



## Linking behaviour and climate change in intertidal ectotherms: insights from littorinid snails



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### ABSTRACT

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

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### 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; Mieszowska et al., 2014; Sinclair et al., 2016) 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 in climate change studies but is increasingly gaining attention (Wichmann et al., 2004; Huey and Tewksbury, 2009; Sih et al., 2010; Huey et al., 2012; Sunday et al., 2014; MacLean et al., 2016).

A few studies (e.g. Wichmann et al., 2004; Kearney et al., 2009) have, however, incorporated the behavioural repertoires of species into predictive models of climate change. Kearney et al. (2009), for example, demonstrated that predictions of lizard body temperatures were

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substantially altered by considering behavioural buffering through selection of shaded areas. Behavioural buffering of thermal environments is, indeed, crucial for ectotherms which rely on external heat sources to regulate their body temperatures to maintain physiological homeostasis (Deutsch et al., 2008; Kearney et al., 2009; Somero, 2010). Such behavioural buffering effects can best be achieved in thermally heterogeneous environments where animals have more opportunities to flee or hide from unfavourable thermal conditions (Huey and Tewksbury, 2009; Huey et al., 2012; Sunday et al., 2014). The role of behavioural buffering associated with temperature is, however, likely to vary between species, with particular environments and especially across latitudes (Deutsch et al., 2008; Huey and Tewksbury, 2009). For temperate ectotherms, that generally occupy environments cooler than their thermal optimum, getting warmer is the priority, whereas staying cool is the goal for many tropical ectotherms living in environments which may exceed their thermal optimum (Stillman, 2003; Deutsch et al., 2008; Tewksbury et al., 2008; Somero, 2010).

Behavioural buffering is especially important in intertidal systems, which are thermally heterogeneous over very small spatial and temporal scales (Williams and Morritt, 1995; Helmuth et al., 2006a, 2006b; Denny et al., 2011; Seabra et al., 2011; Lathlean et al., 2015; Stafford et al., 2015). Being at the margins of the terrestrial and marine realms, intertidal ectotherms are subject to environmental challenges posed by both aquatic and aerial climatic regimes (Helmuth et al., 2006a; Morritt et al., 2007; Firth and Williams, 2009; Little et al., 2009; Williams et al., 2011). Particularly, high-shore marine species living close to the upper limit of the intertidal zone often persist in what are essentially terrestrial conditions for hours, days or even weeks (Finke et al., 2009; Uglow and Williams, 2001; Marshall et al., 2010b; Marshall and McQuaid, 2011). Physiological studies suggest that intertidal ectotherms are particularly vulnerable to climate change because many of them are already living close to their physiological limits (Somero, 2002, 2010; Lima et al., 2016). As such, any changes of these ectotherms at population levels (e.g. in mortality or distribution patterns) and consequent community level changes may be seen as early warnings of the impacts of climate change (Southward et al., 1995; Helmuth, 1998; Helmuth et al., 2002; Harley and Helmuth, 2003; Somero, 2010).

Some studies have, in particular, suggested that high shore species generally have higher heat tolerance but limited acclimation capacity, and hence high shore species are most susceptible to environmental warming (Stillman, 2002, 2003). This generalization is, however, largely based on the physiological response of a single genus (*Petrolisthes*), and it is unclear how much the negative impacts of climate change can be buffered by behavioural responses in intertidal ectotherms. Although intertidal habitats are among the most experimentally examined systems in the context of ecological impacts of climate change (reviewed by Helmuth et al., 2006a), it is noticeable that few previous studies have considered the importance of animal behaviour in buffering these potential impacts (e.g. 1054 publications contain both *climate change* and *intertidal* in their topic but only 101 contain all of the keywords *climate change*, *behaviour* (*behavior*) and *intertidal*; Web of Science: accessed April 23, 2016). There is, nevertheless, increasing evidence that behavioural thermoregulation may indeed play an important role in buffering the impacts brought by increasing temperature on intertidal ectotherms not only in mobile (e.g. McQuaid and Scherman, 1988; Williams et al., 2005; Chapperon and Seuront, 2011a, 2011b; Marshall et al., 2010a, 2011; Seuront and Ng, 2016) but also in sessile species (e.g. Anestis et al., 2007; Nicastro et al., 2010).

This synthesis addresses this knowledge gap by investigating the importance of behavioural thermoregulation in intertidal invertebrates using littorinid gastropods as a case study. These snails are suitable models to address this knowledge gap because (i) they are common herbivores found in almost all intertidal habitats with a near panglobal distribution (Reid, 1989; McQuaid, 1996a, 1996b); (ii) they generally live at higher shore levels and may, therefore, already live close to

their physiological limits as other high shore species (e.g. Somero, 2002, 2010, 2012; Stillman, 2002); and finally (iii) they display a wide range of thermoregulatory behaviours (Table 1; Fig. 1). Firstly, we outline the general experimental approaches that have been used to study thermoregulatory behaviours in littorinids and provide a summary of current findings of potential thermoregulatory behaviours in these snails. We then discuss some of these behaviours in terms of desiccation mitigation, since thermal and desiccation stresses are both tightly associated with environmental temperatures in intertidal habitats (Tomanek and Helmuth, 2002; Helmuth et al., 2006a). Finally, we introduce a simple, conceptual model based on our findings to illustrate how behavioural thermoregulation in terms of *flight* and *fight* responses can provide a buffering effect to both increasing and decreasing environmental temperatures, and highlight the need to integrate behavioural components into predictive models of species responses to climate change.

## 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; Harley, 2008; Denny et al., 2011; Seabra et al., 2011; Lathlean et al., 2016). 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, 2015; Iacarella and Helmuth, 2011; Miller and Denny, 2011). 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, 2011; Marshall and Chua, 2012). Since shell temperatures appear a reliable proxy of body or mantle temperatures in intertidal snails (Caddy-Retalic et al., 2011), some studies have simply compared the difference between shell temperatures and surrounding rock surface temperatures under different behavioural responses of littorinids using either digital thermometers (e.g. Lang et al., 1998; Soto and Bozinovic, 1998; Lim, 2008) or infrared imagery (e.g. Chapperon and Seuront, 2011a; Seuront and Ng, 2016). In particular, the use of infrared imagery has gained popularity since it allows numerous temperature measurements over a relatively short

**Table 1**

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

Behaviour	Species <sup>a</sup>	Location	Reference	
Foot retraction	<i>Afrolittorina africana</i> <sup>1</sup>	South Africa	McQuaid and Scherman (1988)	
	<i>Austrolittorina unifasciata</i> <sup>1</sup>	Vancouver Peninsula, Western Australia	McMahon (1990)	
	<i>Bembicium vittatum</i> <sup>1</sup>	Vancouver Peninsula, Western Australia	McMahon (1990)	
	<i>Echinolittorina natalensis</i> <sup>1</sup>	Natal region, South Africa	Miller and Denny (2011)	
	<i>Littoraria carinifera</i> <sup>2</sup>	Kampong Kranji, Singapore	Vermeij (1971b)	
	<i>Littoraria coccinea</i> <sup>1</sup>	Guam, U.S.	Vermeij (1971b)	
	<i>Littoraria irrorata</i> <sup>3</sup>	South Carolina, U.S.	Iacarella and Helmuth (2011)	
	<i>Littoraria melanostoma</i> <sup>2</sup>	Kampong Kranji, Singapore	Vermeij (1971b)	
	<i>Littoraria pintado</i> <sup>1</sup>	Oahu, U.S.	Vermeij (1971b)	
	<i>Littoraria scabra</i> <sup>1,2</sup>	Oahu and Guam, U.S.	Vermeij (1971b)	
		Western Caroline Islands, Palau		
		Jalan Loyang Besar and Kampong Kranji, Singapore		
		<i>Littoraria undulata</i> <sup>1</sup>	Koror, Palau	Vermeij (1971b)
		<i>Littorina keanae</i> <sup>1</sup>	California, U.S.	Miller and Denny (2011)
		<i>Littorina plena</i> <sup>1</sup>	Washington, U.S.	Miller and Denny (2011)
		<i>Littorina scutulata</i> <sup>1</sup>	California, U.S.	Miller and Denny (2011)
		<i>Littorina sitkana</i> <sup>1</sup>	Washington, U.S.	Miller and Denny (2011)
	Thermal refuge selection	<i>Afrolittorina africana</i> <sup>1</sup>	South Africa	McQuaid and Scherman (1988)
		<i>Echinolittorina malaccana</i> <sup>1</sup>	Hong Kong, China	Cartwright and Williams (2012)
		Jerudong, Brunei Darussalam	Marshall et al. (2013)	
		<i>Echinolittorina peruviana</i> <sup>1</sup>	Las Cruces, central Chile	Soto and Bozinovic (1998)
		<i>Echinolittorina vidua</i> <sup>1</sup>	Hong Kong, China	Cartwright and Williams (2012)
		<i>Littoraria irrorata</i> <sup>3</sup>	South Carolina, U.S.	Iacarella and Helmuth (2011)
		<i>Littoraria scabra</i> <sup>2</sup>	Tailevu, Fiji	Chappon and Seuront (2011a)
		<i>Littorina aspera</i> <sup>1</sup>	Flamenco, Culebra, and Naos Islands, Panama	Garrity (1984)
		<i>Littorina modesta</i> <sup>1</sup>	Flamenco, Culebra, and Naos Islands, Panama	Garrity (1984)
		<i>Littorina sitkana</i> <sup>1</sup>	Vancouver Island, Canada	Jones and Boulding (1999)
Aggregation	<i>Echinolittorina peruviana</i> <sup>1</sup>	Las Cruces, central Chile	Muñoz et al. (2008), Rojas et al. (2013)	
	<i>Littorina saxatilis</i> <sup>1</sup>	North-east England, U.K.	Stafford and Davies (2004)	
	<i>Melarhaphe neritoides</i> <sup>1</sup>	North-east England, U.K.	Stafford and Davies (2004)	
	<i>Nodilittorina unifasciata</i> <sup>1</sup>	New South Wales, Australia	Chapman and Underwood (1996)	
	Shell orientation	<i>Echinolittorina peruviana</i> <sup>1</sup>	Las Cruces, central Chile	Muñoz et al. (2005)
<i>Littorina aspera</i> <sup>1</sup>		Flamenco, Culebra, and Naos Islands, Panama	Garrity (1984)	
<i>Littorina modesta</i> <sup>1</sup>		Flamenco, Culebra, and Naos Islands, Panama	Garrity (1984)	
Shell posturing	<i>Austrolittorina unifasciata</i> <sup>1</sup>	Queensland, Australia	Lim (2008)	
	<i>Echinolittorina malaccana</i> <sup>1</sup>	Hong Kong, China	Seuront and Ng (2016)	
		Jerudong, Brunei Darussalam	Marshall et al. (2010a), Marshall and Chua (2012)	
		<i>Echinolittorina natalensis</i> <sup>1</sup>	Natal region, South Africa	Miller and Denny (2011)
		<i>Echinolittorina radiata</i> <sup>1</sup>	Hong Kong, China	Seuront and Ng (2016)
		<i>Littorina keanae</i> <sup>1</sup>	California, U.S.	Miller and Denny (2011)
		<i>Littorina plena</i> <sup>1</sup>	Washington, U.S.	Miller and Denny (2011)
		<i>Littorina scutulata</i> <sup>1</sup>	California, U.S.	Miller and Denny (2011)
		<i>Littorina sitkana</i> <sup>1</sup>	Washington, U.S.	Miller and Denny (2011)
		<i>Nodilittorina pyramidalis</i> <sup>1</sup>	Queensland, Australia	Lim (2008)

<sup>a</sup> Species found in different habitats are indicated: rocky shore <sup>1</sup>, mangrove <sup>2</sup> and salt marsh <sup>3</sup>.

period and with limited logistics, as compared with more traditional methods. Another advantage of infrared imagery is that it also provides non-invasive, simultaneous, measurements of both the body temperature of multiple snails and the thermal properties of their substrata at appropriate scales, whilst avoiding the possible physiological and behavioural consequences of inserting thermocouples into small organisms (reviewed by Lathlean and Seuront, 2014).

### 3. Potential thermoregulatory behaviours in littorinids

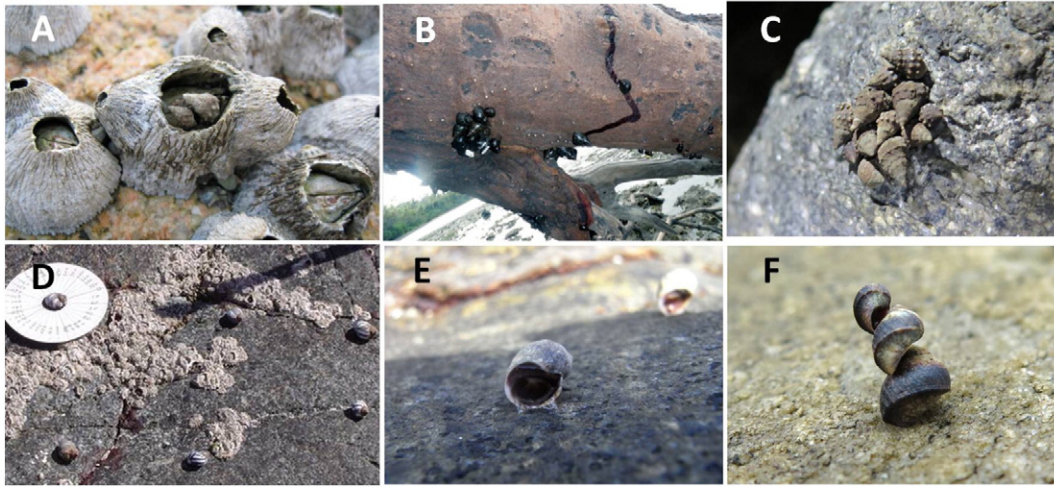
#### 3.1. Foot retraction

Littorinids typically glue their shell to the rock surface with mucus, retract their foot into the shell, and seal the operculum under prolonged or stressful aerial exposure (Bingham, 1972; Vermeij, 1971a, 1971b; Denny, 1984; Garrity, 1984; McMahon and Britton, 1985; Britton and McMahon, 1986). Some species may also leave an opening in the operculum after retracting their foot (termed “gaping”, Iacarella and Helmuth, 2011). The dehydrated mucus holdfasts at the tip of the outer aperture can be as little as 2–3 mm thick but provides adequate anchorage for littorinids to remain physically attached with no physical effort (Denny, 1984). Foot retraction and sealing the operculum, coupled with a mucus holdfast, minimizes heat flux through conduction by removing contact between the body tissue and the rock surface and

also limits water loss through evaporation, reducing both heat and desiccation stresses (Vermeij, 1971b; Britton, 1992; McMahon, 1990; Miller and Denny, 2011; Iacarella and Helmuth, 2011; Rojas et al., 2013). Foot retraction can, therefore, be viewed as a ‘fight’ response, where individuals modify their own thermal environment by adopting a posture. Miller and Denny (2011) showed that individuals of five littorinid species modelled with their foot withdrawn were, on average, 3–5 °C cooler than individuals with their foot attached to the substratum, and that this cooling effect was more pronounced in smaller species. Iacarella and Helmuth (2011), however, showed that the degree of evaporative cooling through foot retraction in littorinids was reduced under high humidity, suggesting that the thermoregulatory effect of this behaviour is context dependent.

Previous studies have found little propensity for lower shore gastropods to withdraw their foot into the shell and attach their shell to the rock with mucus (Vermeij, 1971b, 1973; McQuaid and Scherman, 1988). Foot retraction and mucus holdfast attachment minimizes evaporative water loss, allowing aerial survival for multiple days (Broekhuysen, 1940; Cleland and McMahon, 1986; Britton, 1995; Miller and Denny, 2011). *Echinolittorina malaccana* can, for example, remain inactive (or aestivating) with its foot withdrawn whilst emersed for >40 days (Marshall et al., 2013). Foot retraction behaviour may, however, introduce a trade-off in terms of a reduction in stability and attachment strength as individuals attached by mucus holdfasts can easily





**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).

be dislodged by waves (Miller, 1974; Denny, 1984; Ohgaki, 1988). Survival of dislodged individuals is, nevertheless, typically high, as the majority of dislodged individuals are able to navigate back to their preferred shore levels, suggesting a net selective benefit of this behaviour in littorinids (Evans, 1961; Bock and Johnson, 1967; Miller et al., 2007; Chapperon and Seuront, 2009).

### 3.2. Thermal refuge selection

Many studies have suggested that littorinids benefit from resting in cool habitats by selecting shaded refuges provided by irregularities in the rock surface, such as crevices (or pits); or being associated with sessile organisms such as macroalgae and barnacles (Soto and Bozinovic, 1998; Jones and Boulding, 1999; Cartwright and Williams, 2012; see Fig. 1A and B). Whilst foot retraction can be viewed as a *fight* response, thermal refuge selection resembles a *flight* response to heat stress as littorinids, like other mobile species, gain an advantage from selecting more optimal thermal conditions (Raffaelli and Hughes, 1978; McQuaid and Scherman, 1988; Chapperon and Seuront, 2011b; Chapperon et al., 2013). By selecting these refuges, littorinids gain the benefit of maintaining their body temperatures below their thermal limits (by up to ~11 °C in some situations) during warm periods (Marshall et al., 2013). It is, however, important to note that the amount of shading, and hence the effectiveness of mitigating thermal stress is highly context-dependent (Soto and Bozinovic, 1998; Jones and Boulding, 1999; Chapperon and Seuront, 2011a). For example, the bottom of mangrove roots provide a refuge to reduce heat stress for *Littoraria scabra* during the day but not at night (Chapperon and Seuront, 2011a); *Echinolittorina malaccana* and *E. vidua* only select barnacles as habitats to shelter within during the hot season in Hong Kong (Cartwright and Williams, 2012); and warmer rather than cooler refuges on the shore were preferred by *Echinolittorina peruviana* during cold periods (Soto and Bozinovic, 1998). Littorinids, therefore, select certain microhabitats to moderate body temperatures only at times when these microhabitats function as thermal refuges (e.g. depending on day, tide and season, Soto and Bozinovic, 1998; Jones and Boulding, 1999; Chapperon and Seuront, 2011a).

The preference for certain microhabitats may not, however, be solely associated with thermal stress but with other stressors such as predation and dislodgement risk (Vaughn and Fisher, 1988; Stafford and Davies, 2004; Loke et al., 2017—in this issue). For example, salt marsh littorinids migrate down the stalks of *Spartina* to rehydrate and then crawl back up the stalks to avoid predation (Vaughn and Fisher,

1988). Crevices appear to be more important refuges in winter than in summer for high shore littorinids in Hong Kong due to the overall stronger wave action at this time (T.P.T. Ng unpubl. data). In comparison to adults, juveniles of some species also tend to be restricted to microhabitats without any clear seasonal pattern (Jones and Boulding, 1999), suggesting that juveniles may be more sensitive to a multitude of environmental stressors. Selection of microhabitats is, therefore, a multifunctional behaviour and its effect on thermoregulation can potentially be masked by responses to other stressors.

### 3.3. Aggregation formation

Another multifunctional behaviour that is commonly found in littorinids is aggregation (Chapman, 1995, 1998; Chapman and Underwood, 1996; Stafford et al., 2012a, 2012b; see Fig. 1C). Aggregations in littorinids typically consist of fewer than a hundred individuals, but in extreme cases can involve up to thousands of individuals (Chapman, 1998). This behaviour has been suggested to reduce desiccation stress (e.g. Garrity, 1984; Rojas et al., 2000, 2013; Stafford et al., 2012a, 2012b), dislodgement (Feare, 1971; Raffaelli and Hughes, 1978; Stafford, 2002), and predation risk (Chapman, 1995; Stafford et al., 2007), as well as increasing the chance of copulation (Feare, 1971). The interplay between the multiple different potential causes of aggregation formation may explain why the occurrence and size of aggregations observed in littorinids are temporally and spatially highly variable (Chapman and Underwood, 1996; Chapman, 1998; Stafford and Davies, 2004), and often not correlated with increasing levels of heat and/or desiccation stresses (Chapman, 1995; Soto and Bozinovic, 1998; Rojas et al., 2000; Stafford, 2002; Stafford and Davies, 2004). Aggregation formation has also been suggested to be an emergent function of trail following or microhabitat selection (Chapman, 1995, 1998; Stafford et al., 2007), and computer simulations have demonstrated the vital role of trail following in driving the formation of aggregations (Stafford et al., 2007). Stafford et al. (2012b), however, caution that results from many empirical studies may be confounded as they generally compare water content between aggregated and solitary individuals without considering the time at which individuals joined the aggregations, or individual-level variation in relative hydration levels. As such, the true difference in desiccation stress between aggregated and solitary individuals can be masked by measurement error due to the 'background' variations in water content between individuals within the aggregations (Stafford et al., 2012b). In a recent study Rojas et al. (2013) showed that, in the laboratory, aggregated individuals of

*Echinolittorina peruviana* kept their opercula open for longer in response to desiccation stress than isolated individuals and hence could prolong gaseous exchange, suggesting a selective advantage to this behaviour.

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

### 3.4. Shell orientation

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

### 3.5. Shell posturing

Three shell postures have been suggested to be related to thermoregulation in littorinids and all are coupled with the foot retraction behaviour under aerial conditions mentioned above. Specifically, *shell lifting* (Lim, 2008) involves an individual slightly lifting its shell off the rock surface with its aperture parallel to the substratum; *shell standing* (Garritty, 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 (Garritty, 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). Whilst the magnitude of the temperature gradient of the boundary layer air appears to be the stimulus for standing behaviour, it seems that there is also a thermal threshold to trigger this behaviour in littorinids. *Austrolittorina unifasciata*, for example, only performed standing behaviour when the rock surface temperature was >35 °C (Lim, 2008). A similar threshold has also been observed in *Echinolittorina malaccana* and *E. radiata* which do not exhibit standing behaviour during cooler months (Marshall and Chua, 2012; Seuront and Ng, 2016).

*Towering* behaviour is also a thermoregulatory behaviour (Marshall et al., 2010a; Seuront and Ng, 2016), which can reduce body temperature of individuals by up to ~10 °C in some tropical littorinids (Seuront and Ng, 2016). Similar to aggregation, *towering* has been suggested to be an end product of trail following at benign temperatures (Marshall et al., 2010a). Towers generally consist of two individuals, but can include up to five snails (Seuront and Ng, 2016). In the case of towers with three snails, for example, in *Echinolittorina malaccana*, the uppermost individuals were found to have the lowest body temperatures but only slightly lower (~1 °C) than those of the middle individuals. Both the upper and middle individuals, however, had much lower body temperatures than the basal individuals (3–6 °C, Marshall et al., 2010a; Seuront and Ng, 2016). Although the individuals at the uppermost position may experience increased heating due to greater exposure to direct solar irradiance, they also benefit from improved convective cooling, leading to an overall greater heat reduction (Marshall et al., 2010a). Since towers with three or more snails are generally rare in the field, Marshall et al. (2010a) suggested these towers might be incidental rather than driven by selection. Two-snail towers are, however, not found in cooler, winter months and their occurrence increases with higher temperatures (T.P.T. Ng unpubl. data), supporting

the role of this behaviour as a possible response to heat stress. Interestingly, the size of snails consistently decreases from the bottom to the top of a tower in >95% of the towers observed in *E. malaccana* and *E. radiata*, respectively, and in 100% of heterospecific towers (Seuront and Ng, 2016), and a similar pattern has been recorded in *Afrolittorina knysnaensis* (L. Seuront and T.P.T. Ng unpubl. data; also see Fig. 1F). This pattern of having smaller individuals on the top is likely associated with stability of the tower, as smaller individuals are unlikely to be able to support individuals larger than themselves when their attachment to the substratum is based on a thin layer of mucus holdfast.

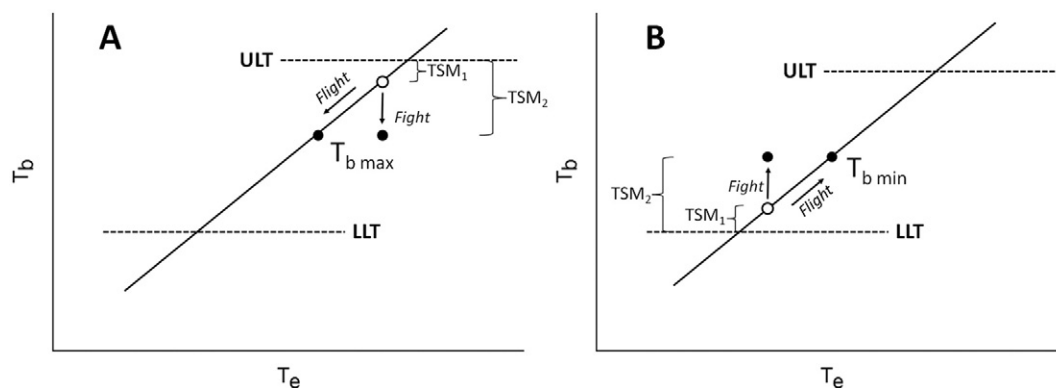
#### 4. Incorporating littorinid thermoregulatory behaviours into a conceptual model for thermal buffering

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 modifying 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 for 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; Wetthey et al., 2011; Chapperon and Seuront, 2012; Firth et al., 2015).

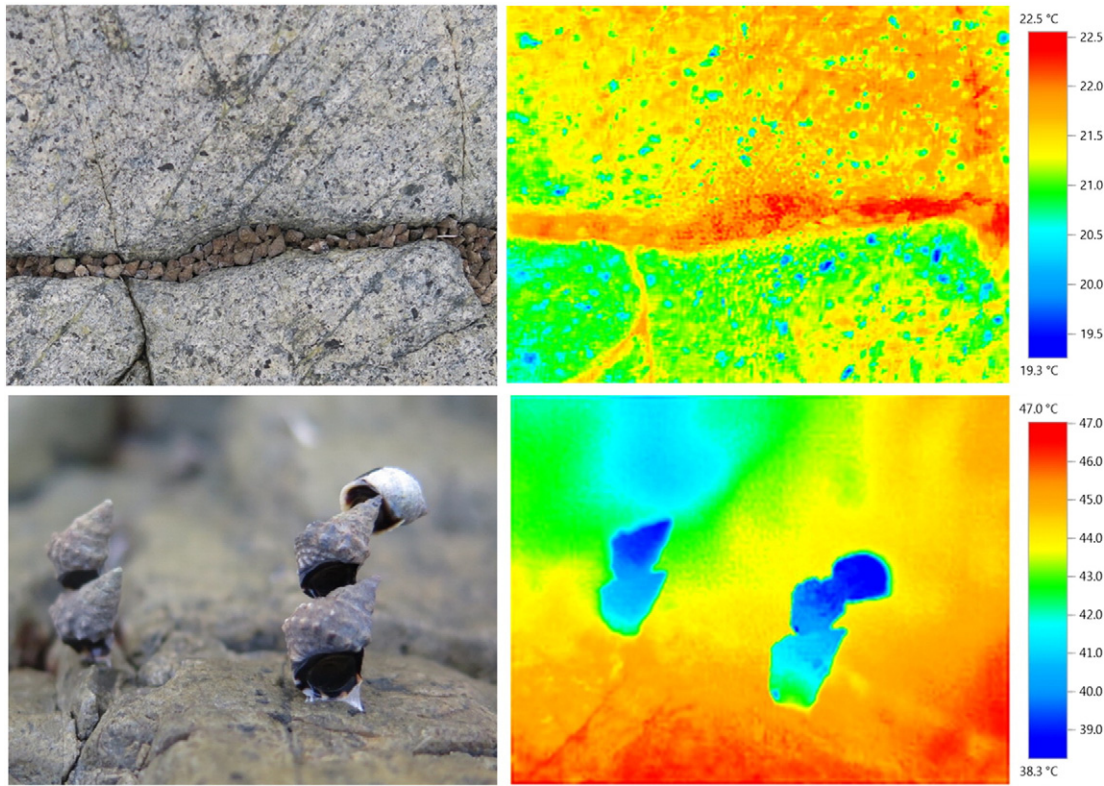
The model (Fig. 2) is based on the fact that the body temperature ( $T_b$ ) of an individual littorinid snail, as in all ectotherms, is expected to be positively and closely related to the realistic environmental temperature ( $T_e$ ) (= rock surface temperature, Marshall et al., 2010b) it experiences. The range between the upper lethal temperature (ULT) and lower lethal temperature (LLT) determines the thermal conditions within which an individual can survive (Somero, 2002, 2010; Huey et al., 2012; Marshall et al., 2015). In the natural environment, under present day conditions, the body temperature of living individuals can reach a maximum ( $T_{b \max}$ ) below the ULT (otherwise, if the body temperature exceeds the ULT, the individual will die) or a minimum ( $T_{b \min}$ ) above the LLT, and the difference between  $T_{b \max}$  and ULT or between  $T_{b \min}$  and LLT represents the thermal safety margin (TSM, Marshall et al., 2013, 2015). The TSM has been widely used to assess the resilience of a species to climate change, although its definition varies in the literature (e.g. Deutsch et al., 2008; Huey et al., 2009; Marshall et al., 2013, 2015; Sunday et al., 2014). The TSM can, for example, also be derived from the difference between  $T_{b \max}$  and heat coma temperature (HCT), as HCT marks the induction of a heat shock response leading to substantial elevation of resting energetic costs, which may cause lethal or sublethal impacts during a single prolonged exposure event (Marshall et al., 2011, 2015). In fact, ecological and evolutionary thermal limits may lie well within the bounds of ULT and LLT, and many studies have highlighted that major negative consequences of climate change may not result from increased exposure to lethal temperatures but from sublethal effects such as energetic imbalances (Dillon et al., 2010; Woodin et al., 2013; Deutsch et al., 2015). For simplicity, and clarity, we illustrate only ULT and LLT in the model as these limits are direct indicators of the temperatures at which death occurs.

Under climate change, as environmental temperatures increase, the  $T_{b \max}$  of individuals will also be higher and, if the new  $T_{b \max}$  reaches ULT, the individual can no longer survive under these new environmental conditions. The width of the TSM, will, therefore, determine the vulnerability of an individual to climate change, such that the wider the TSM, the less likely it will be of  $T_{b \max}$  reaching the ULT. TSM (difference between  $T_{b \max}$  and ULT) is likely to vary with local environmental conditions, being narrower on very hot days and wider during less stressful conditions. The estimation of TSM based on ULT and LLT at a given time may, however, be incomplete in addressing species vulnerability to environment change as these values, and, therefore, the TSM of an individual, can shift through acclimation to local conditions (Stillman, 2003; Calosi et al., 2008; Somero, 2010). The ULT of some species is, for



**Fig. 2.** A conceptual model to illustrate potential differences in individual vulnerability to climate change based on thermal safety margins (TSM) with and without considering thermoregulatory behaviours. TSM is measured as (A) difference between  $T_{b \max}$  and upper lethal temperature (ULT); or (B) difference between or  $T_{b \min}$  and lower lethal temperature (LLT). TSM incorporating thermoregulatory behaviours (TSM<sub>2</sub>) is wider than that without thermoregulatory behaviours (TSM<sub>1</sub>). Circles represent the maximum or minimum body temperature ( $T_{b \max}$  or  $T_{b \min}$ ) before (○) and after (●) considering *flight* and *fight* thermoregulatory behaviours. The solid line represents theoretical relationship between environmental ( $T_e$ ) and body temperatures ( $T_b$ ) of the individual.





**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.

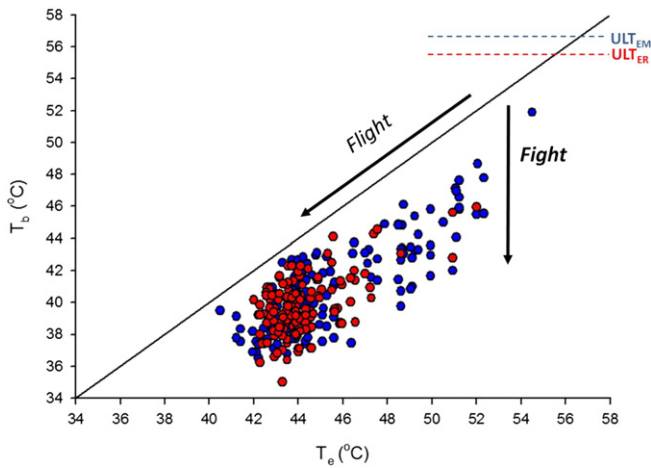
example, higher in more stressful hot seasons as compared to less stressful, cool seasons (e.g. *Echinolittorina malaccana* and *E. radiata*, G.A. Williams unpubl. data; Li, 2012; but see Araújo et al., 2013; Hoffmann et al., 2013; Chapperon et al., 2016).

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

Whilst the differentiation between *flight* and *fight* behaviours provides a mechanistic understanding of how these snails may thermoregulate, the mechanisms that cause an individual to switch between these two types of behaviours under changing temperatures remain unclear. Littorinids exhibit both *flight* and *fight* behaviours to cope with heat stress (Marshall and Chua, 2012; Marshall et al., 2013; Seuront and

Ng, 2016) but seem to adopt only *flight* behaviours when facing cold stress (Soto and Bozinovic, 1998). Marshall et al. (2013) proposed that there is likely a trade-off between the thermal benefit of thermal refuge selection and the cost of evaporative water loss incurred by moving to a refuge under higher temperatures; and therefore an individual may choose to perform *fight* (e.g. standing) rather than *flight* behaviours on sun-exposed rock surfaces when conserving water becomes especially important. In fact, in fast moving species such as crabs which are expected to have a lower cost of water loss when searching for thermal refuges, *flight* behaviour seems to be a dominant thermoregulatory strategy (Navarrete and Castilla, 1990), whereas sessile species are only limited to the use of *fight* behaviours such as gaping in mussels (Nicastro et al., 2010; Lathlean et al., 2016b). The classification of *flight* and *fight* behaviours, therefore, reveals a spectrum of strategies from pure *flight* strategists to pure *fight* strategists, and can provide a better mechanistic understanding of why different groups of intertidal ectotherms utilize different microhabitats under aerial exposure (i.e. fast moving *flight* strategists are found mainly in shaded microhabitats such as spaces beneath rocks, whereas slow moving mixed (*flight* and *fight*) strategists can be found in both shaded and sun-exposed habitats such as bare rock and crevices).

An example of incorporating *flight* and *fight* behaviours in assessing  $T_{b \max}$  and TSM is demonstrated in two high shore littorinids: *Echinolittorina malaccana* and *E. radiata*, in Hong Kong (Fig. 4). The  $T_b$  of these littorinids is positively and tightly correlated with  $T_e$ , and no significant difference between the  $T_e$  and  $T_b$  of individuals was found on the shore when no *shell standing* and *towering* was exhibited by the two species in the winter (Seuront and Ng, 2016).  $T_e$  can, however, readily exceed 50 °C during midday low tides (max.  $T_e$  recorded = 59 °C, T.P.T. Ng unpubl. data), and can exceed the ULTs of the two species (in terms of LT50, the temperature at which 50% mortality of individuals occurs and which is commonly used as an indicator of ULT,



**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 ( $T_{b \text{ max}}$ ) 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.

Somero, 2010, Fig. 4). If behavioural thermoregulation is not considered in these two species in the summer months, and assuming  $T_b$  equals  $T_e$ , as in the winter, individuals of the two species should have already experienced a  $T_b$  which exceeds their ULTs and so should be dead. The *flight* (thermal refuge selection) and *fight* behaviours (foot retraction, standing and towering) exhibited by the two species, however, allow them to maintain their  $T_b$  below their ULTs and hence maintain an effective TSM in the hot summer season of Hong Kong (Fig. 4). In fact, these thermoregulatory behaviours allow most individuals to maintain their  $T_b$  within a range of preferred body temperatures (in this example between 42 and 46 °C). Marshall et al. (2013) showed that *E. malaccana* in Brunei are able to exhibit temperature-insensitive aerobic metabolism (TIM) at 35–46 °C to lower energetic costs under heat stress, but organismal energy homeostasis is disrupted beyond 46 °C. The two species, by keeping  $T_b$  at or below 46 °C, may, therefore, be adopting a strategy to avoid sublethal physiological damage under heat stress.

To our knowledge, mass mortalities of littorinids have not been reported although  $T_e$  in tropical regions often exceeds the upper thermal limits of species (T.P.T. Ng and G.A. Williams unpubl. data), suggesting that the behaviours described and illustrated in the conceptual model can provide a buffering effect to extreme warming (Marshall et al., 2011, 2013, 2015). These snails also appear less vulnerable to climate change as compared to other, lower shore, gastropod species such as limpets and topshells that experience heavy mortality events in the summer on tropical shores such as in Hong Kong (Williams and Morrit, 1995; Williams et al., 2005; Firth and Williams, 2009; G.A. Williams unpubl. data). These observations are, therefore, contradictory to the predictions that high shore species are more vulnerable to climate change based on physiological studies (Stillman, 2002, 2003). Whilst high shore species may indeed live closer to their ULT than their lower shore counterparts (Stillman, 2002, 2003); they may have evolved a greater repertoire of adaptive mechanisms; including behavioural thermoregulation, which has resulted in wider TSMs as compared to lower shore species.

Whilst the various thermoregulatory behaviours may seem advantageous from the view of individual survival, an aspect that is not

incorporated in the model is the trade-off between these behaviours and other fitness associated activities (e.g. foraging and mating) and the resultant longer-term fitness consequences (Gunderson and Leal, 2015, 2016). In other words, behaviours associated with thermoregulation, which may be vital for survival, may potentially lead to sublethal fitness costs by reducing time or energy budgets for growth or reproduction. For example, Jones and Boulding (1999) experimentally compared activity patterns of *Littorina sitkana* between cool and warm days and showed that snails foraged for shorter periods before selecting a refuge microhabitat (where they would remain inactive) on warm days. This study, therefore, showed that littorinids may be able to minimize energetic costs associated with heat stress through thermal refuge selection (as illustrated by the conceptual model), but this may, as a consequence, reduce energy gain by limiting foraging time. Other studies, although not directly investigating activity patterns associated with thermoregulation, generally show that littorinids adjust their activity patterns in response to environmental conditions, suggesting a trade-off between fitness associated activities (Mak, 1996; Lee and Williams, 2002). For example, under conditions of severe heat and desiccation stresses, some littorinids maintain their thermoregulatory behaviours (i.e. will remain inactive in the standing posture) for many days without foraging (Marshall et al., 2013). Some tropical species also shift their distribution downshore in summer months (Mak, 1996), suggesting a strategy to utilize the mid shore barnacles as refuges to mitigate heat stress under warmer conditions, or at least reduce the time emerged (Harper and Williams, 2001; Cartwright and Williams, 2012). Lee and Williams (2002) also showed that some mangrove littorinids foraged more during the night, but spent more time with their foot retracted when environmental temperatures were higher during daytime. Such flexibility in adjusting activity patterns is also common in other intertidal ectotherms (e.g. limpets, Little and Stirling, 1985; whelks, Moran, 1985; Burrows and Hughes, 1989). More quantitative studies are, therefore, needed to examine the association between behaviour and physiology from the view of activity time/energy budgets, and hence to better understand the sublethal impacts of climate change on the life history strategies of intertidal ectotherms.

## 5. Concluding remarks

Whilst 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, 2006b; 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 (Harley et al., 2006; Huey et al., 2012; Zardi et al., 2016), 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 sub-lethal 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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