

Rates of egg production by the copepod *Calanus marshallae* in the laboratory and in the sea off Oregon, USA

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ABSTRACT: Egg production by adult female *Calanus marshallae* Frost was studied in the laboratory by making a census of the number of eggs produced each day by individuals maintained on a diet of the diatom *Thalassiosira weissflogii*. When fed ad libitum individuals produced a clutch of 30 eggs every 30 h on average. Egg production rates were influenced by food concentration, ranging from 0 d⁻¹ when females were kept in filtered seawater up to 24 eggs d⁻¹ at food concentrations ≥ 3500 cells ml⁻¹. Maximum rates of ingestion of phytoplankton cells also occurred at 3500 cells ml⁻¹. Females maintained at food concentrations ranging from 2000 to 3500 cells ml⁻¹ produced the same number of clutches per unit time as females maintained at >3500 cells ml⁻¹, but produced fewer eggs per clutch. At food concentrations < 2000 cells ml⁻¹ the frequency of clutch production declined to one clutch per 4 d. Egg production declined to 0 after 1 d when females were starved. When starved for periods up to 10 d, an interval of 0.4× the starvation interval was required before egg production was re-initiated. Females maintained at 3500 cells ml⁻¹ had a gross efficiency of egg production of 29.0% and a reproductive output of 6.9% of their body weight per day. The latter is 3× the C5-to-female growth coefficient. In situ egg production rates were also determined, using the egg-ratio method, and were usually food-limited. In the sea the functional response of egg production to food concentration in situ was similar to that measured in the laboratory.

INTRODUCTION

The copepod *Calanus marshallae* is common in the coastal plankton of the northeast Pacific Ocean, ranging from the Bering Sea south to northern California, USA. In the Bering Sea this species occurs from March through September (Smith & Vidal 1984, 1986) and off Oregon, USA, from February through October (Peterson & Miller 1977). In both systems the highest population densities occur during summer only in the waters of the middle and inner shelf (depths < 100 m) where chlorophyll concentrations are high, ranging from 5 to 20 µg l⁻¹ off Oregon (Peterson et al. 1979, Small & Menzies 1981) and 1 to 10 µg l⁻¹ in the Bering Sea (Smith & Vidal 1984, 1986). Such food concentrations span the range over which ingestion and egg production rates range from nearly zero to a maximum for the closely-related and similarly-sized *C. pacificus* (Frost 1985). Thus if *C. marshallae* has similar physiological requirements then temporal and spatial variations in phytoplankton concentration could be a key factor

controlling its grazing and egg production rates in the sea, and therefore its potential for maintaining a large population in the waters of the inner continental shelf.

The object of the study described in this paper was to define quantitative relationships between food concentration, feeding rates and rates of egg production by adult female *Calanus marshallae*. One goal was to sort out the effect of food concentration on clutch size and on the frequency at which individual females produce a clutch of eggs. A second was to examine relationships between egg production rate vs food concentration and feeding rate vs food concentration. From these 2 measurements the gross efficiency of egg production was calculated. Third, laboratory measurements of fecundity were compared to in situ measurements to determine if fecundity was food-limited in the sea. Fourth, since during the upwelling season this copepod is frequently subjected to periods of very low food concentration (< 1 µg chlorophyll a l⁻¹ during periods of active upwelling events) the effects of varying periods of starvation on egg production were examined. Finally,

the hypothesis is discussed that high phytoplankton concentration is a necessary but not sufficient condition for population maintenance and population growth in the coastal upwelling zone of the west coast of the USA.

METHODS

Female *Calanus marshallae* Frost were collected at stations 10 to 15 km offshore from Newport, Oregon, USA, by suspending a 0.5 m diameter net of 220 μm mesh at a depth of 10 m for a few minutes while the ship was drifting. Zooplankton was placed into 10 l insulated containers filled with surface seawater and transported to the laboratory. Within 5 h of capture, females were sorted and placed into 600 ml glass containers, 1 per container. When sorting care was taken to select only those females which seemed healthy: individuals which swam erratically, had broken antennules or missing furcal setae were not used in any experiments. Females were fed *Thalassiosira weissflogii* which was grown in f/2 media (Guillard & Ryther 1962). The copepods were held in the laboratory with the phytoplankton food for 48 h before being used in an experiment. Mortality was always low and occurred only during this acclimation period. All work was done in a constant-temperature walk-in chamber set at a temperature of 10 °C, under continuous low light (10 to 30 $\mu\text{E m}^{-2} \text{s}^{-1}$). This temperature was selected because it is the average value observed for the upper 20 m water column over the inner and middle shelf off Oregon during summer (Huyer 1977).

Relationships between phytoplankton concentration and egg production rate were studied by making a census of the number of eggs produced each day by individual females over an 8 to 13 d interval. Food concentration was measured daily using a Fuchs-Rosenthal counting chamber (during 1977) and a Model B Coulter Counter (during 1978). The food suspension was renewed daily. Ingestion rates were calculated using equations in Frost (1972). The volume of the *Thalassiosira weissflogii* clone was 1100 $\mu\text{m}^3 \text{cell}^{-1}$ (= 125 pg carbon cell^{-1} ; from Strathmann 1967). Relations between (1) weight of eggs produced per day vs female weight, known as 'reproductive output' sensu Clarke 1987, and (2) weight of food consumed per day vs female weight were calculated using weight data in Peterson (1986): egg = 0.75 μg dry wt, mean weight of a female = 260 μg dry wt ($n = 23$).

The effect of starvation on egg production was investigated by holding females in glass-fiber (0.8 μm pore size) filtered seawater for periods ranging from 1 to 10 d. After being starved they were fed ad libitum concentrations of *Thalassiosira weissflogii* to determine the time lag between starvation period and resumption of

egg production. Ad libitum food concentrations were determined to be at concentrations of *T. weissflogii* $\geq 3500 \text{ cells ml}^{-1}$ (shown below in Fig. 4).

Egg cannibalism was evaluated in 2 ways. First, eggs which were known to be < 8 h old were placed into 600 ml beakers each containing 1 female which had been underfed for several days. After 24 h the number of eggs remaining were counted. Since it is possible to distinguish between newly-laid and older eggs, the experimental eggs could be differentiated from any eggs which a female might have laid over the course of the experiment. Cannibalism was also evaluated by comparing the number of eggs in clutches that were known to be less than 2.5 h old (i. e. clutches of eggs no older than the 8-cell stage) to the number of eggs in clutches older than 2.5 h. For this analysis I used clutch size data from those females that had been fed ad libitum. The hypothesis tested was based on the assumption that if well-fed females cannibalized their eggs during the experiments then clutches that were composed of 'older' eggs should contain fewer eggs on average than clutches which were recently laid.

Egg production in situ was estimated using the egg-ratio method of Edmondson et al. (1962). Fecundity was calculated from estimates of the abundances of eggs and females in the sea, and from laboratory measurements of egg hatching times as a function of temperature (Peterson 1980). Samples for study of the vertical distribution and abundance of females and eggs were collected from 5 to 9 discrete depths of 1, 5, 10, 15, 20, 30, 50, 70, and 90 m (water depth permitting) at each of 5 stations 1, 3, 5, 7, and 10 n miles from shore on 9 dates along several transect lines over the continental shelf off Oregon and Washington during July and August 1977. Samples were collected with the aid of a pump and 10 cm diameter hose (Miller & Judkins 1981). To collect zooplankton a 0.5 m diameter net of 64 μm mesh was suspended in the pump stream. Sample volumes were 2 m^3 . In addition, 100 ml samples were taken from the pump stream and analysed for chlorophyll concentration following standard techniques (Strickland & Parsons 1972). Egg-ratio fecundity was calculated from egg and female abundances integrated over the upper 50 m (for eggs) and for the entire water column (for females) then averaged for the 1, 3, 5, and 7 nm stations.

RESULTS

Average clutch size

The mean rate of egg production by individual female *Calanus marshallae* fed excess amounts of food (3500 to 8000 cells ml^{-1} of *Thalassiosira weissflogii*) was 23.9 eggs $\text{female}^{-1} \text{d}^{-1}$ (Fig. 1). On many census

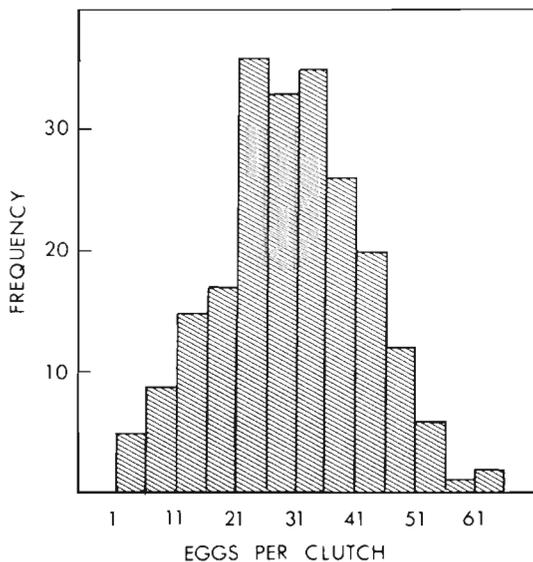


Fig. 1. *Calanus marshallae*. Frequency distribution of the number of eggs per clutch produced by adult females fed excess amounts of *Thalassiosira weissflogii*. Data are from a daily census of individual females kept in separate experimental containers

days no eggs were produced indicating that females do not produce a clutch of eggs every day. A total of 217 clutches were laid in 270 female-days of observations, or an average of 0.8 clutches d^{-1} , equivalent to 30 h between the production of a clutch. The frequency distribution of number of clutches laid each day was: none, 53; one, 209; two, 8. Mean clutch size was 29.7 eggs.

There were some slight but significant seasonal differences in clutch size (based on paired *t*-tests). Table 1 shows that females collected in May produced a significantly greater number of eggs than females collected in January or July to September, 39.2 eggs clutch $^{-1}$ vs the mean of 29.7 eggs clutch $^{-1}$ observed in all other dates combined.

The mean number of eggs clutch $^{-1}$ for females fed ad libitum was regressed on female body length to test the hypothesis that larger females produced more eggs than smaller females. Variations in clutch size were found to be unrelated to female body length ($r = -0.0093$, $n = 26$, $F_{1,24} = 0.0062$).

Effects of food concentration on daily egg production rates

The effect of food concentration on the rate of egg production was measured on 57 individual females. Fig. 2 shows that the rate of egg production increased linearly as food concentration increased up to a maximum of 24 eggs female $^{-1} d^{-1}$ at 3500 cells ml^{-1} . Above that concentration (equivalent to 450 μg carbon l^{-1} or about 10 μg chlorophyll l^{-1}) egg production was constant.

The relation between feeding rate and food concentration for the same 57 females is also shown in Fig. 2. Feeding rate increased linearly over cell concentrations ranging from 300 to 3500 cells ml^{-1} . At concentrations greater than 3500 cells ml^{-1} ingestion was constant at 10 924 cells h^{-1} ($= 1.37 \mu g$ carbon h^{-1} or 32.8 μg carbon d^{-1}). At this rate an average female *Calanus marshallae* (260 μg dry wt, or 104 μg carbon) consumes 31.5% body weight d^{-1} .

The ratio, egg production rate:ingestion rate, is a measure of the gross efficiency of egg production. Table 2 shows that the efficiency of egg production (calculated on a gravimetric basis) increased from 0.22 at the lowest food concentrations (300 cells ml^{-1}) to a maximum of 0.29 at food concentrations in excess of 3000 cells ml^{-1} .

The reproductive output of females fed ad libitum was 0.069 of body weight d^{-1} (6.9%) as eggs. This value is 3 \times greater than the C5-to-female growth rate of 2.4% d^{-1} and 2.5 \times less than the growth rate of younger copepodites, 17.6% d^{-1} (Peterson 1985).

Table 1. *Calanus marshallae*. Egg production by adult females fed *Thalassiosira weissflogii* ad libitum. Females were acclimated to laboratory conditions for 48 h before start of each experiment. Temperatures were $\pm 1^\circ C$ of sea surface temperature on the collection date. Data shown are average number of eggs laid by several individual females (N_φ) over a 4 to 13 d period. N_c is total number of clutches of eggs laid during each experimental period. $S_{\bar{x}}$ is standard error of mean

Date	Temperature ($^\circ C$)	N_φ	N_c	Mean	$S_{\bar{x}}$
6-19 Jan 1977	10	5	54	24.9	1.60
23-30 Jun 1977	10	4	26	27.4	2.60
21-29 May 1978	10	4	32	39.2	1.75
27 Jun-9 Jul 1978	10	7	51	31.3	1.67
7-10 Aug 1978	10	4	14	32.2	2.05
7-14 Sep 1978	10	7	34	27.2	1.60
15-22 Aug 1978	15	5	27	25.8	2.67

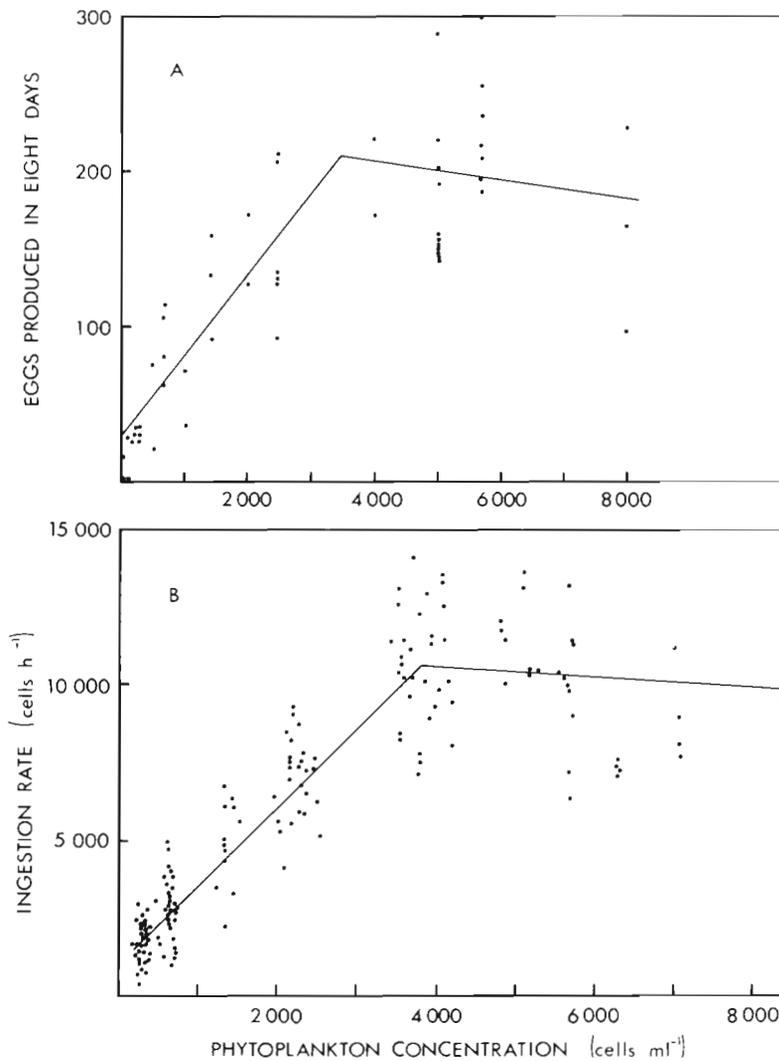


Fig. 2. *Calanus marshallae*. Relation of (A) egg production rate and (B) phytoplankton ingestion rate to phytoplankton concentration for females fed diatom *Thalassiosira weissflogii*. Regression equations for egg production (Y) as function of food concentration (X) were: $Y = 14.94 + 0.0608 X$, ($r = 0.88$) for the steep ascending line, and $Y = 198.5 - 0.0012 X$, ($r = -0.027$) for the plateau. Slope of the plateau did not differ from zero ($F_{1,23} = 0.015$). Corresponding regression equations for ingestion rate (Y) vs phytoplankton concentration (X) were: $Y = 1147.7 + 2.51 X$, ($r = 0.77$) for the ascending line, and $Y = 11677.7 - 0.28 X$, ($r = -0.28$) for the plateau. Slope of the plateau was different from zero ($F_{1,42} = 4.59$).

Table 2. *Calanus marshallae*. Gross efficiency of egg production calculated from egg production and ingestion rate data shown in Fig. 2. 'C' indicates carbon calculated assuming egg C = $0.4 \times$ egg dry wt. The phytoplankton, *Thalassiosira weissflogii*, contained 125 pg carbon cell $^{-1}$

Cells ml $^{-1}$	Eggs d $^{-1}$	Egg C d $^{-1}$	Phytoplankton cells ingested h $^{-1}$	Carbon ingested d $^{-1}$	Gross efficiency of egg production
300	4.1	1.2	1901	5.7	0.22
500	5.7	1.7	2403	7.2	0.24
750	7.6	2.3	3255	9.8	0.24
1000	9.5	2.8	3658	11.0	0.26
2000	24.7	7.4	8678	26.0	0.29
3500	28.5	8.5	9933	29.8	0.28

Effects of food concentration on the frequency of production of a clutch of eggs

Fig. 3 shows that the number of clutches produced during an 8 d interval depended upon food concentration. Females maintained at food concentrations

ranging from 0 to 500 cells ml $^{-1}$ laid 0 to 2 clutches during the 8 d experimental period, whereas females maintained at food concentrations ranging from 2000 to 8000 cells ml $^{-1}$ produced on average 6.8 clutches over an 8 d period. The number of clutches produced reached a maximum at a food concentration of 2000

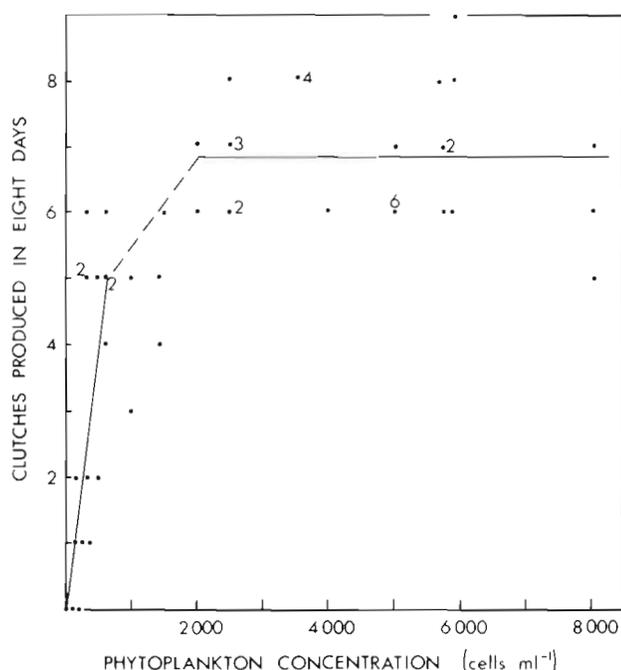


Fig. 3. *Calanus marshallae*. Relation between number of clutches produced in 8 d, and phytoplankton concentration. Integers near various data points indicate number of discrete observations at that coordinate

cells ml^{-1} , lower than the food concentration which produced the maximum number of eggs per clutch ($3500 \text{ cells ml}^{-1}$). This suggests that egg production may be a 2-step physiological process: one step involves the production of a clutch of eggs on a predetermined schedule and the second step, the energetics controlling the number of eggs within that clutch. At food concentrations above $2000 \text{ cells ml}^{-1}$ a clutch is produced every 30 h on average but the number of eggs produced per clutch will not be a maximum until food concentrations exceed $3500 \text{ cells ml}^{-1}$. Below $2000 \text{ cells ml}^{-1}$ ($250 \mu\text{g carbon l}^{-1}$) food-limitation not only decreases the number of eggs produced per unit time but lengthens the usual 30 h time interval between the production of a clutch.

Effects of starvation on fecundity

Females which were placed into filtered seawater produced eggs only during the first 24 h following capture, indicating that eggs result from material obtained from recently ingested food rather than from body reserves. Fig. 4 shows that females fed following a single day of starvation produced eggs after an additional 24 h. However, females that were starved for periods as long as 10 d and then fed, did not resume egg production until an interval 0.4 times the number

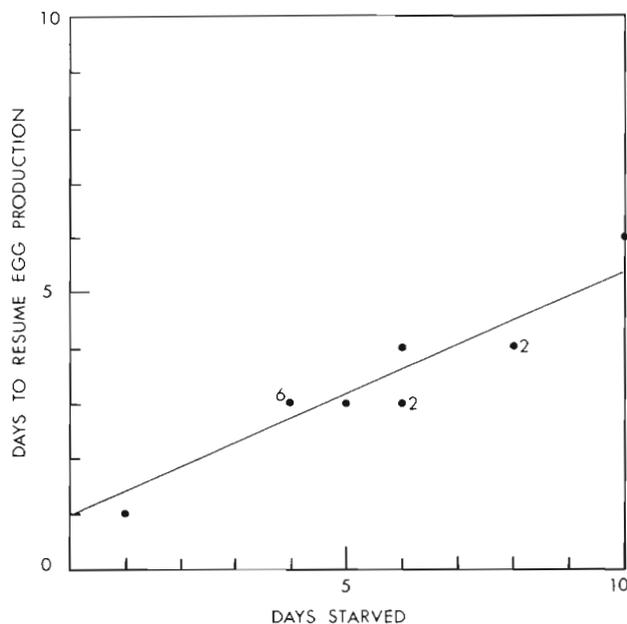


Fig. 4. *Calanus marshallae*. Relation between days starved (X) and time required for resumption of egg production (Y) after females were once again fed, for 14 individual females. Integers near various data points indicate number of discrete observations at that coordinate. Regression equation was $Y = 0.43 X + 1.00$, ($r = 0.92$, $F = 62.2$)

of days starved. For 2 experiments the rate of egg production by females fed ad libitum following a 5 d and a 6 d period of starvation did not return to normal levels until a time lag that was twice the starvation interval (Fig. 5).

Effects of cannibalism on egg production measurements

In 12 experiments, females maintained at food concentrations ranging from 300 to $650 \text{ cells ml}^{-1}$ ate 68 % of the eggs offered over a 24 h period. However among well-fed females there was no evidence of cannibalism: the mean number of eggs in clutches that were < 2.5 h old was not different from the number of eggs in older clutches: 30.2 ± 3.91 (95 % confidence interval) and 29.7 ± 5.94 , respectively.

In situ fecundity

Egg-ratio fecundities were correlated with chlorophyll concentration (Fig. 6). Over the domain $0 < X < 10 \mu\text{g chlorophyll a l}^{-1}$ the slope of the regression (1.96) was the same as the slope obtained for the regression of egg production rate vs phytoplankton concentration measured in the laboratory (slope = 2.00

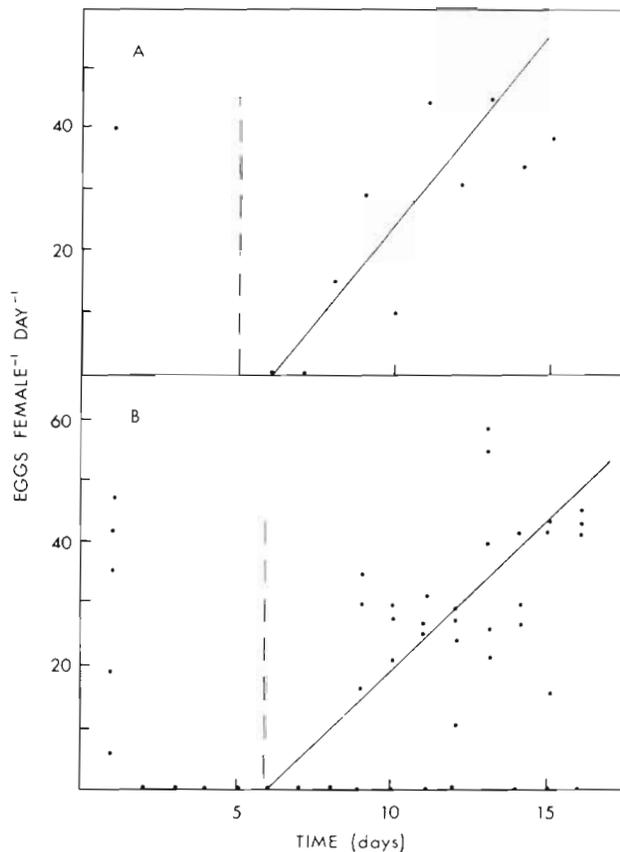


Fig. 5. *Calanus marshallae*. Egg production by females starved for (A) 5 d and (B) 6 d then fed ad libitum, for (A) a single female and (B) 5 females kept individually in separate experimental containers. Relevant statistics are as follows: (A) $Y = 6.36X - 39.36$, ($r = 0.82$, $F = 10.8$, $S_b = 1.93$); (B) $Y = 5.10X - 33.01$, ($r = 0.62$, $F = 16.0$, $S_b = 1.27$)

when the laboratory data were converted into eggs d^{-1} and food concentration data expressed in terms of equivalent chlorophyll concentration, assuming C:chl = 40). At concentrations $> 10 \mu g$ chlorophyll l^{-1} there were too few data points to decide if the overall relation was linear or curvilinear.

DISCUSSION

Results show that in the laboratory and in the sea egg production by *Calanus marshallae* is highly dependent upon food supply. When deprived of food, individuals cease to produce eggs within 24 h. The implication is that female *Calanus* spp. produce eggs from food ingested during the 24 h preceding an egg laying event, suggesting a close coupling between food supply and fecundity, a result noted by others (Checkley 1980 for *Paracalanus parvus*, Durbin et al. 1983 for *Acartia tonsa*, Frost 1985 for *Calanus pacificus*, Hirche

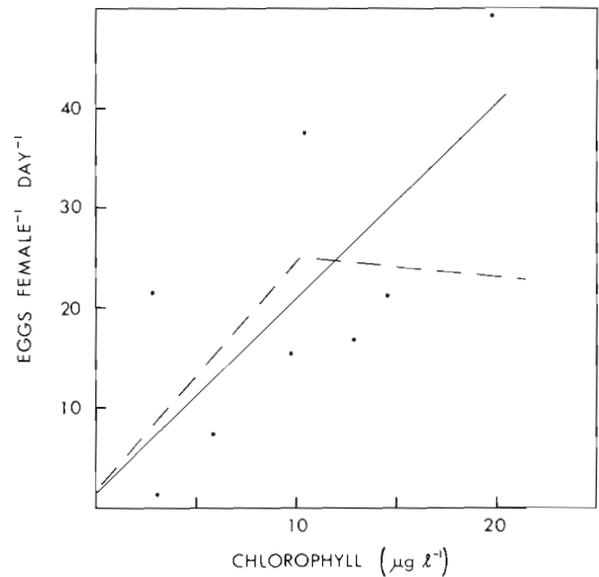


Fig. 6. *Calanus marshallae*. Scattergram of in situ egg production rate calculated from the egg-ratio method, (Y) vs in situ chlorophyll concentration (X). Chlorophyll data are averages over upper 10 m of water column and egg data for upper 50 m of water column. Solid line: regression line for egg-ratio data, $Y = 1.97X + 1.62$ ($r = 0.72$, $F = 6.55$); dashed line: regression lines from laboratory data on egg production vs food concentration redrawn from Fig. 2. Slopes of laboratory and in situ rates (2.00 vs 1.97 were not different)

& Bohrer 1987 for *C. glacialis*, and Peterson & Bellantoni 1987 for *Temora longicornis* and *C. chilensis*). Because of this close coupling between egg production and food supply, fecundity of female *C. marshallae* in the Oregon upwelling zone is likely to be highly dependent upon short-term variations in food concentration caused by upwelling events. The expectation is that egg production should be high during relaxation of upwelling (when chlorophyll concentrations frequently exceed $10 \mu g l^{-1}$) and low during active upwelling events (when chlorophyll concentrations in the nearshore zone are usually less than $1 \mu g l^{-1}$). This was seen in the in situ fecundity data (Fig. 6) thus leading to acceptance of the hypothesis that the presence of high phytoplankton concentrations is a necessary condition for *C. marshallae* to establish a large population in the nearshore zone of the coastal upwelling system off the west coast of the United States.

Prolonged periods of starvation (in excess of a few days) seemed to be detrimental to oogenesis of female *Calanus marshallae*. Individuals which were starved for several days then fed exhibited a lag of 3 to 6 d before resuming egg production. This response is similar to that reported for *C. glacialis* by Hirche & Bohrer (1987). *C. marshallae* living in the Oregon upwelling zone encounter periods of low food concentration during active upwelling events. Such events are charac-

terized by low chlorophyll concentrations ($< 1 \mu\text{g l}^{-1}$), a condition that may persist for periods of 4 to 7 d, occurring several times each month (Small & Menzies 1981). Egg production must nearly cease during active upwelling events. With the onset of relaxation of the upwelling when chlorophyll concentration increases, an immediate resumption of egg production would not be expected because of the time lag between resumption of feeding and renewed oogenesis, shown in Figs. 4 and 5. Thus egg production and food supply become decoupled, and any burst in egg production by *Calanus* spp. would not be expected until after perhaps 3 or 4 d of high chlorophyll concentrations. This suggests that egg production by copepods in upwelling systems depends not only upon the absolute amount of phytoplankton available but on the frequency and duration of periods of active upwelling, a hypothesis previously advanced by Borchers & Hutchings (1986). Thus any study of the degree of coupling between primary production and secondary production should take into account time lags between changes in food supply and fecundity.

Compared to other copepods, *Calanus marshallae* at 24 eggs d^{-1} is not a particularly fecund species, both in terms of absolute number of eggs produced and on a weight-specific basis. Daily egg production rates in excess of 100 to 200 eggs d^{-1} have been reported for *Centropages typicus* (Dagg 1978, Smith & Lane 1985), 60 to 140 eggs d^{-1} for *Acartia tonsa* (Ambler 1985, Beckman & Peterson 1986, Sullivan & McManus 1986), and up to 80 eggs d^{-1} for *C. pacificus* (Hirakawa 1979, Peterson 1980, Runge 1984) and *Calanoides carinatus* (Borchers & Hutchings 1986). Most species fall within the range of 20 to 50 eggs d^{-1} , with several *Calanus* species at the low end of the range (*C. finmarchicus*, Marshall & Orr 1955; *C. glacialis*, Hirche & Bohrer 1987; *C. chilensis*, Peterson & Bellantoni 1987; *C. marshallae*, this study; *Neocalanus tonsus*, Ohman 1987). When weight-specific egg production rates are compared, *C. marshallae* is again among the least fecund producing no more than 7 % of its body weight per day as eggs, compared to 3.0 % for *N. tonsus* (calculated from Ohman 1987), 12 to 18 % for *C. pacificus* (Runge 1985), 37 % for *Paracalanus parvus* (Checkley 1980), and up to 106 % d^{-1} for *A. tonsa* (Ambler 1985; see her paper for a more complete listing of this type of data). The general pattern is that the largest copepods seem to produce the fewest eggs per day with the lowest daily investment of body weight. One hypothesis explaining this low investment in any single egg laying event is that adult female *Calanus* species may be longer-lived on average than, for example, female *A. tonsa*, and so may have an equal or perhaps greater production of eggs over the lifetime of any given female. Thus, as is well known, a complete description

of the population dynamics of any species requires not only information on factors controlling daily egg production rates, but knowledge of a female's lifespan and the total number of eggs produced during her lifetime. Such work was beyond the scope of this study.

This study also demonstrated that the rate at which eggs are produced was directly related to the rate at which food was ingested. Both rates depended upon phytoplankton concentration, and were limiting over the range 0 to 450 $\mu\text{g C l}^{-1}$ (0 to 10 $\mu\text{g chlorophyll a l}^{-1}$), but saturated above the upper limit of that range. The ratio of the 2 rates, which is the gross efficiency of egg production, is nearly the same for the several species which have been studied to date. Values reported are 0.29 for *Calanus marshallae* (this study), 0.32 for *C. pacificus* (calculated from Frost 1985 and Runge 1985), 0.33 for *Paracalanus parvus* (Checkley 1980), and 0.36 for *Acartia tonsa* (Kjørboe et al. 1985a). Kjørboe et al. (1985b) have suggested that if the gross efficiency of egg production is reasonably constant among different coastal copepod species (corroborated in this study) then one can use measurements of egg production as an alternate and independent method of calculating in situ grazing rates. In a study of in situ feeding of several copepod species in the Kattegat and Skagerrak area, good agreement was shown between ingestion rate calculated from gut fluorescence data, egg production data (assuming a 33 % gross efficiency of egg production), rate of particle removal (via Coulter Counter measurements) and disappearance of chlorophyll. Given the difficulties and uncertainties of estimating in situ grazing rates, the incorporation of as many independent techniques, such as egg production, should be encouraged.

Among copepods which broadcast a discrete clutch, the interval between the production of a clutch has been worked out for only 2 species, *Calanus pacificus* and *C. marshallae*. Runge (1984) reported that well-fed females produced a clutch every 17 to 18 h at 12 °C but at low food concentrations the interval between clutches was as long as 5 d. For *C. marshallae* at 10 °C, the interval between clutches for well-fed females was 30 h, increasing to 4 to 8 d for underfed females. Neither Runge's nor my estimate was exactly 24 h, suggesting the absence of an endogenous diel rhythm. Both Runge and I maintained female *Calanus* spp. in the laboratory under continuous dim light (measured to be 10 to 30 $\mu\text{E m}^{-2} \text{s}^{-1}$ in my case) and females were acclimated at least 2 d before being used in any experiments. Thus, the data presented here may represent the *maximum* rates at which a clutch is produced as a function of food supply alone. In the sea however, it is not known if the females adhere to the 18 or 30 h schedule. Diel periodicity in feeding (i.e. a greater nocturnal feeding rate compared to the daytime feed-

ing rate) could impart a diel signal to egg production. Runge (1980) has shown such a feeding behavior for *C. pacificus* and he has also shown (Runge 1985) that in the sea *C. pacificus* lay most of their eggs from midnight until 09:00 h. This suggests that for this species, even though a clutch can be produced as often as once every 18 h in the laboratory, in the sea the interval is probably every 24 h. For female *C. marshallae* evidence for diel vertical migration is equivocal (Peterson unpubl.) and diel variations in feeding have not been looked for in this animal. So, it is an open question whether or not well-fed females produce a clutch once each day, every 30 h (as in the laboratory), or if a diel feeding signal coupled with a 30 h oogenesis cycle might impose a 48 h interval between the production of a clutch. Further study of the relation between the influence of nocturnal feeding and egg production are required to resolve this matter. Endogenous rhythms are possible as well as shown by Marcus (1985).

Evidence was presented showing that well-fed females do not eat eggs but that underfed *Calanus marshallae* were capable of ingesting their own eggs. However, I do not believe cannibalism to have biased any of the egg production data presented in this paper for the following reason: consider, for example, that female *C. marshallae* were producing eggs at maximum rates at food concentrations as low as 2000 cells ml⁻¹ but were later eating some of them during the 24 h experimental period. Under this condition the true gross efficiency of egg production would have to increase greatly with decreasing food concentration, from 0.28 at 3500 cells ml⁻¹ (Table 2) to 0.40 at 2000 cells ml⁻¹ in this example. Such a result would contradict the results of Vidal (1980) who showed that net growth efficiencies decreased with food concentration, and also of Checkley (1980) who found that the gross efficiency of egg production in *Paracalanus parvus* in terms of nitrogen decreased with food concentration. Therefore I suggest that the egg production data are free of any significant influence of cannibalism.

In conclusion, *Calanus marshallae* is a boreal neritic copepod that requires high concentrations of phytoplankton for egg production. Maximum rates of 24 eggs female⁻¹ d⁻¹ occurred only at and above phytoplankton concentrations of 450 µg carbon l⁻¹ (10 µg chlorophyll a l⁻¹). Since eggs are produced only from recently-ingested food, this copepod can only achieve maximum fecundity when its feeding rates are at a maximum. This requirement for high phytoplankton concentrations is met in the waters of the inner and middle continental shelf, and may explain in part the dominance of *C. marshallae* over the inner and mid-shelf (as opposed to the outer shelf) regions of the Oregon and Washington shelf and in the Bering Sea. However, even though high chlorophyll concentration

is a necessary condition for population maintenance and population growth, it is not a sufficient condition. Peterson et al. (1979) and Peterson (1980) have suggested from data on the vertical distribution of *C. marshallae* life cycle stages that the population is retained in the Oregon upwelling zone because copepodites minimize their residence time in the seaward-flowing euphotic zone and because newly-moulted females perform a downward ontogenetic migration into shoreward-moving deep water. Because of this behavior females are carried shoreward to the food-rich waters of the inner shelf where egg production takes place. Without such an ontogenetic migration a large population of this species could not become established within the inner portions of the upwelling zone. It would appear from this study that the ontogenetic migration has adaptive value because the end result is that females are returned shoreward where phytoplankton concentrations are high and where egg production rates are highest.

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