

1 **Linking behaviour and climate change in intertidal ectotherms: insights from**
2 **littorinid snails**

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21

22 **Abstract**

23 A key element missing from many predictive models of the impacts of climate change
24 on intertidal ectotherms is the role of individual behaviour. In this synthesis, using
25 littorinid snails as a case study, we show how thermoregulatory behaviours may
26 buffer changes in environmental temperatures. These behaviours include either a
27 *flight* response, to escape the most extreme conditions and utilize warmer or cooler
28 environments; or a *fight* response, where individuals modify their own environments
29 to minimize thermal extremes. A conceptual model, generated from studies of
30 littorinid snails, shows that various *flight* and *fight* thermoregulatory behaviours may
31 allow an individual to widen its thermal safety margin (TSM) under warming or
32 cooling environmental conditions and hence increase species’ resilience to climate
33 change. Thermoregulatory behaviours may also buffer sublethal fitness impacts
34 associated with thermal stresses. Through this synthesis, we emphasise that future

35 studies need to consider not only animals' physiological limits but also their capacities
36 to buffer the impact of climate change through behavioural responses. Current
37 generalizations, made largely on physiological limits of species, often neglect the
38 buffering effects of behaviour and may, therefore, provide an over-estimation of
39 vulnerability, and consequently poor prediction of the potential impacts of climate
40 change on intertidal ectotherms.

41

42 **1. Introduction**

43 Climate change is undoubtedly one of the most pressing environmental issues today,
44 as it has profound impacts on species viability and hence biodiversity and ecosystem
45 function (Walther et al., 2002; Harley et al., 2006; Parmesan, 2006; Bellard et al.,
46 2012). The past two decades have witnessed a tremendous growth in research on
47 species' responses to climate change (Pörtner, 2001; Garrett et al., 2006; Helmuth et
48 al., 2006a; Somero, 2010; Walther, 2010; Hawkins et al., 2013; Mieszkowska et al.,
49 2014) and biologists have endeavoured to assess and predict the biological
50 consequences of climate change in different species using various predictive models
51 (Helmuth, 1998; Pearson and Dawson, 2003; Araújo et al., 2005; Poloczanska et al.,
52 2008; Kearney et al., 2010; Burrows et al., 2011).

53 To date, both correlative and mechanistic modelling approaches have been used
54 to predict extinction risk and future geographic distributions of species (Hijmans and
55 Graham, 2006; Kearney et al., 2010; Sarà et al., 2011). A substantial amount of
56 research effort has further been allocated to identify and investigate additional
57 physical and biological components that can be incorporated in these models to
58 improve their utility (Helmuth et al., 2005; Brook et al., 2009; Kearney and Porter,
59 2009; Kearney et al., 2009, 2011). Modelling approaches adopted in the past have,
60 however, largely overlooked the fact that organisms are not always 'prisoners' of
61 climate change and may have a suite of behaviours or other adaptations to ameliorate
62 the potential effects of climate change (Huey and Tewksbury, 2009). Indeed, there is
63 increasing realization that species can behaviourally exploit complex small-scale
64 variations in microclimate to regulate their body temperatures (Bogert, 1949; Huey
65 and Tewksbury, 2009; Kearney et al., 2009; Tuomainen and Candolin, 2011).
66 Behavioural thermoregulation is still, however, a relatively under-appreciated process
67 and is rarely included in models to predict the impacts of climate change on species
68 (Wichmann et al., 2004; Huey and Tewksbury, 2009; Sih et al., 2010; Huey et al.,

69 2012; Sunday et al., 2014).

70 A few studies (e.g. Wichmann et al., 2004; Kearney et al., 2009) have, however,
71 incorporated the behavioural repertoires of species into predictive models of climate
72 change. Kearney et al. (2009), for example, demonstrated that predictions of lizard
73 body temperatures were substantially altered by considering behavioural buffering
74 through selection of shaded areas. Behavioural buffering of thermal environments is,
75 indeed, crucial for ectotherms which rely on external heat sources to regulate their
76 body temperatures to maintain physiological homeostasis (Deutsch et al., 2008;
77 Kearney et al., 2009; Somero, 2010). Such behavioural buffering effects can best be
78 achieved in thermally heterogeneous environments where animals have more
79 opportunities to flee or hide from unfavourable thermal conditions (Huey and
80 Tewksbury, 2009; Huey et al., 2012; Sunday et al., 2014). The role of behavioural
81 buffering associated with temperature is, however, likely to vary between species,
82 with particular environments and especially across latitudes (Deutsch et al., 2008;
83 Huey and Tewksbury, 2009). For temperate ectotherms, that generally occupy
84 environments cooler than their thermal optimum, getting warmer is the priority,
85 whereas staying cool is the goal for many tropical ectotherms living in environments
86 which may exceed their thermal optimum (Stillman, 2003; Deutsch et al., 2008;
87 Tewksbury et al., 2008; Somero, 2010).

88 Behavioural buffering is especially important in intertidal systems, which are
89 thermally heterogeneous over very small spatial and temporal scales (Williams and
90 Morritt, 1995; Helmuth et al., 2006a,b; Denny et al., 2011; Seabra et al., 2011;
91 Lathlean et al., 2015; Stafford et al., 2015). Being at the margins of the terrestrial and
92 marine realms, intertidal ectotherms are subject to environmental challenges posed by
93 both aquatic and aerial climatic regimes (Helmuth et al., 2006a; Morritt et al., 2007;
94 Firth and Williams, 2009; Little et al., 2009; Williams et al., 2011). Particularly,
95 high-shore marine species living close to the upper limit of the intertidal zone often
96 persist in what are essentially terrestrial conditions for hours, days or even weeks
97 (Finke et al., 2009; Uglow and Williams, 2009; Marshall et al., 2010b; Marshall and
98 McQuaid, 2011). Physiological studies suggest that intertidal ectotherms are
99 particularly vulnerable to climate change because many of them are already living
100 close to their physiological limits (Somero, 2002, 2010; Lima et al., 2016). As such,
101 any changes of these ectotherms at population levels (e.g. in mortality or distribution
102 patterns) and consequent community level changes may be seen as early warnings of

103 the impacts of climate change (Southward et al., 1995; Helmuth, 1998; Helmuth et al.,
104 2002; Harley and Helmuth, 2003; Somero, 2010).

105 Some studies have, in particular, suggested that high shore species generally have
106 higher heat tolerance but limited acclimation capacity, and hence high shore species
107 are most susceptible to environmental warming (Stillman, 2002, 2003). This
108 generalization is, however, largely based on the physiological response of a single
109 genus (*Petrolisthes*), and it is unclear how much the negative impacts of climate
110 change can be buffered by behavioural responses in intertidal ectotherms. Although
111 intertidal habitats are among the most experimentally examined systems in the context
112 of ecological impacts of climate change (reviewed by Helmuth et al., 2006a), it is
113 noticeable that few previous studies have considered the importance of animal
114 behaviour in buffering these potential impacts (e.g. 1,054 publications contain both
115 *climate change* and *intertidal* in their topic but only 101 contain all of the keywords
116 *climate change*, *behaviour (behavior)* and *intertidal*; Web of Science: accessed April
117 23, 2016). There is, nevertheless, increasing evidence that behavioural
118 thermoregulation may indeed play an important role in buffering the impacts brought
119 by increasing temperature on intertidal ectotherms not only in mobile (e.g. McQuaid
120 and Scherman, 1988; Williams et al., 2005; Chapperon and Seuront, 2011a,b;
121 Marshall et al., 2010a, 2011; Seuront and Ng, 2016) but also in sessile species (e.g.
122 Anestis et al., 2007; Nicastro et al., 2010).

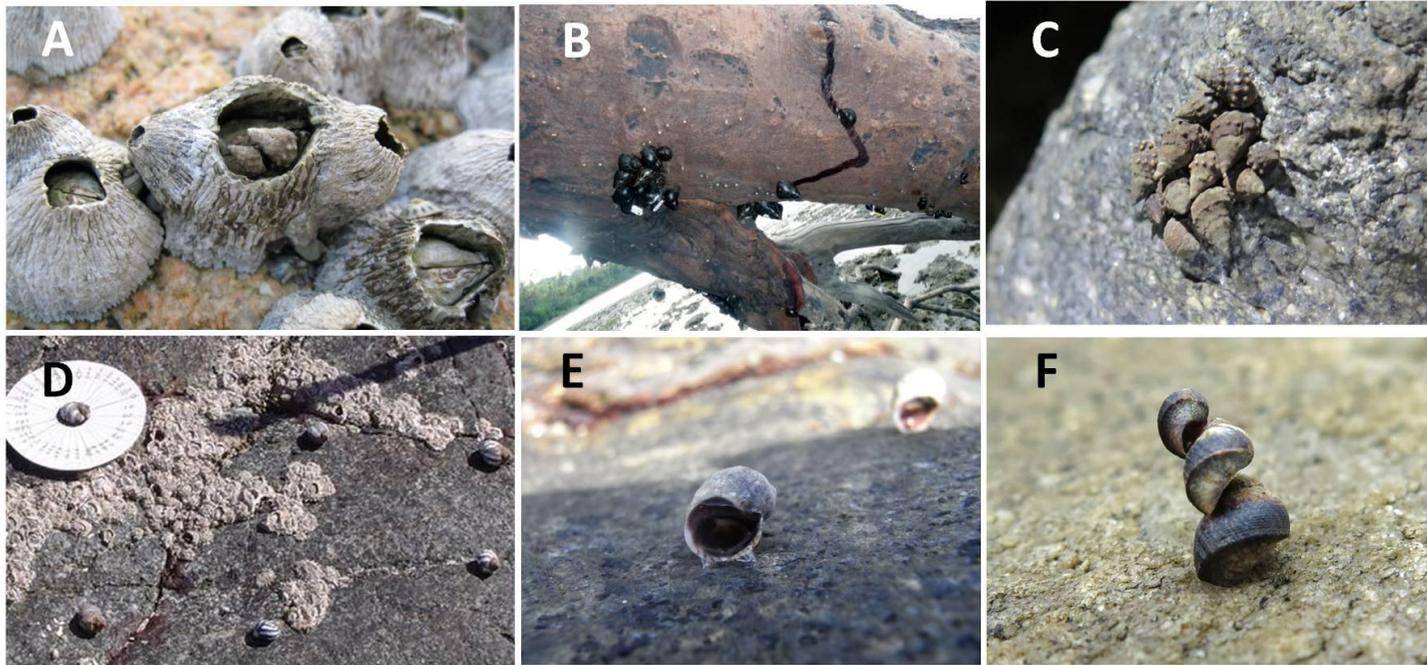
123 This synthesis addresses this knowledge gap by investigating the importance of
124 behavioural thermoregulation in intertidal invertebrates using littorinid gastropods as
125 a case study. These snails are suitable models to address this knowledge gap because
126 (i) they are common herbivores found in almost all intertidal habitats with a near
127 pan-global distribution (Reid, 1989; McQuaid, 1996a,b); (ii) they generally live at
128 higher shore levels and may, therefore, already live close to their physiological limits
129 as other high shore species (e.g. Somero, 2002, 2010, 2012; Stillman, 2002); and
130 finally (iii) they display a wide range of thermoregulatory behaviours (Table 1; Fig. 1).
131 Firstly, we outline the general experimental approaches that have been used to study
132 thermoregulatory behaviours in littorinids and provide a summary of current findings
133 of potential thermoregulatory behaviours in these snails. We then discuss some of
134 these behaviours in terms of desiccation mitigation, since thermal and desiccation
135 stresses are both tightly associated with environmental temperatures in intertidal
136 habitats (Tomanek and Helmuth, 2002; Helmuth et al., 2006a). Finally, we introduce a

137 simple, conceptual model based on our findings to illustrate how behavioural
138 thermoregulation in terms of *flight* and *fight* responses can provide a buffering effect
139 to both increasing and decreasing environmental temperatures, and highlight the need
140 to integrate behavioural components into predictive models of species responses to
141 climate change.
142

Table 1. Published studies that have examined behavioural responses in the context of thermal and/or desiccation regulation in littorinid snails.

Behaviour	Species*	Location	Reference
Foot retraction	<i>Afrolittorina africana</i> ¹	South Africa	McQuaid and Scherman, 1988
	<i>Austrolittorina unifasciata</i> ¹	Vancouver Peninsula, Western Australia	McMahon, 1990
	<i>Bembicium vittatum</i> ¹	Vancouver Peninsula, Western Australia	McMahon, 1990
	<i>Echinolittorina natalensis</i> ¹	Natal region, South Africa	Miller and Denny, 2011
	<i>Littoraria carinifera</i> ²	Kampong Kranji, Singapore	Vermeij, 1971b
	<i>Littoraria coccinea</i> ¹	Guam, U.S.	Vermeij, 1971b
	<i>Littoraria irrorata</i> ³	South Carolina, U.S.	Iacarella and Helmuth, 2011
	<i>Littoraria melanostoma</i> ²	Kampong Kranji, Singapore	Vermeij, 1971b
	<i>Littoraria pintado</i> ¹	Oahu, U.S.	Vermeij, 1971b
	<i>Littoraria scabra</i> ^{1,2}	Oahu and Guam, U.S.	Vermeij, 1971b
		Western Caroline Islands, Palau	
		Jalan Loyang Besar and Kampong Kranji, Singapore	
		Koror, Palau	Vermeij, 1971b
		California, U.S.	Miller and Denny, 2011
		Washington, U.S.	Miller and Denny, 2011
	Thermal refuge selection	<i>Littorina plena</i> ¹	Washington, U.S.
<i>Littorina scutulata</i> ¹		California, U.S.	Miller and Denny, 2011
<i>Littorina sitkana</i> ¹		Washington, U.S.	Miller and Denny, 2011
<i>Afrolittorina africana</i> ¹		South Africa	McQuaid and Scherman, 1988
<i>Echinolittorina malaccana</i> ¹		Hong Kong, China	Cartwright and Williams, 2012
		Jerudong, Brunei Darussalam	Marshall et al., 2013
<i>Echinolittorina peruviana</i> ¹		Las Cruces, central Chile	Soto and Bozinovic, 1998
<i>Echinolittorina vidua</i> ¹		Hong Kong, China	Cartwright and Williams, 2012
<i>Littoraria irrorata</i> ³		South Carolina, U.S.	Iacarella and Helmuth, 2011
<i>Littoraria scabra</i> ²		Tailevu, Fiji	Chapperon and Seuront, 2011a
	Flamenco, Culebra, and Naos Islands, Panama	Garrity, 1984	
	Flamenco, Culebra, and	Garrity, 1984	
	<i>Littorina modesta</i> ¹	Flamenco, Culebra, and	Garrity, 1984

Aggregation	<i>Littorina sitkana</i> ¹	Naos Islands, Panama	Jones and Boulding, 1999
	<i>Echinolittorina peruviana</i> ¹	Vancouver Island, Canada	Muñoz et al., 2008, Rojas et al., 2013
	<i>Littorina saxatilis</i> ¹	Las Cruces, central Chile	Stafford and Davies, 2004
	<i>Melarhappe neritoides</i> ¹	North-east England, U.K.	Stafford and Davies, 2004
	<i>Nodilittorina unifasciata</i> ¹	North-east England, U.K.	Chapman and Underwood, 1996
Shell orientation	<i>Echinolittorina peruviana</i> ¹	New South Wales, Australia	Muñoz et al., 2005
	<i>Littorina aspera</i> ¹	Las Cruces, central Chile	Garrity, 1984
	<i>Littorina modesta</i> ¹	Flamenco, Culebra, and Naos Islands, Panama	Garrity, 1984
Shell posturing	<i>Austrolittorina unifasciata</i> ¹	Flamenco, Culebra, and Naos Islands, Panama	Lim, 2008
	<i>Echinolittorina malaccana</i> ¹	Queensland, Australia	Seuront and Ng, 2016
		Hong Kong, China	Marshall et al., 2010a, Marshall and Chua, 2012
		Jerudong, Brunei Darussalam	Miller and Denny, 2011
	<i>Echinolittorina natalensis</i> ¹	Natal region, South Africa	Seuront and Ng, 2016
	<i>Echinolittorina radiata</i> ¹	Hong Kong, China	Miller and Denny, 2011
	<i>Littorina keenae</i> ¹	California, U.S.	Miller and Denny, 2011
	<i>Littorina plena</i> ¹	Washington, U.S.	Miller and Denny, 2011
	<i>Littorina scutulata</i> ¹	California, U.S.	Miller and Denny, 2011
	<i>Littorina sitkana</i> ¹	Washington, U.S.	Miller and Denny, 2011
<i>Nodilittorina pyramidalis</i> ¹	Queensland, Australia	Lim, 2008	



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146

147 **Fig. 1** Examples of thermoregulatory behaviours associated with thermal and/or desiccation stresses in littorinids. (A) thermal refuge selection
 148 (barnacle test) in *Echinolittorina malaccana*; (B) thermal refuge selection (underside of the roots of mangrove trees) in *Littoraria scabra*; (C)
 149 aggregation in *Echinolittorina malaccana* and *E. radiata*; (D) shell orientation in *Echinolittorina peruviana*; (E) standing in *Echinolittorina*
 150 *vidua*; and (F) towering in *Afrolittorina knysnaensis*. Images courtesy of S.R. Cartwright (A); L. Seuront (B); S.L.Y. Lau (C); J.L.P. Muñoz and
 151 F. Bozinovic (D); M.S. Davies (E); and T.P.T. Ng (F).

152 2. Experimental approaches

153 The thermal environments of intertidal habitats are highly heterogeneous, such that
154 small-scale (typically centimetre- to metre-scale) variability in temperatures can
155 exceed those observed at larger scales (Williams and Morritt, 1995; Helmuth, 2002;
156 Helmuth et al., 2006b; Jost and Helmuth, 2007; Denny et al., 2011; Seabra et al.,
157 2011). Measuring realistic environmental temperatures that are relevant for individual
158 organisms is, consequently, a crucial part of examining thermoregulatory behaviour in
159 littorinids (Helmuth et al., 2006b; Marshall et al., 2010b; Marshall and Chua, 2012).
160 Recent studies have shown that littorinids are primarily impacted by non-climatic heat
161 sources (solar heating and re-radiation from the rock surface, essentially
162 characteristics of latitude and geology) as well as climatic heat sources (air and sea
163 water temperatures, Marshall et al., 2010b). Whilst the heat tolerance thresholds of
164 littorinids are often well above maximum ambient air temperatures, rock surface
165 temperatures can exceed lethal temperatures (Marshall et al., 2010b; T.P.T. Ng and
166 G.A. Williams, unpubl. data). Predictive models of the impacts of climate warming
167 based on climatic heat sources, as have been applied to other marine ectotherms (e.g.
168 Pörtner and Knust, 2007; Harley and Paine, 2009) may not, therefore, be appropriate
169 when considering the potential consequences for these snails. For example,
170 Chapperon and Seuront (2011a) found a strong correlation between body
171 temperatures of the mangrove littorinid, *Littoraria scabra*, and the mangrove roots
172 they were attached to, but no significant relationship with air temperatures
173 (Chapperon and Seuront, 2011a). Subsequent studies confirmed a similar pattern in
174 the nerite, *Nerita atramentosa*, (Chapperon and Seuront, 2011b; Chapperon et al.,
175 2013), suggesting that non-climatic heat sources are better proxies of body
176 temperatures of intertidal ectotherms than climatic heat sources.

177 To address these concerns, biophysical (heat-budget) models that assess operative
178 body temperatures based on heat fluxes due to climatic and non-climatic heat sources
179 at the scale of the organism have been applied to studies of behavioural
180 thermoregulation in littorinids (e.g. Marshall et al., 2010a; Iacarella and Helmuth,
181 2011; Miller and Denny, 2011; Marshall et al., 2015). These models have been
182 validated by comparing the temperatures of live snails to silver or epoxy-filled shells
183 (biomimetics) under various field and laboratory conditions, and then using these
184 biomimetic shells for testing thermoregulation ‘responses’ under different
185 ‘behavioural’ treatments (e.g. Miller and Denny, 2008; Marshall and Chua, 2012).

186 Since shell temperatures appear a reliable proxy of body or mantle temperatures in
187 intertidal snails (Caddy-Retalic et al., 2011), some studies have simply compared the
188 difference between shell temperatures and surrounding rock surface temperatures
189 under different behavioural responses of littorinids using either digital thermometers
190 (e.g. Lang et al., 1998; Soto and Bozinovic, 1998; Lim, 2008) or infrared imagery (e.g.
191 Chapperon and Seuront, 2011a; Seuront and Ng, 2016). In particular, the use of
192 infrared imagery has gained popularity since it allows numerous temperature
193 measurements over a relatively short period and with limited logistics, as compared
194 with more traditional methods. Another advantage of infrared imagery is that it also
195 provides non-invasive, simultaneous, measurements of both the body temperature of
196 multiple snails and the thermal properties of their substrata at appropriate scales,
197 while avoiding the possible physiological and behavioural consequences of inserting
198 thermocouples into small organisms (reviewed by Lathlean and Seuront, 2014).

199

200 **3. Potential thermoregulatory behaviours in littorinids**

201 ***3.1. Foot retraction***

202 Littorinids typically glue their shell to the rock surface with mucus, retract their foot
203 into the shell, and seal the operculum under prolonged or stressful aerial exposure
204 (Bingham, 1972; Vermeij, 1971a,b; Denny, 1984; Garrity, 1984; McMahan and
205 Britton, 1985; Britton and McMahan, 1986). Some species may also leave an opening
206 in the operculum after retracting their foot (termed “gaping”, Iacarella and Helmuth,
207 2011). The dehydrated mucus holdfasts at the tip of the outer aperture can be as little
208 as 2–3 mm thick but provides adequate anchorage for littorinids to remain physically
209 attached with no physical effort (Denny, 1984). Foot retraction and sealing the
210 operculum, coupled with a mucus holdfast, minimises heat flux through conduction
211 by removing contact between the body tissue and the rock surface and also limits
212 water loss through evaporation, reducing both heat and desiccation stresses (Vermeij,
213 1971b; Britton, 1992; McMahan, 1990; Miller and Denny, 2011; Iacarella and
214 Helmuth, 2011; Rojas et al., 2013). Foot retraction can, therefore, be viewed as a
215 ‘*fight*’ response, where individuals modify their own thermal environment by adopting
216 a posture. Miller and Denny (2011) showed that individuals of five littorinid species
217 modelled with their foot withdrawn were, on average, 3–5°C cooler than individuals
218 with their foot attached to the substratum, and that this cooling effect was more
219 pronounced in smaller species. Iacarella and Helmuth (2011), however, showed that

220 the degree of evaporative cooling through foot retraction in littorinids was reduced
221 under high humidity, suggesting that the thermoregulatory effect of this behaviour is
222 context dependent.

223 Previous studies have found little propensity for lower shore gastropods to
224 withdraw their foot into the shell and attach their shell to the rock with mucus
225 (Vermeij, 1971b, 1973; McQuaid and Scherman, 1988). Foot retraction and mucus
226 holdfast attachment minimises evaporative water loss, allowing aerial survival for
227 multiple days (Broekhuysen, 1940; Cleland and McMahon, 1986; Britton, 1995;
228 Miller and Denny, 2011). *Echinolittorina malaccana* can, for example, remain
229 inactive (or aestivating) with its foot withdrawn whilst emersed for more than 40 days
230 (Marshall et al., 2013). Foot retraction behaviour may, however, introduce a trade-off
231 in terms of a reduction in stability and attachment strength as individuals attached by
232 mucus holdfasts can easily be dislodged by waves (Miller, 1974; Denny, 1984;
233 Ohgaki, 1988). Survival of dislodged individuals is, nevertheless, typically high, as
234 the majority of dislodged individuals are able to navigate back to their preferred shore
235 levels, suggesting a net selective benefit of this behaviour in littorinids (Evans, 1961;
236 Bock and Johnson, 1967; Miller et al., 2007; Chapperon and Seuront, 2009).

237

238 **3.2. Thermal refuge selection**

239 Many studies have suggested that littorinids benefit from resting in cool habitats by
240 selecting shaded refuges provided by irregularities in the rock surface, such as
241 crevices (or pits); or being associated with sessile organisms such as macroalgae and
242 barnacles (Soto and Bozinovic, 1998; Jones and Boulding, 1999; Cartwright and
243 Williams, 2012; see Fig. 1A and B). While foot retraction can be viewed as a *fight*
244 response, thermal refuge selection resembles a *flight* response to heat stress as
245 littorinids, like other mobile species, gain an advantage from selecting more optimal
246 thermal conditions (Raffaelli and Hughes, 1978; McQuaid and Scherman, 1988;
247 Chapperon and Seuront, 2011b; Chapperon et al., 2013). By selecting these refuges,
248 littorinids gain the benefit of maintaining their body temperatures below their thermal
249 limits (by up to ~11 °C in some situations) during warm periods (Marshall et al.,
250 2013). It is, however, important to note that the amount of shading, and hence the
251 effectiveness of mitigating thermal stress is highly context-dependent (Soto and
252 Bozinovic, 1998; Jones and Boulding, 1999; Chapperon and Seuront, 2011a). For
253 example, the bottom of mangrove roots provide a refuge to reduce heat stress for

254 *Littoraria scabra* during the day but not at night (Chapperon and Seuront, 2011a);
255 *Echinolittorina malaccana* and *E. vidua* only select barnacles as habitats to shelter
256 within during the hot season in Hong Kong (Cartwright and Williams 2012); and
257 warmer rather than cooler refuges on the shore were preferred by *Echinolittorina*
258 *peruviana* during cold periods (Soto and Bozinovic, 1998). Littorinids, therefore,
259 select certain microhabitats to moderate body temperatures only at times when these
260 microhabitats function as thermal refuges (e.g. depending on day, tide and season,
261 Soto and Bozinovic, 1998; Jones and Boulding, 1999; Chapperon and Seuront,
262 2011a).

263 The preference for certain microhabitats may not, however, be solely associated
264 with thermal stress but with other stressors such as predation and dislodgement risk
265 (Vaughn and Fisher, 1988; Stafford and Davies, 2004). For example, salt marsh
266 littorinids migrate down the stalks of *Spartina* to rehydrate and then crawl back up the
267 stalks to avoid predation (Vaughn and Fisher, 1988). Crevices appear to be more
268 important refuges in winter than in summer for high shore littorinids in Hong Kong
269 due to the overall stronger wave action at this time (T.P.T. Ng unpubl. data). In
270 comparison to adults, juveniles of some species also tend to be restricted to
271 microhabitats without any clear seasonal pattern (Jones and Boulding, 1999),
272 suggesting that juveniles may be more sensitive to a multitude of environmental
273 stressors. Selection of microhabitats is, therefore, a multifunctional behaviour and its
274 effect on thermoregulation can potentially be masked by responses to other stressors.

275

276 **3.3. Aggregation formation**

277 Another multifunctional behaviour that is commonly found in littorinids is
278 aggregation (Chapman, 1995, 1998; Chapman and Underwood, 1996; Stafford et al.,
279 2012a,b; see Fig. 1C). Aggregations in littorinids typically consist of fewer than a
280 hundred individuals, but in extreme cases can involve up to thousands of individuals
281 (Chapman, 1998). This behaviour has been suggested to reduce desiccation stress (e.g.
282 Garrity, 1984; Rojas et al., 2000, 2013; Stafford et al., 2012a,b), dislodgement (Feare,
283 1971; Raffaelli and Hughes, 1978; Stafford, 2002), and predation risk (Chapman,
284 1995; Stafford et al., 2007), as well as increasing the chance of copulation (Feare,
285 1971). The interplay between the multiple different potential causes of aggregation
286 formation may explain why the occurrence and size of aggregations observed in
287 littorinids are temporally and spatially highly variable (Chapman and Underwood,

288 1996; Chapman, 1998; Stafford and Davies, 2004), and often not correlated with
289 increasing levels of heat and/or desiccation stresses (Chapman, 1995; Soto and
290 Bozinovic, 1998; Rojas et al., 2000; Stafford, 2002; Stafford and Davies, 2004).
291 Aggregation formation has also been suggested to be an emergent function of trail
292 following or microhabitat selection (Chapman, 1995, 1998; Stafford et al., 2007), and
293 computer simulations have demonstrated the vital role of trail following in driving the
294 formation of aggregations (Stafford et al., 2007). Stafford et al. (2012b), however,
295 caution that results from many empirical studies may be confounded as they generally
296 compare water content between aggregated and solitary individuals without
297 considering the time at which individuals joined the aggregations, or individual-level
298 variation in relative hydration levels. As such, the true difference in desiccation stress
299 between aggregated and solitary individuals can be masked by measurement error due
300 to the 'background' variations in water content between individuals within the
301 aggregations (Stafford et al., 2012b). In a recent study Rojas et al. (2013) showed that,
302 in the laboratory, aggregated individuals of *Echinolittorina peruviana* kept their
303 opercula open for longer in response to desiccation stress than isolated individuals and
304 hence could prolong gaseous exchange, suggesting a selective advantage to this
305 behaviour.

306 While the study from Rojas et al. (2013) provided evidence for the benefit of
307 aggregation under desiccation stress, most studies have shown little benefit to
308 individuals of joining aggregations during thermally stressful periods in terms of
309 thermoregulation (e.g. Chapman and Underwood, 1996; Chapperon and Seuront,
310 2011a; Stafford and Davies, 2004). Aggregations do, initially, create a wet
311 microclimate, hence delaying the heating of the substratum (Rojas et al., 2013). In
312 some species (Chapman and Underwood, 1996) but not in others (Seuront and Ng,
313 2016), being in an aggregation may also, however, increase body temperatures
314 (compared to solitary individuals) as the substratum dries. The role of aggregation in
315 littorinids has, therefore, generally been attributed to the mitigation of desiccation
316 rather than heat stress (Chapman and Underwood, 1996). There is, however, also
317 evidence that keeping warm through aggregation can be beneficial during cold periods
318 in *Nerita atramentosa* (Chapperon and Seuront, 2012), but such a thermal benefit has
319 yet to be demonstrated for littorinids.

320

321 **3.4. Shell orientation**

322 A few studies have proposed that littorinids orientate their shells to minimize solar
323 gain and hence can reduce their body temperatures by up to 7°C (Muñoz et al., 2005;
324 Fig. 1D). Muñoz et al. (2005) demonstrated that this behaviour is highly
325 context-dependent in *Echinolittorina peruviana*, with most individuals positioning
326 themselves when inactive during emersion to present the front or dorsal face of their
327 shell towards the sun on sunny, summer days, but not on overcast summer or winter
328 days. This behaviour was, therefore, suggested to be mediated by thermally stressful
329 conditions related to solar radiation. No consistency in shell orientation pattern in
330 relation to solar radiation has, however, been recorded in other species (e.g. McQuaid
331 and Scherman, 1988; Lang et al., 1998; Miller, 2008). These contrasting observations
332 suggest that the effectiveness of shell orientation in thermoregulation may vary with
333 local environmental conditions (particularly the direction and magnitude of solar
334 radiation as these animals become exposed to air and, of course, the relative
335 orientation of the shell as the sun moves during the day) or may be species-specific.
336 Littorinid species are highly variable in their shell morphology in terms of size,
337 structure and colour (Vermeij, 1973; Reid, 1989); and such differences may result in
338 variation in absorbance or reflection of solar radiation. The impacts of these shell
339 characteristics may, therefore, lead to contradictory results of the potential thermal
340 benefits of shell orientation in different species. Miller and Denny (2011), for example,
341 showed that the reduction in body temperature as a result of shell structure and colour
342 was negligible in some littorinid species. Shell orientation can also be associated with
343 other functions. Salt marsh littorinids (*Littoraria irrorata*), for example, orientate with
344 their spire facing downwards, which was proposed to help maintain their position on
345 the salt marsh grass stalks (Bingham, 1973). As such, it is difficult to reach any
346 consensus about the role of shell orientation in relation to thermoregulation, and
347 further research is needed to tease apart the various underlying causes of variation in
348 this behaviour.

349

350 **3.5. Shell posturing**

351 Three shell postures have been suggested to be related to thermoregulation in
352 littorinids and all are coupled with the foot retraction behaviour under aerial
353 conditions mentioned above. Specifically, *shell lifting* (Lim, 2008) involves an
354 individual slightly lifting its shell off the rock surface with its aperture parallel to the
355 substratum; *shell standing* (Garrity, 1984; Marshall and Chua, 2012; Fig. 1E) occurs

356 when an individual lifts its shell off the rock surface with its aperture perpendicular to
357 the substratum in a vertical or upright position; and *towering* (Marshall et al., 2010a;
358 Fig. 1F) behaviour occurs when at least one snail attaches itself using pedal mucus to
359 the shell of other snails (either con- or heterospecifics) to form a tower. Individuals
360 involved in the tower may or may not also perform the other two posturing behaviours
361 (Marshall et al., 2010a; Seuront and Ng, 2016).

362 *Shell lifting* behaviour has been widely observed in littorinids (Garrity, 1984;
363 Britton, 1995; Lang et al., 1998; Wada and Ito, 2000; Miller and Denny, 2011) but its
364 role in thermoregulation is still unclear. Lifting the shell from the substratum reduces
365 the area of the shell in contact with the substratum as compared to simply
366 withdrawing the foot (Miller and Denny, 2011). Most studies have, however, shown
367 little reduction in the body temperatures of lifting individuals as compared to the
368 surrounding rock surface or the body temperatures of non-posturing (or 'flat')
369 individuals (Lim 2008; Marshall and Chua, 2012). Lim (2008) suggested that lifting
370 behaviour could be an interrupted stage in the process of standing at times when heat
371 stress becomes so extreme that individuals abort any further attempt to become
372 upright.

373 *Shell standing* behaviour has, however, been widely found to be a very effective
374 *fight* response (Lim, 2008; Miller and Denny, 2011; Marshall and Chua, 2012;
375 Seuront and Ng, 2016), and can reduce body temperatures by up to 6°C on hot, sunny,
376 days in some tropical littorinid species (Marshall and Chua, 2012). This reduction in
377 body temperature is achieved by reducing convective heat gain from the boundary
378 layer air, located 4 mm above the rock surface (Marshall and Chua, 2012). Marshall
379 and Chua (2012) further demonstrated that the thermal gradient in the boundary layer
380 air (a steep decrease in temperature just above the rock surface) may also act as a cue
381 to trigger standing behaviour in littorinids and, when this gradient was not present,
382 individuals did not show this behaviour. Marshall and Chua (2012) also reported
383 *sideways shell standing* (with the aperture being lifted perpendicularly to the surface,
384 but the shell not reaching a vertical or upright position) and proposed that this form of
385 standing resembles a special situation when the temperature gradient in the boundary
386 layer air was not steep enough to stimulate upright standing. If this is the case, the
387 shell lifting behaviour that Lim (2008) interpreted as an interrupted stage in the
388 process of standing may also be a result of heating without the formation of a steep
389 gradient of boundary layer air in windy conditions (Marshall and Chua, 2012). While

390 the magnitude of the temperature gradient of the boundary layer air appears to be the
391 stimulus for standing behaviour, it seems that there is also a thermal threshold to
392 trigger this behaviour in littorinids. *Austrolittorina unifasciata*, for example, only
393 performed standing behaviour when the rock surface temperature was greater than
394 35°C (Lim, 2008). A similar threshold has also been observed in *Echinolittorina*
395 *malaccana* and *E. radiata* which do not exhibit standing behaviour during cooler
396 months (Marshall and Chua, 2012; Seuront and Ng, 2016).

397 *Towering* behaviour is also a thermoregulatory behaviour (Marshall et al., 2010a;
398 Seuront and Ng, 2016), which can reduce body temperature of individuals by up to
399 ~10°C in some tropical littorinids (Seuront and Ng, 2016). Similar to aggregation,
400 *towering* has been suggested to be an end product of trail following at benign
401 temperatures (Marshall et al., 2010a). Towers generally consist of two individuals, but
402 can include up to five snails (Seuront and Ng, 2016). In the case of towers with three
403 snails, for example, in *Echinolittorina malaccana*, the uppermost individuals were
404 found to have the lowest body temperatures but only slightly lower (~1°C) than those
405 of the middle individuals. Both the upper and middle individuals, however, had much
406 lower body temperatures than the basal individuals (3-6°C, Marshall et al., 2010a;
407 Seuront and Ng, 2016). Although the individuals at the uppermost position may
408 experience increased heating due to greater exposure to direct solar irradiance, they
409 also benefit from improved convective cooling, leading to an overall greater heat
410 reduction (Marshall et al., 2010a). Since towers with three or more snails are
411 generally rare in the field, Marshall et al. (2010a) suggested these towers might be
412 incidental rather than driven by selection. Two-snail towers are, however, not found in
413 cooler, winter months and their occurrence increases with higher temperatures (T.P.T.
414 Ng unpubl. data), supporting the role of this behaviour as a possible response to heat
415 stress. Interestingly, the size of snails consistently decreases from the bottom to the
416 top of a tower in >95% of the towers observed in *E. malaccana* and *E. radiata*,
417 respectively, and in 100% of heterospecific towers (Seuront and Ng, 2016), and a
418 similar pattern has been recorded in *Afrolittorina knysnaensis* (L. Seuront and T.P.T.
419 Ng unpubl. data; also see Fig. 1F). This pattern of having smaller individuals on the
420 top is likely associated with stability of the tower, as smaller individuals are unlikely
421 to be able to support individuals larger than themselves when their attachment to the
422 substratum is based on a thin layer of mucus holdfast.

423

424 **4. Incorporating littorinid thermoregulatory behaviours into a conceptual model**
425 **for thermal buffering**

426 The thermal buffering effect provided by various *flight* (thermal refuge selection) or
427 *fight* (foot retraction, aggregation, shell orientation, standing and towering)
428 behaviours in littorinids can be visualized by an individual-level conceptual model
429 (Fig. 2). In this model, *flight* behaviour refers to the selection of a more favourable
430 thermal environment (essentially rock surface temperature, as determined by direct
431 solar heating during aerial exposure), where individuals move to a shaded location
432 during warm periods and unshaded spots during cold periods (Fig. 3). Individuals that
433 join an aggregation or a tower, effectively modifying their local microclimate
434 independently of the solar effect on the rock surface, are classified as exhibiting *fight*
435 behaviour (Fig. 3). The effectiveness in thermoregulation of the *flight* and *fight*
436 behaviours can, however, be variable in time and space due to changes in a range of
437 abiotic and biotic factors (e.g. humidity and topographic features of the substratum,
438 Muñoz et al., 2005; Iacarella and Helmuth, 2011; Marshall and Chua, 2012;
439 individual body condition, Marshall and McQuaid, 2011; Marshall and Chua 2012;
440 and ontogeny, Jones and Boulding, 1999). This model can, however, be generalized to
441 other intertidal ectotherms; for example limpets, which also exhibit *flight* (thermal
442 refuge selection, Williams and Morritt, 1995) and *fight* (mushrooming, Garrity, 1984;
443 Williams et al., 2005) behavioural responses to thermal stress; and neritids which also
444 adopt thermal refuge selection and aggregation as thermoregulatory strategies (Garrity,
445 1984; Chapperon and Seuront, 2011a, 2012; Chapperon et al., 2013). Whilst most
446 predictions of climate change focus on increasing temperatures, the impacts of climate
447 change also involve changing weather patterns and extreme climatic events (Katz and
448 Brown, 1992; Easterling et al., 2000; Helmuth et al., 2014; Seabra et al., 2015). As
449 such, the model incorporates not only the scenario for warming but also for cooling.
450 In fact, behavioural thermoregulation can also be important to the viability of
451 littorinid species and other intertidal ectotherms during cold periods, especially in
452 temperate regions where cold stress can be severe (e.g. Crisp, 1964; Murphy and
453 Johnson, 1980; Sinclair et al., 2004; Wethey et al., 2011; Chapperon and Seuront,
454 2012; Firth et al., 2015).

455 The model (Fig. 2) is based on the fact that the body temperature (T_b) of an
456 individual littorinid snail, as in all ectotherms, is expected to be positively and closely
457 related to the realistic environmental temperature (T_e) (= rock surface temperature,

458 Marshall et al., 2010b) it experiences. The range between the upper lethal temperature
459 (ULT) and lower lethal temperature (LLT) determines the thermal conditions within
460 which an individual can survive (Somero, 2002, 2010; Huey et al., 2012; Marshall et
461 al., 2015). In the natural environment, under present day conditions, the body
462 temperature of living individuals can reach a maximum ($T_{b \max}$) below the ULT
463 (otherwise, if the body temperature exceeds the ULT, the individual will die) or a
464 minimum ($T_{b \min}$) above the LLT, and the difference between $T_{b \max}$ and ULT or
465 between $T_{b \min}$ and LLT represents the thermal safety margin (TSM, Marshall et al.,
466 2013, 2015). The TSM has been widely used to assess the resilience of a species to
467 climate change, although its definition varies in the literature (e.g. Deutsch et al. 2008;
468 Huey et al., 2009; Marshall et al., 2013, 2015; Sunday et al., 2014). The TSM can, for
469 example, also be derived from the difference between $T_{b \max}$ and heat coma
470 temperature (HCT), as HCT marks the induction of a heat shock response leading to
471 substantial elevation of resting energetic costs, which may cause lethal or sublethal
472 impacts during a single prolonged exposure event (Marshall et al., 2011, 2015). In fact,
473 ecological and evolutionary thermal limits may lie well within the bounds of ULT and
474 LLT, and many studies have highlighted that major negative consequences of climate
475 change may not result from increased exposure to lethal temperatures but from
476 sublethal effects such as energetic imbalances (Dillon et al. 2010; Woodin et al. 2013;
477 Deutsch et al. 2015). For simplicity, and clarity, we illustrate only ULT and LLT in the
478 model as these limits are direct indicators of the temperatures at which death occurs.

479 Under climate change, as environmental temperatures increase, the $T_{b \max}$ and T_b
480 $_{\min}$ of individuals will also be higher and, if the new $T_{b \max}$ reaches ULT, or the new T_b
481 $_{\min}$ reaches LLT, the individual can no longer survive under these new environmental
482 conditions. The width of the TSM, will, therefore, determine the vulnerability of an
483 individual to climate change, such that the wider the TSM, the less likely it will be of
484 $T_{b \max}$ or T_b $_{\min}$ reaching the ULT and LLT, respectively. TSM is likely to vary with
485 local environmental conditions, being narrower on very hot days and wider during
486 less stressful conditions. The estimation of TSM based on ULT and LLT at a given
487 time may, however, be incomplete in addressing species vulnerability to environment
488 change as these values, and, therefore, the TSM of an individual, can shift through
489 acclimation to local conditions (Stillman, 2003; Calosi et al., 2008; Somero, 2010).
490 The ULT of some species is, for example, higher in more stressful hot seasons as
491 compared to less stressful, cool seasons (e.g. *Echinolittorina malaccanna* and *E.*

492 *radiata*, G.A. Williams unpubl. data; Li, 2012; but see Araújo et al., 2013; Hoffmann
493 at al., 2013; Chapperon et al., 2016).

494 The major focus of the model (Fig. 2) is to demonstrate how bias in assessing T_b
495 $_{max}$ and T_b $_{min}$, by neglecting behavioural thermoregulation, may result in a poor
496 assessment of a species' TSM and hence erroneous predictions of species
497 vulnerability to climate change. Physiological studies often assume that intertidal
498 ectotherms would not survive when the maximum environmental temperature ($T_{e\ max}$)
499 recorded in the field exceeds the ULT of the species under predicted climate warming
500 scenarios (Stillman, 2003; Somero, 2010). These studies, therefore, infer $T_{e\ max}$ as T_b
501 $_{max}$, and, based on such an assumption, high shore ectotherms are suggested to already
502 live in environments where the T_b $_{max}$ is close to their ULTs under present day
503 conditions (Stillman, 2002, 2003). While this assumption may be true for some
504 intertidal species that rest in the shade (e.g. porcelain crabs, Stillman, 2002), the
505 model addresses a potential over-estimation of vulnerability in other species,
506 especially those that can invoke *flight* and/or *fight* behaviours. As such, the model
507 compares between hypothetical T_b $_{max}$ and T_b $_{min}$ as well as TSMs before (assuming
508 these values to be close to the species ULT or LLT) and after considering the buffering
509 effect of thermoregulatory behaviours and illustrates how *flight* or *fight* behaviours
510 can adjust the T_b $_{max}$ or T_b $_{min}$ of an individual to create a wider TSM, and, therefore,
511 enhance the potential for a species to survive when environmental temperatures are
512 close to their ULTs/LLTs.

513 While the differentiation between *flight* and *fight* behaviours provides a
514 mechanistic understanding of how these snails may thermoregulate, the mechanisms
515 that cause an individual to switch between these two types of behaviours under
516 changing temperatures remain unclear. Littornids exhibit both *flight* and *fight*
517 behaviours to cope with heat stress (Marshall and Chua, 2012; Marshall et al., 2013;
518 Seuront and Ng, 2016) but seem to adopt only *flight* behaviours when facing cold
519 stress (Soto and Bozinovic, 1998). Marshall et al. (2013) proposed that there is likely
520 a trade-off between the thermal benefit of thermal refuge selection and the cost of
521 evaporative water loss incurred by moving to a refuge under higher temperatures; and
522 therefore an individual may choose to perform *fight* (e.g. standing) rather than *flight*
523 behaviours on sun-exposed rock surfaces when conserving water becomes especially
524 important. In fact, in fast moving species such as crabs which are expected to have a
525 lower cost of water loss when searching for thermal refuges, *flight* behaviour seems to

526 be a dominant thermoregulatory strategy (Navarrete and Castilla, 1990), whereas
527 sessile species are only limited to the use of *flight* behaviours such as gaping in
528 mussels (Nicastro et al. 2010). The classification of *flight* and *fight* behaviours,
529 therefore, reveals a spectrum of strategies from pure *flight* strategists to pure *fight*
530 strategists, and can provide a better mechanistic understanding of why different
531 groups of intertidal ectotherms utilize different microhabitats under aerial exposure
532 (i.e. fast moving *flight* strategists are found mainly in shaded microhabitats such as
533 spaces beneath rocks, whereas slow moving mixed (*flight* and *fight*) strategists can be
534 found in both shaded and sun-exposed habitats such as bare rock and crevices).

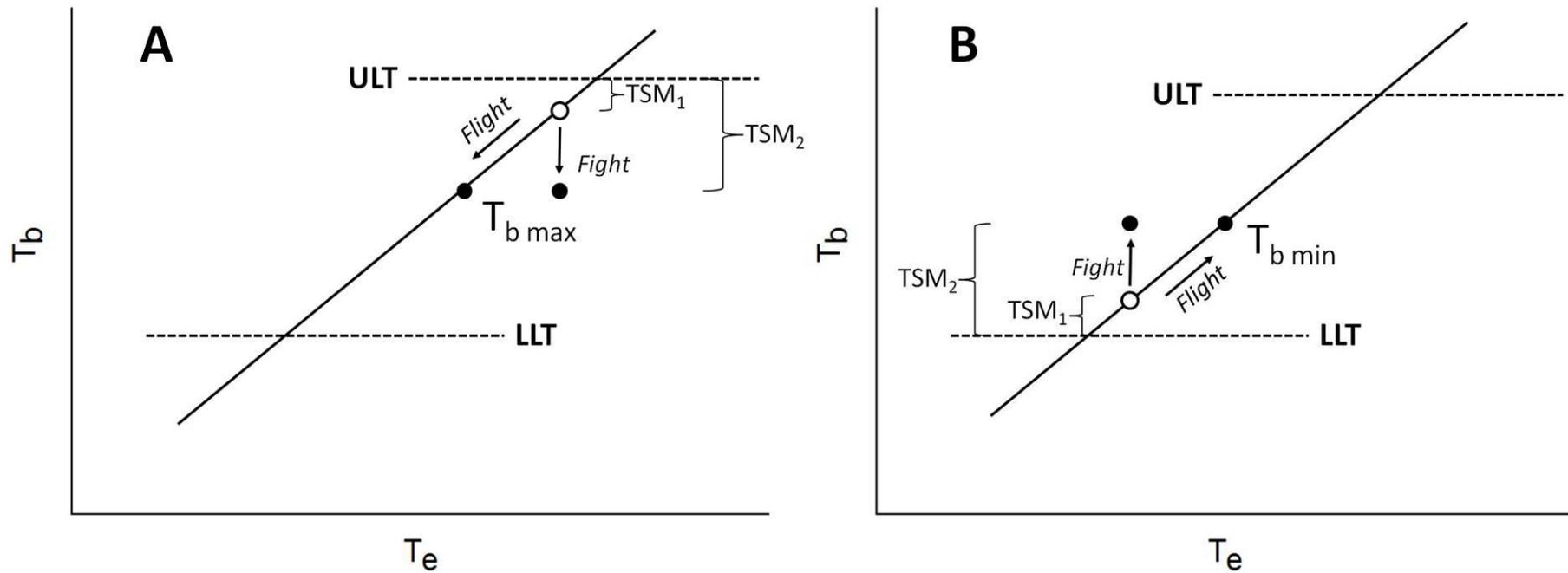
535 An example of incorporating *flight* and *fight* behaviours in assessing $T_{b\ max}$ and
536 TSM is demonstrated in two high shore littorinids: *Echinolittorina malaccana* and *E.*
537 *radiata*, in Hong Kong (Fig. 4). The T_b of these littorinids is positively and tightly
538 correlated with T_e , and no significant difference between the T_e and T_b of individuals
539 was found on the shore when no *shell standing* and *towering* was exhibited by the two
540 species in the winter (Seuront and Ng, 2016). T_e can, however, readily exceed 50°C
541 during midday low tides (max. T_e recorded = 59°C, T.P.T. Ng unpubl. data), and can
542 exceed the ULTs of the two species (in terms of LT50, the temperature at which 50%
543 mortality of individuals occurs and which is commonly used as an indicator of ULT,
544 Somero, 2010, Fig. 4). If behavioural thermoregulation is not considered in these two
545 species in the summer months, and assuming T_b equals T_e , as in the winter,
546 individuals of the two species should have already experienced a T_b which exceeds
547 their ULTs and so should be dead. The *flight* (thermal refuge selection) and *fight*
548 behaviours (foot retraction, standing and towering) exhibited by the two species,
549 however, allow them to maintain their T_b below their ULTs and hence maintain an
550 effective TSM in the hot summer season of Hong Kong (Fig. 4). In fact, these
551 thermoregulatory behaviours allow most individuals to maintain their T_b within a
552 range of preferred body temperatures (in this example between 42 and 46°C).
553 Marshall et al. (2013) showed that *E. malaccana* in Brunei are able to exhibit
554 temperature-insensitive aerobic metabolism (TIM) at 35-46°C to lower energetic costs
555 under heat stress, but organismal energy homeostasis is disrupted beyond 46 °C. The
556 two species, by keeping T_b at or below 46°C, may, therefore, be adopting a strategy to
557 avoid sublethal physiological damage under heat stress.

558 To our knowledge, mass mortalities of littorinids have not been reported although
559 T_e in tropical regions often exceeds the upper thermal limits of species (T.P.T. Ng and

560 G.A. Williams unpubl. data), suggesting that the behaviours described and illustrated
561 in the conceptual model can provide a buffering effect to extreme warming (Marshall
562 et al., 2011, 2013, 2015). These snails also appear less vulnerable to climate change as
563 compared to other, lower shore, gastropod species such as limpets and topshells that
564 experience heavy mortality events in the summer on tropical shores such as in Hong
565 Kong (Williams and Morritt, 1995; Williams et al., 2005; Firth and Williams, 2009;
566 G.A. Williams unpubl. data). These observations are, therefore, contradictory to the
567 predictions that high shore species are more vulnerable to climate change based on
568 physiological studies (Stillman, 2002, 2003). Whilst high shore species may indeed
569 live closer to their ULT than their lower shore counterparts (Stillman, 2002, 2003);
570 they may have evolved a greater repertoire of adaptive mechanisms; including
571 behavioural thermoregulation, which has resulted in wider TSMs as compared to
572 lower shore species.

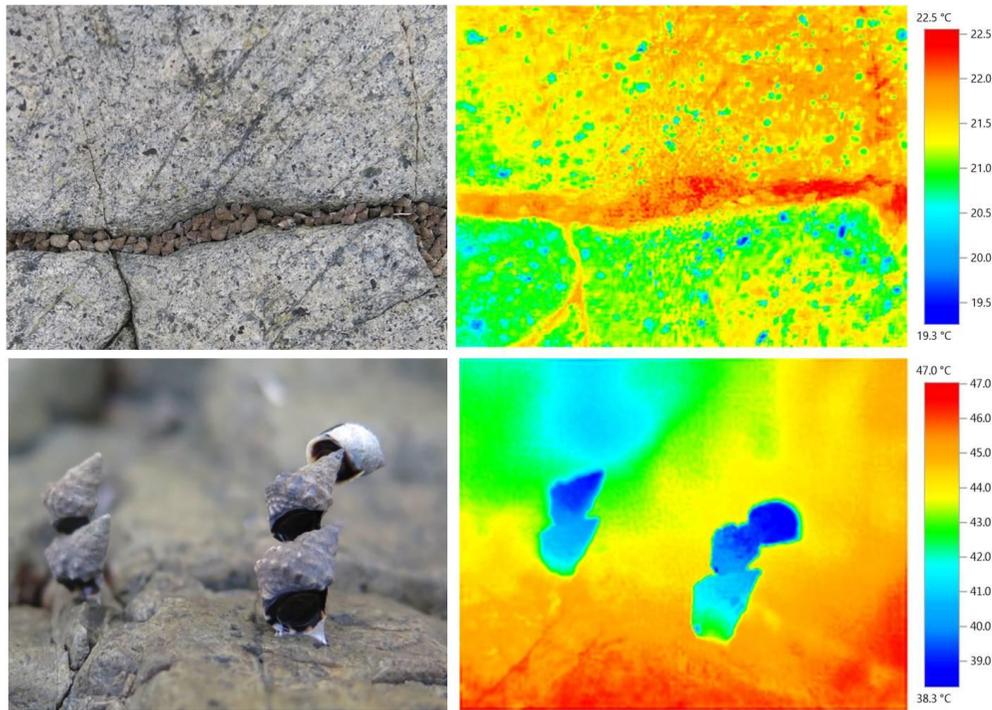
573 Whilst the various thermoregulatory behaviours may seem advantageous from the
574 view of individual survival, an aspect that is not incorporated in the model is the
575 trade-off between these behaviours and other fitness associated activities (e.g.
576 foraging and mating) and the resultant longer-term fitness consequences (see
577 Gunderson and Leal, 2015). In other words, behaviours associated with
578 thermoregulation, which may be vital for survival, may potentially lead to sublethal
579 fitness costs by reducing time or energy budgets for growth or reproduction. For
580 example, Jones and Boulding (1999) experimentally compared activity patterns of
581 *Littorina sitkana* between cool and warm days and showed that snails foraged for
582 shorter periods before selecting a refuge microhabitat (where they would remain
583 inactive) on warm days. This study, therefore, showed that littorinids may be able to
584 minimise energetic costs associated with heat stress through thermal refuge selection
585 (as illustrated by the conceptual model), but this may, as a consequence, reduce
586 energy gain by limiting foraging time. Other studies, although not directly
587 investigating activity patterns associated with thermoregulation, generally show that
588 littorinids adjust their activity patterns in response to environmental conditions,
589 suggesting a trade-off between fitness associated activities (Mak, 1996; Lee and
590 Williams, 2002). For example, under conditions of severe heat and desiccation
591 stresses, some littorinids maintain their thermoregulatory behaviours (i.e. will remain
592 inactive in the standing posture) for many days without foraging (Marshall et al.,
593 2013). Some tropical species also shift their distribution downshore in summer

594 months (Mak, 1996), suggesting a strategy to utilize the mid shore barnacles as
595 refuges to mitigate heat stress under warmer conditions, or at least reduce the time
596 emersed (Harper and Williams, 2001; Cartwright and Williams, 2012). Lee and
597 Williams (2002) also showed that some mangrove littorinids foraged more during the
598 night, but spent more time with their foot retracted when environmental temperatures
599 were higher during day time. Such flexibility in adjusting activity patterns is also
600 common in other intertidal ectotherms (e.g. limpets, Little and Stirling, 1985; whelks,
601 Moran, 1985; Burrows and Hughes, 1989). More quantitative studies are, therefore,
602 needed to examine the association between behaviour and physiology from the view
603 of activity time / energy budgets, and hence to better understand the sublethal impacts
604 of climate change on the life history strategies of intertidal ectotherms.



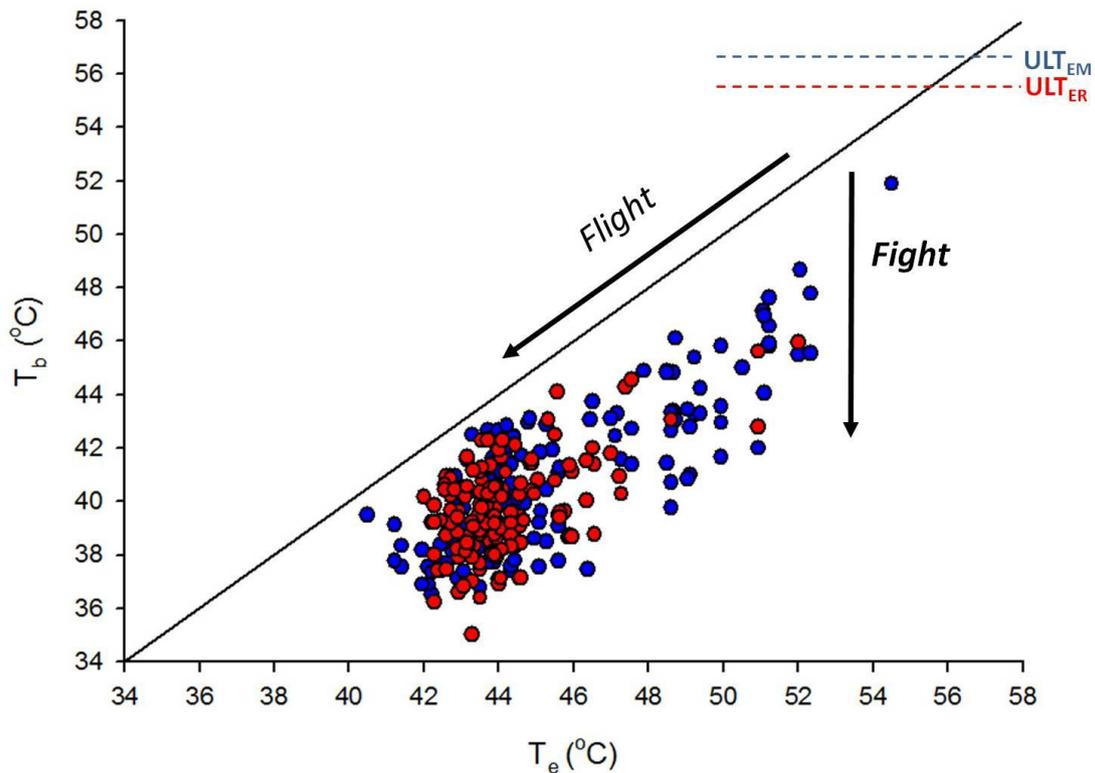
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606 **Fig. 2.** A conceptual model to illustrate potential differences in individual vulnerability to climate change based on thermal safety margins (TSM)
 607 with and without considering thermoregulatory behaviours. TSM is measured as (A) difference between $T_{b \max}$ and upper lethal temperature
 608 (ULT); or (B) difference between or $T_{b \min}$ and lower lethal temperature (LLT). TSM incorporating thermoregulatory behaviours (TSM₁) is wider
 609 than that without thermoregulatory behaviours (TSM₂). Circles represent the maximum or minimum body temperature ($T_{b \max}$ or $T_{b \min}$) before (○)
 610 and after (●) considering *flight* and *fight* thermoregulatory behaviours. The solid line represents theoretical relationship between environmental
 611 (T_e) and body temperatures (T_b) of the individual.



612
613

614 **Fig. 3.** An illustration of *flight* and *fight* behaviours in littorinids . Upper panel demonstrates a *flight* behaviour where *Echinolittorina malaccana*
615 and *E. radiata* select a thermal refuge with higher temperatures (T_e) than surrounding habitats in the cooler winter period to maintain their T_b
616 (taken on a sunny day, 19th January 2016). Lower panel shows a *fight* behaviour where the two species enhance convective cooling (i.e. reduce
617 their T_b from the T_e of the habitat they are in) by forming towers (conspecific *E. malaccana* tower on the left and heterospecific tower on the
618 right with *E. radiata* on the top) in the summer (taken on a sunny day, 5th August 2014; recaptured from Seuront and Ng, 2016) Thermal images
619 were taken with Testo 875-1iSR (thermal sensitivity < 0.05°C, Testo AG, Germany) in Cape d' Aguilar, Hong Kong.



620
621

622 **Fig. 4.** An example (modified from Seuront and Ng, 2016) of incorporating *flight* and
 623 *fight* behaviours in assessing TSM for *Echinolittorina malaccana* (EM, blue circles)
 624 and *E. radiata* (ER, red circles). Data were taken during low tide at ~1500-1600 on
 625 5th August 2014 (summer) in Cape d' Aguilar, Hong Kong. Upper lethal temperatures
 626 (ULTs) of the two species in terms of lethal temperatures in summer (LT50; EM:
 627 56.8°C; ER: 55.7°C, average from G.A. Williams unpubl. data and Li, 2012) are
 628 indicated by the dashed lines. Despite the fact that rock surface temperatures (T_e)
 629 readily exceeded 50°C during the survey period, individuals of the two species mostly
 630 experienced T_e below this temperature, which indicates thermoregulation through
 631 *flight* behaviour. In general, T_b were lower (average 4.4°C, maximum 10.3°C) than T_e
 632 which indicates thermoregulation through *fight* behaviours (foot retraction, standing
 633 and towering). Maximum body temperatures ($T_{b\ max}$) of *E. malaccana* and *E. radiata*
 634 were 51.9°C and 45.9°C, and hence the thermal safety margins (TSMs) of the two
 635 species were 4.9°C and 9.8°C respectively.
 636

637 **5. Concluding remarks**

638 While behavioural buffering is clearly important for organisms living in intertidal
639 habitats that have a great degree of small-scale spatial and temporal variability in
640 environmental temperatures (Helmuth et al., 2006a,b; Marshall et al., 2010b; Denny et
641 al., 2011), the importance of behavioural responses of organisms remains relatively
642 unexplored in climate change studies. This synthesis, using littorinid snails as a case
643 study, demonstrates that behaviour is an important, though largely overlooked,
644 component which should be included into predictive models of the responses of
645 species to climate change. Predictions based solely on morphological properties or
646 physiological limits of ectotherms, without considering the capacity for behavioural
647 thermoregulation, may result in over-estimates of the negative impacts of extreme
648 climatic events associated with longer-term climate change. The need to incorporate
649 behavioural responses into studies addressing the responses of ectotherms has been
650 previously highlighted (Huey and Tewksbury, 2009; Kearney et al., 2009). The simple,
651 conceptual model that we illustrate, however, provides a framework for understanding
652 those behaviours in the form of *flight* and/or *fight* responses and for integrating these
653 behaviours with other, more traditionally invoked mechanisms when trying to predict
654 how intertidal ectotherms may respond to climate change. Distinguishing between
655 *flight* and *fight* behaviours also allows a mechanistic understanding of different
656 thermoregulation processes in intertidal ectotherms. Although we emphasize mainly
657 the importance of behavioural strategies in this synthesis, we believe that future
658 studies should adopt an integrated approach, that distinguishes between *flight* and
659 *fight* behaviours, in addition to an array of other components including morphology
660 and physiology, potential for acclimation and genetic adaptation, as well as species
661 interactions (Kearney et al., 2009; Harley et al., 2011; Huey et al., 2012), to generate a
662 better picture of how species may respond to climate change. Such an approach would
663 generate an improved, mechanistic, understanding of intra- and inter-specific
664 variations in response to both sublethal and lethal stresses which, ultimately, will help
665 scientists better predict which species will be winners and losers under future climate
666 change scenarios.

667

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674

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