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Growth and development of *Calanus finmarchicus* related to the influence of temperature: Experimental results and conceptual model

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Abstract

A large number of weight values for the different stages of *Calanus finmarchicus* permits us to show that no overlapping takes place between ranges of structural weights (i.e. without storage) of successive copepodite stages at a given temperature and that structural growth is exponential at all temperatures. Nevertheless, in each instar, weights are negatively correlated with temperature. The hypothesis of critical molting weights is discussed in the framework of the elaboration of a conceptual model coupling growth and development.

To estimate the production of copepods, and more generally zooplanktonic production, we must know the common characteristics of growth and development for the individuals of the same population and the sources of their variability. Weight integrates the whole feeding history and the influences of physical parameters on physiology. The development as a whole appears as a succession of identical phases for all individuals of the same population. For crustaceans, development in each stage includes a phase of tissue differentiation followed by a growth phase (Skinner 1985), and the passage into a new stage depends on one or more signals (e.g. metabolisms, hormonal productions).

In all studies of population dynamics, the individuals of a population exhibit variability in growth and time of development, even in stable conditions (Båmstedt 1988). This phenotypic variability is expressed by standard deviations of the mean growth curve and mean development time. There are other sources of variability of weights of copepods. Numerous observations of copepods in situ have revealed strong seasonal variability of weight for adults and late instars (Comita et al. 1966; Tande 1982; Grigg et al. 1989), supposedly due to temperature or food supply, or both. In this paper, we analyze the influence of temperature on the observed weights of *Calanus finmarchicus* for each stage.

In a model coupling growth and development of small copepods, Carlotti and Sciandra (1989) suggested that molting, within a given stage, takes place at a fixed weight, called the "critical molting weight." In other words, under given temperature and food conditions, the individuals present a range of weights between the critical weights on entering and leaving this stage. Carlotti and Sciandra supposed that these critical weights could be changed by temperature and food supply, and proofs for this critical molting weight were given for small copepods by a literature review in which the range of weights for a given instar did not overlap that of the previous and the next instar. Here we test whether the above assumption is also acceptable for large copepods. As an example, we take *C. finmarchicus* because it plays an important ecological role in the marine envi-

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ronment, being the preferred prey of cod and haddock, and dominates the zooplankton in large parts of the oceans (Williams and Lindley 1980; Smith 1988). It is extensively studied, and numerous weight data of the stages are available to derive common rules of growth and development. Results of Harris (1983) and McLaren (1986) support the hypothesis of a critical molting weight for this species but only for the structural weight, thus without storage. McLaren (1986) showed that no overlap takes place between the ranges of structural weights of successive copepodite stages at 5°C and that structural growth of *C. finmarchicus* is exponential at this temperature.

To test the critical molting weight hypothesis and McLaren's exponential-growth hypothesis in a large range of temperatures, we used weights of *C. finmarchicus* from two sources. The first is a nonexhaustive review of published weights of *C. finmarchicus,* the second source is data collected by M. Krause during several cruises.

Materials and methods

Review of literature—To compare the weight values found in the literature, we distinguish three regional groups. The first group is mainly constituted of results from the NW Atlantic by McLaren (1986) and McLaren et al. (1989) with the temperature values of McLaren and Corkett (1986, figure 3). McLaren (1986, figure 1) presented ranges of body weights discounting the variable lipid storage, which is taken in reference in our study. For summer, we considered the temperature above the thermocline (*see* figure 2 of McLaren et al. 1989). We add weight values used by Davis (1987) for modeling.

The second group consists of values obtained in the North Sea. We collected values obtained from in situ sampling either in various seasons (Gauld 1951; Marshall and Orr 1956; Hirche 1983; Grigg et al. 1989) or obtained for 1 yr (Marshall and Orr 1955; Comita et al. 1966). Corner et al. (1967) presented values for body nitrogen of individuals cultivated at 10°C from egg to adult. Values given in C and N were converted to dry weight considered respectively as 50 and 10% of dry weight. From the Fladen Ground experiment FLEX'76, dry weights of *C. finmarchicus* were estimated by different investigators (Daro 1980; Franz and van Arkel 1980; Williams and Lindley 1980). Temperature was at 6°C in the homogeneous water column at the beginning of cohort development, whereas mixed-layer temperatures of 8–9°C had developed when the copepods were maturing into stage CV and adults.

The third group corresponds to values from the Norwegian coast (Tande 1982, figure 5; Båmstedt and Ervik 1984; Båmstedt 1988) and Fram Strait (Smith 1988, 1990), concerning essentially CV, males, and females.

McLaren et al. (1989) and Smith (1988, 1990) used a chemical preservation method, but corrected the dry weight estimates for an average loss of 25 and 26%, respectively. Others stored their samples by deep-freezing or weighed animals freshly sampled.

Original data—Krause's data originated from three different stations in the North Sea between 1982 and 1985 and from grouped stations in the Fram Strait region between East Greenland and Svalbard in 1984. Parts of the data from the North Sea (1983–1984) and data from Fram Strait have been published (Kattner and Krause 1987; Kattner et al. 1989). Those papers reported the lipid and wax ester contents as well as the fatty acid and alcohol composition of *C. finmarchicus* and *Calanus hyperboreus*. Stations, sampling methods, counting, storing and drying methods, and lipid analysis have also been described in detail (Kattner and Krause 1987; Kattner et al. 1989).

The unpublished data used here have been obtained following the same methods and covering a longer period, from 1982 to 1985. The data were related to temperature according to the following procedure. At all stations, we have profiles of temperature. At most stations, we obtained vertical distributions of the different stages from bottle samplers. Since there is no direct information about the amplitude of the diel vertical migration, it was extrapolated from investigations of Krause and Radach (1989). Thus, when the vertical distribution of a stage was known, we took the temperature corresponding to the depth of maximum abundance. When no clear peaks appeared (case of CV), we took the mean temperature of the water where we found individuals. When vertical distributions were unknown, either the water column was isothermal, and we used this temperature value, or the water column presented a thermo-

cline. In this latter case, the hypothesis was made, following Williams and Lindley (1980) and Krause and Radach (1989), that CI–CIV were above the thermocline (thus we used the mean temperature in the mixed layer), and CV, adult males, and females were distributed over the entire water column, in which case we used a mean value of temperature of the whole water column.

Results

Literature data—The literature review indicates that weights of naupliar stages are seldom studied. Figure 1 presents values from egg to NVI. Egg weights range from 0.25 to 0.6 μg. Runge's value (cited by McLaren et al. 1989) appears higher than the others. Only two complete sets for the entire naupliar development were found (Fransz and van Arkel 1980; Davis 1987). Corner et al. (1967) investigated groups, namely eggs, NI–NII, NIII–NIV, NV–NVI, but the numbers of determinations are very different for these groups (one measure for NIII–NIV, 14 for NI–NII). Their values appear close to those of Davis. Nevertheless, his values must be considered cautiously because they were derived from length data connected to weight by a power curve. Because their weighing was performed with great numbers of individuals, particularly for the first four stages, the weight values of Fransz and van Arkel (1980) give a complete and reliable set (*see* their tables 1 and 4). Their set clearly shows a decrease of weight after hatching.

Values in the literature for CI–CIII (Fig. 2) fall into the weight range presented by McLaren (1986). For CIV (Fig. 2) and for CV, adult females, and adult males (Fig. 3), literature values exceed the upper limit of the range of structural weight measured by McLaren (1986), but rarely the lower one. Variability in CV weight seems very important, particularly for populations living in cold waters. Thus, following McLaren (1986), weights of CI–CIII are only structural, whereas we must consider a storage compartment for CIV, CV, and adults. It is possible to discern an influence of temperature only for the values of females.

Original data—Krause's data (Fig. 4) are in good agreement with the preceding values. They showed that for a given temperature there is no overlap between weights of instars from CI to CV. Moreover, upper limits of a given

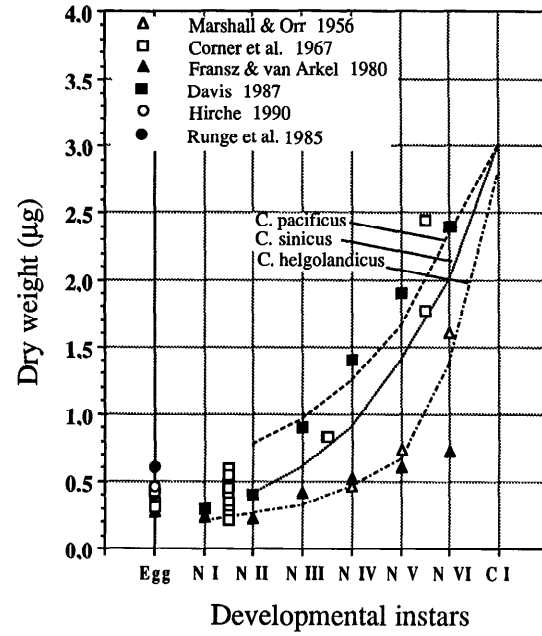

Fig. 1. Growth of *Calanus finmarchicus* from egg to NVI. Growth curves of *Calanus pacificus* (Fernandez 1979), *Calanus sinicus* (Uye 1988) and *Calanus helgolandicus* (Mullin and Brooks 1970) added for comparison.

stage coincide with the lower limits of the next instar over the whole range of temperatures. The weights in all stages have slightly negative correlations with temperature. Weight ranges of CV, adult males, and females are comparable. Some values of CV at 15°C seem higher than others, but, as described in the methods, it is possible to attribute this to individuals below the thermocline, where temperatures of ~6°C are found. Two groups of stage CV are clearly separated by the thermocline.

Synthesis of the data—All data have been grouped in a semilogarithmic graph of weight vs. relative time (Fig. 5). Relative time has been defined by Corkett et al. (1986) assuming equiproportional development. Because equiproportional development means that the duration of a given stage occupies a constant proportion of the embryonic development time across temperature, we can introduce weight vs. temperature graphs for each instar in the graph with weight vs. relative time. We have kept the ranges of structural weights presented by McLaren (1986) and plotted two straight lines against the limits of these ranges. Figure

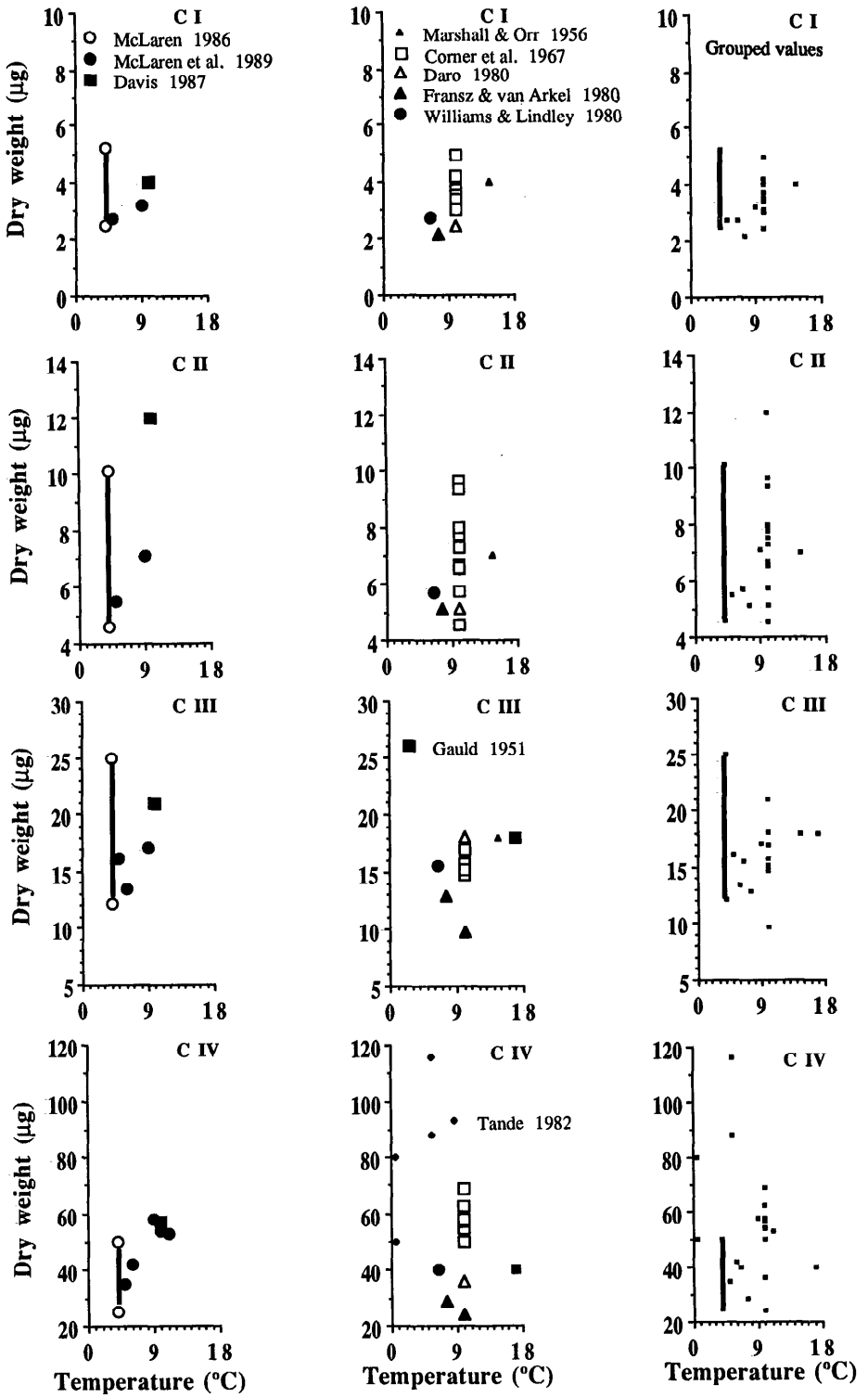

Fig. 2. Dry weights of stages CI–CIV of *Calanus finmarchicus* vs. temperature based on literature data. Straight lines correspond to the ranges of structural weights found by McLaren (1986, figure 1).

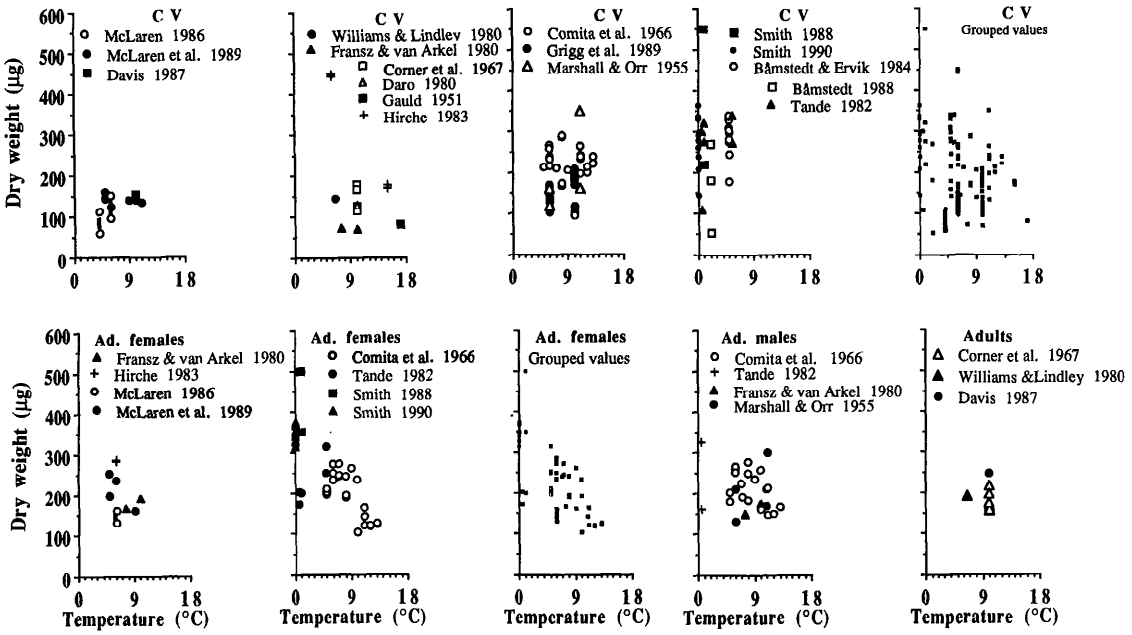

Fig. 3. As Fig. 2, but of stages CV, adult females, and adult males of *Calanus finmarchicus*.

5 shows that growth of *C. finmarchicus* is exponential, at least for its structural part. The heaviest CIII, CIV, and CV exceed the upper limits of structural weight in the proportions of 23, 120, and 200%, respectively. These proportions could be attributed to increased storage in these stages, which would correspond to 19, 54, and 66% of their dry weight.

Discussion

Growth of nauplii—As stated by McLaren et al. (1989), knowledge about growth of the naupliar stages is insufficient. It will be difficult to appreciate the ecological role of nauplii without better knowledge of their growth and development. Judging from the literature reviewed, it is likely that the values of Fransz and van Arkel (1980) for the stages from eggs to NV (their NVI value seems suspiciously low) and the values of Marshall and Orr (1956) for NIV–NVI yield the most realistic growth curve of the naupliar phase of *C. finmarchicus* (Fig. 1). The curve confirms that the weight decreases from eggs to NII due to the inability of these stages to feed (Marshall and Orr 1955) and shows the important growth rate during stage NIII to recover the loss of weight during the previous nonfeeding stages, as shown for *Calanus marshallae* (Peterson 1986).

Naupliar growth curves for other species of *Calanus* largely agree with values for *C. finmarchicus*. Among the three other species presented, *Calanus helgolandicus* is certainly the species closest to *C. finmarchicus* (Bradford 1988).

Growth of copepodites—The comparison between the data and the range of structural weight obtained by McLaren (1986) suggests that the whole weight is essentially structural for the first three copepodite stages, and storage represents a large part of weight in CIV and CV and in adults. Heavier CVs exceed the upper limit of structural weight found by McLaren (1986) by 200%. In other words, stores should correspond to 66% of dry weight. This value is in very good agreement with results of Håkanson (1984, figure 1) on the lipid contents of copepodite stages of *Calanus pacificus*. Figure 2 also clearly shows that the highest variability in CV weights occurs in the data obtained from Fram Strait and the Norwegian coast—the coldest waters. Part of this variability of weights in CV is due to overwintering observed for the population at very high latitudes. The animals stay in deep water in winter and metamorphose into adults in spring (Båmstedt and Tande 1988). Tande (1982) showed a decrease in dry weight (300–

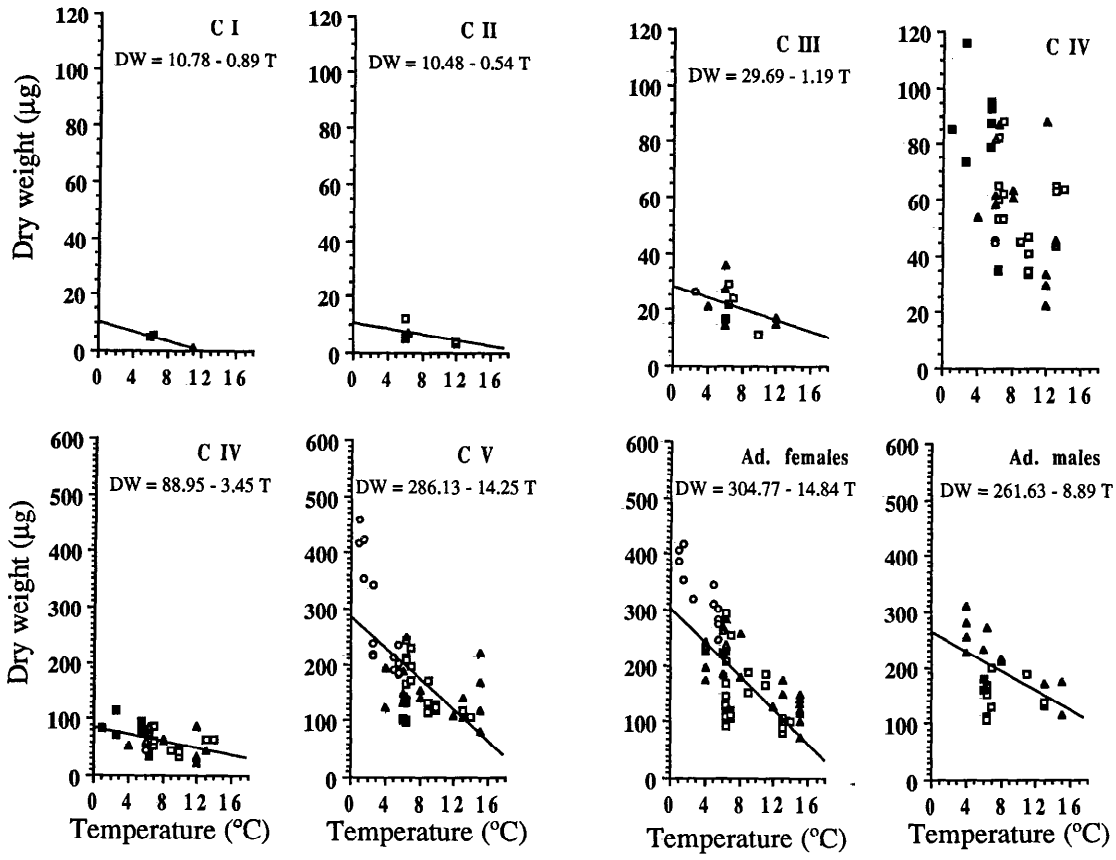

Fig. 4. Dry weights of the copepodites and adults of *Calanus finmarchicus* vs. temperature from three stations in the North Sea (▲, □, ■) and from Fram Strait (○). For each stage, the equation of the least-square regression is given.

108 µg) in CV from December to March, coupled to a change in chemical composition and the onset of sexual differentiation in stage CV. Thus, we can suppose utilization of stores inducing a decrease of ~64% of dry weight. Such a value falls into the range of lipid content of *C. hyperboreus* (Conover 1962). The fat reserves of stage CV go directly into egg formation by adult females (Båmstedt and Tande 1988), and the grazing of females permits continuity of spawning (Kattner et al. 1989).

Krause's values (Fig. 4) show no overlap between the weight ranges of consecutive instars from CI to CV at a given temperature. These values are adequate to validate the hypothesis of critical molting weights because for both the North Sea and Fram Strait the lipid content of individuals was low in all stages, as can be seen in table 2 of Kattner and Krause (1987), and in table 2 of Kattner et al. (1989). Thus, molting from one instar to the following instar occurs at a fixed critical structural weight, which depends on temperature. The values also show that the correlation of temperature with body weight is negative. Such a correlation has been shown by Corkett and McLaren (1978, figure 27) for *Pseudocalanus*. Moreover, they showed that the percentage of reduction in length per °C increased with stage. If we graph the slopes of the regressions of dry weight vs. temperature ($W = a - bT$) obtained in Fig. 4 for consecutive stages, we also obtain such an increase with stage (Fig. 6A). It is more convenient to normalize each regression coefficient with the origin of the regression (Fig. 6B). The variance of slope (b) and origin of regression (a) could be calculated from residual variance in the regression and from these estimates the variance of $b : a$ (relative slope) has been calculated. The standard deviation is indicated in Fig. 6B. A

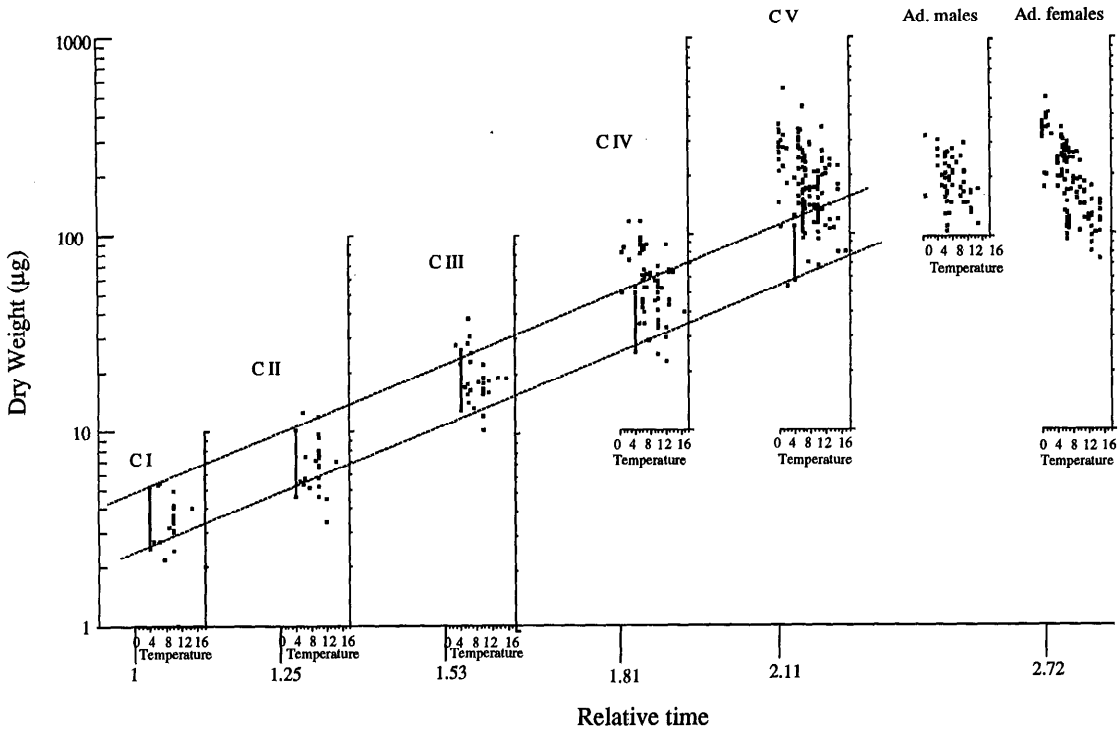

Fig. 5. Synthesis of the data of Figs. 2, 3, and 4 in a semilogarithmic graph: weights vs. relative time as defined by Corkett et al. (1986).

Bartlett test (Sokal and Rohlf 1981) has shown that variances of $b : a$ for the different copepod stages are not significantly heterogeneous ($P = 0.05$). The relative slopes of CIII, CIV, and adult males are not significantly different ($P = 0.05$), but they are different from CV and adult females which are themselves not significantly different. It is suggested that the relative slope for CI is different from others; however, the data are too few to take the statistical result as a strong hypothesis. For the same reason the value of the relative slope for CII cannot be considered.

McLaren (1986) suspected that adequate tests of the exponential-growth hypothesis barely exist, but the grouped data of Fig. 5 allow such a test. A short literature review concerning growth of other *Calanus* species confirms the hypotheses of exponential growth and of critical molting weights. For *C. marshallae,* Peterson (1986, figure 7) showed exponential growth and no overlap between ranges of stage weights from NIV to CIII, but overlap between CIII–CIV and CIV–CV. Frost (1980) suggested exponential growth for *C. pacificus,* and results of Vidal (1980) do not present overlap between ranges of copepodite weights. It is probably more difficult to prove exponential growth phases for species with multiyear cycles, because growth stops for long periods. Nevertheless, weight ranges of *Calanus glacialis* shown by Slagstad and Tande (1990, figure 4) do not exhibit overlap, and growth seems exponential from CI to CIV in the period from spring to summer. Similar relations may be hidden by the high variability in the data of Bottrell and Robins (1984) for *C. helgolandicus.* Nevertheless McLaren (1986), using their data, found agreement with the exponential-growth hypothesis.

A good way to test these hypotheses experimentally would be the use of *Calanus* species that have little lipid storage. For instance, *Calanus sinicus* (Uye 1988) has exponential growth, and ranges of weights do not overlap between successive stages. Moreover, mean body lengths in each stage are negatively correlated with temperature.

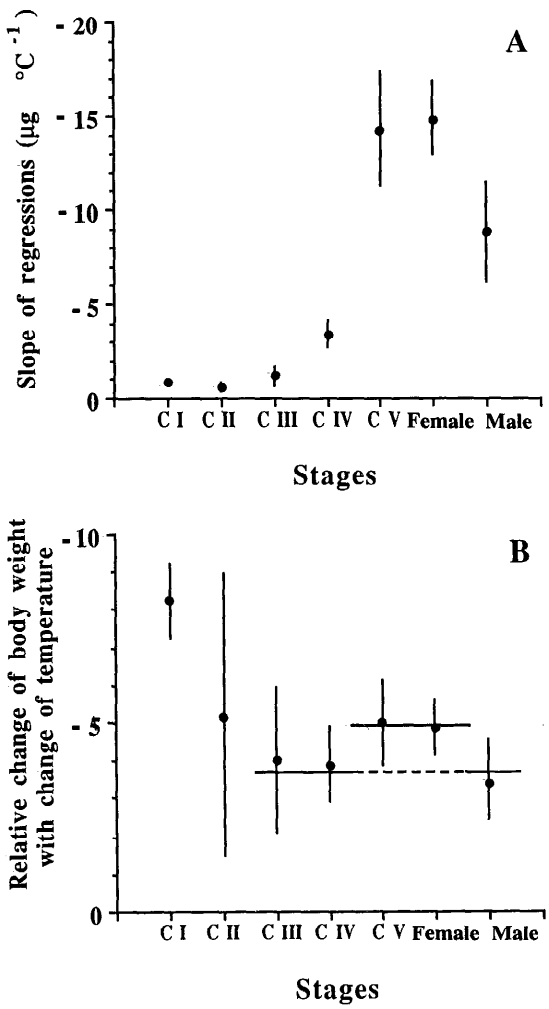

Fig. 6. A. Comparison of the effect of temperature on dry weight of copepodites and adult stages, using the slope of the regressions (*b*) from Fig. 4. Vertical lines—standard deviation. B. Effect of temperature on the weight-specific ratio (*b* : *a*). Vertical lines—standard deviation. Horizontal lines join means that are not significantly different (*see text*).

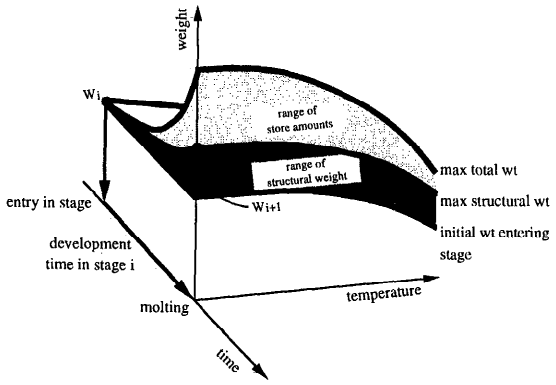

Fig. 7. Suggested time scales of structural and storage components during the molt cycle in an instar for different temperature conditions.

Conceptual model of growth within each stage—To summarize the results of our data analysis, we suggest the following conceptual model (Fig. 7). A copepod enters in stage *i* with a structural weight W_i. Then the structural body weight grows (exponentially if the external conditions are good) until a maximum structural weight is reached, which is the critical structural weight for the next stage W_{i+1}. Thus, development is linked to structural growth, and the time of development in stage *i* depends on the growth rate between structural weights W_i and W_{i+1}. These critical weights are lower for high temperatures than for low temperatures, and the observed weights in a stage appear to be negatively correlated with temperature. The observed total body weight is the sum of the structural weight and the lipid content. From the physiological point of view, it is sufficient to consider the structural weight in the molting process because hormones of molting (ecdysone) act on young tissues with cells having a high potential of multiplication (Skinner 1985). Afterward, these cells will have a phase of differentiation and will grow during the molting cycle.

McLaren (1986, p. 1345) said that "it is unlikely that weight variations in nature can be understood without identification of cohorts, recognition of resting stages, and separation of the lipid 'store' from other components." To test the model suggested from this analysis, it would be interesting to repeat his experimental work for different temperatures, distinguishing between structural weight and lipid stores, to see if the time scales of development of these compartments during the course of the individual molt cycle are consistent with our conceptual model.

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