Usage guidelines

1 **Linking behaviour and climate change in intertidal ectotherms: insights from**
2 **littorinid snails**
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4 Terence P.T. Ng[a], Sarah L.Y. Lau[a], Laurent Seuront[b], Mark S. Davies[c], Richard
5 Stafford[d], David J. Marshall[e], Gray A.Williams[a*]
6

7 [a] The Swire Institute of Marine Science and School of Biological Sciences, The
8 University of Hong Kong, Pokfulam Road, Hong Kong SAR, China
9 [b] Centre National de la Recherche Scientifique, Laboratoire d'Oceanologie et de
10 Geosciences, UMR LOG 8187, 28 Avenue Foch, BP 80, 62930 Wimereux, France
11 [c] Faculty of Applied Sciences, University of Sunderland, Sunderland, U.K.
12 [d] Faculty of Science and Technology, Bournemouth University, U.K.
13 [e] Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam,
14 Gadong BE1410, Brunei Darussalam
15

16 Corresponding author: The Swire Institute of Marine Science, The University of Hong
17 Kong, Cape d' Aguilar, Shek O, Hong Kong; hrsbwga@hku.hk (G.A. Williams)
18

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

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

1. Introduction

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

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

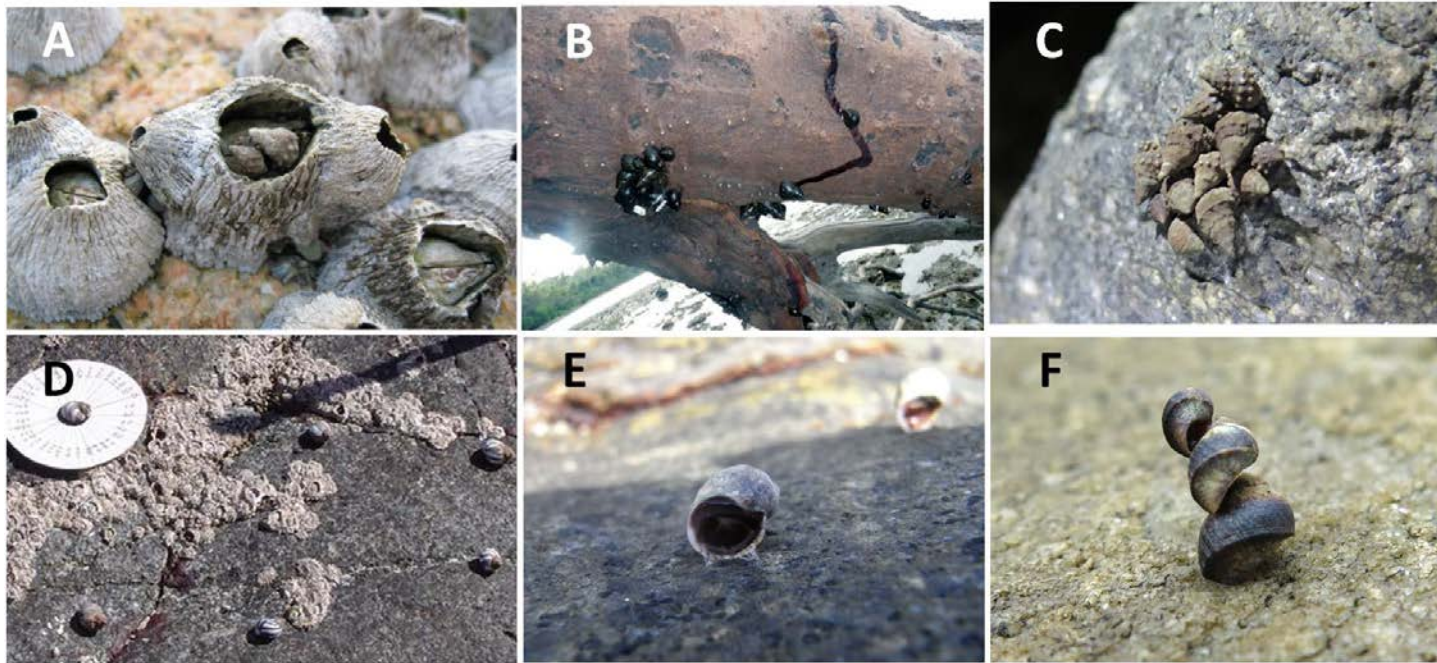122 Anestis et al., 2007; Nicastro et al., 2010).

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

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

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

144 * Species found in different habitats are indicated: rocky shore [1], mangrove [2] and salt marsh [3].

Fig. 1 Examples of thermoregulatory behaviours associated with thermal and/or desiccation stresses in littorinids. (A) thermal refuge selection (barnacle test) in *Echinolittorina malaccana*; (B) thermal refuge selection (underside of the roots of mangrove trees) in *Littoraria scabra*; (C) aggregation in *Echinolittorina malaccana* and *E. radiata*; (D) shell orientation in *Echinolittorina peruviana*; (E) standing in *Echinolittorina 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 F. Bozinovic (D); M.S. Davies (E); and T.P.T. Ng (F).

2. Experimental approaches

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

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

205   Britton, 1985; Britton and McMahon, 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; McMahon, 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

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

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

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

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

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

The model (Fig. 2) is based on the fact that the body temperature (T_b) of an individual littorinid snail, as in all ectotherms, is expected to be positively and closely 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 $T_{b\,min}$

480   of individuals will also be higher and, if the new $T_{b\,max}$ reaches ULT, or the new $T_{b\,min}$

481   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 invike *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 *fight* 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 ^{o}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.
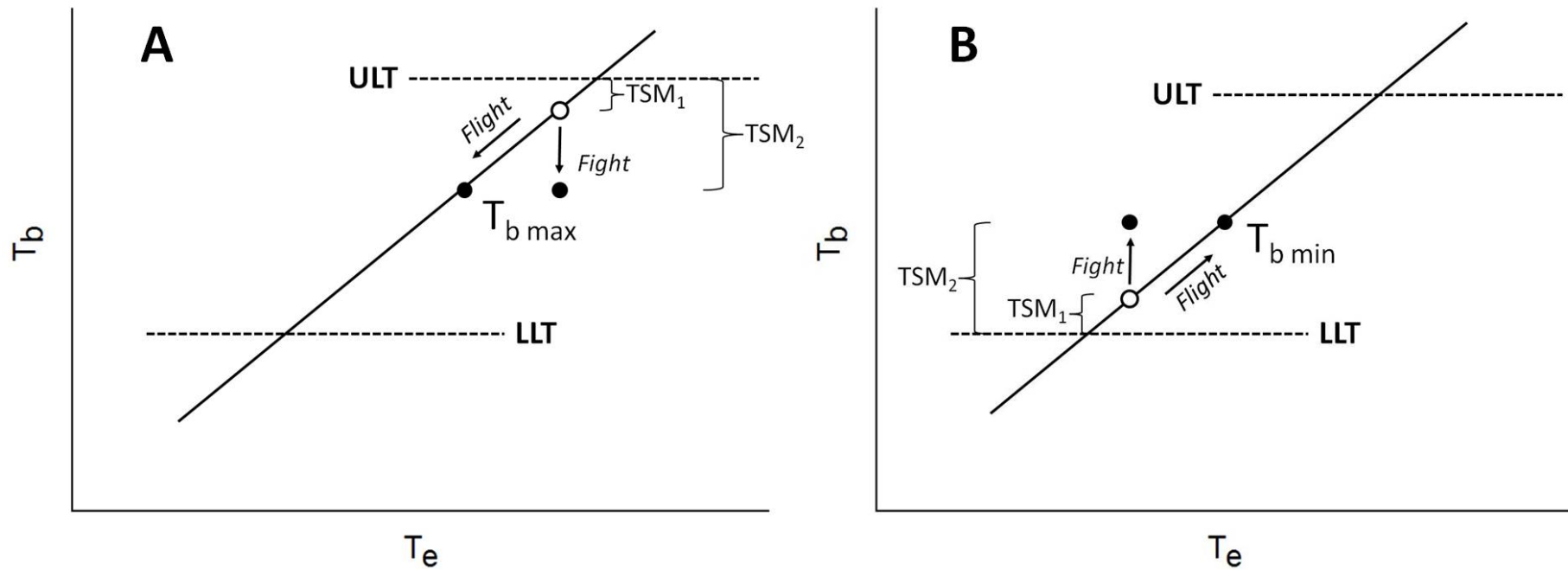
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606 **Fig. 2.** A conceptual model to illustrate potential differences in individual vulnerability to climate change based on thermal safety margins (TSM)

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 (TSM_1) is wider

609 than that without thermoregulatory behaviours (TSM_2). Circles represent the maximum or minimum body temperature ($T_{b\ max}$ or $T_{b\ min}$) before ($\circ$)

610 and after ($\bullet$) 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.

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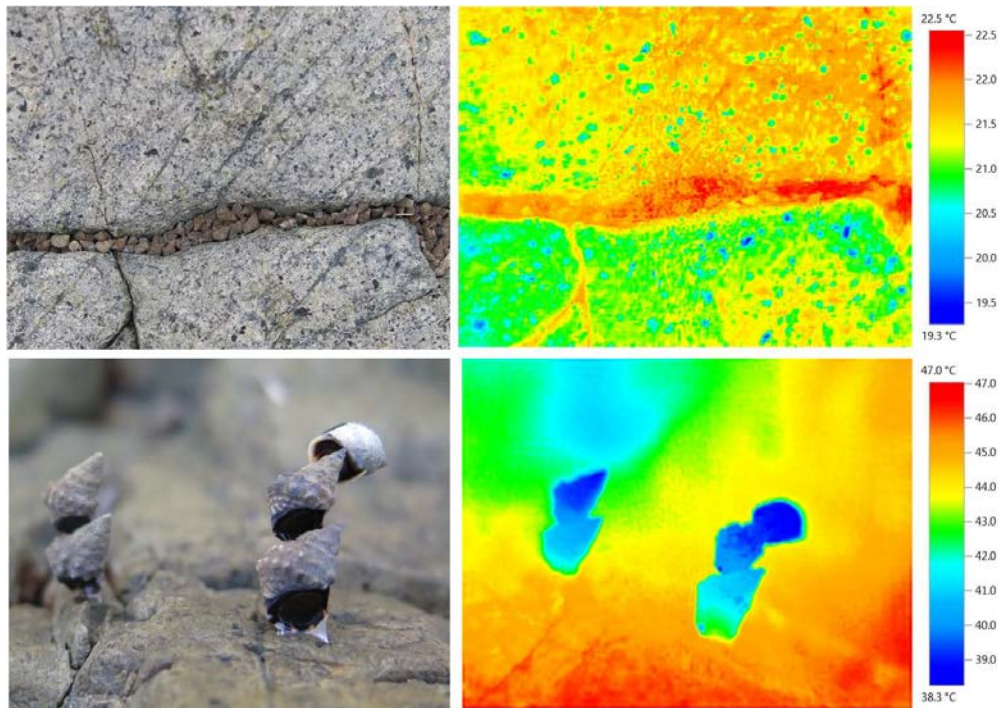
Fig. 3. An illustration of *flight* and *fight* behaviours in littorinids . Upper panel demonstrates a *flight* behaviour where *Echinolittorina malaccana* and *E. radiata* select a thermal refuge with higher temperatures (T_e) than surrounding habitats in the cooler winter period to maintain their T_b (taken on a sunny day, 19th January 2016). Lower panel shows a *fight* behaviour where the two species enhance convective cooling (i.e. reduce 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 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 were taken with Testo 875-1iSR (thermal sensitivity < 0.05°C, Testo AG, Germany) in Cape d' Aguilar, Hong Kong.
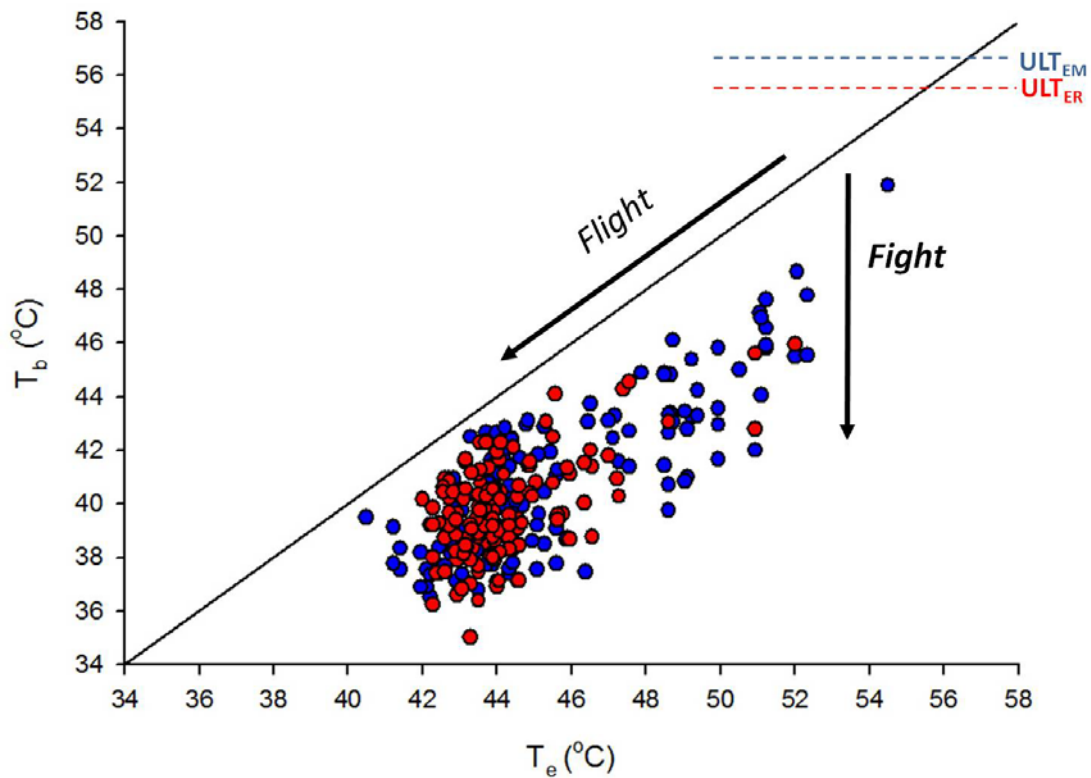
Fig. 4. An example (modified from Seuront and Ng, 2016) of incorporating *flight* and *fight* behaviours in assessing TSM for *Echinolittorina malaccana* (EM, blue circles) and *E. radiata* (ER, red circles). Data were taken during low tide at ~1500-1600 on 5th August 2014 (summer) in Cape d' Aguilar, Hong Kong. Upper lethal temperatures (ULTs) of the two species in terms of lethal temperatures in summer (LT50; EM: 56.8°C; ER: 55.7°C, average from G.A. Williams unpubl. data and Li, 2012) are indicated by the dashed lines. Despite the fact that rock surface temperatures (T_e) readily exceeded 50°C during the survey period, individuals of the two species mostly experienced T_e below this temperature, which indicates thermoregulation through *flight* behaviour. In general, T_b were lower (average 4.4°C, maximum 10.3°C) than T_e which indicates thermoregulation through *fight* behaviours (foot retraction, standing and towering). Maximum body temperatures ($T_{b\ max}$) of *E. malaccana* and *E. radiata* were 51.9°C and 45.9°C, and hence the thermal safety margins (TSMs) of the two species were 4.9°C and 9.8°C respectively.

5. Concluding remarks

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

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