The Rate of Development of *Balanus balanoides* (L.) Larvae

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**Abstract**

Experiments are described on the rate of transition of State I to State II *B. balanoides* larvae at a series of temperatures. A value of 2.2 was found for $Q_{10}$ between 1° and 18° C. The data regarding the length of the planktonic phase over the area of distribution are reviewed and new data also given. There is little indication of a high correlation with temperature. The discrepancy may be accounted for by acclimation, but it is suggested that the quality and quantity of food should be considered as interacting with and perhaps compensating for the effect of temperature.

*Balanus balanoides* (L.) is widely distributed over the arctic-boreal regions; the conditions of its environment, therefore, differ widely, and information regarding rate processes at any stage of the life cycle is clearly of importance in any interpretation of the ecology of the species. Plankton collections at a number of places have given some information regarding the rate of development of the free living larval stages, but there is no recorded experimental work. While such work on the late larval stages involves all the difficulties associated with the culture and maintenance of marine planktonic organisms, the Stage I to Stage II transition may be easily studied. Ripe embryos, teased out from the egg lamellae present in the mantle cavity of the adult readily hatch into Stage I nauplii and soon pass into Stage II nauplii.

**Material and Methods**

A number of lamellae of the same apparent degree of ripeness were teased out into sea water contained in a petri dish; the liberated Stage I nauplii accumulate on the lighter side of the dish and may be easily pipetted off. Since the rate of transition from Stage I to II changes during the season (under constant experimental conditions) presumably according to the ripeness of the lamellae, all the following experiments were run on a single batch of nauplii after the techniques had been tested in a series of preliminary experiments.

Small samples of active nauplii were pipetted into large test tubes containing 5 ml sea water, brought to and subsequently maintained at constant temperature in water baths; experiments were run at 1.0, 5.5, 6.1, and 18.5°C. Some 40–50 such tubes were set up at each temperature. All the tubes were held in the multiple arms of a single mechanical shaker and gently agitated throughout the experiments, since the preliminary experiments had shown that without gentle shaking the rate of transition is reduced and the results are very erratic. This may be due to the fact that without agitation the nauplii were often crowded together and tended to be less active in the relatively small volume of water used. Whether the lower rate of transition in the absence of gentle agitation is the result of less activity per se or whether it is perhaps due to the greater ease of ecdysis among actively swimming animals is unknown. From time to time formalin in the usual strength was added to three replicate tubes at each temperature, the appropriate intervals being selected on the basis of earlier experiments. The number of Stage I and Stage II nauplii were subsequently counted...
under a low power binocular microscope. From the results the mean percentage of larvae that had moulted to Stage II at any time (corrected for viability by expressing as percentage of ultimate numbers of Stage II) was plotted against the time, and from the smoothed curves the rate of transition, that is, time of half change, was calculated.

RESULTS

These are shown in Figure 1 in which the reciprocal of the time of half change (relative rate of transition) is plotted on a logarithmic scale against temperature. The two are linearly related over the whole range with a \( Q_10 \) of about 2.2. Such a value might have been anticipated for an arctic-boreal species at the range of temperatures of the normal habitat, namely 0–8°C for the planktonic phase (see Scholander et al. 1953). However, it is a little surprising that no falling off in the value of \( Q_10 \) is apparent at the higher temperatures—higher than those at which the larvae are normally found but not higher than those to which the adult is subjected in the southern parts of its distribution. This may indicate that the larvae are completely viable up to 18°C and that up to this limit temperature effects on the larval stage do not limit the distribution of the species. However, the Stage I to II transition takes place rapidly; the later stages which take much longer in development may not be viable at the higher temperatures.

COMPARISON WITH PLANKTONIC DATA

The results may be compared with what is known of the length of planktonic life under natural conditions. When sampling problems are taken into account, even with collections taken at short intervals, it is difficult to estimate with any accuracy the length of individual stages—usually a matter of only a few days. We may consider the planktonic life up to the cypris; the cypris stage may be variable and estimates based on the settlement dates are even more crude.

There is satisfactory data from the Firth of Clyde (Scotland). Pyefinch (1948) making hauls every three days during the spring months estimated the time for development up to the cypris stage was 32 days in 1944 and 30 days in 1947. We have confirmed these results taking daily hauls with the Hardy plankton indicator; the estimates are the same whether first appearances or peak values are used. The mean sea-surface temperature for this region during the month of March when the larval population is developing is about 7°C (Barnes 1955). Although there is a considerable amount of data on the general biology of \( B. \) balanoides both round the coast of Britain and Northern France, there are no further reports on plankton collections which allow satisfactory estimates of the larval life to be made.

Again, although there is much literature on the plankton of the Norwegian coast, little attention has so far been paid to the cirripede larvae. However, through the courtesy of Dr. F. K. Wiborg, we have been able to examine plankton hauls taken in the Lofoten area. For the present purpose the hauls were taken too infrequently, but the best estimate using the results from all the stations is some 27–30 days at a temperature of 3–4°C. Runnström (1924–25) while stressing that there may be some variability from year to year gives a plankton life of 30 days for the waters near Bergen at a temperature of 4°C. He also states that in Liverpool Harbour nauplii appeared on February 22 and cyprids on April 6, a period of 43 days.
Table 1. Rate of development of planktonic phase of B. balanoides

<table>
<thead>
<tr>
<th>Place</th>
<th>Days</th>
<th>Sea surface temperature °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ungava Bay (Canada)</td>
<td>48</td>
<td>1</td>
</tr>
<tr>
<td>Halifax Harbour (Canada)</td>
<td>40</td>
<td>1-2</td>
</tr>
<tr>
<td>Woods Hole (U. S. A.)</td>
<td>21</td>
<td>0.6</td>
</tr>
<tr>
<td>Newport (Rhode Is., U. S. A.)</td>
<td>33</td>
<td>1.0</td>
</tr>
<tr>
<td>Millport (Scotland)</td>
<td>32</td>
<td>7.0</td>
</tr>
<tr>
<td>Bergen (Norway)</td>
<td>30</td>
<td>4.3</td>
</tr>
<tr>
<td>Lofoten (Norway)</td>
<td>27-30</td>
<td>3.0</td>
</tr>
</tbody>
</table>

Bousfield (1952-53) has given much information on B. balanoides around the Canadian coast, but the plankton data cover only Halifax Harbour. Weekly samples during the spring of 1952 indicated the first appearance of nauplii on February 26 and Stage VI on April 4; cyprids were settling on the shore by April 10, so that a period of 40 days may be taken as the best estimate for Stage I-VI. During this period ice was observed in the harbor, and Bousfield states that the surface temperatures were less than 3°C. Data by Banks (1955) for Halifax Inner Harbour indicates that 1-2°C is a better estimate for the temperature, a value substantiated by those for Eastport, Maine (U. S. Coast and Geodetic Survey 1955).

We have been able, through the courtesy of Dr. M. J. Dunbar, to examine plankton hauls taken by the Eastern Canadian Arctic Investigations in the Ungava Bay Region. In 1949, Stage II nauplii were first taken on June 4 and cyprids on August 11, which is a period of 48 days for development.

Fish (1925) found in plankton collected at Woods Hole that nauplii first appeared during December and cyprids in February. However, we have recently examined bi-weekly collections taken by Dr. C. S. Rao at Woods Hole, and while confirming the occurrence of nauplii on December 6 found they were followed by cyprids 21 days later. The mean sea surface temperature at this time was 6.6°C. It would seem that due to conditions pertaining at the time of Fish's collections his nauplii did not give rise to viable cyprids (see Barnes 1956).

Fish also records that he observed large quantities of early stage nauplii on January 30 somewhat further to the south at Newport (Rhode Island), and that these were followed by abundant cyprids on March 4, 33 days later; the temperature may be taken as similar to that at Woods Hole for February, namely 1.0°C (U. S. Coast and Geodetic Survey 1955). The data discussed above are collected together in Table 1.

Discussion

It is evident from Table 1 that while at some of the colder places the period of larval development is somewhat longer, there is no regular relation with temperature. In most cases a period of about 30 days is required whatever the temperature. The results stand, therefore, in marked contrast to the effect of temperature on the Stage I to II transition as determined experimentally. It is realised that there is some doubt about feeding in Stage I and that the absolute rates of the different stages may vary; one might expect nevertheless the value of Q10 to be similar for all stages. It is possible that acclimation is responsible for the roughly constant period of development, but in this connection it must be noted that the temperature during the later stages of embryonic development varies widely; for example the adults have been buried under the ice in the Canadian Arctic, while at Woods Hole the temperature falls only from 15° in October to 11°C in November. Acclimation to habitat conditions has been shown to be a common feature among poikilothermous animals (Bullock 1955) and has been suggested for a number of planktotrophic larvae by Thorson (1946); the comparisons are, however, largely interspecific.

On the other hand the availability of the right kind of food has been shown to be of fundamental importance in the development of planktonic larvae with high metabolic rates, and it is suggested that this factor may interact with and compensate for temperature effects.
REFERENCES

Banks, R. E. 1955. Seasonal changes in the water temperature of Halifax Harbour and Bedford Basin. Naval Research Department, Nova Scotia, U/P Section IV, Research Note 55/1.


