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Thermal tolerance ranges and climate variability: A comparison between bivalves from differing climates

Tanya J. Compton [a,b,c,*], Micha J.A. Rijkenberg [a], Jan Drent [a], Theunis Piersma [a,b]

[a] *Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ),*
P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
[b] *Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands*
[c] *Western Australian Department of Environment and Conservation (DEC), WA Wildlife Research Centre,*
P.O. Box 51, Wanneroo, WA 6065, Australia

Abstract

The climate variability hypothesis proposes that in variable temperate climates poikilothermic animals have wide thermal tolerance windows, whereas in constant tropical climates they have small thermal tolerance windows. In this study we quantified and compared the upper and lower lethal thermal tolerance limits of numerous bivalve species from a tropical (Roebuck Bay, north western Australia) and a temperate (Wadden Sea, north western Europe) tidal flat. Species from tropical Roebuck Bay had higher upper and lower lethal thermal limits than species from the temperate Wadden Sea, and Wadden Sea species showed an ability to survive freezing temperatures. The increased freezing resistance of the Wadden Sea species resulted in thermal tolerance windows that were on average 7 °C greater than the Roebuck Bay species. Furthermore, at a local-scale, the upper lethal thermal limits of the Wadden Sea species were positively related to submersion time and thus to encountered temperature variation, but this was not the case for the Roebuck Bay species. A review of previous studies, at a global scale, showed that upper lethal thermal limits of tropical species are closer to maximum habitat temperatures than the upper lethal thermal limits of temperate species, suggesting that temperate species are better adapted to temperature variation. In this study, we show for the first time, at both local and global scales, that the lethal thermal limits of bivalves support the climate variability effect in the marine environment.
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Keywords: Bivalves; Intertidal mud flat; Inundation time; Physiological tolerances; Thermal niche width

1. Introduction

The greater magnitude of temperature variation at temperate latitudes is expected to select for wider physiological tolerance windows in poikilothermic animals, whereas the smaller magnitude of temperature variation at tropical latitudes is expected to lead to narrower tolerance windows (Dobzhansky, 1950; Stevens, 1989). The relationship between climate variation and thermal tolerance windows has been termed the *climate variability hypothesis* (Stevens, 1989). It has far-reaching implications for geographical range sizes and species richness patterns (Gaston et al., 1998).

Direct evidence for the climate variability hypothesis in the marine environment is scarce (Gaston et al., 1998; Spicer and Gaston, 1999). The reason for a lack of support

* Corresponding author. Present address: Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands. Tel.: +31 222 369 592; fax: +31 222 319 674.
E-mail address: compton@nioz.nl (T.J. Compton).

for the climate variability hypothesis, especially in the marine environment, is that few studies have examined the lower lethal thermal limits of organisms (Spicer and Gaston, 1999). Thus, the effects of thermal acclimation on both heat and cold tolerance have seldomly been reported in multiple species adapted to different thermal habitats (Pörtner et al., 2006; Osovitz and Hofmann, 2007). A large scale approach of examining physiological traits, macrophysiology (Chown et al., 2004), has proven promising in insects, and is expected to be important for understanding species' distributions in the marine environment (Osovitz and Hofmann, 2007). For example, a meta-analysis of the thermal limits of insects has shown that the lower rather than the upper lethal thermal limits of insects are correlated with latitude (Addo-Bediako et al., 2000; Sinclair et al., 2003).

Based on available knowledge, tolerance windows in marine organisms as estimated by lethal and critical thermal limits have displayed a relationship with climate regime. Note that lethal thermal limits can be used as relevant indirect correlates to examine biogeographical limits (Pörtner, 2002). Fishes and bivalves from the Antarctic are known to have narrow thermal tolerance windows relative to temperate fishes with broad thermal tolerance windows that reflect the higher variation in their environmental temperatures (Somero and Devries, 1967; Brett, 1970; Peck and Conway, 2000; Peck et al., 2002). An adaptation to climate regime has also been shown in the upper lethal thermal limits of crabs and bivalves, as tropical species displayed higher upper lethal thermal limits than temperate species (Vernberg and Tashian, 1959; Stillman and Somero, 2000). In addition, where lower lethal thermal limits have been estimated in crabs it appears that tropical species have higher lower lethal thermal limits than temperate species (Vernberg and Tashian, 1959). Interestingly, an examination of the upper thermal limits of porcelain crabs (Genus *Petrolisthes*) along the Pacific coast indicated that temperate species have a larger safety buffer in their upper thermal limits than temperate species (Stillman and Somero, 2000; Stillman, 2002).

To investigate whether congeneric bivalve species from intertidal sedimentary habitats display evidence of a climate variability effect, we measured lethal thermal limits of 18 bivalve species from a tropical (Roebuck Bay, North West Australia) and a temperate tidal flat (Wadden Sea, The Netherlands) in relation to the local climate regime at each location. Thermal tolerance windows were compared between bivalves from both locations to test for a climate variability effect. Seasonal acclimatisation was examined to observe whether

differences between locations would be greater than seasonal differences. The upper lethal thermal limits were related to the local habitat to examine relationships with submergence time. To examine whether at a global scale bivalves display a relationship between their upper lethal thermal limits and habitat temperature we obtained additional values from the literature and examined this correlation.

2. Materials and methods

2.1. Local temperature variation

Annual climate regimes of the Roebuck Bay, north western Australia (17°S and 122°E) and the Wadden Sea, The Netherlands (53°N and 5°E) tidal flats were recorded using Stowaway Tidbit™ loggers (hourly readings, buried 5 cm deep into the sediment) for periods of 6 to 12 months over a four year period (2002 to 2006). We averaged daily measurements to show seasonal trends in temperature, including yearly maxima and minima. The annual temperature range at each location was determined by subtracting the upper from the lower quartile value for each year.

2.2. Collection of bivalve species

The species sampled in this experiment represent all the numerically important species (Pearson et al., 2003; Piersma et al., 2001). At both locations most species were sampled at the tidal flat and one species was collected from a hard substrate (*Mytilus edulis* in Wadden Sea and *Barbatia pistachia* in Roebuck Bay). In The Netherlands one species was collected in the subtidal North Sea, *Spisula subtruncata* (although this species does appear in the intertidal occasionally, T.P. pers obs.). Overall, the thermal limits of eleven species in Roebuck Bay, and seven species in the Wadden Sea were determined. Bivalve species were collected directly before placement into the experiment, and thus the field temperature at the time of collection is regarded as the acclimatization temperature for each trial. All collection and handling of animals was completed according to the legal requirements of each country.

2.3. Experimental trials

The tested range of temperatures was 0–45 °C for the bivalves from Roebuck Bay and −10 to 40 °C for bivalves from the Wadden Sea; in both cases treatments were separated by 5 °C intervals. All lethal thermal

tolerance ranges were determined in the local sea-water. Each experiment tested only one species at a time. Each species' experiment was terminated at 24 h, and at the end of the experiment a gaping response indicated death; i.e. the lack of adductor muscle contractions (Ansell et al., 1980a). In aquatic organisms, lethal limits are determined in the time-frame when survival is passive and time-limited at high temperatures, i.e. at the end-point of survival. During passive survival blood oxygen levels are minimal and life is supported by anaerobic metabolism, heat shock proteins and an antioxidative defence (Pörtner and Knust, 2007).

Seasonal variation in the upper lethal thermal limits was examined for six of the 11 species in Roebuck Bay and five of the seven species in the Wadden Sea. Replicate species' trials within a season were completed for all species, except for *Gafrarium dispar* and *Mya arenaria*. In Roebuck Bay the winter species trials ran from July to August (2003), and the summer species trials ran in November (2003). In the Wadden Sea the winter trials ran from February to March (2003), and the spring species trials ran in May (2003). In Roebuck Bay, the lower lethal thermal limits of all species were determined in November 2003. In the Wadden Sea species the lower temperatures from 20 °C to −5 °C were examined in May 2003, and as no species died, we tested another level of freezing tolerance (−10 °C) in June 2004. Freezing tolerance limits were tested in spring due to logistical reasons.

Replicate ($n=2$) temperature treatment basins were used for both the warm (20–45 °C) and cool (15–0 °C) temperature treatments. Within each basin salt water filled aquaria ($n=3$–6, size: $11.5 \times 18 \times 18$ cm, WS salinity 28‰, RB salinity 35‰) held the experimental species at the desired temperature. Temperatures above 20 °C were maintained in basins with aquarium heaters (Tetra™ (20 °C, 25 °C), Reptistat™ (35 °C, 40 °C) and Schlego™ heaters (40 °C, 45 °C)). In Roebuck Bay, temperatures below 20 °C were maintained in basins that were held in air-conditioned rooms (20 °C, 15 °C), Engel™ refrigerator units (10 °C, 5 °C) and ice (0 °C). For the Wadden Sea species, cool temperature basins were maintained in a climate room (15 °C), a temperature controlled water bath using anti-freeze (MGW Lauda K2R) (10 °C, 5 °C), basins with ice (0 °C) and a temperature controlled cabinet (Weiss Enet Model HETK 3057.S, The Netherlands) (−5 °C, −10 °C). In the temperature treatment of −5 °C, aquaria filled with sea water were placed directly into the refrigerator unit. Temperature readings were taken every four hours. As temperatures varied by 1–2 °C, the average temperature from each basin, during an experimental trial, was used in the final analysis.

2.4. Phylogenetic analysis

Related species can share similar adaptations such that species can no longer be regarded as independent samples (Felsenstein, 1985). To establish whether such effects of evolutionary history should be of concern, we examined whether the lethal thermal limits at both sites were related to phylogeny. In this study the phylogenetic topology of the bivalve species was drawn from Giribet and Wheeler (see Fig. 11, p 296, in Giribet and Wheeler, 2002) and family descriptions from Beesley, Ross, and Wells (1998). To examine whether the bivalve thermal limits were phylogenetically constrained (Harvey and Pagel, 1991), a test for serial independence was run (Abouheif, 1999; Reeve and Abouheif, 2003). In each simulation the relationship between lethal thermal limits and phylogeny was non-significant: upper lethal thermal limits $P=0.48$, lower lethal thermal limits $P=0.36$, lethal thermal range $P=0.38$. Therefore, as the lethal thermal limits were not significantly correlated with phylogeny, traditional statistical analyses can be safely applied (Abouheif, 1999; Ackerly and Reich, 1999).

2.5. Tidal height and upper thermal limits

Submergence time was calculated from the two spatial mapping databases available for each location (see Pepping et al., 1999; Piersma et al., 2001). Based on the positive occurrence of species in the spatial mapping database we calculated an average submergence time (hours) for each species. The average submergence time was then converted into a percentage (12.42 h is a full tidal cycle). Average submergence time (%) was estimated for all species, except for the two hard substrate species.

2.6. Statistical analyses

As mortality is a sigmoid function of temperature, a logit linear regression was used to separately estimate the upper and lower thermal limit of each species trial (day $n=2$, season $n=2$), and each replicate within a trial (basin $n=2$). The coefficients of the logit linear regression were used to calculate the temperature at which half of the sample population died within 24 h. All lethal thermal limit values are presented as a mean and standard error in the results.

Upper lethal thermal limits were tested separately for each species using a two-way ANOVA to examine differences between season and replicate species' trials. In species where season was not tested, a one-way ANOVA was used to examine differences between replicate species' trials. A summary of these statistical

Table 1
Lethal thermal limit values of the Roebuck Bay and Wadden Sea species

	Season	Upper thermal tolerance limits (°C)							n	Lower thermal tolerance limits (°C)							n	Range (°C)	Subm. Time (%)
		Mean	S.E.	DF	F-value	P (S.T.)	F-value	P (season)		Season	Mean	S.E.	DF	F-value	P (S.T.)				
Roebuck Bay species																			
Anadara granosa (Linné)	Spring	41.45	1.31	2,3	330.39	<0.01		–	6	4.82	1.31	0.01	1,2	142.20	0.01		4	36.63	21.97
Barbatia pistachia (Lamarck)	Spring	36.22	0.53	1,5	0.043	0.85	0.99	0.37	8	6.01	0.81	0.07	1,2	13.21	0.07		4	30.21	
	Winter	36.87	0.29																
Anadontia bullula (Reeve)	Spring	36.31	0.81	1,2	9.56	0.09		–	4	7.17	1.65	0.62	1,2	0.33	0.62		4	29.14	39.87
Divericella irpex (Smith)	Spring	36.94	0.51	1,2	2.42	0.26		–	4	5.51	0.52	0.93	1,2	0.01	0.93		4	31.43	39.38
Anomalocardia squamosa (Linné)	Spring	37.30	0.42	1,5	0.63	0.81	0.45	0.53	8	3.05	0.73	0.37	1,2	1.35	0.37		4	34.25	25.63
	Winter	37.76	0.45																
Gafrarium dispar (Holten)	Spring	41.76	1.44			–		–	2	7.32	0.49				–		2	34.44	17.14
Siliqua sp.	Spring	33.45	0.80	1,5	5.75	0.06	1.23	0.32	8	6.14	0.40	0.31	1,2	1.81	0.31		4	27.31	40.64
	Winter	31.99	1.57																
Tellina capsoides (Lamarck)	Spring	37.97	0.85	1,5	2.35	0.19	0.13	0.74	8	3.35	0.24	0.00	1,2	9147.56	0.00		4	34.61	17.09
	Winter	38.25	0.21																
Tellina piratica (Hedley)	Spring	37.58	0.10	1,5	0.69	0.44	0.28	0.62	8	3.63	0.87	0.03	1,2	37.97	0.03		4	33.95	34.54
	Winter	37.42	0.28																
Tellina sp. (oval)	Spring	36.31	0.81	1,5	0.24	0.65	0.42	0.54	8	3.52	0.95	0.12	1,2	7.00	0.12		4	32.80	11.17
	Winter	35.75	0.08																
Corbula sp.	Spring	37.72	0.92	1,2	59.50	0.02		–	4	5.46	0.60	0.95	1,2	0.01	0.95		4	32.26	58.97
Wadden Sea species																			
Mytilus edulis (Linné)	Winter	28.34	0.11	1,5	0.41	0.55	1.02	0.36	8	−13.40	1.49	0.09	1,2	10.20	0.09		4	41.73	
	Spring	27.41	0.87																
Cerastoderma edule (Linné)	Winter	32.19	0.63	1,5	0.10	0.77	3.23	0.13	8	−6.18	0.34	0.48	1,2	0.74	0.48		4	38.38	60.03
	Spring	33.98	0.67																
Spisula subtruncata (da Costa)	Winter	26.97	0.64	1,5	0.95	0.38	0.09	0.78	8	–	–								100.00
	Spring	26.60	1.07																
Mya arenaria (Linné)	Winter	30.46	0.20	1,2		–	2.91	0.23	4	–	–								62.27
	Spring	31.32	0.47																
Abra tenuis (Montagu)	Winter	33.44	0.73	1,2	0.00	0.99		–	4	−1.68	0.07	0.88	1,2	0.03	0.88		4	35.12	45.03
Macoma balthica (Linné)	Winter	29.43	0.39	1,5	1.89	0.23	15.62	<0.01	8	−7.01	0.61	0.44	1,2	0.92	0.44		4	36.45	65.69
	Spring	30.97	0.14																
Tellina tenuis (da Costa)	Winter	27.57	0.50	1,2	109.35	<0.01		–	4	–	–								72.37

The mean upper and lower lethal thermal limits (including standard error (SE)) are shown. The one- and two-way ANOVA's results for differences between replicate species' trials (S.T.) and seasons are included (degrees of freedom (DF), F-value and P-value). No data is indicated by a slash (−). The replicate trials are indicated by n. The lethal thermal tolerance range and the average submergence (subm.) time are included for each species. Authority names from McMillan (1968) and from Lamprell and Whitehead (1992).
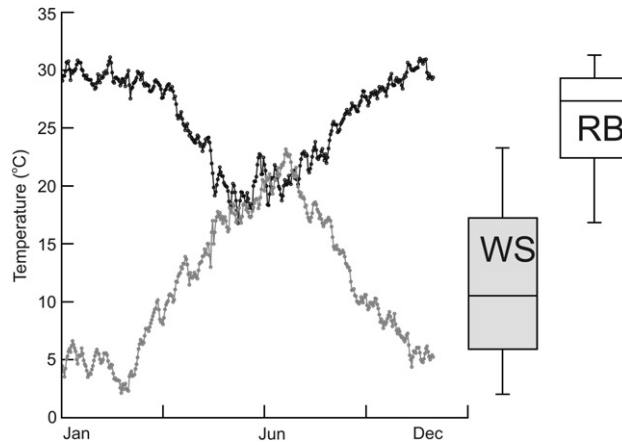
Fig. 1. Annual and daily temperature variation at a tropical and temperate tidal flat. The dots represent the average daily temperature at each location. The black line represents Roebuck Bay (RB) and the grey line represents the Wadden Sea (WS). June temperatures are winter in Roebuck Bay and summer in the Wadden Sea. The boxplots show the annual temperature range. A boxplot shows 50% of the measured values, with the whiskers representing the outliers. The line in the middle of the boxplot represents the median value.

results are presented in Table 1. To determine whether the upper and lower lethal thermal limits are correlated, we ran a Pearson correlation. The lethal thermal tolerance windows (upper–lower thermal limits) of all the species were calculated and tested for a difference between the two locations in a one-way ANOVA. All
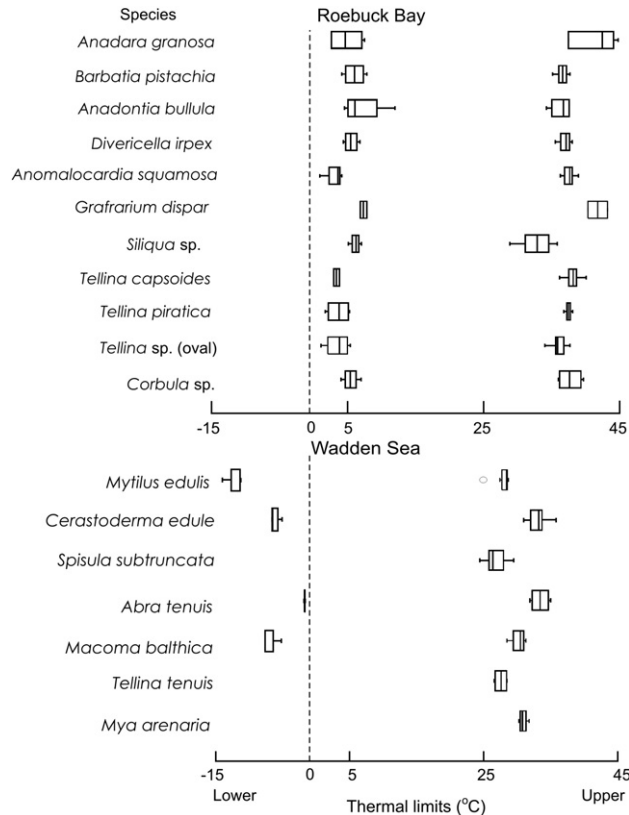

Fig. 2. Upper and lower lethal thermal limits of bivalve species from Roebuck Bay and the Wadden Sea. The boxplot of each species represents the range of basin, day and season estimates. The stippled line represents the 0 °C value. A boxplot displays the median, the upper and lower quartile. The values lying outside of the box are shown as whiskers, and large and small outliers are indicated by circles and asterisks, respectively.
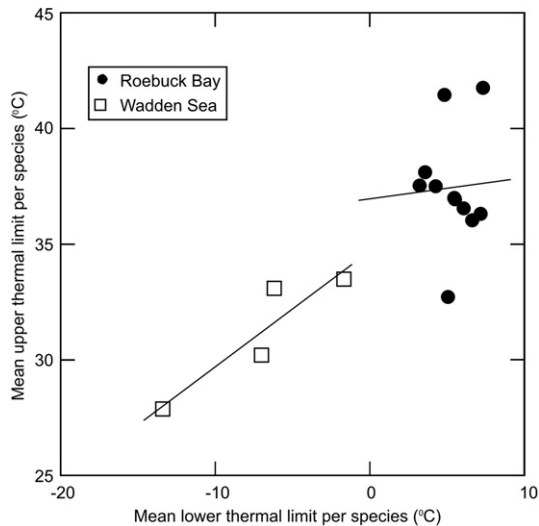
Fig. 3. The relationship between the upper and lower lethal thermal limits at each location. In Roebuck Bay there is no correlation between the mean upper and lower lethal thermal limits, whereas in the Wadden Sea a correlation is apparent but not significant.

statistical analyses were performed in the statistical package, Systat® version 11.

3. Results

The temperature data demonstrated that the tidal flat temperatures at Roebuck Bay showed less annual variation (5.64±2.05 °C, mean±SD of difference between upper and lower quartile) than the Wadden Sea (9.74±2.11 °C, mean±SD of difference between upper and lower quartile) (Fig. 1). The Roebuck Bay tidal flat also attained higher maximum (32.51±0.17 °C, mean±SE) and minimum (18.82±0.75 °C, mean±SE) average daily temperatures relative to the Wadden Sea tidal flat (22±1.14 °C maximum and 1.89±0.59 °C minimum, mean±SE).

The average lethal thermal tolerance windows of the Roebuck Bay bivalve species were significantly narrower ($F_{1,56}=42.29$, $P<0.01$, 32.25±0.52 °C) than the four Wadden Sea species (38.52±0.78 °C, Fig. 2). Furthermore, consistent with the field temperatures, the Roebuck Bay species displayed both higher average upper (37.11±0.33 °C) and higher average lower lethal thermal limits (4.98±0.32 °C, Fig. 2), than the Wadden Sea species whose average upper lethal thermal limits were 29.80±0.42 °C and average lower lethal thermal limits were −7.07±1.14 °C. Thus, the Roebuck Bay bivalves can survive about 5 °C above their average maximum habitat temperatures, whereas the Wadden Sea species can survive by about 7 °C above their average maximum habitat temperatures. The lower lethal

thermal limits of the Roebuck Bay bivalves were about 14 °C below their average minimum field temperatures, and the Wadden Sea bivalves survived about 9 °C below their minimum field temperatures. In the Wadden Sea species there was also a tendency for the average upper and lower lethal thermal limits to be positively correlated ($P=0.10$, Fig. 3), with no trend in the Roebuck Bay species ($P=0.93$).

In the Wadden Sea tidal flat, the average field temperature in February was approximately 4 °C and in May was approximately 14 °C (Fig. 1). These seasonal differences in field temperature are, however, not reflected by a change in the upper lethal thermal limits of the Wadden Sea bivalves ($P\geq0.05$ in Table 1). Only Macoma balthica showed a slight increase of 1.5 °C in temperature tolerance from winter to spring ($F_{1,5}=15.62$, $P=0.01$ in Table 1). Within the sediment of the Roebuck Bay tidal flat, the average field temperature in June was approximately 19 °C and in November was approximately 29 °C. The upper lethal thermal limits of the Roebuck Bay bivalve species, however, did not show a response to an increase in seasonal temperature ($P\geq0.05$ in all cases, Table 1). Furthermore, the statistical effect of replicate species' trial was mainly not significant at both locations ($P\geq0.05$ in most cases, Table 1), as only three out of 16 species showed a significant difference. This suggests that the experimental results are robust.

Within the Roebuck Bay tidal flat, the bivalves showed no significant relationship between their upper lethal thermal limits and average submergence time ($r=-0.38$,
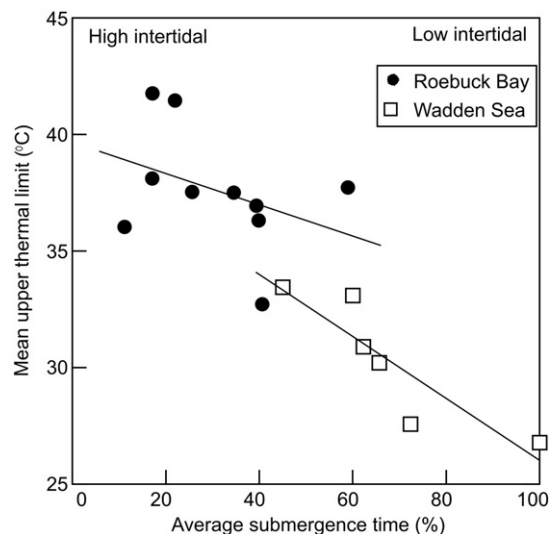

Fig. 4. The relationship between the upper lethal thermal limits of each species and submergence time (%). The upper lethal thermal limits of the Wadden Sea species are correlated with submergence time, whereas the upper lethal thermal limits of the Roebuck Bay species are not.

$n = 10$, $P = 0.28$, Fig. 4). However, in the Wadden Sea tidal flat the bivalves did show a significant negative relationship between upper lethal thermal limits and average submergence time ($r = -0.88$, $n = 6$, $P = 0.02$) (Fig. 4). In the Wadden Sea, the two high intertidal species (*Cerastoderma edule* and *Abra tenuis*) showed higher upper thermal limits than the predominantly low intertidal and subtidal species (*Tellina tenuis* and *S. subtruncata*) (Fig. 4). In addition, the hard substrate species (*M. edulis*) in the Wadden Sea displayed a significantly reduced upper lethal thermal limit relative to the other tidal flat species (excluding the subtidal North Sea *S. subtruncata*, $F_{1,34} = 7.69$, $P < 0.01$) (Table 1). In contrast, the hard substrate species at Roebuck Bay (*B. pistachia*) did not have a significantly reduced upper lethal thermal limit ($F_{1,66} = 0.33$, $P = 0.57$) compared to the temperate species (*M. edulis*).

4. Discussion

In agreement with the climate variability hypothesis, the temperate species from the Wadden Sea tidal flat had lethal thermal tolerance windows approximately 7 °C greater than those of the tropical Roebuck Bay species that appeared to reflect the greater temperature variation measured in the temperate sediments. This shows that the Wadden Sea species can survive across a wider range of temperatures before they cease to function. The tropical Roebuck Bay species displayed an ability to survive higher temperatures in their upper lethal thermal limits than the temperate species, whereas the temperate Wadden Sea species survived cooler temperatures than the tropical species. These results are consistent with studies on crabs Decapoda. Tropical fiddler crabs (*Uca*) could not survive cool temperatures (Vernberg and Tashian, 1959), and tropical crabs from the Genus *Uca* and *Petrolisthes* had higher upper lethal thermal limits than temperate crabs (Vernberg and Tashian, 1959; Stillman and Somero, 2000; Stillman, 2002).

In the temperate Wadden Sea the local tidal flat temperatures dropped markedly from summer to winter, and concurrent with this observation, the species showed a remarkable ability to survive freezing temperatures. Freezing resistance has also been reported in other molluscs (Davenport and Davenport, 2005; Peck and Conway, 2000). Although the exact cause of death as the result of freezing is still debated, cell damage due to either or both changes in osmotic gradients and ice-crystal damage are considered most likely (Loomis, 1995). In insects, lower lethal thermal limits show the most dramatic change with latitude (Addo-Bediako et al., 2000; Sinclair et al., 2003). Whether lower lethal thermal limits display the greatest change with latitude in marine invertebrates is unknown. However, our results indicate that the lower lethal thermal limits display greater differences between the tropical and temperate species than the upper lethal thermal limits. In marine invertebrates it is expected that freeze tolerance enabled range expansion into colder waters (Aarset, 1982).

Seasonal acclimatization differences were not apparent in the upper and lower lethal thermal limits of most species at both locations. The lack of a seasonal effect is not necessarily surprising, as previously established seasonal changes in bivalve lethal thermal limits were generally small, only a 1–2 °C change in lethal thermal limits with an increase of 10–15 °C in water temperature (Ansell et al., 1980a,b). Furthermore, interspecific differences in upper lethal thermal limits have been shown to be greater than acclimation-induced effects in porcelain crabs (Stillman and Somero, 2000). Although acclimation of lethal limits was very limited, this does not exclude the importance of thermal acclimation for physiological processes in the normal "operating temperature ranges".

Like Davenport and Davenport (2005) for rocky intertidal molluscs, we found that the upper and lower lethal thermal limits of the Wadden Sea species were positively correlated, with a 10% likelihood that the correlation represents a chance event. A positive correlation between the upper and lower lethal thermal limits might suggest a trade-off in the physiological mechanisms needed to deal with upper and lower thermal limits (Pörtner, 2002). A trade-off suggests that in adapting to new environments and acquiring new characters or greater performance, organisms sometimes experience a correlated decline in other structures or functions (Pörtner et al., 2006).

At a local-scale the average upper lethal thermal limits and submergence time were negatively correlated in the Wadden Sea, and thus to encountered temperature variation. This result is in agreement with other studies from buffered sandy substrates that have only studied one to three bivalve species across a tidal gradient (Ansell et al., 1980a,b). In porcelain crabs (*Petrolisthes*), upper lethal thermal limits were related to tidal height, and are expected to have evolved in response to microhabitat temperatures as they were not related to phylogeny (Stillman and Somero, 2000; Stillman, 2002). This suggests that at a local scale lethal thermal limits in bivalves can predict local distributions. Interestingly, recent evidence has shown that temperatures within the 'normal' performance range of an organism are also important for understanding species' distributions. For example, a small rise in temperature just outside the

'normal operating temperature range' of an organism, rather than heat-induced death per se, can result in a lowered scope for growth and reproduction (Pörtner and Knust, 2007; Wang and Overgaard, 2007).

The lack of a negative correlation between upper lethal thermal limits and submergence time in Roebuck Bay might be due to the species' occurrences over a more limited range of higher intertidal areas than the Wadden Sea species. Alternatively, the larger range of sediment and habitat types at Roebuck Bay (Pepping et al., 1999) might provide a wider variety of microhabitats that enable lower body temperatures to be maintained at higher tidal elevations (Helmuth, 2002), i.e. species at high intertidal levels do not experience more temperature variation than low intertidal species.

The upper lethal thermal limit of *M. edulis*, from the Dutch Wadden Sea, showed a significantly lower upper lethal thermal limit relative to the other species at this location. This is surprising as it could be expected that a rocky intertidal species would have higher upper lethal thermal limits, than sedimentary tidal flat species, which are buffered by a layer of sediment and interstitial water. One explanation for a lower upper lethal thermal limit in *M. edulis*, relative to the tidal flat species, is that this species usually lives as a cluster of bivalves attached together by byssal threads. Living as a cluster protects this species from temperature extremes (Helmuth, 1998). In contrast to *M. edulis*, a lower lethal thermal limit is not displayed in the rocky intertidal species (*B. pistachia*) from Roebuck Bay that lives in clusters within rock crevices. These contradicting results might suggest that upper lethal thermal limits are dependent on the microhabitat of an individual species (Helmuth, 2002).

Results from our study suggested that the tropical species live closer to their maximum habitat temperature (~ 4.6 °C) than the temperate species (~ 7.8 °C). To examine whether this trend was general at a global scale, we compiled data from the literature, and compared the upper lethal thermal limits in relation to the maximum habitat temperature of bivalve species from sites in the northern and southern hemisphere, using an analysis of covariance (Fig. 5, Appendix A). The upper lethal thermal limits of bivalves were correlated with maximum habitat temperature ($F_{1,47} = 12.87$, $P < 0.01$), and exceeded maximum temperatures by an average of 7.12 ± 0.52 °C, in all but two (*Donax semistriatus* (G) and *Siliqua* sp. (J)) cases. There was no difference in the regression slopes of the northern and southern hemisphere species ($F_{1,46} = 2.38$, $P = 0.13$). Most strikingly, the species inhabiting higher temperatures live closer to their maximum habitat temperatures (*t*-value 4.33, $P < 0.01$). In crabs upper thermal limits were also closer to maximum habitat

temperatures at tropical sites than temperate sites (Stillman and Somero, 2000; Somero, 2002).

The observed relationship between upper lethal thermal limits and habitat temperatures at both global and local habitat scales, in this study, tally well with the suggestions of Stillman and associates (Stillman and Somero, 2000; Stillman, 2002). Stillman et al. suggested that there are physiological costs involved in maintaining higher thermal tolerance limits, and that temperate species maintain a broader capacity to survive changes in temperature. Furthermore, it can be expected that differing thermal window widths in various climates are associated with physiological costs (Pörtner et al., 2006).

The thermal tolerance windows of bivalves, as estimated by lethal thermal limits, are consistent with the climate variability hypothesis; revived by Stevens (1989). To quantify thermal limits at a global-scale, future studies might increase the geographic range of study, and determine whether differently defined thermal limits, i.e. pejus temperatures, show a similar or stronger response to geographical location (Pörtner, 2002; Osovitz and Hofmann, 2007). Finally, our finding of narrower lethal thermal tolerance ranges in tropical species places the suggestion that tropical areas act as source habitats for bivalve speciation and range expansion towards temperate and high-latitude zones (Jablonski et al., 2006) in an
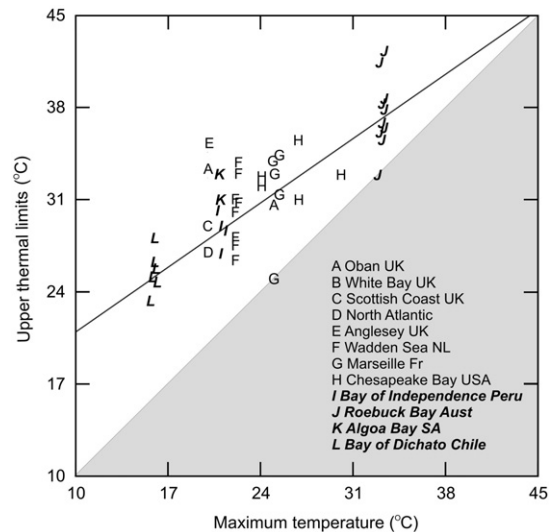

Fig. 5. The relationship between the upper lethal thermal limits and the maximum habitat temperature of bivalves from a number of sites shows a difference between warmer and colder living bivalves. As the regression slope of the bivalve upper lethal thermal limits is significantly different from 1 (i.e. the grey shaded area), this indicates that species inhabiting warmer temperatures live closer to their maximal habitat temperatures than temperate species. The basic data are presented in Appendix A.

interesting light. On the basis of our results only, we would predict temperate species to have a higher chance to invade tropical areas rather than the reverse.

Appendix A

The mean upper lethal thermal limits (ULT50) from other bivalve studies at northern and southern latitudes. The place name indicates where the study was conducted. The maximum temperature reported with the studies at each site is included (MaxT). The acclimation (Acc) temperature used prior to testing the upper thermal limits is also included. The majority of studies share the same protocol of observing death in bivalves after 24 h. Missing location positions (latitude and longitude) were estimated using Google Earth™. The maximum temperature at Algoa Bay has been taken from another article (Hicks et al., 2001), and the maximum temperature for White Bay was estimated from UK DMAP.

Species	Site	Location	Habitat	Acc	ULT50	MaxT	Latitude	Longitude	Author
Donax vittatus	Scottish Coast	Scotland, UK	Sediment	15	29	20	56.24N	5.28W	Ansell et al. (1980a)
Donax semistriatus	Marseille	France	Sediment	15	25	25	43.17N	5.22E	Ansell et al. (1980a)
Donax trunculus	Marseille	France	Sediment	15	33	25	43.17N	5.22E	Ansell et al. (1980a)
Tellina fabula	North Atlantic	Scotland, UK	Sediment	15	27	20	56N	5W	Ansell et al. (1980b)
Tellina tenuis	Oban	Scotland, UK	Sediment	15	31	25	56.24N	5.28W	Ansell et al. (1980b)
Tellina tenuis	Marseille	France	Sediment	15	34	25	43.17N	5.22E	Ansell et al. (1980b)
Cardium edule	Oban	Scotland, UK	Sediment	15	33	20	56.24N	5.28W	Ansell et al. (1981)
Cardium glaucum	Marseille	France	Sediment	15	34	25	43.17N	5.22E	Ansell et al. (1981)
Cardium tuberculum	Marseille	France	Sediment	15	31	25	43.17N	5.22E	Ansell et al. (1981)
Donax serra	Algoa Bay	South Africa	Beach	20	33	21	34.01S	25.42E	Ansell and McLachlan (1980)
Donax sordidus	Algoa Bay	South Africa	Beach	20	31	21	34.01S	25.42 E	Ansell and McLachlan (1980)
Mytilus edulis	White Bay	Scotland, UK	Rocks		30.7		55.47N	4.54W	Davenport and Davenport (2005)
Mya arenaria	Chesapeake Bay	N.E. America	Estuarine	20	31	27	36.55N	76.24W	Kennedy and Mihursky (1971)
Gemma gemma	Chesapeake Bay	N.E. America	Estuarine	20	35.6	27	36.55N	76.24W	Kennedy and Mihursky (1971)
Mulinia lateralis	Chesapeake Bay	N.E. America	Estuarine	20	32.4	24	36.55N	76.24W	Kennedy and Mihursky (1971)
Macoma balthica	Chesapeake Bay	N.E. America	Estuarine	20	32.6	24	36.55N	76.24W	Kennedy and Mihursky (1971)
Macoma phenax	Chesapeake Bay	N.E. America	Estuarine	20	32.9	30	36.55N	76.24W	Kennedy and Mihursky (1971)
Mytilus galloprovincialis		France			31	22	42N	5E	Masse and Parache (1984)
Abra tenuis	Wadden Sea	N.W. Europe	Sediment	4 and 14	33.44	22	53N	4-6E	This study
Cerastoderma edule	Wadden Sea	N.W. Europe	Sediment	4 and 14	33.09	22	53N	4-6E	This study

Appendix A (*continued*)

Species	Site	Location	Habitat	Acc	ULT50	MaxT	Latitude	Longitude	Author
Macoma balthica	Wadden Sea	N.W. Europe	Sediment	4 and 14	30.20	22	53N	4-6E	This study
Mytilus edulis	Wadden Sea	N.W. Europe	Sediment	4 and 14	27.87	22	53N	4-6E	This study
Mya arenaria	Wadden Sea	N.W. Europe	Sediment	4 and 14	30.89	22	53N	4-6E	This study
Spisula subtruncata	Wadden Sea	N.W. Europe	Sediment	4 and 14	26.78	22	53N	4-6E	This study
Tellina tenuis	Wadden Sea	N.W. Europe	Sediment	4 and 14	27.57	22	53N	4-6E	This study
Anadara granosa	Roebuck Bay	N.W. Australia	Sediment	19 and 29	41.45	33	17S	122E	This study
Anadontia bullula	Roebuck Bay	N.W. Australia	Sediment	19 and 29	36.31	33	17S	122E	This study
Anomalocardia squamosa	Roebuck Bay	N.W. Australia	Sediment	19 and 29	37.53	33	17S	122E	This study
Corbula sp.	Roebuck Bay	N.W. Australia	Sediment	19 and 29	37.72	33	17S	122E	This study
Divericella irpex	Roebuck Bay	N.W. Australia	Sediment	19 and 29	36.94	33	17S	122E	This study
Grafrarium dispar	Roebuck Bay	N.W. Australia	Sediment	19 and 29	41.76	33	17S	122E	This study
Barbatia pistachia	Roebuck Bay	N.W. Australia	Sediment	19 and 29	36.55	33	17S	122E	This study
Siliqua sp.	Roebuck Bay	N.W. Australia	Sediment	19 and 29	32.72	33	17S	122E	This study
Tellina capsoides	Roebuck Bay	N.W. Australia	Sediment	19 and 29	38.11	33	17S	122E	This study
Tellina sp. (oval)	Roebuck Bay	N.W. Australia	Sediment	19 and 29	36.03	33	17S	122E	This study
Tellina piratica	Roebuck Bay	N.W. Australia	Rocks	19 and 29	37.50	33	17S	122E	This study
Laseaea rubra	Anglesey	Wales, U.K.	Rocks	15	34.95	20	53.18N	4.38W	Tyler-Walters and Davenport (1990)
Gari solida	Bay of Independencia	Peru	Sediment	16	26.9	21	14.15S	76.10W	Urban (1994)
Semele solida	Bay of Independencia	Peru	Sediment	16	28.5	21	14.15S	76.10W	Urban (1994)
S. corrugata	Bay of Independencia	Peru	Sediment	16	30.6	21	14.15S	76.10W	Urban (1994)
Actopecten purpuratus	Bay of Independencia	Peru	Sediment	16	29	21	14.15S	76.10W	Urban (1994)
Gari solida	Bay of Dichato	Chile	Sediment	13	23.7	16	36.32S	73.57W	Urban (1994)
Semele solida	Bay of Dichato	Chile	Sediment	13	25.1	16	36.32S	73.57W	Urban (1994)
Protothaca thaca	Bay of Dichato	Chile	Sediment	13	28.1	16	36.32S	73.57W	Urban (1994)
Venus antiqua	Bay of Dichato	Chile	Sediment	13	25.6	16	36.32S	73.57W	Urban (1994)
Tagelus dombeii	Bay of Dichato	Chile	Sediment	13	25.1	16	36.32S	73.57W	Urban (1994)
Ensis macha	Bay of Dichato	Chile	Sediment	13	25	16	36.32S	73.57W	Urban (1994)
Choromytilus chorus	Bay of Dichato	Chile	Sediment	13	26.3	16	36.32S	73.57W	Urban (1994)
Aulocomya ater	Bay of Dichato	Chile	Sediment	13	25.6	16	36.32S	73.57W	Urban (1994)

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