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Development, growth, and survivorship of the copepod *Calanus marshallae* in the laboratory

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ABSTRACT: Development times from egg to adult *Calanus marshallae* (Copepoda, Crustacea) were 36 d at 15 °C, 62 d at 11 °C and 64 d at 10 °C. Stage-by-stage development was not isochronal but followed a sigmoidal pattern. Egg, N1 and N2 together took 3.4 d at 10 °C (= 5.3 % of the total development time). N3 had the second longest duration of any stage (6.8 d at 10 °C; 10.7 % of total development). Stage duration decreased from N3 through N6, with N6 having the shortest duration of any stage (2.6 d), then development became progressively slower through each copepodite stage. C5 had the longest duration (20.9 d; 32.8 % of total development time). Body lengths of laboratory-raised stages N1 to C3 were the same as of field-collected specimens; C4 and C5 were shorter than in wild copepods, but laboratory-raised females were significantly longer than wild females. This suggests that laboratory growth conditions were probably as good as, if not better than, conditions in the field. Weight was gained at a rate of 0.05 $\mu g\ \mu g^{-1}\ d^{-1}$ from egg through N4; 0.18 d^{-1} from N5 to C5; 0.02 d^{-1} from C5 to adult female. It is argued that observed deviations from isochronal development in *Calanus marshallae* may reflect differential mortality rates among developmental stages such that stages that on average experience high mortalities will develop most rapidly.

INTRODUCTION

The copepod *Calanus marshallae* is common in the zooplankton of the coastal upwelling zone of the northeast Pacific Ocean off Washington, Oregon and northern California, USA (Peterson & Miller 1975, 1977). Individual *C. marshallae* were often referred to as *Calanus finmarchicus* until Frost (1974) showed that it was a third sibling species within a *'Calanus finmarchicus'* complex: *C. marshallae* in the North Pacific, along with *C. finmarchicus* in the north Atlantic, and *C. glacialis* in the Arctic Ocean. Even though all 3 species are morphologically similar, their life-history characteristics may be quite different because each is adapted to a different environment. Aspects of the life history and ecology of *C. finmarchicus* and *C. marshallae* have been worked out by Marshall & Orr (1955) and Peterson (1980), respectively.

This paper presents information on several life history parameters for *Calanus marshallae* including development, growth and survivorship, where possible in comparison with similar data for *C. finmarchicus*, for other *Calanus* species, and other coastal copepods (e.g. Landry 1983). Both laboratory and field data are presented. All results are discussed within a framework of life history and evolutionary ecology.

METHODS

Female *Calanus marshallae* were collected 5 to 10 km offshore from Newport, Oregon, USA. To start an experiment on development time, a known number of eggs was placed in a glass Petridish. After hatching, the nauplii were pipetted to glass containers (600 ml to 3.8 l) where all subsequent development took place. All laboratory work was done under continuous low light intensity except for 1 experiment (Exp 'I'; Table 2) under a 12 h LD cycle. Copepods were fed excess amounts of a mixture of the diatom *Thalassiosira weissflogii* and the flagellate *Isochrysis galbana*, grown in batch cultures at 12 °C using f/2 medium (Guillard & Ryther 1962). New phytoplankton cultures were inoculated at weekly intervals ensuring that food provided to the copepods was always in log phase and never more than 1 wk old. Twelve 10 °C experiments were started with eggs of females collected in January and February 1977, five 11 °C experiments in June and

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July 1976, and two 15 °C experiments in August 1977. Nine of the 10 °C experiments began from single clutches of eggs of individual females. All other experiments began with eggs from several females.

Preliminary experiments showed that mortality of nauplii and early copepodites was high with dense concentrations of phytoplankton so these were avoided. When nauplii were developing, diatoms were kept at ca 2,000 cells ml^{-1}, and the flagellate at ca 50,000 cells ml^{-1} (cell counts determined by microscope). When copepodites appeared, *Thalassiosira weissflogii* was increased to ca 6,000 cells ml^{-1}. Cell counts were converted to carbon units using Strathmann's (1967) equation: Carbon = $0.378 \cdot V \cdot \exp 0.758$. The mean cell volume (V) of the *Thalassiosira* clone was 2,100 μm^3, equal to 125 pg C $cell^{-1}$. Therefore the food concentrations in the experiments ranged from 250 to 750 µg C l^{-1} over the range of 2,000 to 6,000 cells ml^{-1} of the diatom. Each experimental container was inspected daily for food build-up or depletion, and phytoplankton was added as needed. Copepods in Experiments 'H' through 'N' (Table 2) were fed twice daily, and in Experiments 'M' and 'N', copepods were fed such excess amounts of *T. weissflogii* as to color the water yellow-brown. Fecal pellets and other debris were removed from the containers daily, or as necessary. The containers were not stirred because the particular clone of *T. weissflogii* which was used remained in suspension without stirring.

A census was made of the copepods in the 10 and 11 °C experiments at weekly intervals, and at 4 d intervals in the 15 °C experiments. On the census day, water in each container was gently poured through a 64 µm Nitex screen and the copepods rinsed into a Petridish. Individuals were enumerated by developmental stage then returned to the experimental containers. Anesthetics were never used.

Stage-specific development times and stage duration were calculated from observed changes in stage-frequency over time. Through regression analysis of the data on percent-frequency of stage over time, the median development time (MDT) was calculated, following Landry (1983) and Vidal (1980). Three regression analyses were performed: ordinary least-squares, ordinary least-squares with arc sine transformation of the percents (Sokal & Rohlf 1981), and a non-parametric regression technique (the Brown-Mood method; Daniel 1978).

For analysis of growth during these experiments, total length of individuals was measured from the tip of the head to the end of the furcae (not including furcal rami). Weights were obtained from unpreserved copepods. Various life cycle stages were removed from plankton collections or laboratory cultures, placed on absorbent paper, rinsed with 1 drop of distilled water, transferred to a piece of aluminum foil, dried overnight at 60 °C, then weighed using a Cahn Gram Electrobalance.

RESULTS

Survivorship

Survival from egg to adult at 10 °C (Fig. 1) ranged from 10 to 68 % (mean = 41 %). Mortality was highest during the first 40 d of development (to fifth copepodite) after which it dropped to zero in most experiments. Survivorship from egg to adult in the five 11 °C experiments averaged 15 %; in the two 15 °C experiments, 0 and 19 % respectively. At 15 °C, 7 of 9 individuals in 1 experiment died before the molt into fifth copepodite; the remaining 2 died during C5 stage. The other 15 °C experiment produced 5 adult females from 26 eggs.

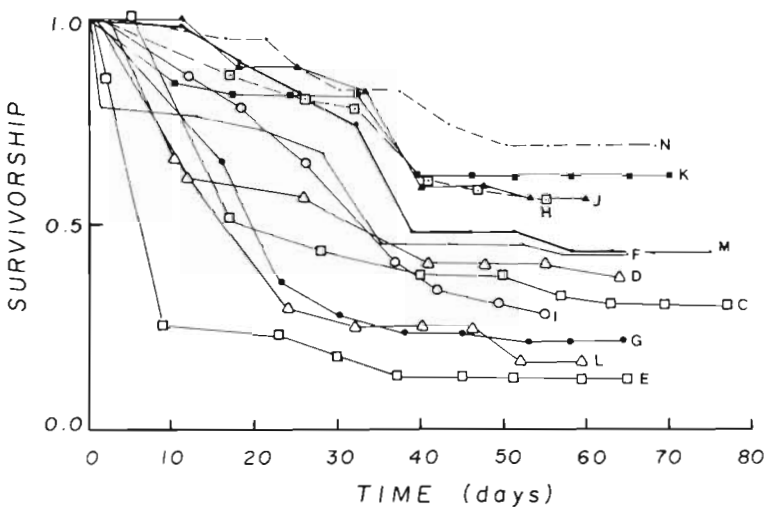

Fig. 1. *Calanus marshallae*. Survivorship in 10 °C experiments. Letters: experiments listed in Table 2

The twelve 10 °C experiments began with a total of 551 eggs, 136 of which became adult females and 1 a male. Many of these laboratory-born females were maintained for more than 2 mo after adulthood was reached; the single male was kept alive for 73 d before being preserved. Longevities of field-collected copepods were similar. Wild females were maintained for up to 77 d and males for 50 d before being preserved.

Development at 10 °C

Fig. 2 shows the cumulative percent of the population that was younger than each indicated developmental stage, for the fourth nauplius through female, for all experiments. Estimates of median development times (MDT) calculated from each of the 3 regression methods are listed in Table 1. The 3 methods gave nearly identical results; hence for all subsequent analyses the MDT calculated from ordinary least-squares methods will be used. Estimates of developmental rates of eggs and development time to the third nauplius stage come from direct observations. Egg hatching times were as follows: 42 h at 9.2 °C and 9.4 °C; 41.3 h at 9.5 °C; 40.0 h at 10.0 °C; 39 h at 10.8 °C; 2 observations of 39 h at 11 °C; 38.8 h at 11.5 °C; 37 h at 12.0 °C; less than 24 h at 15 °C. Most eggs hatched within 30 min of each other, so the variance in hatching time was not great. The average time from egg laying to the beginning of the third nauplius stage was 85 h (mean of 4 experiments; $s_{\bar{x}} = 7.2$ h). The combined duration of nauplius Stages 1 and 2 (time from hatching to the beginning of nauplius Stage 3) was 45 h, an average of 22.5 h stage^{-1}.

Median development time (MDT), duration of each developmental stage, and percentage of the total

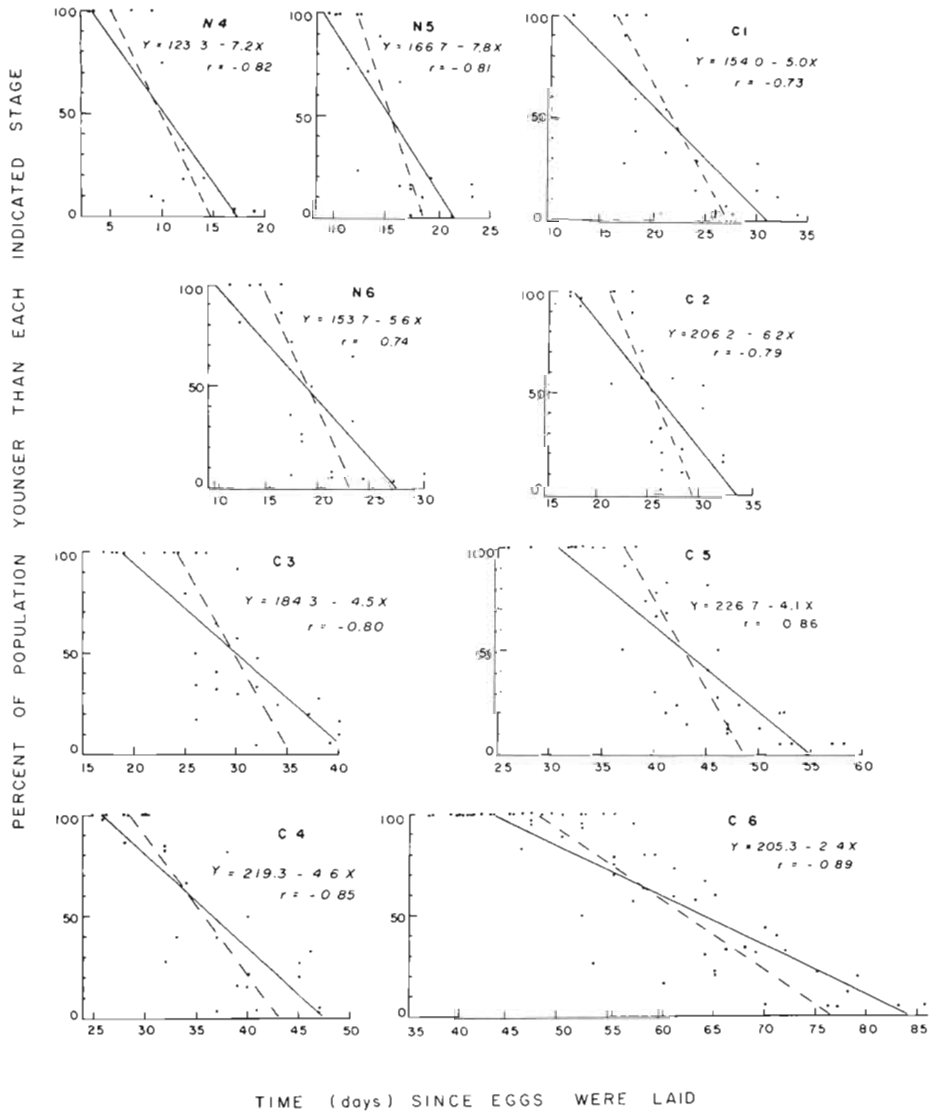

Fig. 2. *Calanus marshallae*. Scattergrams of cumulative percent of the population that was as young, or younger, than the indicated stage, *vs* time, in the 10 °C experiments. The 2 lines shown on each panel are regressions calculated from parametric (——) and nonparametric (- - -) techniques. Regression equations and correlation coefficients are from parametric analysis

Table 1. *Calanus marshallae.* Median development time (MDT), in days to reach each successive developmental stage at 3 temperatures. MDT was calculated from 12 experiments at 10 °C; 5 at 11 °C; 2 at 15 °C

Stage	Median development time (MDT), 10 °C			Stage duration (d)	% of 63.8 d	MDT 11 °C	MDT 15 °C
	Non parametric	Least ordinary	Arc sin				
Egg	–	–	–	1.6	2.5	–	–
N1	–	–	–	0.9	1.4	–	–
N2	–	–	–	0.9	1.4	–	–
N3	–	–	–	6.8	10.7	3.4	–
N4	10.0	10.2	10.9	4.8	7.5	10.3	5.8
N5	15.1	15.0	15.4	3.4	5.3	13.9	8.5
N6	18.6	18.4	18.9	2.6	4.1	17.1	8.5
C1	21.6	21.0	21.6	4.3	6.7	20.4	8.6
C2	25.6	25.3	25.7	4.6	7.2	24.1	13.4
C3	29.8	29.9	30.8	6.8	10.7	26.7	15.6
C4	35.8	36.7	37.3	6.2	9.7	35.0	19.2
C5	41.0	42.9	43.8	20.9	32.8	41.4	27.1
C6	62.2	63.8	64.5	>75		62.3	35.8

development time represented by each stage is given in Table 1. Median development times for each stage in the 10 °C experiments are plotted in Fig. 3A. The overall pattern in development from N3 to C5 can be approximated by a linear function with a slope of 4.6 d stage^{-1}. However, the true pattern of development seems to follow a sigmoidal model with periods of rapid development alternating with periods of slower development. Median development times for the 11 and 15 °C experiments are also listed in Table 1 and plotted in Fig. 3B. The MDTs for each stage at these temperatures were faster than those at 10 °C, and the overall pattern of development is sigmoidal, rather than linear.

Variability in developmental rates

Regression lines from Fig. 2 are sequentially arranged in Fig. 4. The slope of each line is a measure of the variance in development time for individuals within that stage. If the variance in development increases with time (i.e. if slow individuals develop progressively slower and fast individuals faster), the slopes of the regression line for each successive stage should decrease. The hypothesis that all slopes were equal was tested by calculating the 95 % confidence interval estimates for each slope. The test was done using both untransformed and arc sine transformed percentages. Interval estimates were found to include

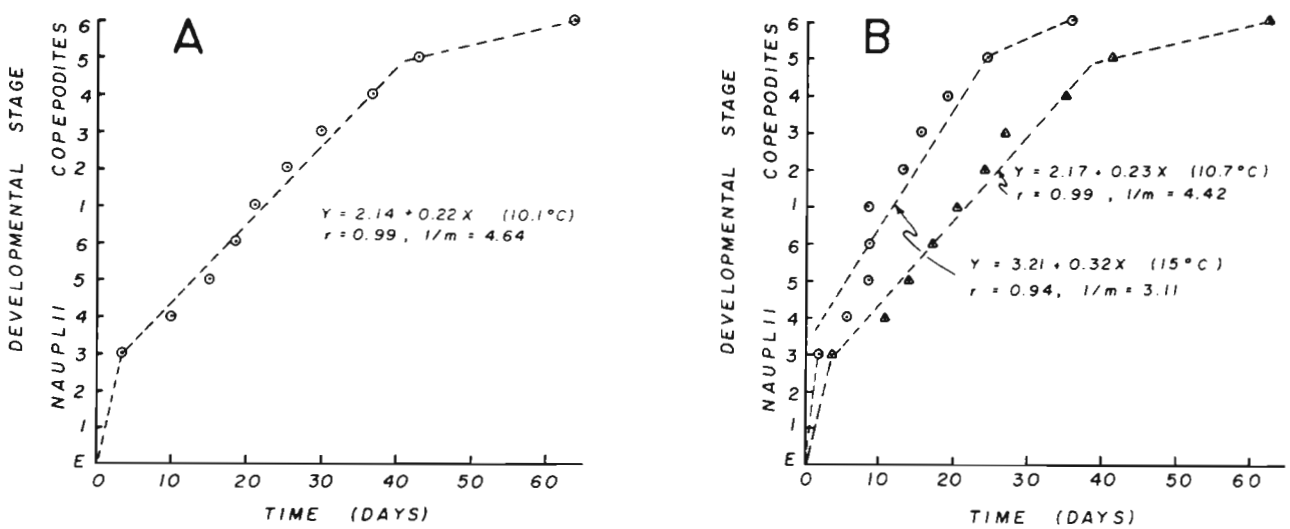

Fig. 3. *Calanus marshallae.* (A) Progression of developmental stages through time. Dots: times when the median individual had just entered a stage, at 10 °C. (B) Same, at 11 and 15 °C

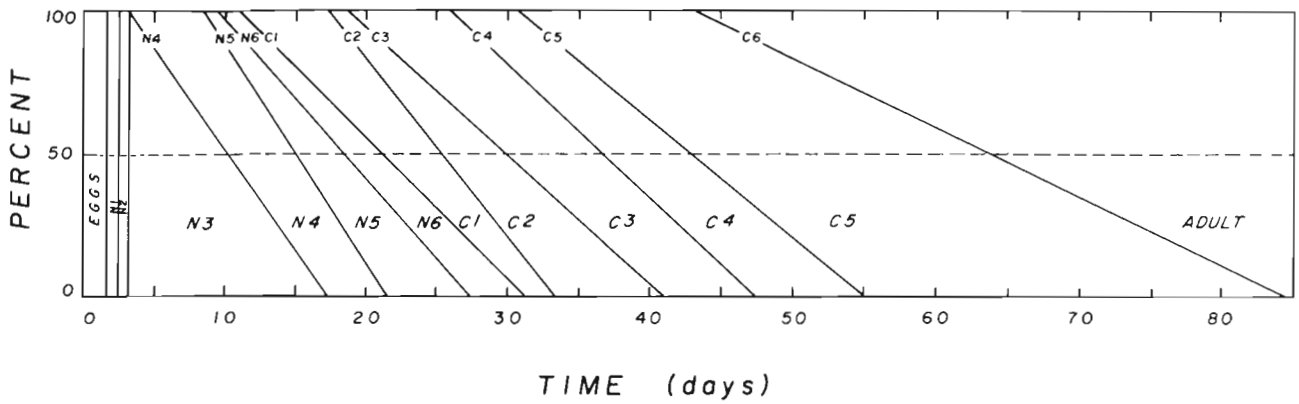

Fig. 4. *Calanus marshallae*. Development of each indicated stage at 10 °C showing the least squares regression lines from Fig. 2

all slopes except egg through N3, and C6. I conclude that the variance in development *to* all stages from N4 to C5 is about equal. Most of the variance arises during the development of the third nauplius and the fifth copepodite. This suggests that once some variable point of development is reached during the N3 stage, molting of most individuals proceeds on some pre-set nonvariable schedule. Additional variability reappears as C5 individuals prepare for the molt to adult. I therefore conclude that both the N3 and C5 stages have some 'special' status during the developmental process, a matter discussed later in this paper.

Variability in development among families

Most of the 10 °C experiments were initiated from a single clutch of eggs so that variations in stage-specific development times among families could be investigated. The age of the median individual at each developmental stage for each of the 9 family lines was calculated, and is listed in Table 2. Due to shortage of data, only median development times to copepodite Stages 2, 3, 5 and 6 could be analysed for differences among families.

Several conclusions may be drawn from the data listed in Table 2. First, among families the range in days between the arrival of the median individual to a given stage is great. The median individual from a fast-developing clutch (e.g. 'F') could be 2 developmental stages ahead of the median individual from a slower developing clutch (e.g. 'G'). In 'G', the median C1 appeared at 26.7 d while in 'F' the median individual was a C3 at 26.1 d.

Second, if copepods in one experiment got ahead of another experiment for whatever reason, they did not necessarily keep this lead through to the end. For example, individuals in the 'H' experiment were the first to arrive at C2 and C3, the second to C5 but last to arrive at female. Conversely, individuals in 'G' were last to arrive at the younger stages but fifth to become female. The rank-order arrival to Stages C2, C3 and C5 among the twelve 10 °C experiments was tested for concordance using Kendall's coefficient of concordance, 'W', from Daniel (1978). The result was W = 0.59 (significant at the 0.005 level); there was substantial agreement among the ranks as to fast and slow developing clutches. The situation was reversed when rank-order arrivals to Stages C3–C5–C6, and C5–C6 were examined. In these 2 cases, no concordance was found (W = 0.39, p = 0.3; W = 0.54, p = 0.4 respectively) because in 4 of the 12 experiments, individuals

Table 2. *Calanus marshallae*. Time (d) when the median individual had reached each listed developmental stage, for 12 separate experiments at 10 °C. Times in parentheses are inferred from a single data point. With the exception of C, H and I, all experiments began with eggs from a single clutch of an individual female. All experiments conducted under continuous low light except I (12:12 LD cycle)

Code	Copepodite stage						Elapsed time
	C1	C2	C3	C4	C5	C6	C5 to C6
C		23.2	(< 28)	35.7	45.0	65.3	20.3
D		(24.6)	26.0		44.9	68.3	23.4
E	26.1	28.9	31.6	38.0	45.3	68.1	22.8
F		21.9	26.1		(39)	59.1	20
G	26.7	30.6	35.2	41.8	47.7	61.4	13.7
H		21.5	23.6	32.0	39.1	69.8	30.1
I	18.5	22.2	24.1		36.6	63.0	26.4
J	19.2	22.7	29.6	32.9	40.3	51.9	11.6
K	23.8	27.3	31.8	35.5	42.5	59.8	17.3
L		25.4	32.0	40.9	43.4	52.7	9.3
M	24.7	(27.8)	31.7		42.2	67.7	25.5
N	20.5	24.2	28.9	33.6	40.2	63.5	23.3
N (early)	19.0	23.8	28.5	33.8	39.6	59.1	
N (late)	20.9	24.5	29.3	33.5	41.1	69.4	
Average	22.8	24.8	29.1	36.3	42.5	62.5	20.0

molted from C5 to female at a much slower rate (C, D, H, I), in 4 at a faster rate (G, J, K, L) and in 4 at intermediate rates (E, F, M, N) as compared to molting during the earlier copepodite stages. When only the 9 clutches representing different families were analysed by the same methods, the same result was found. All of this again suggests that development through the later stages (copepodite Stage 5 in particular) is controlled by a genetic mechanism different from that for development from N3 to C5.

Variability in development within a family line

The hypothesis was tested that the eggs which were the first to hatch from a clutch developed at a faster rate than those which hatched last. In this experiment, the first 20 nauplii which hatched from a clutch of 40 eggs were maintained separately from the last 20 nauplii. The median development times of these 2 groups are shown at the bottom of Table 2 as experiments 'N-early' and 'N-late'. (The pooled results of this experiment are 'N' in Table 2.) The median individual within the early-hatching group became an adult 59.5 d after hatching whereas among the late-hatching group, adulthood was reached 9 d later, 68.1 d after hatching.

Change in length with stage

The relation between body length and developmental stage for *Calanus marshallae* (Fig. 5) shows that change in length with stage occurred in 4 linear phases. First, nauplius (N) Stages 1 and 2 (0.017 mm stage^{-1}); second, N2 through N6, 0.06 mm stage^{-1}; third, N6 through third copepodite (C), 0.29 mm stage^{-1}; fourth, C3 through C6, 0.41 mm stage^{-1}. Mean lengths of nauplii from the laboratory and field were equal. Mean length of each copepodite stage from the Lab-77 experiments was significantly greater than Lab-76 copepodites (paired t-tests). With the exception of C4 and C5, laboratory-raised individuals were significantly longer than wild individuals. These results suggest that the laboratory conditions under which the copepods were raised were as good as if not better than conditions in the field.

Maternal effects on terminal size

Table 3 shows that laboratory females (Lab-77) were significantly longer than field females and that the range in length of laboratory females was greater than field females. Since the laboratory conditions represent a nearly constant environment with food in excess,

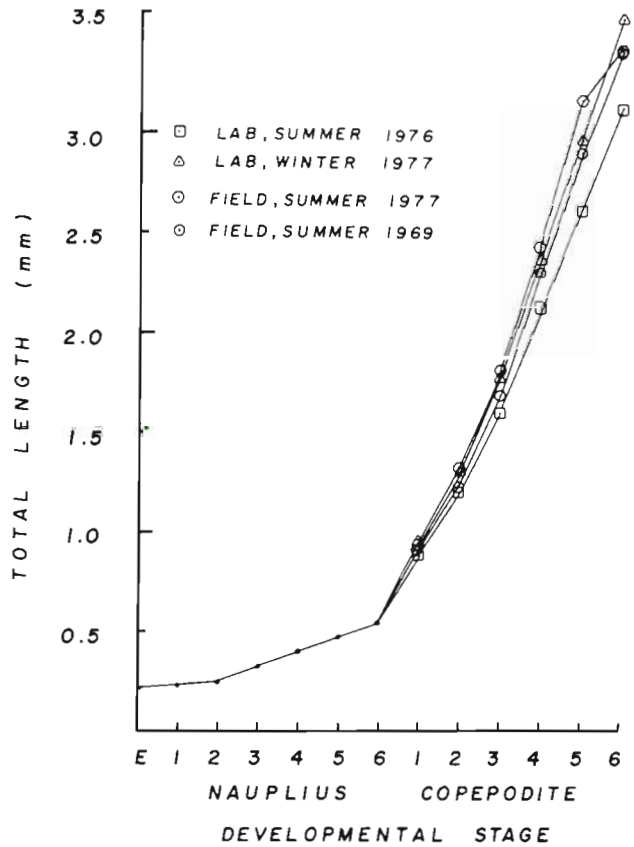

Fig. 5. *Calanus marshallae*. Comparison of average lengths of laboratory-raised and field-collected developmental stages. Lengths of nauplii were the same in both lab and field specimens so data are shown by a single dot for each stage

the great range in terminal size may be due almost entirely to genetic effects. This hypothesis was further examined by comparing terminal size of daughters with that of their mothers (Fig. 6). The trend of the data suggests that larger mothers produce *smaller* daugh-

Table 3. *Calanus marshallae*. Comparison of total length of females either raised in the laboratory or collected off the Oregon coast. Laboratory females were significantly longer than field females ($t = 7.04$; 270 df)

Size classes (mm)	Lab 1977 No. of individuals	%	Field 1977 No. of individuals	%
2.60–2.76	0	0.0	1	0.1
2.80–2.96	0	0.0	1	0.1
3.00–3.16	2	2.0	79	6.1
3.20–3.36	14	14.1	400	30.8
3.40–3.56	22	22.2	572	44.1
3.60–3.76	44	44.4	213	16.4
3.80–3.96	16	16.2	29	2.2
4.00–4.16	1	1.0	2	0.2
Total	99		1,297	

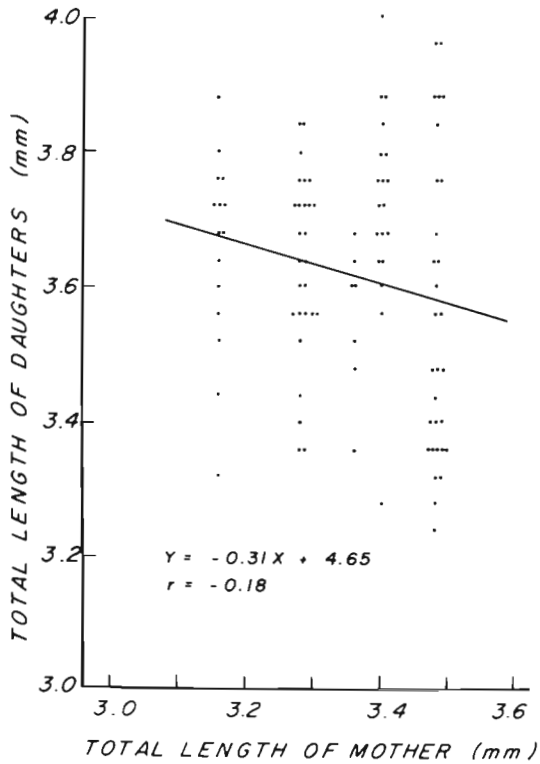

Fig. 6. *Calanus marshallae.* Scatter diagram showing length of daughters *vs* length of mother. Slope of regression line was not significantly different from zero

ters on the average, although the slope of the regression line was not significantly different from zero ($F = 3.24$, 1,98 df). Only 3 % of the variability in terminal size of all daughters was explained by size of their mothers. I conclude that length of a female has little direct influence on the average length of her daughters, and that terminal size of offspring within any given clutch of eggs is extremely variable. The observed differences in total length between laboratory and field females may have resulted from any number of vagaries of differences in diet between lab and field, as well as variable water temperature in the field. Size-selective predation is an alternate hypothesis, but this factor was not examined during my study.

Length-weight relations

Length-weight data were only available for Stages C4 through C6. The coefficients of the power function ($W = a L^b$) were determined by least-squares methods after transforming both L and W to logarithms. The relation was $W = 2.00\ L^{3.94}$ ($n = 57$; $r = 0.96$; 95 % confidence interval of the slope $\pm$ 0.02). It seems that a cubic relation ($W = aL^3$) does not apply to older copepodite stages of *Calanus marshallae.* Individuals in the older stages are heavier than the cubic law would predict probably because they contain appreciable amounts of wax esters.

Change in weight with stage and time

Weight gained between egg and N4 was small, but from N4 to C6, weight was gained at on overall stage-specific rate of 0.73 µg stage^{-1} (Fig. 7A). The functional relation between change in weight and *time* was examined by plotting dry weight of stages *vs* the cumulative median development time (Fig. 7B) using the development time data from the 10 °C experiments. Three phases in the growth processes were seen: (1) egg through N4: weight was gained at a rate of 0.050 µg µg^{-1} d^{-1}; (2) N5 through C5: 0.176 µg µg^{-1} d^{-1}; (3) C5 to female: 0.024 µg µg^{-1} d^{-1}. Even though growth rate on a *per stage* basis was constant from N4 through female, growth on a *daily* basis was slow between C5 and female for example, because of the extended interval between recruitment of C5 to adult female. Females do gain the weight predicted by the weight-stage linear regression (from Fig. 7), but it takes them longer to achieve the predicted weight.

DISCUSSION

Survivorship

Survivorship from egg to adult in the 10 °C experiments averaged 41 %. Similar results were obtained by Mullin & Brooks (1967, 1970) for *Rhincalanus nasutus* and *Calanus pacificus.* Hirche (1980) reported 12 % for *Calanoides carinatus,* and Paffenhöfer (1970) 41 to 100 % for *C. pacificus.* In Paffenhöfer's experiments, mortality rates were very nearly zero after the first copepodite stage but in my study, mortality did not reach zero until the fourth copepodite stage. Virtually all *Calanus marshallae* copepodites which died did so during the molt, an observation also noted by Raymont & Gross (1942) and Corkett (pers. comm.) for *Calanus finmarchicus.*

Sex ratio

Of 137 adults produced in the laboratory, only 1 was a male. Males did not appear in Mullin & Brook's (1970) experiments on *Calanus pacificus,* but the sex ratio was 1:1 for *Rhincalanus nasutus* cultured at the same time under the same conditions. Hirche (1980) obtained only females of *Calanoides carinatus* and *Calanus helgolandicus.* Conover (1965) and Tomasini & Petit (1977, cited in Hirche 1980) maintained fifth

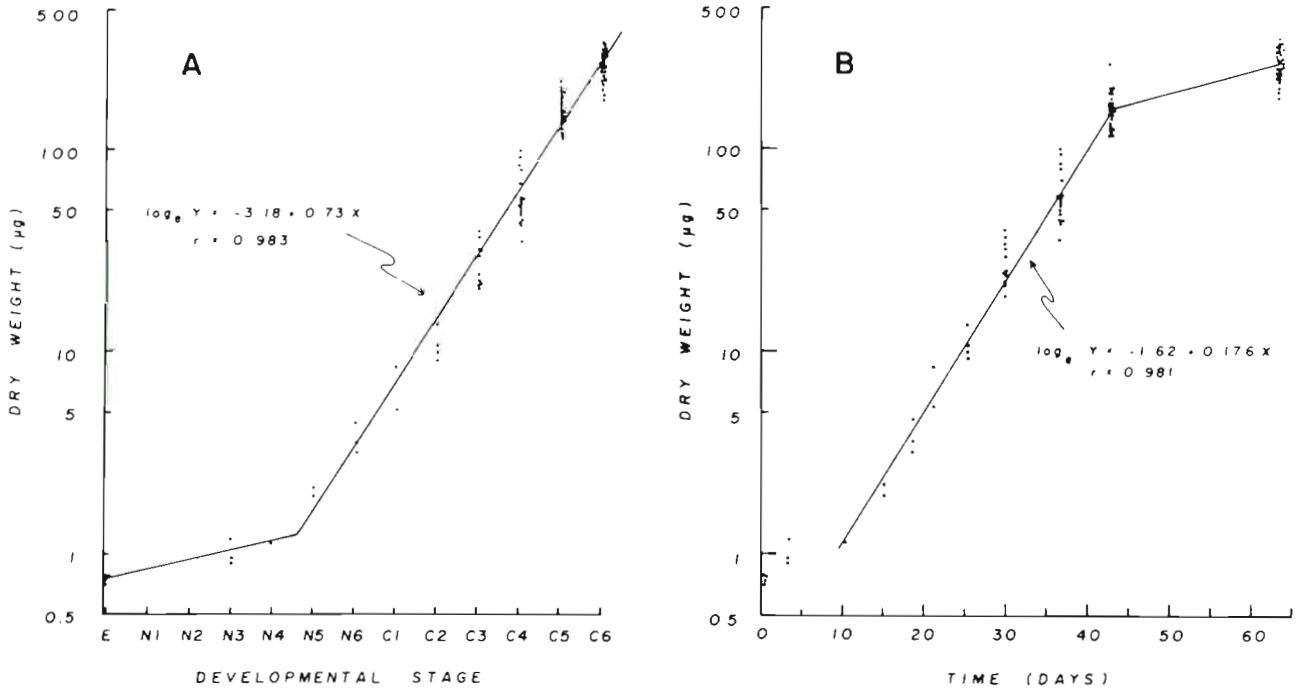

Fig. 7 *Calanus marshallae*. (A) Change in weight with developmental stage. (B) Change in weight with time. Three linear growth phases are seen: (1) from Day 0 to Day 10 (Egg to N4); (2) from Day 10 to Day 43 (N4 to C5); (3) from C5 to female. Specific growth rate from N4 to C5 was 0.176 µg µg^{-1} d^{-1}

stage *Calanus hyperboreus* and *C. carinatus* respectively in the laboratory and obtained only females although some males appeared in Conover's experiments on copepods collected during winter. Both Paffenhöfer (1970) and Vidal (pers. comm.) got as many as 25 to 40 % males respectively in their laboratory cultures of *C. pacificus*. Landry (1983) reported a proportion of male *R. nasutus* and *C. pacificus* of 0.44 and 0.31. Paffenhöfer suggested that both food concentration and phytoplankton species composition may be important for sex determination, but in Vidal's (pers. comm.) experiments, food concentration had no apparent effect on sex ratio.

An excess of females is frequently observed in nature, and differential mortality of adults has been suggested (Marshall & Orr 1955) as an explanation. *Calanus marshallae* averaged 12.0 % males in 195 vertical plankton net hauls taken off Newport, Oregon, from 1969 to 1972 (Peterson & Miller 1976) and 13.6 % in 360 samples collected from discrete depths during the summer of 1977 (Peterson 1980). Similar results (10 % male) were reported by Marshall & Orr (1955) for *Calanus finmarchicus* in the Clyde Sea. Raymont & Gross (1942) found that male *C. finmarchicus* survived only 1 to 2 wk whereas females lived more than 9 wk in the laboratory. They also showed that males took very little if any food suggesting that the mouthparts were reduced. Hirche (1980) reported that *Calanoides carinatus* males lived only 10 to 12 d in the laboratory. Very different results were found for *C. marshallae:* both males and females survived for at least 8 wk in the laboratory. Males have fully developed mouthparts and produce copious amounts of fecal pellets in the laboratory, suggesting that they do feed and that skewed sex ratios in nature are not due to higher physiological mortality of males.

Development time

Individual *Calanus marshallae* developed from egg to adult at a much slower rate than other related species. Corkett (pers. comm.) found for *Calanus finmarchicus* an egg-to-adult development time of 35 d at 10 °C. *Calanus pacificus* reached adulthood after about 23 and 45 d at 15 and 10 °C respectively (Mullin & Brooks 1970, Paffenhöfer 1970), and 20 d at 15 °C (Landry 1983). Thompson (1982) reported development times for *Calanus* spp. (collected from the southern North Sea) of 26 and 42 d at 15 and 10 °C, and Hirche (1980), 22 d at 15 °C for *Calanoides carinatus*. *C. marshallae* reached adulthood after 36 and 64 d at the same 2 temperatures. Each of these estimates are 34 % greater than those for other *Calanus* species.

Growth

In my experiments, log-phase phytoplankton was usually added to the copepod growth chambers in dense enough concentrations to at least color the water lightly. Some evidence that the copepods were not food-limited comes from the facts that body lengths of all nauplii and of copepodites Stages 1 to 3 and adult females in the laboratory were the same as (or in adult females, greater than) field-collected individuals. This contrasts with the results of Paffenhöfer (1970) whose laboratory female *Calanus pacificus*, raised on various diatom species, were significantly smaller than wild females, and only achieved the lengths of wild females with *Gymnodinium splendens* as food. Curiously, laboratory-raised C4 and C5 *Calanus marshallae* in my experiments were shorter than wild specimens. A likely explanation is that in the field C4 and C5 are diel migrators, which grow at temperatures that average lower than 10 °C, and experience a different food environment compared to non-migrating stages. Other evidence that feeding conditions were adequate comes from experiments on the fecundity of *C. marshallae*. Maximum egg production rates of 25 eggs female^{-1} d^{-1} occurred at 3,500 cells ml^{-1} of *Thalassiosira weissflogii* (Peterson 1980), a concentration near the low end of the range in food concentration used in the development time experiments.

Growth in weight of *Calanus marshallae* was exponential from N4 to C5. This result differs from laboratory studies on most other coastal copepods in which specific growth rates decreased through the late copepodite stages, as shown for *Rhincalanus nasutus, Calanus helgolandicus* and *Calanus pacificus* (Mullin & Brooks 1970, Paffenhöfer 1976, Vidal 1980), and for *Pseudocalanus elongatus* and *Temora longicornis* (Paffenhöfer & Harris 1976, Harris & Paffenhöfer 1976). My result may have been obtained because growth rates were calculated from weights of laboratory-raised N3 to C3 but wild C4 to C6. Hakanson (1984) has shown that wild C5 of *C. pacificus* are considerably heavier than laboratory-raised individuals, but that weights of laboratory and wild C4 were equal. Similarly, Paffenhöfer's (1976) diatom-raised C5 and female *C. pacificus* reared on diatoms were lighter than those raised on dinoflagellates or from the wild. If my C5 and adult *C. marshallae* raised on *Thalassiosira weissflogii* grew similarly to Hakanson's *C. pacificus* raised on *T. weissflogii*, and to Paffenhöfer's *C. pacificus* raised on diatoms, then specific growth rates of *C. marshallae* (if calculated from weights of laboratory-raised individuals) would have declined between C4 and adult female. Hakanson (1984) suggested that differences in lipid (wax ester) content in laboratory *vs* 'wild' phytoplankton may explain observed differences in weight between laboratory and wild C5 and adult *Calanus*. The decline in growth rate with stage in laboratory-raised copepods may be due to lipid-limitation of growth.

Development

The overall pattern of development of *Calanus marshallae* largely conforms to patterns described by Landry (1983) for the coastal copepods *Acartia clausi, Acartia tonsa, Rhincalanus nasutus, Calanus pacificus, Labidocera trispinosa, Paracalanus parvus* and *Pseudocalanus* spp. First, the duration of the pre-feeding naupliar stages is relatively short, only 42 h for N1 + N2 in *C. marshallae*. Second, the first-feeding stage, N3, has the second-longest duration of any stage. Third, the female C5 had the longest duration. Landry (1983) suggested that the first 2 naupliar stages are short because they do not feed, that N3 is long because it needs time to recover weight lost during the previous 2 non-feeding stages, and that the extended duration of C5 is needed to accumulate lipid reserves. Landry's observation that egg development times cannot be used to predict egg-to-adult development times holds for *C. marshallae* as well. The primary difference between the development of *C. marshallae* and other coastal copepods is the sigmoidal pattern of stage-by-stage developmental times. In particular, development from N3 through N6 was progressively faster, with N6 the stage with the shortest duration. This was followed by progressively slower development through each copepodite stage.

Adaptive features of *Calanus* development

The arguments presented here assume that any deviations from isochronal development will have evolved in response to differential mortality rates among developmental stages. Stages with a long duration are considered to be relatively 'safe' while those with a short duration are 'vulnerable'. Along these lines, Miller et al. (1977) and Johnson (1981) argued that the observed rapid development through late copepodite stages of *Acartia* species evolved in response to high mortality rates of older copepodite stages, especially of the adults.

The pattern in *Calanus marshallae* was rapid development to N3, followed by quasi-isochronal development to C5 then extremely slow development to adult. One can hypothesize that the pattern evolved in response to constantly high egg and N1 + N2 mortalities, or both, moderate death rates through the other nauplii and early copepodites, followed by greatly

enhanced survival rates of C5 and adults. Evidence in support of this model follows.

First, compared to other neritic copepods, the eggs of *Calanus marshallae* hatch quickly: 1.8 d at 10 °C compared to 3.3 d for *Acartia clausii* (Landry 1976), 3.5 d for *Pseudocalanus minutus* and 4.1 d for *Tortanus discaudatus* (McLaren 1966). Second, in the field, mortality of eggs seems to be high. From 360 samples collected from discrete depths along 9 zonal transects off the Oregon coast in July-August 1977 (Peterson 1980), the ratio, number of N3 recruits produced each day: number of eggs produced per day, averaged 0.017 (Table 4). Furthermore, on 3 dates when N1, N2, and

Table 4. *Calanus marshallae*. Estimated number of daily recruits from egg, N1 + N2 and N3 stages, calculated from abundance estimates of these stages in samples collected off the Oregon and Washington State coast during summer 1977. On average, about 1.7 % of the eggs produced each day reach the third nauplius stage

Date (1977)	Daily recruits Eggs d^{-1}	N1+N2 d^{-1}	N3 d^{-1}	Ratio N1+N2/ Eggs	Ratio N3/ Eggs
8 Jul	537,806	2,245	1,668	.004	.003
15 Jul	1,008,131	–	18,533	–	.018
21 Jul	67,379	540	802	.008	.012
23 Jul	202,316	–	23,879	–	.031
24 Jul	401,620	1,114	2,679	.003	.007
26 Jul	187,948	–	932	–	.005
29 Jul	880,510	–	4,535	–	.005
4 Aug	97,874	–	1,640	–	.017
13 Aug	2,074	–	109	–	.053
Average					.017

N3 were each enumerated (Table 4), the number of recruits from these stages were about equal, suggesting that almost all mortality came during the egg stage. If this has been true over evolutionary time, selection would have shortened the time spent in the vulnerable egg. The evolution of an egg which hatches quickly may also be related to egg sinking rates. The eggs of *C. marshallae* sink at a rate of 36.0 m d^{-1} (n = 68; Peterson 1980). In 1.8 d an egg could sink well below the food-rich upper 0 to 10 m mixed layer off Oregon. The rapid development to a swimming nauplius would aid in the return to the euphotic zone. In contrast, the eggs of *A. clausii* sink at rates of only 5 m d^{-1} (Valentin 1972) so would not leave the euphotic zone during their 3 to 4 d developmental period. Egg sinking does not seem to be a problem for the Oregon population of *C. marshallae* because eggs were found to be most abundant between 0 and 10 m (Peterson et al. 1979, Peterson 1980), but may be important where upwelling is limited (such as in the Bering Sea). Eggs of *Calanus* spp. are known from English Channel sediments (Williams & Lindlay 1980).

Another key stage in the life history of *Calanus marshallae* is the third nauplius, which I considered as having some special developmental status because: (1) this stage has a relatively long duration and (2) it shows the most variable development time. I suggest that this is the case because a number of developmental events take place during N3, including a general thickening of the ectoderm, a greater development of muscles which work the limbs, development of the gut, and initiation of development of the genital system as noted by Marshall & Orr (1955, p. 46–47). In my experiments, the N3 gained very little weight compared to the later naupliar stages, suggesting that most of the energy it uses goes into production of new machinery rather than new biomass. In order to assure that this stage has sufficient energy to complete development (even when food is scarce), individuals may be able to subsist on yolk alone. To test this hypothesis, a number of batches of eggs were hatched in 0.45 µm filtered seawater. Development proceeded to N3 at the regular pace, but no further. Individual N3 survived for 10 d on average.

Other species of *Calanus* may have a similar early life history. Eggs of *C. finmarchicus* hatch quickly (40 h at 10 °C), N3 is reached within 3 d (Marshall & Orr 1955), and the N3 stage is long-lived (Lebour 1916). Fernandez (1979) found that eggs of *C. pacificus* hatch within 24 h at 15 °C, that N3 was reached in 1.5 d, and that at 15 °C, starved N3 lived up to 6 d. However, in his experiments, the nauplii all molted to N4 before dying. From Landry (1983) and Thompson (1982), it could be concluded that many coastal copepods share this pattern of rapid development to the first feeding stage.

After N3 is successfully passed, all other stages have a pre-set schedule with little change in variability of stage duration. Stage durations become progressively shorter from N3 to N6. The sixth nauplius lasted only 2.6 d (4.1 % of the total development time) which was surprising because many morphological changes take place here. Individuals develop maxillules, maxillae, maxillipeds, and 2 pairs of swimming legs along with the musculature to operate them. Landry (1978) has shown that for some copepod predators, late nauplii stages are preferred as prey over younger stages, therefore if predation pressure is intense enough, selection could act to accelerate development of the N6. Rapid development through N6 is not common however, only being found by Thompson (1982) for *Pseudocalanus elongatus* and *Calanus sp.*, and for *Labidocera trispinosa* in Landry's (1983) study of 7 coastal species.

At C5, developmental problems may be responsible

for lengthening the stage duration: the copepods develop gonads and make a decision about diapause. If they molt to adult, the oil sac is partially resorbed and the gonads develop. The differential ability of individuals to handle all of these events likely explains why some arrive to adulthood faster than others. All coastal copepods studied to date have delayed C5 development (Landry 1983), but *Calanus marshallae* seems to have the longest duration at this stage.

Some insights into the heritability of several fitness characteristics were gained from this study. First, total development time from N3 to older copepodite stages was highly variable among families suggesting that this is not a major factor affecting individual fitness. This is further supported by the observation that families that arrived to C5 first did not reach adulthood first. Additional among-family variability in development time came during the fifth copepodite. Such a change in rate of development and overall variability in development among families was noted by McLaren & Corkett (1978) who found that for *Pseudocalanus* the variability in the N1 to C1 developmental time was greater than for the period N1 to adult. This suggests that the overall egg-to-adult developmental process comes under control of different genetic mechanisms at several points. For *Calanus marshallae,* changes in genetic control probably come at N3 and C5 stages.

Another parameter often associated with fitness is female body size. For *Calanus marshallae,* length of females was highly variable. Also, there was no relation between total length of females and total length of their female offspring. These facts suggest that there is no selective advantage to being large, a conclusion supported by the observation that fecundity among individual female *C. marshallae* is unrelated to body length (Peterson 1980). MacLaren & Corkett (1978) found the opposite, that large female *Pseudocalanus* produce large daughters. This result would be expected because fecundity in this copepod is positively correlated with body size.

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