thermal tolerance in a tropical
657 limpet, *Cellana grata*. *Mar. Ecol. Prog. Ser.* 124, 89–103.

658 Zar, J.H., 2010. *Biostatistical analysis*, Fifth edit. ed.

659

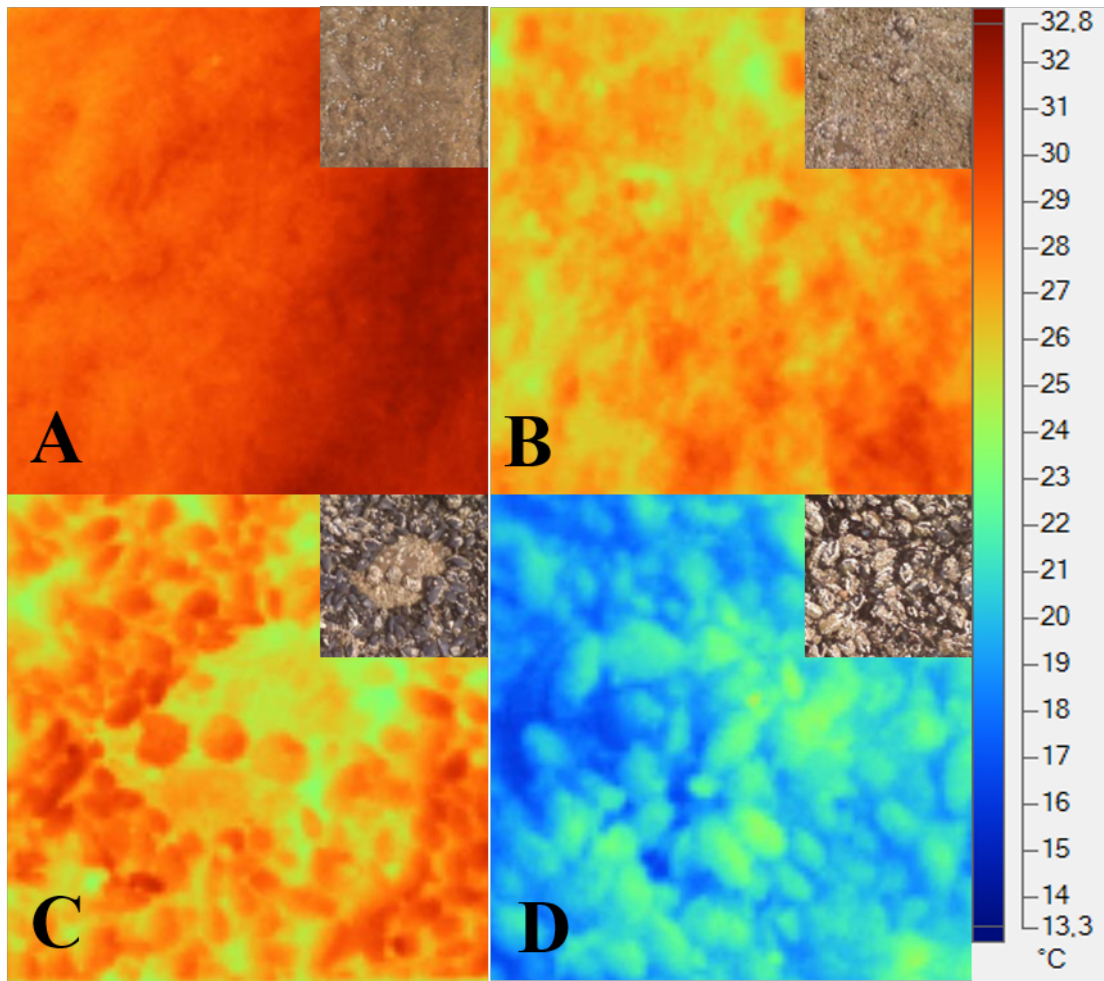
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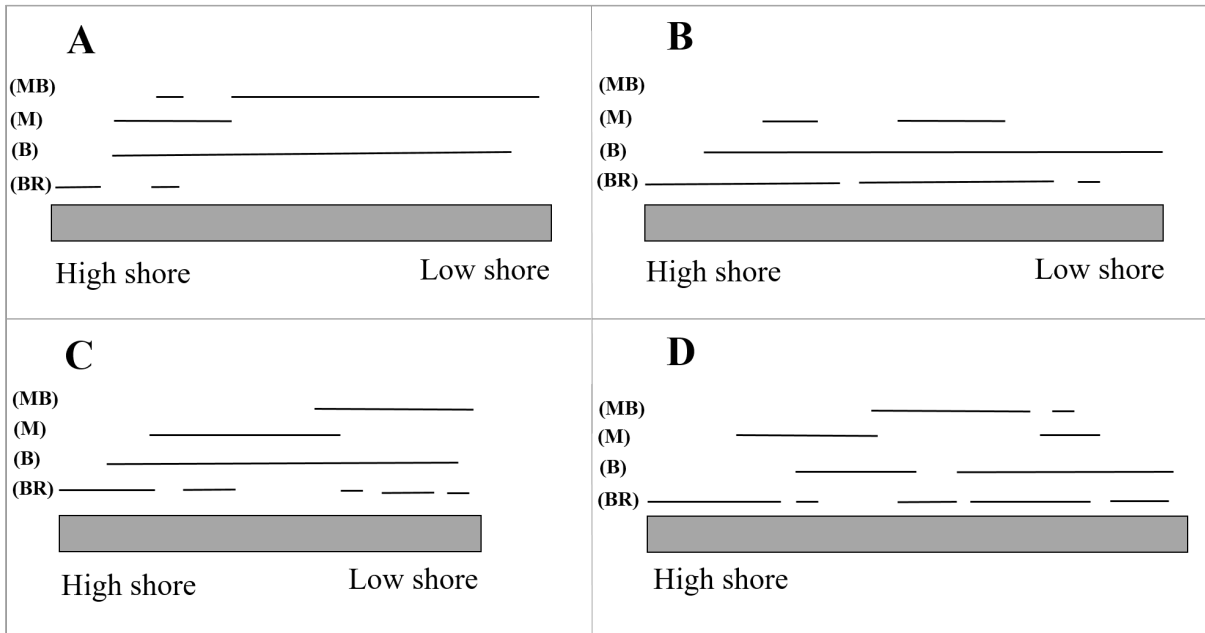
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666 Fig. 1. Thermal images and associated digital pictures of the four types of habitats found on the rocky platform
 667 (A) bare rock, (B) rock covered by barnacles, (C) rock covered by mussels and (D) rock covered by mussels with
 668 barnacles. These images were taken in June.

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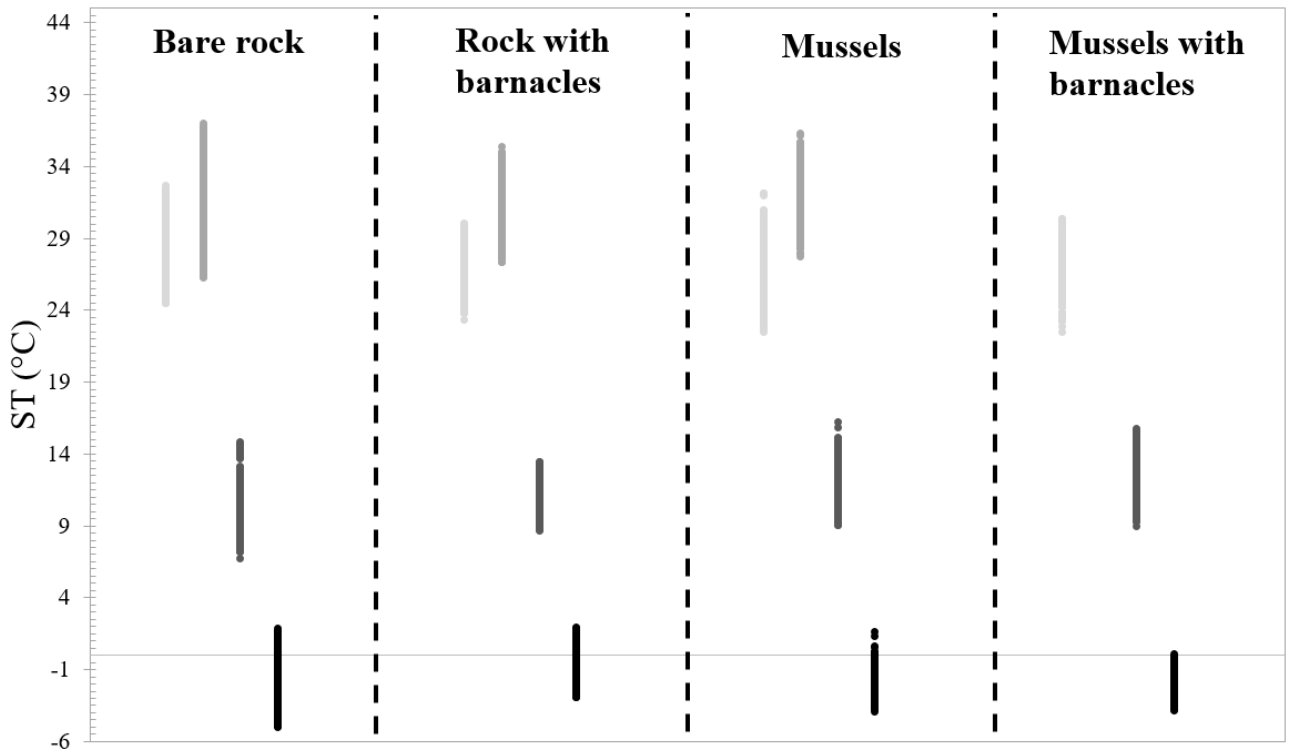


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673 Fig. 2. Distribution of the four habitats found along the rocky platform (in grey) (BR) bare rock, (B) rock
 674 covered by barnacles, (M) mussels, (MB) mussels encrusted by barnacles at the different months (A) June, (B)
 675 July, (C) November and (D) December. The black line represents the presence of the habitat.

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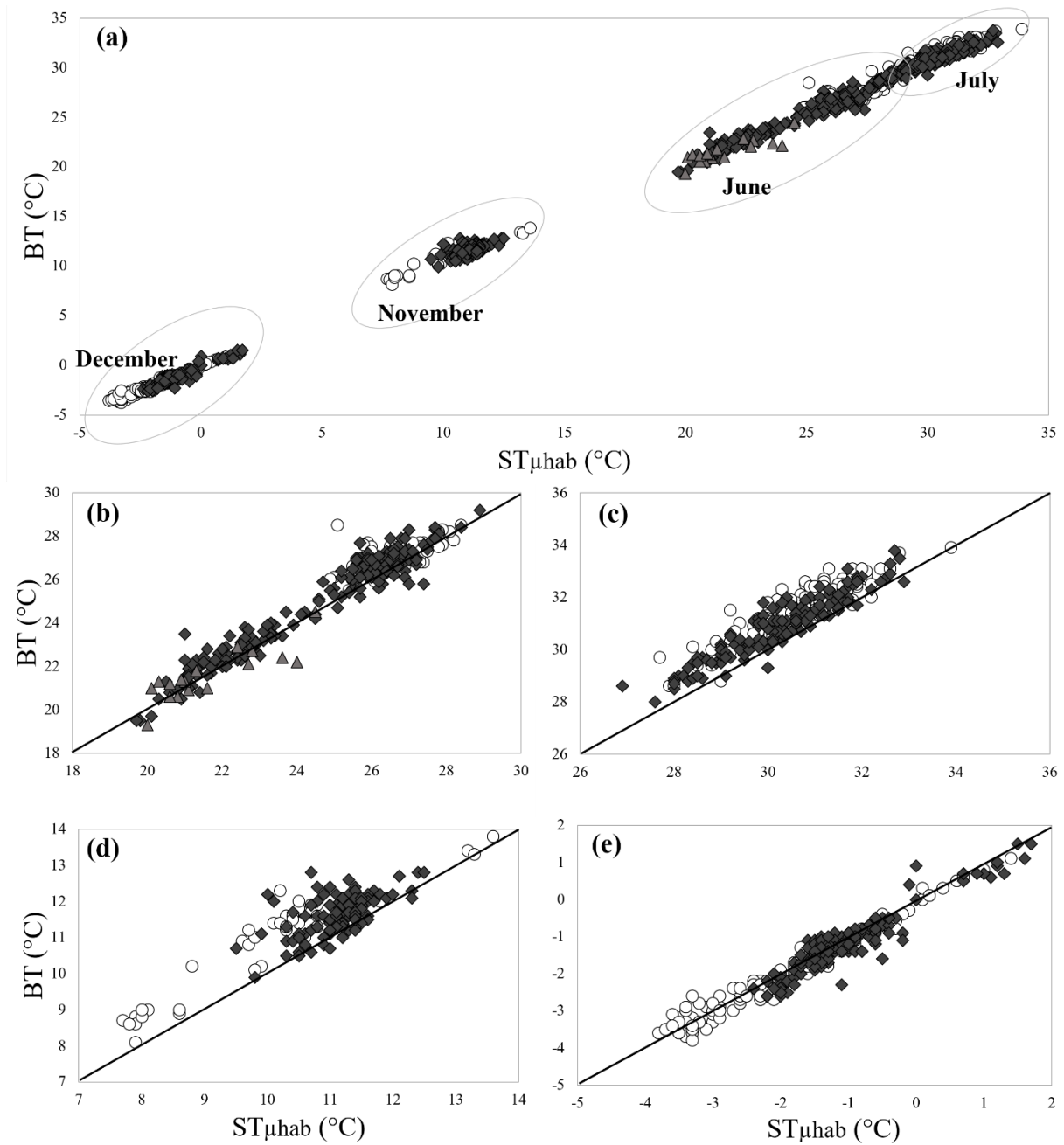
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679 Fig. 3. Substrate temperature (*ST*) found on the different habitats in June (light grey), in July (grey), in
 680 November (dark grey) and in December (black). The habitat mussels with barnacles was absent in July.

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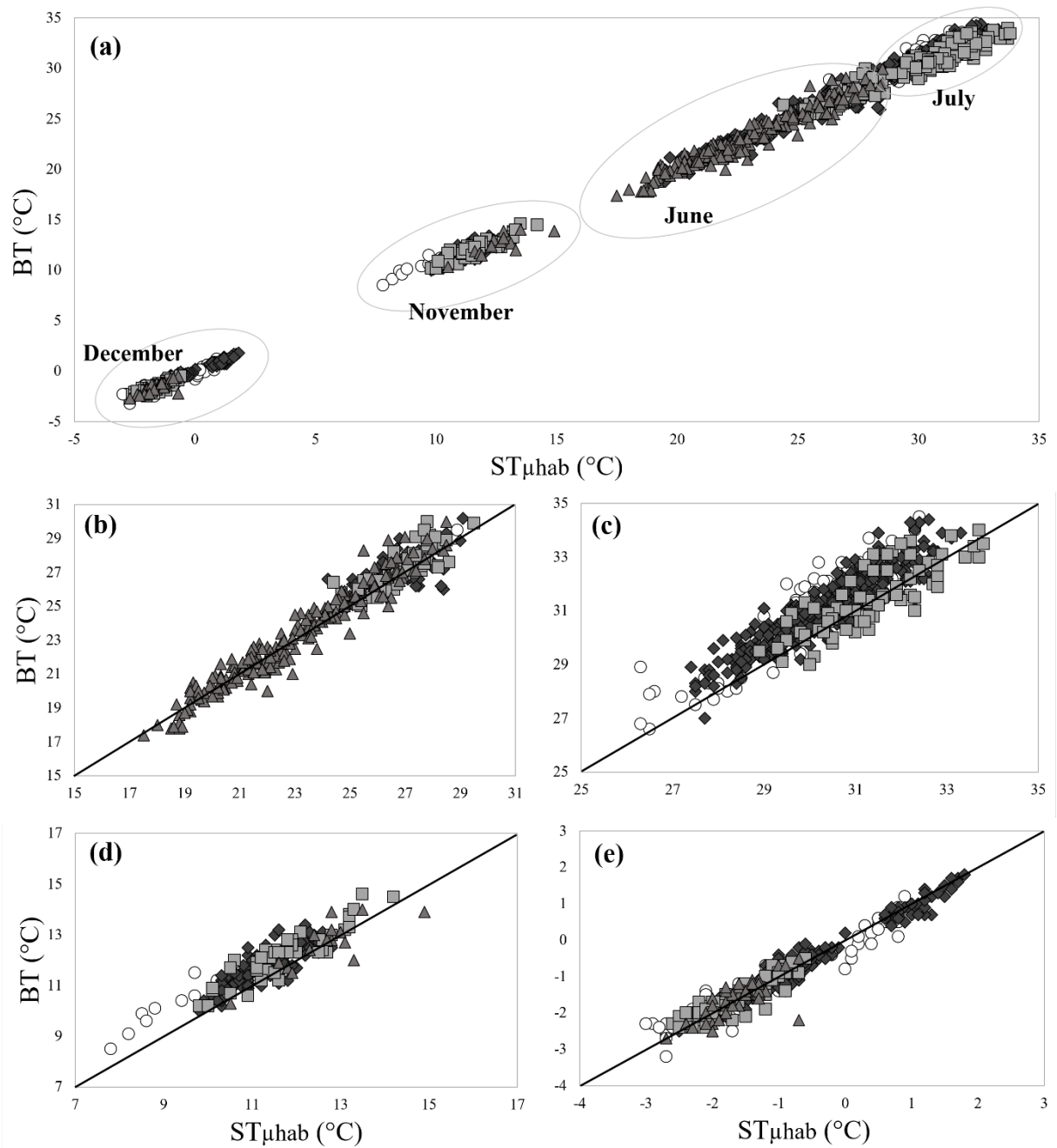
683 Fig. 4. Body temperature (*BT*) as a function microhabitat substrate temperature (*ST μ hab*) for *Patella vulgata* for
 684 the four months studied (a) and in particular for June (b), July (c), November (d) and December (e). The open
 685 dots represented the bare rock habitat, the diamond ones rock with barnacles, the square markers mussels and the
 686 triangle markers represented mussels with barnacles. The black line represents the first bisectrix, i.e. *BT* =
 687 *ST μ hab*.

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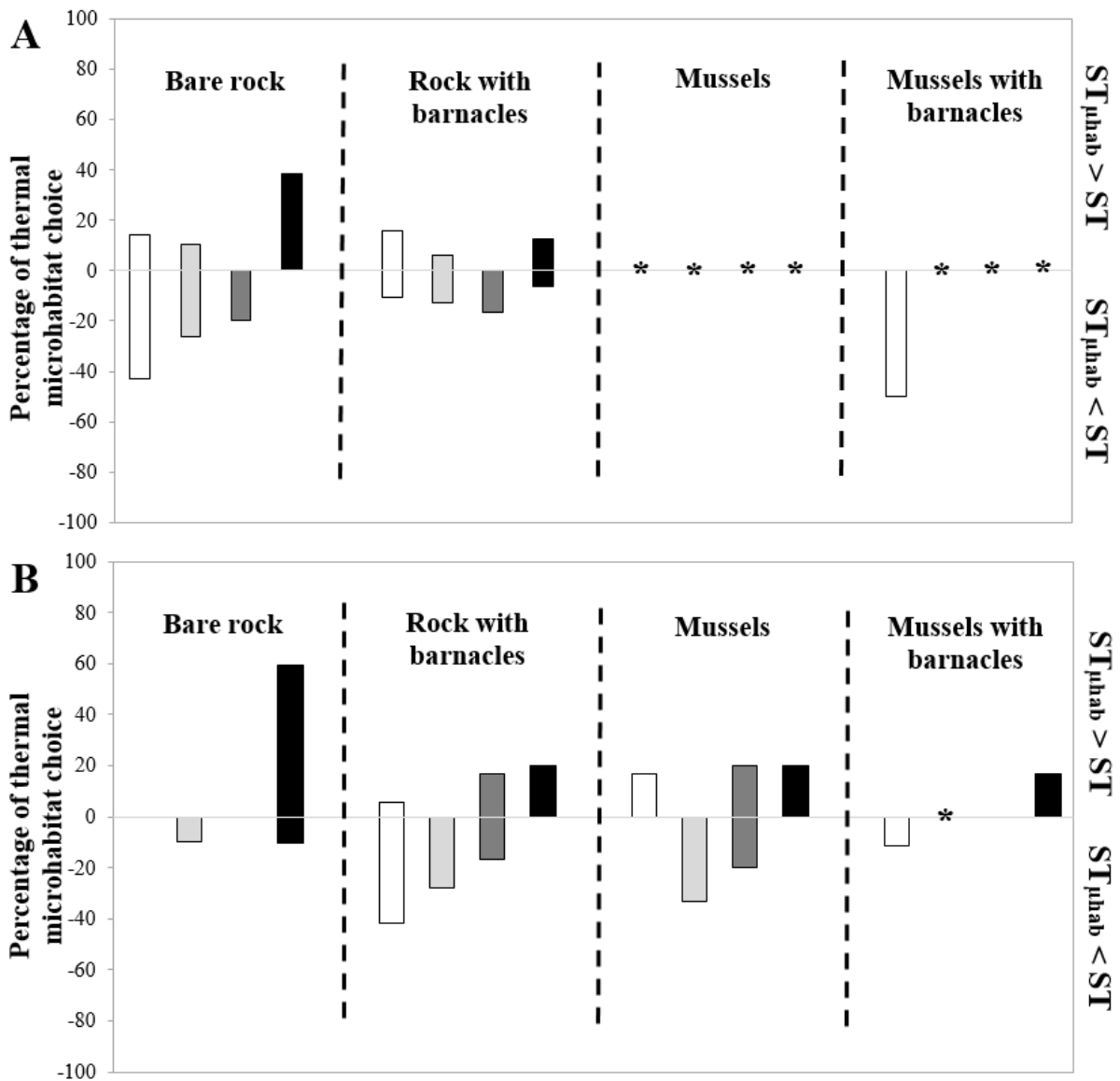
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693 Fig. 5. Body temperature (*BT*) as function of microhabitat substrate temperature (*ST* μ hab) for *Littorina littorea*
 694 for the four months studied (a) and in particular for June (b), July (c), November (d) and December (e). The open
 695 dots represented the bare rock habitat, the diamond ones rock with barnacles, the square markers mussels and the
 696 triangle markers represented mussels with barnacles. The black line represents the first bissectrix, i.e. *BT* =
 697 *ST* μ hab.

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700 Fig. 6. Percentage of thermal microhabitat choice for *Patella vulgata* (A) and for *Littorina littorea* (B) in June in
 701 white, in July in light grey, in November in dark grey and in December in black, in the different four habitats
 702 found on the rocky reef. The asterisk means that *P. vulgata* and *L. Littorina* were absent from the habitat.

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711 Table 1. Maximal abundance (ind.m⁻²) of *Patella vulgata* and *Littorina littorea* on the different studied months
 712 in the four habitats. The number of patches of *P. vulgata* are given within brackets. *L. littorea* was never found
 713 on aggregate in this study.

		Bare rock	Rock with barnacles	Mussels	Mussels with barnacles
<i>Patella vulgata</i>	June	240 (8)	336 (8)	ABS	176 (1)
	July	256 (6)	208 (5)	ABS	ABS
	November	272 (4)	320 (7)	ABS	ABS
	December	288 (10)	384 (14)	ABS	ABS
<i>Littorina littorea</i>	June	80	700	416	320
	July	272	944	288	ABS
	November	96	352	160	64
	December	400	416	320	144

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