

Physioecology of Zooplankton. II. Effects of Phytoplankton Concentration, Temperature, and Body Size on the Development and Molting Rates of *Calanus pacificus* and *Pseudocalanus* sp.*

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Abstract

Development time and stage duration for *Calanus pacificus* Brodsky and *Pseudocalanus* sp. and the rate of loss of body carbon by molting for *C. pacificus* were estimated for copepodite stages cultured under various combinations of phytoplankton concentration and temperature. Mean development time and stage duration for *C. pacificus* decreased hyperbolically with increasing food concentration, and the minimum time required for reaching a given stage decreased logarithmically with a logarithmic increase in temperature. Low temperature retarded the development of early stages proportionally more than that of late stages, and stage duration increased logarithmically with increasing body weight. Therefore, copepodite development was not isochronal. The rate of loss of body carbon by molting was small, ranging from 0.2 to 2% day⁻¹. This rate increased hyperbolically with food concentration and was linearly related to the growth rate. The critical food concentration for the rates of development and molting increased with temperature and stage of development, but these rates were less dependent on food concentration than the growth rate. The development rate of *Pseudocalanus* sp. was higher than that of *C. pacificus*, and was less influenced by changes in food concentration and temperature. It is postulated that the inverse relationship between temperature and body size results from a differential effect of temperature and body size on the rates of growth and development. That is, with increasing body size the growth rate tends to become temperature-independent, but the development rate remains proportional to temperature. Thus, copepodites growing at low temperature can experience a greater weight increment between molting periods than individuals growing at high tem-

perature, because the growth rate is similar at all temperatures but stage duration is longer at low temperature.

Introduction

Temporal and spatial fluctuations in composition and abundance of zooplankton populations must result from changes in distribution and in rates of recruitment, growth, development, and mortality of various species, induced by changes in biotic and abiotic environmental factors. Information on the effects of environmental factors on rates of various biological and physiological processes can, therefore, contribute to the understanding of population fluctuations by providing clues on whether certain species may succeed under given environmental conditions. For example, body-size-related growth patterns of planktonic herbivores in relation to changes in phytoplankton concentration and temperature suggest that medium- to large-sized copepods, because of the increase in the food concentration required for maximum growth with increasing body size and temperature, are likely to be excluded from warm waters with limited food supply (Vidal, 1980a).

Information on the effects of food concentration, temperature, and body size on development rates of zooplankton is also required in studies of population dynamics. The influence of temperature on embryonic development of planktonic copepods is well understood (e.g. McLaren, 1966; McLaren *et al.*, 1969; Corkett and McLaren, 1970; Corkett, 1972; Landry, 1975a), but for postembryonic stages, the nauplii and copepodites, the information available is mostly qualitative. On the basis of studies on species of *Acartia* and *Pseudocalanus*, it was postulated that under optimal food conditions the duration of all life stages is similar (referred to as isochronal development by Miller *et al.*, 1977), and that with changes in temperature, stage duration varies in a

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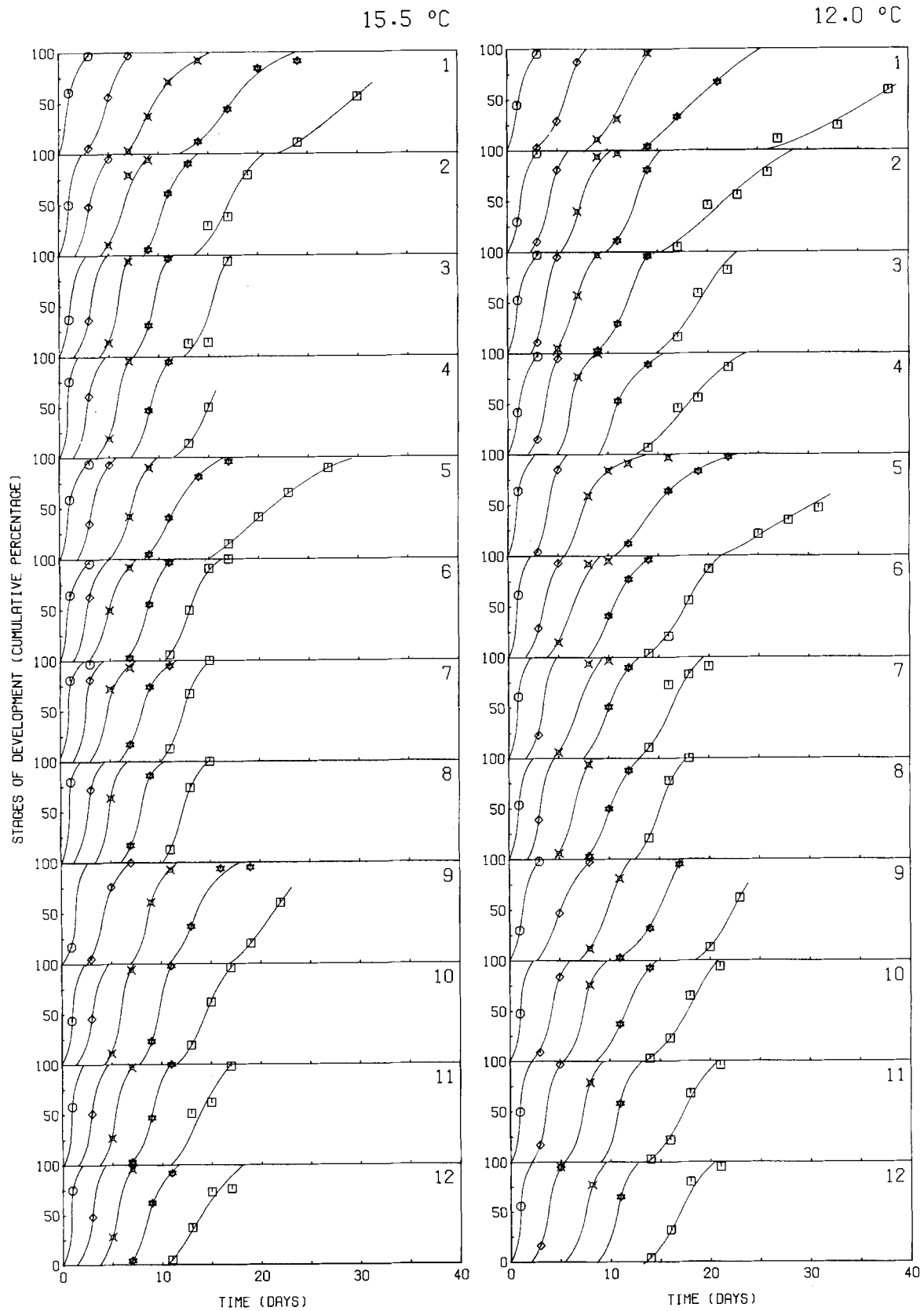


Fig. 1. *Calanus pacificus*. Development sequence for Stages CII (circles), CIII (diamonds), CIV (crosses), CV (stars), and CVI (squares) cultured at 12 food concentrations (1 = 0.67 ppm, 2 = 2.28 ppm, 3 = 4.70 ppm, 4 = 9.39 ppm, 5 = 0.99 ppm, 6 = 3.36 ppm, 7 = 6.93 ppm, 8 = 13.85 ppm, 9 = 1.16 ppm, 10 = 4.15 ppm, 11 = 8.63 ppm, and 12 = 17.18 ppm) and 3 temperatures. Time zero = start of experiments, when copepod populations consisted exclusively of Stage CI. Curves were hand-fit to data

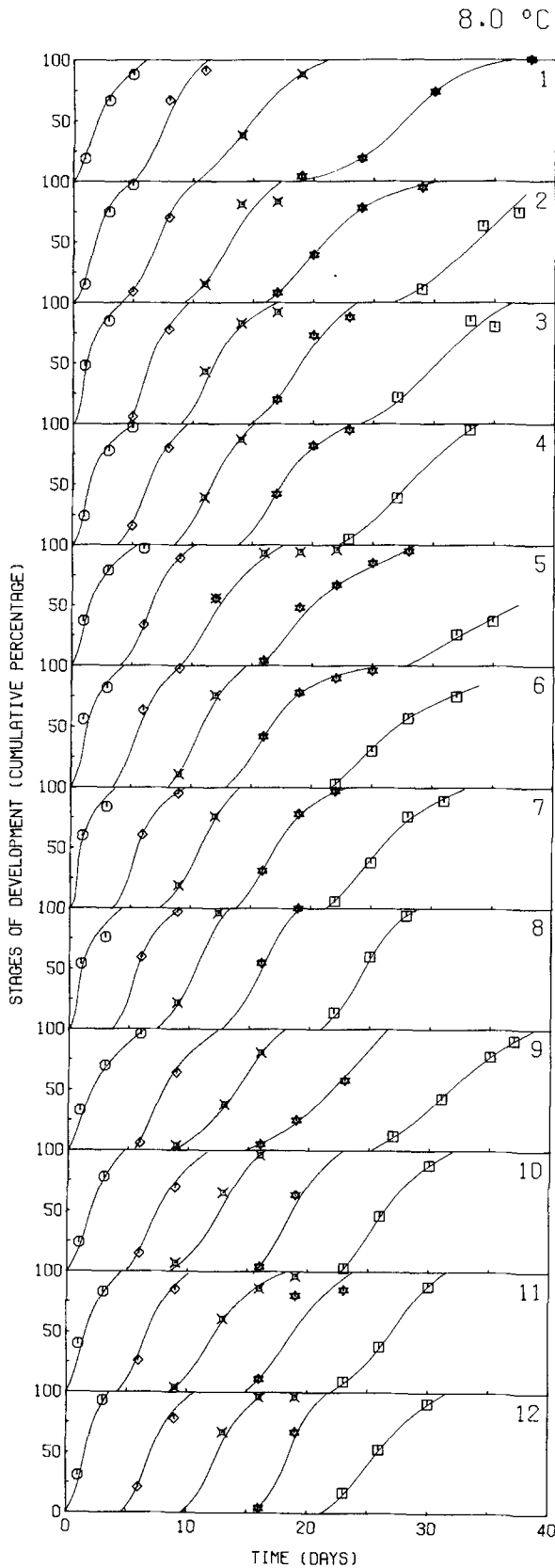


Fig. 1. (continued)

constant proportion to that of the egg stage (e. g. Corkett and McLaren, 1970; Landry, 1975b, Corkett and McLaren, 1978). That is, within species the development rate is independent of body size and of interactions between temperature and body size. Therefore, the development time of any stage at any temperature could be estimated from data on postembryonic development at a single temperature and egg development throughout a range of temperatures. Isochronal development was not confirmed in other studies with marine planktonic copepods cultured under controlled conditions (e. g. Mullin and Brooks, 1967, 1970; Heinle and Flemer, 1975), but the data collected on development were perhaps less precise than those of the studies cited above. However, in more detailed studies on freshwater copepods, the duration of postembryonic stages again did not remain constant (e. g. Geiling and Campell, 1972; Ivanova, 1973; Munro, 1974).

Information on the effect of phytoplankton concentration on development rates of marine copepods is less precise than that on the effect of temperature. Low food concentration retarded markedly the development of several species in culture (e.g. Mullin and Brooks, 1970; Paffenhöfer, 1970; Harris and Paffenhöfer, 1976; Landry, 1976; Paffenhöfer and Harris, 1976); but the exact nature of the relationship between development rate and food concentration was not established. Development rates in natural populations of copepods, on the other hand, have been assumed to be independent of food supply (McLaren, 1978).

The rate of loss of body carbon by shedding of molts during ecdysis (referred to here as molting) is one of the least studied physiological processes in planktonic crustaceans; often, it is assumed to be unimportant and therefore is neglected. Although data on this rate are needed in studies of production and in energy budgets for zooplankton, they have been obtained for only one species of marine planktonic copepod (Mullin and Brooks, 1967).

The present study is part of a continuing effort to establish general body size-related patterns of change in rates of physiological processes of planktonic copepods with changes in phytoplankton concentration and temperature (Vidal 1980, a,b,c). Its purpose was to assess the effects of these factors on the development rate of the marine planktonic copepods *Calanus pacificus* Brodsky and *Pseudocalanus* sp. (a species resembling *P. minutus*; B. W. Frost, personal communication) and on the rate of loss of body carbon by molting in *C. pacificus*. Changes in development and molting rates were investigated for a broad range of experimental conditions, and the relationship between these rates and the factors under study was formulated with emphasis on their dependence on food concentration and body size.

Materials and Methods

Culture techniques, experimental conditions, and procedures for determining stage composition and dry

weight of copepodite stages of *Calanus pacificus* Brodsky and *Pseudocalanus* sp. cultured under various concentrations of single species of diatoms at 3 temperatures (15.5 °C, 12 °C, and 8 °C) have been described earlier (Vidal, 1980a). Mean development times and intermolt periods for copepodite stages of *C. pacificus* were estimated from data on stage composition. Mean development time for Stages CIII to CVI is defined as the time required for development from mean Stage CII (the time at which 50% of each copepod population had reached Stage CII) to mean stage of a later copepodite (the time at which 50% of each population had reached the later stage). Intermolt period between two successive copepodites, or stage duration, is defined as the difference between mean development times of two successive stages. Mean development times were estimated from curves of cumulative percentages of Stages CII to CVI. Intermolt periods for copepodites of *C. pacificus* cultured at various food concentrations were estimated from equations describing the relationship between mean development time for various stages and food concentrations.

Because fewer observations were available for *Pseudocalanus* sp. than for *Calanus pacificus*, development rates for *Pseudocalanus* sp. were estimated from graphs of cumulative percentages for Stages CIV to CVI.

Rates of loss of body carbon by molting in copepodites of *Calanus pacificus* were obtained from measurements of mean carbon content in the exuviae of various stages and from estimates of intermolt periods. In some experiments, exuviae were collected periodically and frozen for subsequent carbon analysis. Intact exoskeletons were sorted by stage of development, rinsed with distilled water, and placed in silver containers for carbon determination with a Carlo Erba Elemental Analyzer (Model 1100). The percentage of body carbon lost with each molt was estimated as the ratio of the carbon content in the exoskeletons to the mean body carbon of the preceding development stage (x100), and the rate of loss of body carbon by molting (as % body carbon per day) was obtained by dividing the percentage of body carbon loss with each molt by the respective intermolt period.

Results

Development Rate of *Calanus pacificus*

The developmental sequence from Stages CII to CVI of *Calanus pacificus* in 36 experiments is shown in Fig. 1. At the start of the experiments (Time zero in Fig. 1), each copepod population consisted exclusively of Stage CI. Observations at later times indicate the proportion of each population that had reached or passed a particular stage of development. For example, Graph 1 for 15.5 °C shows that after three days, 97% of the population had reached or passed Stage CII (circles in Fig. 1) and 6% had reached Stage CIII (diamonds in Fig. 1), i.e., this population consisted of 3% CI, 91% CII, and 6% CIII.

The curves in Fig. 1 were hand-fit to the data. S-shaped curves were preferred to straight lines for these fits, because when sufficient observations were available they suggested a sigmoid relationship between the cumulative percentage of each development stage and the age of the copepods ("Time" in Fig. 1). These curves were used for estimating mean development times for Stages CIII to CVI (in relation to mean Stage CII) under various experimental conditions.

The relationship between mean development time and food concentration for copepodites of *Calanus pacificus* (Fig. 2) was described with the reciprocal of a hyperbolic function,

$$D = D_{\min} (1 - e^{-\epsilon P})^{-1}, \quad (1)$$

where D is the mean development time for a given copepodite (in relation to mean Stage CII), D_{\min} is the minimum time required to reach that stage (from mean Stage CII), ϵ is an exponent specifying the slope of the curve, and P is the food concentration (in ppm). The parameters of Eq. (1) for various temperatures and stages of development, and the food concentration at which 90% of D_{\min} was attained (critical food concentration for development, P_c) are given in Table 1. Mean development times for copepodite stages of *C. pacificus* decreased asymptotically to a minimum value (D_{\min} , attained at maximum development rate) with increasing food concentration (Fig. 2). The critical food concentration for development increased with increasing temperature and stage of development (Table 1).

D_{\min} decreased logarithmically with a logarithmic increase in temperature. This relation was described with the equation

$$\log D_{\min} = \log a - b \log T. \quad (2)$$

As shown in Table 2, the slope of the equations decreased with increasing stage of development, which implies that low temperature retarded the development rate of younger stages proportionally more than that of older ones.

The effects of food concentration, temperature, and stage of development (and therefore body size) on the development rate of *Calanus pacificus* were consistent with the effects of these factors on the growth rate of this species (Vidal, 1980a), and interactions among the critical food concentration, temperature, and stage of development (and therefore body size) had similar effects on both rates. However, the critical food concentration for development of all stages was consistently and considerably lower than the critical food concentration for growth (Vidal, 1980a), which implies that the development rate was less affected by changes in food concentration than the growth rate.

Intermolt periods for successive copepodite stages (or stage duration) of *Calanus pacificus*, computed with Eq. (1) (Table 1) for various food concentrations and temperatures, are given in Table 3. Stage duration decreased hyperbolically with increasing food concentra-

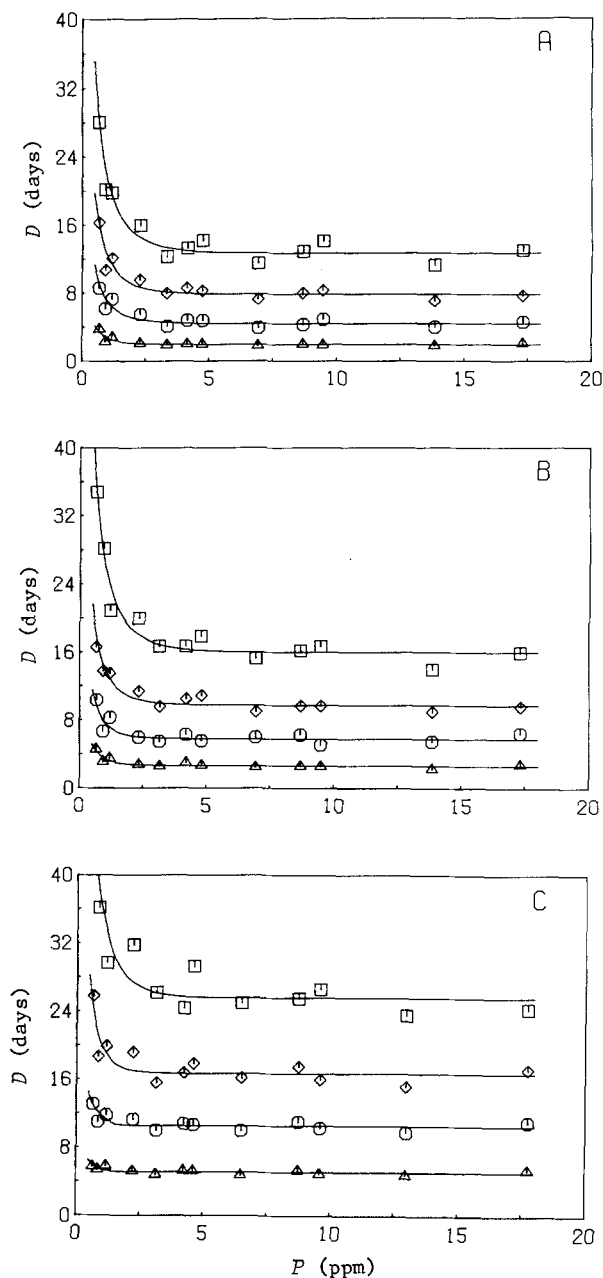


Fig. 2. *Calanus pacificus*. Relationship between mean development time (D) and food concentration (P) for Stages CIII (triangles), CIV (circles), CV (diamonds), and CVI (squares) cultured at 15.5 °C (A), 12 °C (B), and 8 °C (C). Development times are given in relation to that of mean Stage CII (i.e., Development Time zero = time at which 50% of each population had reached Stage CII). Curves were fit using Eq. (1); parameters of equations are in Table 1

tion, and was inversely related to experimental temperature (Table 3). Stage duration also increased with stage of development (and therefore with body size), and for copepods cultured at high food concentrations (> 5 ppm) the intermolt period increased logarithmically with a linear increase in mean body weight of successive copepodite stages (Table 3). Such a relationship was described with the equation

Table 1. *Calanus pacificus*. Parameters of Eq. (1) for Stages CII to CVI cultured at various food concentrations and 3 temperatures. P_c = critical food concentration for development

Temperature and stage	D_{min} (days)	e	P_c (ppm)
15.5 °C			
CIII	1.93	1.253	1.84
CIV	4.40	0.984	2.34
CV	7.86	1.012	2.28
CVI	12.68	0.895	2.57
12.0 °C			
CIII	2.63	1.428	1.61
CIV	5.81	1.407	1.64
CV	9.75	1.196	1.93
CVI	16.00	0.942	2.44
8.0 °C			
CIII	5.11	3.062	0.75
CIV	10.54	2.612	0.88
CV	16.70	1.796	1.28
CVI	25.62	1.246	1.85

Table 2. *Calanus pacificus*. Intercepts (a) and slopes (b) of Eq. (2), and correlation coefficients (r), for copepodite stages cultured at food concentrations higher than the critical concentration for development and at 3 temperatures

Stage	$\log a$	b	r
CIII	2.044	-1.487	0.994
CIV	2.221	-1.334	0.994
CV	2.259	-1.157	0.987
CVI	2.373	-1.073	0.996

$$\log IMP = a + b W, \tag{3}$$

where IMP is the intermolt period or stage duration (in days) and W is the mean dry weight of two successive copepodite stages in μg . Values for the coefficients a and b for the three temperatures are given in Table 4. The increase in the slopes (b) of these relations with increasing temperature shows that the body-size dependence of the maximum developmental rate of *C. pacificus* (under optimal food conditions), like that of the maximum growth rate (Vidal, 1980a), was more pronounced at high than at low temperatures. Therefore, the maximum developmental rate of younger stages, as noted above, was more sensitive to changes in temperature than that of later stages.

Development Rate of *Pseudocalanus* sp.

The development sequence from Stages CIV to CVI of *Pseudocalanus* sp. in 12 experiments is shown in Fig. 3. These experiments started with Stage CII, and the copepods were cultured at only four different food concentrations; consequently, fewer samples were collected throughout the development of this species, and only general trends can be noted from Fig. 3. S-shaped curves were fit to these data for the reasons given above for *Calanus pacificus*.

Table 3. *Calanus pacificus*. Intermolt periods (*IMP*), in days, estimated from Fig. 2 using Eq. (1); rate of loss of body carbon by molting (*MT*) as % per day; mean dry body weight (*W*) in μg ; and weight-specific growth rate (*G*), computed using Eq. (19) of Vidal (1980a); data are for Stages CII-CIII, CIII-CIV, CIV-CV, and CV-CVI cultured at various food concentrations (*P*), in ppm, and at 3 temperatures

Temperature														
15.5 °C					12.0 °C					8.0 °C				
<i>P</i>	<i>IMP</i>	<i>MT</i>	<i>W</i>	<i>G</i>	<i>P</i>	<i>IMP</i>	<i>MT</i>	<i>W</i>	<i>G</i>	<i>P</i>	<i>IMP</i>	<i>MT</i>	<i>W</i>	<i>G</i>
CII-CIII														
0.68	3.37	1.13	11.2	14.7	0.66	4.30	0.88	12.7	12.7	0.66	5.89	0.65	13.1	11.4
0.93	2.81	1.35	12.2	20.4	0.93	3.57	1.06	13.2	18.2	0.86	5.50	0.69	15.0	13.7
1.18	2.49	1.53	12.6	24.9	1.19	3.21	1.18	13.0	20.2	1.19	5.25	0.72	14.1	16.3
2.30	2.05	1.85	15.5	33.7	2.33	2.73	1.39	15.5	28.7	2.24	5.11	0.74	14.6	18.3
3.36	1.96	1.94	16.4	36.8	3.15	2.66	1.43	13.3	31.0	3.15	5.11	0.74	14.9	18.5
4.15	1.94	1.96	16.3	37.9	4.18	2.63	1.44	14.8	31.3	4.23	5.11	0.74	14.2	18.5
4.75	1.94	1.96	17.5	37.8	4.80	2.63	1.44	16.8	31.0	4.61	5.11	0.74	14.1	18.5
6.93	1.93	1.97	17.0	38.5	6.93	2.63	1.44	15.9	31.4	6.49	5.11	0.74	15.6	18.5
8.69	1.93	1.97	16.0	38.9	8.69	2.63	1.44	17.6	31.4	8.74	5.11	0.74	14.6	18.5
9.48	1.93	1.97	16.3	38.8	9.48	2.63	1.44	19.1	30.7	9.59	5.11	0.74	15.7	18.5
13.85	1.93	1.97	16.0	38.9	13.85	2.63	1.44	15.9	31.4	12.97	5.11	0.74	15.6	18.5
17.31	1.93	1.97	16.6	38.7	17.31	2.63	1.44	15.1	31.5	17.44	5.11	0.74	13.9	18.6
CIII-CIV														
0.68	5.64	0.67	22.3	9.8	0.66	5.31	0.72	25.8	8.5	0.66	6.94	0.55	34.2	7.7
0.93	4.52	0.84	25.6	13.7	0.93	4.39	0.87	26.9	13.0	0.86	6.28	0.61	32.1	10.6
1.18	3.88	0.98	27.5	17.1	1.19	3.94	0.96	28.0	16.1	1.19	5.78	0.66	36.9	12.9
2.30	2.86	1.33	35.0	24.8	2.33	3.31	1.15	34.3	22.8	2.24	5.46	0.70	34.3	16.6
3.36	2.60	1.46	39.9	27.6	3.15	3.22	1.18	36.7	24.8	3.15	5.43	0.70	32.5	17.3
4.15	2.53	1.50	40.0	29.4	4.18	3.20	1.19	39.5	25.8	4.23	5.43	0.70	41.1	16.9
4.75	2.50	1.52	39.1	30.6	4.80	3.19	1.19	39.8	26.3	4.61	5.43	0.70	32.7	17.4
6.93	2.47	1.54	40.6	31.6	6.93	3.18	1.19	44.7	26.1	6.49	5.43	0.70	36.5	17.2
8.68	2.47	1.54	39.2	32.2	8.69	3.18	1.19	42.3	26.6	8.74	5.43	0.70	35.4	17.3
9.48	2.47	1.54	41.3	31.7	9.48	3.18	1.19	52.3	25.0	9.59	5.43	0.70	33.9	17.4
13.85	2.47	1.54	43.4	31.3	13.85	3.18	1.19	45.5	26.1	12.97	5.43	0.70	39.2	17.1
17.31	2.47	1.54	41.6	31.8	17.31	3.18	1.19	41.0	26.9	17.44	5.43	0.70	38.8	17.1
CIV-CV														
0.68	6.80	0.56	39.0	5.7	0.66	8.24	0.46	48.4	4.6	0.66	11.22	0.34	60.3	5.1
0.93	5.57	0.68	44.5	8.5	0.93	6.56	0.58	45.6	8.8	0.86	9.45	0.40	56.8	7.8
1.18	4.87	0.78	51.5	10.1	1.19	5.69	0.67	62.8	8.8	1.19	7.90	0.48	92.7	7.6
2.30	3.81	1.00	69.0	14.9	2.33	4.35	0.87	75.8	13.9	2.24	6.43	0.59	70.5	13.6
3.36	3.58	1.06	76.9	17.4	3.15	4.10	0.93	80.8	15.9	3.15	6.22	0.61	72.9	14.6
4.15	3.51	1.08	85.2	17.7	4.18	3.98	0.95	93.4	16.1	4.23	6.17	0.62	110.8	13.0
4.75	3.49	1.09	74.4	21.1	4.80	3.96	0.96	93.3	17.0	4.61	6.16	0.62	70.9	15.2
6.93	3.47	1.10	88.2	20.5	6.93	3.94	0.96	97.4	18.1	6.49	6.16	0.62	83.5	14.7
8.69	3.46	1.10	88.2	21.3	8.69	3.94	0.96	105.9	17.5	8.74	6.16	0.62	109.9	13.4
9.48	3.46	1.10	95.3	20.2	9.48	3.94	0.96	106.7	17.6	9.59	6.16	0.62	76.4	15.1
13.85	3.46	1.10	98.8	20.1	13.85	3.94	0.96	103.4	18.3	12.97	6.16	0.62	95.6	14.1
17.31	3.46	1.10	99.5	20.1	17.31	3.94	0.96	104.4	18.2	17.44	6.16	0.62	109.0	13.5
CV-CVI														
0.68	12.00	0.32	62.1	2.3	0.66	16.98	0.22	77.0	1.9	0.66	21.65	0.18	84.9	3.3
0.93	9.54	0.40	70.4	4.2	0.93	12.90	0.29	72.5	5.0	0.86	17.73	0.21	93.0	4.9
1.18	8.11	0.47	93.6	3.6	1.19	10.90	0.35	123.9	2.5	1.19	14.21	0.27	179.1	2.5
2.30	5.81	0.65	114.7	7.0	2.33	7.61	0.50	130.1	6.9	2.24	10.29	0.37	126.4	9.7
3.36	5.20	0.73	124.1	9.1	3.15	6.89	0.55	133.6	8.9	3.15	9.37	0.41	133.2	11.0
4.15	5.01	0.76	147.4	7.9	4.18	6.50	0.58	167.0	7.6	4.23	9.04	0.42	223.9	7.8
4.75	4.93	0.77	130.4	11.1	4.80	6.39	0.59	156.8	9.4	4.61	9.00	0.42	124.7	12.4
6.93	4.83	0.79	151.9	10.7	6.93	6.27	0.61	160.5	11.0	6.49	8.92	0.43	148.2	11.7
8.69	4.82	0.79	159.9	10.9	8.69	6.26	0.61	196.6	8.9	8.74	8.92	0.43	227.2	9.0
9.48	4.82	0.79	167.2	10.4	9.48	6.25	0.61	186.6	9.9	9.59	8.91	0.43	152.5	11.6
13.85	4.82	0.79	174.6	10.6	13.85	6.25	0.61	182.0	11.0	12.97	8.91	0.43	181.6	10.9
17.31	4.82	0.79	179.3	10.5	17.31	6.25	0.61	203.8	9.7	17.44	8.91	0.43	230.4	9.0

The time required for development from Stages CII to CVI of *Pseudocalanus* sp. was inversely proportional to food concentration at 15.5 ° and 12 °C and independent of this factor at 8 °C. At the highest food concentrations (Graphs 3 and 4 in Fig. 3) the development rate was inversely related to temperature, but at the lowest food levels (Graphs 1 and 2 in Fig. 3), the rate was similar at all temperatures, and even slightly higher at 8 °C than at 12 ° or 15 °C. Since fewer observations on stage composition were available for copepods cultured with low food concentrations at 8 °C than at higher temperatures, it is not clear whether the trends noted above for the development of *Pseudocalanus* sp. at 8 °C are real or simply reflect analysis of limited data. However, since the critical food concentration for growth of this species was extremely low at 8 °C (Vidal, 1980a), it is possible that even at the lowest food concentration tested here (0.3 ppm) the development of

Pseudocalanus sp. may have proceeded at near maximum rates for this temperature.

The development rate of *Pseudocalanus* sp. was higher than that of *Calanus pacificus*, and the difference in rate between the two species was greater at the lowest temperature. For example, the time required for *C. pacificus* to develop from 100% CII to 50% CVI at food concentrations above the critical value was about 12, 14, and 23 days at temperatures of 15.5°, 12°, and 8 °C respectively, whereas *Pseudocalanus* sp. cultured at the same temperatures and at a food concentration of 3.5 ppm developed from 100% CII (Time zero in Fig. 3) to 50% CVI in 8, 9, and 12 days, respectively. This also shows that the development rate of *Pseudocalanus* sp., like the growth rate of this species (Vidal 1980a), is less dependent on temperature in *Pseudocalanus* sp. than in *C. pacificus*.

Table 4. *Calanus pacificus*. Intercepts (*a*) and slopes (*b*) of Eq. (3) for copepodite stages cultured at food concentrations > 5 ppm and 3 temperatures (data from Table 3 were used to obtain equations)

Temperature (°C)	<i>a</i>	<i>b</i> (× 10 ⁻³)
15.5	0.27	2.57
12.0	0.39	2.12
8.0	0.68	1.39

Rate of Loss of Body Carbon by Molting in *Calanus pacificus*

The carbon content in exoskeletons of Stages CII to CVI of *Calanus pacificus* ranged from 2.8 to 5.1% of the body carbon content of the preceding development stage. The mean was 3.8% (*n* = 21, standard deviation = 0.9) and the deviations from the mean were uncorrelated with changes in temperature and body size. Therefore, regardless of experimental conditions, a constant proportion of body carbon was lost with each molt.

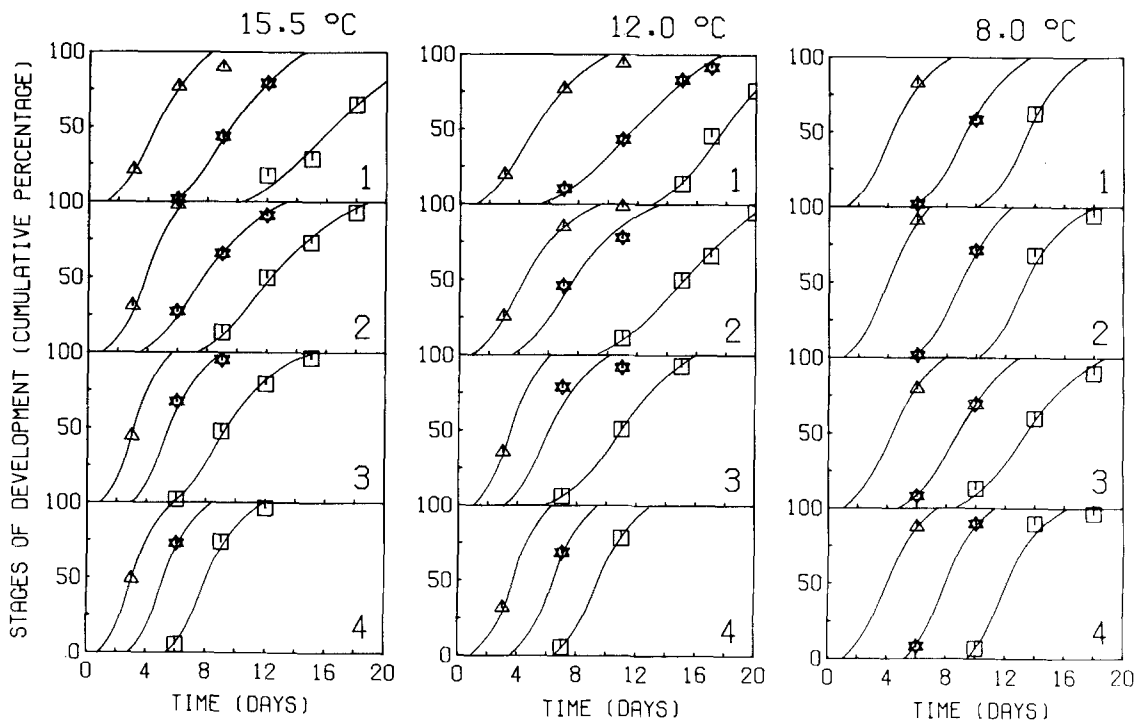


Fig. 3. *Pseudocalanus* sp. Development sequence for Stages CIV (triangles), CV (stars), and CVI (squares) cultured at 4 food concentrations (1 = 0.30 ppm, 2 = 0.50 ppm, 3 = 1.50 ppm, and 4 = 3.50 ppm) and 3 temperatures. Time zero = start of experiments, when copepod populations consisted exclusively of Stage CII. Curves were hand-fit to data (curves for Stage CIV do not pass through the origin because at the first sampling period all populations had reached or passed Stage CIII)

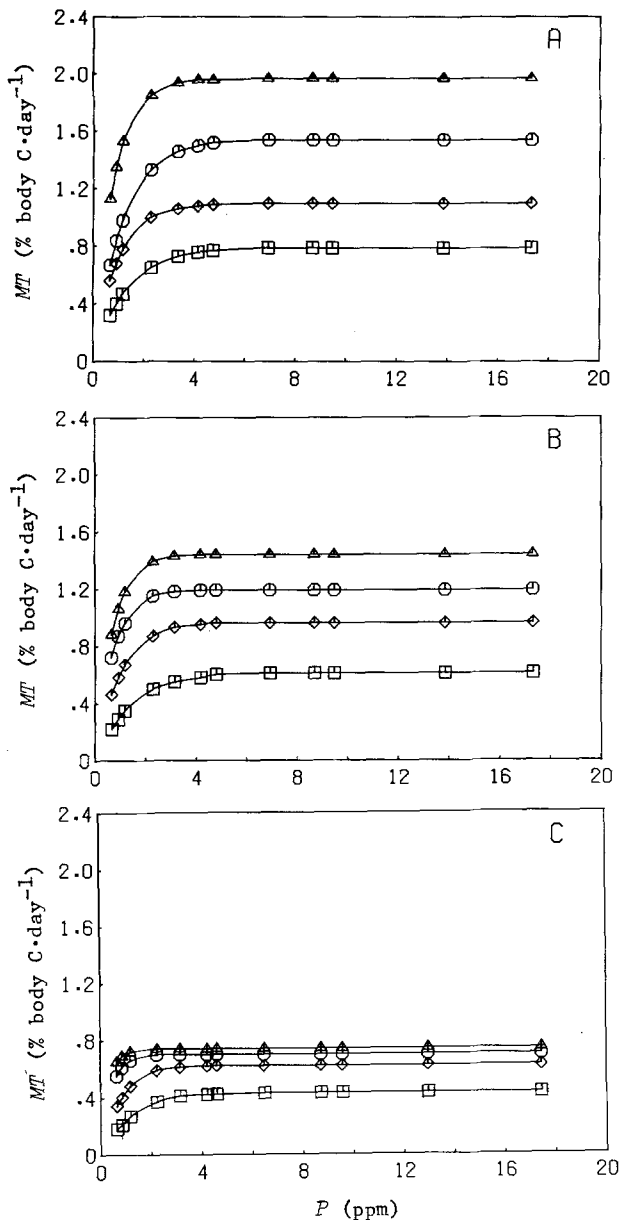


Fig. 4. *Calanus pacificus*. Relationship between rate of loss of body carbon by molting (MT) and food concentration (P) for Stages CII-CIII (triangles), CIII-CIV (circles), CIV-CV (diamonds), and CV-CVI (squares) cultured at 15.5 °C (A), 12 °C (B), and 8 °C (C). Data from Table 3. Curves were fit using Eq. (4); parameters of equations are in Table 5

Rates of loss of body carbon by molting for successive copepodite stages of *Calanus pacificus* in various experiments are given in Table 3. The relationship between this rate and food concentration was described with a hyperbolic function,

$$MT = MT_{\max} (1 - e^{-\lambda P}), \quad (4)$$

where MT is the rate of loss of body carbon by molting (in % body C per day), MT_{\max} is the maximum value of MT , λ is an exponent specifying the slope of the

Table 5. *Calanus pacificus*. Parameters of Eq. (4) for copepodite stages cultured at various food concentrations and 3 temperatures. P_c = critical food concentration for the rate of loss of body carbon by molting

Temperature and stage	MT_{\max}	λ	P_c
15.5 °C			
CII-CIII	1.97	1.254	1.84
CIII-CIV	1.54	0.850	2.71
CIV-CV	1.10	1.043	2.21
CV-CVI	0.97	0.759	3.03
12.0 °C			
CII-CIII	1.44	1.432	1.61
CIII-CIV	1.19	1.401	1.61
CIV-CV	0.96	0.998	2.31
CV-CVI	0.74	0.706	3.26
8.0 °C			
CII-CIII	0.74	3.166	0.73
CIII-CIV	0.70	2.356	0.98
CIV-CV	0.62	1.220	1.89
CV-CVI	0.43	0.824	2.79

Table 6. *Calanus pacificus*. Intercepts (a) and slopes (b) of Eq. (5) for copepodite stages cultured at various food concentrations and 3 temperatures (data from Table 3 were used to obtain equations)

Temperature (°C)	a	b
15.5	0.3198	0.0416
12.0	0.2714	0.0375
8.0	0.1539	0.0320

curves, and P is the food concentration (in ppm) (Fig. 4). The parameters of Eq. (4) for various temperatures and development stages and the critical food concentration for MT are given in Table 5. MT_{\max} decreased with increasing stage of development (and therefore body size), but with changes in temperature, MT_{\max} changed proportionally more for smaller than for larger copepodites. This resulted in larger differences between MT_{\max} of early and late stages at 15.5 °C than at 8 °C (Fig. 4). A similar effect of interactions between temperature and stage of development (and body size) was found for the maximum growth rate of this species (Vidal, 1980a).

The critical food concentration for the molting rate (P_c), like that for the growth rate (Vidal, 1980a), increased with increasing stage of development and temperature (Table 5). However, P_c was considerably lower for the molting rate than for the growth rate. This implies that the rate of loss of body carbon by molting, like the development rate, was less dependent on food concentration than was the growth rate.

The rate of loss of body carbon by molting in *Calanus pacificus* (MT) increased linearly with increasing growth rate (Fig. 5), and the relationship between these rates was described by the equation

$$MT = a + bG, \quad (5)$$

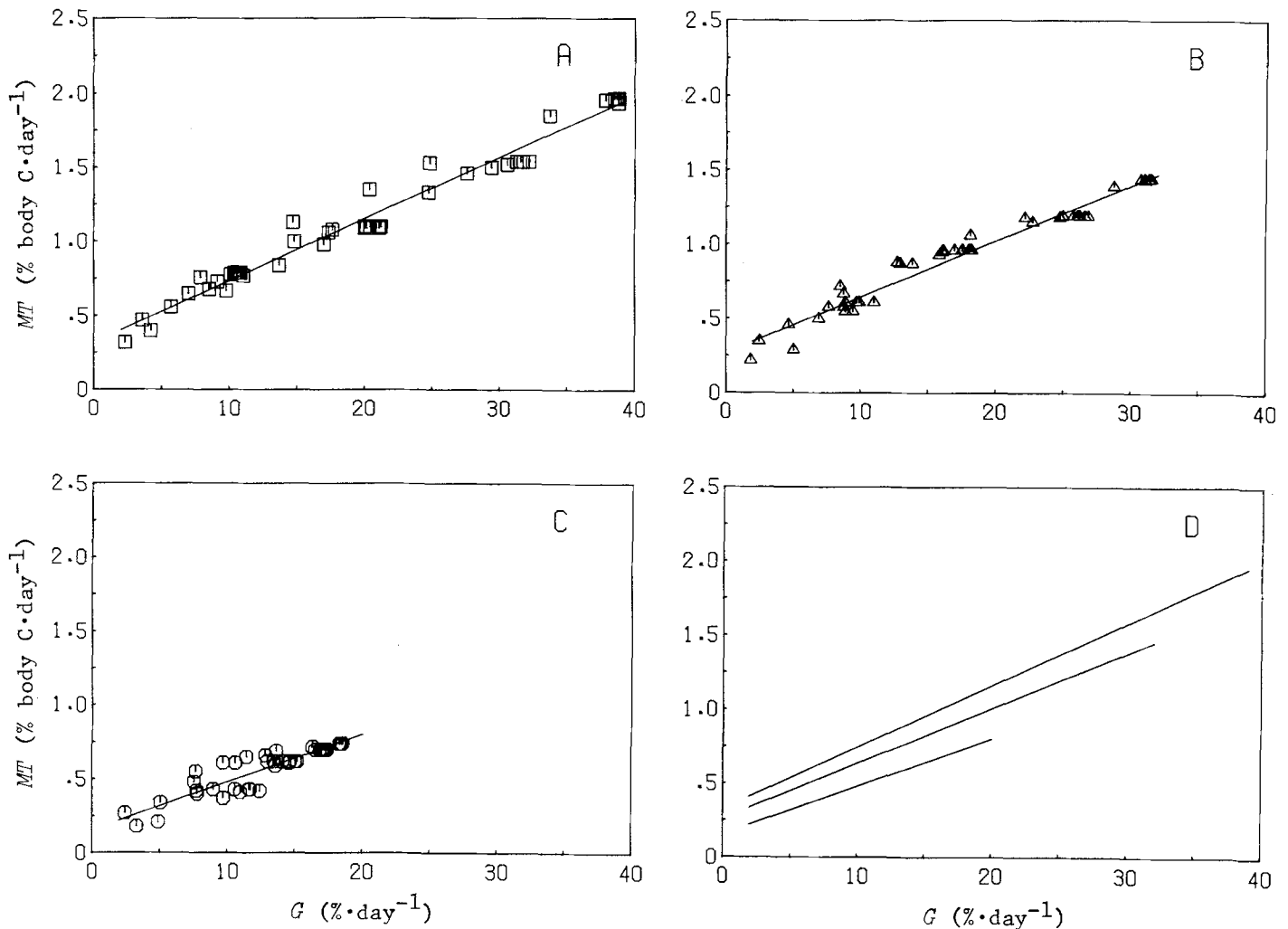


Fig. 5. *Calanus pacificus*. Relationship between rates of loss of body carbon by molting (MT) and growth (G) for Stages CII to CVI cultured at various food concentrations at 15.5 °C (A), 12 °C (B), and 8 °C (C). Data from Table 3. Lines fit using Eq. (5) are shown in (A) to (C) and those fit using Eq. (6) in (D)

where MT is defined as above, and G is the weight-specific growth rate (in % per day). The coefficients a and b of Eq. (5) for the three experimental temperatures are given in Table 6. MT was more than an order of magnitude smaller than G , as the highest values of MT , about 2% per day at 15.5 °C, occurred at growth rates of about 40% per day. The intercepts of the lines in Fig. 5 (Table 6) increased linearly with a logarithmic increase in temperature ($r = 0.99$) and the slopes of the lines also increased linearly with temperature ($r = 0.99$). Thus, by substitution of a and b for their respective temperature-dependent relations into Eq. (5), the following expression describing the rate of body carbon loss by molting as a function of temperature (T) and growth rate was obtained:

$$MT = (-0.371 + 0.586 \log T) + (2.193 \times 10^{-2} + 1.278 \times 10^{-3} T) G \quad (6)$$

Discussion

The proportion of body carbon lost with each molt in *Calanus pacificus* was similar to losses of body carbon by molting reported for other planktonic crustaceans. Losses of body carbon of about 3 to 7% with each molt were found for a mysid and a euphausiid (Lasker, 1966; Clutter and Theilacker, 1971; Sameoto, 1976). Slightly higher losses of about 9 to 10% of body carbon per molt were reported for species with apparently thicker exoskeletons, such as the marine amphipod *Calliopius laeviusculus* (Dagg, 1976) and the copepod *Rhincalanus nasutus* (Mullin and Brooks, 1967). Since the intermolt period for these crustaceans ranged from about 3 to >10 days, the rate of loss of body carbon by molting ranged from about 3 to <1% per day. The rate of loss of body carbon by molting for *Calanus pacificus* in the present study ranged between 2 and 0.2% per day (Fig. 5). This shows that the energetic cost of molting in planktonic

crustaceans is small in relation to that of other physiological processes and to the total carbon metabolism.

The development of *Calanus pacificus* and *Pseudocalanus* sp. was retarded at very low food concentrations (Figs. 1 and 2; Table 4). A similar trend was evident for the copepods *C. helgolandicus* (Mullin and Brooks, 1970; Paffenhöfer, 1970), *Acartia clausi* (Landry, 1976), *Pseudocalanus elongatus* (Paffenhöfer and Harris, 1976), and *Temora longicornis* (Harris and Paffenhöfer, 1976), and for the larvae of the prawn *Palaemon serratus* (Reeve, 1969). Type of food also affects development rate, as shown for *Rhincalanus nasutus* (Mullin and Brooks, 1970) and *C. helgolandicus* (Paffenhöfer, 1970). Low food concentration, and poor food quality also reduced the molting frequency of the freshwater cladoceran *Daphnia hyalina* (Vijverberg, 1976). Protracted delay in development may be caused by extremely low food concentrations, as reported for nauplii of *Pseudocalanus minutus* (Corkett and McLaren, 1970) and for species of freshwater copepods (Coker, 1933). These observations suggest that growth and development in natural populations of planktonic herbivores is likely to be highly dependent on phytoplankton concentration, particularly in medium- to large-sized species, since the critical food concentration for growth and development increases with increasing body size (Vidal 1980a, and present paper).

On the basis of analyses of data by Marshall *et al.* (1934) and Marshall (1949) on abundance, distribution, and size of development stages of marine copepods in Loch Striven, McLaren (1978) concluded that development rates in nature were unaffected by variations in phytoplankton concentration. McLaren did not take into account changes in food supply reported by Marshall *et al.* (1934), and assumed that significant delays in development of late copepodites, e. g. that found for Stage CV of *Calanus finmarchicus* from mid-April to late May, may have been adaptive. During this time, CV and adults were found almost exclusively in the upper 10 m, where the concentration of diatoms at the surface was the lowest of the year, ranging only from 7 to 26 cells per 20 ml of seawater (Table 4 in Marshall *et al.*, 1934). The extremely low food concentration at that time, rather than seasonal adaptations, most likely caused the arrest in development of late stages of *C. finmarchicus*, since during the same period the previous year, when diatoms were present in larger numbers, the development of late copepodites proceeded without delay (Nicholls, 1933; Marshall *et al.*, 1934).

Detailed data on stage duration of marine planktonic copepods in relation to temperature and stage of development are lacking, since in most studies measurements were limited to total development time from egg hatching to Stages CI or CVI. Landry (1975b) assessed the effect of temperature on naupliar and copepodite development of *Acartia clausi*. He found that the duration of all stages was similar (referred to as isochronal development by Miller *et al.*, 1977), and that with changes in temperature stage duration changed in a proportion constant to that of the egg stage, as proposed by Corkett and

McLaren (1970). These latter authors (1978), reviewing the pertinent literature, found the same trends for *Pseudocalanus* spp., but in some of the studies they reviewed stage duration did increase with stage of development. In the present investigation, stage duration of *Calanus pacificus* also increased with increasing stage of development, and low temperature retarded the development of early stages proportionally more than that of late stages (Fig. 2, Table 3). For late stages of *Pseudocalanus* sp., stage duration seemed to increase with stage of development, but the reduced number of observations precludes a definitive conclusion. However, for other species of marine (*C. helgolandicus*, *Rhincalanus nasutus*, and *Eurytemora affinis*) and freshwater (*Acanthocyclops viridis*, *Cyclops vicinus*, *Microcyclops fuscus*, and *Eudiaptomus* spp.) copepods, stage duration increased with increasing stage of development (Mullin and Brooks, 1967, 1970; Ivanova, 1973; Munro, 1974; Heinle and Flemer, 1975).

In several other species of crustaceans, stage duration increased logarithmically with a linear increase in body size (Kurata, 1962; Mauchline, 1977a,b), as found in the present study for *Calanus pacificus* [Eq. (3), Table 3]. This relationship, because of its log-linear nature, implies that the difference in stage duration between two successive development stages must decrease with decreasing body size, and therefore that in small species and in early development stages of larger ones, stage duration must be similar. This also implies that the narrow range of body size found in small species would be insufficient to allow detection of small differences in the duration of various stages, and thus under standard sampling intervals development would appear to be isochronal. Present data on development of small species have not been collected at sufficiently close-spaced intervals to check the validity of this postulation. Furthermore, consideration of the effect of temperature on growth and development makes the problem more difficult, since a decrease in temperature can retard the growth and development of younger stages proportionally more than that of older stages, as shown above for *C. pacificus* and *Pseudocalanus* sp. Thus, low temperature, by prolonging stage duration in younger stages, also seems to induce a development pattern approaching isochronal development.

The inverse relationship between temperature and body size has intrigued biological oceanographers for decades. Growth and development patterns for *Calanus pacificus* and *Pseudocalanus* sp. in relation to temperature and body size found in this and in a previous study (Vidal, 1980a) suggest an explanation for such a relationship. The body-size dependence of the maximum growth rate of these species was more pronounced at high than at low temperatures, and this caused large differences in growth rates of early copepodites cultured at high and low temperatures, while late stages experienced similar rates at all temperatures (Vidal, 1980a). The development rate followed a similar trend, except for its body-size dependence, which was less affected by temperature than that of growth rate. For example, at food concentrations >5 ppm the growth rate of mean Stages CII-

CIII was about 38.8% per day at 15.5 °C and 18.5% per day at 8 °C, but stage duration was 2.0 and 5.1 days, respectively, whereas for the larger Stages CV-CVI the growth rate was 10.6% per day at 15.5 °C and 10.4% per day at 8 °C, but stage duration was 4.8 and 8.9 days, respectively (Table 3). Thus, as the copepods grew, their growth rate became temperature-independent but stage duration remained inversely related to temperature. The final body weight of any stage must be equal to the body weight just after molting plus the weight increment during the following intermolt period; therefore, late copepodites must attain a greater body weight at low temperature, since the growth rate is similar at all temperatures but stage duration is longer at low temperature.

This trend is illustrated in Table 7, where the percentage increment in body weight ($G \times IMP$) of *Calanus pacificus* in various intermolt periods is compared at the three experimental temperatures. For all stages, and particularly for late copepodites, body weight increments are greater at 8 °C than at 15.5 °C. Such an inverse relationship between temperature and body weight was experimentally confirmed for intermediate and late copepodites of *C. pacificus* (Vidal 1980a), while for early copepodites body weight was independent of temperature. This suggests that perhaps the effect of temperature was not sufficiently developed in early copepodites, since the experiments started with Stage CI. However, in cultures of the copepod *Acartia clausi* (Landry, 1976) and the amphipod *Calliopius laevisculus* (Dagg, 1976), in which experiments at various temperatures started with the egg stage, the inverse relationship between temperature and body size became apparent during early development.

The differential effect of temperature on the body-size dependence of the rates of growth and development also explains the inverse relationship between temperature and body size found for late stages of *Pseudocalanus* sp. (Vidal, 1980a); the maximum growth rate was similar at all temperatures (Vidal, 1980a), but development time at high food concentration was inversely related to temperature (Fig. 3). Additional support for this type of interaction is found in Dagg's (1976) data for the marine amphipod *Calliopius laevisculus* cultured at three temperatures and optimal food conditions. The weight-specific growth rate for amphipods of intermediate and large body size was slightly affected by temperature (Vidal, 1980a), but the molting frequency was markedly retarded at low temperature (Dagg, 1976).

The inverse relationship between temperature and body size must occur also at low food concentrations, especially for late development stages, since the critical food concentration for both growth and development increased with increasing temperature, body weight, and stage of development (Vidal, 1980a, and present study). Data on body weight of late copepodites of *Calanus pacificus* and *Pseudocalanus* sp. cultured at various food concentrations and temperatures (Vidal, 1980a) support this hypothesis since, regardless of food concentration, body size was greater at low temperature, and the dif-

Table 7. *Calanus pacificus*. Weight-specific growth rate (G) in % per day, intermolt period (IMP) in days, and their product ($G \times IMP$), or percentage body weight increment during an intermolt period, for copepodite stages cultured at food concentrations > 5 ppm and at 3 temperatures (G and IMP from Table 3)

	Temperature (°C)		
	15.5	12.0	8.0
CII-CIII			
G	38.8	31.3	18.5
IMP	1.93	2.63	5.11
$G \times IMP$	74.9	82.3	94.5
CIII-CIV			
G	31.7	26.1	17.2
IMP	2.47	3.18	5.43
$G \times IMP$	78.3	83.0	93.4
CIV-CV			
G	20.4	17.9	14.2
IMP	3.46	3.94	6.16
$G \times IMP$	70.6	70.5	87.5
CV-CVI			
G	10.6	10.1	10.4
IMP	4.82	6.25	8.91
$G \times IMP$	51.1	63.1	92.6

ference in body weight between copepodites raised at various temperatures increased with increasing stage of development and body size of species.

Growth and development patterns discussed above may also explain the inverse relationship between temperature and body size in natural populations of zooplankton (e.g. Deevey, 1960, 1964; discussed by Vidal, 1980a), since interactions between temperature and body size seem to have a similar effect on the growth rate of animals from various phylogenetic groups (Vidal, 1980a).

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