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The effect of temperature on the oxygen uptake and rate of development of the egg-masses of two common cirripedes, *Balanus balanoides* (L.) and *Pollicipes polymerus* J. B. Sowerby.

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The egg-masses in many cirripedes take the form of two compact lamellae occupying much of the adult mantle cavity in which they are incubated until the ripe embryos are hatched. Under optimal conditions, this period of incubation in a typical warm water species, may be quite short (10—15 days) as one brood follows another in rapid succession. By contrast, incubation in some arctic or boreo-arctic species may occupy several months. For example, in the Arctic, the eggs of *Balanus balanoides* are fertilized in the late summer and remain in the mantle cavity until the following June-July; during much of this time the animals may be frozen under the ice foot. Further south, for example, at Millport, Scotland, the embryos are retained from November to the following spring. At Woods Hole, Mass., U.S.A., where planktonic conditions are somewhat atypical for a north temperate coastal region (Fish, 1925), incubation may last only from October to December (Barnes 1958; Barnes and Barnes, 1959a).

In view of these facts the respiratory activity of the egg-masses of two intertidal cirripedes namely *B. balanoides* (L.) and *Pollicipes polymerus* J.B Sowerby has been investigated The former, common on both sides of the Atlantic and recorded from the Alaskan coast, is a typical boreo-arctic operculate and the latter, common on the Pacific coast of both North and South America, a temperate and possibly sub-tropical pedunculate.

Development of the embryos.

The embryology of a number of common barnacles has been examined in some detail by Groom (1895); the earlier stages of embryogenesis in *Balanus balanoides* was given particular attention by Delsman (1917) and Batham (1946) has given an account of the formation and development of the egg-mass of *Pollicipes spinosus* Quoy and Gaimard. Embryonic development appears to be very similar in many cirripedes; the following stages are recognised by Groom (loc. cit):

Stage A. Formation of polar bodies and first blastomere; the freshly laid ovum consists of granular protoplasm, coarse and fine yolk granules, together with oil globules of various sizes. The first polar body is soon formed and the egg is probably fertilized prior to the formation of the second polar body.

Stage B. Formation of blastomeres and growth of blastoderm over yolk; blastoderm, formed by repeated division, gradually extends from the anterior to the posterior pole until it eventually comes to cover the whole yolk. The position of the blastopore appears to be variable.

Stage C. Formation and extension of mesoblast and hypoblast; closure of the blastopore is followed by division of the yolk within the single layered epiblast.

Stage D. Formation of naupliar segments.

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Stage E. Marking out of naupliar appendages; this stage differs from the preceding only in that the epiblast and mesoblast are traversed by the dorsal longitudinal groove.

Stage F. Origin of labrum, oesophagus and intestine; the furrows on the dorsal side of the embryo become more marked forming very considerable depressions.

Stage G. Appendages long with short setae; the embryo at this stage is much transparent; various organs and body cavity can be distinguished.

Stage H. Development of the ultimate naupliar form ready for hatching; the appendageslengthen, thespines become very distinct and the embryo is even more transparent than in the preceding stage. It is particularly characterized by the development of a single median eye which in the later phases becomes deeply pigmented. The yolk endoderm, at first forming a solid mass, later separates and eventually yolk endoderm surrounds a wide cavity.

The Material and Methods

The animals were collected and brought to the laboratory as quickly as possible while still attached to substrata such as rock, stones or shells. Where they had to be transported for some distance, delay was reduced to a minimum and the material kept at ambient air temperature and immersed at intervals in sea water. For each set of experiments, egg lamellae were carefully removed from adult mantle cavities, transferred to a dish of sea water, and each lamella examined under a binocular microscope. The lamellae were then graded according to GROOM's classification; the required numbers in any given stage of development were lightly dried on filter paper and quickly weighed before being transferred to a manometer vessel containing a measured volume of sea water.

The oxygen uptake was measured using standard Warburg constant volume respirometers. The vessels (volume 15—21 ml.) had 3 or 5 ml. of sea water containing 1 mg/l of choloromycetin to prevent bacterial action but had no addition of any substrate; 10% KOH and filter papers were used in the centre cups. The gas phase was air. Preliminary experiments showed that, under the conditions employed, oxygen uptake was not affected by the presence of chloromycetin and that O_2 uptake/g. wet tissue/hr. (or $\mu l\, O_2$/mg. N/hr.) was independant of the duration of the experiment and amount of material used. 30 minutes were allowed for equilibration. Experiments were run for 2—4 hrs. (depending upon the temperature) at 0^0, 5^0, 10^0, 15^0 and 20^0 C, and check readings were taken at intervals.

After the oxygen uptake had been determined the lamellae were transferred to a Kjeldahl flask wet ashed and their nitrogen contents determined by a standard semimicro technique.

The results are expressed ether as μlO_2/g. wet tissue/hr. or μlO_2/mg N/hr.

As stated above each lamella was characterized according to GROOM's scheme; however, because this grading was done as rapidly as possible to avoid deterioration of the material and because lamellae had often to be pooled in order to obtain adequate manometer readings, the results from the various stages have been pooled into four categories, namely GROOM's A+B, C+D+E, F+G and H. These are relatively natural divisions in development and except for the last stage, take about equal times at moderate temperatures; stage H takes longer than the others and includes several phases of development prior to hatching.

All the experiments on *Balanus balanoides* were done at Woods Hole; much of the material was collected either from the nearby Institution pier or from Rocky Beach — a small stoney shore at the entrance to Buzzards Bay. In addition animals were investigated from two points in Maine some 200 miles (latitudinal) to the north — collections

being made at Cundy's Harbor, a relatively well sheltered inlet several miles from the open coast, and at Small Point on the outer exposed coast. A single series of comparisons was also made on lamellae taken from animals collected further to the south (150 miles, latitudinal) at Sandy Hook, New Jersey. The experiments on *Pollicipes polymerus* were made on material collected at Will Rogers State Beach, near Santa Monica, California and at Friday Harbor, Washington some 1000 miles (latitudinal) further north.

The Results

It was possible to obtain sufficient numbers of embryos in different stages from these widely separated places to compare their oxygen uptake even although for *Balanus balanoides* their initial fertilization had taken place more or less synchronously. The

Table 1

Balanus balanoides: oxygen uptake (µl/g/hr) of lamellae in different stages of development at different temperatures. Animals from Maine (Small Point S.P.M.; Cundy's Harbor C.H.M.) and Woods Hole (Pier, W.H.P.; Rocky Beach, W.H.R.B.).

T°C. / Stage	5	10	15	20
D	—	—	—	S.P.M. 107 W.H.P. 109 W.H.R.B. 98
E	C.H.M. 23 W.H.P. 27 W.H.R.B. 41	—	S.P.M. 85 C.H.M. 79	C.H.M. 126 W.H.P. 126
F	S.P.M. 29 W.H.P. 34	W.H.P. 58 W.H.R.B. 57	W.H.P. 103 S.P.M. 100	—
G	—	S.P.M. 79 W.H.R.B. 67	—	—

results are shown in Tables 1 and 2. (In the limited time available and in view of the fact that some of the material had to be transported several hundred miles, a comparison of all stages at all the selected temperatures was not possible). Irrespective of the stage of development or the temperature at which the estimations were made there is no

Table 2.

Pollicipes polymerus: oxygen uptake (µl/g/hr) of lamellae in different stages of development at different temperatures. Animals from Los Angeles, California (L.A.) and Friday Harbor, Washington (F.H.)

T°C. / Stage	15	20	25
C	—	—	L.A. 237 F.H. 245
G	—	L.A. 342 F.H. 323	L.A. 375 F.H. 410
H	L.A. 190 F.H. 188	L.A. 282 F.H. 305	—

indication in the case of either species of any significant regional difference in regard to oxygen uptake. For *Balanus balanoides* this is further evidence in support of a previous suggestion that is little indication of any sub-speciation adequate to separate physiologically distinct races in this area (BARNES and BARNES, 1959 a). The orgin of the animals will, therefore, be neglected in the further treatment of the results that follows.

The results are shown in Figure 1, in which log. oxygen uptake/mg. N/hr. for the several pooled stages of development described above has been plotted against the reciprocal of the absolute temperature. They are plotted in this conventional form for convenience of discussion; nothing is thereby implied regarding any theoretical interpretation of such curves in relation to the energy of activation of complex biological processes. Although discrete breaks are shown, the curves may in reality be continous curves with constantly changing slope. In both species, as is commonly the case when embryos cannot be (or are not) separated from yolk, the earlier stages with their smaller quantity of active protoplasm give the lower respiratory rates at any given temperature. With *B. balanoides* the initial stages of the curves are of similar slope, but with rising temperature there is a marked 'inflexion' (change of slope if the curves are continuous) which occurs at a successively higher temperature with advancing stage of development. The effect of increase in temperature on the rate of respiration is greatest at low temperatures on the early stages. It may be noted that there is an indication that a rise of temperature from 15—20° C. has a deleterious effect on the late stage (H) embryos. Between 0—5° C. there is little difference in oxygen uptake between the stages of development up to that in which the nauplii appendages are marked out (CDE). Elsewhere over the temperature range investigated *B. balanoides* shows a marked increase in respiratory rate from stage to stage. The slope of the lower parts of these curves approximates to a Q_{10} value of 4.2 and of the upper parts above the 'inflexion' of 2.2.

No data are available for the early stages of *Pollicipes polymerus*. For the later stages (CDE onwards) the curves show a marked change of slope at 10° C, this change taking place at the same temperature for all the stages in contrast to the situation found in *Balanus balanoides*. The most striking difference, however, is the relative independence of temperature (above 10°) of the CDE stage in *Pollicipes*; changes in respiratory rate as one passes from this to the next are, therefore, very marked at the higher temperatures. Below 10° C. the slope corresponds to a Q_{10} of 4.2, as in *Balanus*, but above 10° C. for all the stages except CDE the value approximates to 2.5.

Because the inflexion varies with the embryonic stage in *Balanus balanoides* the relative rates at which the two species take up oxygen will change with the temperature at which the comparison is made, although *Pollicipes* embryos always respire at a higher rate over the range investigated. At 15° the rate for the latter species is 1.25 times that of the former, but at 5° the differences are greater in the earlier stages (2.2 for CDE). However the eggs of *Pollicipes* are much smaller than those of *Balanus*, the former averaging 0.08 × 0.15 mm. and the latter 0.19 × 0.31 mm. The volume of a single egg of *Pollicipes* is about $^1/_{12}$ that of a *Balanus* egg. However, the ratio of wet weight to nitrogen is somewhat greater, (1.5 times) in *Pollicipes* so that on the basis of a single egg corrected for the difference in nitrogen content the rate of oxygen uptake of a *Pollicipes* egg approximates to $^1/_6$ to $^1/_3$ that of a *Balanus* egg. (The densities of these similar eggs are presumed equal).

Development of the embryos in vitro

The in vitro development of cirripede embryos has not often been reported although BATHAM (1946) has given an account of the culture of *Pollicipes spinosus* embryos. A number of species have now been reared including *Balanus balanoides*. As indicated by the work of OPPENHEIMER (1955) success would seem to depend upon keeping the growth of

bacteria and fungi in check; adequate aeration is also essential. The following method has been found satisfactory for barnacles. Two or three egg-masses are placed in a series of small containers through which a continuous flow of sea water at the selected temperature is maintained. Over the outlet tube of each container a piece of fine plankton gauze is fastened to prevent the escape of nauplii after they have hatched. This gauze may be changed at intervals to prevent clogging. The sea water is adjusted to the selected temperature before reaching the containers and the latter are maintained in a constant temperature bath. At the inlet to the train a two-way tap allows the system to be cut off from the main supply and to be put into connection with a vessel containing a bactericide. After cutting off the main supply the system was flushed out daily with 2 litres of sea water containing 1 mg. chloromycetin per litre. Embryos treated in this way were inspected frequently, and after passing through all the sequence of colour changes observed when they are incubated in the adult mantle cavity, normal and fully viable nauplii were hatched out. There was no apparent arrest in the eyed stage consequent upon the lamellae being outside the mantle cavity (for discussion, see BARNES, 1954; BARNES and BARNES, 1959b; CRISP and SPENCER, 1958). *Balanus balanoides* took 32 days at 5^0 and 11 days at 15^0 C. to hatch, the original material being in the 8—16 cell stage. This is equivalent to a Q_{10} of almost 3.●, and is similar to the value found by Crisp and DAVIES (1955) for *Elminius modestus*, an Australian barnacle now common in Britain. Between 5^0—15^0 C the Q_{10} of oxygen uptake is 2.2 for the first and in part the second stages, and 4.2 for the two later stages. Since each of these pooled stages takes about the same time for complete development, it is evident that the Q_{10} for total development time is similar to the overall value for the rate of respiration obtained experimentally.

Development of the embryos on the shore

In addition to following the development of *Balanus balanoides* embryos in vitro, shore populations at Millport, Scotland, and Woods Hole, have been investigated. Samples were taken at fortnightly intervals and again staged according to GROOM's classification. Careful check had been kept on the state of the animals so that at any particular collecting locality the time when they fertilized was known to within a few days.

It has already been stressed that naupliar release is related to the spring diatom increase in the eastern Atlantic and Arctic regions (BARNES, 1957; CRISP and SPENCER, 1958). At Woods Hole with a considerable winter diatom population it might be expected that with constant feeding activities nauplii would be released as soon as embryonic development is complete. This is the case as regards a proportion of the population — but a considerable number delay release which takes place over several weeks. The samples taken from the Woods Hole Institution pier will be first considered. Here the whole population behaved similarly. The animals were fertilized during the second half of October. Within three-four days all the animals in the samples were found to

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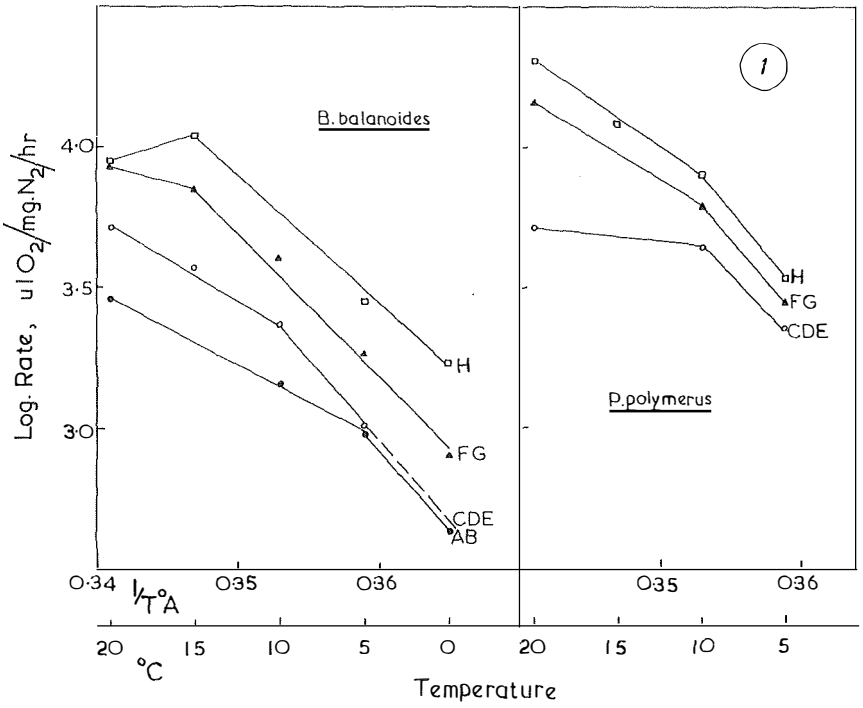
Fig. 1: Oxygen uptake (μlO^2/mg.N/hr.) for *Balanus balanoides* and *Pollicipes polymerus* eggmasses at various temperatures and stages of development; logarithmic scales.

Fig. 2: *Balanus balanoides* at Woods Hole; development of egg lamellae at various levels on the shore during the latter part of the season: e = empty, nauplii released.


1
B. balanoides
P. polymerus
Log. Rate, $ul O_2/mg.N_2/hr$
4·0
3·5
3·0
H
FG
CDE
AB
0·34
1/T°A
0·35
0·36
20
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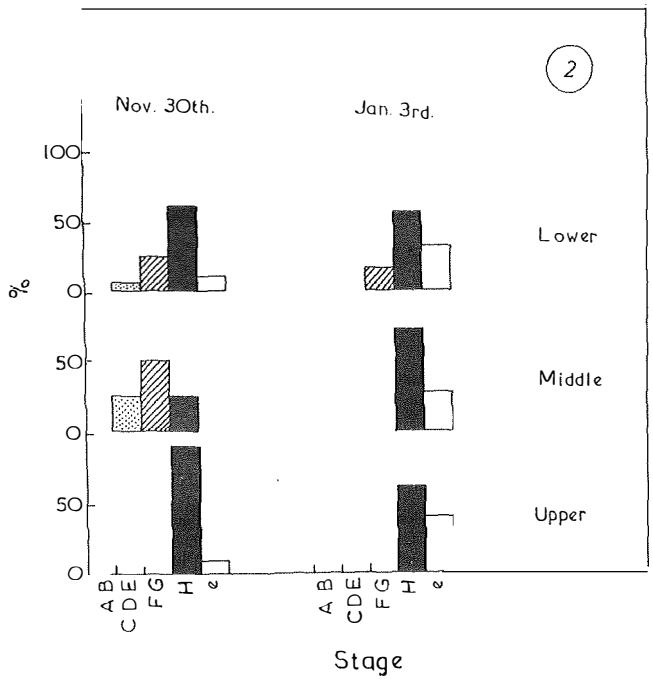
2
Nov. 30th.
Jan. 3rd.
100
50
0
%
Lower
Middle
Upper
A B
C D E
F G
H
e
Stage

Tafel 49

contain embryos; on 30th October 100% were in the AB stage. By 11th December 99% were in Stage H and 1% had released their nauplii. This gives a period of about 45 days for development; this is in good agreement with the in vitro results when it is remembered that during November both sea and air temperatures were falling rapidly. For these months the mean sea surface temperature is 11° falling to 6.6° C (mean max. 10.1° C, mean min. 3.1° C) and reaching 3.5° C. (mean max. 6.7° C; mean min. 1.5° C.) in December. Although hardly affecting the pier population the shores were often frozen during the mornings but no ice cover was formed during this period. The pier population in stage H, however, released nauplii for two months, some 3% still containing stage H embryos on 4th February. During this period, however, air temperatures were around zero — (January, mean max. 3.7° C.: mean min. —2.9° C: February, mean max. 4.2° C: mean min. — 3.1° C.) and the mean water temperatures were 1.7° C. and 0.7° C. for the two months. The shores during this period in 1957 both at Woods Hole and elsewhere in the Buzzards Bay region were frozen up.

Detailed continuous observations on the shore, where samples were taken at several levels, were started later and the early stages of development of the population missed. The animals began to be fertilized earlier (Oct. 11th—15th) than on the pier. Even so, certain features are worthy of comment. On 16th November only 18% of the poputon of the upper shore had lamellae in stage FG, the remainder being at early stage H, and yet at the lowest levels of the shore 10% were still at stage AB, 80% at CDE, and 10% at stage FG and none had reached the eyed stage. Evidence has been presented (Crisp, 1957; Barnes, 1958, 1959) that there is a temperature bar to the processes associated with the fertilization or final maturation of the gametes; at Woods Hole these are well developed during the late summer. It is considered that the upper shore will be released from this temperature barrier sooner than the lower shore since although water temperatures even in October are still high, air temperatures are falling very rapidly. On the upper shore the period of development appears again to be of the order of 40 days; Moreover, although by 15th December some 10% had released their nauplii — entire release of the population was not completed until February to March. During much of this time the shores were iced-up. At the lowest levels of the shore not only was fertilization much delayed but it was much less synchronous. However, once initiated, development was more rapid. The interpretation placed upon these facts is that once the temperature barrier has been removed at the lower levels of the shore which happens somewhat later in the season than at the upper levels, the higher sea temperatures and freedom from ice will not only allow development to proceed more rapidly but will also allow naupliar release to take place once development is completed.

At Millport the eggs are not usually fertilized until November; it is initiated fairly regularly during the first fortnight. Development to Stage H occupies some 50—60 days and in 1957 samples (100%) taken from the pier remained in this stage during the whole of February. There is, therefore, a delay either in the final stages of development or in the actual release of the nauplii. Release was, however, fairly synchronous being completed during March and indeed over 50% of it during the early part of the month. Temperatures — both sea and air — are much higher at Millport during this period of embryonic development than at Woods Hole (the mean air temperature lying between 6.5° and 4° C and mean sea temperatures between 10.5° and 7.0° C). The long time of development to stage H is, quite apart from the delayed release, therefore, unexpected and as has been suggested previously, may be due to inadequate ventilation of the mantle cavity consequent upon inactivity resulting not from low sea temperatures but from the absence of diatoms in the water (Barnes, 1957).

Rather less precise data is available for the development under natural conditions of *Pollicipes polymerus* lamellae and none for in vitro development. BATHAM (1946) has given a period of 30 days for development of *P. spinosus* in the laboratory at an unspecified temperature. Since breeding is continous during the warmer months and since the state of the lamellae in a single animal cannot be followed through the whole period of development, an estimate of this period cannot be made by examination of a series of random samples from the population. An estimation of the proportion of the time spent in each stage is, however, readily obtained by regular sampling.

At weekly intervals, collections were made at Friday Harbor and Los Angeles and lamellae graded according to the previous scheme; this was done throughout the summer. Since sampling was carried out at regular intervals and the same number (20) of animals staged on each occasion the fraction of the total generation time spent in any stage is given by the percentage of animals in that stage over the whole sampling period. The following results were obtained.

Table 3.

Percentage animals (*Pollicipes polymerus*) in given stage of development. Samples (20 animals taken) weekly throughout the summer; Los Angeles and Friday Harbor.

Stage	AB	CDE	FG	H	Empty
Los Angeles (July—September	2.7	6.5	5.2	15.0	70.6
Friday Harbor (July—August)	3.7	6.9	5.6	25.7	58.1

There are two notable features of these results; first the relatively long time spent in the "empty" phase and secondly the relatively longer time in stage H at Friday Harbor. The prolonged time during which the animals have no lamellae indicates that in any animal one brood does not succeed another in rapid succession. It is suggested that this is in keeping with the known sluggish behaviour of the animal; for example, BATHAM (1946) has pointed out that growth in the related *P. spinosus* is extremely slow, and it may be assumed that in view of a generally low metabolic activity this long period in between broods is required for building up of the ovary. This would also be in accord with the observed low rate of oxygen uptake when expressed on an egg basis (p. 245).

Discussion

There are few references in the literature to the oxygen consumption of crustacean eggs over the whole period of embryonic development and indeed relatively few Q_{10} values during this process for marine invertebrates other than echinoderms. NEEDHAM (1931) determined the oxygen consumption of *Carcinus maenas* embryos at 17° and 35° C — pointing out, however, that the latter temperature was lethal to the adult. His results are expressed in terms of weight of eggs and on this basis, as in the present experiments, the earliest stages with the smallest amount of active protoplasm showed the least respiratory activity. Between 15° and 37° C NEEDHAM found some — though not a great — variation of Q_{10} with the stage of development; all his values lay between 2.03 and 2.5. It is of interest to note that MELVIN (1928) found that in the development of a number of insects temperaure had very little effect on oxygen uptake during the early stages but its influence was considerable during the late stages; it is evident from his figures

that, while in the early stages Q_{10} was little more than unity, in the late stages it reached values greater than 3.0.

Apart from the apparent insensitivity of the CDE stage to temperature in *Pollicipes polymerus*, the major difference between it and *Balanus balanoides* is that in the former the Q_{10} for all stages above 10° C. approximates to 2.2, whereas in the latter such a value is only found at the higher temperatures. Now although it is well known that under certain experimental conditions respiratory activity and morphological development can be dissociated, the available evidence suggests that, as regards the effect of temperature, they are closely linked in these two cirripedes. This is particularly indicated by the fact that similar values of oxygen uptake are obtained for a particular stage of development whatever its previous temperature history (pp. 244 and 245). This may not be the case outside the temperature range investigated or under natural or experimental stresses other than temperature. *B. balanoides* is a northern form and the development of the egg-masses takes place at a relatively low temperature (below 10° C.) since this development succeeds a phase (the final stages of the maturation of the gametes) which has an upper critical temperature. With the exception of the early stages (AB) a Q_{10} of about 4.0 will be applicable to animals in their natural environment. If the respiratory and developmental processes are closely linked with respect to their Q_{10} values, the high value of the latter would seem to be of ecological significance. It has previously been stressed (Barnes, 1957) that the time available for development in artic regions is an important determinant in the distrioution of the species; in such places, once released from ice-cover under which the embryos, within the mantle cavity, have spent the winter, a high value of Q_{10} allows development to be accelerated with the rising temperatures during the artic spring so that the embryos are ripe early during the diatom bloom. Falling temperatures during the autumn subsequent to fertilization will similarly tend to retard embryonic development so that the animals will become frozen under the ice foot when the embryos are in a relatively early stage. There is some evidence (personal, unpublished) that early stages are better able to withstand the freezing and melting that occurs at the onset of winter than are the late stages. In contrast it may be noted that, except in Stage H, between 15° and 20° C there is apparently little deleteriouse ffect of tempratures above the normal habitat range on respiratory activity during embryonic develop-ment.

The time of development on the shore at Woods Hole agrees reasonably well with that estimated from the in vitro experiments on *B. balanoides*. At Millport, however, the time required to reach the H stage is somewhat longer than expected from the temperature conditions; Barnes (1957) has suggested that this may be due to somewhat inadequate ventilation of the mantle cavity during the winter months when feeding is minimal. There is then a further delay at Millport in the H stage and this is associated with processes concerned in the hatching of the embryos that lead to liberation at the time of the spring diatom increase.

There has recently been much interest in homeostasis in poikilothermous animals (Segal, Rao and James, 1953; Bullock, 1955; Segal, 1956; Dehnel, 1956). There is much evidence that animals living in colder regions have, at the temperature of their environment, a relatively higher metabolic rate than animals in warmer regions have at the same low temperature.

Relatively little is known concerning the mechanism of homeostasis and some discussion has centred round the effect of temperature on Q_{10} values since a low value of Q_{10} clearly results in homeostatic tendencies. Rao and Bullock (1954) have maintained that there is a tendency for lower values of Q_{10} to play a part in homeostatis

whereas SCHOLANDER, FLAGG, WALTERS and IRVING (1953) consider changes in sensitivity to temperature play no part in climatic adaptation which, they believe, is brought about by a shift in the metabolism (or activity) — temperature curve and not a change in its slope. One of the objects of the current work was to compare the metabolism of egg lamellae of the two different species as well as the same species over a range of latitude. On the one hand, it might be expected that in a sessile animal acclimation would be more marked since there is no possibility of retreat to a more favourable micro-habitat; on the oher, the great changes in the environment to which intertidal animals are constantty subjected might be expected to mitigate against such a hypothesis. However, acclilmation has been indicated with regard to a number of rate functions in intertidal species and KIRBERGER's work (1953) indicates that some animals can 'average' temperature fluctuations.

In the present instance, as far as it was possible to test, there is no acclimation as regards the oxygen uptake of embryos in either *B. balanoides* or *Pollicipes polymerus*. At each temperature employed and with all the stages tested the oxygen uptake was the same for animals taken over a wide range (see Tables 1 and 2) although there were considerable variations in habitat temperature. Furthermore, there is no evidence of a reduction in Q_{10} at low temperatures. It is clear that any acclimation in embryonic development would have to take place at the metabolic rather than the behavioural level and as PROSSER (1956) has pointed out there is general evidence that activity acclimation is more common than that of basal metabolic processes.

Summary.

1. Data are presented on the oxygen uptake, determined by the Warburg technique, of the isolated egg-masses of *Balanus balanoides* and *Pollicipes polymerus*.

2. Oxygen uptake of egg-nasses from widely separated places (latitudinal) showed no significant differences at any of the stages of development tested.

3. The earlier stages of development give low respiratory rates.

4. In *Balanus balanoides* the Q_{10} changes with stage and temperature whereas above 10^0 C all stages of *Pollicipes polymerus*, except CDE, have the same value of Q_{20}.

5. The oxygen uptake (on a per egg basis) of the pedunculate is $^1/_3$ rd. to $^1/_6$ th. that of the northern operculate.

6. The in vitro development of egg-masses is described.

7. An account of development in some natural shore populations and the effect of temperatures on them is presented.

8. The ecological significance of the results is discussed.

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