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Geographical variation in heat coma temperatures in *Littorina* species (Mollusca: Gastropoda)

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Upper critical thermal limits were measured as heat coma temperatures in *Littorina* species (Mollusca: Gastropoda) from sites around the British Isles. Thermal tolerance was found to be stable within a population but extensive variation occurred between populations and species. The majority of species examined displayed heat coma values of around 30°C and did not show a positive correlation with shore height. The highest capacity for thermal tolerance was found along the coast of South Wales, while the lowest was found on the south-west coast of Ireland and on the east coast of Scotland.

INTRODUCTION

Biodiversity has been defined as 'the variability among living organisms from all sources, including *inter alia* terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems' (Rio Convention, 1992). Most studies on biodiversity simply focus on the number of species occurring, although other aspects such as cladistic, morphological and physiological diversity are also of importance (Gray, 1997). This study is one of a series examining the diversity that exists within a group of littoral snails, the Littorinidae, that possess contrasting life histories, reproductive strategies and degrees of intraspecific pheno- and genotypic variation. They occupy a variety of habitats on the shore, from the eulittoral, where animals get wetted by every incoming tide, to the eulittoral fringe where animals are only wetted periodically.

There are currently between six and eight recognized species of periwinkles (*Littorina*) occurring around northern European shores, displaying a variety of life history strategies and degrees of intraspecific pheno- and genotypic variation. *Littorina littorea* (L.), the edible periwinkle, produces planktonic eggs and larvae, so populations experience substantial gene flow. In contrast, the flat periwinkle species, *Littorina obtusata* (L.) and *Littorina fabalis* (W. Turton), are both oviparous. The remaining species (the rough periwinkles) comprise the '*Littorina saxatilis*' species complex, where between three and five sibling species are currently recognized (Barnes, 1993; Reid, 1996). The status of *Littorina arcana* Hannaford Ellis and *Littorina compressa* Jeffreys within this complex is non-contentious. However, *L. saxatilis s.s.* (Olivi) is an extremely variable taxon, occupying a wide range of habitats, from exposed intertidal shores to sheltered lagoons, and clearly identifiable forms exist within this taxon. Among these forms, three clearly recognizable ones occur on North Yorkshire (and other) coasts; a high shore form (*L. saxatilis* 'H'), which is typically a thin, high spired dark shell with pronounced ridging, in contrast to a mid-shore form (*L. saxatilis* 'M') which possesses thicker, lighter coloured shells, sculptured with very fine spiral lines. Not only are these clearly morphologically divergent, there is also evidence that there is some reproductive isolation between the two (Hull et al., 1996), and that they may, indeed, be genetically divergent (Wilding et al., 1998). The third form is a small ecotype, living low down on the shore in the interstices between barnacles (*Semibalanus balanoides*) and in their empty tests (*L. saxatilis* 'B') (Johannesson & Johannesson, 1990a,b). The other two taxa, tentatively referred to as *Littorina neglecta* Bean, another barnacle dweller and *Littorina tenebrosa* (Montagu), a lagoonal dwelling animal, are of controversial status (Grahame et al., 1995; Gosling et al., 1998), and may also be ecotypes of *L. saxatilis s.s.* (Olivi).

Measures of thermal tolerance have long been employed to examine the thermal capacities of marine invertebrates to tolerate their environment (Southward, 1958; Fraenkel, 1966, 1968; Vermeij, 1971; McMahon, 1990, 1992; Britton, 1992; Cannon & Hughes, 1992). Physiological tolerances are integral to our understanding of species distribution and adaptation. Since temperature moderates the effect of almost all environmental and biological factors it is thought to explain at least a portion of the diversity of physiological and behavioural adaptations among organisms (Lutterschmidt & Hutchison, 1997a). The aim of this study is to examine the variation in thermal tolerance that occurs in *Littorina* species around the British Isles.

MATERIALS AND METHODS

Animals and holding conditions

Adult specimens of *Littorina arcana*, *L. saxatilis*, *L. compressa*, *L. neglecta*, *L. littorea*, *L. obtusata*, and *L. fabalis* were collected at low tide from shores around the British Isles (Figure 1, Table 1) between late June and early September 1997. Prior to experimentation, animals were acclimated to 12°C in the laboratory for a minimum of

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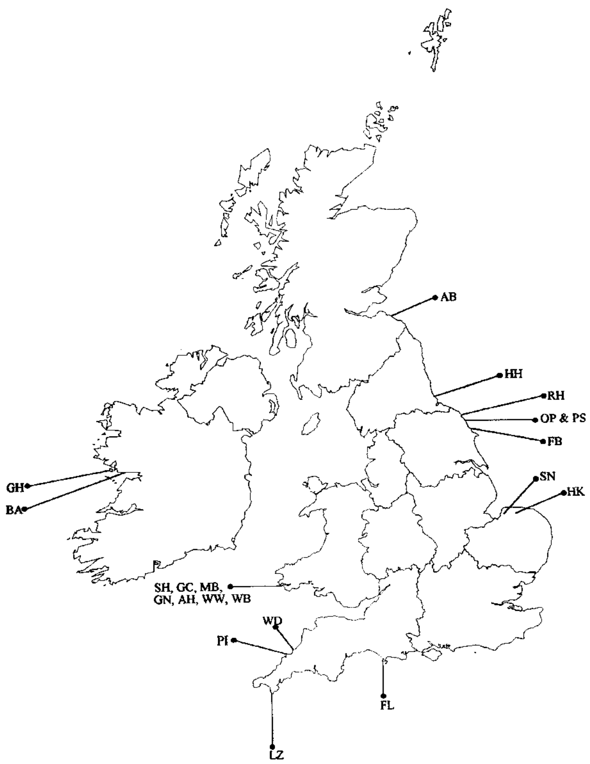

Figure 1. Map showing location of sites used in present study.

ten days in aquaria containing artificial seawater (Instant Ocean™).

Determination of upper thermal tolerance limits

Upper thermal tolerance limits were determined as mean heat coma temperatures (HCT) using a method modified from McMahon (1990). By definition, heat coma observed in gastropods, is a reversible condition characterized by the loss of nervous integration and manifested by a cessation of locomotion, ventral curling of the foot and an inability to remain attached (McMahon, 1976). Individuals were placed in test tubes (30 ml) containing 25 ml of artificial seawater and allowed to attach. For larger specimens (some *L. littorea* and *L. obtusata*), individuals were placed in 50 ml test tubes and allowed to attach in 45 ml of seawater. The bath heater was switched manually to raise the water temperature of both the bath and test tube water by approximately a 1°C increase in temperature every 5 min, a rate of increase which makes any lag between tube water and snail tissue temperatures negligible (Broekhuysen, 1940). Water temperatures in the test tubes were monitored using a series of fine thermocouples (Omega) connected to a digital thermometer (Omega). In species where identification on the basis of shell character was uncertain (*L. saxatilis* and *L. arcana*), individuals were subsequently dissected for identification. The only reliable criterion for distinguishing between these two species being the presence of a brood pouch in female *L. saxatilis* and a jelly gland in *L. arcana* (Hannaford Ellis, 1979; Grahame & Mill, 1989). The columella length (CL) (Grahame & Mill, 1989) of individuals was also measured with dial calipers to the nearest 0.1 mm. Where the size of the animals were notably varied (*L. littorea*) the animals collected were divided into three samples: <10 mm (small), 10–20 mm (medium), 20–30 mm (large). Each HCT determination began at the acclimation temperature (12°C). Snails were allowed to attach to the tube walls and actively locomote; any specimens remaining inactive during this time were discarded. The number of individuals entering heat coma was recorded for every 1°C increase in tube water temperature.

Table 1. *Location of sites used in the present study.*

Site Code	Location	Grid Reference	Species Collected
AB	St Abbs Head, Scotland	NT 907692	A, S, C, L
HH	Hawthorn Hive, Durham	NZ 443460	A
RH	Robin Hood's Bay, North Yorkshire	NZ 955045	A, S, O, L, F
OP	Old Peak, Ravenscar, North Yorkshire	NZ 984021	A, S^H, S^M, L, F
PS	Peak Steel, Ravenscar, North Yorkshire	NZ 979027	A, S^B, N, O, F
FB	Filey Brigg, North Yorkshire	TA 137815	A, S^H, S^M, L, O, F
SN	Snettisham, Norfolk	TF 649319	T
HK	Holkham Hole, Norfolk	TF 886451	S^L
FL	East Fleet, Dorset	SY 664757	S
LZ	Lizard, Cornwall	SW 699114	A, S, C
PI	Port Isaac, Cornwall	SW 996807	A, L
WD	Widemouth, Devon	SS 197026	S, L
SH	Sandyhaven, Pembrokeshire	SM 856068	S, C, L
GC	Great Castle Head, Pembrokeshire	SM 797056	A, S, C
MB	Musslewick Bay, Pembrokeshire	SM 818063	S, C
GN	The Gann, Pembrokeshire	SM 817065	S, C, O
AH	St Ann's Head, Pembrokeshire	SM 809028	S, C
WW	Watwick Bay, Pembrokeshire	SM 818042	A, S, C
WB	Westdale Bay, Pembrokeshire	SM 796059	A, S^H, S^M, C
GH	Golam Head, Galway	L 826214*	S, T
BA	Baile na hAbhann, Galway	L 992202*	S, C, L

Species abbreviations: *Littorina arcana*, A; *Littorina saxatilis*, S^H high shore form, S^M mid-shore form, S^B barnacle-dwelling form, S^L lagoonal dwelling form; *Littorina neglecta*, N; *Littorina compressa*, C; *Littorina littorea*, L; *Littorina obtusata*, O; *Littorina fabalis*, F. *, Irish Grid Reference.

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Statistical analysis

Differences between *L. saxatilis* 'H' and 'M' morphs on the same shore were determined using *t*-tests, while differences within a species were determined using one-way ANOVA. Where differences occurred, Tukey tests were performed to determine which of the populations were different (*Q* values). Due to the contentious nature of *L. neglecta* and *L. tenebrosa* as species, these data were analysed with that of *L. saxatilis*. Overall trends in population data are presented as box plots showing the distribution of data in terms of the mean, quartiles and the range.

RESULTS

All species examined displayed a characteristic distribution of HCT, with all individuals typically entering heat coma over a range of 5–10°C (Figure 2). *Littorina saxatilis* (Figure 3), the most studied species (18 sites), showed extensive variation in thermal tolerance both over long and short distances, and with position on the shore (Table 2A). Mean HCT in *L. saxatilis* ranged between 26.7°C ±0.4 (SE) (Lizard, Cornwall) and 33.9°C ±0.2 (Great Castle Head, Pembrokeshire), with most animals typically having coma temperatures around 31–32°C. Where different morphs of *L. saxatilis* occurred on the same shore ('H' and 'M'), no significant differences in thermal tolerance were found in the Yorkshire animals (sites OP, FB), but the higher shore morphs from Pembrokeshire (site WB) possessed significantly higher HCT (P=0.004, t=2.981, df=55). On shores where barnacle-dwelling littorinids (*L. saxatilis* 'B' and *L. neglecta*) occurred together (Peak Steel, Ravenscar), no differences were found between the two taxa. Where animals were found occupying lagoonal environments (Norfolk), no differences in thermal tolerance were found between *L. saxatilis s.s.* (site SN) and *L. tenebrosa* (site HK), although they both displayed significantly depressed thermal capacities compared to many of the coastal animals examined; a similarly low HCT was found in animals from the tidal lagoon (East Fleet, Dorset). However, significant differences in thermal tolerance were found to occur between English and Irish *L. tenebrosa* ($P<0.05$, Q=6.70, $Q_{0.05}$=5.14) with Irish animals possessing even lower HCT (26.8°C ±0.3 compared with 29.1°C ±0.3). Geographically, coastal *L. saxatilis* generally show a decline in thermal tolerance northwards along the east coast of Britain, with Scottish *L. saxatilis* (St Abbs) having significantly lower values than their Yorkshire counterparts (sites RH, OP and PS) ($P<0.05$, $Q>9.54$, $Q_{0.05}$=5.14). Low coma temperatures occur at the Lizard on the south coast, but are higher at Widemouth, Devon. The highest HCT were found along the Pembrokeshire coast and were either similar to, or significantly higher, than those found on the Yorkshire coast. For example, all Welsh animals examined were significantly higher in HCT than those from Robin Hood's Bay, North Yorkshire ($P<0.05$, $Q>5.35$, $Q_{0.05}$=5.14), while all Yorkshire animals examined possessed significantly lower HCT than those from Great Castle Head, Pembrokeshire ($P<0.05$, $Q>9.58$, $Q_{0.05}$=5.14). The lowest capacities for thermal tolerance were found on Irish coasts (27°C); similar to those found in Scotland.

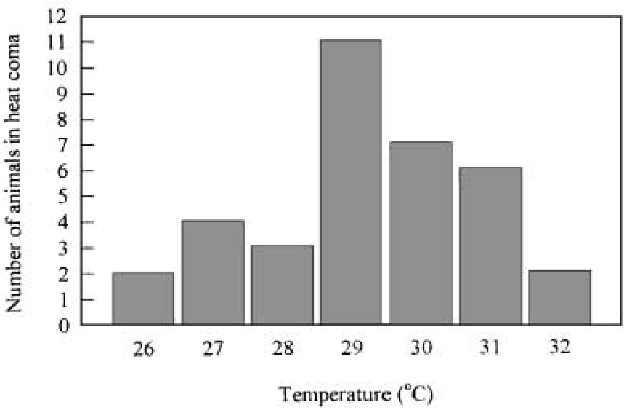

Figure 2. A typical distribution of upper thermal limits measured as heat coma temperatures (HCT) in *Littorina saxatilis* from Widemouth, Devon (site 11). Mean=39.67°C ±0.27 (SE); N=34.

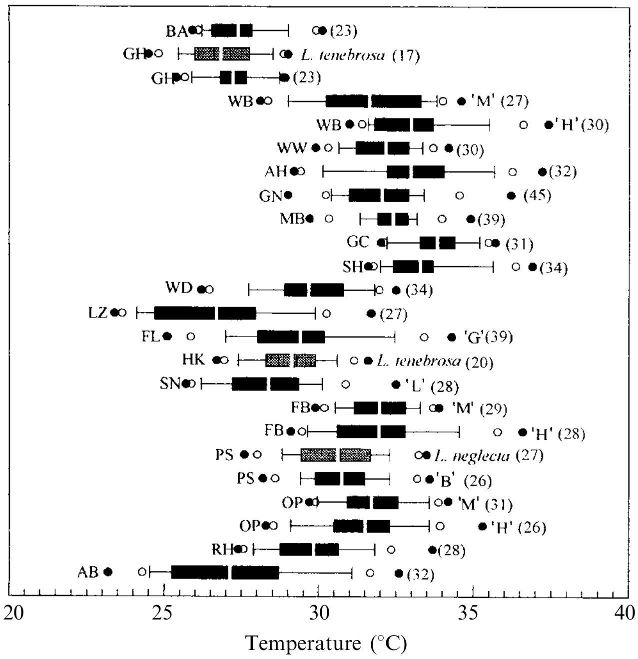

Figure 3. Box plot illustrating heat coma temperatures in *Littorina saxatilis*. White bars, the mean; solid bars, 25th and 75th percentiles; whiskers, 10th and 90th percentiles; hollow circles, 5th and 95th percentiles (2SE); solid circles, range; N, numbers in parentheses. Site number is shown to the left of each bar.

Heat coma temperatures in *L. arcana*, a sibling species of *L. saxatilis*, show much less variation than thermal tolerance in *L. saxatilis* (Table 2C & Figure 4). Mean HCT ranged from 29.2°C ±0.4 (Widemouth, Devon) to 33.7°C ±0.3 (Great Castle Head, Pembrokeshire), with typical coma temperatures falling between 31–32°C (similar to *L. saxatilis*). Geographically, as with *L. saxatilis*, a slight decline in HCT is observed down the east coast of Britain, with significantly lower HCT ($P<0.05$, $Q>4.65$, $Q_{0.05}$=4.62) occurring in south west England. Again the highest capacities for thermal tolerance were found in Welsh animals, where coma temperatures are typically around 33°C compared to around 31°C seen on Yorkshire shores.

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Table 2A. *Results of one-way ANOVA for* Littorina saxatilis.

Site	N	Sum	Mean	Variance
AB	32	868.5	27.14	5.82
RH	28	835.7	29.85	2.19
OP (S^H)	26	819.4	31.52	2.61
OP (S^M)	31	983.2	31.7	21.53
PS (S^B)	26	799.8	30.76	1.64
PS N	27	827.1	30.63	2.21
FB (S^H)	28	894.8	31.96	3.56
FB (S^M)	29	927.2	31.97	1.17
SN	28	795	28.39	2.44
FL	39	1146.9	29.41	4.37
LZ	27	720.4	26.68	4.73
PI	8	240.3	30.04	1.25
WD	34	1008.9	29.67	2.41
WB (S^H)	30	990.1	33.00	2.78
WB (S^M)	27	854.3	31.64	3.18
GN	45	1441.8	32.04	1.94
MB	39	1263.9	32.41	0.95
WW	30	965	32.167	1.12
SH	34	1131.7	33.29	1.92
AH	32	1055.5	32.99	3.65
GC	31	1049.1	33.84	0.98
GH	23	626.2	27.23	0.92
BH	23	629.9	27.39	1.27
HK (T)	20	582.7	29.14	1.52
GH (T)	18	481.4	26.74	1.58

Source of Variation	SS	df	MS	F	*P*-value	F crit
Between Sites	3258.88	24	135.79	56.85	9.3E-146	1.53
Within Sites	1647.96	690	2.39			
Total	4906.84	714				

Table 2B. *Results of one-way ANOVA for* Littorina arcana.

Site	N	Sum	Mean	Variance
AB	32	1000.9	31.28	7.15
HH	72	2287.7	31.78	1.35
RH	32	996.9	31.15	2.72
OP	41	1300.2	31.71	2.78
PS	32	1034.5	32.33	2.26
FB	27	883.2	32.71	5.30
LZ	39	1154.2	29.60	5.40
PI	58	1740.4	30.01	3.10
WD	16	466.6	29.16	2.12
WB	91	3014.7	33.13	2.82
WW	39	1264.7	32.43	2.45
GH	31	1043.5	33.66	1.93

Source of Variation	SS	df	MS	F	*P*-value	F crit
Between Sites	822.83	11	74.80	24.22	5E-40	1.81
Within Sites	1537.96	498	3.09			
Total	2360.79	509				

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Table 2C. *Results of one-way ANOVA for* Littorina compressa.

Site	N	Sum	Mean	Variance
AB	27	730.7	27.06	4.86
LZ	25	661	26.44	5.75
WB	30	1041.1	34.70	1.25
GN	38	1218.5	32.07	1.69
MB	36	1146.6	31.85	3.21
WW	31	997.5	32.18	1.67
SH	30	1024.7	34.16	5.45
AH	30	987.1	32.90	3.10
GH	30	1000.2	33.34	2.31
BH	30	812.7	27.09	1.99

Source of Variation	SS	df	MS	F	*P*-value	F crit
Between Sites	2457.84	9	273.09	90.31	1.19E-79	1.91
Within Sites	898.13	297	3.02			
Total	3355.97	306				

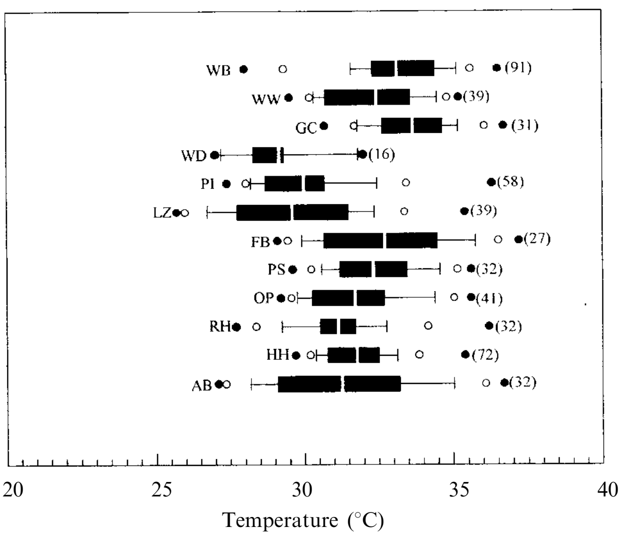

Figure 4. Box plot illustrating heat coma temperatures in *Littorina arcana*. White bars, the mean; solid bars, 25th and 75th percentiles; whiskers, 10th and 90th percentiles; hollow circles, 5th and 95th percentiles (2SE); solid circles, range; N, numbers in parentheses. Site number is shown to the left of each bar.

Littorina compressa, also a sibling species of *L. saxatilis* (Table 2D & Figure 5), showed greater variation in thermal tolerance than *L. arcana*, although it should be noted that it is much more limited in its geographical distribution. Heat coma temperatures ranged from 26.4°C ±0.5 (Lizard, Cornwall) to 34.2°C ±0.4 (Sandyhaven, Pembrokeshire). Unlike *L. arcana* and *L. saxatilis*, mean HCT typically fall around two distinct temperatures of 27°C and 33°C. As with the other rough periwinkle species, the lowest coma temperatures were found to occur in Ireland and on the south-east coast of Scotland, and in south-west England. Again, elevated coma temperatures occurred along the Pembrokeshire coast.

Thermal tolerance in the edible periwinkle, *L. littorea*, also varied with geographical location, although size (measured as columella length) may also be important on some shores where extremes in animal sizes were found (Table 2D & Figure 6). On a geographical scale, similar patterns in thermal tolerance to the rough periwinkle species were observed. Actual mean HCT varied from 25.5°C ±0.4 (St Abbs, Scotland) to 33.4°C ±0.3 (Sandyhaven, Pembrokeshire) with coma temperatures typically occurring around 30°C, similar to the majority of other *Littorina* species examined. The possible effect of size on thermal tolerance was only observed in animals from St Abbs, where significantly lower HCT were seen in the largest size class. Here, differences ($P<0.05$, $Q>14.1$, $Q_{0.05}=4.62$) of around 5°C were observed (30.4°C ±0.4 small animals compared with 25.5°C ±0.4 large animals). A slight decrease in mean thermal tolerance was also seen in the other site where these extremes in size occurred (Filey Brigg, North Yorkshire), although this was not significant.

No differences in thermal tolerance were found to occur in the flat periwinkle species, *L. fabalis* (Table 2E & Figure 7), although only three sites over a relatively small distance were examined. Mean HCT were very similar with values only varying by 0.5°C. The range of HCT measured was also very similar and typically ranged from 27–34°C. However, much more variation was observed in the other flat periwinkle species examined, *L. obtusata* (Table 2F & Figure 7). Heat coma temperatures were typically much higher than any other species examined (around 32°C), with mean coma temperatures ranging from 30.7°C ±0.5 (Ravenscar, North Yorkshire) to 35.9°C ±0.6 (Gann, Pembrokeshire). The range of thermal tolerances measured was also larger, with most animals entering heat coma over a span of 10°C. Significant differences ($P<0.05$, $Q=2.14$, $Q_{0.05}=1.98$) were also found to occur over a smaller geographical distance (North Yorkshire sites FB and PS), although the same overall geographical pattern in thermal tolerance between these animals and those occurring on the Welsh coast was observed.

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Table 2D. *Results of one-way ANOVA for* Littorina littorea.

Site	N	Sum	Mean	Variance
AB (large)	30	765.7	25.52	5.82
AB (small)	34	1034.3	30.42	5.21
RH	30	849.4	28.31	2.05
OP	27	814.4	30.16	1.10
PS	31	940.5	30.34	1.02
FB (small)	29	937.6	32.33	3.80
FB (med)	31	975.9	31.48	2.85
FB (large)	37	1158.4	31.31	4.18
PI	30	873.3	29.11	6.87
WD	27	795.7	29.47	9.55
SH	21	702	33.43	2.31
BH	25	688.4	27.54	0.85

Source of Variation	SS	df	MS	F	*P*-value	F crit
Between Sites	1413.99	11	128.54	33.21	1.57E-47	1.82
Within Sites	1315.86	340	3.87			
Total	2729.85	351				

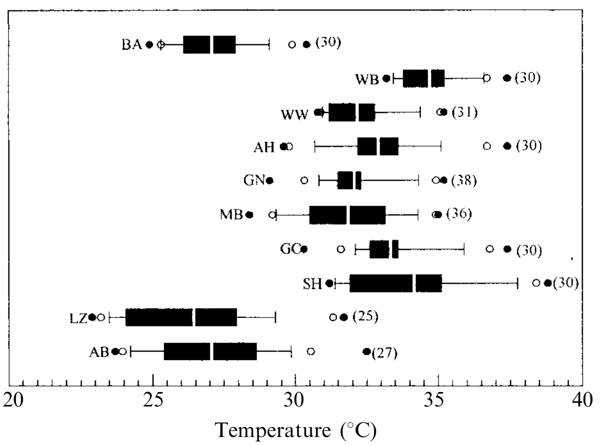

Figure 5. Box plot illustrating heat coma temperatures in *Littorina compressa*. White bars, the mean; solid bars, 25th and 75th percentiles; whiskers, 10th and 90th percentiles; hollow circles, 5th and 95th percentiles (2SE); solid circles, range; N, numbers in parentheses. Site number is shown to the left of each bar.

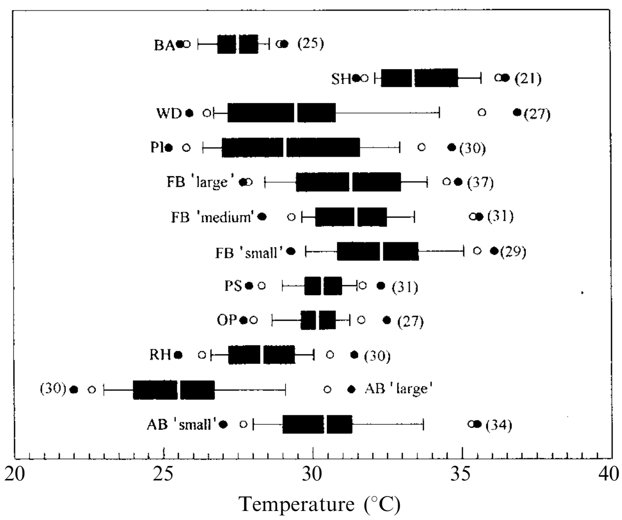

Figure 6. Box plot illustrating heat coma temperatures in *Littorina littorea*. White bars, the mean; solid bars, 25th and 75th percentiles; whiskers, 10th and 90th percentiles; hollow circles, 5th and 95th percentiles (2SE); solid circles, range; N, numbers in parentheses. Site number is shown to the left of each bar.

Table 2E. *Results of one-way ANOVA for* Littorina fabalis.

Site	N	Sum	Mean	Variance
RH	29	883.6	30.47	3.76
OP	22	673.2	30.60	3.49
PS	26	804.5	30.94	1.70

Source of Variation	SS	df	MS	F	*P*-value	F crit
Between Sites	3.21	2	1.60	0.54	0.59	3.12
Within Sites	221.05	74	2.99			
Total	224.25	76				

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Table 2F. *Results of one-way ANOVA for* Litorina obtusata.

Site	N	Sum	Mean	Variance
RH	25	821	32.84	5.27
PS	31	950.5	30.66	7.59
FB	30	961.9	32.06	13.89
GN	21	754.5	35.93	6.74

Source of Variation	SS	df	MS	F	*P*-value	F crit
Between Sites	359.26	3	119.75	13.84	1.19E-07	2.69
Within Sites	891.47	103	8.66			
Total	1250.73	106				

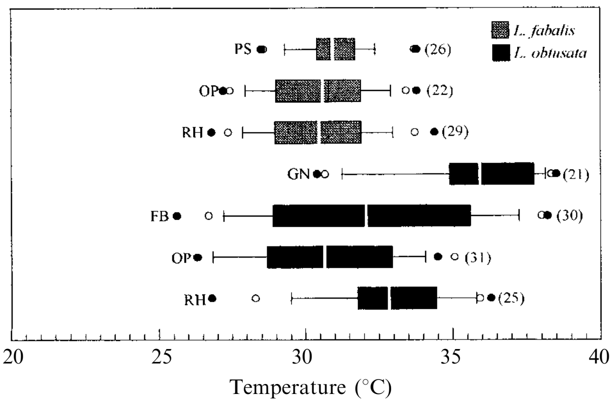

Figure 7. Box plot illustrating heat coma temperatures in flat *Littorina* species. White bars, the mean; solid bars, 25th and 75th percentiles; whiskers, 10th and 90th percentiles; hollow circles, 5th and 95th percentiles (2 SE); solid circles, range; black line in grey boxes, median; N, numbers in parentheses. Site number is shown to the left of each bar.

DISCUSSION

Littorinid gastropods are cosmopolitan and ubiquitous in intertidal and shallow marine ecosystems (McQuaid, 1996) and, where populations of the same species occur in varied habitats, adapt themselves to the prevailing conditions in terms of thermal tolerance. The importance of temperature as a factor in both the horizontal and vertical distribution of intertidal animals has been stressed by many investigators (Southward, 1958; Fraenkel, 1966, 1968; Vermeij, 1971) since these animals may frequently be subjected to sudden and large changes in temperature between tidal cycles. It is therefore unsurprising that thermal tolerance has been studied extensively in intertidal animals (Markel, 1971; McMahon, 1990, 1992; Britton, 1992; Cannon & Hughes, 1992). In the present study, heat coma temperatures were found to be stable within a population but extensive variation was noted between populations.

Examining thermal tolerance across large geographical distances allows for assessment of a species' ability to adapt to different thermal regimes. Differences in thermal tolerance were observed in most species between Yorkshire and Welsh coasts, with the Yorkshire animals possessing coma temperatures approximately 2°C (or more) lower. Geographical differences in coma temperature have also been reported by Sandison, (1967) (also incorporating data from Evans (1948)), where littorinids on the east coast of Scotland displayed slightly lower coma temperatures than those from the west coast of Britain. These data suggest that ambient sea and air temperatures are mostly responsible for these adaptations. It has also been suggested that harsh thermal environments select for genotypes that allow for plasticity in physiological traits, which will ultimately produce community changes (Lutterschmidt & Hutchison, 1997b). Indeed, McMahon & Payne (1980) have reported that selective pressures of thermal regimes appear to be capable of generating genetic differences in populations of pulmonate snails. It is also well documented that thermal tolerance in intertidal gastropods varies according to season (Hamby, 1975; Cannon & Hughes, 1992) and a sibling paper indicates that factors such as acclimation temperature, size, salinity and previous thermal history are also important (Clarke et al., 2000).

Littorina saxatilis s.s. is an extremely variable taxon occupying a wide range of habitats, from the exposed intertidal to sheltered lagoonal environments. This is reflected in the upper critical thermal maximums of different populations, *L. saxatilis* dwelling in sheltered or permanently submerged environments showing lower coma temperatures than those in exposed intertidal environments. The lagoonal *L. tenebrosa* has previously been ascribed to *L. saxatilis* on the grounds of genetic similarity and the occurrence of phenotypic intermediates, although some investigators feel it warrants separate status, albeit at the 'variety' level (Barnes, 1993). Physiologically, lagoonal dwelling *L. saxatilis* and *L. tenebrosa* do not differ in terms of thermal tolerance, but this may be due to the type of environment they occupy (stable and permanently submerged). A corresponding similarity was observed between the barnacle dwelling ecotype of *L. saxatilis* and *L. neglecta*, the latter also being a problematic taxon (Grahame et al., 1995; Reid, 1996). Cannon & Hughes (1992) examined thermal tolerance in both *L. neglecta* and intertidal *L. saxatilis* (not the barnacle dwelling ecotype).

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They reported that similar aged juveniles also showed no difference in thermal tolerance (despite size differences), although mature *L. neglecta* possessed a lower thermal tolerance than intertidal *L. saxatilis*; they attributed these differences to the relatively sheltered environment occupied by *L. neglecta*. In this study, the non-contentious sibling species, *L. arcana* and *L. compressa*, appeared to show less variation in thermal tolerance than *L. saxatilis*. However, where all species occurred together (with the exception of Lizard, Cornwall), no significant differences were found between them. At Lizard, *L. arcana* possessed a significantly higher mean HCT ($P<0.05$) than *L. saxatilis* and *L. compressa*. However, both *L. saxatilis* and *L. compressa* were obtained submerged from a large pool, as opposed to *L. arcana* which were collected from the slopes around the pool.

Thermal tolerance in intertidal littorinids was found not to form a discrete relationship with shore height. In contrast, many earlier studies have indeed demonstrated a positive correlation between intertidal height and thermal tolerance (Southward, 1958; Fraenkel, 1966, 1968; Davis, 1970; Markel, 1971; Stirling, 1982). However, the reverse has also been reported (Evans, 1948; Sandison, 1967; McMahon, 1990; Britton, 1992). In the present study, most species examined possessed similar mean HCT of around 30–31°C on the north-east coast and 32–33°C on the south-west coast of Britain.

Littorina obtusata appeared to possess a similar, or higher, capacity for thermal tolerance than the rough periwinkle species that occupy the top of the shore. Reid (1990) has suggested that the ancestors of these North Atlantic littorines originated from the Pacific. Since the majority of these Pacific Littorinidae are upper eulittoral fringe species, invading stocks may initially have occupied the upper shore and later radiated downwards to form the eulittoral species of the North Atlantic. Retention of relatively high thermal tolerance in these North Atlantic littorines, as is seen in *L. obtusata*, may therefore have occurred (McMahon, 1992).

In the present study, thermal tolerance has been reported to be very diverse among some of the *Littorina* species examined. It should be stressed, however, that heat coma does not determine the *in situ* survival of these animals. The tolerance of these animals towards a single environmental factor such as temperature may well be greater than their tolerance of combinations of environmental factors studies together (Southward, 1958). However, these methods do provide an insight into aspects of physiological diversity that exist within the *Littorina*, making it useful in the context of biodiversity.

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