Growth rules in the marine copepod genus *Acartia*[1,2]

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Abstract

Several species of the copepod genus *Acartia* are shown from existing data to complete each molt-to-molt phase of the life cycle in a constant time period. This molting pattern is termed *isochronal development*. Increase in mass at each stage is a nearly constant fraction of the weight at the beginning of the stage (with the exception of the late naupliar stages). Coupled with isochronal development this implies that growth in *Acartia* is exponential in time through most of the life cycle. Under isochronal development a proportionately shorter part of the total development is spent in the copepodite stages than in forms with stages of progressively greater duration. This may be a response to preference of the predators of *Acartia* for the older stages or a general adaptation leading to a shorter life cycle and higher rates of population increase.

Figure 1 is a graph of the results presented in table 1 of Landry (1975a). The conclusion is striking. When food is present in excess of demand, the progression of *Acartia clausi* Giesbrecht through its developmental stages is linear in time. Therefore, the duration of the stages must be close to constant throughout development after hatching of the egg. This holds for all temperatures tested except for the last male stage at 15°C. The data at lower temperatures are incomplete. The conclusion drawn by Landry from the data is that the time required after hatching to reach any stage at a given temperature is proportional to the time required for the eggs to hatch at that temperature. That conclusion could be true regardless of the relative times required for different stages. It is an additional fact that the durations of the stages are about equal. We will call this molting pattern *isochronal development*.

M. Landry (personal communication) feels that the duration of the first naupliar stage (N_1) is consistently shorter, of N_2 longer, and of the fifth copepodite (C_5)

longer than the times for N_3 through C_3, and further that males consistently reach maturity before females. Because Landry's data about the variability of development times at a given temperature are not yet available, these possible deviations from constant duration of the stages cannot be evaluated. On the whole the stages are each passed in the same amount of time.

Isochronal development is found in at least one other member of the genus *Acartia*. Heinle (1969a,b) has demonstrated it for an Atlantic population of
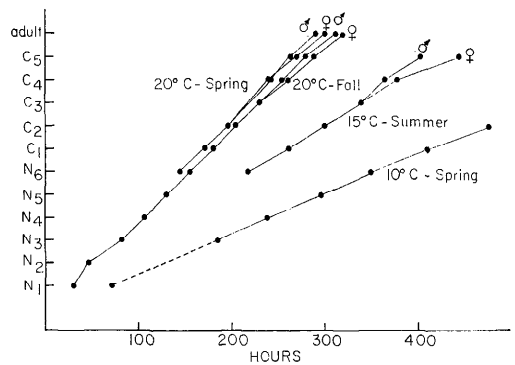

Fig. 1. Median times required for development of *Acartia clausi* from Jakle's Lagoon to stages shown on ordinate at several temperatures and seasons of collection. Data from Landry (1975a).
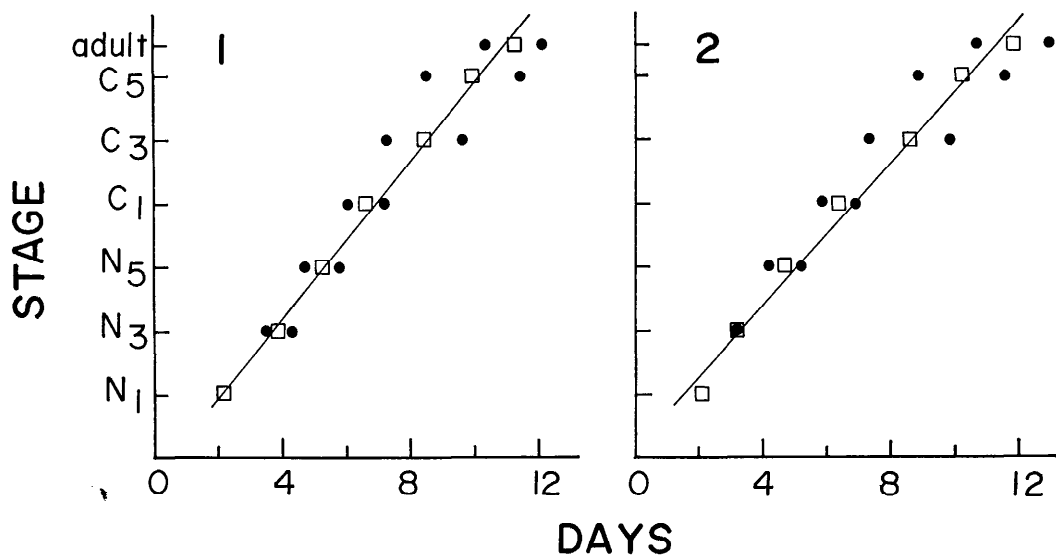
Fig. 2. Squares are median times required for development of *Acartia tonsa* from Yaquina Bay to stages shown on ordinate in two replicate experiments, 1 and 2. Line is fitted by least squares to these medians. Solid circles are range of development times predicted by linear regression of percent having reached the stage against time for all times after first appearance and before slowest termination of the stage. Data from Johnson (1974).

Acartia tonsa Dana, although constancy broke down near the thermal tolerance limit. Figure 2 is a similar demonstration for *A. tonsa* from Yaquina Bay, Oregon, reared at 21°C in 25‰ salinity (Johnson 1974). Heinle and Flemer (1975) have suggested that isochronal development probably pertains for *Eurytemora affinis* (Poppe). While a plot of the data from table 1 in that paper, from which the conclusion is taken, do not bear this out, they feel their culture conditions may have been less than optimal. Katona (1971) found isochronal development for all stages of the same species. His data are excellent and seem definitive.

Data on other marine copepods are in general less precise. In their table 1, Mullin and Brooks (1967) give some general data for *Rhincalanus nasutus* Giesbrecht and *Calanus pacificus* Brodsky. These data imply that naupliar instars must be considerably shorter than copepodite instars, since all of egg and naupliar development (6 stages) takes only 25% of the fastest egg-to-adult development time (13

steps) for *R. nasutus* and only 19% of the only estimate given for *C. pacificus*. M. Mullin (personal communication) has confirmed in later experiments with *C. pacificus* from off southern California that times per stage increase markedly, but somewhat irregularly, through the life cycle. The early data of Nicholls (Marshall and Orr 1955) showed *Calanus finmarchicus* (Gunnerus) to have increasing time per stage through all copepodite stages, although control of temperature, food, and other conditions did not approach modern standards. Field data on growth of *Pseudocalanus minutus* (Krøyer) in Ogac Lake (McLaren 1965) also suggested increasing duration of instars during growth, but it is not certain that adequate nutrition was available, even for the portion of the data based on individuals raised in fertilized plastic bags suspended in the lake. A selection of the better data from a study by Katona and Moodie (1969) on development time of *Pseudocalanus elongatus* (Boeck) at 15°C gives an average of about 8.6% of the total development time per
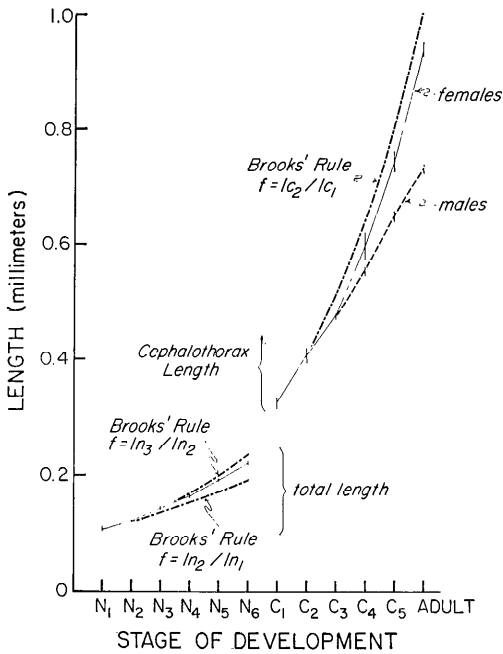
Fig. 3. Increase in length with stage in *Acartia tonsa* from Yaquina Bay. Vertical bars are 95% confidence limits for mean length of stage. Comparisons to various versions of Brooks' Rule are shown.

naupliar instar and 9.6% per copepodite instar. Results of Paffenhofer and Harris (1976) are more disparate: 7.5% and 11.0% for the same measures. More detailed data may show that development in *Pseudocalanus* is more nearly isochronal. However, it seems likely, on present evidence, that isochronal development will not be found to be the general situation for marine copepods.

A considerable body of data has been developed in recent years about the relative durations of instars of freshwater copepods. Munro (1974) and Ivanova (1973) have reviewed these results. Some forms seem to be isochronal, such as *Cyclops vicinus* Uljanin (Munro 1974); others have progressively increasing instar durations, such as *Diaptomus laciniatus* (Eckstein 1964) and *Eudiaptomus gracilis* Sars (Munro 1974). In the data for *E. gracilis*, first copepodite through third copepodite instars are of very nearly equal duration, but

they are longer than the average naupliar stage, and they are shorter than the duration of fourth and fifth copepodite instars at all but the highest temperature tested. None of the studies give a stage-by-stage development schedule during the naupliar phase.

Because the molting interval is constant, the developmental biology of *Acartia* must have some special properties. Since length increases with stage (Fig. 3), and since weight has approximately an exponential relationship to length as in other organisms (Heinle 1966), constant time per stage implies that *Acartia* grows exponentially in weight throughout its developmental period. At each stage the amount of tissue that must be accumulated before molting increases in absolute amount and is in constant ratio to the amount already present. An early period of exponential growth (a first "growth stanza") is typical of a wide variety of organisms (*see* Warren 1971). In *Acartia* this stanza may simply extend throughout development. Since feeding is probably accomplished by setal filtration, it may appear that this requires that the filter area increase relative to copepod length in order for food gathering ability to have a constant relation to the copepod's mass (e.g. *see* Egloff and Palmer 1971). However, the conditions of the experiments are that food is present in excess. Individuals at all stages are able to filter as much food as they require to saturate the available digestive and assimilative capacities. When excess food is not present, isochronal, and thus exponential, growth does not occur (Landry 1975a; Johnson 1974; Heinle 1966).

Methods

Measurements of *A. tonsa* originating from Yaquina Bay and reared in the laboratory at 21°C, 25‰ salinity, with full nutrition have been used to more precisely define the growth patterns implied above. The animals were fed a mixture of *Isochrysis galbana*, *Pseudoisochrysis* sp., and *Thalassiosira fluviatilis* at an approximate concentration of 150,000 to 200,000 cells

ml⁻¹. Lengths of nauplii were measured by camera lucida projection at 1,612 diameters. Copepodites were measured by ocular micrometer. Weights of adults, copepodites, and sixth stage nauplii were determined for a minimum of three lots of 25 to 267 individuals (depending on stage) dried at 60°C in tared foil cups after a brief rinse in distilled water on a filter. Individual animals were transferred by forceps tipped with swine eyelashes to prevent puncturing the body (M. W. Johnson personal communication). Weights were measured with a Cahn electrobalance. Animals for weighing were taken from cultures well mixed with respect to stage, so that weights of many pooled individuals will represent the mean weight of the stage.

Weights of younger nauplii were estimated by multiplying an estimate of naupliar volume by the dry weight density determined for the sixth naupliar stage. Volumes of individual nauplii were measured by approximating their shape (as shown by camera lucida projections in several orientations) with a series of prismatic disks whose volumes could be graphically determined. The volumes of the labrum and limbs were also approximated by prisms and included in the total volume estimate.

Results

Increase of length with stage in *A. tonsa* (Fig. 3) falls into three phases: naupliar instars, first through fourth copepodites, and fifth and sixth (adult) copepodites. The third phase is different from the second only in the female. In the naupliar period length increases by slightly larger increments at each molt. This increase in increment does not follow a Brooks' Rule, however. According to Brooks' Rule, first derived for stomatopods (Brooks 1886), the ratios of lengths of successive stages should be nearly constant. Let this ratio be f, and lengths of stages be designated by l_{n1} for the first nauplius, and so on. Curves based on $f = l_{n2}/l_{n1}$ and $f = l_{n3}/l_{n2}$ are shown in Fig. 3. Growth is intermediate between those rules. In the early copepo-
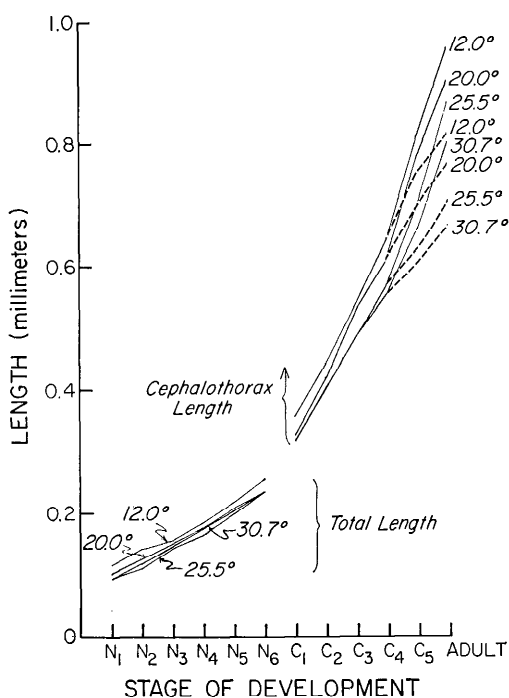

Fig. 4. Increase in length with stage in *Acartia tonsa* from Chesapeake Bay at various temperatures. Male lengths in later stages are shown by dashed lines. Data from Heinle (1969a).

dite stages (and in all stages for the male) growth is linear, length increases by the same increment at each molt. The last molts in female individuals produce larger increments. These rates of increase are less than predicted by a Brooks' Rule based on $f = l_{c2}/l_{o1}$. Figure 4, taken from table 10 of Heinle (1969a) demonstrates that *A. tonsa* from Chesapeake Bay grow in length by the same rule as those from Yaquina Bay (except that the naupliar phase seems more linear) and that the same basic rule applies to growth at a wide range of temperatures.

Naupliar volume determinations for *A. tonsa* are plotted against nauplius length in Fig. 5. The observed values fall on a straight line given by the regression equation, volume = (1.07×10^{-2}) length − (9.63×10^{-4}), where volume is in cubic millimeters and length is in millimeters. It would be expected than an object of
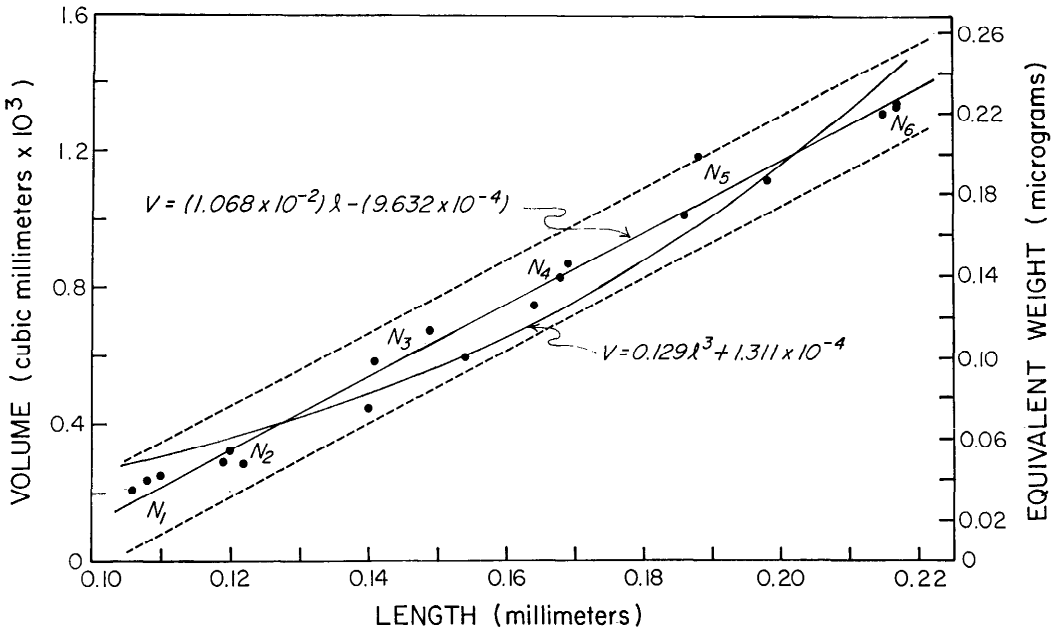
Fig. 5. Relationship between body volume and body length for nauplii of *Acartia tonsa* from Yaquina Bay. Equivalent dry weights are from known weight of sixth naupliar stage. Linear (with 95% confidence limits of predicted volume) and cubic regressions fitted by least squares.

constant shape would increase in volume by some multiple (depending on shape) of the cube of the length, not linearly with length. There is, however, no apparent change in the shape of the nauplii as they grow. The ratios (length:width) and (length:body depth) are almost constant throughout naupliar growth at 2.12 and 2.13 (standard deviations of distribution = 0.15 and 0.13). Subjectively determined variations of "roundness" and other features of shape are also constant. A cubic relationship, $V = k_1 l^3 + k_2$, was fitted by least squares, and the result is plotted in Fig. 5. At all points it falls within the 95% confidence limits for predicted volume at a given length derived from the linear regression (note: these are not the same as confidence limits for the position of the linear relationship). This implies either that the underlying relationship may well be cubic or that the differences in shape that cause deviation from the cubic are very subtle. The linear relationship was used to approximate naupliar weights.
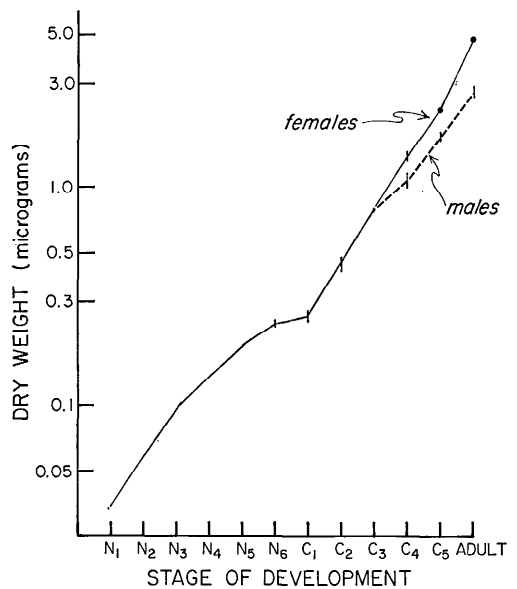

Fig. 6. Increase in dry weight with stage in *Acartia tonsa* from Yaquina Bay. Vertical bars are 95% confidence limits for mean weight of stage (dots used where limits were too narrow to show). Naupliar weights derived from volume estimates (*see Fig. 5 and text for explanation*).
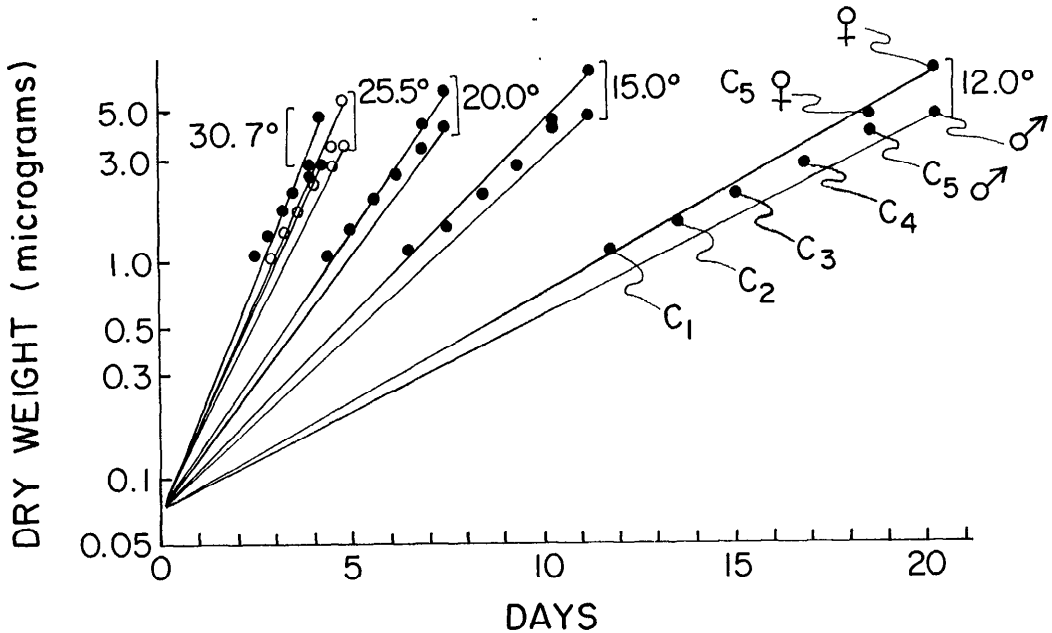
Fig. 7. Increase in weight with development time in *Acartia tonsa* from Chesapeake Bay at various temperatures on semilogarithmic scales. Stages are shown for 12°C case and are in same order at higher temperatures. Lines showing exact exponential growth are straight lines from egg weight to adult weight. Open circles are only to help distinguish 25.5°C case.

Dry weight density for the sixth nauplius was found to be 1.676×10^2 μg mm^{-3}. This was multiplied by volumes predicted by the regression of Fig. 5 for the mean length of each naupliar stage. The result is plotted together with direct weighing of older stages in Fig. 6. The growth pattern is exponential with an overall (n_1 to adult) relative rate of 0.45 μg·μg^{-1} stage^{-1} for females. However, growth slows almost to a halt during the sixth naupliar stage. Presumably most of the available food is required for the metamorphosis which occurs in preparation for the molt to the first copepodite stage, and little is available for growth. Growth rates for the copepodite stages are again exponential at a relative rate of 0.58 μg·μg^{-1} stage^{-1}. Females filled with ripe eggs weigh more (5.14 μg dry wt) than the early females shown in Fig. 6.

Figure 7 (after Heinle 1969a) shows that for the Chesapeake Bay form of *A. tonsa* the basically exponential character of

growth in mass throughout the life cycle is affected by temperature only in its rate. Figure 6 adds only detail to this earlier result. The data presented in Fig. 6 show that the younger nauplii of *A. tonsa* weigh much less than the approximately 1 μg implied by table 6 in Heinle (1966). That result was based on an incorrect application of a regression equation. This change necessitates downward revision of the estimate of production of *A. tonsa* given in that paper by a factor of 2.5 to 3 (*see also* Heinle 1969a).

Discussion

It is a well known fact of copepod biology that terminal size is inversely related to the developmental temperature (Deevey 1960; McLaren 1963, 1965; Lock and McLaren 1970). This holds for species of *Acartia* (Deevey 1960; Heinle 1966, 1969b), at least in the upper part of the temperature tolerance range. When this is combined with isochronal development at
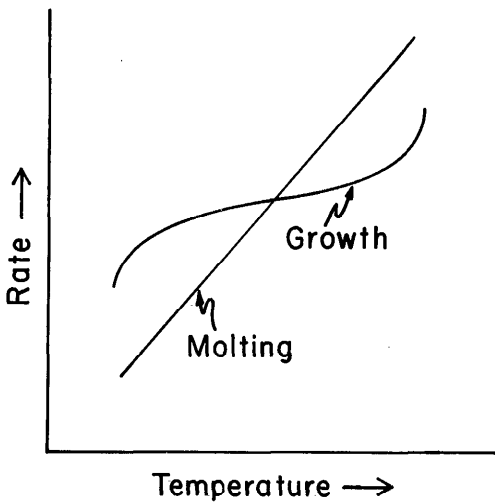
Fig. 8. Hypothetical relationship of molting and growth rates to temperature. Growth is temperature regulating over a wide temperature range. Molting is not.

any fixed temperature, it must be true that molting in *Acartia* is under control of a physiological process which is independent of size. A strictly hypothetical control mechanism can be postulated: it is as if there were a molting titer which has to build up to a threshold level to permit molting. Once this threshold is reached, molting proceeds. The rate of accumulation of the titer is dependent on temperature and on nutrition, but is independent of size per se and of stage. Either the threshold is constant and passing it is all that is required to induce all the rest of the molting cycle regardless of the animal's size, or else the required titer and the rate at which it is accumulated increase together and both in proportion to growth. In copepods in which molting intervals increase with stage, a similar titer and threshold must be present, but the rate of accumulation or the threshold must change with stage. These must remain independent of size, since size of any given stage decreases as temperature increases, just as in *Acartia*.

The physiological equivalents of the hypothetical titer and molting threshold re-main to be discovered. Carlisle and Pittman (1961) have shown that marine copepods have a neurosecretion in the forebrain whose concentration varies with the molting cycle. *Calanus* and *Euchaeta* contain an ecdysone that will induce molting in shrimp (*Leander*) and crabs (*Carcinus*) (Carlisle 1965). Therefore, it is likely that molting in copepods is under hormonal control substantially like that of other crustacea. However, nothing is known of details. In fact, details of molting control are still open to conjecture in crustaceans in general. Warner and Stevenson (1972) discuss some of the complexities.

An alternate way to express the apparent relation between molting and growth is to say that growth of both mass and linear dimensions in *Acartia* must have smaller temperature coefficients than molting (Heinle 1969*b*). This relationship is shown diagrammatically in Fig. 8. Thus, if an animal is forced through its fixed quota of molts quickly by high temperature, it simply has no chance to grow large. The maintenance of growth rate in the face of low temperature allows large size to be achieved thanks to slow molting. Lack of temperature independence in molting of *Acartia* is a major point of Landry's (1975*a*) paper. Munro's (1974) data for *C. vicinus* are convincing that either molting rate in that form is constant over a substantial temperature range or that growth rate is limited by factors other than temperature above 10°C.

One consequence of isochronal development like that of *Acartia*, as contrasted with nonisochronal development, is that a proportionately shorter part of the total development is spent in the older stages. This can be seen by comparing the growth pattern of *A. tonsa* to the mean growth pattern given by Ivanova (1973) for a variety of diaptomids and cyclopoids (and for *C. finmarchicus*) (Fig. 9). The group mean has used only 36% of the total development period by the molt to C_1, whereas *A. tonsa* has used 54%. It is possible, although there is no evidence whatever, that more of the

differentiation of cells and organs takes place in naupliar and younger copepodite stages in *A. tonsa* than is the case for other copepods.

There are several ways in which this distribution of developmental time could be selectively advantageous. If predation rates on different stages are such that the loss of reproductive value (a product of the integrated survivorship of stages older than that for which the value is calculated and the total of prospective births to older stages: Fisher 1958) from the population is concentrated in later stages, then any shortening of those stages relative to earlier ones will be promoted. This selective mechanism can work even if absolute mortality rates of nauplii are higher than those of copepodites, as has been shown to be the case for *A. tonsa* in the Patuxent River (Heinle 1966).

There is evidence that the life table for *A. tonsa* in Yaquina Bay, Oregon, is such that this mechanism could work. In the upper reaches of that bay there is a population explosion of this copepod in the summer and fall months. During this period of increase the seven consecutive generations remain discrete in time (Johnson and Miller 1974). Population modeling (in progress) has shown that the only way that this is possible is for the adults to survive and lay eggs for only a very brief period. Otherwise prolonged production of young by each generation of adults will cause many generations to be present at once, and soon all life cycle stages will be present at all times in constant proportions (stable age distribution). Thus the observed population dynamics provide evidence that older stages of *A. tonsa* are in fact suffering intense mortality and that the condition required for the proposed selective mechanism may well be met. Study of the gut contents of the dominant planktivorous fish of the bay, *Engraulis mordax mordax* Girard and *Clupea harengus pallasi* Valenciennes, has shown that *A. tonsa* and *A. clausi* are extremely important in their diet, and that they are eaten almost exclusively in the adult and
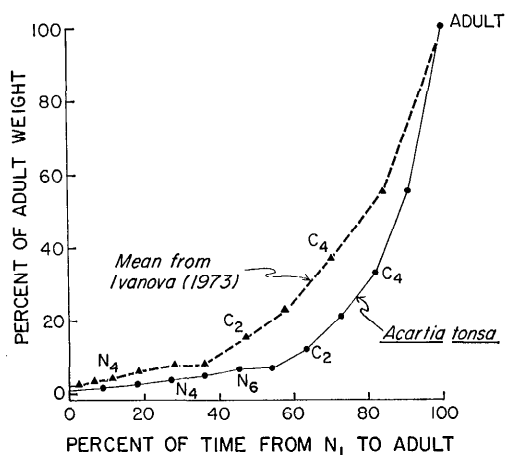

Fig. 9. Relative growth in weight of *Acartia tonsa* from Yaquina Bay compared to mean pattern derived by Ivanova (1973) for a variety of copepods (primarily from freshwater).

oldest copepodite stages (unpublished data of J. K. Johnson). We understand that a similar situation prevails for *A. clausi* in Jakle's Lagoon, the source of Landry's experimental animals (M. Landry personal communication). Thus a source of mortality that is relatively concentrated in older stages exists.

There is little evidence about the relative susceptibility to predation of copepod life cycle stages in the neritic and oceanic habitats in which copepods lacking isochronal development are found. If the selective argument above is correct, and if both modes of development are available for selection to act upon, then the finding that molting interval increases with stage for these forms suggests loss of reproductive value is concentrated in younger stages, and they must, therefore, be hurried through. A similar conclusion is suggested for the diaptomids studied by Munro (1974).

M. Mullin has suggested to us that the difference between the more neritic and the more oceanic habitats which results in the difference in development schedules could be nutritional. If nauplii are generally less efficient feeders than copepo-

dites, there will be an advantage to making the naupliar stages as small a fraction of the total development time as possible, and that advantage will be stronger in nutritionally poorer oceanic habitats.

Many of the copepod species apparently lacking isochronal development (e.g. *Calanus* and *Pseudocalanus*) pass periods of low temperature or food scarcity as late copepodites in a state of arrested growth. *Acartia clausi* and *A. tonsa* produce resting eggs to achieve the same purpose (Zillioux and Gonzalez 1972; Kasahara et al. 1974; Landry 1975*b*; J. K. Johnson unpublished data). Isochronal growth may be a feature of this alternate strategy for surviving unfavorable conditions found in species in highly variable neritic and estuarine environments. Shortening of the later life cycle stages could lead to a shorter total development time and hence to faster population increase. Thus these species of *Acartia* can increase with great rapidity when conditions are good and can leave the pelagic habitat completely when conditions are bad.

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