

# Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna

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**ABSTRACT:** Environmental temperature is a controlling factor in ecology and is influenced by global climate change. Upper/lower thermal limits for 10 species of sessile/sedentary invertebrates were established on a single rocky shore. Two species with different reproductive strategies (*Littorina littorea*, *Nucella lapillus*) from 3 Scottish and 3 Irish shores were investigated to test effects of small scale (<10 km) or larger scale (ca. 500 km) distances, and shore height on upper lethal temperature. At 3 sheltered and 3 exposed shores in Ireland, thermal responses of *N. lapillus* from the middle of their vertical distribution were compared. Amongst the 10 species from a single shore, thermal niche width rose asymptotically with maximum height of distribution on the shore and maximum emersion time. Median upper lethal temperature and median lower lethal temperature were closely correlated. For 8 species on the middle and upper shore, there were significant linear relationships between shore height and the variables upper lethal temperature, lower lethal temperature and thermal niche width. *L. littorea* upper lethal temperature was found not to vary with shore height, varied little over small geographical distances, but was significantly higher in Ireland than in Scotland. *N. lapillus* upper lethal temperature was higher in animals collected from the upper limit of distribution on the shore than in dogwhelks from the lower limit of distribution, was higher in animals taken from sheltered shores than from exposed shores and showed significant local differences. Upper lethal temperature was higher in Scottish than Irish dogwhelks.

**KEY WORDS:** Thermal niche · Intertidal invertebrates · *Littorina* · *Nucella*

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## INTRODUCTION

Temperature is regarded as the most important abiotic stress affecting ectothermic animals, since it has influences from population to molecular levels (e.g. Hochachka & Somero 2002). Relationships between environmental temperature, and organismal distribution and temperature tolerance have been widely studied, particularly in recent years as the impact of anthropogenically driven climate change has focused attention on thermal biology (e.g. Taschler & Neuner 2004). However, there has been controversy over the importance of thermal tolerance to intertidal vertical distribution of fauna. Some believe that physical factors, particularly temperature, control zonation pat-

terns (e.g. Lewis 1964, Newell 1979). Others have suggested that biotic factors determine zonation through competition for space/energy (e.g. Stephenson & Stephenson 1972), with animals subsequently becoming adapted to withstand thermal and desiccation stress (which are often intertwined) (e.g. Underwood 1979). Both factor categories probably contribute (Simpson 1976, Moore & Powell 1985). Connell (1961a,b) suggested that upper limits of distribution were set by environmental tolerances, while lower limits were controlled by biotic interactions. Several others have pointed out that the strengths of biotic influences are themselves influenced by temperature (e.g. Wethey 1983, 1984, Little 1990, Hodgkinson 1999). Sorte & Hofmann (2004) have recently demonstrated that the

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Pacific dogwhelk *Nucella canaliculata* shows greater levels of physiological stress (measured as concentrations of the heat shock protein Hsp70) at the southern (warm) limit of its distribution than at the cooler 'abundance centre' of the species, reinforcing the idea of physiological tolerance and distribution being linked. Somero (2002) provides a recent comprehensive review of the literature devoted to thermal tolerance in relation to vertical distribution in the intertidal zone.

Temperature tolerances of intertidal invertebrates, and temperature-related mortalities have long been recorded (e.g. Evans 1948), notably in Europe in the wake of the prolonged cold winter of 1962–63 (e.g. Crisp 1964). Several researchers have provided evidence to support the commonly held perception that animals living higher on the shore are more thermally tolerant than those living nearer to low water (e.g. Southward 1958, Vernberg & Vernberg 1972, Newell 1979, Underwood 1979). This is to be expected as sea temperatures vary much less than air temperatures, while the temperature of intertidal substrata will vary as a result of air temperature or insolation variations to a greater extent the longer the period of emersion. However, Helmuth (1998, 1999), Helmuth et al. (2002) and Harley & Helmuth (2003) have shown that the body temperatures of sessile/sedentary intertidal invertebrates have extremely complicated relationships with environmental conditions. Exposure, splash, wind velocity, aspect, body size, gregariousness and behaviour, local microclimates and timing of extreme tidal cycles combine to yield poor relationships with air temperature. For example, crevice dwelling in the limpet *Helcion pectunculus* was found to reduce body temperature by around 10°C (Gray & Hodgson 2004). As a consequence, the relationships between climate, climate change, latitude and thermal tolerance are unlikely to be straightforward (see Helmuth et al. 2002).

Few comparative estimations of temperature tolerance without temporal, acclimatory or geographical confounding have been attempted. Tyler Walters & Davenport (1990) found significant differences amongst median upper lethal temperatures (MULT) of different in-bred lines of the self-fertilizing hermaphrodite intertidal bivalve *Lasaea rubra*, with upper-shore 'clones' having significantly higher MULT values (by about 9°C) than genetically-distinct lower-shore populations. Davenport & MacAlister (1996) measured MULT and median lower lethal temperature (MLLT) in relation to maximum shore height (MSH) amongst 7 subantarctic sedentary/sessile intertidal species during summer at South Georgia. They found a significant linear relationship between MSH and MULT (with MULT rising with MSH), and between MSH and thermal niche width (TNW; difference between MULT and MLLT). This conflicted with McMahon's (1990) synthesis (based on

work on prosobranch molluscs) that indicated little or no change in thermal or desiccation resistance with tidal height until the eulittoral fringe was reached. Clarke et al. (2000) compared upper thermal tolerances of littorinid gastropod species from around the British Isles, using the heat coma criteria pioneered by McMahon (1990). They reported no effect of shore height on temperature tolerance, but variations between populations and species. Although they conducted experiments in summer (June to September), the total period of experimentation exceeded 70 d, while all animals were pre-acclimated to 12°C before experiments.

The objectives of the study were: (1) to study the thermal responses of common sedentary/sessile European rocky shore invertebrates in narrow time windows in summer and winter on a single shore, and (2) to test the hypothesis that MULT and MLLT are related to MSH. Acute, 24 h thermal tolerances were determined, since these allow ready comparison between different taxonomic groups and between upper and lower lethal temperatures (unlike otherwise useful criteria such as heat coma temperature [McMahon 1990], or use of programmed rates of temperature change [Davenport 1982]). Secondly, 2 abundant species with uncontroversial taxonomy and differing reproductive strategies (*Littorina littorea*, *Nucella lapillus*) were studied to investigate differences in thermal response between specimens collected (1) from different shore heights, (2) from different local shores (<10 km distance), (3) from shores ca. 500 km apart. Finally, for *N. lapillus*, differences in thermal response between specimens collected from neighbouring sheltered and exposed shores were investigated.

## MATERIALS AND METHODS

**Collection of species and assessment of distribution on shore.** White Bay, Great Cumbrae, Scotland (55° 45' N, 4° 57' W), was the site chosen for the main comparative study. It is a gently sloping, very sheltered shore (using the criteria of Hiscock 1996) and selected for its diversity and negligible exposure-driven elevation of zonation. The shore features early morning and early evening low spring tides; this minimizes heat stress to lower shore organisms. It is also north-facing, with a hill providing further inland protection from the morning sun. Specimens of target species (Table 1) were collected by hand and transferred to tanks supplied with running sea water (salinity ca. 33 psu) at ambient temperature; they were used in experiments within 48 h. It should be noted that all of the sedentary species appear to show no seasonal vertical migration on the shore. The availability of a nearby Admiralty recording tide gauge at the University Marine Biologi-

Table 1. Upper and lower thermal limits for 10 species of sedentary/sessile invertebrate species collected from White Bay, Great Cumbrae, Scotland. Median Upper Lethal Temperature (MULT) values were established in summer (July 2002), Median Lower Lethal Temperature (MLLT) in winter (January 2004). UC: upper 95% confidence limit for median value; LC: lower 95% confidence limit. Note that confidence intervals for median lethal temperatures derived from probit analysis are asymmetrical. Thermal niche width (TNW) = MULT – MLLT. Maximum shore height (MSH) is mean height above chart datum (n = 3). % time emersed' means % time emersed during the September 2003 spring-neap cycle at MSH

Species	MSH (m)	% time emersed	MULT (°C)	UC (°C)	LC (°C)	MLLT (°C)	UC (°C)	LC (°C)	TNW (°C)
Gastropods									
<i>Tectura tessulata</i>	0.803	8.5	25.5	25.7	25.2	-7.4	-7.0	-8.0	32.8
<i>Gibbula cineraria</i>	2.567	70.8	27.0	27.3	26.6	-1.1 <sup>a</sup>	-1.5	-1.9	28.1
<i>Nucella lapillus</i>	2.590	71.6	28.2	28.5	28.0	-6.4	-6.1	-6.6	34.6
<i>Littorina fabalis</i>	3.063	87.4	29.9	30.0	29.7	-13.3	-13.0	-13.4	43.3
<i>Littorina obtusata</i>	3.077	87.8	29.6	29.9	29.4	-13.0	-12.7	-13.2	42.9
<i>Littorina littorea</i>	3.073	87.7	35.3	35.6	35.0	-13.0	-12.9	-13.2	48.3
<i>Littorina saxatilis</i>	3.407	95.7	35.0	35.2	34.7	-16.4	-15.9	-17.0	51.4
Bivalves									
<i>Mytilus edulis</i>	2.900	82.5	30.5	30.7	30.2	-8.2	-7.4	-8.6	38.7
Barnacles									
<i>Balanus crenatus</i>	0.907	10.8	25.2	25.5	24.8	-1.4 <sup>a</sup>	-1.3	-1.6	26.6
<i>Semibalanus balanoides</i>	3.130	89.3	34.9	35.1	34.6	-14.6	-14.2	-15.0	49.5

<sup>a</sup>Died at a temperature above the freezing point of sea water so not killed by freezing

cal Station Millport allowed the ready determination of maximum upper level of distribution (maximum shore height, MSH) for each of the 10 sedentary/sessile species studied. On a spring tide, 3 transect lines perpendicular to the shoreline were set up, about 10 m apart. The position of the uppermost specimen observed within 2 m on either side of each transect line was determined for each species. As the tide rose, the time at which each uppermost specimen was inundated was recorded. Later, the corresponding tidal height above chart datum was obtained (accuracy ~2 cm) from the tide gauge record. In the case of one species (*Balanus crenatus*), it should be noted that all specimens recorded were phoretic, living on shells of living organisms (gastropods, mainly limpets *Patella vulgata*).

**Assessment of thermal tolerances.** Thermal tolerances were assessed as follows. For each target species (or population sample in shore height/wave exposure/geographical studies on periwinkles and dogwhelks), 20 freshly collected animals were exposed to each of a variety of temperatures within the range -20 to 40°C. Several temperature baths (accurate to ±0.1°C) were used simultaneously, so that all upper lethal temperatures were measured within a 10 d summer period (15 to 25 July 2002), and all lower lethal temperatures were measured within a 10 d winter period (12 to 22 January 2004); seasonal changes in lethal temperature were therefore minimized. September and January were chosen as they represent the warmest and coldest months of the year in Clyde Sea habitats. Animals were held in air in lidded glass or plastic vessels appropriate to their size together with

water-saturated paper towelling to ensure 100% relative humidity and placed in the temperature baths. A water-saturated atmosphere was used since achieving relative humidities below 100% is logistically extremely difficult (moving air is essential). Exposure temperatures were selected pragmatically to allow MULT and MLLT to be established for each species, using probit analysis (Finney 1971). Animals were exposed to temperatures for 24 h, then allowed to recover at ambient temperature for at least 2 h before assessment of mortality using binocular microscopes, forceps and needles to test for responsiveness. Probit analysis yields median values with asymmetrical 95% confidence intervals. Throughout this paper, significant differences between means ( $p < 0.05$ ) are assumed if 95% confidence intervals do not overlap. An exposure period of 24 h was chosen, partly because no single duration of exposure is biologically relevant to animals ranging from the lower shore to the upper shore, but also because short MLLT experiments are vulnerable to the relatively slow progress of the freezing process; cooling is dramatically slowed when freezing of body fluids starts. Pilot experiments showed that (1) all study species could tolerate emersion in humid air for at least 2 d and (2) at freezing temperatures, the tissues of all species reached the designated exposure temperatures within 12 h.

**Shore height and geographical experiments on periwinkles and dogwhelks.** *Littorina littorea*: To test the effect of shore height on MULT, periwinkles were collected in Co. Cork, Ireland on 14 September 2003 from 3 sites: Sandy Cove (51° 40.628' N, 8° 31.426' W: shel-

tered), Bullens Bay (51° 38.584' N, 8° 33.052' W: 4 km west of Sandy Cove, moderately exposed) and Garretstown Bay (51° 38.581' N, 8° 35.097' W: 2 km west of Bullens Bay, exposed). At each site, 200 periwinkles were collected from the uppermost part of the species' distribution and 200 from the lowest part of the intertidal distribution. Upper shore collections took place on the ebb tide. Lower shore collections took place between 1.5 h before and 1.5 h after LWS (at all 3 sites, the lowest point of distribution was elevated above LWS on that date). All collections took place within a period of 5 h. Collected periwinkle samples were held separately in plastic bags with wet seaweed until transferred to aerated seawater in the laboratory. Their acute 24 h MULT values were established (as above) in 3 d.

To test the effect of geographical distance (at ca. 10 and 500 km scales), periwinkles were collected from 3 sites on the island of Great Cumbrae, Scotland on 28 September 2003: White Bay (55° 47.499' N, 04° 54.5826' W), Ballochmartin Bay (55° 46.3452' N, 04° 53.9166' W: 3 km southwest of White Bay) and Farland Point (55° 44.781' N, 04° 54.6198' W: 3 km south of Ballochmartin Bay). They were transported to Ireland by air and held in aerated sea water. In Ireland, periwinkles were collected from the 3 Co. Cork sites described above on 30 September 2003 (i.e. 2 d later). The Irish shores were approximately 540 km in direct line from the Scottish shores. In both Scotland and Ireland, the periwinkles were collected from the middle of their distribution on the shore. Acute 24 h MULT values were established for all 6 sites over a period of 3 d.

***Nucella lapillus*:** To test the effect of shore height on MULT, dogwhelks were collected in Co. Cork, Ireland on 20 May 2004 from Sandy Cove, Bullens Bay and Garretstown Bay. At each site, 200 dogwhelks were collected from the uppermost part of the species' distribution and 200 from the lowest part of the intertidal distribution. Collection and holding were as described above for *Littorina littorea*. The dogwhelks' acute 24 h MULT values were established (as above) in 3 d.

To test the effect of geographical distance (at ca. 10 and 500 km scales), dogwhelks were collected from the same 3 Great Cumbrae Scottish sites and the 3 Co. Cork sites on 2 June 2004. The Scottish dogwhelks were transported to Ireland by air and held in aerated sea water. In both Scotland and Ireland, the dogwhelks were collected from the middle of their distribution on the shore. Acute 24 h MULT values were established for all 6 sites within 3 d.

**Wave exposure experiments on dogwhelks.** To test the effect of wave exposure on MULT, dogwhelks were collected from the middle of their distribution on each of 3 exposed and 3 sheltered shores within a total distance of 25 km on the coast of Co. Cork, Ireland on 16 August 2004. Three very exposed shores (using the cri-

teria of Hiscock 1996) were to the west of the Old Head of Kinsale, facing SW into the prevailing weather with no interrupting islands. Located between Garretstown and Fitzpatrick, over a total distance of 2.5 km, they are here described as Garretstown 1, 2 and 3; they were separated from one another by sandy beaches and had the following GPS locations: Garretstown 1, 51° 38.591' N, 08° 35.097' W; Garretstown 2, 51° 38.542' N, 08° 34.688' W; Garretstown 3, 51° 38.213' N, 08° 33.822' W. The 3 sheltered shores (criteria of Hiscock 1996) were all to the east of the Old Head of Kinsale and located over a distance of 18 km. They were protected from the prevailing weather, first by the Old Head, and secondly by being located in SE-facing coves: Sandy Bay Cove (51° 40.590' N, 08° 31.410' W), Roberts Cove (51° 44.641' N, 08° 18.653' W) and Myrtleville (51° 46.932' N, 08° 17.672' W). Acute 24 h MULT values were established for all 6 sites in 3 d. It should be noted that extreme daytime low tides occur at all 6 sites at around midday; this means that aspect-related thermal effects will be minimal (but not eliminated).

## RESULTS

### Shore distribution

For the 10 Scottish study species, maximum heights of distribution on the shore, together with corresponding maximum periods of emersion are displayed in Table 1 and Fig. 1. It is immediately evident that 2 of the 10 species (*Tectura tessulata* and *Balanus crenatus*) were limited to the lower shore and were emersed for <11% of a September spring-neap cycle, even at their uppermost position on the shore. The remaining 8 species, though variously distributed on the middle and upper shore, were all emersed for >70% of the tidal cycle at their maximum shore height. *Littorina saxatilis* had a noticeably higher limit on the upper shore than all other species, uppermost animals being emersed for about 96% of a September spring-neap cycle.

### Comparative thermal tolerances

Thermal tolerance data for 10 species at White Bay, Great Cumbrae, are displayed in Table 1. There were great differences in thermal tolerance amongst the species studied. It is evident that, for MULT, there was a 10°C difference between the lowest value (for *Tectura tessulata*) and the highest (*Littorina littorea*). For MLLT, the difference was greater, with about 15°C difference between the highest MLLT of *Gibbula cineraria* and the lowest of *Littorina saxatilis*. From Fig. 2, it is evident that there is a statistically significant curvi-

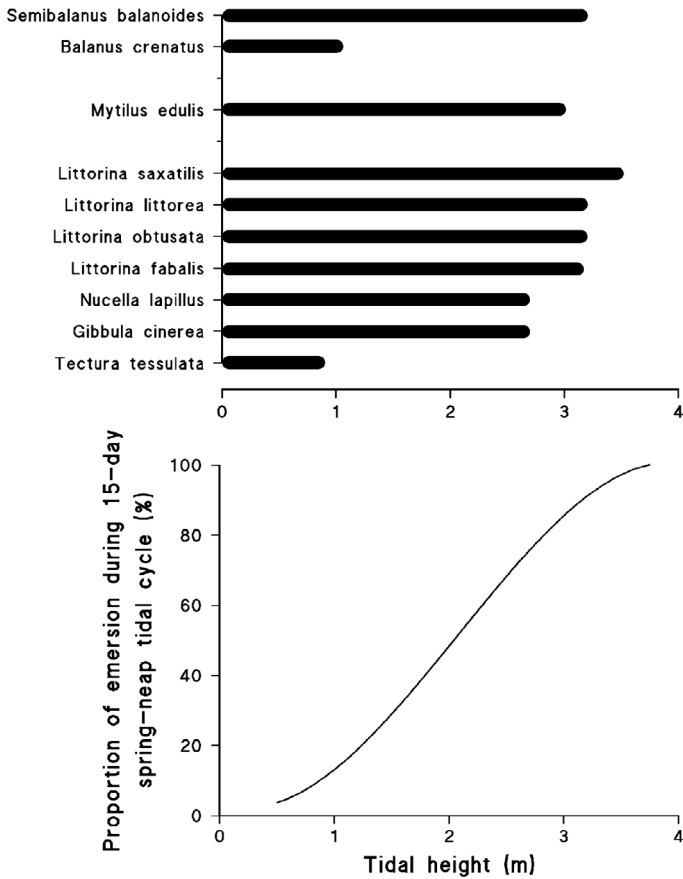


Fig. 1. Maximum shore height of 10 species of invertebrates and cumulative period of emersion during a September 2003 spring-neap tidal cycle at different tidal heights at White Bay, Great Cumbrae, Scotland (raw tidal data courtesy of the University Marine Biological Station Millport)

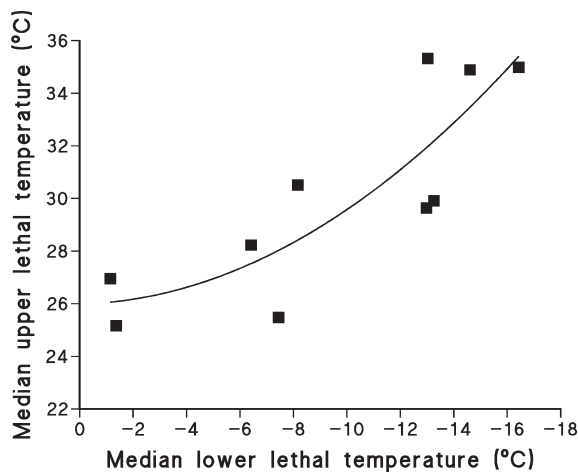


Fig. 2. Relationship between median upper lethal temperature (MULT: summer) and median lower lethal temperature (MLLT: winter) in 10 species of invertebrates (see Table 1 for species' names). (■) data for each species. Solid line: quadratic regression of data. Regression equation is:  $MULT = 25.98 - 0.0270 MLLT + 0.033 MLLT^2$  ( $r^2 = 72.5\%$ ,  $p = 0.011$ )

linear relationship between MULT and MLLT for the 10 species; animals that are tolerant of high temperatures are also tolerant of low temperatures. When thermal niche width is calculated (Table 1), it can be seen that the most tolerant upper shore species (*L. saxatilis*) has roughly double the thermal niche width (TNW) of the least tolerant (*Balanus crenatus*). From this table, it may be seen that 2 species could not tolerate freezing and died at temperatures above the freezing point ( $-1.9^{\circ}\text{C}$ ) of sea water (*G. cineraria*, *B. crenatus*). Otherwise, all species tolerated freezing temperatures.

Amongst the littorinid species, it was noteworthy that the closely related *Littorina fabalis* and *L. obtusata* exhibited virtually identical MULT and MLLT values. *L. littorea* had a significantly higher MULT, but similar MLLT. *L. saxatilis* showed a similar MULT to *L. littorea*, but a significantly lower MLLT (by  $3.4^{\circ}\text{C}$ ).

Figs. 3 to 5 consider the relationships between MSH and MULT, MLLT and TNW, respectively. Using MINITAB, curves were first fitted to the data for all 10 species. In all 3 cases, linear regression of temperature data against exponentiated MSH (i.e.  $MSH^x$ ) data yielded curves that were statistically significant and provided reasonable visual representation of the data. For MULT, the curve showed an initial steep increase in MULT with shore height, and then an asymptotic reduction in rate of increase in MULT towards the top of the shore. For MLLT, the curve showed an initial steep decrease in MLLT that also became asymptotic at high shore levels. Asymptotes were approximately

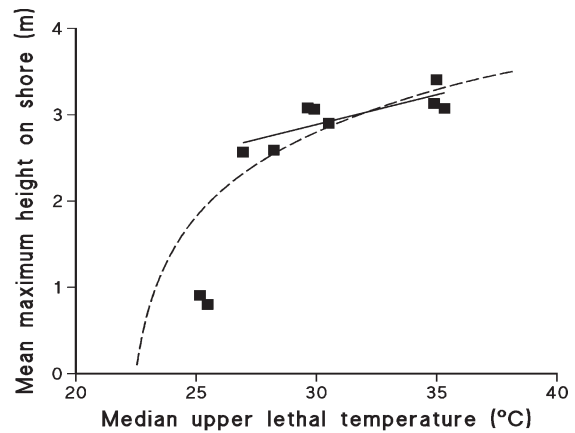


Fig. 3. Relationship between shore distribution (mean maximum shore height above chart datum, MSH) and median upper lethal temperature (MULT: summer) in 10 species of invertebrates (see Table 1 for species' names). (■) MULT values for each species. (a) Dashed line indicates exponential regression of all 10 species. Regression equation is:  $MULT = 23.9 + 0.373e^{(MSH)}$  ( $r^2 = 76.5\%$ ,  $p = 0.01$ ). (b) Solid line indicates linear regression of data for 8 species (omitting *Tectura tessulata* and *Balanus crenatus*). Regression equation is:  $MULT = 3.23 + 9.43 MSH$  ( $r^2 = 65.1\%$ ,  $p = 0.015$ )

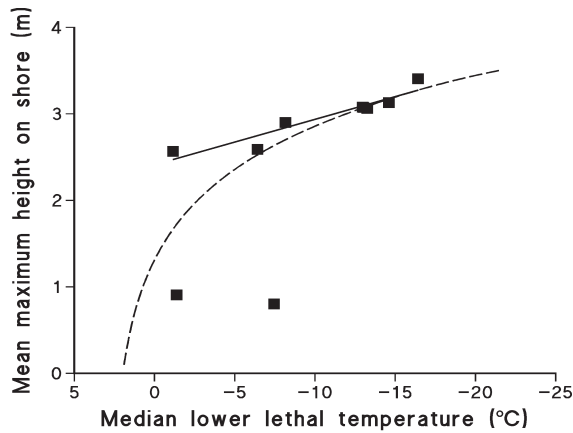


Fig. 4. Relationship between shore distribution (mean maximum shore height above chart datum, MSH) and median lower lethal temperature (MLLT winter) in 10 species of invertebrates (see Table 1 for species' names). (■) MLLT values for each species. (a) Dashed line indicates exponential regression of all 10 species. Regression equation is:  $MLLT = -1.20 - 0.496e^{(MSH)}$  ( $r^2 = 67.9\%$ ,  $p = 0.003$ ). (b) Solid line indicates linear regression of data for 8 species (omitting *Tectura tessulata* and *Balanus crenatus*). Regression equation is:  $MLLT = 38.86 - 17.01 MSH$  ( $r^2 = 89.2\%$ ,  $p = 0.0004$ )

35°C for MULT and -20°C for MLLT. TNW (dependent on MULT and MLLT) inevitably showed a similar asymptotic curve. This analysis indicates a general exponential curvilinear relationship between shore height and thermal tolerance, with exponential regressions explaining 68 to 78% of the data. Secondly, the 8 species that were emersed for >70% of the time at the uppermost limit of their distributions (i.e. omitting *Tectura tessulata* and *Balanus crenatus*) were further studied by simple linear regression analysis. This approach yielded statistically significant relationships for the remaining 8 species, with MULT rising with increased shore height and MLLT falling with increased shore height. The relationship between MSH and TNW was particularly strong ( $p = 0.0006$ ), with shore height explaining nearly 90% of the variation in TNW. Interestingly, the slope of the MULT regression (9.43) is shallower than the slope of the MLLT regression (17.01). This suggests that these 8 species are more constrained by high rather than low temperatures.

Similarly significant exponential and linear relationships (not presented) between % time emersed at MSH during spring neap cycles and MULT, MLLT and TNW were also found. For the 2 lower shore species (*Tectura tessulata* and *Balanus crenatus*), MULT was similar and much lower than for the other 8 species. For MLLT, the situation of these 2 species was less clear-cut; *B. crenatus* could not tolerate freezing temperatures, while *T. tessulata* tolerated lower temperatures than *Nucella lapillus* and could survive temperatures as low as those tolerated by *Mytilus edulis*.

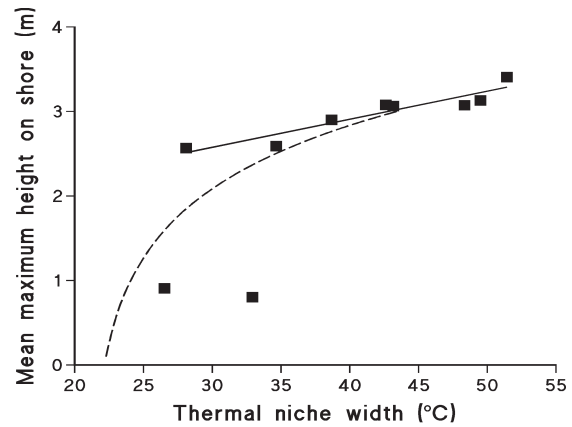


Fig. 5. Relationship between shore distribution (mean maximum shore height above chart datum, MSH) and thermal niche width (TNW: see text for definition) in 10 species of invertebrates (see Table 1 for species' names). (■) TNW values for each species. (a) Dashed line indicates exponential regression of all 10 species. Regression equation is:  $TNW = 25.1 + 0.869e^{(MSH)}$  ( $r^2 = 78.0\%$ ,  $p = 0.001$ ). (b) Solid line indicates linear regression of data for 8 species (omitting *Tectura tessulata* and *Balanus crenatus*). Regression equation is:  $TNW = 26.44 MSH - 36.67$  ( $r^2 = 87.7\%$ ,  $p = 0.0006$ )

### Shore height and geographical experiments on periwinkles and dogwhelks

#### *Littorina littorea*

Fig. 6 displays MULT values for periwinkles collected at the top and bottom of intertidal distributions on 3 shores in Co. Cork, Ireland. On all 3 shores, there

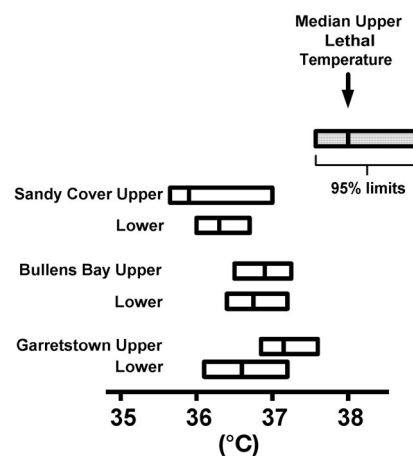


Fig. 6. *Littorina littorea*. Upper lethal temperatures of periwinkles collected on 14 September 2003 from 3 shores in Co. Cork, Ireland. For each shore, animals were collected at low water from the lowest part of the intertidal distribution ('Lower') and the highest point ('Upper'). Note that confidence intervals for median upper lethal temperature derived from probit analysis are asymmetrical

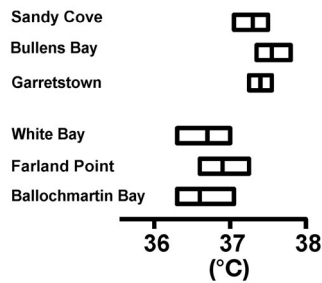


Fig. 7. *Littorina littorea*. Upper lethal temperatures of periwinkles collected from 3 shores (White Bay, Farland Point, Ballochmartin Bay) on Great Cumbrae, Scotland, on 28 September 2003, and 3 shores (Sandy Cove, Bullens Bay, Garretstown) in Co. Cork, Ireland on 30 September 2003 (i.e. 48 h apart). In both countries, periwinkles were collected from the middle of the distribution. Key as in Fig. 6

was no significant difference (i.e. 95% confidence intervals for median values overlapped) in MULT between upper and lower animals. This was confirmed by calculations on pooled data (upper shore MULT 37.0°C, lower 95% confidence limit [lcl] 36.8°C, upper 95% confidence limit [ucl] 37.2°C; lower shore MULT 36.6°C lcl 36.4°C, ucl 36.9°C). Generally, there was little inter-shore difference in MULT; the only statistically significant difference (i.e. 95% confidence intervals for median values non-overlapping) was between the sample from the lower limit of distribution at Sandy Cove and the sample from the upper limit of distribution at Garretstown.

Fig. 7 displays MULT values for periwinkles collected from the middle of the distribution on 3 Irish and 3 Scottish shores. There were no significant differences between MULT values within countries, but the Irish samples had rather higher MULT values than the Scottish ones (significantly so when pooled data were compared: Scottish MULT 36.7°C, lcl 36.5°C, ucl 36.9°C; Irish MULT 37.4°C, lcl 37.2°C, ucl 37.6°C). However, the difference in pooled MULT was small (0.7°C).

#### *Nucella lapillus*

Fig. 8 displays MULT values for dogwhelks collected at the top and bottom of intertidal distributions on 3 shores in Co. Cork, Ireland. On 2 out of 3 shores (Sandy Cove, Garretstown), there were significant differences between the MULT values of dogwhelks from the upper and lower limits of intertidal distribution, with upper limit animals displaying significantly higher MULT values. This was particularly marked at Garretstown, where the difference in MULT was about 1.6°C. Pooled data for all 3 shores (upper shore

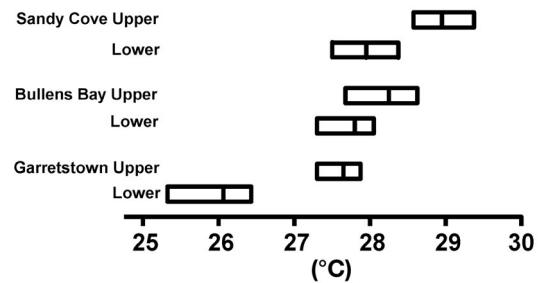


Fig. 8. *Nucella lapillus*. Upper lethal temperatures of dogwhelks collected on 20 May 2004 from 3 shores in Co. Cork, Ireland. For each shore, animals were collected at low water from the lowest part of the intertidal distribution ('Lower') and the highest point ('Upper'). Key as in Fig. 6

MULT 28.3°C, lcl 28.0°C, ucl 28.3°C; lower shore MULT 27.1°C, lcl 26.8°C, ucl 27.4°C) confirm a significant intraspecific effect of shore height on MULT (difference in median = 1.2°C).

Fig. 9 displays MULT values for dogwhelks collected from the middle of the distribution on 3 Irish and 3 Scottish shores. There were significant differences between MULT values within both countries; Garretstown values were lower than the other 2 Irish sites; Farland Point values were significantly lower than those recorded from Ballochmartin Bay in Scotland. Values at 2 Irish sites (Sandy Cove, Bullens Bay) did not differ from those of 2 Scottish sites (White Bay, Farland Point), but overall, the Scottish samples had rather higher MULT values than the Irish ones (significantly so when pooled data are compared: Scottish MULT 28.8°C, lcl 28.4°C, ucl 29.3°C; Irish MULT 27.1°C, lcl 26.6°C, ucl 27.5°C). The difference in pooled MULT was 1.7°C.

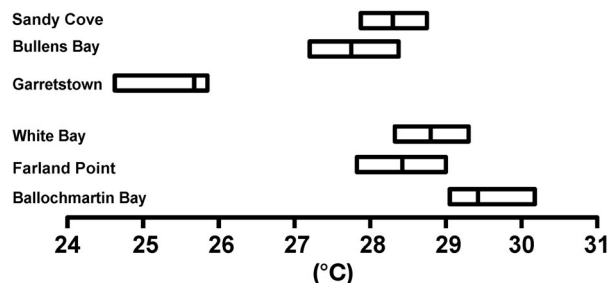


Fig. 9. *Nucella lapillus*. Upper lethal temperatures of dogwhelks collected from 3 shores (White Bay, Farland Point, Ballochmartin Bay) on Great Cumbrae, Scotland, and 3 shores (Sandy Cove, Bullens Bay, Garretstown) in Co. Cork, Ireland, on 2 June 2004 (i.e. same day). In both countries, dogwhelks were collected from the middle of the distribution. Key as in Fig. 6

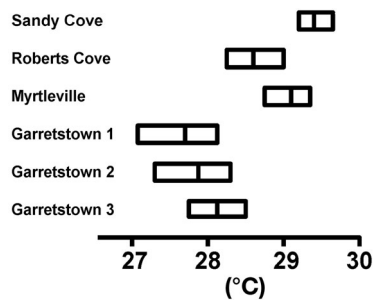


Fig. 10. *Nucella lapillus*. Upper lethal temperatures of dogwhelks collected on 16 August 2004 from 3 sheltered shores (Sandy Cove, Roberts Cove, Myrtleville) and 3 exposed shores (Garretstown 1, 2, 3) in Co. Cork, Ireland. For each shore, animals were collected from the middle part of the intertidal distribution. Key as in Fig. 6

### Wave exposure experiments on dogwhelks

Fig. 10 displays MULT values for dogwhelks collected from the middle of the distribution on 3 sheltered and 3 exposed Irish shores. Pooled data (sheltered shore MULT 29.1°C, lcl 28.8°C, ucl 29.3°C; exposed shore MULT 27.9°C, lcl 27.6°C, ucl 28.2°C) showed a significant difference, with sheltered shore dogwhelks having a significantly higher MULT than exposed shore animals (by 1.2°C). However, data for individual shores (Fig. 10) provided further evidence of the variability of MULT in this species. Dogwhelks from 2 out of the 3 sheltered shores showed MULT values significantly higher than all 3 exposed shores, but one sheltered shore (Roberts Cove) yielded data that differed significantly from data for one of the other sheltered shores (Sandy Cove), and did not differ significantly from 2 of the exposed shores (Garretstown 2, 3).

### DISCUSSION

The 3 main findings of this study were: (1) confirmation of the hypothesis that MULT, MLLT (and hence TNW) are strongly correlated with MSH (and hence duration of emersion during the tidal cycle), (2) a strong (curvilinear) relationship between MULT and MLLT in 10 intertidal invertebrate species, (3) demonstration of significant differences in thermal tolerances between dogwhelks *Nucella lapillus* living high on the shore and those living low on the same shore, and between dogwhelks living on exposed shores and those living on nearby sheltered shores (though it should be noted that the exposed and sheltered shores inevitably differed to some extent in aspect).

Asymptotic analysis of the data collected for the 10 intertidal species living on Great Cumrae indicated

that asymptotes were about 35°C for MULT and -20°C for MLLT. These would, therefore, appear to be the extreme temperatures tolerable by intertidal species distributed to uppermost levels on the shore at this location. Splash zone temperatures close to 35°C appear to be much more likely than does the occurrence of -20°C. The suggestion that intertidal animals are more sensitive to high rather than low temperatures is reinforced by the results of linear regression analysis on the 8 species living higher on the shore (slope of the MULT:MSH regression much shallower than slope of MLLT:MSH regression).

The study also provided good evidence of small geographical differences in MULT for *Littorina littorea* and *Nucella lapillus*, with no confounding effects of seasonality or pre-acclimation. Thermal responses of *L. littorea* were evidently less plastic than those of *N. lapillus*. The finding that *N. lapillus* MULT varies over short distances far more than *L. littorea* MULT seems likely to be in part due to the much greater capacity for gene flow inherent in the *L. littorea* life history; the direct-developing *N. lapillus* is known to show local population allozyme substructuring (Kirby 2000), while the planktonic larvae of *L. littorea* must inevitably limit local differences in thermal tolerance to phenotypic plasticity alone.

The finding that animals that tolerate high temperatures also tolerate low temperatures reflects substantial overlap in the biochemical adaptations required to deal with both types of stress. The seminal review of Pörtner (2001) demonstrates the close relationship between upper lethal temperature and the following attributes: (1) an extended aerobic scope, (2) the ability to switch to anaerobic metabolism and (3) in extremis, the ability to protect molecules by deployment of heat shock proteins and antioxidative defence. Key factors in surviving freezing temperatures are the ability to respire anaerobically during ischaemia, inevitable when circulation ceases in frozen animals, the deployment of ice-nucleating and thermal hysteresis proteins, and the ability to adjust the size of the osmotically active intracellular amino-acid pool as ice formation in extracellular fluid threatens osmotic dehydration of the intracellular milieu (Storey & Storey 1988, Davenport 1992).

The confirmation of asymptotic curvilinear relationships between maximum height of distribution on the shore and MULT, MLLT and TNW when all 10 study species are considered, plus the finding of very strong linear relationships between MSH and MULT, MLLT and TNW in those 8 species emersed for >70% of a spring-neap cycle at that maximum height, reconciles 2 positions that previously appeared contradictory: (1) the suggestion that there are simply 2 groups of animals living on shores, stenothermal animals living



close to low water spring tide level, and eurythermal animals that reach the eulittoral fringe (e.g. McMahon 1990); and (2) the finding (on subantarctic South Georgia) that shore height and thermal tolerance were closely correlated (Davenport & MacAlister 1996).

It is also evident that species that have extensive vertical ranges and moderately high upper limits on northern European shores (e.g. *Mytilus edulis*, *Semibalanus balanoides*, *Littorina littorea*) have much wider tolerances than species that are only emersed on spring tides, and then for short periods (e.g. *Tectura tessulata*, *Balanus crenatus*). However, differences in extreme thermal limits are significantly correlated with relatively small differences in maximum height of distribution, and such species are less eurythermal than an upper shore/splash zone specialist such as *L. saxatilis*.

Of the 10 species studied, 8 were sedentary, so capable of movement within their vertical ranges and between exposed and sheltered microhabitats. Two species, the barnacles *Semibalanus balanoides* and *Balanus crenatus*, were sessile, so cannot control their position, though the studied specimens of the latter lower shore species were all phoretic, so could be moved by their sedentary hosts. There is no evidence of any consistent effect of sedentary/sessile life style on thermal tolerance in the data presented here. Logistically, the design of experiments to further elucidate this point would be very difficult.

The littorinid data presented here can be compared with the work of Clarke et al. (2000). They were concerned particularly with *Littorina saxatilis* s.s. and its various sibling species (none of the latter being present on the White Bay shore studied); they also measured heat coma temperatures that cannot be directly compared with our MULT values. Unlike them, we did find significant interspecific relationships between maximum height of distribution and thermal tolerances in the White Bay littorinids, with *L. littorea* and *L. saxatilis* being generally more tolerant than the flat periwinkles *L. obtusata* and *L. fabalis*. In agreement with their data, we found significant differences in response between geographically separated populations of *L. littorea* (with greater discrepancies at the 500 km scale than at the 10 km scale), though our finding (in Ireland) that there is no intraspecific shore height-related difference in thermal tolerance in *L. littorea* is novel. A major discrepancy between the present study and that of Clarke et al. (2000) concerns the flat periwinkles; in their study, they reported *L. obtusata* to be of similar upper thermal tolerance to *L. saxatilis* s.l. and significantly more tolerant of high temperature than *L. fabalis*. The 2 White Bay flat periwinkle species showed virtually identical thermal responses, and occupied very similar habitats and shore heights.

Thermal tolerances of *Nucella lapillus* have attracted limited study before, though it was one of a number of species apparently unaffected by the severe winter of 1962–63 (Crisp 1964). The plasticity of MULT demonstrated in our study, within shores and between neighbouring shores, suggests that the dogwhelk will be a useful model species for further thermal studies. The finding that dogwhelks living on the lower shore tend to have a lower MULT than those living at the upper limit of shore distribution makes sense in terms of phenotypic plasticity, with the higher animals needing to deploy more effective responses to high temperature. It is tempting to explain the significantly lower MULT of sheltered shore animals than the MULT of exposed shore animals in similar fashion, because of greater exposure to moderating winds in the latter case. However, it is virtually impossible to avoid confounding wave exposure and solar aspect, though in the study reported here, both exposed and sheltered shores were approximately 45° from due south.

The findings of this study reinforce the conclusions of Helmuth et al. (2002) that prediction of effects of global climate change on the distribution of intertidal animals will not be straightforward. Identifiable latitudinal changes in species range appear less likely in the short term than do subtle local changes in height of distribution on the shore, coupled with micro-distributional changes, such as a tendency towards crevice-dwelling and avoidance of sun-exposed surfaces.

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