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ON THE BEHAVIOUR OF BARNACLES

II. THE INFLUENCE OF HABITAT AND TIDE-LEVEL ON CIRRAL ACTIVITY

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During a study of the relation between temperature and cirral activity of barnacles, reported in Part I of this series (Southward, 1955), specimens for investigation were collected from those habitats and tide-levels where the particular species was most abundant. However, it is possible that some variation in behaviour may arise from local environmental factors such as tide-level and degree of exposure to wave action, and experiments were carried out to test this possibility.

The experimental conditions under which the barnacles were observed, and the methods of measuring cirral activity, were similar to those described in Part I. In all experiments the material was dealt with within 24 h of collection from the shore. Only one or two temperature levels were used to obtain temperature-frequency relations, as this was sufficient to enable a comparison of behaviour to be made between samples from different localities or tide-levels. Most frequently the temperature of the laboratory sea water supply was used since it required no regulation and remained at uniform temperatures (within 0·5 to 1·0°) for long periods.

The investigations were carried out during the first half of 1954, during the tenure of a D.S.I.R. Senior Research Award. I am grateful to Dr D. J. Crisp for help and advice in this work.

Investigations at Plymouth

Chthamalus stellatus

The work at Plymouth was confined largely to the commonest barnacle in the neighbourhood, *C. stellatus*. Specimens were first taken from two tide-levels at Tinside, below the laboratory, and examined at two temperatures. At both temperatures the two age-groups present in the sample from low water showed a 40–50% greater frequency of cirral beat than that of specimens of corresponding age from high water (Table I). This difference, when tested by the t distribution, was found to be significant in comparison with the individual variation (P less than 0·1% that the samples from the two tide-levels came from the same population).

Subsequently, however, specimens were taken from high and low tide levels at Wembury, and similarly compared. In this case there was very little difference in the frequency of cirral beat, and the slight differences that were observed were not statistically significant (Table II). The experiments were

TABLE I. FREQUENCY OF BEATING OF THE CIRRI, AS BEATS/10 SEC, OF SPECIMENS OF *CHTHAMALUS STELLATUS*

From two different tide-levels at Tinside, Plymouth, 15. xii. 53.

Temperature (° C)	Year-group	Tide-level	No. in sample	Frequency Mean	Range	S.D.	t
13·8	1+	M.H.W.S.	6	3·516	2·2–4·5	0·893	3·33
		M.L.W.N.	12	5·466	3·8–8·4	1·205	
	2+	M.H.W.S.	9	3·188	2·3–3·7	0·459	6·36
		M.L.W.N.	10	5·810	4·1–8·1	1·184	
20·4	1+	M.H.W.S.	8	5·962	4·5–7·4	0·976	7·65
		M.L.W.N.	20	9·725	7·8–12·1	1·240	
	2+	M.H.W.S.	9	4·822	3·7–6·1	0·882	4·78
		M.L.W.N.	12	8·350	6·4–10·2	1·389	

TABLE II. THE FREQUENCY OF BEATING OF THE CIRRI, AS BEATS/10 SEC, OF SPECIMENS OF *CHTHAMALUS STELLATUS*, APPROXIMATELY $1\frac{1}{2}$ YEARS OLD

From two different tide-levels at Wembury, near Plymouth.

Date	Temperature (° C)	Tide-level	No. in sample	Frequency Mean	Range	S.D.	t
22. i. 54	20·4	M.H.W.S.	9	5·220	3·8–6·6	0·788	1·07
		M.L.W.N.	10	5·630	4·3–7·2	0·869	
19. ii. 54	19·6	M.H.W.S.	7	5·185	4·2–7·3	1·083	1·21
		M.L.W.N.	8	5·837	4·4–7·1	0·985	

TABLE III. THE FREQUENCY OF BEATING OF THE CIRRI, AS BEATS/10 SEC, OF SPECIMENS OF *CHTHAMALUS STELLATUS*, APPROXIMATELY 1 YEAR OLD

From two different tide-levels at two places in Plymouth Sound, 1–2. vi. 54, temperature 14·9° C.

Place	Tide-level	No. in sample	Frequency Mean	Range	S.D.	t
Tinside	M.H.W.S.	9	6·355	5·3–7·7	0·705	3·03
	M.L.W.N.	10	7·780	6·3–9·5	1·014	
Rum Bay	M.H.W.S.	17	6·576	4·9–8·9	1·368	0·45
	M.L.W.N.	10	6·370	5·6–7·2	0·566	

therefore repeated on some more specimens from Tinside, and simultaneously observations were made on barnacles from Rum Bay, a nearby site in Plymouth Sound (Table III). Again the specimens from L.W.N. at Tinside had a significantly faster cirral beat than those from high water, while there was no significant difference between the two sets of barnacles from Rum Bay.

The matter rests there at the moment. It can only be suggested that the *Chthamalus* at low water at Tinside are anomalous compared with those from all other levels and localities, but the reason for this anomaly is not clear.

Elminius modestus

Further tests were made on another barnacle, *E. modestus*, which at Plymouth is common only in the estuaries. Specimens under 1 year old showed a significant difference in cirral beat between individuals from different tide-levels (Table IV). Those from low water had a mean frequency of beat some 20% greater than those living at high water. The older age groups of this species were not tested, as the older specimens among the high water sample could not be induced to beat regularly under laboratory conditions.

TABLE IV. THE FREQUENCY OF BEATING OF THE CIRRI, AS BEATS/10 SEC, OF SPECIMENS OF *ELMINIUS MODESTUS*, UNDER 1 YEAR OLD

From two different tide-levels at Hen Point, near Plymouth, 22. ii. 54, temperature 12·4° C.

Tide-level	No. in sample	Frequency			
		Mean	Range	S.D.	t
M.H.W.N.	6	15·350	13·3–16·7	1·126	3·10
M.L.W.N.	9	18·200	15·6–21·8	1·857	

TABLE V. OBSERVATIONS ON *CHTHAMALUS STELLATUS* FROM M.H.W.N., HEN POINT (TAMAR ESTUARY), 23. vi. 54, TEMPERATURE 16·6°

Age group, in years	Percentage of total sample showing rhythmic beating of cirri	Mean frequency of beating, as beats/10 sec
1	50	8·066
2	30	6·433
3 and over	12	5·200

Effect of Age

The difficulty of obtaining regular beating from the older barnacles was frequently encountered during the work described in Part I. The irregular behaviour of the older barnacles seems to be linked with their generally lower mean frequency of cirral beat (see Table I). Some comparative observations showed a decrease, with increasing age, of both the frequency of beat and the proportions of the sample regularly beating (Table V). The two phenomena are probably characteristic of the ageing process in barnacles.

Unfortunately it is not possible to determine critically the effect of age on cirral activity without more exact information of the age of the barnacles examined. The age-groups given here were separated only by estimation, based on experience of the barnacle in question, its size at settlement and its known rate of growth. Although this was sufficient to show that the younger barnacles have more lasting and frequent cirral activity, further investigation with barnacles of definite age is clearly desirable.

The work at Plymouth indicated that habitat variations might have some influence on the cirral activity of barnacles. It was therefore arranged to continue the work in the Anglesey area (from the Marine Biology Station at Menai Bridge), where a greater variety of habitats were within easy reach, and where the other common British intertidal barnacle, *Balanus balanoides*, was plentiful.

Investigations at Menai Bridge

The experimental conditions at Menai Bridge were similar to those at Plymouth. The water currents used in the apparatus, in addition to a regular flow of water through it, were set up by a jet of compressed air instead of a paddle wheel.

TABLE VI. THE FREQUENCY OF BEATING OF THE CIRRI, AS BEATS/10 SEC, OF TWO SPECIES OF BARNACLES

From two different tide-levels at Criccieth, 26. iv. 54, temperature 10·4° C.

Species	Approximate age (years)	Tide-level	No.	Frequency Mean	Range	S.D.	t
Chthamalus stellatus	$1\frac{1}{2}$	M.H.W.N.	10	2·970	2·1–4·2	0·602	0·72
		M.L.W.N.	10	2·950	1·9–3·7	0·632	
Balanus balanoides	1	M.H.W.N.	20	3·155	2·1–4·1	0·584	12·53
		M.L.W.N.	20	4·705	3·9–6·0	0·664	

Effect of Tide-Level

Specimens of *Chthamalus stellatus* and *Balanus balanoides* were collected from two tide-levels at the north end of Cardigan Bay, and examined the same day. As can be seen from Table VI, there was no significant difference in the frequency of beat of the *Chthamalus* from the two tide-levels. In the case of *Balanus balanoides*, however, the specimens from low water had a markedly faster cirral beat than those from higher up the shore. This difference in behaviour of two species living side by side under identical conditions is surprising, in view of the great similarity, at the temperature used, of the frequency of beat of the high water individuals of both barnacles. It is interesting to note that, again at this temperature, the low water *B. balanoides* would probably be more successful in obtaining food than the *Chthamalus* at the same level.

Further experiments on the same barnacles during subsequent days showed a change in behaviour. After the specimens had been kept for 24 h in running sea water from the laboratory supply the former difference between the high and low water *Balanus balanoides* disappeared, the mean frequencies being, at 18°: high water, 7·45; low water, 7·72. The corresponding frequencies for *Chthamalus* at 17° were: high water, 5·17; low water, 4·85. The similarity between the two sets of *Balanus balanoides* was found again the following day, when the mean frequencies at 10·4° were: high water, 5·62; low water, 5·56, Comparison with Table VI shows that both the high-water and the low-water samples of *B. balanoides* had increased their frequency of beat after only 3 days in the laboratory, but that the increase was greater among the individuals from the higher tide-level.

These experiments serve to show the extent of acclimatization that may occur. It is not known whether the change in the frequency of beating was a reaction to some quality of the laboratory water (temperature, salinity, pH, silt, etc.), or merely to the continued immersion. Cole (1929, 1932) found no change in the frequency of beat of continuously immersed *B. balanoides* at Mt Desert Island, Maine, but, as noted in Part I, there are important differences in the behaviour of the British and American specimens of this species.

Effect of Habitat

Some preliminary experiments suggested that the fast type of beat (see Part I) was more commonly shown by individuals from sheltered habitats, than by those living on the open coast. A full investigation was therefore undertaken with *B. balanoides*, by collecting a series of samples from four different habitats on the same day. This was possible since the variation in the time of low water around Anglešey permits several localities to be visited on one tide. To avoid acclimatization changes the samples were kept out of water at the laboratory, in a cool place, and examined within 24 h. The measurements of the cirral beat were made at approximately the time of high water the following day, to minimize any inherent tidal rhythm of the animals. Before counting the frequency of beating each sample of barnacles was allowed 30 min in water to eject the air that is often present in the mantle cavity, and to settle down to regular beating. The numbers showing fast beat, normal beat, and those closed or irregular were then noted (Table VII).

It was found that there was invariably a larger proportion of closed or non-beating individuals among the specimens from high water compared with those from lower down on the shore. Furthermore, a much lower percentage of rhythmically beating individuals occurred among the barnacles from the open coast site exposed to wave action than was found at the three sheltered localities. This was evident in samples from both tide-levels. This difference may be habitual, for those barnacles living at high water may be used to rhythmic beating only for short periods when covered by the tide. Individuals from a wave beaten place may also be unused to beating continuously for a different reason. If the continuous water movement resulting from wave action brought an abundant supply of food and oxygen to the barnacles, only limited periods of cirral activity might be necessary for normal growth and respiration.

TABLE VII. THE FREQUENCY OF BEATING OF THE CIRRI, AS BEATS/10 SEC, AND THE PROPORTION OF INDIVIDUALS ACTIVE, OF SAMPLES OF APPROXIMATELY 1 YEAR OLD *BALANUS BALANOIDES*

From different tide-levels and habitats, Anglesey, 30. iv. 54

Locality, and type of habitat	Temperature °C	Tide-level	Fast beat: % of sample	Fast beat: No. examined	Fast beat: Frequency: Mean	Fast beat: Frequency: Range	Fast beat: Frequency: S.D.	Ordinary beat: % of sample	Ordinary beat: No. examined	Ordinary beat: Frequency: Mean	Ordinary beat: Frequency: Range	Ordinary beat: Frequency: S.D.	% closed or not beating
Aberffraw, open coast exposed to wave-action	13·0	M.H.W.N.	0	—	—	—	—	55	8	3·975	2·6–5·9	1·149	45
		M.L.W.N.	0	—	—	—	—	64	10	5·010	3·9–6·9	0·898	36
Aberffraw, open coast sheltered from wave-action	12·2	M.H.W.N.	0	—	—	—	—	81	11	3·127	2·5–4·1	0·735	19
		M.L.W.N.	2	—	One only 13·3			87	12	5·950	3·1–9·8	2·153	11
Menai straits, exposed to currents	12·6	M.H.W.N.	3	—	One only 10·2			82	10	2·930	1·9–4·4	0·707	15
		M.L.W.N.	3	—	One only 10·8			86	10	6·010	4·2–7·4	1·275	11
Menai straits, sheltered from currents	11·6	M.H.W.N.	68	10	15·560	13·9–16·7	0·938	12	3	9·400	7·7–10·5	1·493	20
		M.L.W.N.	0	—	—	—	—	89	10	5·640	4·5–8·3	1·153	11

Note: the number examined is not the number on which the percentages are based, except in one case.

Turning to the mean frequency of the normal cirral beat shown by these samples (Table VII, col. 11) it can be seen that, except for the specimens from the sheltered site without currents, the low-water samples had a mean 30–100% greater than that of the high-water individuals. The least difference was shown by the barnacles from the wave beaten locality at Aberffraw, and the greatest by those from the site in the Menai Straits exposed to currents.

The fast type of beat was not shown by any individuals from the wave-beaten site, and only one fast-beating specimen occurred in the sample from the sheltered open coast site, and two among those from the site with currents. However, among those individuals from the site without wave action or currents, a remarkably high proportion of fast-beating specimens was found in the high-water group. At low water in the same place not a single fast-beating specimen was obtained. On ecological grounds it seems possible that the fast type of beat could, in this case, be an adaptation to life in comparatively still water, a replacement of the natural movement of water over the cirri found in the other habitats. It might only be found regularly among barnacles from high water, since these would have the greatest need of such an adaptation on account of the short time available for feeding and respiratory exchange.

Effect of Oxygen Content

If respiratory need were the driving factor in stimulating the fast type of cirral beat, it should be possible to investigate the relation by varying the oxygen content of the medium, and recording the effect on the type and frequency of beat. Specimens of *B. balanoides* together with *Chthamalus stellatus* for comparison were observed in a small dish holding about 200 ml. water with a lid ground on and sealed with vaseline. Gases were led in through calibrated flowmeters of the manometer type, and bubbled through the water in a manner that caused currents to be set up. Observations were made at regular intervals, the flow of gas being turned off momentarily to arrest the water currents. The temperature was kept fairly constant by immersing the dish in a trough of running tap water.

The effects of lowering the oxygen content by bubbling nitrogen through the water, and of increasing the oxygen content by bubbling that gas through the water, are given in Table VIII, for individual specimens of *Balanus balanoides* and *Chthamalus*. It should be noted that, as the supply of nitrogen and oxygen did not contain any carbon dioxide, the latter may have been driven off from the water. The loss of some of the carbon dioxide, and the resulting decrease in the hydrogen-ion concentration, may have had some influence on the behaviour of the barnacles. The results can only be accepted as indications of responses to variations in the oxygen content on the assumption that the possible changes of carbon dioxide content and pH had a negligible effect. Previous work (Roaf, 1912; Fox & Johnson, 1934) suggests that the effects of a decrease in the carbon dioxide content and hydrogen-ion concentration are indeed negligible, though an *increase* may influence the cirral beat.

From the table it can be seen that lowering the oxygen content of the water caused a reduction in the cirral activity of both fast and normally beating specimens of *Balanus balanoides*, and had a similar effect on *Chthamalus*. In

TABLE VIII. THE EFFECT OF VARYING THE OXYGEN CONTENT OF THE WATER ON THE FREQUENCY AND TYPE OF CIRRAL BEAT OF INDIVIDUAL BARNACLES, 28–29 iv. 54

A. Oxygen decreased by passing nitrogen through the water at 6 ml./min; temperature 13° C.

Time in min since start of N_2 bubbling	Frequency of individual specimens*											
	Balanus balanoides								*Chthamalus stellatus*			
	From Menai Straits				From Criccieth				From Criccieth			
	a	*b*	*c*†	*d*†	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
0	4·3	3·6	14·1	13·0	3·7	5·0	3·1	4·2	2·6	3·7	3·1	2·9
15	—	—	4·8	4·9	4·1	4·5	—	3·2	2·9	3·0	1·6	4·1
30	G	G	G	G	2·7	2·3	G	G	G	G	0·5	G

B. Oxygen increased by passing the gas through the water at 6 ml./min, temperature 13° C.

Time in min since start	Frequency of individual specimens*												
	Balanus balanoides								*Chthamalus stellatus*				
	From Menai Straits				From Criccieth				From Criccieth				
	w†	*x*†	*y*†	*z*†	*w*	*x*	*y*	*z*	*v*	*w*	*x*	*y*	*z*
0	17·9	11·9	13·9	14·1	3·8	3·5	3·8	3·5	2·1	1·7	2·8	1·3	1·8
15	18·5	C	14·3	9·9	2·3	2·7	2·2	1·8	1·7	1·7	2·6	E	3·2
30	19·3	C	13·7	C	2·3	3·1	2·4	1·1	2·8	4·7	3·3	3·8	4·1
45	18·5	C	C	C	2·3	2·9	2·6	C	2·7	3·7	4·0	E	4·2
	Only one out of 17 of this group open												

Notes. C, terga and scuta tightly closed; G, terga and scuta open, cirri inactive, and in some, protruding; E, cirri remaining extended for longer than usual during open phase of beat.

* As beats per 10 sec.

† Specimens showing the fast type of beat.

each case, the first response was a slowing down of the frequency of beating, followed by a cessation of beating altogether. At the end of the experiments practically all specimens had the terga and scuta slightly open, often with the cirri protruding. This reaction can be termed the gaping response, and probably indicates acute respiratory difficulties (cf. Fox & Johnson, 1934). It will be noted that before the fast-beating specimens became inactive they changed over to the normal type and frequency of beat. From this it might be inferred that the fast type of beat is not related to respiratory need, but it must be remembered that the fast beat in itself may utilize more oxygen than the normal type, and may thus be the first to be inhibited by severe oxygen lack.

The two species of barnacles reacted differently to an increase in the oxygen content of the water. In five specimens of *Chthamalus* the mean frequency of beating increased from 1·94 to 3·75 beats/10 sec, a gain of nearly 90 %. The frequency of *Balanus balanoides*, on the other hand, slowed down, the mean of the normal beat decreasing from 3·6 to 2·6 beats/10 sec, while all but one of the specimens showing the fast type of beat gave the closing response.

The more rapid beat of *Chthamalus* in oxygen-enriched water suggests that the species is adapted to an oxygen content higher than that of the laboratory sea water supply, which may not have been fully saturated with air. In Britain this barnacle is most abundant in wave-beaten places, where the water will nearly always be fully saturated. The cessation or slowing down of both types of beat in *Balanus balanoides* suggests that in these specimens oxygen lack was the main driving factor behind cirral activity. From this assumption it could be argued that the fast type of beat was in fact respiratory in function.

The problem of the fast type of beat therefore remains unsolved by these experiments. It is hoped that it will be dealt with again in a later paper in this series.

Discussion

The studies described here and in Part I take no account of possible inherent diurnal rhythms in the behaviour of barnacles. Diurnal rhythms, generally related to the tidal cycle, have been shown to occur in the rate of feeding, respiration, and other processes in many intertidal (and sublittoral) animals, and may persist even after periods of continuous immersion in the laboratory (literature in Rao, 1954). Although during the present work no signs of diurnal variations in behaviour were noticed, the possibility of their existence in barnacles cannot be discounted. However, in the investigations into the effects of tide-level and habitat on cirral activity, any diurnal rhythms would not have affected the comparisons of different samples of barnacles, as the latter were taken practically simultaneously, treated identically in the laboratory, and examined at about the same time of day and period of tidal cycle.

Segal, Rao & James (1953) have shown differences in the rate of activity of limpets and mussels from different tide-levels in California. They suggest that the differences are related to similar differences found in examples of the species from different latitudes, and that the greater activity, at a given temperature, of the forms from low water is comparable to the greater activity of cold-adapted forms from higher latitudes. This is, of course, possible, since animals living at low water in relatively warm latitudes, and exposed to the air for only a short time, will have a more uniform and cooler environment than those at high water that are exposed to the heat of the sun and air for longer periods. But it must be noted that, except for activities such as heart beat, most of the other activities of an intertidal animal (feeding, movement of feeding or respiratory appendages, gaseous exchange) take place mainly under water, when the conditions governing the high- and low-water individuals will be almost identical.

However, at first sight the suggestion of Segal *et al.* might seem to explain the greater cirral activity of the British specimens of *B. balanoides* from low water. As was shown in Part I, this barnacle is at its southern limits in Britain, and its behaviour here must represent its extreme limit of adaptation to higher temperatures, i.e. there is probably ample scope for cold-adaptation by those forms living at low water. At the same time the absence, except in one instance, of any difference in the behaviour of *Chthamalus* from different tide-levels could be due to this species having already, at high water, reached its limit of adaptation to low temperature.

Attractive as this explanation might seem, since it would link up with the restriction of *Chthamalus* to high water and of *Balanus balanoides* to lower down the shore at their respective extreme limits of distribution, it does not fit all the observed facts. The differences in the behaviour of barnacles from different habitats, and the acclimatization that can occur in the laboratory, suggest that, in these animals, the tidal differences are not entirely a matter of temperature. It is well known that the rate of growth of intertidal animals is slower at high water than further down the shore, and that correspondingly their life is longer at high water. It seems possible that the whole life and vital activities of the animal living at high water might be keyed to the slower tempo, and that not only growth, but rate of feeding, respiration, and other processes would therefore be slower than at low water.

Finally, it seems worthwhile pointing out the need for caution in comparing the behaviour or activity of intertidal animals from different tide-levels or latitudes until the effect of other habitat variations have been thoroughly investigated.

SUMMARY

The frequency of beating, and other aspects of cirral activity, were observed in samples of three species of intertidal barnacles taken from various habitats and from different tide-levels.

At Plymouth a more rapid beat was found among individuals of *Chthamalus stellatus* from low water at one locality than among those from high water at the same place. At two other localities, however, there was no significant difference in behaviour between samples from high and low water. A difference was found in samples of *Elminius modestus*, those from low water having a more rapid cirral beat than those from high water.

There was again no difference in the frequency of beating of the cirri of *Chthamalus* collected near Anglesey. Samples of *Balanus balanoides* from the same district, however, with one exception, showed a greater frequency of beat

among those individuals from low water, and had more regular cirral activity, than individuals from high water. Among the specimens from the exceptional locality, which was sheltered from wave action and currents, nearly all the high-water individuals showed the fast type of beat, while the low-water individuals showed only the normal beat.

It was suggested that the fast type of beat was an adaptation to assist feeding or respiration in still water. Experiments with varying oxygen content of the water failed to show whether or not the adaptation was respiratory.

The work suggests that the older a barnacle becomes, the slower is its cirral beat, and the less often it shows cirral activity.

The difference in activity of animals from high- and low-tide levels may be related as much to the difference in rate of growth, and possibly of general metabolism, as to any adaptation to temperature differences between the two levels.

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