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Resource-satiated population growth of the copepod *Pseudocalanus* sp.

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With 10 figures and 1 table in the text

Abstract

The hypothesis of resource-limitation of population growth of *Pseudocalanus* sp. was tested in Dabob Bay, Washington state. Five independent indices were inconsistent with the resource-limitation hypothesis: (1) interannual variations in abundance depend on the initial conditions, independent of within-year fluctuations in resources, (2) generation times in the field correspond to those for food-satiated copepods, (3) seasonal changes in prosome length are consistent with those for food-satiated animals, (4) ambient phytoplankton abundance nearly always meets or exceeds the critical concentration for growth, (5) females reproduce continuously, exhibiting only damped seasonal changes in reproductive rate as assessed from a modified egg ratio method. The food limitation paradigm is not applicable to *Pseudocalanus* sp., for which predation is a more likely mechanism of population regulation.

Introduction

Three principal mechanisms regulate the growth and abundance of natural populations: physical processes, resource-limitation, and predation. In the plankton, McLaren (1969, 1978) has argued that temperature is a physical mechanism of overriding importance in regulating population growth. Physical transport processes may also alter rates of population increase (e. g., Wroblewski 1982). On the other hand, the view that the growth and coexistence of natural populations are controlled by resource-limitation has been widely adopted in investigations in marine pelagic ecosystems (e. g., Steele 1974; Steele & Frost 1977; Conover & Huntley 1980; Durbin et al. 1983). The assumption of resource-limited growth also underlies numerous studies of suspension-feeding mechanisms. By contrast, Hrbáček (1962), Brooks & Dodson (1965), Zaret (1980), Wright & O'Brien (1984), and others have emphasized the importance of predation in influencing the abundance patterns and species composition of zooplankton assemblages, particularly in freshwater environments.

In the present study, I test the hypothesis of resource-limited growth of *Pseudocalanus* sp., a small-bodied planktonic copepod which is numerically dominant in much of the north temperate ocean (Corkett & McLaren 1978). The study site is Dabob Bay, a fjord contiguous with Puget Sound. Selection of this study site reduced the effects of advection as a population control mechanism and permitted repeated sampling of a population over time. Five independent indices were used to

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evaluate the importance of resource-limitation in controlling the growth dynamics of *Pseudocalanus*. These indices included measures of food requirements of individual copepods as well as population level responses to available resources. The importance of predation in controlling *Pseudocalanus* population growth is documented elsewhere (Ohman 1983).

The present investigation builds on a foundation of laboratory investigations of biology of *Pseudocalanus*. These experiments have established that species of the genus *Pseudocalanus* have low food requirements for maximum rates of ingestion (Frost 1974, 1980; Paffenhöfer & Harris 1976), growth (Paffenhöfer & Harris 1976; Vidal 1980 a, Klein Breteler et al. 1982), development (Vidal 1980 b), and maximum body size (Vidal 1980 b; Klein Breteler & Gonzalez 1982). Here I investigate the realized dynamics of a natural copepod population in contrast to the potential dynamics as inferred from laboratory study.

Materials and methods

Sampling and analytical methods

Sampling was performed at Sta. D, the deepest location in Dabob Bay (mean depth = 185 m) from the R/V's ONAR, HOH, or a float plane. Temperature profiles were determined with a conductivity-temperature-depth unit or occasionally with reversing thermometers or a calibrated bathythermograph. Hydrocasts for chlorophyll *a* (Chl *a*) were made with 2.5–5.0 l Niskin bottles, usually at 6–8 depths. Chl *a* retained on a Gelman A/E glass fiber filter was extracted in 90 % acetone either by sonication or by cold extraction at 4 °C in the dark for 24–36 hours, then analysed fluorometrically after the method of Lorenzen (1966). Seawater from 6–12 m was also size-fractionated through 73- μ m Nitex screens. Each aliquot flowed through a single screen under low vacuum. Chl *a* was converted to organic carbon assuming the average ratio of Chl *a* : C was 0.025 for the depths where size fractionation was performed (Welschmeyer & Lorenzen 1984). Temperature and Chl *a* data are reported completely in Ohman (1983).

Pseudocalanus sp. was sampled with a 73- μ m, 0.50-m diameter net during 1979–1980 except for one sampling date (12-I-79) when a 110- μ m, 0.75-m net was used. Replicate samples (2–4) were usually taken in the daytime within one half hour of each other. Vertical hauls were made from a depth of 150–0 m on most dates in 1979 and early 1980 and from 180–0 m after April 1980. The abundance of overwintering copepodids on 7-I-1973 and 16-I-1982 was determined from replicate vertical hauls with a 73- μ m mesh net, from ca. 180–0 m. The maximum abundance of *Pseudocalanus* sp. females in these two years was determined with a 216- μ m, 1-m net hauled vertically over the same depths. Samples were preserved in 10 % formalin buffered with sodium borate. Eggs and copepodids were stained with Phloxine B and enumerated from quantitative splits from a Folsom splitter. Usually 200–300 *Pseudocalanus* copepodids (range: 177–1109) and 300–500 *Pseudocalanus* eggs (range: 40–1453) were counted per sample.

Three forms of *Pseudocalanus* occur in Dabob Bay. These are probably sibling species (B.W. Frost pers. comm.). The *P. elongatus*-like form (designated *Pseudocalanus* sp. herein) comprised 90 % or more of the *Pseudocalanus* in Dabob Bay during 1979–1980 and is the sole form reported on here.

Prosome length and mass-length determinations

Pseudocalanus sp. females were randomly subsampled and prosome length measured on 200–300 preserved individuals from each date. Nonparametric confidence intervals were calculated for the median length and one half of the measurement error of 19.6 μ m added to both tails. Preservation had no detectable effect on prosome length ($P > 0.10$, Mann-Whitney U; $N_{\text{fresh}} = 91$, $N_{\text{preserved}} = 101$). Length and mass determinations were made on fresh copepods collected in April and May when females did not have prominent lipid droplets. Eggs were teased away from ovigerous females on moist Nuclepore filters, females rinsed with 10 μ l of distilled

water, then measured and placed in shallow foil wells. Copepods were dried at 55 °C for at least 24 h, then weighed individually on a Cahn 25 electrobalance to the nearest 0.1 µg. After regression of \log_e transformed values of dry mass vs. prosome length, a minimum variance unbiased estimator was calculated for the antilogged regression equation (Beauchamp & Olson 1973) and the same procedure carried out for clutch size vs. prosome length.

Definition of generations

Sequential generations of *Pseudocalanus* sp. were identified by changes in the modal size of adult females and by peaks in relative abundance of copepodid stages IV and V (CIV and CV), after the method of McLaren (1978). With the appearance of a new generation the modal length changes abruptly, then remains relatively stable until the following generation appears. For purposes of illustration prosome length changes are shown as variations in median length, although median and modal length do not change in an identical manner. The generation time was approximated as the time in days between the appearance of new, dominant size modes of adult females or, in midsummer, between peaks in relative abundance of CIV + CV.

The 24-h average temperature experienced by nauplius I (NI) through CII and the daytime temperature experienced by CIII through adult (and eggs) was estimated from the temperature in the chlorophyll maximum layer (TCM). In Dabob Bay variations in TCM with Julian day (JD) can be described by a modified Gamma function:

$$TCM = 7.5 + 6.0 X^{1.319} e^{0.385(1-X^{3.426})} \quad (1)$$

$$\text{where: } X = \frac{(365-JD)}{143}$$

Regardless of the stimuli for vertical aggregation of copepods, TCM appears to be a suitable approximation of the average temperature experienced by the *Pseudocalanus* population. Night temperatures for stages CIII-CVI (and eggs) were estimated from the temperature at the weighted mean depth where females occurred by night (range: 7.6–11.4 °C), since late developmental stages exhibit reverse vertical migration behavior (Ohman et al. 1983). The fraction of a day spent at the day temperature was estimated from seasonal variation in daylight hours (HD) from a modified Gaussian function:

$$HD = 8.37 + 7.68 e^{-\frac{(Y-172)^2}{11327}} \quad (2)$$

$$\text{where: } Y = JD \quad \text{for } JD < 355$$

$$Y = JD - 365 \quad \text{for } JD \geq 355$$

(see Ohman [1983] for details.) Egg duration (ED, in days) as a function of temperature (T) was calculated from Corkett & McLaren (1978, data of Thompson 1982):

$$ED = 1845 (11.45 + T)^{-2.05} \quad (3)$$

Results

Population growth of *Pseudocalanus* sp. occurs primarily from March through July or August (Fig. 1), despite the episodic availability of phytoplankton later in the year. Eggs and young copepodid stages occur in the water column year-round, but major recruitment to the population takes place over a more limited period during spring and summer. Beginning in summer, 1979, the proportion of late copepodid stages (CIV and CV) increased until they comprised 64 % of the population in January, 1980, as compared with 66 % from the previous January (Fig. 2). In autumn and winter stages CIV and CV usually contain conspicuous lipid droplets and appear to be in a state of diapause. Despite recruitment of younger copepodid

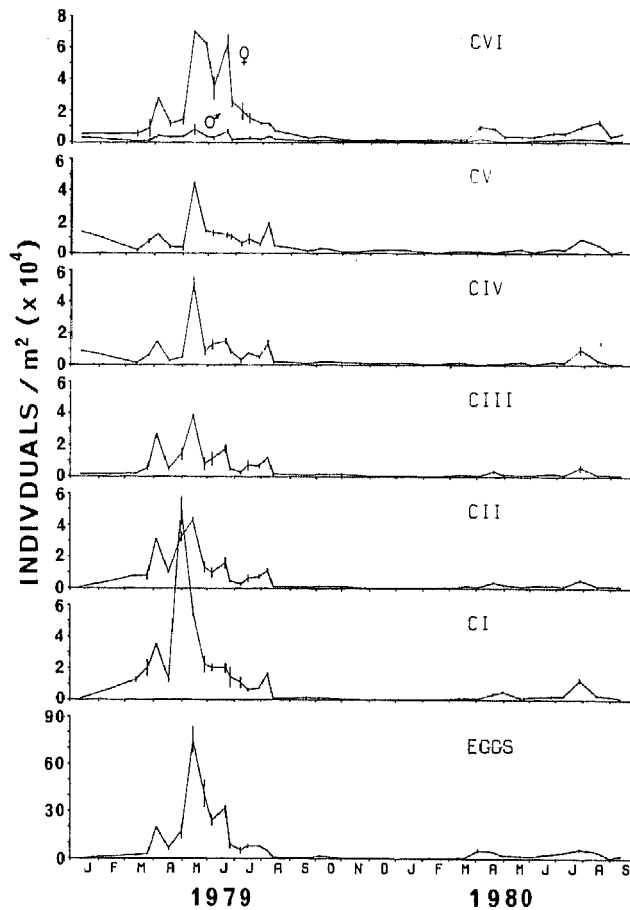


Fig. 1. Abundance of eggs and copepodid of *Pseudocalanus* sp. at Sta. D in Dabob Bay ($\bar{x} \pm$ s.d.).

stages throughout the year, development is usually arrested at stages CIV–CV during autumn and winter when phytoplankton concentrations are low or unpredictable.

If after stages CIV and CV break diapause in early spring subsequent population growth is strongly dependent on phytoplankton fluctuations, then there should be no relationship between the initial number of overwintering copepodids and the subsequent maximum number of adult females. Year-to-year differences in food supply should have a stronger effect than the initial conditions on abundance patterns. Fig. 3 provides evidence to the contrary. The annual maximum of adult female *Pseudocalanus* sp. is dependent on the number of overwintering copepodids ($r^2 = 0.744$, $P < 0.15$). Although only a 4 year time series was available for the comparison, this is a first line of evidence that population growth is not severely resource-limited. Interannual variations in abundance of *Pseudocalanus* appear to depend more on the initial conditions (number of overwintering copepodids) than

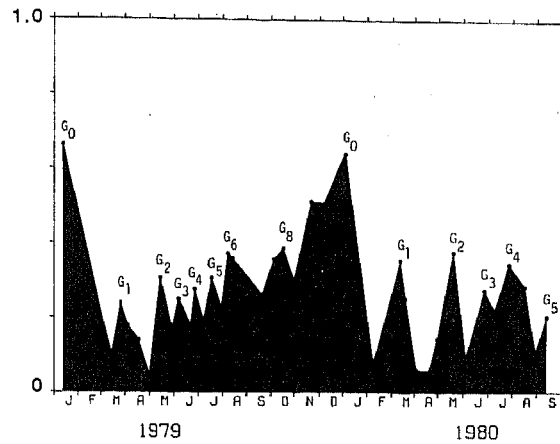


Fig. 2. Proportion of total copepodids of *Pseudocalanus* sp. in stages CIV + CV (shaded region). Sequential generations (G_n) denoted as peaks in relative abundance of CIV + CV (see also Fig. 4). G_7 was missed due to a long sampling interval.

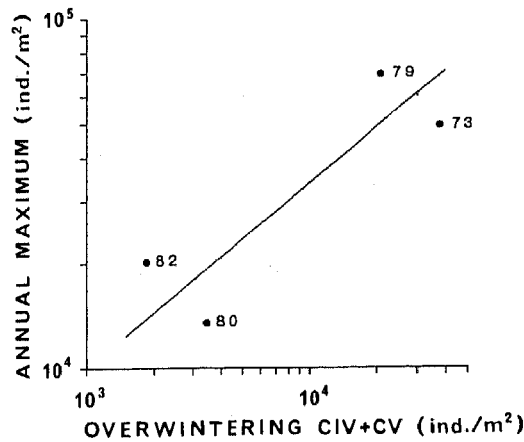


Fig. 3. The annual maximum of adult female *Pseudocalanus* sp. (F) vs. the abundance of overwintering CIV + CV *Pseudocalanus* sp. in early January. Points are labelled by year. $\log F = 0.534 \log (CIV + CV) + 2.397$.

on subsequent variations in phytoplankton resources within the primary season of population growth.

Comparison of observed generation times in a natural population with predictions from food-satiated populations in the laboratory tests the sufficiency of food resources to support optimal development rates. The inferred sequence of generations of *Pseudocalanus* sp. is illustrated in Figs. 2 and 4. G_0 denotes the generation of females that appears in March after overwintering CIV and CV break diapause and molt to adults. This usage of G_0 differs from that in Corkett & McLa-

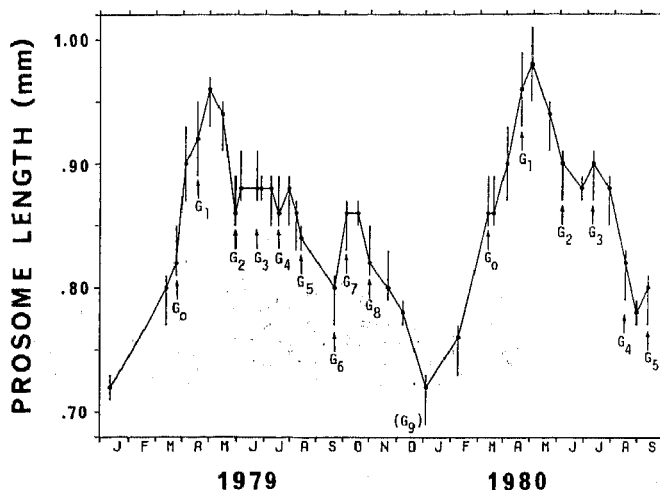


Fig. 4. Seasonal variation in prosome length of adult female *Pseudocalanus* sp. in Dabob Bay (median \pm 95 % C. L.). Sequential generations of adult females denoted G_0 to G_n , where G_0 females develop from overwintering CVs (see also Fig. 2).

ren (1978). G_1 and subsequent generations are numbered sequentially in the year in which spawning and development occurred. The median prosome length may continue to change even when the modal length (not shown) is relatively stable. A new generation is typically preceded by, or coincides with, an increase in the relative abundance of CIV and CV stages (Fig. 2), except for G_7 when the sampling interval changed. A small fraction of the late copepodid stages continue development to the adult stage in late autumn, as reflected by size changes and by the continued presence of reproductively active females throughout the year (Fig. 1 and Fig. 9 below).

The observed time between the appearance of new generations was calculated from the generations designated in Fig. 4. The predicted time between generations is obtained from the relation between temperature (T) and development time (D , in days) for food-satiated animals:

$$D = 18229 (T + 11.45)^{-2.05} \quad (4)$$

(modified from Corkett & McLaren 1978; see Ohman 1983), where T is estimated from equation (1) applied at the mid-point of each generation. Predicted mean temperatures for different generations range from 8.1°C for G_1 (1979 and 1980) to 13.4°C for G_5 (1979) and G_4 (1980).

The correspondence between observed and predicted generation time is close (Fig. 5) considering the sampling interval. G_6 and G_7 are combined in Fig. 5 because the long sampling interval preceding G_6 gives an unrealistically brief generation time of 14 days for G_7 . There is no significant difference between observed and predicted times ($P > 0.10$, Wilcoxon signed rank test). The average difference, $|d|$, was 5 ± 4 days ($\bar{x} \pm \text{s.d.}$). Developmental rates of *Pseudocalanus* sp. in Dabob Bay are consistent with predictions for food-satiated animals.

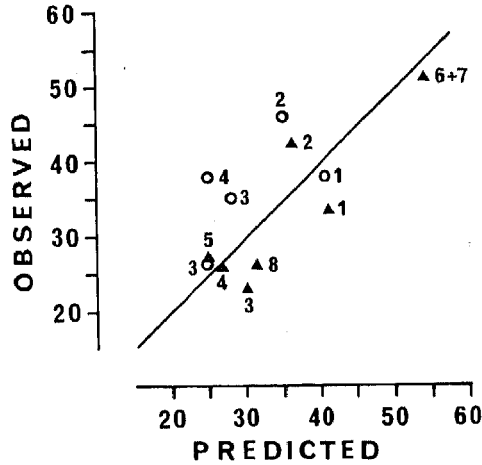


Fig. 5. Observed vs. predicted generation time (days) for *Pseudocalanus* sp. Generations numbered sequentially for 1979 (\blacktriangle) and 1980 (\circ). G_6 and G_7 were combined because of a long sampling interval. Line indicates perfect agreement between observations and predictions.

A third, independent measure of the sufficiency of food resources is the seasonal variability in prosome length. Assuming that food supply is adequate and that the qualitative pattern of predation between the two years is similar, then body size variations should be predictable by changes in temperature. Maximum body size (as dry mass) of Puget Sound *Pseudocalanus* females varies with temperature (Vidal 1980 a, his Fig. 2). From Vidal's data, the dependence of maximum dry mass (M , in μg) on temperature (T) can be expressed as:

$$M = -0.664 T + 20.273 \quad (5)$$

from 8°C to 15.5°C ($r^2 = 0.939$, $P < 0.10$, $N = 4$). From Fig. 6 the relationship between M and prosome length (PL, in mm) is:

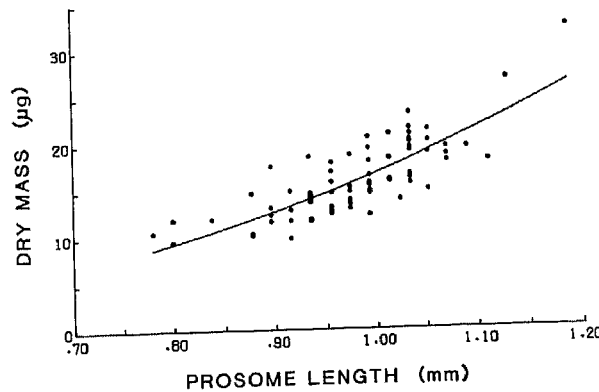


Fig. 6. Relationship between dry mass (μg) and prosome length (mm) of *Pseudocalanus* females. $M = 16.716 \text{ PL}^{2.399}$.

$$M = 16.716 PL^{2.399} \quad (6)$$

($r^2 = 0.622$, $P < 0.001$). Substituting equation (5) into equation (6), PL can be predicted from temperature:

$$PL = (-0.040 T + 1.213)^{0.417} \quad (7)$$

Using the average temperature experienced by each generation (eq. 1) and the observed median length at the onset of each generation from Fig. 4, the correspondence between observed and predicted prosome lengths is shown in Fig. 7. Note that the predicted prosome length is based on maximum size in culture while the observed prosome length is the median from the field. Temperature alone predicts the primary seasonal trends in body size variations in Dabob Bay, although a barely significant ($0.04 < P < 0.05$; Wilcoxon signed rank) difference was detected between observed and predicted values. The average difference between predicted and observed prosome length, $|d|$, is $3.2 \pm 2.6\%$ ($\bar{x} \pm s.d.$). However, if the maximum size of each field generation (as upper 95 % C. L. of the median) is used for the comparison, as obtained from the laboratory, there is no significant difference ($P > 0.20$). Body size variations, as well as generation times, suggest that resources are typically not in short supply.

As a fourth test of the resource-limitation hypothesis, the food requirements of *Pseudocalanus* from laboratory experiments were compared with an estimate of resources available in Dabob Bay. The critical concentration for growth of copepodid stage V (P_{CV} ; the food concentration at which CV growth is 90 % of the asymptotic maximum) is used as a measure of food requirements. Since younger developmental stages have lower food requirements than CVs (Vidal 1980 a) if CVs are food-satiated other stages should be as well (providing the other stages use similar resources). Estimates of P_{CV} can be obtained from Vidal (1980 a; his Table 5 and Fig. 8) at 8, 12 and 15.5 °C (0.45, 1.51, 2.68 ppm, respectively). Of two experiments at

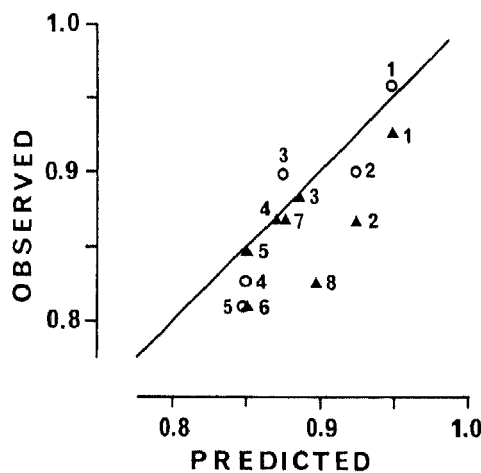


Fig. 7. Observed vs. predicted prosome length (mm) for sequential generations of CVI females of *Pseudocalanus* sp. in 1979 (▲) and 1980 (○).

(6) 12 °C, one yielded a higher value of P_{CV} due to retardation of copepod growth from clumping of cells (Vidal pers. comm.) and is therefore excluded. When these estimates of P_{CV} are converted to organic carbon (from Table 1, Vidal 1980 a), a linear relationship exists between P_{CV} ($\mu\text{g C/l}$) and temperature:

$$(7) \quad P_{CV} = 16.67 T - 91.49 \quad (8)$$

($r^2 = 0.999$; $P < 0.01$).

Ambient food supply was estimated from size-fractionated Chl *a* assuming (1) that cells retained on a 73- μm mesh were too large or too spiny to be handled effectively by *Pseudocalanus*, (2) that the only food available is live phytoplankton containing Chl *a*, (3) and that *Pseudocalanus* feeds at the depth where phytoplankton is most concentrated. Fig. 8 illustrates the comparison between ambient phytoplankton and the temperature-dependent critical concentration as estimated from eq. (8). On most dates throughout 1979–1980 the ambient food supply meets or exceeds the critical food concentration ($P < 0.002$, Wilcoxon signed rank), often surpassing food requirements several-fold. Based on Runge's (1981) analysis of the variability associated with the maximum chlorophyll concentration in Dabob Bay, on only three dates (4 January, 19 July, and 31 July 1979) was the ambient concentration of phytoplankton significantly different ($P < 0.05$) from the estimated critical concentration. Nonsignificant differences occurred on other occasions. Even throughout most of winter ambient food supply appears to meet requirements for growth of CV stages. This analysis is in further support of the hypothesis of generally satiating food resources.

Another index of the adequacy of the resources available to a natural population is the fecundity of adult females. However, care must be taken to correct for the effects of body size, stage structure, and mortality of adult females, if the causes for changes in fecundity of a natural population are to be correctly understood. In

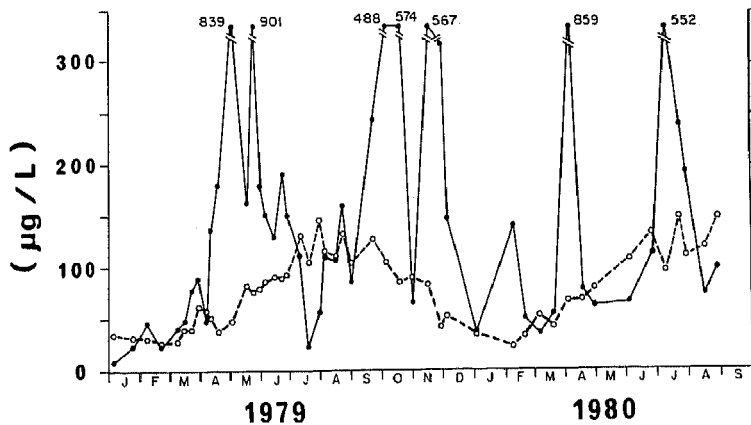


Fig. 8. Seasonal variation in concentration of phytoplankton (from a depth of 6–12 m) passing through a 73- μm screen (solid line) and in the critical concentration for growth of CV *Pseudocalanus* (dashed line).

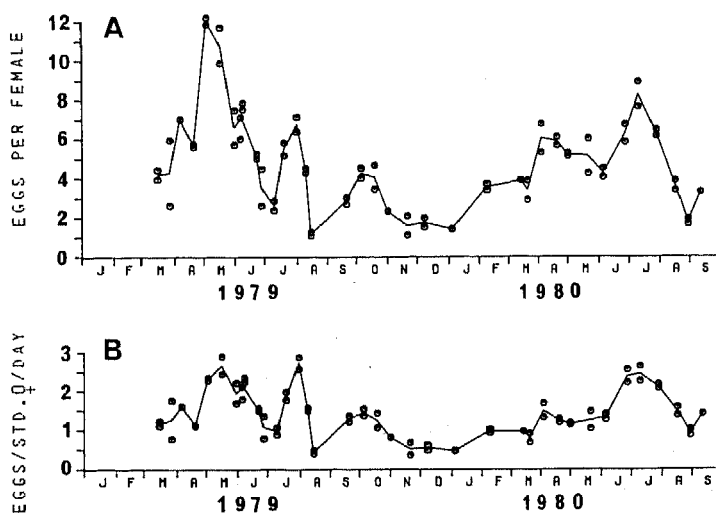


Fig. 9. Seasonal variation in fecundity of *Pseudocalanus* sp. in Dabob Bay. (A) Egg ratio (eggs/♀) and (B) egg hatching rate (eggs · standard ♀⁻¹ · d⁻¹), which corrects for seasonal changes in body size and temperature.

Dabob Bay the uncorrected values of the egg ratio vary by more than an order of magnitude (1.16 to 12.06 eggs/total females) over the duration of the investigation (Fig. 9 A). (No egg data are available for January 1979 because the net mesh size (110- μ m) used on this date was unsuitable for retaining eggs). Seasonal variations in the egg ratio are significantly correlated with seasonal changes in prosome length in both 1979 ($r^2 = 0.555$, $P < 0.001$, $N = 44$) and 1980 ($r^2 = 0.622$, $P < 0.001$, $N = 29$), suggesting that much of the variability of fecundity is attributable to variations in body size.

Corrections for seasonal variation in body size and temperature were made as follows. From laboratory experiments with food-satiated *Pseudocalanus*, clutch size (E) was found to vary with prosome length (PL, in mm):

$$E = 18.219 \text{ PL}^{2.298} \quad (9)$$

($r^2 = 0.474$, $P < 0.001$; $N = 102$; unpublished data of B. W. Frost). From eq. (9) the expected egg number was calculated for median-sized females from each field observation (Fig. 4) and divided by the expected number for a standard-sized female of 0.862 mm prosome length (the annual average prosome length). The observed egg ratio was then divided by this quotient to correct all egg ratios to that of a "standard" female. The average temperature was approximated as indicated in "Methods" and egg duration calculated from eq. (3). The egg hatching rate (EHR) is then: $\text{EHR} = \text{Eggs}/(\text{Std } \text{♀} \cdot \text{ED})$.

Seasonal variation in egg hatching rate is illustrated in Fig. 9 B. This panel shows markedly damped fluctuations by comparison with the egg ratio in the panel above. Although variations in EHR between dates exceed the precision of replicate samples on the same date, these variations do not follow phytoplankton fluctuations closely.

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Declines in phytoplankton abundance were not necessarily accompanied by decreases in the EHR (e. g., July 1979) nor were increases in phytoplankton consistently associated with increases in EHR (e. g., October, November 1979; April 1980). The striking feature of Fig. 9 B is the low variability. On 90 % of the dates investigated the average EHR was between 0.81 and 2.72 eggs · female⁻¹ · d⁻¹, a 3.4-fold difference over a two year time period. The low amplitude seasonal variation in fecundity provides a fifth line of evidence that resources are adequate to support population growth nearly year-round.

The analysis of seasonal variability in egg ratio assumes that the observed fecundity is close to the potential fecundity. The egg ratio observed in the field

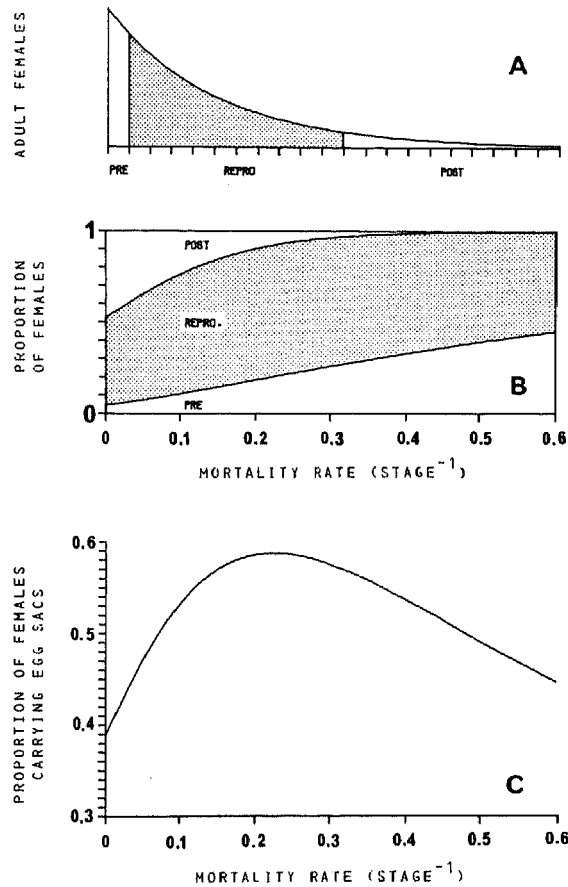


Fig. 10. Variation in reproductive state of adult female *Pseudocalanus*. (A) Instantaneous distribution of females of different reproductive states (pre-reproductive, reproductive, post-reproductive) under constant mortality. Life span of females is divided into 21 stages on the abscissa. (B) Distribution of reproductive states as a function of mortality rate. (C) Proportion of total females carrying egg sacs as a function of mortality rate. Stippling indicates the reproductive portion of the population.

(Fig. 9 A) is lower than that observed in the laboratory (eq. 9). However, even if individuals in a natural population are food-satiated, females will not carry an egg sac if they are pre-reproductive, reproductive but currently between clutches, or post-reproductive. In an extension of the analysis by Corkett & McLaren (1978) Fig. 10 A illustrates a model for the reproductive states of adult female *Pseudocalanus*. The following assumptions are made: (1) a newly molted female has a pre-reproductive period equivalent to the time between clutches, (2) inter-clutch duration is 1.25 times the embryonic duration, (3) the reproductive span of a female averages 10 clutches, and (4) the post-reproductive period is equivalent to the duration of the reproductive period (see Corkett & McLaren 1978). Assuming constant exponential mortality at rate m , the number of females in different reproductive states is described by $\int e^{-mx} dx$, evaluated between stages 0-1, 1-11, and 11-21 (Fig. 10 A). The proportion of total females which are reproductive is then indicated by the stippled area under the curve (Fig. 10 A), which varies with mortality rate (Fig. 10 B). (The abscissa in Fig. 10 B can be converted to daily instantaneous rates by dividing the daily rate per stage by 1.25 times the egg duration.) The proportion of females carrying egg sacs, which also varies with mortality rate (Fig. 10 C), is 0.816 times the proportion of reproductive females. For *Pseudocalanus* females experiencing mortality rates spanning 0.001 to 0.300 per stage the proportion of ovigerous females should range between 39-59 % of total females.

This analysis confirms that the expected proportion of ovigerous females in a natural population is substantially lower than might be projected from laboratory experiments. Furthermore, copepod populations experiencing variable mortality should show variations in fecundity, even if food-satiated.

Discussion

Five independent indices suggest that resources are usually sufficient to sustain maximal rates of development, growth, and reproduction of *Pseudocalanus* sp.. Contrary to the food limitation paradigm, phytoplankton fluctuations are a poor predictor of rates of population growth and recruitment. *Pseudocalanus* sp. population growth appears not to be regulated in a density-dependent manner by the phytoplankton production cycle, as is commonly assumed for suspension-feeding zooplankton. Evidence suggests that predation by carnivorous zooplankton is the primary factor explaining seasonal and interannual variations in abundance patterns of *Pseudocalanus* sp. in Dabob Bay (Ohman 1983).

McLaren (1969, 1978) and Corkett & McLaren (1978) have suggested that other species of *Pseudocalanus* are not food-limited, in other regions. McLaren (1978) also concluded that competitive interactions have little influence on population fluctuations or on patterns of coexistence of *Pseudocalanus* with other members of the zooplankton. This conclusion appears applicable to the present population, but is inapplicable to other zooplankton species with which *Pseudocalanus* sp. co-occurs (Frost 1985; Runge 1985). Apart from open ocean populations of *Pseudocalanus*, for which birth and death rates remain poorly known, population growth of species of *Pseudocalanus* may generally be regulated by factors other than abundance of resources.

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In parallel with the present results, Colebrook (1982) concluded that the distribution of *Pseudocalanus elongatus* in the Northeast Atlantic and the North Sea was determined by the size of the overwintering population. Although a positive relationship was suggested between the abundance of overwintering animals and phytoplankton concentration in the latter study, it is not clear how phytoplankton standing stock was measured or what the developmental stage composition was of the overwintering population.

The indices used to evaluate the effects of resource supply on growth of *Pseudocalanus* sp. rest upon assumptions which merit further discussion. Point estimates are used for the average temperature and food conditions encountered by the *Pseudocalanus* population although vertical gradients in these properties exist in Dabob Bay (Runge 1981; Ohman et al. 1983; Welschmeyer & Lorenzen 1984), as elsewhere. Thus those individuals which experience conditions deviating from the estimated mean are not accounted for. Neither is demographic stochasticity within a population exposed to uniform conditions. While a range of conditions and individual responses to those conditions surely exists, it was not feasible to incorporate environmental and population variances into the hypothesis tests made above. Moreover, the agreement of averaged population responses with predictions suggests that the assumptions were suitable first approximations to the average temperature and food conditions experienced by the population.

Concerning estimates of critical concentration, there is close agreement for *Pseudocalanus* species from different regions and different laboratories. At 12 °C, the critical concentration for ingestion of CVI females was ca. 120 µg C/l (Frost 1980), and the critical concentration for growth of CVs was ca. 110 µg C/l (Vidal 1980 a; omitting clumped cell experiment). Note that Vidal's experiments were conducted with animals raised on a nearly uniform food type from egg to adult, providing ample time for digestive enzyme induction (e. g., Hassett & Landry 1983). Critical concentrations for both body mass of adult females and growth of CIII/IV to adult in experiments by Paffenhöfer & Harris (1976) can be approximated as 100 µg C/l at 12.5 °C. From Klein Breteler et al. (1982) the critical concentration for growth of CV at 15 °C can be estimated as < 180 µg C/l (1/4 feeding level), comparing favorably with 170 µg C/l at 15.5 °C from Vidal (1980 a). Higher critical concentrations have, however, been observed in experiments where no stirring mechanism was employed (Corkett & McLaren 1978) and when natural particle concentrations have been assessed with an electronic particle counter (e. g., Mayzaud & Poulet 1978). However, the particle counting method fails to account for the presence of inedible particles such as spiny chains and inorganic particulate matter (Harbison & McAlister 1980).

The size fractionation technique used here permits exclusion of most elongate cells or chains (Runge & Ohman 1982). Several instances of reduced ingestion or avoidance of large or spiny particles by *Pseudocalanus* spp. have been reported (Parsons et al. 1967; Hargrave & Geen 1970; Schnack 1975; Skiver 1980; Angelidis 1983). Although the flavor of particles may also influence their capture (cf. Rassoulzadegan et al. 1984) and the smallest suspended particles are probably captured with low efficiency by *Pseudocalanus*, most particles of intermediate size range appear to be ingested (Zagorodnyaya 1974; Poulet 1974; Koeller et al. 1979; Harris 1982). The effective food concentrations for *Pseudocalanus* were more likely underestimated than overestimated in the present study because of the presence of unsampled microscale layers of phytoplankton, microzooplankton as a

Table 1. Comparative in situ reproductive rates of marine copepods, uncorrected for variations in body size.

Species	Time interval	Reproductive rate (eggs · female ⁻¹ · d ⁻¹)	Max/min	Reference
<i>Calanus pacificus</i>				
Dabob Bay	March - Sept	0.0 - 38.0	> 100	Runge (1981)
Puget Sound	April - Sept	1.5 - 48.0	32	Runge (1981)
	May - Jan	5.0 - 230.0	46	Dagg (1978)
<i>Centroages typicus</i>	Feb - March and Aug - Sept	2.1 - 83.1	40	Checkley (1980)
<i>Paracalanus parvus</i>	July - Sept	1.6 - 50.3	31	Durbin et al. (1983)
<i>Acartia tonsa</i>	Aug - Feb	2.6 - 66.0	25	Uye (1981)
<i>Acartia steueri</i>	July - Oct	1.0 - 16.9	17	Kimmerer (1984)
<i>Acrocalanus inermis</i>	year round	4.0 - 55.0	14	Uye (1981)
<i>Acartia clausi</i>	Aug - Feb	0.3 - 3.9	13	Koeller et al. (1979)
<i>Pseudo calanus</i> sp.	year round	0.3 - 3.3	11	present study

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Comparison of laboratory-derived egg production rates with egg hatching rates observed in the field suggest that potential as well as realized reproductive rates of *Pseudocalanus* are low. From laboratory experiments, Corkett & Zillioux (1975) reported a mean of 3.4 eggs produced per female per day at 12.5 °C. From Corkett & McLaren (1978, Fig. 21) it can be seen that the maximum expected egg production rate of *Pseudocalanus* varies with body size and temperature. For a population experiencing natural mortality, 1.0-mm *Pseudocalanus* should produce approximately 3.3–3.9 eggs per female per day at 8–10 °C and 0.80-mm *Pseudocalanus*, 2.2–2.4 eggs per female per day at 12–14 °C. These values correspond reasonably well with observations in Dabob Bay.

The experiments of Koeller et al. (1979) with *Pseudocalanus* sp. in Saanich Inlet during autumn–winter show a range in fecundity comparable to that in Dabob Bay year-round (Table 1). Other copepod species show greater seasonal excursions in fecundity than *Pseudocalanus* (Table 1), an indication of their greater susceptibility to resource fluctuations. (Experiments in Table 1 reflect in situ rates of egg production although Dagg (1978) fed copepods for 14–17 h after capture.) Seasonal variability in reproductive output of other copepods ranges from a factor of 14 for *Acartia clausi* (Uye 1981) to > 100 for *Calanus pacificus* (Runge 1981). Furthermore, while the maximum fecundity of *Pseudocalanus* sp. in Dabob Bay was 3.26 eggs per female per day (uncorrected for body size), the comparable maximum for other species was between 17–230. All of the species in Table 1 broadcast eggs, in contrast to *Pseudocalanus* which carries its eggs in an attached sac. One consequence of carrying an egg sac may be restricted reproductive output. However, the drawback associated with this reproductive bottleneck may be compensated by sustained, nearly steady-state recruitment and by enhanced survivorship of eggs when ovigerous females avoid predators (Ohman et al. 1983).

Investigations of the dynamics of marine copepods indicate that species other than *Pseudocalanus* are frequently resource-limited in the field (e. g., Landry 1978; Huntley 1981; Runge 1981; Frost et al. 1983). Other taxa of suspension-feeding zooplankton such as euphausiids (Ohman 1984), larvaceans (King 1981), and salps (Harbison & Gilmer 1976) also demonstrate far greater food requirements than *Pseudocalanus*. Of those marine planktonic suspension-feeders studied intensively to date *Pseudocalanus* appears unusual in its capability for sustaining population growth nearly independently of ambient resource fluctuations. However, though the physiological adaptations governing growth and reproduction of *Pseudocalanus* may be unusual, the genus is widely distributed and abundant. Low food requirements, brooded eggs, and continuous iteroparous reproduction, coupled with the seasonal development of predator-avoidance behavior (Ohman et al. 1983), probably account for the numerical dominance of *Pseudocalanus* in many north temperate marine zooplankton communities.

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