

The relationship between temperature and rhythmic cirral activity in some Cirripedia considered in connection with their geographical distribution

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KURZFASSUNG: Die Beziehung zwischen Temperatur und rhythmischer Rankenfußaktivität bei einigen Cirripedia, betrachtet im Zusammenhang mit ihrer geographischen Verbreitung. Balaniden vermögen einen weiten Temperaturbereich zu ertragen. Auf äußere Reize reagieren sie aber nur innerhalb eines kleineren Bereiches, und ihre volle Aktivität entfalten sie nur innerhalb relativ enger Temperaturgrenzen. Für die Beurteilung ihres ökologischen Potentials in verschiedenen Arealen der Verbreitungsgebiete ist der zuletzt genannte Bereich der wichtigste. Während der letzten 10 Jahre wurde die Aktivität vieler europäischer und amerikanischer Arten aus einer Vielzahl verschiedener Habitats und Klimate untersucht, wobei die Schlagfrequenz der Rankenfüße – ein temperaturabhängiger Indikator der allgemeinen Stoffwechselrate – als Kriterium diente. Bei einigen weitverbreiteten Arten konnten physiologische Varietäten oder Subspezies nachgewiesen werden und frühere, rein morphologische Beurteilungen zur Validität von Arten und anderen taxonomischen Einheiten bestätigt oder abgelehnt werden. Im Vergleich zu den Anpassungen an Gezeitenhöhe und der Intensität der Welleneinwirkung wurden bei einigen weitverbreiteten Formen nur geringfügige Längs- und Temperaturadaptationen gefunden. Ganz allgemein unterstreichen die Ergebnisse die Bedeutung physiologischer Daten für taxonomische Beurteilungen ebenso wie die Notwendigkeit systematischer Exaktheit in der Physiologie.

INTRODUCTION

It is generally assumed that temperature is the most important single factor controlling distribution. Although we can often point to extremely good correlations between the limits of species and particular isotherms, a causal relationship is difficult to prove. The results of experiments made on the upper lethal temperatures in several groups of animals show a general agreement, in that tropical forms tolerate much higher temperatures than arctic forms (KINNE 1963). But it seems unlikely that directly lethal effects are ever important in controlling distribution, as DARWIN pointed out nearly 100 years ago (1872). Except possibly for the high arctic regions, temperature is more likely to act as a modifying influence on competition between species and varieties.

Cirripedes are affected by extremes of temperature in the same way as other organisms. They can tolerate a very wide range of temperature without actually being

killed; they remain responsive to stimuli over a somewhat narrower range; but are fully active only within relatively narrow limits (Fig. 1). As far as competition between species is concerned it is the last range that is most important in determining the fitness or otherwise of a species to its geographical limits. The most obvious activity

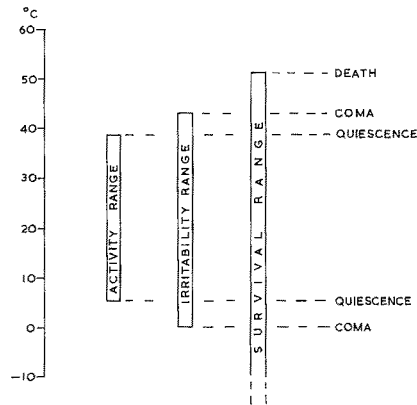


Fig. 1: The three ranges of temperature tolerance, as illustrated by *Chthamalus stellatus* from S. W. England. The low temperature lethal point has not been determined

of a barnacle is the rhythmic extensions and withdrawals of its cirri and the associated openings and closings of the shell valves. We know from the work of Cole and his collaborators (COLE 1929, 1932, COLE & ALLISON 1937) that cirral beat is temperature dependent, and hence may reflect the general metabolic level of the barnacle. This view is strengthened by recent investigations carried out on the different types of cirral rhythm that may be found in a single species (CRISP & SOUTHWARD 1961). One of these, fast beat, seems to be an ecological adaptation for feeding, and will not be considered further here, but the other two, which we call normal beat and pumping beat, seem to be largely respiratory in unfed specimens. In any species there is a close correspondence in rate of normal beat and rate of pumping beat, and both types are equally temperature dependent. In the following account, when cirral beat is mentioned, these two types of activity are meant.

TEMPERATURE AND CIRRAL ACTIVITY

During the past ten years the relationship between temperature and cirral activity has been investigated in most European species, and recently the American forms have been studied. Cirral activity has always been observed with the barnacles subjected to a flow of water, gentle for some species, strong for others. This minimizes any response to other stimuli, particularly variation in light intensity or mechanical shock, which might otherwise interrupt regular beating. As in all investigations of this type, whether movement of respiratory appendages, rate of heart-beat or oxygen uptake, there is considerable variation between individual animals, and comparisons can only

be made by using the mean rates from fairly large groups, ten or more at each temperature point. The rate of change of temperature has been restricted to about 5° C per hour, to prevent or reduce overshoot or hysteresis in the response.

In each species the observations on rate of activity have been made mostly on the dominant size-group in the population, taken from the habitat and tide-level at which the species is most abundant. However, it must be realised that considerable differences in rate of activity may be found in older or younger specimens, or in those of the same size group from a different level or habitat (SOUTHWARD 1955a, 1955b, 1957, 1962) (cf. Fig. 9).

European species

Some typical results are shown in Figure 2 for the two common European barnacles, *Balanus balanoides* and *Chthamalus stellatus*, with the range of observations and the standard deviation shown on each side of the mean. As well as a difference in rates of activity there is a shift in position of the curve, showing adaptation to low temperature in the northern form and adaptation to higher temperatures in the

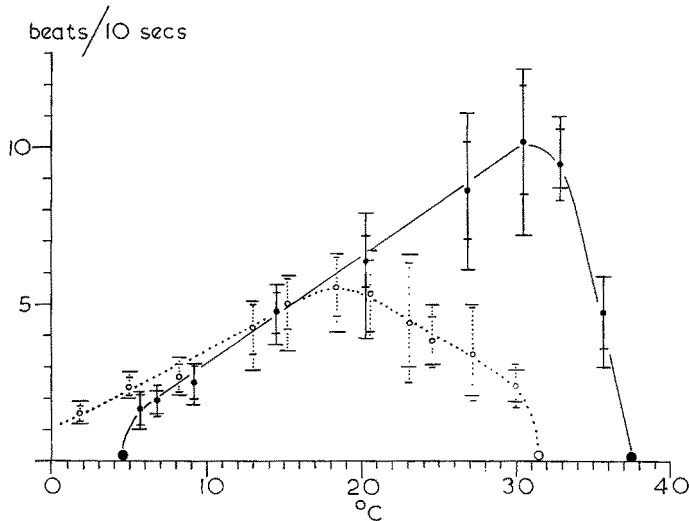


Fig. 2: Example of cirral activity/temperature data for *Chthamalus stellatus* ●—● and *Balanus balanoides* ○.....○. The small circles show the mean rate at each temperature, the large cross lines the range of observations and the small cross lines the standard deviation on each side of the mean. The large circles indicate absence of cirral beating

southern form. The shift is such that the cold water species (*Balanus*) ceases cirral beating completely at a temperature at which the warm water form (*Chthamalus*) shows maximum activity. Obviously in the limited areas of Britain, France and N. W. Spain where these two species are found together, the local temperature regime must be the most important factor in determining their relative success.

A shift of this type is well known in comparisons of the metabolism of arctic and tropical poikilotherms (e. g. SCHOLANDER et al. 1953, FOX 1939). However, the adaptation found in barnacles appears to be much smaller than that found by these wor-

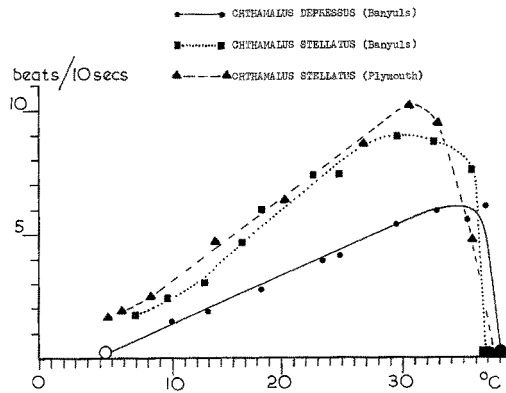


Fig. 3: Cirral activity/temperature curves of *Chthamalus depressus* and *Chthamalus stellatus* from two localities

kers in other groups of animals. Among the European species of *Chthamalus* for example, *C. depressus*, which does not occur north of the Mediterranean, is somewhat better adapted to high temperatures than *C. stellatus*, but the difference is not large (Fig. 3). An apparent slight low temperature shift shown by the specimens of *C. stellatus* in England is not statistically significant.

Arctic and tropical forms

Somewhat greater differences, though still smaller than in some other invertebrate groups, can be found when comparing fully arctic barnacles with species from the tropics. For example the two pairs of species of about the same physical size but unfortunately not quite the same ecological niche; *Balanus crenatus* from Point Barrow, Alaska, and *Balanus amphitrite* from Miami; and *Balanus balanus* from Point Barrow and *Tetraclita squamosa* from Miami, Florida, shown in Figure 4. These are classical examples of adaptation to the particular environments, ranging from below -1° C to about 6° for the arctic specimens, and from 22° to over 30° C at Miami.

Atlantic coast of U.S.A.

Quite understandably, the differences in rates of activity and temperature curves are not always as simple as this, particularly over the wide range of temperatures and habitats available on the American coast. On the east coast the cold water species reach their southern limits in Long Island Sound, except for *Bala-*

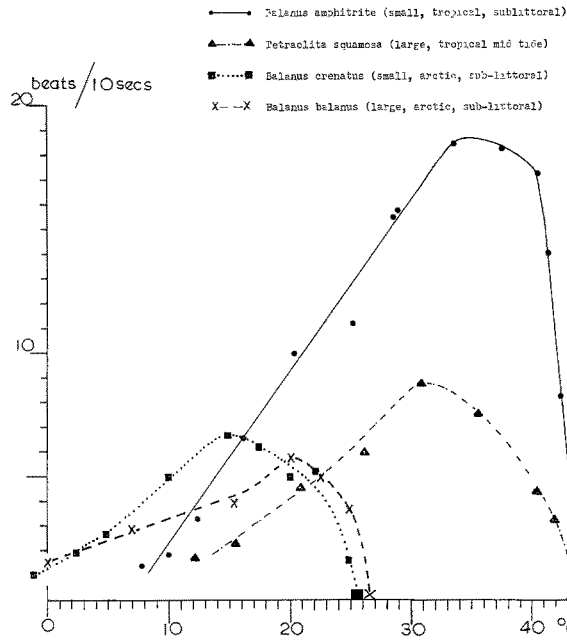


Fig. 4: Cirral activity/temperature curves for pairs of arctic and tropical species

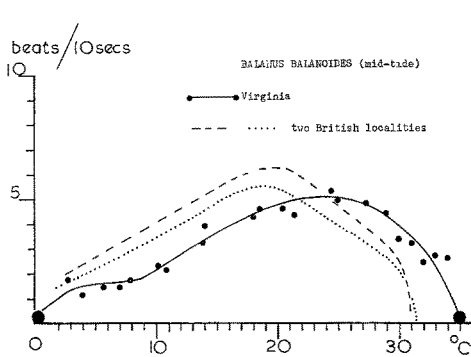


Fig. 5

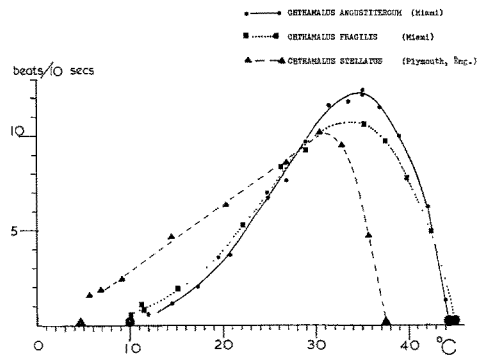


Fig. 6

Fig. 5: Cirral activity/temperature curves of specimens of *Balanus balanoides* from each side of the Atlantic

Fig. 6: Cirral activity/temperature curves of two species of *Chthamalus* from the east coast of America, compared with *C. stellatus* from Europe

nus balanoides which occurs as far south as Cape Hatteras on the wave-beaten open coast. Cape Hatteras is, incidentally, the locality showing the greatest rate of change of temperature in the whole area being considered here. The penetration of *Balanus balanoides* into water that is comparatively warm in summer is clearly shown in the temperature-activity curve of specimens from near the southern limit, at Virginia

Beach (Fig. 5). Compared with south-west England there is a shift of some 5 degrees in the maximum activity and in upper limit. Otherwise the form of the curve is similar in both areas, except for signs of a possible break in the slope of the Virginian specimens, perhaps adapting them to the comparatively cold winter north of Cape Hatteras.

Both species of *Chthamalus* found on the Atlantic coast of U.S.A. show a high temperature adaptation, particularly in Florida, where their distributions overlap (Fig. 6). At Miami there is really little difference between *C. fragilis* and *C. angustitergum*, where the latter is at the northern limit of its range, but both differ considerably in form of curve from European specimens of *C. stellatus*, of which they have been regarded as subspecies. Evidence obtained by Dr. D. J. CRISP (personal communication) suggests that *C. fragilis* is locally adapted along the coast; and specimens from Woods Hole, near the northern limits of the species, show a certain amount of low temperature shift.

Pacific coast

Perhaps the most interesting distributional problems are encountered on the Pacific coast of North America, where the cool temperate region is expanded at the expense of the warm temperate and arctic regions. An allied problem in the region is the large number of local sub-species that have been described, and their exact rela-

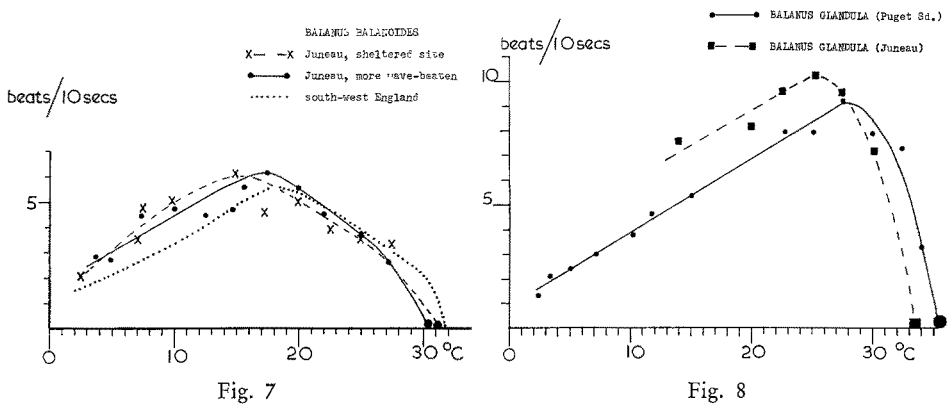


Fig. 7: Cirral activity/temperature curves of Pacific coast specimens of *Balanus balanoides*, compared with European forms

Fig. 8: Cirral activity/temperature curves of *Balanus glandula* from two localities

tionship to the parent species of circum-boreal distribution. On this coast *Balanus balanoides* appears to be restricted to the coldest parts of the temperate zone, in fact to south-eastern Alaska only, and near its southern limit it is abundant only in the presumably cooler sheltered inlets. The temperature-activity curve is, however, very similar to those of European specimens, displaying an insignificant amount of low temperature shift (Fig. 7). Of course, in the Pacific, *B. balanoides* is in competition

with a more widely distributed related species, *Balanus glandula*, which lives from Mexico to the Aleutians. *B. glandula* is obviously better fitted for this area: at low temperatures its rate of activity is comparable with that of *B. balanoides*, yet it is able to continue beating some 10 degrees higher before showing signs of disturbance (Fig. 8). There would appear to be some local acclimation, as for example between

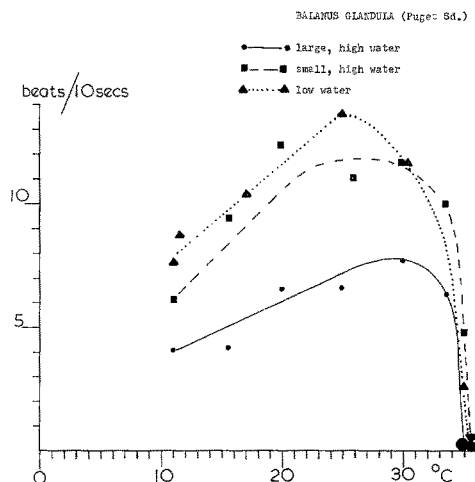


Fig. 9: Differences in cirral activity of specimens of *Balanus glandula* of differing size and tide-level

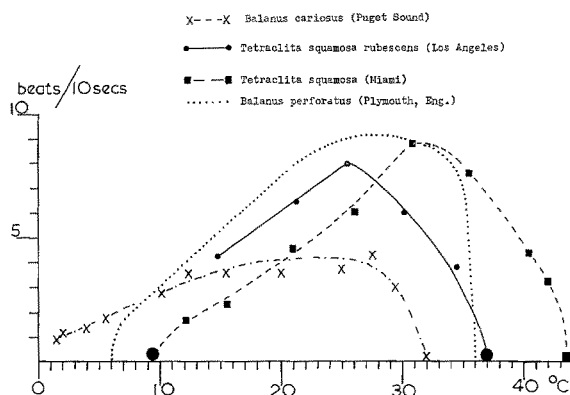


Fig. 10: Cirral activity/temperature curves of four species of large mid-tide and low water barnacles

Puget Sound and Juneau (Fig. 8), though it has not yet been possible to observe the behaviour of the species at its southern limits in California. On the other hand, there is as much variation between age groups and species from different habitats (cf. Figs. 8 and 9).

Another widely distributed barnacle of the Pacific coast is *Balanus cariosus*; which occupies the niche of mid-tide and low water large barnacle. It is interesting to com-

pare its wide flat-topped temperature-activity curve with that of *Tetraclita squamosa rubescens*, which occupies the same niche over a very limited region from San Francisco to Lower California (Fig. 10). The curve shows the sharpest peak of all species investigated and appears to be quite distinct from the parent species which was, however, examined only at Miami. In western Europe the same niche is occupied by

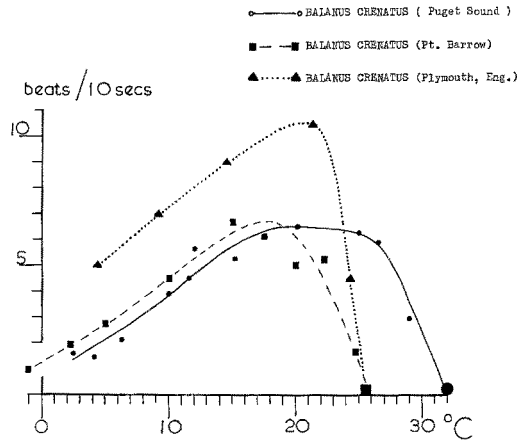


Fig. 11: Cirral activity/temperature curves of two lots of *Balanus crenatus* from N.W. America, compared with European specimens

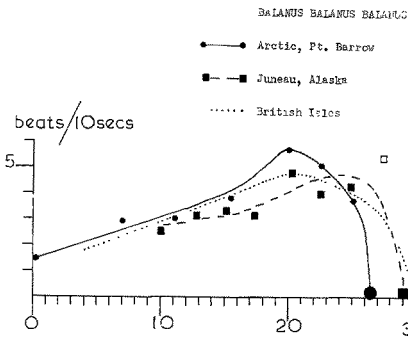


Fig. 12

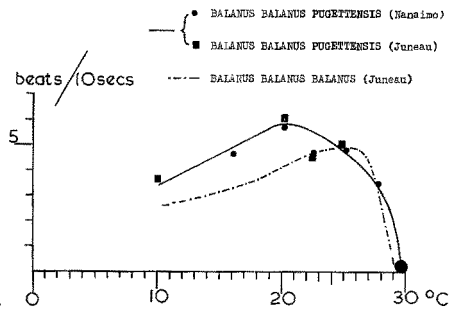


Fig. 13

Fig. 12: Cirral activity/temperature curves of *Balanus balanus balanus* from three localities
 Fig. 13: Comparison of cirral activity of *Balanus balanus pugettensis* and *Balanus balanus balanus*

Balanus perforatus, with a fairly wide distribution from England to West Africa and a correspondingly broad cirral activity-temperature curve (Fig. 10).

Balanus crenatus is another circum-boreal form, and occurs on the Pacific coast down to north California. Specimens from Puget Sound show a flat-topped curve indicating a wide degree of acclimation, but arctic specimens are more strictly adapted to colder conditions (Fig. 11). Both these arctic and temperate specimens of *Balanus*

crenatus show a different type of curve to that of the same species in Europe, and further investigations are needed.

In contrast to *B. crenatus*, another circum-boreal species, *Balanus balanus*, displays little difference in the form of the curve at three different localities, and only a slight degree of high temperature adaptation in the more southerly places (Fig. 12). However, a sub-species of *B. balanus*, examined at two localities, showed a constant

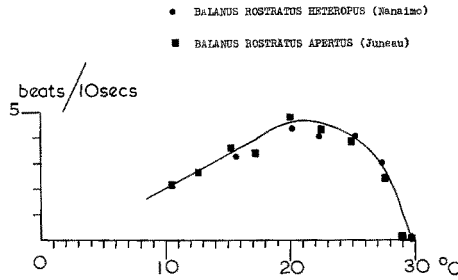


Fig. 14: Cirral activity/temperature data for two supposed sub-species of *Balanus rostratus*

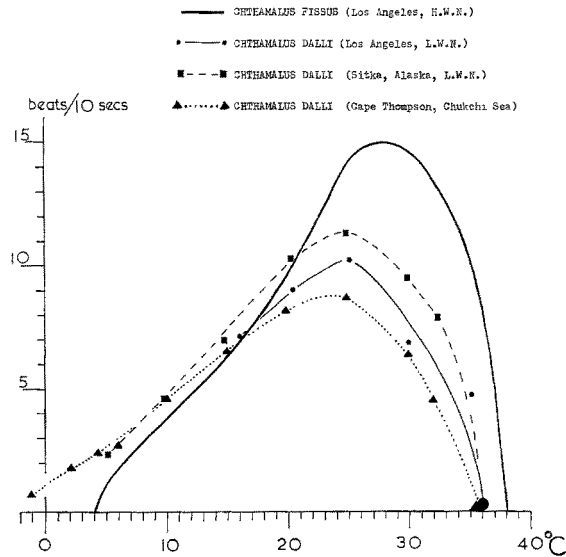


Fig. 15: Cirral activity/temperature curves of two species of *Chthamalus* found on the Pacific coast of N. America

slight difference in pattern of activity compared with the parent species, reinforcing the separation on morphological reasons (Fig. 13). In a related species, *B. rostratus*, much divided up by the systematists, two of the commonest varieties from two different localities and habitats, showed almost exact agreement in shape and form of curve (Fig. 14) suggesting that the morphological differences are phenotypic only.

Perhaps the most interesting cirral activity-temperature data are provided by the species of *Chthamalus* along the Pacific coast. The warm temperate species *Chthama-*

lus fissus (Fig. 15), which is found from Monterey to North Mexico, shows only slight high temperature adaptation compared with the more widely distributed form *C. dalli*. The latter occurs towards low water in South California, is the dominant open coast species at high water from San Francisco to the Aleutians, and extends to well within

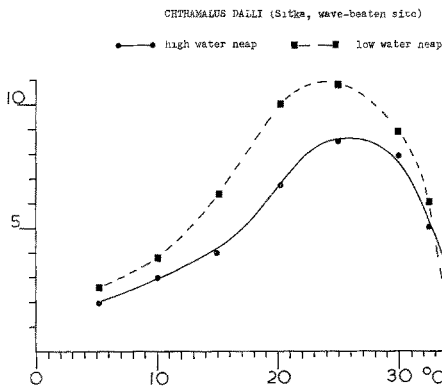


Fig. 16

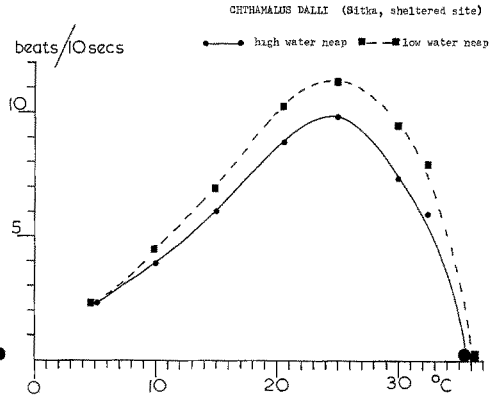


Fig. 17

Fig. 16: Comparison of cirral activity of *Chthamalus dalli* from two tide levels exposed to wave action

Fig. 17: Comparison of cirral activity of *Chthamalus dalli* from two tide levels sheltered from wave action

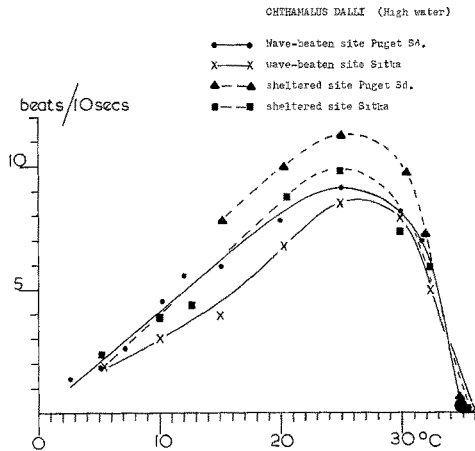


Fig. 18: Cirral activity/temperature curves of high-water specimens of *Chthamalus dalli* from two wave-beaten and two sheltered sites

the arctic regions in the Chukchi Sea. In this wide area it shows almost the same temperature-activity curve. Specimens from Cape Thompson in the Chukchi Sea survive 6 months frozen in the ice-foot, and begin breeding at 5° C, yet display only the slightest low temperature adaptation, statistically insignificant, compared with specimens from the warm temperate region where the temperature never falls below 15° C.

C. dalli does, however, show some interesting differences in rate of activity of specimens from different tide levels and habitats. For example, high water and low water forms at the same locality and between nearby sheltered and wave-beaten sites (Figs. 16, 17, 18). These two sets of differences are of the same order, that is, high water forms have a depressed rate of beating compared with low water forms, further depressed in high water forms from very wave-beaten localities. In the absence of significant adaptation with latitude, it can hardly be maintained that these differences are a matter of adaptation to temperature, as suggested for other groups of intertidal animals (e. g. SEGAL et al. 1953, SEGAL 1956, DEHNEL 1956, see also SEGAL 1961), and an alternative theory of correlation with relative rates of growth – usually maximal at low water and minimal in high water wave-beaten places – would seem to be confirmed (SOUTHWARD 1955b).

CONCLUSIONS

The investigations described here are far from complete, but from the examples quoted above it would seem that cirral activity/temperature relationships offer a useful basis for comparing species and populations of barnacles. Among other things, it is possible to show the degree of adaptation of a species to its habitat, to demonstrate the occurrence of physiological races or varieties, and to confirm or deny the validity of species or other taxa that have been separated upon morphological characters. In general the results emphasize the importance of physiological data in taxonomy, as well as the need for systematic exactness in physiology.

SUMMARY

1. Barnacles can tolerate quite a wide range of temperature without being killed, remain responsive to stimuli over a more limited range, but are fully active only within relatively narrow limits. It is the last range that is most important in determining the fitness of a species to its geographical distribution and the extent of competition between species.
2. During the past ten years work has been carried out on many European and American species from a wide variety of habitats and climates. Activity has been measured as rate of rhythmic beating of the cirri, a temperature-dependent process which is an index to general metabolic rate.
3. It has been possible to show the existence of sub-species or physiological varieties in some apparently widespread species, and to confirm or deny previous assumptions made on morphological grounds as to the validity of species and other taxa.
4. In a few widespread forms little latitudinal or temperature adaptation was found compared with differences related to tide-level and degree of exposure to wave-action.
5. In general the results emphasize the importance of physiological data in taxonomy as well as the need for systematic exactness in physiology.

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LITERATURE CITED

- COLE, W. H., 1929. The relation between temperature and the pedal rhythm of *Balanus*. *J. gen. Physiol.* **12**, 599-608.
- 1932. The sensitivity of the cirri and the variability of their movements in the barnacles *Balanus tintinnabulum* and *B. balanoides*. *J. exp. Zool.* **63**, 143-153.
- & ALLISON, J. B., 1937. Responses of the barnacle to some strong electrolytes and to urea, glucose and glycerol. *Physiol. Zool.* **10**, 405-411.
- CRISP, D. J. & SOUTHWARD, A. J., 1961. Different types of cirral activity of barnacles. *Phil. Trans. (B)* **243**, 271-308.
- DARWIN, C., 1872. The origin of species by means of natural selection. 6th Ed., ch. 3. John Murray, London.
- DEHNEL, P. A., 1956. Growth rates in latitudinally and vertically separated populations of *Mytilus californianus*. *Biol. Bull. Woods Hole* **82**, 26-46.
- FOX, H. M., 1939. The activity and metabolism of poikilothermal animals in different latitudes. V. *Proc. zool. Soc. Lond.* **109**, 141-156.
- KINNE, O., 1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanogr. Mar. Biol. Ann. Rev.* **1**, 301-340.
- SCHOLANDER, P. F., FLAGG, W., WALTERS, V. & IRVING, L., 1953. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* **26**, 67-92.
- SEGAL, E., 1956. Microgeographic variation as thermal acclimation in an intertidal mollusc. *Biol. Bull. Woods Hole* **111**, 129-152.
- 1961. Acclimation in molluscs. *Am. Zoologist* **1**, 235-244.
- RAO, K. P. & JAMES, T. W., 1953. Rate of activity as a function of intertidal height within populations of some littoral molluscs. *Nature, Lond.* **172**, 1108-1109.
- SOUTHWARD, A. J., 1955a. On the behaviour of barnacles I. The relation of cirral and other activities to temperature. *J. Mar. biol. Ass. U. K.* **34**, 403-422.
- 1955b. On the behaviour of barnacles II. The influence of habitat and tide-level on cirral activity. *J. Mar. biol. Ass. U. K.* **34**, 423-433.
- 1957. On the behaviour of barnacles III. Further observations on the influence of temperature and age on cirral activity. *J. Mar. biol. Ass. U. K.* **36**, 323-334.
- 1962. On the behaviour of barnacles IV. The influence of temperature on cirral activity and survival of some warm-water species. *J. Mar. biol. Ass. U. K.* **42**, 163-177.

Discussion following the paper by SOUTHWARD

LILLELUND: Zwei Dinge haben mich besonders beeindruckt. Da ist zunächst die außerordentliche Variabilität der untersuchten Vorgänge: Die Beobachtung, daß wir generell drei verschiedene Rhythmustypen unterscheiden müssen, daß die Temperatur-Cirren-Aktivitätskurve nicht nur von Art zu Art unterschiedlich sein kann, sondern daß darüber hinaus eine Abhängigkeit innerhalb der Art von der Körpergröße und vom Standort mit all seinen verschiedenen Milieufaktoren bestehen kann. Zum anderen sind die Arbeiten von Dr. SOUTHWARD ein Musterbeispiel dafür, wie Untersuchungen, die zunächst dem Studium einer einfach erscheinenden Lebensäußerung eines Tieres gewidmet waren, sich ausweiten und zu hochinteressanten, nicht

vorherzusehenden Schlüssen führen können und so letztlich neue Erkenntnisse für die Tiergeographie und Evolution liefern.

PROSSER: To what extent are the differences genetic and to what extent environmentally induced? I suggest that with the intertidal populations where the upper limits are the same and the rates in the mid-range are different, the effects may result from environmental induction. This agrees with many other data.

SOUTHWARD: It depends on the species. There would appear to be both in some species but not in others. An interesting case in point is *Chthamalus fissus*, which we examined for cirral activity within 24 hours of collection at Los Angeles. Then we put them in the trunk of the car, just damp in a polythene bag, took them up the coast, dipping them in sea water whenever possible. On arriving at Friday Harbor, two weeks after collecting them, we did another run on activity, and there was really very little difference in spite of their being subjected to higher and lower temperatures than usual on the way. Then we kept them at Friday Harbor at a constant low temperature (12° to 13° C, which is low compared with Los Angeles) for two weeks. We did another run on those that survived, and the results were again little different. I was very surprised that no environmental modification occurred.

WELLS: Dr. SOUTHWARD is to be congratulated on the fertility of his data and, I think, on *not* having studied oxygen consumption. As we heard several times during this symposium, a respiration rate pools together activity, basal metabolism, etc., and the apparent simplicity of a respiratory rate figure may be illusory. But here we know what we are talking about. I would like to ask whether the rhythm varies with size, and how Dr. SOUTHWARD allowed for this factor.

SOUTHWARD: Yes, the results differed for different sizes, but there was no time to go into this in detail. The dominant size group was used in each species. In general, small specimens are faster, and old specimens are slower, but sometimes the differences can be quite small.

CRISP: I would like to add one point in relation to Dr. PROSSER's first question. In *Balanus balanoides* the difference in upper limits for activity may indeed be due to a genetic difference, since such differences are shown in comparing populations from America and Britain, but not in comparing populations within one continent. On other grounds genetic differences seem probable between American and European forms of this species. The only differences in cirral activity observed within one area were very small shifts in the temperature for maximal activity, perhaps caused by temperature acclimation, and therefore phenotypic.

SOUTHWARD: The temperature/activity curve has the same pattern in forms from both localities. It shows the level of relationship between the forms.

PROSSER: I would like to add one other suggestion. It appeared that with the animals taken from intertidal levels, the upper limit seemed to be the same, but that the rate of beating over the mid-range temperatures was different. This agrees with a great deal of other evidence that what Professor PRECHT has called resistance adaptation is genetically determined, whereas capacity adaptation can be more easily modified. I would suggest that perhaps in the case of intertidal populations the difference may be environmentally rather than genetically determined.