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ON THE BEHAVIOUR OF BARNACLES

III. FURTHER OBSERVATIONS ON THE INFLUENCE OF TEMPERATURE AND AGE ON CIRRAL ACTIVITY

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(Text-figs. 1–3)

The results of investigations into the relation between temperature and cirral activity in certain barnacles were described in Part I of this series (Southward, 1955*a*). It was shown that in each of five species commonly found on the shore in Britain, the range of temperature over which the cirri were active and the temperature at which this activity was greatest could be related to the geographical distribution of the species and to the temperatures experienced in the normal habitat. In a further paper it was shown that in one of these species (*Chthamalus stellatus*) the frequency of beating was apparently lower in older individuals (Southward, 1955*b*). These results have been confirmed and extended by experiments made on a further five species of barnacles from a wider range of habitats (Table 1).

TABLE 1. SPECIES OF BARNACLES INVESTIGATED

Species	Where collected	Tide-level or depth	Speed of water current in apparatus
Lepas anatifera L.	Growing on cork lifebelt, found off Plymouth	—	Nil
Balanus improvisus Darwin	Upper reaches of Tamar estuary, near Weir Quay	L.W.N.	0·5 cm/sec, with occasional bursts of 5–10 cm/sec
B. amphitrite Darwin var. *denticulata* Broch	On piles near outflow of warm water from power station, Plym estuary	L.W.N.	As *B. improvisus*
B. balanus L.	On shells of *Modiolus* from Anglesey	*ca.* 12 fathoms	As *B. improvisus*
Hexelasma hirsutum Hoek	Continental slope in vicinity of 48° 33′ N., 10° 4′ W.	570–770 fathoms	4–16 cm/sec

All temperatures are quoted in degrees Centigrade. Climatic details have been taken from the following references: Admiralty, 1946; Air Ministry, 1949; International Council, 1933.

I am indebted to Dr D. J. Crisp, who supplied living *Balanus balanus*, for advice in this work and to Mr F. G. C. Ryder for construction of apparatus. The experiments were carried out during the tenure of a D.S.I.R. Senior Research Award.

EXPERIMENTAL CONDITIONS

The experimental conditions differed slightly from those of the earlier work. The animals were observed in a long trough of Perspex, divided by a central partition. The trough was filled with filtered offshore water, which was replenished from time to time. All water movement was set up by means of an enclosed paddle wheel, also of Perspex, placed at one end of the trough and driven by belt and pulleys from an electric motor.

The temperature of the water in the trough was raised or lowered by immersing in it small vessels containing hot water or ice. During the duration of each experiment the temperature was easily controlled to within 0·5°, the temperature limits adopted in the previous work. However, for temperatures below 4° some difficulty was experienced because of warming by the air during the long period of observation necessitated by the slow frequency of beating at low temperatures, and a smaller number of barnacles was placed in a finger bowl standing in ice water or freezing mixture. Under these circumstances water movement was set up by a jet of compressed air.

In the trough, the water currents could be controlled by means of a resistance in series with the electric motor. The current speed was measured approximately by timing the movement of small particles in the water. As previously, the frequency of beating was assessed by noting the time taken for ten complete openings and closings of the valves accompanied by partial or complete protrusion of the cirri. The values so obtained were converted to the number of beats per 10 sec. Approximately ten specimens were examined at each temperature. The temperature intervals were about 4° or 5° and the rate of heating or cooling was adjusted to 4°/h.

Except for *Balanus amphitrite* (see below) all specimens were observed while still attached to small pieces of the substratum.

Only *B. improvisus* and *B. amphitrite* were examined within 24 h of collection; *B. balanus* was sent by post and nearly 7 days elapsed between collection and examination; *Lepas* was examined after an unknown period out of water followed by nearly 24 h in the aquarium water at Plymouth; *Hexelasma* was brought back on R.V. *Sarsia* under running sea water and examined within 7 days of being dredged up. Chances of acclimatization to temperatures other than those normally experienced must therefore be allowed for in interpreting the results.

RESULTS

Lepas anatifera (Fig. 1; Table 3)

All specimens of *Lepas* at times showed a tendency to hold the cirri extended (extension response—see Part I), even in still water. The rate of water movement had no observable effect on the proportion of individuals beating, and the actual measurements were made without a current. It was necessary to observe a large number of specimens and choose those that were showing rhythmic beating.

Some beating was noted below 1·5°, although there was almost instantaneous and complete chill coma on lowering the temperature to 0·5°. The mean frequency of beating increased almost linearly between 3·8° and 19·8°, from 0·55 to 2·85 beats per 10 sec. Above 20° the frequency slowed down, and all beating ceased at 33°. More than half the specimens succumbed to heat coma at 33·5°.

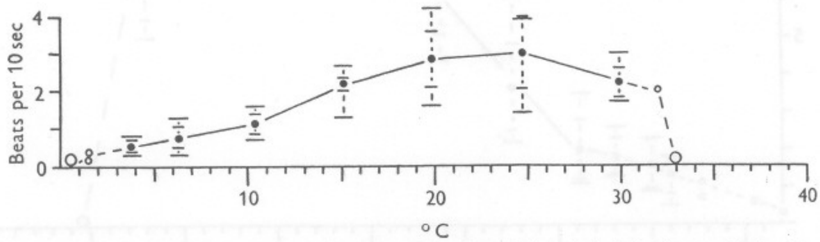

Fig. 1. *Lepas anatifera*: frequency and range of beating of the cirri. The larger circles denote absence of beating, and the smaller circles single observations; the dots indicate the mean frequency at each temperature, while the large and small cross-lines mark, respectively, the range and standard deviation of the samples on either side of the mean.

Both the optimum cirral activity and the position of maximum cirral frequency shown by these specimens occur at relatively low temperatures for a species which has been recorded from all the oceans (see Darwin, 1854). There is, therefore, a strong possibility that the species contains physiological varieties adapted to different temperature regimes. Certainly, these specimens would be ill-suited to temperature conditions prevailing in the Atlantic north of Nova Scotia and North Norway, or south of Cape Cod and Gibraltar.

Balanus improvisus (Fig. 2A; Table 4)

Specimens of *B. improvisus* showed cirral activity over a wide range of temperatures. Between 8·8° and 20° the mean frequency increased uniformly from 2 to over 8 beats/10 sec, and a maximum was reached at 30°. Above 30° the frequency of beating declined sharply, and beating was not detected above 35·5°.

The behaviour at low temperatures was most interesting. There was a change in the temperature coefficient at about 8–9°, and the mean frequency of beating declined only slowly as the temperature was lowered. Most specimens continued to beat rhythmically down to 4°, and one or two continued to do so down to −2°, the lowest temperature tested. Even after remaining at this low temperature for 10 min, less than half the specimens (4 out of 10) showed chill coma.

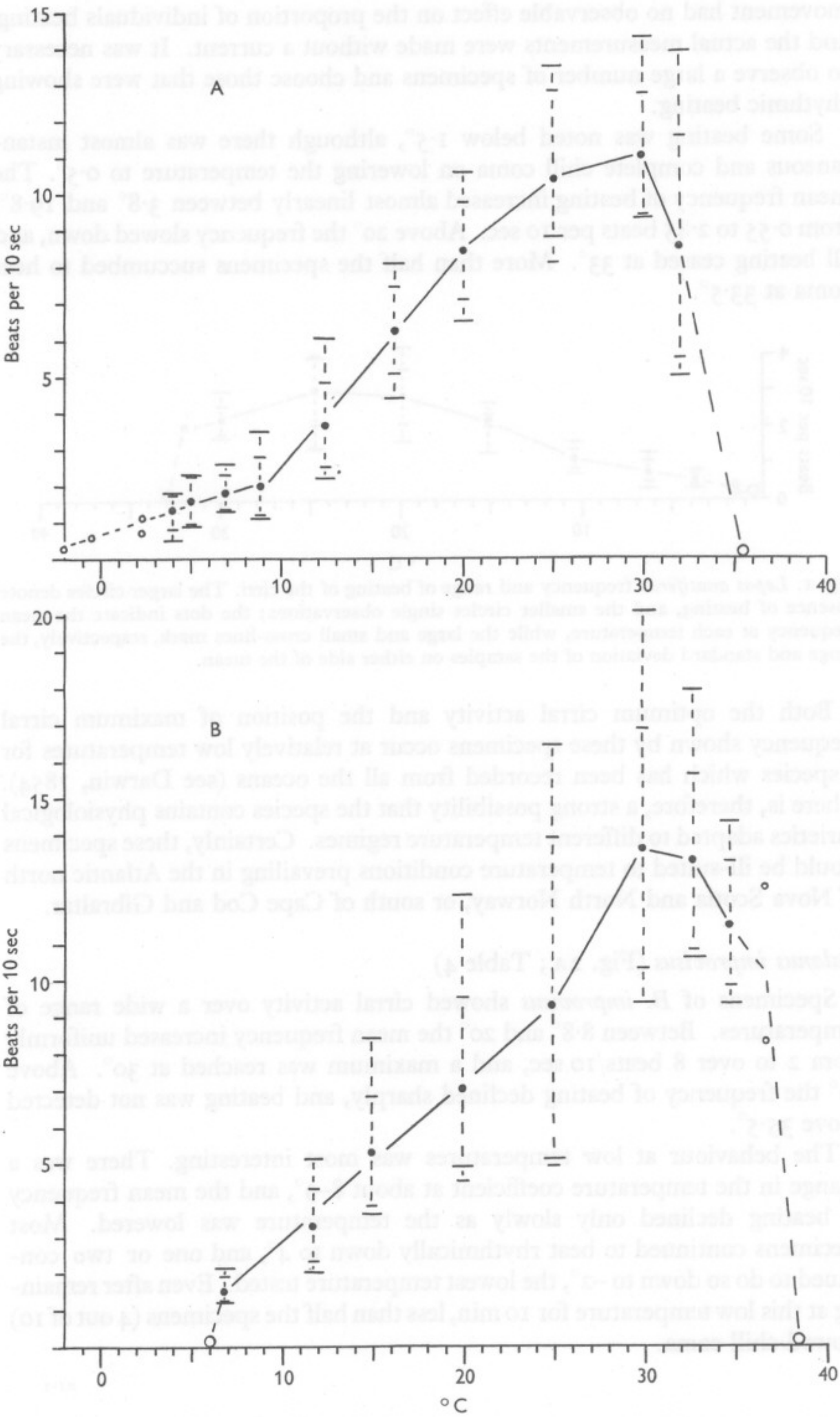

Fig. 2. The frequency and range of beating of the cirri of (A) *Balanus improvisus*, (B) *B. amphitrite*. For explanation of symbols refer to Fig. 1.

The wide range of optimum temperature in this species is in accordance with its wide geographical range; it has been recorded from Nova Scotia and the Baltic, and extends through the tropics to southern South America (Darwin, 1854; Pilsbry, 1916; Segerstråle, 1953). Nevertheless, the position of the maximum cirral frequency is more characteristic of a tropical species.

Balanus amphitrite (Fig. 2B; Table 5)

Only twelve specimens of *B. amphitrite* were collected with their calcareous bases intact; they were mounted on glass slides with SIRA wax before being placed in the trough. A few specimens showed the fast type of beat at some temperatures; they have not been included in the results. At most temperatures it was possible to measure the cirral frequency of nine specimens. Below 10° only five individuals were active, and beating was not observed below 6°. Between 6·8 and 24·9° the mean frequency of beating increased linearly from 1·5 to 9·3 beats/10 sec. The maximum frequency was reached at 29·9°, with a mean of 13·5 beats/10 sec. Beating slowed down slightly between 30° and 36°, and ceased completely at 38·4°.

The high upper limit to the temperature range, and the relative ease with which beating was carried on above 30°, agree well with the predominantly tropical and warm temperate distribution of the species. Its normal northern limit appears to be northern Spain (Fischer-Piette, 1955), and beyond this it is found only in docks, harbours or estuaries that are artificially warmed (see Bishop, 1950; Crisp & Molesworth, 1951). At Plymouth after a warm summer I have found young specimens on the shore of the Sound, as well as in the Plym estuary, but the adults survive only in the vicinity of the warm water outlet from the power station. The absence of beating below 6°, and the difficulty of obtaining beating between this temperature and 10° suggest that little, if any, acclimatization has taken place in the local population.

Balanus balanus (Fig. 3; Table 6)

The specimens of *B. balanus* sent by Dr Crisp consisted of four groups. The first three groups consisted of freshly collected specimens showing respectively one, two and three growth rings; the fourth group of specimens with two or three growth rings had been kept in the laboratory at Menai Bridge for 4 months without food. *B. balanus* is the only British barnacle that has been found to show clear growth marks, and the groups with one, two and three rings correspond to individuals in their second, third and fourth years since settlement (Crisp, 1954).

The behaviour of each group was noted separately, but as each group contained less than ten specimens and only the two- and three-ring groups were active at all temperatures, the results from these groups have been combined to show the effect of temperature on cirral activity. For this purpose specimens showing the fast type of beat have been ignored. One specimen showed signs of beating at −2°, but none was active below this temperature. Above zero the frequency of beating increased fairly linearly, from between 1·1 and 1·3 beats/10 sec at 1·9° to a maximum of 4·8 beats at 20·2°. Above 20° the frequency of beating declined, at first slowly up to 26°, then more rapidly; beating ceased at 30°.

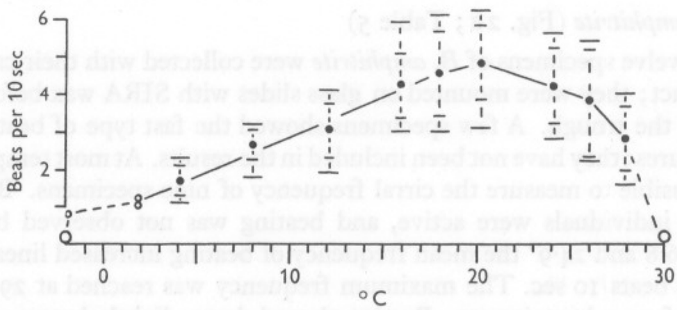

Fig. 3. *Balanus balanus*: frequency and range of beating of the cirri. For explanation of symbols refer to Fig. 1.

This species is predominantly of Arctic and Boreal distribution (Darwin, 1854; Weltner, 1900), and it seems doubtful whether it ever occurs south of the Bristol Channel and North Sea (Crisp & Southward, 1957). Thus in its normal habitat it is hardly likely to be subjected to sea temperatures above 17°; even when it occurs on the shore it is found in places well protected from the sun and the air, such as beneath *Ascophyllum* (Crisp, 1954) or in crevices and under stones (personal records). The species, therefore, is not operating at the extreme upper limit of its optimum range, unlike the other northern form *B. balanoides* (Southward, 1955*a*).

The effect of age on cirral activity in this species is shown in Table 2. The range and the mean of the cirral frequency is given for each group at four temperatures; at other temperatures one or more of the groups failed to beat the cirri. It can be seen that the younger barnacles had the highest frequency of cirral beat, and that the cirri beat progressively more slowly in the older groups. The lowest frequency of all was found in the starved specimens; except at 4° the differences between these specimens and all the others were greater than between any two age-groups of the fresh specimens.

The differences between the means are not very great for such small samples and statistically they are hardly significant. For example, in tests by the t distribution that the one-ring and three-ring groups belonged to the same statistical population, the value of P varied from 0·05 to 0·1.

However, the evidence tends to support the earlier observation that ageing in barnacles is accompanied by a slowing down of the cirral activity. It seems that starvation has a similar effect. Probably there is a depression of the metabolic rate in both old and in starved individuals.

These differences relate to the ordinary rhythmic beat. A fast type of beat was shown by a few individuals at some temperatures, but only among the youngest specimens and in the starved group. These are the groups in which the fast type of beat would be expected if it was largely a feeding reaction (cf. Southward, 1955*b*).

Further differences between the four groups of *B. balanus* were noticed at the upper limit of temperature for cirral activity. All starved specimens ceased beating at 27·9°, all three-ring and two-ring specimens at 29° and 30° respectively, while more than half the youngest group continued active to 30·5°. These differences are of the same order as those of cirral frequency.

TABLE 2. CIRRAL BEHAVIOUR IN THE DIFFERENT AGE-GROUPS OF *BALANUS BALANUS*

Temperature (° C)	Age-group	No. tested	No. showing ordinary beat	Frequency of ordinary beat			No. showing fast beat	No. not beating
				Mean	Range	S.D.		
4·0	1 ring	7	3	2·333	2·0–2·8	±0·417	0	4
	2 ring	7	4	1·950	1·6–2·3	±0·310	0	3
	3 ring	5	3	1·366	1·1–1·7	±0·307	0	2
	Starved	5	2	0·950	0·7–1·2	±0·353	1	2
8·0	1 ring	7	6	2·883	2·4–3·3	±0·338	0	1
	2 ring	7	6	2·816	2·5–3·2	±0·260	0	1
	3 ring	5	4	2·40	1·8–2·8	±0·454	0	1
	Starved	5	5	1·140	0·9–1·5	±0·251	0	0
15·9	1 ring	7	3	4·833	4·1–5·2	±0·637	0	4
	2 ring	7	6	4·583	3·4–5·9	±0·855	0	1
	3 ring	5	5	3·760	3·0–4·8	±0·695	0	0
	Starved	5	4	2·775	1·6–3·4	±0·801	1	0
20·2	1 ring	7	3	5·433	4·8–6·2	±0·711	3	1
	2 ring	7	5	4·920	3·9–5·9	±0·837	0	2
	3 ring	5	5	4·70	3·1–6·2	±1·332	0	0
	Starved	5	4	3·075	2·3–3·7	±0·684	1	0

Hexelasma hirsutum

So far, only a preliminary investigation has been made into the behaviour of *Hexelasma*. Of twenty-four specimens tested in the trough none could be induced to show rhythmic beating of the cirri under any variation of temperature, water movement or illumination. With a water current from 4 to 16 cm/sec an extension response was given by up to eight specimens simultaneously at temperatures between 2·7° and 8°. Below 2·7° and down to −2° one or two specimens showed very slight movements of the valves and reacted to touch by closing. Above 8° a few specimens showed what has been called the pumping type of beat (Southward & Crisp, 1957). The cirri were not protruded, but minor movements of the prosoma and valves caused a current of water to enter the mantle cavity near the mouth; this water passed through the mantle cavity and was ejected in puffs behind the prosoma (see Crisp & Southward, 1956). The frequency of these exhalant puffs increased from 0·05 and 0·06/10 sec at 8·5° to 0·10 and 0·18/10 sec at 19°. The temperature was not taken higher than 19° to avoid risk of damage to the specimens, but even at this temperature there were signs of jerky movements similar to those that precede heat coma in other barnacles.

Hexelasma hirsutum has been recorded elsewhere from the Faroe-Shetland Ridge (59° 40′ N., 7° 21′ W.) at 516 fathoms (Hoek, 1883) and from the Azores (38° 31′ N., 26° 49′ W.) at 465 fathoms (Gruvel, 1920). The bottom-water temperatures at all localities at which the species has been found, or at nearby stations of similar depth, vary from 7° to 9° (Hoek, 1883; Rouch, 1948; Cooper, 1952) and the annual variation is probably less than 1° (Dr L. H. N. Cooper, personal communications). As far as cirral extension is concerned, the specimens of *Hexelasma* examined were thus living very close to the upper limit of their optimum range. Probably the species can live in colder and deeper water when other conditions allow.

The absence of rhythmic beating within the optimum range suggests that respiratory needs are satisfied by the passage of water over the branchiae caused by the twisting movements of the extended cirri, by the occasional withdrawing movements of the cirri, or by external water currents. The pumping beat at higher temperatures suggests the onset of respiratory difficulties; the low frequency of the pumping movements may indicate lack of co-ordination for rhythmic activity.

DISCUSSION

In three of the five species dealt with in this Part, namely *Balanus improvisus*, *B. amphitrite* and *B. balanus* the range of cirral activity is closely related to the geographical distribution.

The behaviour of *B. amphitrite*, and, in the upper part of its range, *B. improvisus* is similar to that of one of the two southern species discussed in Part I, *B. perforatus*. These three species belong to the same subgroup, or closely related subgroups, of the genus *Balanus* (Darwin, 1854; Pilsbry, 1916); the resemblance in behaviour is not therefore unexpected. *B. improvisus* is the only species of the group to occur in genuinely cold climates, and the form of its behaviour suggests that it is a tropical species that has been able to extend the lower end of its range of optimum temperature. This adaptation may be connected with the remarkable euryhalinity shown by the species (Darwin, 1854; Pilsbry, 1916). It seems probable that a more flexible metabolism is needed to cope with the osmoregulatory requirements of a brackish water habitat, and this may have facilitated tolerance of a wider range of temperatures.

The range of optimum temperature in *B. balanus*, and the temperature at which maximum cirral frequency was shown, differ considerably from those of the related species, *B. crenatus*, investigated previously (Part I). There is, in fact, more resemblance between *B. balanus* and *B. balanoides*. All three species are of generally northern distribution, but their exact southern limits vary. As stated, *B. balanus* does not apparently occur as far south as the English Channel, where *B. crenatus* has its southern limit; *B. balanoides* is present in the Bay of Biscay (Southward & Crisp, 1956) and in a limited area of north-west Spain (Fischer–Piette & Prenant 1956). The order of increasing tolerance of high temperatures is *B. crenatus–B. balanus–B. balanoides*, while the position of maximum cirral frequency increases *B. balanoides–B. balanus–B. crenatus*. There is thus no exact relation between the extreme southern limits of the species and their temperature tolerances for cirral activity. No doubt other environmental factors besides temperature affect the limits of the species.

The temperature relations of *Lepas* and *Hexelasma* have already been discussed (pp. 325 and 330). The behaviour of the latter species reflects the relatively uniform temperatures experienced in deep water compared with the intertidal or shallow water habitats favoured by the species of *Balanus*.

SUMMARY

The range of temperature over which the cirri were active, and the frequency of beating of the cirri at different temperatures were measured in a further five species of barnacles from a variety of habitats. In three of the species the temperature range and frequency of cirral beat were related to the geographical distribution of the species. The tropical and warm temperate species *Balanus amphitrite* was active at higher temperatures, and showed a greater frequency of beating than the northern species *B. balanus*; conversely, the latter was active to much lower temperatures than *B. amphitrite*. The species with the widest geographical range, *B. improvisus*, showed cirral activity over the widest range of temperatures, although its behaviour at high temperatures was similar to that of the related species *B. amphitrite*. It is suggested that *B. improvisus* is a tropical species that has adapted itself to colder climates; its tolerance of a wide range of temperatures may be associated with its tolerance of low salinities.

The stalked barnacle *Lepas anatifera* showed too restricted a temperature range for its supposed world-wide distribution, and it is suggested that the species may contain physiological races adapted to different climates. The extremely restricted range of temperatures over which the cirri of the deep-sea barnacle *Hexelasma hirsutum* were active can be correlated with the almost uniform temperature conditions at great depths.

In *B. balanus* age-groups can be clearly distinguished by growth rings on the shell, and the cirral frequency was found to be slower in the older specimens. Even slower cirral beating was found in some starved specimens.

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APPENDIX

TABLE 3. FREQUENCY OF BEATING OF THE CIRRI OF *LEPAS ANATIFERA*

From off Plymouth, 1. x. 56; examined 2. x. 56

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
0·5	—	Nil	—
1·5	2 specimens only	0·2, 0·4	—
3·8	0·557	0·3–0·8	±0·161
6·3	0·770	0·3–1·3	±0·292
10·4	1·130	0·7–1·6	±0·283
15·1	2·20	1·3–2·7	±0·125
19·8	2·850	1·6–4·2	±0·760
24·7	2·50	1·4–2·9	±0·454
29·7	2·185	1·7–3·0	±0·422
32·0	1 only	2·0	—
33·0	—	Nil	—

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

From the Tamar estuary, 13. ii. 56 and 15. ii. 56

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
−2·0	1 only	0·3	—
−0·5	1 only	0·6	—
2·3	2 only	0·7, 1·1	—
4·0	1·344	0·5–1·8	±0·470
5·0	1·595	0·9–2·3	±0·703
6·9	1·833	1·3–2·6	±0·477
8·8	2·018	1·1–3·5	±0·778
12·4	3·677	2·2–6·1	±1·171
16·2	6·266	4·4–8·1	±1·180
20·0	8·440	6·5–10·6	±1·318
25·0	10·420	8·8–13·5	±2·360
30·0	11·057	9·3–14·3	±1·674
32·0	8·550	5·0–13·9	±3·078
35·5	—	Nil	—

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

From the Plym estuary, 9–10. ii. 56

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
6·0	—	Nil	—
6·8	1·520	1·2–2·1	±0·311
11·7	3·322	2·0–5·1	±0·983
14·9	5·30	3·6–8·4	±1·495
19·9	6·988	4·9–12·3	±2·467
24·9	9·337	5·1–16·4	±4·547
29·9	13·562	9·3–20·0	±3·271
32·7	13·20	10·6–17·9	±2·371
34·7	11·487	9·3–14·3	±1·739
36·7	2 only	8·3, 12·5	—
38·4	—	Nil	—

TABLE 6. FREQUENCY OF BEATING OF THE CIRRI OF *BALANUS BALANUS*

From Anglesey, examined 17–18. iii. 56: 2-ring and 3-ring

Temperature (° C)	Frequency of beating, as beats per 10 sec		
	Mean	Range	S.D.
−2·0	1 only	0·8	—
1·9	2 only	1·1, 1·3	—
4·0	1·70	1·1–2·3	±0·420
8·0	2·650	1·8–3·2	±0·389
12·1	3·044	1·9–4·1	±0·731
15·9	4·209	3·0–5·9	±0·862
18·0	4·544	3·0–6·1	±1·115
20·2	4·810	3·1–6·2	±1·009
24·1	4·211	2·8–5·6	±1·003
26·0	3·775	2·3–5·4	±1·563
27·9	2·80	1·6–4·0	±0·868
30·0	—	Nil	—