

Rates of warming and the global sensitivity of shallow water marine invertebrates to elevated temperature

S.A. MORLEY¹, A.E. BATES², M LAMARE³, J RICHARD⁴, K.D. NGUYEN⁵, J BROWN⁶ AND L.S. PECK¹

¹British Antarctic Survey, High Cross, Madingley Road, Cambridge, Cambridgeshire, CB3 0ET, UK, ²National Oceanography Centre, University of Southampton Waterfront Campus, Southampton SO14 3ZH, UK, ³Department of Marine Science, University of Otago, Dunedin, New Zealand, ⁴Université de Bretagne Occidentale, Institut Universitaire Européen de la Mer, Laboratoire de Sciences de l'Environnement Marin (UMR CNRS 6539), Technopôle Brest-Iroise, Place Copernic, F-29280 Plouzané, France, ⁵Tropical Marine Science Institute, National University of Singapore, 14 Kent Ridge Road, Singapore 119223, Singapore, ⁶Environmental Management Division, Environment and Natural Resources Directorate, St Helena Government, Essex House, Jamestown, St Helena STHL 1ZZ

Assessing the sensitivity of ectotherms to variability in their environment is a key challenge, especially in the face of rapid warming of the Earth's surface. Comparing the upper temperature limits of species from different regions, at different rates of warming, has recently been developed as a method to estimate the long term sensitivity of shallow marine fauna. This paper presents the first preliminary data from four tropical Ascension Island, five temperate New Zealand and six Antarctic McMurdo Sound species. The slopes and intercepts of these three assemblages fitted within the overall pattern for previously measured assemblages from high temperature tolerance in tropical fauna and a shallow slope, to low temperature tolerance and a steep slope in Antarctic fauna. Despite the tropical oceanic Ascension Island being subject to upwelling events, the fit of the intercept and slope within the overall assemblage pattern suggests that the upwelling is sufficiently predictable for the fauna to have evolved the plasticity to respond. This contrasts with previously analysed species from the Peruvian upwelling region, which had a steeper slope than other temperate fauna. The speed and capacity of faunal assemblages to acclimatize their physiology is likely to determine the shape of the rates of warming relationship, and will be a key mechanism underpinning vulnerability to climate warming.

Keywords: climate change, assemblage, vulnerability, warming, rates of warming, Ascension Island, New Zealand, McMurdo Sound, Antarctica

Submitted 10 December 2013; accepted 3 February 2014; first published online 11 March 2014

INTRODUCTION

Understanding how animals respond to climate variation, and the mechanisms underlying changes in species distributions, are key scientific challenges (Pennisi, 2005). One of the most common ways to address these challenges is to compare geographical differences in physiological tolerance and plasticity between populations, species and communities across latitudes (see Gaston *et al.*, 2009 for recent review). Estimates of physiological limits can then be combined with climate envelope models to improve predictions of how patterns of biodiversity will change in the future (Helmuth, 2009; Peck *et al.*, 2009). Studies have, however, highlighted the importance of comparing physiological traits at an environmental scale that is relevant to the variability of the organisms experienced microhabitat, otherwise there may be a poor match between species range (realized niche) and the range predicted by physiological tolerance (physiological niche, Helmuth, 2002; Helmuth *et al.*, 2002; Sanchez-Fernandez *et al.*, 2012).

Whilst many physical and biological factors are known to affect the distribution of marine ectotherms, temperature is pervasive, as it affects the rates of all biochemical reactions (Hochachka & Somero, 2002). When testing temperature limits, the rate of warming markedly affects the measured temperature limit, which is set by a combination of the magnitude and duration of temperature exposure; limits are expected to be lower at slower rates of warming (Mora & Moya 2006; Terblanche *et al.*, 2007; Chown *et al.*, 2009; Peck *et al.*, 2009). However, if the rate of warming is slow enough, then animals may be able to adjust their physiology to a new stable state, with this acclimation is expected to lead to an increase in temperature limits (Beneficial Acclimation Hypothesis; e.g. Leroi *et al.*, 1994). Different life history stages may have different degrees of physiological plasticity, potentially altering their vulnerability. Acclimatory capacity may, therefore, be the component of phenotypic plasticity that confers most resistance to environmental change (Somero, 2010; Peck *et al.*, 2014). Modelling relationships of species' thermal limits at different rates of warming has recently been developed as a technique for extrapolating the results of short term laboratory experiments, run over hours to months, towards annual and decadal scales, which are more closely related to the scales over which climate is

Corresponding author:
S.A. Morley
Email: smor@bas.ac.uk

changing (Peck *et al.*, 2009; Barnes *et al.*, 2010). The upper temperature limits of ectotherms are set by a combination of both the magnitude of temperature exposure and the duration of that exposure. This results in ectotherms having higher lethal limits at faster rates of warming and lower limits at slower rates. If the lethal limits of species within an assemblage are tested at different rates of warming in the laboratory, then long term limits can be estimated from the resultant relationship (Peck *et al.*, 2009). The shape of the relationship also allows assessment of the relative vulnerability of different assemblages to the rate at which climate is warming. The intercept indicates the maximum CT_{max} of the assemblage which is expected to be correlated with habitat temperature. A steeper relationship between CT_{max} and the rate of warming will indicate a reduced ability to cope with long term warming. The slope will also be shallower if species within an assemblage have the capacity to acclimate their physiology at slower rates of warming.

Assemblage level studies have shown that marine species from the Antarctic (Peck *et al.*, 2009) and coastal tropics (Nguyen *et al.*, 2011), which experience stable year round water temperatures, are more sensitive to acute elevated temperature than temperate species, which experience a wider annual range (Richard *et al.*, 2012). A similar pattern was found for the ability of the same marine ectotherms to acclimate their physiology; tropical and polar species had reduced physiological capacity compared to temperate species (Peck *et al.*, 2014). This differs from findings for a range of terrestrial species, which are more sensitive in the tropics than temperate regions, but also have increased tolerance capacities to cope with the hugely variable air temperature range in high latitudes (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Sunday *et al.*, 2012).

To further test the global patterns of thermal sensitivity in shallow subtidal marine ectotherms, this study presents the first, preliminary, data on the effect of different rates of temperature change on the upper temperature limit of common shallow subtidal marine ectotherms, collected from additional tropical (the oceanic Island of Ascension), temperate (Dunedin New Zealand) and Antarctic (McMurdo Sound) locations. Methodologies were standardized so that data sets could be directly compared with published data for a coastal tropical site in Singapore (Nguyen *et al.*, 2011), temperate regions (Richard *et al.*, 2012) and the Antarctic Peninsula (Peck *et al.*, 2009).

MATERIALS AND METHODS

Shallow water subtidal species were collected by divers from less than 20 m depth; four species were studied from Ascension Island, five from Dunedin, New Zealand and six from McMurdo Sound, Antarctica (Table 1). Apart from Ascension, which is tropical, all samples were collected in summer. For these trials, the size-range of each species was deliberately limited to reduce the variability in thermal limits attributable to size (e.g. Peck *et al.*, 2009). Ascension Island is an isolated volcanic Island on the Mid-Atlantic Ridge (7.89°S 14.38°W) and is subject to an annual seawater temperature range of 22–28°C (Irving, 1989; Weber *et al.*, 2011). The Island has a narrow shelf and is surrounded by deep water, which leads to a cooler and more variable sea surface temperature than many coastal tropical sites (e.g.

Singapore, 27–31°C (Chou & Lee, 1997)). Species were collected from Dunedin Harbour on the south-east coast of New Zealand (45°49.67'S 170°38.49'E) and Doubtful Sound, on the south-west Fiordland coast (45°25'S 167°6'E). Dunedin Harbour has a narrow entrance with an annual temperature range of 7.1–16.1°C (Shaw *et al.*, 1999). Doubtful Sound is a narrow fjord, surrounded by mountains, and has a reduced annual temperature range, at 15 m, of 12–18°C (Goodwin & Cornelisen, 2012). Species were also collected from McMurdo Sound, by US Antarctic Program divers (77°51'S 166°40'E). McMurdo Sound has the coldest and one of the most stable marine temperature regimes (−1.9 to −0.5°C (Hunt *et al.*, 2003)). In each location specimens were transported in insulated containers to marine aquarium systems, in the nearest laboratory facility. During trials carnivores were fed to satiation twice a week on pieces of fish, whilst herbivores were fed on recently collected macroalgae, algal cultures or algae in the water column, which were replaced through daily water changes or a flow-through system in longer incubations at Portobello Marine Laboratory. Daily water exchange, with water pre-heated to the experimental temperature, also ensured water quality never deteriorated. Mortality in controls (at ambient temperature) was monitored to check for any adverse effects of culture conditions. Any species that suffered significant mortality of control animals was removed from the analysis.

In Ascension Island, specimens were transported to the Ascension Island Conservation Office where they were placed in 100 l aerated water baths with 500 W titanium heaters (Aqua Medic) controlled by a 0.1°C digital thermostat (MJA Heat trace Ltd). The species were separated, with two compatible species in each water bath, and then temperature was either kept at ambient (control 26.1 ± 0.1°C; mean ± 1 standard error), or raised at one of three rates 0.04 d °C⁻¹, 1 d °C⁻¹ and 1.3 d °C⁻¹ (Table 1; Supplementary Figure S1). Trials at slower rates of warming were not possible because of logistical constraints.

In New Zealand, specimens were transported to a flow-through aquarium system at the Portobello Marine Laboratory. Controls were kept at ambient aquarium temperature, 18.7 ± 0.3°C (Supplementary Figure S1). Acute temperature tolerance tests were conducted in insulated jacketed tanks attached to thermocirculators (Grant Instruments, LTDG20) which were able to maintain seawater temperature to a precision of ± 0.1°C. Temperatures were raised at 0.04 d °C⁻¹ (1.0°C h⁻¹) and 1 d °C⁻¹ (1.0°C d⁻¹). Longer term temperature tolerance was estimated following the methodology of Peck *et al.* (2009). Animals used in longer term experiments were housed in insulated flow-through aquaria (~10 l). Briefly, seawater was heated in a header tank (50 l) with 50 W aquarium tank heaters and inflow was via gravity into aquaria at a rate of 60 ml min⁻¹ (controlled by the diameter of the outflow valves). Flow of cold seawater into the header tank was maintained with a float valve so that the header pressure remained constant. Temperature was raised at 5 d °C⁻¹ until target temperatures of 22.9 ± 0.3°C and 26.2 ± 0.6°C were reached. These temperatures were then maintained until more than 50% mortality had occurred. The number of days that 50% of individuals survived at elevated temperature was converted into a rate of temperature change by dividing the number of degrees that temperature was elevated by the number of days (following Peck *et al.*, 2009).

Table 1. Rates of warming, species used and higher taxon in experiments on species collected from three locations; Ascension Island, Dunedin in New Zealand and McMurdo Sound, Antarctica.

Location	Collection depth	Collection temperature (annual temperature range) °C ⁻¹	Species	Taxon	Rates of warming	CT _{max} °C ⁻¹ Median (inter-quartile range)
Ascension Island, English Bay	3–9 m	24 (22–28)	<i>Acar domingensis</i>	Bivalve	0.04 d °C ⁻¹	39 (39–40.2)
					1 d °C ⁻¹	37.1 (36.4–37.9)
					1.3 d °C ⁻¹	36.3 (34.8–38.5)
			<i>Echinomerta lucunter</i>	Echinoid	0.04 d °C ⁻¹	37.1 (36.4–37.9)
					1 d °C ⁻¹	36.3 (34.8–38.5)
					1.3 d °C ⁻¹	36 (35.8–36)
			<i>Eucidaris tribuloides</i>	Echinoid	0.04 d °C ⁻¹	36 (35.8–36)
					1 d °C ⁻¹	34 (34.0–34.0)
					1.3 d °C ⁻¹	35 (35.0–35.2)
			<i>Ophiostigma abnorme</i>	Ophiuroid	0.04 d °C ⁻¹	35.6 (35.0–35.6)
					1 d °C ⁻¹	31.1 (30.9–33.3)
					1.3 d °C ⁻¹	31.1 (30.9–33.3)
New Zealand, Doubtful Sound	15–20 m	13 (12–18)	<i>Cnemidocarpa bicornuta</i>	Ascidian	0.04 d °C ⁻¹	29.0 (27.0–29)
					1 d °C ⁻¹	26.4 (26.0–26.6)
					2.3 d °C ⁻¹	26.2
					8.9 d °C ⁻¹	22.9
					0.04 d °C ⁻¹	32.7 (32.5–32.9)
					1 d °C ⁻¹	31.0 (27–31.6)
Dunedin Harbour	5–10 m	16 (7.1–16.1)	<i>Cookia sulcata</i>	Gastropod	3.2 d °C ⁻¹	26.2
					0.04 d °C ⁻¹	29.4 (28.3–29.4)
Doubtful Sound			<i>Liothyrella neozelanica</i>	Brachiopod	1 d °C ⁻¹	25.6 (21.7–26.0)
Dunedin Harbour			<i>Ophioneries fasiata</i>	Ophiuroid	0.04 d °C ⁻¹	31.8 (31.3–32.4)
					1 d °C ⁻¹	23.9 (0.33)
					2.7 d °C ⁻¹	26.2
Doubtful Sound			<i>Pseudechinus huttoni</i>	Echinoid	10.5 d °C ⁻¹	22.9
					0.04 d °C ⁻¹	26.8 (26.6–27.6)
					1 d °C ⁻¹	19.5 (19.2–21.1)
McMurdo Sound, Antarctica	10–20 m	–1.7 (–1.9 to –0.5)	<i>Odontaster validus</i>	Asteroid	0.04 d °C ⁻¹	23.7 (18.6–23.7)
					1 d °C ⁻¹	14.9 (13.5–16.1)
			<i>Sterechinus neumayeri</i>	Echinoid	0.04 d °C ⁻¹	19.3 (17.7–20.4)
					1 d °C ⁻¹	12.1 (11.3–13.5)
			<i>Limatula hodgsoni</i>	Bivalve	0.04 d °C ⁻¹	12.7 (11.7–15.7)
					1 d °C ⁻¹	13.3 (11.7–14.5)
			<i>Laternula elliptica</i>	Bivalve	0.04 d °C ⁻¹	17.4 (15.7–19.3)
					1 d °C ⁻¹	13.4 (12.1–13.4)
			<i>Trophon longstafi</i>	Gastropod	1 d °C ⁻¹	14.5 (14.5–16.1)
			<i>Adamussium colbecki</i>	Bivalve	1 d °C ⁻¹	11.7 (9.8–12.4)

At Scott Base (Antarctica New Zealand) animals were transferred to a flow-through aquarium at ambient temperature (–1.7°C). Acute temperature tolerance tests were conducted in insulated jacketed tanks attached to thermo-circulators which were able to maintain seawater temperature to a precision of ±0.1°C. Temperatures were raised at 0.04 d °C, 0.6 d °C⁻¹ and 1 d °C⁻¹. Trials at slower rates of warming were not possible.

Mortality was assessed every hour in 0.04 d °C⁻¹ experiments or two to three times a day at slower rates of temperature change (after the method of Peck *et al.*, 2009). For species that normally live attached to the substratum, e.g. starfish, sea urchins and gastropod molluscs, the first sign that competence had been compromised was when they lost their ability to remain attached. Unattached individuals were stimulated with a blunt seeker to illicit a response; non-response (loss of equilibrium) was recorded as CT_{max} and the size of each individual was measured. Temperature limits for individual species in the current study were not normally distributed even after

transformation, and so non-parametric Mann–Whitney multiple comparisons were used with a Bonferroni corrected acceptance probability. The global comparison of temperature limits was conducted using a linear mixed effects model with species as a random factor and natural logarithm of rate of change as the covariate. The model fit and residual behaviour were visually inspected to ensure that the test assumptions were met; to normalize the residual variance the variance for each location was modelled independently using the function ‘varIdent’ and the form ~1|Location applied as a weights argument.

RESULTS

Ascension Island

There was no mortality of control animals. All species had a significantly higher CT_{max} at the fastest rate of change (Tables 1, 2). At warming rates of 0.04 d °C⁻¹ and 1 d °C⁻¹,

Table 2. Mann–Whitney comparison tests of thermal limits of 4 species of invertebrate at the fastest rates of temperature change.

Location	Species	Mann–Whitney values for quoted rate of warming $d\ ^\circ C^{-1}$	Comparisons		
		0.04 vs 1.0	0.04 vs 1.2	0.04 vs 1.3	1.0 vs 1.3
Ascension	<i>Acar domingensis</i>	W = 532 P < 0.01		W = 434 P < 0.01	W = 736 P = 0.67
	<i>Echinometra lucunter</i>	W = 408 P < 0.01		W = 472 P < 0.01	W = 234 P = 0.24
	<i>Eucidaris tribuloides</i>	W = 493 P < 0.01		W = 340 P < 0.01	W = 230 P < 0.01
	<i>Ophiostigma abnorme</i>	W = 350 P < 0.01		–	–
New Zealand	<i>Cnemidocarpa bicornata</i>	W = 134 P < 0.01			
	<i>Cookia sulcata</i>	W = 456 P < 0.01			
	<i>Liothyrella neozelanica</i>	W = 190 P < 0.01			
	<i>Ophioneries fasiata</i>	W = 36 P < 0.01			
	<i>Pseudechinus huttoni</i>	W = 120 P < 0.01			
McMurdo Sound	<i>Laternula elliptica</i>		W = 66 P < 0.01		
	<i>Odontaster validus</i>		W = 133 P < 0.01		
	<i>Sterechinus neumayeri</i>		W = 120 P < 0.01		
	<i>Limatula hodgsoni</i>		W = 196 P = 0.54		

the bivalve, *Acar domingensis* was the most temperature tolerant (medians of 39.0 and 37.1 $^\circ C$, respectively; Tables 1, 2) and the brittlestar, *O. abnorme*, was the least tolerant at both these rates of change (35.6 and 31.1 $^\circ C$ respectively; Tables 1, 2). At the slowest rate of change, 1.2 or 1.3 $d\ ^\circ C^{-1}$, there was no difference in the temperature limits of *Acar domingensis* or *Echinometra lucunter*, but *Eucidaris tribuloides* had a significantly higher temperature limit at 1.3 $d\ ^\circ C^{-1}$ than at 1.0 $d\ ^\circ C^{-1}$.

New Zealand

After 45 d there were mortalities in controls of *Pseudechinus huttoni* (8 out of 12) and *Liothyrella neozelanica* (9 out of 13). Data from beyond 30 d were, therefore, not used for these species. Mortalities in controls of *Cnemidocarpa bicornata* (N = 2), *Cookia sulcata* (N = 1) and *Ophioneries fasiata* (N = 1) were low, and so mortality could be estimated from long term trials. This was with the exception of *C. sulcata*, which did not suffer 50% mortality during the incubation period at 22.9 $^\circ C$. Long term mortality could, therefore, not be estimated at 22.9 $^\circ C$ for this species.

In all cases upper temperature CT_{max} was lower at 1 $d\ ^\circ C^{-1}$ than at the fastest rate of warming, 0.04 $d\ ^\circ C^{-1}$ (Tables 1, 2). 50% of *Cnemidocarpa bicornata* survived for a median of 17 and 37.5 d at 26.2 $^\circ C$ and 22.9 $^\circ C$, for which calculated rates of change were 2.3 $d\ ^\circ C^{-1}$ and 8.9 $d\ ^\circ C^{-1}$ respectively. 50% of *Cookia sulcata* survived for a median of 23 d at 26.2 $^\circ C$ which gave a rate of change of 3.2 $d\ ^\circ C^{-1}$. 50% of *Ophioneries fasiata* survived for a median of 20 and 44 d at 26.2 $^\circ C$ and 22.9 $^\circ C$ for which calculated rates of change were 2.7 $d\ ^\circ C^{-1}$ and 10.5 $d\ ^\circ C^{-1}$, respectively.

McMurdo Sound

In all but *Limatula hodgsoni* upper temperature limits were lower at 1 $d\ ^\circ C^{-1}$ than at the fastest rate of warming, 0.04 $d\ ^\circ C^{-1}$ (Tables 1, 2).

Global comparisons between assemblages

In the global comparison of CT_{max} at 1 $d\ ^\circ C^{-1}$, each assemblage had a tolerance that was positively correlated with their mean environmental temperature, except McMurdo Sound, which although a colder environment than the Western Antarctic Peninsula, had a higher tolerance than

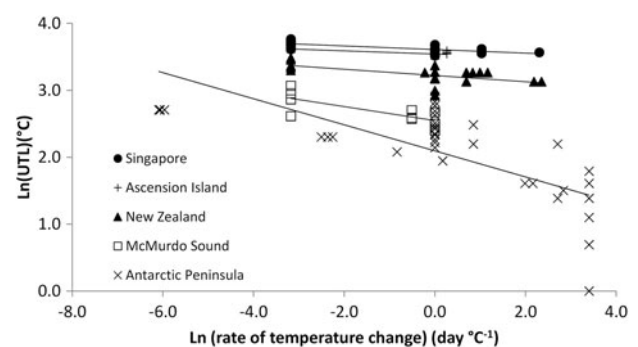


Fig. 1. Temperature limits of different faunal assemblages from the tropics to the Antarctic. Tropical Singapore data from Nguyen *et al.* (2012), Antarctic Peninsula data from Peck *et al.* (2009), and new data from Ascension Island, New Zealand and McMurdo Sound. Fitted lines from linear mixed effect regression fits (Table 3).

Table 3. Summary table for the linear mixed effects model estimates fitted using restricted maximum likelihood for the global relationship of upper temperature limit as a function of the predictor, the rate of temperature change, with location as a factor and species as a random factor. WAP, Western Antarctic Peninsula. Akaike information criterion = 145.8; log likelihood = 88.9; SE, standard error; d.f., degrees of freedom.

Assemblage	Slope					Intercept				
	Estimate	SE	d.f.	t-value	P-value	Estimate	SE	d.f.	t-value	P-value
Singapore	-0.028	0.0021	66	13.3	<0.01	3.61	0.01	66	280.9	<0.01
Ascension	-0.0258	0.006	66	0.37	0.71	3.5388	0.03	43	2.66	0.01
McMurdo	-0.104	0.027	66	2.87	<0.01	2.549	0.057	66	18.6	<0.01
New Zealand	-0.047	0.01	66	1.83	0.07	3.2385	0.031	43	12.09	<0.01
WAP	-0.1949	0.02	66	6.71	<0.01	2.099	0.071	66	21.23	<0.01

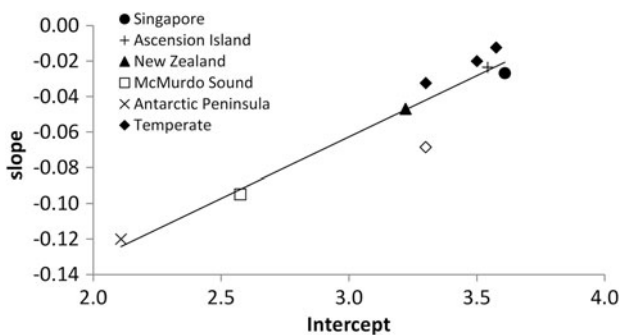


Fig. 2. For groups of marine invertebrates from different locations, the slope of the regression between upper temperature limit and rate of warming (as in Figure 1) is plotted against the intercept. Singapore data from Nguyen *et al.* (2012), temperate data from Richard *et al.* (2012) with the Peruvian upwelling fauna indicated with an open diamond, Antarctic Peninsula data from Peck *et al.* (2009). The regression line was fitted excluding this outlying Peruvian fauna. Slope = $0.071\text{intercept} - 0.27$, $R^2 = 0.97$, $F = 252$, $P < 0.01$.

the Western Antarctic Peninsula. Singapore had a significantly higher intercept than Ascension Island (Figure 1; Table 3), and New Zealand fauna were between these. Ascension Island, Singapore and New Zealand assemblages had slopes that were not significantly different. The slopes for the two Antarctic faunal assemblages were significantly steeper than the warmer-water species. There was, therefore, a strong relationship between the slope and intercept across assemblages (Figure 2). Assemblages that had higher intercepts (higher CT_{\max}) also had shallower slopes than those from cooler environments (Figure 2).

DISCUSSION

As expected, CT_{\max} values were generally lower at slower rates of warming. The only species that had a temperature limit that was significantly higher at a slower rate of warming was the urchin *Euchidaris tribuloides* from Ascension Island. This is the first evidence that a shallow water Ascension Island species has the capacity to rapidly adjust its physiology. Tropical species are expected to have limited acclimatory capacity as they live in thermally stable environments, with little variation in temperature through the year (Spicer & Gaston, 1999; Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Peck *et al.*, 2014). However, the shelf seas around Ascension Island are surrounded by deep oceanic water and so the water temperature is cooler and more variable than in

coastal tropical locations. The near-shore water temperature rose gradually between September 2012 and June 2013, from 24 to 28°C (Brickle, unpublished data). If this is a predictable seasonal change in seawater temperature, then Ascension Island marine species may have evolved the plasticity to adjust their physiology in response to this variation. When warm water species have the capacity to acclimate their physiology, acclimation is expected to be rapid, occurring within a few hours to days (Spicer & Gaston, 1999; Verberk & Calosi, 2012; Peck *et al.*, 2014). In polar waters, which are also thermally stable through the year, species are similarly expected to have limited acclimatory capacity (Peck *et al.*, 2014). When acclimation of invertebrates does take place at the poles, it may take many months. For example, the acclimation of the Antarctic limpet, *Nacella concinna*, took between 2 and 5 months (Peck *et al.*, 2014). It is possible that longer duration experiments will find that McMurdo Sound fauna will also have limited acclimation capacity but the preliminary experiments conducted here do not allow this to be tested.

Assemblages from warmer environments had higher intercepts, indicating their higher CT_{\max} (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Sunday *et al.*, 2011). The overall relationship shows that the CT_{\max} of each assemblage was negatively correlated to the slope of the relationship between CT_{\max} and the rate of warming; the slope was also shallower in assemblages from warmer environments (Figure 3). Tropical species are often thought to be living at temperatures close to the upper limit that can be sustained through acclimatization and, therefore, have limited ability to further adjust their temperature limits (Stillman & Somero, 2000; Stillman, 2003; Deutsch *et al.*, 2008; Richard *et al.*, 2012). This is thought to result in tropical species having temperature limits that are only slightly above their experienced environmental temperatures and a rates-of-warming relationship with a reduced slope. Temperate marine assemblages, such as the New Zealand fauna tested here, generally live in cooler, but more variable environments, and their intercepts and slopes are closer to those of tropical species than polar ones. To cope with the variability of their environments they have evolved higher thermal tolerances with higher buffers above their experienced environmental maxima (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Sunday *et al.*, 2011). The increased acclimatory capacity of temperate species would also tend to reduce the slope of the rates-of-warming relationship closer to those of tropical rather than polar species (Figure 3). Whilst the maintenance of physiological heat tolerance is expensive and is generally expected to be lost in species from colder latitudes (Stillman

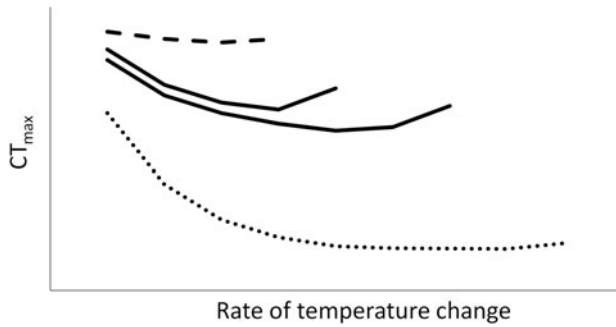


Fig. 3. Theoretical representation of the effect of the rate of warming on the lethal limits of marine ectotherms across latitudes. The dashed line represents a tropical assemblage with a shallow slope, due to rapid but limited acclimation capacity. The solid lines represent a temperate assemblage with an intermediate slope, a slower rate of acclimation, but with greater acclimation capacity. Two examples are shown with different rates of acclimation. The dotted line represents a polar assemblage with a steep slope and very slow and limited acclimation capacity.

& Somero, 2000), the reduced, and extended duration of, acclimatory capacity in polar species leads to the steeper slope of the relationship for this assemblage (Figure 3), indicating their increased sensitivity to long term elevated temperature. The compression of upper temperature limits, and therefore shallower slopes, at higher temperatures was also apparent when the slopes and intercepts of temperate species were compared between summer and winter (Richard *et al.*, 2012).

Isolated oceanic islands are often regions of upwelling, as they have narrow shelves and are surrounded by deep water (Pinheiro *et al.*, 2010). Rapid changes in temperature, of up to 2.5°C in less than 24 h, were recorded at Ascension Island, particularly during March and April 2013 (Brickle, unpublished data). Whilst the occurrence of upwelling events at Ascension Island may be predictable enough that faunal species have sufficiently regular cues to acclimate their physiology, the assemblage living in the Peruvian upwelling region, studied by Richard *et al.* (2012), did not have the ability to respond to the episodic warming associated with El Niño events. When the slopes of regression fits were plotted against the intercept for each assemblage (following Richard *et al.*, 2012), the relationship was consistent across assemblages, except for the Peruvian upwelling fauna. This indicates that the Peruvian faunal species have a reduced long term temperature tolerance, compared to other temperate assemblages, and are less likely to be able to adjust their thermal tolerance to cope with the warmer temperatures experienced during unpredictable El Niño warming events (Figure 1). This is supported by evidence that species experience large scale mortality during these periods. Although further data are required, the fact that Ascension Island fauna fit with the general pattern provides preliminary evidence that the annual variation in temperature at Ascension (6°C) is sufficiently variable yet predictable, that some of the marine fauna have the ability to acclimate their physiology. The Ascension experiments were conducted in August, when the water temperature was close to its annual minimum of 22°C. If Ascension Island invertebrates can acclimatize their physiology in response to seasonal changes in temperature, they might be expected to have higher temperature limits when water is at its annual maximum (28°C). Experiments testing more species, and at different times of

year, are required to confirm the presence of seasonal plasticity. Comparisons of thermal tolerance across environments are often, out of necessity, conducted in different years and whilst temperate and polar experiments were conducted in summer, there can be inter-annual differences in thermal limits (e.g. Morley *et al.*, 2012). Assessing long term thermal limits through projections based on different rates of warming are likely to reduce the impact of differences between years and give a better assessment of the differences between assemblages.

The relationship between CT_{max} and the rate at which temperature is increased measures a combination of acute thermal tolerance and acclimatory capacity. These relationships between CT_{max} and the rate of warming help explain why tropical species, which are already living close to their upper limits, have limited capacity for acclimation to warmer temperatures (Stillman & Somero, 2000; Stillman, 2003), whilst temperate latitude freshwater beetles with higher CT_{max} 's had higher acclimation capacity (Calosi *et al.*, 2008). The global relationship between these parameters is consistent across assemblages allowing long term thermal sensitivities to be predicted for other assemblages. This pattern, however, only holds in environments where predictable temporal cues have led to the development of the ability to respond to environmental variability.

ACKNOWLEDGEMENTS

Bev Dickson and the staff at both Portobello and Doubtful Sound provided vital technical support in New Zealand. Jess Ericson, Tom and Linnaea Bird helped maintain the long term incubations in Portobello Marine Laboratory. The United States Antarctic Program divers, under the leadership of Rob Robbins, collected specimens at McMurdo. We are grateful to the Shallow Marine Surveys Group and the South Atlantic Environmental Research Institute for organizing the expedition. We are also very grateful to the Ascension Island Government, the members of staff at the Conservation Centre and Ascension Island Dive Club for their cooperation, accommodation and hospitality.

FINANCIAL SUPPORT

This research was funded by NERC British Antarctic Survey Polar Science for Planet Earth funding (Adaptations and Physiology work package), the University of Otago Research Committee, Antarctica New Zealand (event no. K-068), the TransAntarctic Association (TAA05/08). A.E.B. was funded by a Natural Science and Engineering Research Council of Canada post-doctoral fellowship. The funding for work in Ascension came from a grant to Dr Paul Brickle from the Darwin Initiative (EIDCF012).

SUPPLEMENTARY MATERIALS AND METHODS

The supplementary material referred to in this article can be found online at journals.cambridge.org/mbi.

REFERENCES

- Barnes D.K.A., Peck L.S. and Morley S.A. (2010) Ecological relevance of laboratory determined temperature limits: colonization potential, biogeography and resilience of Antarctic invertebrates to environmental change. *Global Change Biology* 16, 3164–3169.
- Calosi P., Bilton D.T and Spicer I. (2008) Thermal tolerance, acclimatory capacity and vulnerability to climate change. *Biology Letters* 4, 99–102.
- Chou R. and Lee H.B. (1997) Commercial fish farming in Singapore. *Aquaculture Research* 28, 767–776.
- Chown S.L., Jumban K.R., Sørensen J.G. and Terblanche J.S. (2009) Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Functional Ecology* 23, 133–140.
- Deutsch C.A., Tewksbury J.J., Huey R.B., Sheldon K.S., Ghalambor C.K., Haak D.C. and Martin P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Science of the United States of America* 105, 6668–6672.
- Gaston K.J., Chown S.L., Calosi P., Bernado J., Bilton D.T., Clarke A., Clusella-Trullas S., Ghalambor C.K., Konarzewski M., Peck L.S., Porter W.P., Pörtner H.O., Rezende E.L., Schulte P.M., Spicer J.I., Stillman J.H., Terblanche J.S. and van Kleunen M. (2009) Macrophysiology: a conceptual reunification. *American Naturalist* 174, 595–612.
- Goodwin E. and Cornelisen C.D. (2012) Near-surface water temperatures in Doubtful Sound and response to natural and anthropogenic drivers. *New Zealand Journal of Marine and Freshwater* 46, 411–429.
- Helmuth B.H. (2002) How do we measure the environment? Linking intertidal physiology and ecology through biophysics. *Integrative and Comparative Biology* 42, 837–845.
- Helmuth B.H. (2009) From cells to coastlines: how can we use physiology to forecast the impacts of climate change? *Journal of Experimental Biology* 212, 753–760.
- Helmuth B., Harley C.D.G., Halpin P.M., O'Donnell M., Hofmann G.E. and Blanchette C.A. (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298, 1015–1017.
- Hochachka P.W. and Somero G.N. (2002) *Biochemical adaptation: mechanism and process in physiological evolution*. New York: Oxford University Press.
- Hunt B.M., Hoefling K. and Cheng C.H.C. (2003) Annual warming episodes in seawater temperatures in McMurdo Sound in relationship to endogenous ice in notothenioid fishes. *Antarctic Science* 15, 333–338.
- Irving R.A. (1989) A preliminary investigation of the sublittoral habitats and communities of Ascension Island, South Atlantic. *Progressive Underwater Science* 13, 65–78.
- Leroi A.M., Bennett A.F. and Lenski R.E. (1994). Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proceedings of the National Academy of Science of the United States of America* 91, 1917–1921.
- Mora C. and Moya M.F. (2006) Effect of the rate of temperature increase of the dynamic method on the heat tolerance of fishes. *Journal of Thermal Biology* 31, 337–341.
- Morley S.A., Martin S.M., Bates A.E., Clark M.S., Ericson J., Lamare M. and Peck L.S. (2012) Spatial and temporal variation in the heat tolerance limits of two abundant Southern Ocean invertebrates. *Marine Ecology Progress Series* 450, 81–92.
- Nguyen K.D.T., Morley S.A., Lai C.-H., Clark M.S., Tan K.S., Bates A.E. and Peck L.S. (2011) Upper temperature limits of tropical marine ectotherms: global warming implications. *PLoS One* 6, e29340. doi:10.1371/journal.pone.0029340.
- Peck L.S., Clark M.S., Morley S.A., Massey A. and Rossetti H. (2009) Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology* 23, 248–256.
- Peck L.S., Morley S.A., Richard J. and Clark M.S. (2014) Acclimation and thermal tolerance in Antarctic marine ectotherms. *Journal of Experimental Biology* 217, 16–22.
- Pennisi E. (2005) What determines species diversity? *Science* 309, 90.
- Pinheiro H.T., Gasparini J.L. and Joyeux J.-C. (2010) Reef fish mass mortality event in an isolated island off Brazil, with notes on recent similar events at Ascension, St Helena and Maldives. *Marine Biodiversity Records* e47, 1–4. doi:http://dx.doi.org/10.1017/S1755267210000424.
- Richard J., Morley S.A., Thorne M.A.S. and Peck L.S. (2012) Estimating long-term survival temperatures at the assemblage level in the marine environment: towards macrophysiology. *PLoS One* 7, e34655. doi:10.1371/journal.pone.0034655.
- Sanchez-Fernandez D., Aragón P., Bilton D.T. and Lobo J.M. (2012) Assessing the congruence of thermal niche estimations derived from distributions and physiological data. A test using diving beetles. *PLoS One* 7, e48163. doi:10.1371/journal.pone.0048163.
- Shaw A.G.P., Kavalieris L. and Vennell R. (1999) Seasonal and inter-annual variability of SST off the east coast of South Island, New Zealand. *Geocarta International* 14, 29–34.
- Somero G.N. (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology* 213, 912–920.
- Spicer J.I. and Gaston K.J. (1999) *Physiological diversity and its ecological implications*. Oxford: Blackwell Science.
- Stillman J.H. (2003) Acclimation capacity underlies susceptibility to climate change. *Science* 301, 65.
- Stillman J.H. and Somero G.N. (2000) A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus *Petrolisthes*: influence of latitude, vertical zonation, acclimation, and phylogeny. *Physiological and Biochemical Zoology* 73, 200–208.
- Sunday J.M., Bates A.E. and Dulvy N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society of London, B* 278, 1823–1830.
- Terblanche J.S., Deere J.A., Clusella-Trullas S., Jannion C. and Chown S.L. (2007) Critical thermal limits depend on methodological context. *Proceedings of the Royal Society of London, B*, 274, 2935–2942.
- Tewksbury J.J., Huey R.B. and Deutsch C.A. (2008) Putting the heat on tropical animals. *Science* 320, 1296–1297.
- Verberk C.E.P. and Calosi P. (2012) Oxygen limits heat tolerance and drives heat hardening in the aquatic nymphs of the gill breathing damselfly *Calopteryx virgo* (Linnaeus, 1758). *Journal of Thermal Biology* 37, 224–229.
- and
- Weber S.B., Blount J.D., Godley B.J., Witt M.J. and Broderick A.C. (2011) Rate of egg maturation in marine turtles exhibits 'universal temperature dependence'. *Journal of Animal Ecology* 80, 1034–1041.

Correspondence should be addressed to:

S. A. Morley
British Antarctic Survey, High Cross, Madingley Road
Cambridge, Cambridgeshire, CB3 0ET, UK
email: smor@bas.ac.uk