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Development of Neritic Copepods *Acartia clausi* and *A. steueri*

II. Isochronal Larval Development at Various Temperatures[1),2)]

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Abstract

Isochronal development is a general feature in stage succession of neritic copepods *Acartia clausi* and *A. steueri*, when they are cultured at optimal temperatures with excess food. However, stage duration of NI is shorter and of NII is compensatingly longer than the other later stages which are almost equal in time. The time required from egg-laying to reach any developmental stage at a given temperature can be calculated from the Bělehrádek equation by proper multiplication of proportional constant for embryonic development at that temperature. Isochronal development may be more advantageous than nonisochronal development for some species of the genus *Acartia* to ensure high reproductive potential of the population by reducing the mortality during copepodite stages.

It has been a general agreement that when food is excessively abundant the rates of post-embryonic development of copepods are dependent on temperature (MCLAREN 1963, 1965). CORKETT & MCLAREN (1970) have used the Bělehrádek equation, $D=a(T-\alpha)^b$ (D: development time, T: temperature in Celsius, a, b, and α: fitted constants), to describe the development time of eggs and larval stages of 4 species of calanoid copepod as a function of temperature. They have argued that the values of b and α derived from egg development may also be applied to describe larval development, whereas the value of a derived from embrycnic development increases with successive developmental stages. This means that once the development rate of eggs has been determined it is only necessary to measure the development rates of older stages at one temperature in order to calculate these rates at any temperature.

MILLER et al. (1977) have recently found a growth rules for *Acartia* species by reviewing the previous works. They refer the data reported for *A. clausi* from Jakle's lagoon, Washington by LANDRY (1975), *A. tonsa* from Patuxent River estuary, Maryland by HEINLE (1969) and *A. californiensis* (*A. tonsa*, ref.) from Yaquina Bay, Oregon by JHONSON & MILLER (1973). The rule MILLER et al. (1977) found is that *Acartia* develops at a constant time interval throughout whole larval stages and such a molting pattern has been termed "isochronal development" by them.

Isochronal development is also found in *A. clausi* and *A. steueri* from Onagawa Bay,

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[2)] 内湾性橈脚類 *Acartia clausi* と *A. steueri* の発生. II. 等時生長

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northeast mainland of Japan, under their optimal temperatures with excess food. To supplement the evidence of this characteristic developmental mode, this paper reports the post-embryonic development of *A. clausi* and *A. steueri* under various temperature conditions.

Materials and Methods

Several hundreds to about a thousand of eggs of *A. clausi* and *A. steueri* either spawned by females in the laboratory or isolated from the natural sea-bottom muds were introduced into Pyrex beakers containing approximately 900 ml of Millipore (HA type: 0.45 μm) filtered seawater. The beakers were placed in a water bath maintaining temperature gradient from 2.5 to 29.6°C. After hatching, cultured *Isochrysis galbana* and *Dunaliella tertiolecta* were supplied as food. As nauplii grew beyond NIV, *Thalassiosira decipiens* was also added. An excessive food condition in the vessels was maintained by monitoring color of the rearing medium with naked eyes (generally no less than 10^6 cells • ml^{-1}). At 2-5 days intervals, fecal pellets and residual food on the bottom of the vessels were carefully pipetted or siphoned out, and freshly prepared medium was added. Illumination was not specially controlled, although direct sun light was avoided, daytime lighting in the laboratory was 300-500 lx. At appropriate intervals, 20-25 individuals were subsampled with a large-mouthed pipette after the culture was gently stirred, and preserved with formalin to check their developmental stages under the dissecting microscope. Then the percentage composition of stages in each subsample was calculated.

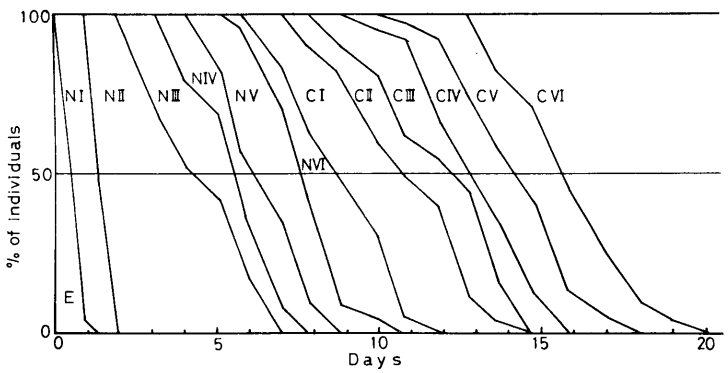

Fig. 1. Post-embryonic development of *Acartia clausi* at 20.3°C.

Results

Fig. 1 shows the variations in percentage composition of successive stages during time course from egg through adult observed at 20.3°C within a batch of *A. clausi* eggs which were produced in the laboratory. From this figure, the time of entering into each stage was defined graphically by the time when 50 % of the animals had molted into that stage. By the same method, the development rate under various temperature conditions could be estimated. Figs. 2 and 3 show larval development of *A. clausi* hatched from eggs spawned in

the laboratory and from resting eggs sorted from bottom muds, respectively. Since there were few eggs in the mud, the development of *A. steueri* was examined from eggs spawned in the laboratory only (Fig. 4). It is clear as in embryonic development (cf. UYE 1980), that the rate of larval development is dependent on temperature. The rate increases with increasing temperature, while the rate of *A. clausi* is no longer increased beyond 20.3°C.

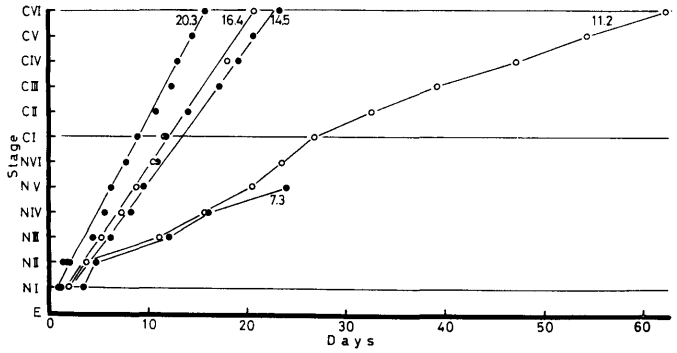

Fig. 2. Post-embryonic development of *Acartia clausi* at 7.3, 11.2, 14.5, 16.4 and 20.3°C. Each point is the time required for 50 % of individuals molting into each stage. Straight lines are fitted by the least squares to all points except one entering into NII.

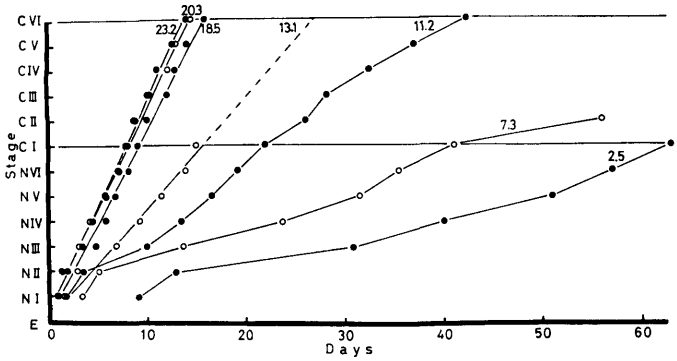

Fig. 3. Post-embryonic development of *Acartia clausi* hatched from the resting eggs at 2.5, 7.3, 11.2, 13.1, 18.5, 20.3 and 23.2°C. Further details as in Fig. 2. Points at 2.5°C denote the time for the fastest growing individual.

Regardless of temperature and species, the consistent acceleration and delay of development were observed in NI and NII stages, respectively, then an isochronal development was evident in post-NII stages. However, at lower temperatures the isochronism was slightly biased toward hyperbolic curve; the duration of more advanced stages became longer. Although *A. clausi* hatched from the resting eggs developed faster than those hatched from the laboratory-spawned eggs when reared at lower temperature, e.g. 11.2°C, there was no discernible difference in the development rate under optimal temperature condition between two different origins.

As mentioned before, since the development from NIII through CVI at optimal temperature was isochronal, a straight line was fitted by the least squares, which can describe development time to reach a given stage, omitting NII. The development time from egg to CI and CVI estimated from the fitted lines and the observed time to NII are shown with that of embryonic development in Table 1. The latter was calculated from the Bělehrádek

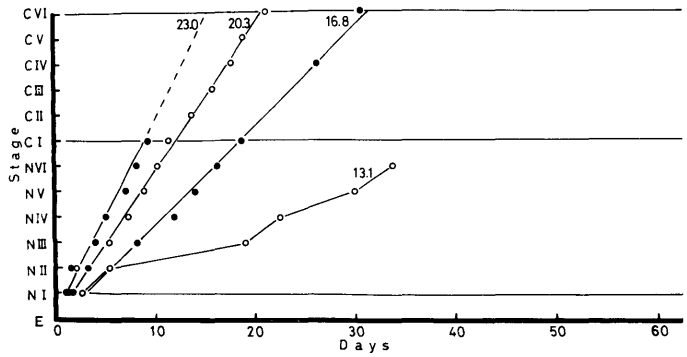

Fig. 4. Post-embryonic development of *Acartia steueri* at 13.1, 16.8, 20.3 and 23.0°C. Further details as in Fig. 2.

TABLE 1. EMBRYONIC AND POST-EMBRYONIC DEVELOPMENT TIMES OF *Acartia clausi* AND *A. steueri* AT VARIOUS TEMPERATURES.

Temperature (°C)	Development time (days) egg development (1)	egg to NII (2)	egg to CI (3)	egg to CVI (4)		(2)/(1)	(3)/(1)	(4)/(1)
Acartia clausi								
13.1	1.6	2.8	15.6	27.0		1.75	9.77	16.9
14.5	1.3	2.1	13.1	22.7		1.62	10.1	17.5
16.4	1.1	1.8	12.2	21.1		1.64	11.1	19.2
18.5	0.93	1.8	9.2	15.6		1.94	9.86	16.7
20.3	0.81	1.2	9.1	15.8		1.48	11.3	19.5
20.3	0.81	1.3	7.9	14.2		1.60	9.78	17.9
					Mean	1.67±0.16	10.3±0.70	17.9±1.18
Acartia steueri								
16.8	1.6	3.1	18.2	31.1		1.94	11.4	19.4
20.3	1.2	2.0	11.9	20.7		1.67	9.96	17.3
23.0	0.9	1.4	9.26	16.2		1.56	10.3	18.0
					Mean	1.72±0.20	10.6±0.75	18.2±1.07

equation in the previous paper (UYE 1980). The ratios of the time for post-embryonic development to the embryonic one calculated for *A. clausi* between 13.1 and 20.3°C and *A. steueri* between 16.8 and 23.0°C were quite constant and identical between two species. The delayed development at lower temperature was probably due to unfavorable food conditions which might be easily created at lower temperature by slow growing and inactively settling phytoplankton in the vessels. If provided with cold-water phytoplankters, the copepods might

have followed a similar pattern of development to those cultured within optimal temperature range, or the development of *Acartia* in nature must be isochronal over their thermal range. The larval development at lower temperature then could be extrapolated from duration of the egg development. A schematic pattern of the isochronal development at various temperatures is given in Fig. 5. In these figures shorter stay at NI and longer stay at NII are also taken into account.

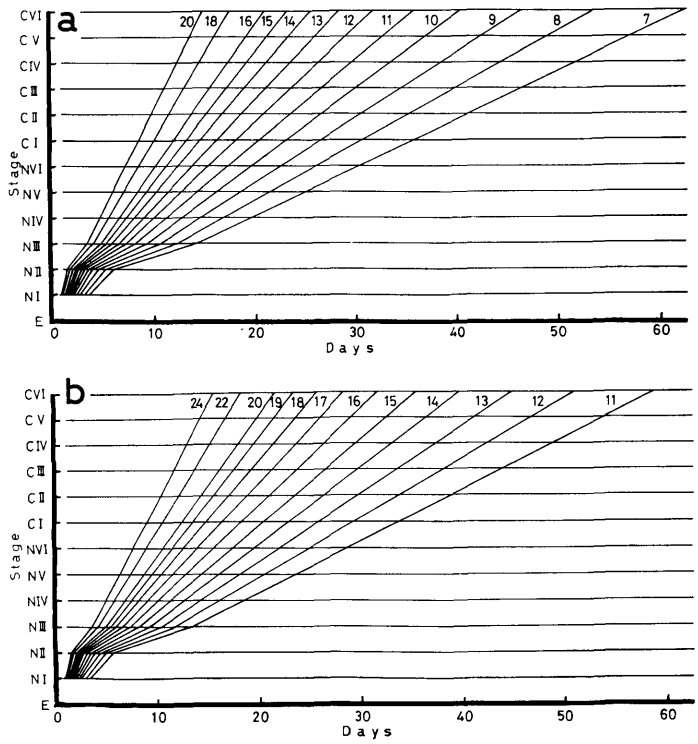

Fig. 5a, b. Schematic pattern of post-embryonic development of (a) *Acartia clausi* at temperatures from 7 to 20°C, and (b) *A. steueri* from 11 to 24°C.

Discussion

Following the proposition by CORKETT & MCLAREN (1970), my assumption was also that the time taken to reach any stage was the same multiple of embryonic duration at any given temperature for *A. clausi* and *A. steueri*. The Bělehrádek equation applied to define the relationship between embryonic development time (in days) and temperature is $D=650(T+5.8)^{-2.05}$ and $D=747(T+3.2)^{-2.05}$ for *A. clausi* and *A. steueri*, respectively (UYE 1980). The multiples of embryonic time to the time to reach NII and NIII are 1.67 and 4.22 respectively for *A. clausi*. Corresponding values are 1.77 and 4.52 for *A. steueri*. Beyond NIII to adult, this multiple is increased by 1.52 for both species as their stage progresses. Therefore, one can easily calculate the time required from egg-laying to reach any developmental stage by

the equation for embryonic duration, with changes only in the proportional constant (650, 747 for the respective species) by proper multiplication. From the results presented in Table 1 of LANDRY (1975), when *A. clausi* collected in fall were reared at 20°C, it took 13.3 days before the females molted into adult stage, and the multiples of embryonic duration to the time to reach NII, NIII, CI and CVI♀ were 1.51, 2.65, 5.78 and 10.2, respectively. However, the data from the present experiments show that at the same temperature it takes a longer period (14.9 days) to reach adult and the corresponding multiple is much larger than his data.

LANDRY (1975) has found that the duration of NI is shorter and of NII is longer than the other later stages, and that the males reach maturity consistently before the females. Since no attempt has been made to separate sex in this paper, the difference in sexual maturation is obscure. As mentioned above, however, similar anomalous duration of NI and NII are also found. Since no NII develops to further stages under starved condition, it can be concluded that, while yolk is available by NI, NII is to start feeding. The longer stay of NII may imply that the animals at this stage need much time to accumulate energy by means of initiatory feeding or the NII stage is the critical period for these copepods.

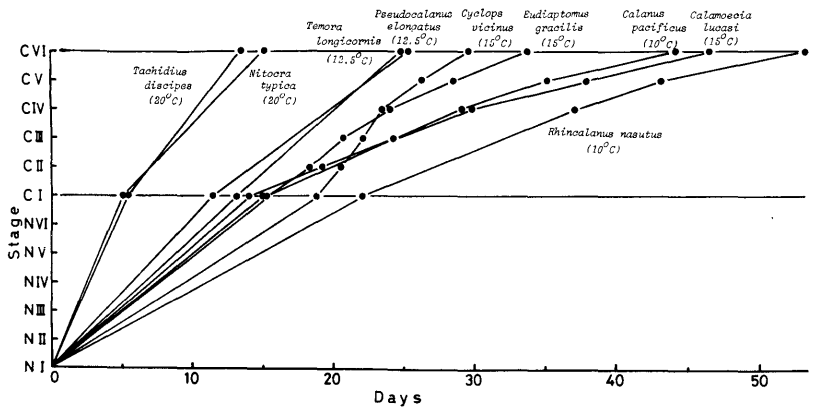

Fig. 6. Post-embryonic development of *Calanus pacificus* and *Rhincalanus nasutus* at 10°C (from MULLIN & BROOKS 1970), *Temora longicornis* (from HARRIS & PAFFENHÖFER 1976) and *Pseudocalanus elongatus* (from PAFFENHÖFER & HARRIS 1976) at 12.5°C, *Cyclops vicinus* and *Eudiaptomus gracilis* (from MUNRO 1974), and *Calamoecia lucasi* (from GREEN 1976) at 15°C, and *Tachidius discipes* and *Nitocra typica* at 20°C (from HEIP & SMOL 1976).

Fig. 6 summarizes the published data on post-embryonic development of copepods at various temperatures, which are in general less precise. It seems to be a general principle for most species that naupliar instars are considerably shorter than copepodite instars, showing nonisochronal development. Only *Temora longicornis* and *Pseudocalanus elongatus* develop nearly in isochronal manner, though no stage-by-stage data available. The development of *Cyclops vicinus* is exceptional; the development time through copepodite stages is shorter

than that through naupliar stages. While we need more detailed data for many species before generalization, it is most likely that the isochronal development is characteristic to some limited group of copepods.

One consequence of the isochronal development, as contrasted with nonisochronal development, is that a proportionally shorter part of life history is spent in the older stages. The shortening of the later stages could, as has already been discussed by MILLER et al. (1977), lead an adaptive significance that is advantageous in faster development and hence in rapid population increase.

MILLER et al. (1977) have also suggested that the selective advantages of the isochronal development are to reduce mortality during copepodite stages by shortening the stage duration relative to naupliar stages. From the study on population dynamics of *A. clausi* at the innermost part of Onagawa Bay, it has been found that only 10–20 % of spawned eggs recruit to the planktonic population. Such a large loss during egg stage has also been demonstrated by LANDRY (1978) in the population study of *A. clausi* in a small temperate lagoon. Although I have no comparable data for other species of copepod, this large loss in egg stage may be specific for the population dynamics of *A. clausi*. To compensate this loss, the population needs higher reproductive potential, although the data shows the females can live for only a very short period. Thus, this species is required to increase the female abundance by reducing mortality in later life stages.

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