J. mar. biol. Ass. U.K. (1962) 42, 163-177
Printed in Great Britain

ON THE BEHAVIOUR OF BARNACLES. IV

THE INFLUENCE OF TEMPERATURE ON CIRRAL ACTIVITY AND SURVIVAL OF SOME WARM-WATER SPECIES

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(Text-figs. 1–3)

In previous papers (Southward, 1955, 1957, 1958) it has been shown that, in the species of barnacles investigated, the range of temperatures over which the cirri were active, the range of optimum activity, and the range within which the animal could survive were related both to the geographical distribution of the species and the ecological niche occupied. This relationship has been confirmed by further work on some strictly warm-water species, and some light thrown on possible systematic differences between species or varieties.

The barnacles came from three localities, as noted in Table 1, but cirral activity was studied only on the European material. The specimens of *Chthamalus* were collected and examined at Banyuls within a few days; the material

TABLE 1. THE SPECIES OF BARNACLES INVESTIGATED

Species	Where collected	Tide level
(*a*) From Banyuls-sur-Mer, Pyrénées-Orientales, France		
Chthamalus depressus (Poli)	East side of Île Grosse	0·5–1·0 m above sea level in April/May
C. stellatus (Poli)	East side of Île Grosse	Approx. at sea level in April/May
(*b*) From St Jean de Luz, Basses-Pyrénées, France		
Balanus eburneus Gould	*ca.* 0·5 km up estuary of la Nivelle from bridge carrying R.N. 10	Approx. M.L.W.N.
B. amphitrite var. *denticulata* Broch	*ca.* 0·5 km up estuary of la Nivelle from bridge carrying R.N. 10	M.L.W.N. to M.T.L.
(*c*) From Port-of-Spain, Trinidad, West Indies, exact tide level not known		
Chthamalus fragilis Darwin	On mangroves, Monos Islands, and Diego Martin River	
Balanus amphitrite var.	On piles in harbour, and on mangroves, Monos Island	
B. tintinnabulum (L.)	Piles, Monos Island	
Tetraclita radiata Blainville	Rocks, S.W. end of Monos Island	
T. squamosa (Bruguière) (var. not determined)	Rocks, S.E. side of Gaspare Grande	

from St Jean de Luz was examined at Banyuls within 2–5 days; the Trinidad material was sent by air to England and though some specimens died during the 5 days in transit to Plymouth, the remainder survived for several months and appeared normal.

All temperatures are quoted in degrees Centigrade.

I wish to acknowledge the assistance of my wife, Dr E. C. Southward, in the experiments on cirral activity and for help with Russian literature. I am indebted to Dr D. J. Crisp for invaluable criticism of the manuscript.

The work at Banyuls formed part of an investigation supported by the NATO funds for scientific research; I am grateful to the Science Adviser and the Advisory Panel on Research Grants for their support, and to Prof. G. Petit and his colleagues of the Laboratoire Arago for laboratory facilities and advice. The Trinidad material was despatched by the Trinidad and Tobago Electricity Commission by arrangement with Messrs Howard Humphreys and Sons, and I am indebted to Mr E. Guevara for collection of samples.

METHODS

To measure cirral activity the barnacles were placed in a long trough of 'Perspex' in which the sea water was circulated by an enclosed paddle wheel driven by an electric motor controlled by a variable resistance (Southward, 1957). The temperature of the water in the trough was raised or lowered by placing in it small flasks of hot water or of ice and salt. The temperature was not controlled exactly but remained stable long enough for each series of observations within a range of 0·2–0·5°, the mean temperature for a series being reported. The beats of at least ten barnacles of each species were counted at each temperature level, the time taken for a sequence of 10 beats being noted. About twenty to fifty barnacles were placed in the trough, and at the higher and lower ends of the temperature range the proportion beating or active was also observed, after trying different speeds of current flow to find the velocity producing optimum activity. With most of the species tested the records imply 'normal' cirral beating unless stated otherwise, but for species of *Chthamalus*, 'pumping' beat, which is more usual in this genus, was also included (see Crisp & Southward, 1961).

Tolerance of high temperatures was assessed as previously (Southward, 1958). The barnacles were placed in a beaker of sea water at room temperature (15–20°) and immersed in a water bath of the type intended for round-bottomed flasks. The water in the bath was heated slowly to obtain a rate of increase of temperature of about 1° every 1 or 2 min, the water around the animals being stirred and aerated by bubbling through it filtered compressed air. Batches of animals were removed at intervals to dishes of cool sea water (15–20°), and those failing to react to pricking with a needle after 12 h were considered dead. One or two preliminary experiments were needed to narrow down the range of lethal temperature, and the results are reported as the means of subsequent experiments with steps of 1°. The temperatures at which 50% and 100% of the animals failed to recover are both given, but only the former are statistically reliable.

A few experiments were also carried out to show the effect of more prolonged immersion in water at high temperatures. The animals were taken from water at room temperature and dropped into large vessels of sea water maintained at a given temperature in a thermostatically controlled bath. The water was stirred and aerated with compressed air, and batches of animals removed at short intervals for recovery and testing as above.

CIRRAL ACTIVITY

Full details of experiments on cirral activity are given in Tables 2–5 (Appendix). Graphs are shown here and the more interesting points commented on under separate headings.

Chthamalus depressus (Fig. 1 A)

The rate of activity in *C. depressus* was much lower than in *C. stellatus*. From approximately 1·5 beats per 10 sec at 10·9°, the mean rate increased linearly to a maximum of 5·95 beats at 32·7°. Above this temperature the rate decreased slightly to 5·58 at 35·3°, several of the specimens showing signs of heat stress in irregular beating and rocking of the valves. Above 36·0° only one specimen at a time was ever found beating out of forty-five individuals, and all activity ceased at 38·0°. Heat coma, from which recovery was made later, set in at 40° (50% of the individuals) and was complete at 41° (all individuals).

Rhythmic activity, even of the pumping type, was rare below 10°. One specimen out of forty-five gave a full sequence of 10 beats at 7·8°, but all others were irregular, and below this temperature no rhythmic activity was observed. However, cirri were still protruded and withdrawn at long intervals down to the lowest level tested, 5·2°. At these low temperatures more than half the barnacles might be found on occasion with their cirri fully extended in the flow of water (extension reaction, Crisp & Southward, 1961), and much lower velocities were needed to elicit this response than at higher temperatures. This species occurs at very high levels on the shore, well above the narrow range of tidal movement in the Mediterranean, and will thus be exposed to great extremes of temperature. It is not therefore surprising that cirral activity is continued down to almost as low a temperature as in *C. stellatus*, which occurs farther north in Europe, but which is not usually found at such high levels as *C. depressus* in the Mediterranean.

Chthamalus stellatus (Fig. 1 B)

Specimens of *C. stellatus* from Banyuls showed rhythmic activity over a range from 8·0° to 35·6°. The mean rate increased more or less linearly from 1·75 beats per 10 sec at 8·0° to 8·97 beats at 29·5°. Above 30° the rate decreased slightly to 8·74 at 32·5°, and then fell off rapidly, only two out of twenty showing rhythmic beating at 35·6°. All activity ceased at 36·6°, and heat coma supervened at 39·5° (50%) to 40° (100%).

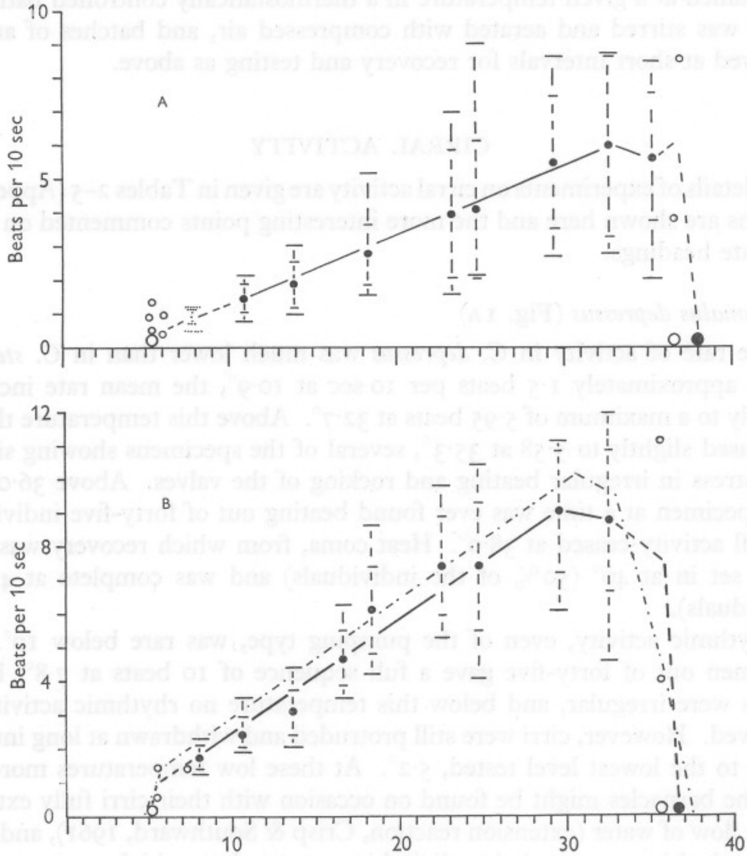

Fig. 1. A. The range of cirral activity in *Chthamalus depressus*. The small black circles show the mean rate of beating at each temperature, the standard deviation and range being indicated by the large and small cross-lines respectively on either side of the mean. Small open circles show single observations too few to supply a mean value, while the series of counts given as dotted lines refers to single beats only, not a sequence of ten beats for each specimen. Large open circles show cessation of cirral activity by 50% of the individuals, large black circles total lack of activity. B. The range of cirral activity in *C. stellatus*. Symbols as above, the solid black line and broken line showing the trend of the Banyuls specimens, while the trend of Plymouth material examined earlier is given as a lighter broken and dotted line.

At low temperatures only a few specimens showing an occasional beat were observed below 8·0°, and all but three out of twenty were completely inactive at 5·3°. Unlike *C. depressus*, specimens of *C. stellatus* were not easily induced to extend their cirri at low temperatures.

The cirral activity of the specimens of *C. stellatus* from Banyuls was substantially the same as that of the Plymouth specimens examined some years ago (Southward, 1955). The latter had an extreme range of activity from 5·7° to 35·7°, with a maximum of 10·18 beats per 10 sec at 30·5°. The mean rate of the Plymouth specimens is shown on Fig. 1B, together with that of the Banyuls material. Although at all temperatures the Plymouth specimens beat slightly faster, of the order of 0·2–0·7 beats per 10 sec, this difference was well within one standard deviation (or at some points on the graph, two) and is probably not significant. More significance should be attributed to the similarity in the rate of change of activity with temperature in both groups of *C. stellatus*, and their difference in this respect from *C. depressus*.

Balanus eburneus (Fig. 2)

Although recorded from the Mediterranean coast of France at Agdè (Utinomi, 1959), *Balanus eburneus* was not found at localities near Banyuls in the short time available for searching, and material was therefore obtained from the Atlantic coast, at St Jean de Luz. Both *B. eburneus* and *B. amphitrite* are very abundant in the port and estuary at St Jean.

The rate of cirral activity increased rather irregularly, from a mean of 2·92 beats per 10 sec at 10·1° to 13·01 beats at 25·0°. A very slight decrease was noted to 12·86 beats at 29·7°, but it is possible that a peak of optimum activity was missed by the absence of observations between 25·0° and 29·7°. Above 30° the rate declined to 10·37 beats at 34·9°, with an increasing proportion of specimens showing jerky or irregular beating. Above 35·0 the numbers or irregularly beating specimens increased, the mean rate falling to 6·91 beats at 37·1°, and only two specimens were observed to give a full sequence of ten beats at 38·0°. All ceased beating at 38·5°, at which temperature over 50% showed no spontaneous activity. Heat coma set in at 41·0 (50%), and was complete at 42·0° (100%).

At temperatures below 10° the mean rate of activity showed a different rate of change, the decrease with decreasing temperature being much less than that found above 10°. Full rhythmic beating was seen at 8·2°, with a mean rate of 1·94 beats, and seven out of forty specimens were still beating at 7·4°. At 5·0° only four specimens were active, and only three showed a full sequence of 10 beats at 3·2°. A few specimens continued to show irregular single protrusions of the cirri down to −0·5°, the lowest temperature available, at which point 50% were in chill coma. It is surprising that this species should be capable of activity at very low temperatures since in Europe it is not found north of the Gulf of Gascony, and is not subjected to such conditions in nature. However, on the American coast *B. eburneus* is recorded from Massachusetts (Pilsbry, 1916), where a greater range of temperature is experienced (cf. Bigelow, 1928), and where the high summer temperatures inshore will balance the low winter minima.

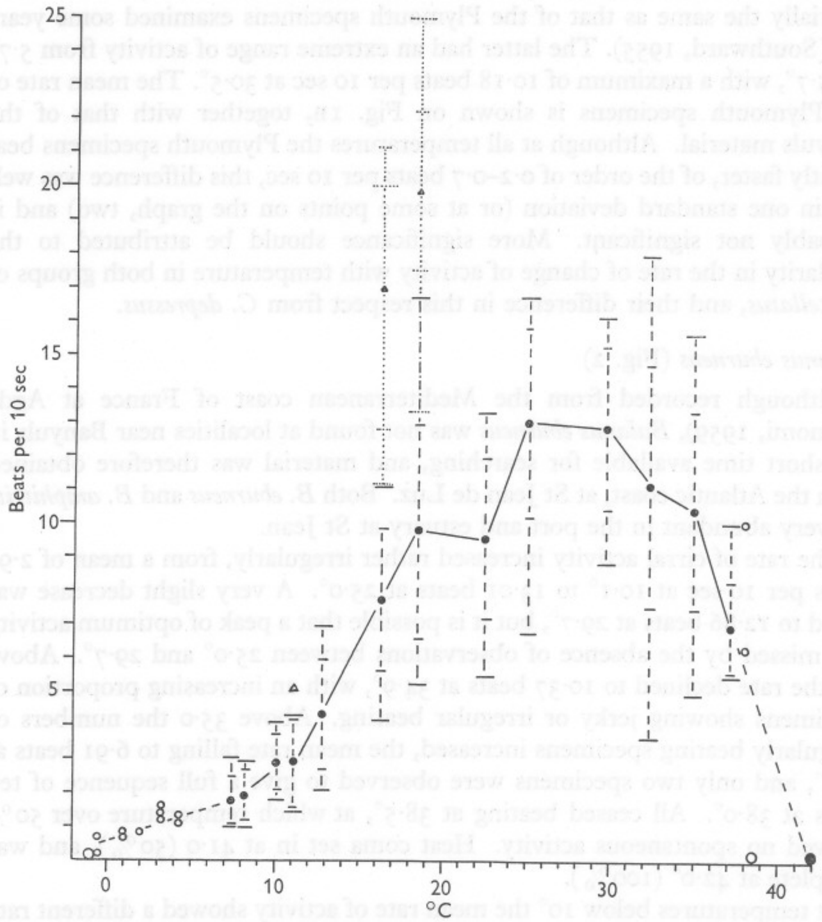

Fig. 2. The range of cirral activity in *Balanus eburneus*. The dotted lines and black triangles show the fast beating specimens, the open triangle a single observation of fast beat. Other symbols (for explanation see Fig. 1) refer to normal beat.

Balanus amphitrite var. *denticulata* (Fig. 3)

The specimens of *Balanus amphitrite* from St Jean de Luz appear to belong to the same variety as those occurring near the Power Station at Plymouth and used for earlier experiments (Southward, 1957). They correspond in all respects with the var. *denticulata* (Broch, 1927), which Utinomi (1959) believes is identical with var. *hawaiiensis* (Broch, 1922). However, Tarasov & Zevina (1957) regard var. *denticulata* Broch as the same as var. *communis* Darwin. Until this difficulty can be settled, it seems best to continue to refer to the European specimens as var. *denticulata*; they do not closely resemble either var. *hawaiiensis* Broch or var. *communis* as described by Utinomi.

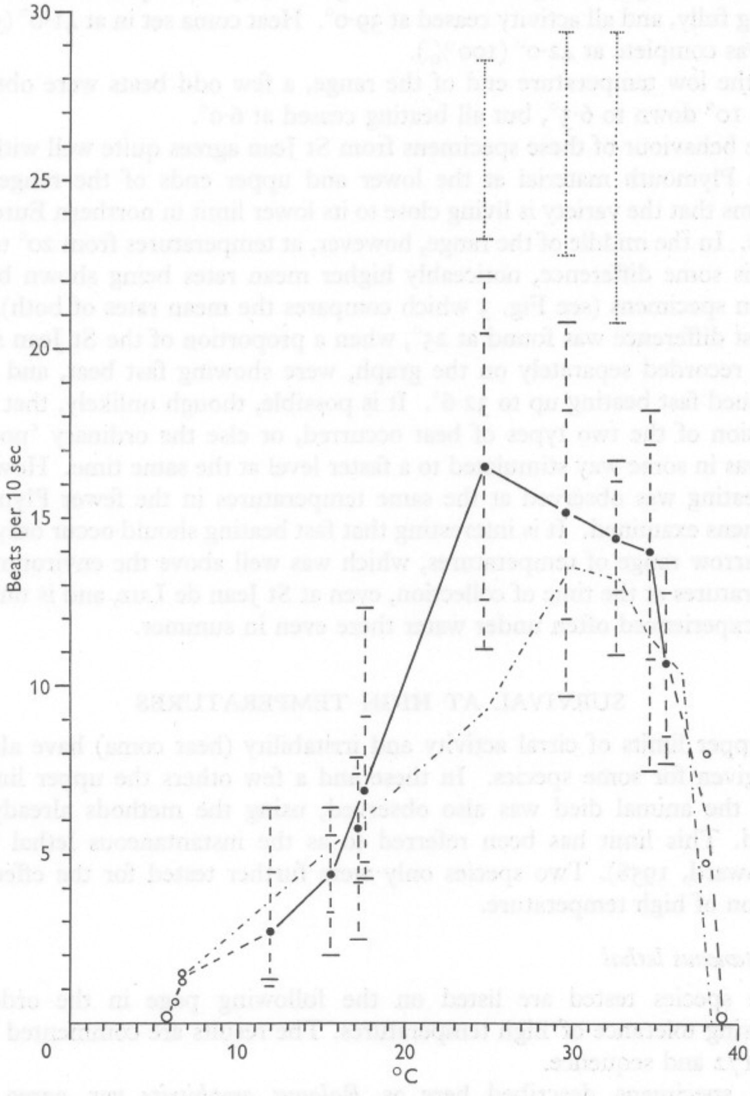

Fig. 3. The range of cirral activity in *Balanus amphitrite* var. *denticulata*. The dotted lines show the range of fast beating specimens at certain temperatures. Other symbols (for explanation see Fig. 1) refer to normal beat of specimens from St Jean de Luz, while the broken and dotted light line shows the trend of Plymouth material examined earlier.

A full sequence of cirral activity was shown between 10° and 35°, the rate increasing non-linearly from 2·77 beats per 10 sec at 11·9° to a peak of 16·55 at 24·7°. Above 25° there was a slight decline in the mean rate to 14·0 beats at 35·6°, and then a sharp decline to 10·67 at 35·6°. At the latter temperature only seven out of thirty specimens were showing a full sequence of beats, the remainder irregular single strokes. At 38·0° only one specimen was seen beating fully, and all activity ceased at 39·0°. Heat coma set in at 41·0° (50%) and was complete at 42·0° (100%).

At the low temperature end of the range, a few odd beats were obtained below 10° down to 6·3°, but all beating ceased at 6·0°.

The behaviour of these specimens from St Jean agrees quite well with that of the Plymouth material at the lower and upper ends of the range, and confirms that the variety is living close to its lower limit in northern European waters. In the middle of the range, however, at temperatures from 20° to 32°, there is some difference, noticeably higher mean rates being shown by the St Jean specimens (see Fig. 3 which compares the mean rates of both). The greatest difference was found at 25°, when a proportion of the St Jean specimens, recorded separately on the graph, were showing fast beat, and some continued fast beating up to 32·6°. It is possible, though unlikely, that some confusion of the two types of beat occurred, or else the ordinary 'normal' beat was in some way stimulated to a faster level at the same time. However, fast beating was observed at the same temperatures in the fewer Plymouth specimens examined. It is interesting that fast beating should occur only over this narrow range of temperatures, which was well above the environmental temperatures at the time of collection, even at St Jean de Luz, and is unlikely to be experienced often under water there even in summer.

SURVIVAL AT HIGH TEMPERATURES

The upper limits of cirral activity and irritability (heat coma) have already been given for some species. In these and a few others the upper limit at which the animal died was also observed, using the methods already described. This limit has been referred to as the instantaneous lethal point (Southward, 1958). Two species only were further tested for the effects of duration of high temperature.

Instantaneous lethal

The species tested are listed on the following page in the order of decreasing tolerance of high temperatures. The results are commented upon on p. 172 and sequence.

The specimens described here as *Balanus amphitrite* var. agree with Utinomi's (1960) description of var. *communis*, but not Tarasov & Zevina (1957). They agree more or less with Darwin's (1854) description, and differ consistently

Species	Temp. at which 50 % or more failed to recover	Temp. at which 100 % or more failed to recover
Chthamalus depressus	54·0	54·5
C. fragilis	52·5	*ca.* 54
C. stellatus	52·5	53·0
C. stellatus (Plymouth, from Southward (1955))	52·5	53·7
Balanus amphitrite var. *denticulata*	50·5	51·0
Tetraclita squamosa	49·5	—
Balanus eburneus	47·5	48·5
Tetraclita radiata	47·0	—
Balanus amphitrite var.	46·25	48·0
Balanus tintinnabulum	< 45·0	—

from specimens attributed to var. *denticulata* obtained from Plymouth, Swansea (South Wales), St Jean de Luz, and from the Mediterranean at Sète (on a boat in the harbour, and inside the Etang de Thau). This difference is clearly reinforced by the difference in the upper lethal temperatures of the two forms; further work is obviously needed, but we may well have two distinct species as Utinomi has suggested.

Duration

The results of two series of experiments on the effect of time and high temperature are listed here:

Species	Temperature	Time in minutes to 50 % lethal	Time in minutes to 100 % lethal
Chthamalus fragilis	50·0 ± 0·2°	15	45
Balanus amphitrite var.	45·0 ± 0·3°	10	20

DISCUSSION

All these experiments have the defect, already noticed (Southward, 1958), that the extreme temperatures are experienced under water, whereas in nature the intertidal species would experience their greatest extremes while exposed to the air. Of course, full cirral activity is possible only when the barnacle is covered by the tide or splashed by the waves, but a reduced level of activity such as testing, or even pumping, may be carried on when the shell and aperture are wet enough. Nevertheless, the observations do provide a guide to purely temperature effects and are clearly related to the animal's distribution. To study the influence of temperature on the barnacles while they are out of water involves the complication of desiccation. A further defect is that the activity of the brackish water species (see below) was assessed at normal salinity (*ca.* 35·0‰) for comparison with the other species; at lower salinities they may well show different behaviour.

The pattern of cirral activity in *Balanus eburneus* resembles that of *B. improvisus* reported previously (Southward, 1957). These species are closely related morphologically and tend to favour brackish water habitats. Both show optimum cirral activity at high temperatures and a change in rate below 10° allowing them to continue cirral beating down to much lower temperatures than other warm water species. However, *B. eburneus* is much the more tropical of the two, if we exclude *B. improvisus* var. *assimilis* Darwin, and in Europe *B. improvisus* occurs in colder waters. This difference is reflected in their behaviour: *B. eburneus*, which has a generally higher rate of beating shows an optimum at a considerably higher temperature than *B. improvisus*; all activity stops in *B. improvisus* above 35°, but *B. eburneus* is still active and continues to beat up to 37 or 38°.

Balanus eburneus is often found associated with *B. amphitrite*, and except at the lower range of activity below 10°, their behaviour is quite similar. *B. amphitrite* var. *denticulata*, however, has a somewhat greater tolerance of high temperatures, possibly connected with its ability to live at higher levels on the shore, where it will be subjected longer to the heat of the sun. It is worth noting that during the experiments *B. amphitrite denticulata* tended to keep its valves tightly closed while being heated, whereas *B. eburneus* opened up sooner. This difference is often found when comparing species of barnacles from different levels on the shore; other low-tide or sublittoral forms such as *B. perforatus* and *B. crenatus* open and display cirral activity more readily than *B. balanoides* and *Chthamalus stellatus* which can exist much higher up the shore.

The relatively low tolerance of high temperatures shown by the specimens of *B. amphitrite* var. from Trinidad is surprising, since the variety is more restricted to the Tropics than var. *denticulata*. It seems possible that the Trinidad var. is a low-level form, more comparable with *B. eburneus*, but the exact intertidal distribution is not known. There is less difference in the lethal temperatures of *B. eburneus* and *B. amphitrite* from Trinidad than between the two varieties of *B. amphitrite*.

Apart from *Chthamalus fragilis*, the remaining species of barnacles from Trinidad were not examined in detail. The low lethal temperature of *Balanus tintinnabulum* compared with *Tetraclita squamosa* needs comment since the species is generally distributed in the Tropics. Probably its lesser tolerance of heat reflects the relatively low level it occupies on the shore compared with *Tetraclita*. In West Africa, for example (Lawson, 1956), *B. tintinnabulum* is common above low water only on wave-beaten shores.

The results of the experiments on the three species of *Chthamalus* confirm previous impressions that species of this genus are much better adapted to withstand heat than the species of *Balanus* or *Tetraclita*, and this adaptation with, we can assume, a concomitant higher resistance to desiccation, explains their ability to live at higher levels on the shore. Of the three species tested, *C. depressus*, which occurs well above the normal intertidal zone at levels reached only by the waves, had the greatest tolerance of high temperatures.

The rate of cirral activity of *C. depressus* was significantly lower than that of *C. stellatus* at all temperatures up to the optima. The rate of change with temperature was also different, and these other differences between the two forms, which were once regarded as varieties, are sufficient to justify separation as distinct species, a procedure already suggested for morphological and ecological reasons (Utinomi, 1959). The lower rate of beat in *C. depressus* may perhaps be related to the rather precarious habitat it occupies, where a generally lower level of metabolic activity may be an advantage, or it may be a latitudinal effect (Fox, 1939), the metabolic rate being less at a given temperature in *C. depressus* than in the more northern form *C. stellatus*. The latter possibility would appear to be supported by the higher temperature at which optimum activity is reached in *C. depressus* and its reluctance to show rhythmic activity below 10°, but further comment must wait for more information on the distribution of the species. At the moment *C. depressus* is known with certainty only from the Mediterranean Sea and Black Sea; West African records refer to other, possibly new, species, while records from north of the Mediterranean seem to be only of growth forms of *C. stellatus* (Utinomi, 1959; personal observations; personal communications Dr H. G. Stubbings and Dr G. B. Zevina).

In conclusion, it is worth noting that the differences in temperature tolerance and cirral activity are less between species of almost wholly tropical distribution and those capable of penetrating into the temperate regions, than between the latter forms and those of Arctic–Boreal distribution. For example, widely distributed forms such as *Balanus perforatus*, *B. amphitrite denticulata* and *Chthamalus stellatus* differ much more from Arctic–Boreal species such as *Balanus balanoides* and *B. crenatus* than they do from *B eburneus*, *Chthamalus depressus* and the other tropical species examined. In fact, in the North Atlantic area it seems that only two main distributional groups of acorn barnacles exist, Arctic and Tropical, which overlap in the Temperate regions, and that there are few or no species of intermediate distribution such as are common among intertidal gastropods (e.g. the genera *Gibbula* and *Monodonta*).[1] A possible exception is *Verruca stroemia*; this species and other members of the genus have not yet been investigated, but as rhythmic beating is rarely found different techniques will have to be used.

A further conclusion is that in the genera of acorn barnacles examined so far, no evidence has been found for the occurrence of physiological races comparable with those reported by Mayer (1914) in *Aurelia aurita*, and suspected to occur in other groups of animals. Differences in temperature effects have been found to be significant only between species or well established varieties. An exception that might have been made in the case of the American

[1] From its range of cirral activity, the immigrant Australasian species *Elminius modestus* seems fitted to qualify as an intermediate form of neither tropical nor Arctic distribution. It is still spreading in Europe and its final distribution is awaited with much interest.

form of *Balanus balanoides* examined by Cole (1929) seems no longer valid as far as cirral activity is concerned: Dr D. J. Crisp informs me that his examination of specimens of *Balanus balanoides* from Massachusetts and from Wales shows no significant difference in the general pattern of cirral behaviour in relation to temperature (cf. Southward, 1955). It would seem therefore that Cole was examining another species of *Balanus* in Maine.

Finally, the investigations carried out in this and previous reports emphasize the value of physiological investigations in systematic work, as well as the importance of systematic correctness in physiological studies.

SUMMARY

The range of temperatures over which the cirri were active and the frequency of beating at different temperatures were measured in four species of barnacles collected on the southern and south-western coasts of France. The extremes of high temperature at which the animal remained irritable or could survive were assessed in these species and in a further group of species from Trinidad, West Indies.

The results are discussed in comparison with previous evidence for species of more northern distribution, and related to the geographical range of the species and the ecological niche occupied. For example, the brackish water species, *Balanus eburneus* and *B. improvisus*, have similar patterns of cirral activity, but the greater tolerance of high temperatures shown by the former is obviously connected with its more tropical distribution. Differences in temperature tolerances of varieties of *B. amphitrite* from Europe and Trinidad, possibly related to differences in the tide levels at which they live, tend to reinforce their separation on morphological grounds. More pronounced differences between *Chthamalus depressus* and *C. stellatus* confirm the separation of these two species which were formerly regarded as varieties. The relatively lower rate of beating of *C. depressus* which is not found north of the Mediterranean and its greater tolerance of high temperatures compared with *C. stellatus*, may be related to its more southern distribution and its ability to live at very high levels on the shore. These two species and *C. fragilis* from Trinidad all show greater tolerance of high temperatures than the species of *Balanus* and *Tetraclita*, which are found at lower levels on the shore.

It is concluded that in the North Atlantic area there may be only two main distributional groups of species of acorn barnacles, Arctic and Tropical, overlapping in the Temperate regions, with few or no intermediate forms, and that there is as yet no evidence for the existence of physiological races in these species.

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ADDENDUM

Dr J. P. Harding has kindly allowed me to see the manuscript of his forthcoming account in *Bull. Brit. Mus.* (N.H.) of Darwin's varieties and type specimens of *Balanus amphitrite*. *Balanus amphitrite* var. *denticulata* Broch is identical with Darwin's *communis*, and the correct name is simply *Balanus amphitrite* Darwin. The Trinidad variety does not have a multidenticulate labrum and is not therefore *B. amphitrite*. Very similar material, possibly from the West Indies, but lacking opercula and soft parts, is present in the Darwin collection, but not named. At the moment the West Indian specimens are best regarded as a variety of *Balanus variegatus* Darwin (formerly *B. amphitrite* var. *variegatus*) related to *B. variegatus* var. *cirratus* (formerly *B. amphitrite* var. *cirratus*).

APPENDIX

TABLE 2. FREQUENCY OF BEATING OF THE CIRRI OF *CHTHAMALUS DEPRESSUS*

As number of beats per 10 sec. Banyuls-sur-Mer, 27–29 April 1961

Temperature (° C)	Mean	Frequency range	Standard deviation
5·2	Nil, but 1/45 slight activity		
5·4	Nil, but 4/45 slight activity		
7·8	One only	1·2	—
10·9	1·48	0·81–2·14	0·42
13·9	1·87	1·0–3·03	0·67
18·3	2·77	1·55–5·15	0·91
23·3	3·94	1·55–6·94	1·92
24·8	4·11	2·14–9·02	2·04
29·4	5·44	2·72–8·62	1·96
32·7	5·95	2·74–8·70	2·68
35·5	5·58	2·0–8·47	1·92
36·6	One only	3·79	—
37·0	One only	8·55	—
38·0	—	Nil	

TABLE 3. FREQUENCY OF BEATING OF THE CIRRI OF *CHTHAMALUS STELLATUS*

As number of beats per 10 sec. Banyuls-sur-Mer, 27–29 April 1961

Temperature (° C)	Mean	Frequency range	Standard deviation
5·3	Nil, 2/20 slight activity		
5·5	Nil, 3/20 slight activity		
7·3	Nil, 2/20 slight activity		
8·0	1·75	1·35–2·30 (5 individuals)	0·35
10·6	2·42	2·04–3·51 (8 individuals)	0·52
13·6	3·07	2·04–4·38	0·67
16·6	4·66	4·47–6·25	0·81
18·3	6·07	4·20–8·63	1·31
22·5	7·40	5·24–9·80	1·48
24·7	7·38	4·03–10·4	1·89
29·5	8·97	6·03–11·1	1·80
32·5	8·74	4·55–11·9	2·08
35·6	Two only	4·0, 11·1	—
36·6	—	Nil	

TABLE 4. FREQUENCY OF BEATING OF THE CIRRI OF *BALANUS EBURNEUS*

As number of beats per 10 sec. Collected St Jean de Luz, 2 May 1961

Temperature (° C)	Mean	Frequency range	Standard deviation
−0·5	Nil, 50 % chill coma, 5/20 slight activity		
1·0	Nil, 5/20 slight activity		
2·0	Nil, 3/20 slight activity		
3·2	Three only	1·18, 1·25, 1·67	—
4·3	Two only	1·11, 1·33	—
7·4	1·80	1·0–3·05 (7 individuals)	0·71
8·2	1·94	0·98–2·94 (7 individuals)	0·76
10·1	2·92	1·79–4·12 (8 individuals)	0·82
11·1	2·97	1·43–4·31	1·22
12·8	4·35	2·13–6·95	1·62
16·3	7·76	4·17–11·1	2·08
16·3 fast beat	17·0	11·1–20·0	4·17
18·5	9·81	5·27–16·7	3·15
18·5 fast beat	19·88	13·3–25·0	2·32
22·5	9·56	5·44–13·3	2·38
25·1	13·01	6·76–16·7	2·82
29·7	12·86	8·85–16·1	2·44
32·25	11·12	3·63–17·8	3·58
34·9	10·37	4·90–15·6	2·91
37·1	6·91	5·44–10·0	1·35
38·0	Two only	6·25, 10·0	—
38·5	Nil, 14/40 slight activity		
40·0	Nil, 6/40 slight activity		
41·5	Nil, 1/40 slight activity		
42·0	No activity		

TABLE 5. FREQUENCY OF BEATING OF THE CIRRI OF *BALANUS AMPHITRITE DENTICULATA*

As number of beats per 10 sec. Collected St Jean de Luz, 2 May 1961

Temperature (° C)	Mean	Frequency range	Standard deviation
5·8	No activity		
6·3	Nil, 1/30 slight activity		
6·8	Nil, 2/30 slight activity		
11·9	2·77	1·32– 6·42	1·70
15·5	4·46	2·0–6·42	1·18
17·2	5·82	2·50–7·88	1·59
17·6	6·95	4·30–12·35	2·13
24·7	16·55	11·1–22·2	3·93
24·7 fast beat	—	23·3–28·6 (4 only)	—
29·6	15·18	9·70–20·8	3·01
29·6 fast beat	—	22·8–29·4 (3 only)	—
32·6	14·42	10·9–16·7	1·67
34·6	14·0	7·47–18·2	3·18
35·6	10·67	7·70–13·7 (6 only)	2·15
38·0	One only 2/30 slight activity	8·0	
39·0	No activity		