

# LIMNOLOGY AND OCEANOGRAPHY

November 1972

VOLUME XVII

NUMBER 6

## EFFECTS OF SIZE AND CONCENTRATION OF FOOD PARTICLES ON THE FEEDING BEHAVIOR OF THE MARINE PLANKTONIC COPEPOD *CALANUS PACIFICUS*<sup>1</sup>

B. W. Frost

Department of Oceanography, University of Washington, Seattle 98195

### ABSTRACT

When adult females of *Calanus pacificus* are fed on monospecific cultures of centric diatoms which grow as single cells, a predictive relationship is found between feeding behavior of the copepods and size and concentration of food particles. Ingestion rate of copepods increases linearly with cell concentration up to a maximal rate. This maximal ingestion rate, expressed as carbon, is the same for copepods feeding on diatoms ranging in diameter from 11–87  $\mu$ . As the size of food particles increases, the carbon concentration at which this ingestion rate is achieved decreases. Thus females of *C. pacificus* can obtain their maximal daily ration at relatively low carbon concentrations of large cells.

### INTRODUCTION

In oceanic food webs, calanoid copepods constitute prominent pathways for energy flow between primary producers and the larger predatory species of zooplankton and nekton. An understanding of quantitative trophic interactions between phytoplankton and herbivorous copepods is required to elucidate the nature of marine food webs in terms of rates. Much progress has been made in studies of species of *Calanus* and related genera.

The mechanics of filter feeding in copepods are well known (Marshall and Orr

1955). Unlike the more automatic, relatively unselective filter-feeding crustaceans such as *Artemia* (Reeve 1963) and *Daphnia* (McMahon and Rigler 1965; *but see also* Burns 1969), copepods apparently feed discontinuously and show considerable discrimination when presented with a choice of several food organisms. The latter behavior is known for copepods feeding on both mixed laboratory cultures of phytoplankton (Harvey 1937; Mullin 1963, 1966; Petipa 1965; Mullin and Brooks 1967) and on natural phytoplankton (Parsons et al. 1967, 1969; Parsons and LeBrasseur 1970; Hargrave and Geen 1970). Selective feeding may be based on quality of food but copepods also apparently tend to pick large-sized particles when given a choice (Mullin 1963; Richman and Rogers 1969).

It has not been clearly established whether size-selective feeding in *Calanus*

<sup>1</sup>Contribution No. 661 from the Department of Oceanography, University of Washington. This work was supported by National Science Foundation Grants GA-25385, GB-20182, and GA-31093, and U.S. Atomic Energy Commission Contract AEC AT(45-1)-2225, TA 26 (ref. RLO-2225-T26-6).

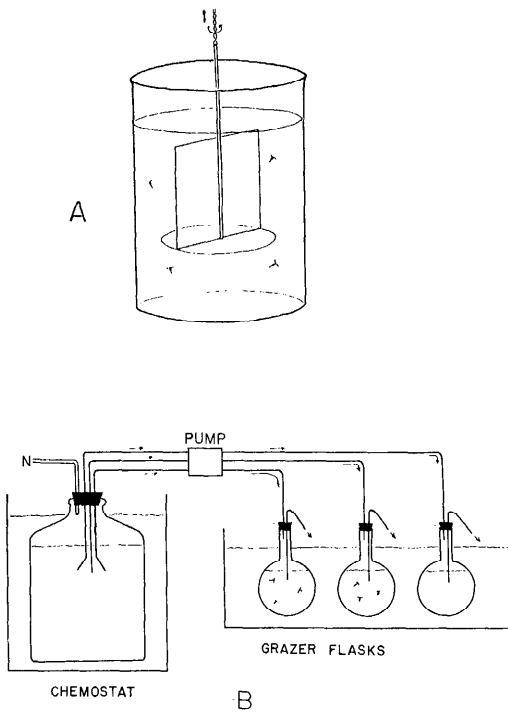


FIG. 1. A. Experimental container used in batch culture feeding experiments with *Calanus*. The Plexiglas stirrer, driven by a 1 rpm motor, rotates and oscillates up and down within the 4-liter beaker. B. Experimental apparatus used for continuous (chemostat) feeding experiments with *Calanus*. The seawater-nutrient mixture enters the 16-liter chemostat at N. Arrows indicate flow of *Thalassiosira fluviatilis* into and out of the 3-liter flasks.

reflects active hunting for larger cells (Richman and Rogers 1969) or is simply due to greater feeding efficiency of the animals on larger cells. Further, the relationship between cell concentration and feeding behavior has not been properly established in selective feeding experiments. In unialgal cultures the ingestion rate of *Calanus* increases with concentration of food up to some maximal rate, then decreases (Mullin 1963) or, more likely, remains constant with further increases in cell concentration (McAllister 1970, 1971). How ingestion curves vary with different sizes of food particles was usually confounded in previous investigations by the

use of algae of markedly different shapes or chemical composition.

In this paper I describe the feeding behavior of adult females of *Calanus pacificus* exposed to batch and continuous cultures of centric diatoms. This is the species described by Brodsky (1948, 1965) and is probably conspecific with the populations called *Calanus helgolandicus* by Mullin (1963), Mullin and Brooks (1967), Richman and Rogers (1969), and Paffenhöfer (1971). The purpose of this work is to demonstrate predictable relationships between feeding behavior of *Calanus* and both concentration of food and size of food particles.

I thank Dr. J. Lewin for providing cultures of diatoms and for advice on maintaining laboratory cultures of phytoplankton. B. Booth identified the diatoms isolated from Puget Sound and J. Vidal gave valuable technical assistance.

#### MATERIAL AND METHODS

##### *Batch culture feeding experiments*

Copepods feed at abnormally high rates during the first few hours of a grazing experiment, because of previous starvation or of handling during transfer (Mullin 1963; Hargrave and Geen 1970; McAllister 1970). Since this abnormal behavior may be evident for up to 12 hr, long-term (2–5 day) grazing experiments were used. Ten to thirty adult females of *Calanus* were placed in each of two 4-liter beakers containing 3.5 liters of twice glass-fiber filtered seawater; both the copepods and seawater were freshly collected at a depth of 50 m or more in Puget Sound (Washington). The contents of beakers were kept homogeneous by modified plunger-jar stirrers (Fig. 1A). The effect of food concentration on feeding behavior was assessed by adding a suspension of algae to the beakers and following the changes in concentration in the beakers as the animals grazed the suspension down. A single control beaker, containing algae but no grazers, was always used. Feeding behavior was monitored at short, irregular intervals (5–14 hr) by pipetting a 100–200-ml

TABLE 1. Dimensions and estimated carbon content of diatoms used in grazing experiments. The two species of *Thalassiosira* were isolated from Long Island Sound by R. R. L. Guillard. The other three species were obtained from Puget Sound

	Mean cell diam ( $\mu$ )	Mean cell vol ( $\mu^3$ )	Estimated carbon/cell ( $\mu\text{g} \times 10^{-6}/\text{cell}$ )
<i>Thalassiosira pseudonana</i>	3.8	55	8
<i>Thalassiosira fluviatilis</i>	11	1,450	94
<i>Coscinodiscus angatii</i>	35	26,000	840
<i>Coscinodiscus eocentricus</i>	75	63,000	1,644
Centric sp.*	87	160,000	3,334

\* Cf. *Coscinodiscus angatii* var. *granulomarghatus*.

sample from each beaker and making 6-8 cell counts with a model B Coulter counter. After counting, the remaining portions of the samples were returned to the beakers. The control was sampled and counted each time the beakers containing grazers were counted. On two occasions, at the end of long grazing experiments, copepods were removed from both grazer beakers and the growth rates of the algae determined after further incubation; in both cases no difference in algal growth rates was found between grazer beakers and the control beaker, indicating that the copepods were not affecting the growth of algae by remineralizing nutrients. All experiments were run at 12.5C in continuous dim light.

The effect of size of food particles on feeding behavior of *Calanus* was studied by using as food centric diatoms which grow as single cells in culture. Five species were used; all are of similar pill-box shape, but differ markedly in size (Table 1). Cultures of diatoms were maintained in medium "F" (Guillard and Ryther 1962). Cultures less than 6 days old, still in logarithmic growth, were used for grazing experiments. Average cell volumes of diatoms were determined with the Coulter counter, which was periodically calibrated with pollen grains of two different sizes. The carbon content of diatom cells was estimated from average cell volumes (Strathmann 1967). Only monospecific cultures of diatoms were fed to *Calanus*; no selection experiments are reported here.

Ingestion rates were calculated from cell counts of the control beaker and sepa-

rately for each beaker with grazers. The growth constant for algal growth,  $k$ , was calculated from

$$C_2 = C_1 e^{k(t_2 - t_1)},$$

where  $C_1$  and  $C_2$  are cell concentrations (cells/ml) in the control beaker at  $t_1$  and  $t_2$ . For each beaker with grazers the grazing coefficient,  $g$ , was calculated from

$$C_2^* = C_1^* e^{(k-g)(t_2 - t_1)},$$

where  $C_1^*$  and  $C_2^*$  are cell concentrations in a beaker with grazers at time  $t_1$  and  $t_2$ . Using values of  $k$  and  $g$  the average cell concentration,  $\langle C \rangle$ , for each grazer beaker during a time interval  $t_2 - t_1$  is:

$$\langle C \rangle = \frac{C_1^* [e^{(k-g)(t_2 - t_1)} - 1]}{(t_2 - t_1)(k - g)}.$$

Although *Calanus* obtains its food by means of filtering maxillae, true filtering rate (volume of water passing through the maxillary filter per unit time) cannot be directly measured. The volume swept clear,  $F$  (Harvey 1937), is given by

$$F = Vg/N \quad (\text{ml copepod}^{-1} \text{ hr}^{-1}),$$

where  $V$  is the volume (ml) of the beaker and  $N$  is the number of copepods in the beaker. "Volume swept clear" is defined as the volume of ambient medium from which cells are completely removed by copepods to achieve the measured ingestion rate. Volume swept clear, as used here, is synonymous with the term "filtering rate" used in many studies of filter-feeding crustaceans and the term "grazing

rate" used by Mullin (1963). Notice that filtering rate and volume swept clear are equivalent only if a copepod is 100% efficient at removing particles from the water passing through the maxillary filter. The ingestion rate,  $I$ , is then

$$I = (C) \times F \quad (\text{cells eaten copepod}^{-1} \text{ hr}^{-1}).$$

The effect of cell concentration on volume swept clear and ingestion rate is demonstrated by plotting the rates against the average cell concentration for each period of grazing.

#### *Continuous culture feeding experiments*

A continuous culture (chemostat) containing *Thalassiosira fluviatilis* was run with artificial seawater (Kester et al. 1967) enriched with solutions of nutrients, trace metals, and vitamins. The nutrient limiting algal growth was ammonium or silicate. The chemostat in steady state was used for four experiments by connecting separate outflow tubes from the chemostat through a peristaltic pump to 3-liter flasks (Fig. 1B) or 4-liter beakers. The contents of the containers were mixed with stirring bars and by air bubbling. Twenty to forty adult females of *C. pacificus* were used in feeding experiments. Diatom cells were counted periodically in the inflowing and outflowing medium of each copepod container. Both the chemostat and copepod containers were maintained in a water bath at 12.5C in a light-dark cycle (16L:8D). The chemostat was illuminated directly by a fluorescent light bank (0.099 ly/min); fluorescent light to the grazer containers was first passed through a blue Plexiglas sheet and a 50% light screen, and the resultant flux was 0.019 ly/min.

In the large steady-state chemostat the growth rate of *Thalassiosira* was always kept low (about 0.6% per hour). About the same or a lower algal growth rate prevailed in the grazer containers since the illumination was a fifth as great as in the chemostat. Flow rates and numbers of copepods were adjusted so that the effect of these factors on cell concentration in the grazer containers was much greater than the effect of algal growth.

In only one experiment were the copepod containers run long enough to achieve steady state. For nonsteady-state conditions the growth rate of algae in the grazer flasks was assumed to be the same as the growth rate of algae in the chemostat (turnover rate of algal population in steady-state chemostat = turnover rate of liquid volume in chemostat). Ingestion rates were calculated from an equation that balanced, for each grazer flask, 1) inflow of cells, 2) growth of cells, 3) outflow of cells, and 4) removal of cells by grazers. In the one long steady-state experiment the number of grazers in the two flasks was slightly different (23 and 26 copepods/flask); the growth rate of algae was assumed to be identical in the two flasks containing copepods and ingestion rates were then calculated simply from the difference between cell concentrations in the outflows of the two flasks at steady state. Obviously the algal growth rate should be slightly higher in the flask containing more grazers if all copepods graze at the same rate and if a true steady state is reached; in this experimental design the result of assuming equal algal growth rates is that the ingestion rate of the copepods may be slightly underestimated.

At the end of all experiments the copepods were fixed in filtered seawater with 5% Formalin. After 2-3 weeks they were removed from the preservative, washed briefly with distilled water, dried at 60C on preweighed aluminum pans, and weighed on a Cahn electrobalance.

#### RESULTS

In three batch culture experiments, I could not measure ingestion rates when *Calanus* was fed *Thalassiosira pseudonana*, even though a few fecal pellets were produced. The average spacing of filtering setules on the scivelike second maxilla of adult *Calanus* is significantly greater than the cell diameter of the diatom, so that most cells probably pass between the setules.

*Calanus* displays a predictable feeding behavior when fed in batch cultures at

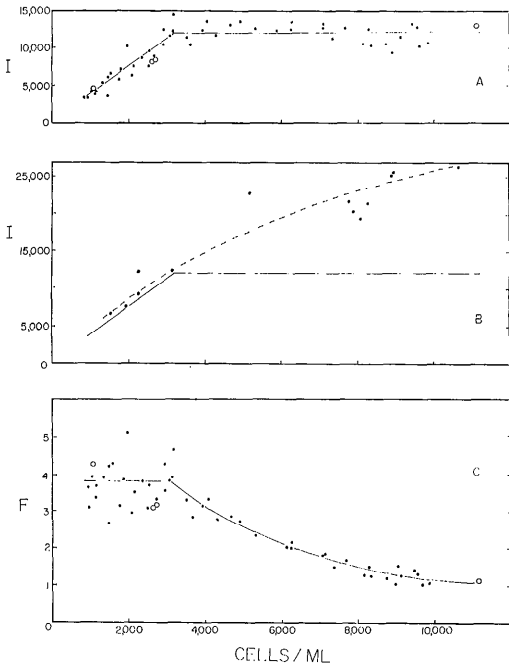


FIG. 2. Results of batch culture (dots) and continuous culture (circles) experiments with *Calanus* feeding on *Thalassiosira fluviatilis*. A. Effect of cell concentration on ingestion rate,  $I$  (cells eaten copepod<sup>-1</sup> hr<sup>-1</sup>). B. Ingestion rates of starved (dots and dashed line) and unstarved (solid line from part A) *Calanus* in batch cultures; starvation rates were those measured in the first 4–12 hr of a feeding experiment. C. Effect of cell concentration on volume swept clear,  $F$  (ml copepod<sup>-1</sup> hr<sup>-1</sup>).

different concentrations of *T. fluviatilis* (Fig. 2A). The ingestion rate increases with cell concentration up to a maximal rate that remains essentially unchanged with further increase in cell concentration. The cell concentration at which the maximal ingestion rate is first achieved will be referred to below as the critical concentration (McMahon and Rigler 1963). Figure 2A includes rates determined for unstarved copepods. An unstarved *Calanus* adjusts its feeding rate at high concentrations of cells (>4,000 cells/ml), since starved animals can ingest at unusually high rates (Fig. 2B). The adjustment in feeding behavior is also evident from the pattern of volume swept clear ( $F$ ). Going from high

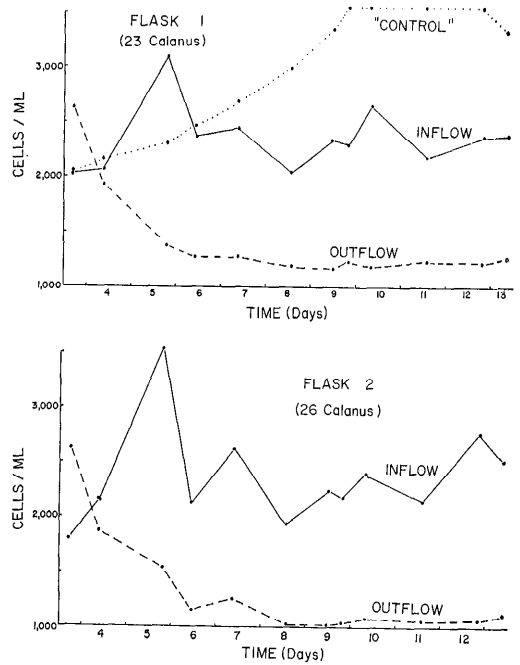


FIG. 3. Results of experiments in which females of *Calanus* fed on *Thalassiosira fluviatilis* from a continuous culture (see Fig. 1B). Inflow: concentration of cells in medium flowing into grazer flask from the continuous culture (flow rate 96 ml/hr). Outflow: concentration of cells in medium flowing out of grazer flask. "Control" represents the concentration of cells in a flask containing no grazers. Average concentrations in the inflows to flask 1 (2,326 cells/ml) and flask 2 (2,288 cells/ml) are not statistically different.

to low concentrations of *T. fluviatilis*,  $F$  increases curvilinearly to an average maximal rate about which it oscillates with considerable amplitude (Fig. 2C). While true filtering rate of *Calanus* cannot be measured, volume swept clear is useful for comparative purposes since it seems to represent, when it is measured at low food concentrations, the physiologically maximal rate at which a copepod can process a particular type of food. Thus, although at high cell concentrations (>4,000 cells/ml) a starved *Calanus* ingests at a higher rate than an unstarved *Calanus*, at cell densities below the critical concentration starved animals feed like unstarved animals (Fig. 2B).

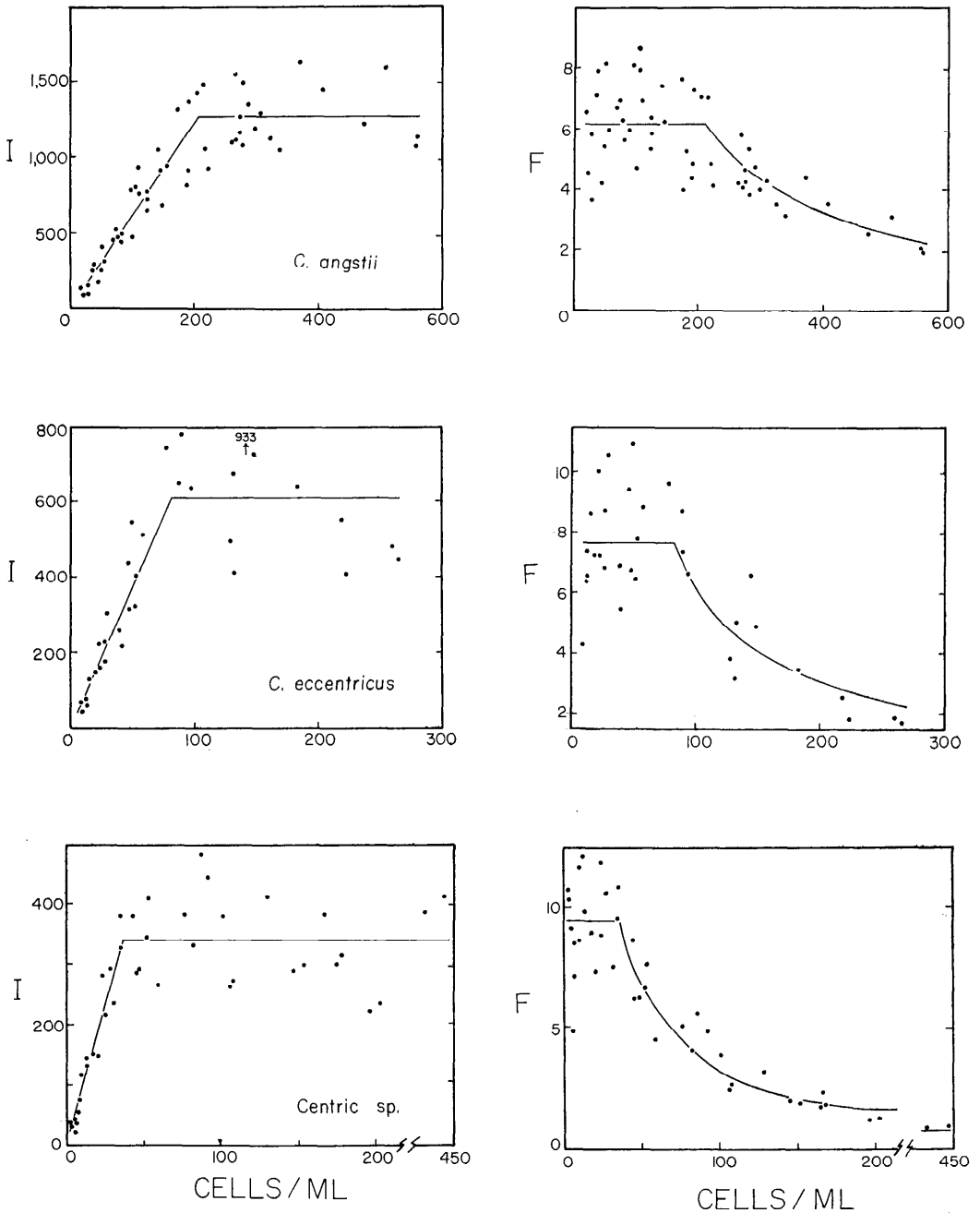


FIG. 4. Effect of cell concentration on ingestion rate,  $I$ , and volume swept clear,  $F$ , of adult females of *Calanus* feeding on *Coscinodiscus angstii* (top graphs), *Coscinodiscus eccentricus* (center graphs) and centric sp. (lower graphs).

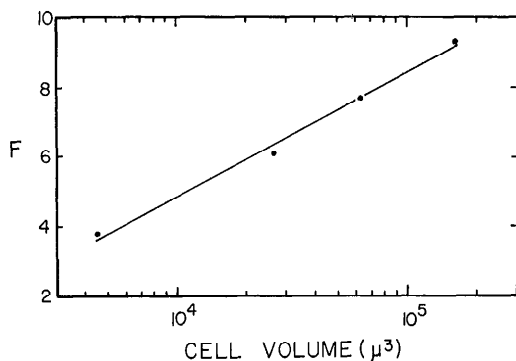


FIG. 5. Relationship between volume swept clear,  $F$ , for adult females of *Calanus* and mean cell volume of diatoms used as food. Values of  $F$  are means based on rates measured at cell densities below the critical concentration for each species of diatom (Figs. 2 and 4).  $F$  is predicted by the least-squares regression line  $F = 2.61(\log V) - 4.84$ , where  $V$  is the cell volume ( $\mu^3$ ) of the centric diatom used as food. The correlation coefficient between  $\log V$  and  $F$  is 0.79 ( $N = 95$ ).

The curved part of the line in Fig. 2C represents the volume that must be swept clear by a *Calanus* female to obtain the maximal ingestion rate ( $12,066$  cells copepod $^{-1}$  hr $^{-1}$  based on 26 points for cell concentrations exceeding  $3,500$  cells/ml). The straight part of the line in Fig. 2C represents the average volume swept clear ( $3.81$  ml copepod $^{-1}$  hr $^{-1}$ ) at cell concentrations below  $3,500$  cells/ml. Thus  $I$  represents the relationship between ingestion rate of *Calanus* and cell concentration of *T. fluviatilis* as two intersecting straight lines (Fig. 2A). Note that the slope of the ascending part of the line in Fig. 2A is equivalent to the average maximal volume swept clear. A curvilinear function could be fitted to Fig. 2A (e.g. Parsons et al. 1967) but there is no a priori reason for doing so and my representation seems to me to provide clearer insight into the feeding behavior of *Calanus*.

The above results describe how adult females of *Calanus* might feed on a patch of *T. fluviatilis*. But the batch culture system is somewhat unreal in the sense that it is a completely closed system; the algal population often ceased growing in both

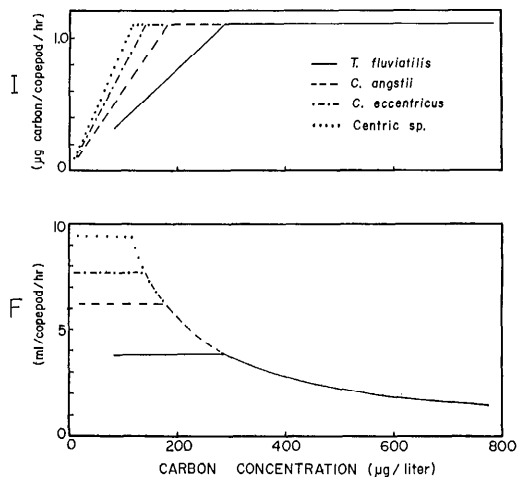


FIG. 6. Effect of size (species) and concentration (as carbon) of food particles on ingestion rate,  $I$ , and volume swept clear,  $F$ , of adult females of *Calanus*.

the control and grazing beakers before the end of a long feeding experiment. The results of feeding experiments in continuous cultures of *T. fluviatilis* are therefore of interest because cell concentrations remain high and the cells are always in a logarithmic phase of growth. Ten days of results from a long steady-state experiment (Fig. 3) show that *Calanus* fed continuously and at a constant rate from day 8 onward. Ingestion rate ( $4,610$  cells copepod $^{-1}$  hr $^{-1}$ ) and volume swept clear ( $4.3$  ml copepod $^{-1}$  hr $^{-1}$ ) were calculated from the averaged data for days 8 to 13. These rates and those of three other experiments agree well with the results of batch culture experiments (Fig. 2, A and C).

When larger diatoms are fed to *Calanus* (Fig. 4) the effect of cell concentration on ingestion rates and volumes swept clear parallels that described above, with one important exception. Average maximal volumes swept clear increase with the size of cell, evidently in a predictable way (Fig. 5). The effects of cell concentration and size of cell on feeding behavior may be more clearly seen by replotting the data after converting cell concentrations and ingestion rates to carbon equivalents (Fig. 6). Above the critical concentrations of

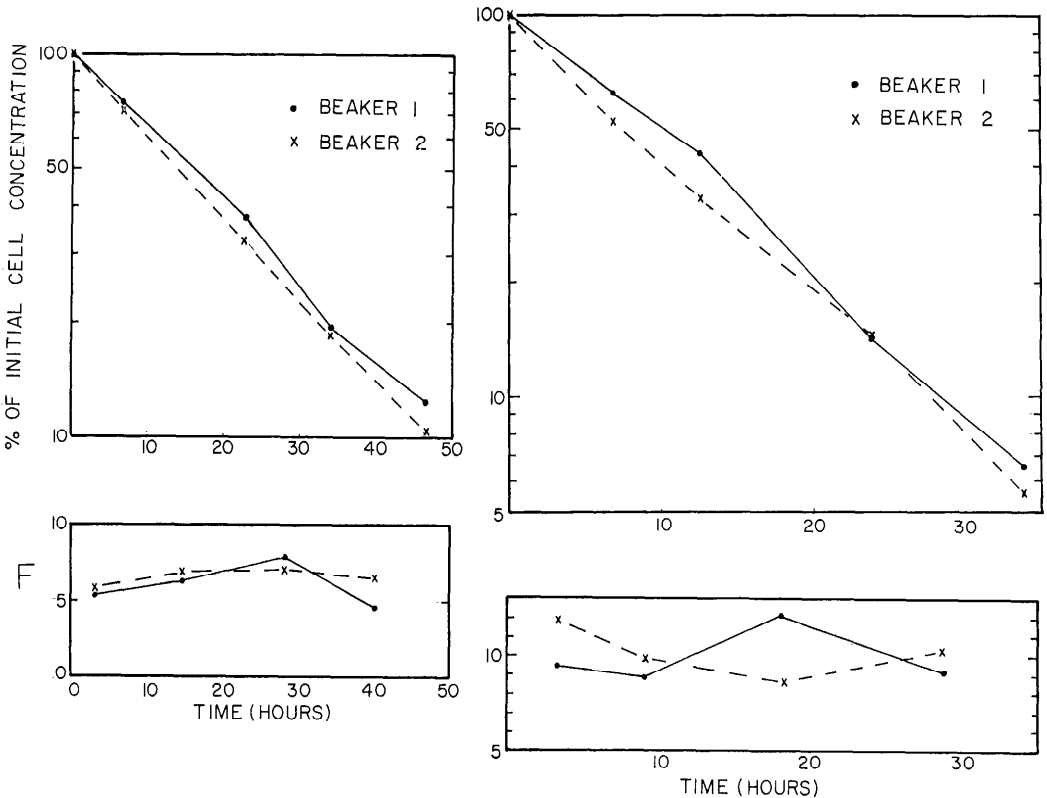


FIG. 7. Changes in cell concentration and volume swept clear,  $F$ , with time during experiments in which the initial cell concentration was below the critical concentration. Left graphs: *Calanus* feeding on *Coscinodiscus angustii* (initial cell concentrations: beaker 1—140 cells/ml; beaker 2—143 cells/ml). Right graphs: *Calanus* feeding on centric sp. (initial cell concentrations: beaker 1—47 cells/ml; beaker 2—32 cells/ml). Each beaker contained 30 *Calanus*.

plant carbon for all species of diatom, the copepods ingest and sweep clear water at the same rate regardless of the species of diatom used for food (Table 2). From this I conclude that *Calanus* does not distin-

TABLE 2. Mean ingestion rate ( $A$ ) ( $\mu\text{g C copepod}^{-1} \text{ hr}^{-1}$ ) of adult females of *Calanus pacificus* feeding on diatoms of different sizes. Means are based only on rates measured at cell densities above the critical concentration for each species of diatom. SE = standard error; N = number of observations

	A	SE	N
<i>T. fluviatilis</i>	1.13	0.031	26
<i>C. angustii</i>	1.07	0.038	18
<i>C. eccentricus</i>	1.01	0.072	14
Centric sp.	1.13	0.051	23

guish between these four species of diatom with respect to food quality, at least over the 3–5 day term of an experiment. Thus, the progressively higher carbon ingestion rates measured just at critical concentrations of larger cells (Fig. 6) most likely reflects differences in the efficiency with which *Calanus* handles and eats cells of different sizes. Clearly, females of *Calanus* can obtain their maximal daily ration at relatively low concentrations when feeding on the larger centric diatoms.

I suggest that below the critical cell densities of a particular diatom, *Calanus* ingests at a rate directly proportional to the amount of food available. This implies that volume swept clear is constant at low food concentrations. Feeding experiments

initiated at cell densities just below critical food concentrations and run for 1.5–2 days demonstrate that this is essentially true. Cell concentrations decrease exponentially and volumes swept clear are independent of cell concentrations (Fig. 7).

Mean dry weight of the copepods ranged from 130–210  $\mu\text{g}$  with no apparent systematic variation between experiments. If an average dry weight per copepod of 170  $\mu\text{g}$  is used and the bodily carbon is taken as 40% of dry weight (Mullin 1969), then unstarved females of *Calanus* ingest daily an amount of carbon equivalent to about 39% of their bodily carbon when feeding at food concentrations above the critical concentration (Table 2).

#### DISCUSSION

When feeding on monospecific cultures of centric diatoms which grow as single cells, a female of *C. pacificus* displays an ingestion rate which is directly dependent on the concentration and size of cell at low food concentrations, but constant and apparently independent of concentration, size and type of cell at high food concentrations. A model of this behavior is simple: it assumes no preference for food quality (i.e. species of centric diatom), a maximal daily ration (~39% of the body weight at 12.5°C) at high food concentrations, a critical food concentration (measured as carbon) that decreases with increasing cell volume, and an ingestion rate that (below the critical concentration) is linearly dependent on food concentration. Thus in Fig. 6 only four of a large family of ingestion lines are shown; lines for centric diatoms of other sizes could be found from Fig. 5 which gives the slope of the ingestion line for cell densities below the critical concentration. For now, I prefer this model because it is the simplest fit to the data in Figs. 2 and 4.

My model is not of the usual curvilinear form describing the feeding rate of predators in response to food concentration; however, Holling (1965) has pointed out that a rectilinear type of response curve may be typical of filter-feeding crusta-

ccans (e.g. McMahon 1965). The response curve is characteristic of an animal which searches at random for prey and has a searching rate which is not affected by density of prey organisms. This applies to filter-feeding copepods, since food particles—diatoms at least—can be ingested only after falling from a feeding current onto the scivelike second maxillae (Conover 1966). Ingestion rate for such a feeder increases in direct proportion to increase in concentration of food up to a saturation point above which ingestion may be determined by the passage rate of food through the alimentary canal. Other mathematical expressions for feeding behavior of copepods (e.g. Parsons et al. 1967; Cushing 1968) were tried, but do not fit my data particularly well.

Below critical food concentrations volumes swept clear by *Calanus* increase as the size of food particles increases. For the range of cell volumes used in this study the relationship can be considered monotonic and linear when plotted as in Fig. 5. From this I conclude that *Calanus* probably feeds as a filterer on both large and small cells but handles and eats larger cells with greater effectiveness than it handles and eats small cells. The actual mechanism behind this phenomenon is not clear. Obviously there must be a maximal rate at which *Calanus* can filter water. For benthic filter-feeding molluscs, the maximal filtering rate is usually found for animals exposed to particle-free seawater or very dilute suspensions of food (e.g. Loosanoff and Engle 1947; Davids 1964). Cushing (1968) suggested that the maximal filtering rate of *Calanus* depends on swimming speed; however, a consequence of this is that he predicts the same volume swept clear by *Calanus* at low concentrations of different-sized cells, a feature not actually found in feeding experiments. Since calculation of volume swept clear is based on the number of cells eaten, it is possible that a few large cells might be manipulated and passed to the mouth more quickly than many small cells of equivalent total carbon content. If this is

so, then *Calanus* could be filtering at the same rate on cells of all sizes, and the measure of volume swept clear could be indicative of how effectively *Calanus* handles and eats different-sized cells. Direct observations, designed after those of McMahon and Rigler (1963) and Burns (1968) on *Daphnia*, are needed.

*Calanus* may feed preferentially on larger cells when presented with a spectrum of particle sizes (see Richman and Rogers 1969). My results do not deny this possibility. However, consideration of the efficiency with which *Calanus* handles and eats cells of different sizes might shed light on some of the results of selective feeding experiments. Further, selective feeding experiments must be carefully designed with consideration of possible unwanted effects of cell concentration on feeding behavior. Adult females of *C. pacificus* feeding on a mixture of *T. fluviatilis* and *Coscinodiscus angustii* (each at a low concentration of carbon, i.e. <100 µg C/liter) ought to display a much higher ingestion rate, in terms of carbon, on the larger *Coscinodiscus*. When both diatoms are present at densities greater than the critical concentration for each, no selection by *Calanus* should be apparent. Richman and Rogers (1969) found that *Calanus* fed at significantly higher rates on paired cells than on single cells of the diatom *Ditylum brightwellii*. Inexplicably, the relationship in Fig. 5 qualitatively predicts this result but greatly overestimates the volume swept clear by *Calanus* when feeding on cultures of *Ditylum* dominated by single cells. This could be due to the difference in shape between a *Ditylum* cell and the cells used in my experiments. Alternatively, my study, utilizing unialgal cultures as food for *Calanus*, may possibly have missed other patterns of feeding behavior that emerge only when *Calanus* is exposed to heterogeneous mixtures of particle sizes or food species.

## REFERENCES

- BRODSKY, K. A. 1948. Free-living Copepoda of the Sea of Japan [transl. from Russian]. *Izv. Tikhookean. Nauch.-Issled. Inst. Rybn. Khoz. i Okeanogr.* **26**: 3-130.
- . 1965. Variability and systematics of the species of the genus *Calanus* (Copepoda) 1 [transl. from Russian]. *Akad. Nauk SSSR Zool. Inst., Issled. Fauni Morei* **3**(11): 22-71.
- BURNS, C. W. 1968. Direct observations of mechanisms regulating feeding behavior of *Daphnia* in lakewater. *Int. Rev. Gesamten Hydrobiol.* **53**: 83-100.
- . 1969. Particle size and sedimentation in the feeding behavior of two species of *Daphnia*. *Limnol. Oceanogr.* **14**: 392-402.
- CONOVER, R. J. 1966. Feeding on large particles by *Calanus hyperboreus* (Kröyer), p. 187-194. In H. Barnes [ed.], *Some contemporary studies in marine science*. Allen and Unwin.
- CUSHING, D. H. 1968. Grazing by herbivorous copepods in the sea. *J. Cons., Cons. Perm. Int. Explor. Mer* **32**: 70-82.
- DAVIDS, C. 1964. The influence of suspensions of microorganisms of different concentrations on the pumping and retention of food by the mussel (*Mytilus edulus* L.). *Neth. J. Sea Res.* **2**: 233-249.
- GUILLARD, R. R. L., AND J. II. RYTHER. 1962. Studies on marine planktonic diatoms 1. *Can. J. Microbiol.* **8**: 229-239.
- HARGRAVE, B. T., AND G. H. GEEN. 1970. Effects of copepod grazing on two natural phytoplankton populations. *J. Fish. Res. Bd. Can.* **27**: 1395-1403.
- HARVEY, W. H. 1937. Note on selective feeding by *Calanus*. *J. Mar. Biol. Ass. U.K.* **22**: 97-100.
- HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* **45**. 60 p.
- KESTER, D. R., I. W. DUEDALL, D. N. CONNORS, AND R. M. PYTEKOWICZ. 1967. Preparation of artificial seawater. *Limnol. Oceanogr.* **12**: 176-178.
- LOOSANOFF, V. L., AND J. B. ENGLE. 1947. Effect of different concentrations of microorganisms on the feeding of oysters (*O. virginica*). *Fish. Bull.* **51**: 29-57.
- MCALLISTER, C. D. 1970. Zooplankton rations, phytoplankton mortality and the estimation of marine production, p. 419-457. In J. H. Steele [ed.], *Marine food chains*. Univ. Calif.
- . 1971. Some aspects of nocturnal and continuous grazing by planktonic herbivores in relation to production studies. *Fish. Res. Bd. Can. Tech. Rep.* 248.
- MCMAHON, J. W. 1965. Some physical factors influencing the feeding behavior of *Daphnia magna* Straus. *Can. J. Zool.* **43**: 603-611.
- , AND F. H. RIGLER. 1963. Mechanisms regulating the feeding rate of *Daphnia magna* Straus. *Can. J. Zool.* **41**: 321-332.
- , AND ———. 1965. Feeding rate of

- Daphnia magna* Straus in different foods labeled with radioactive phosphorus. *Limnol. Oceanogr.* **10**: 105-114.
- MARSHALL, S. M., AND A. P. ORR. 1955. The biology of a marine copepod. Oliver and Boyd. 188 p.
- MULLIN, M. M. 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. *Limnol. Oceanogr.* **8**: 239-250.
- . 1966. Selective feeding by calanoid copepods from the Indian Ocean, p. 545-554. In H. Barnes [ed.], *Some contemporary studies in marine science*. Allen and Unwin.
- . 1969. Production of zooplankton in the ocean: the present status and problems. *Oceanogr. Mar. Biol. Annu. Rev.* **7**: 293-314.
- , AND E. R. BROOKS. 1967. Laboratory culture, growth rate, and feeding behavior of a planktonic marine copepod. *Limnol. Oceanogr.* **12**: 657-666.
- PAFFENHÖFER, G. A. 1971. Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. *Mar. Biol.* **11**: 286-298.
- PARSONS, T. R., AND R. J. LEBRASSEUR. 1970. The availability of food to different trophic levels in the marine food chain, p. 325-343. In J. H. Steele [ed.], *Marine food chains*. Univ. Calif.
- , ———, AND J. D. FULTON. 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. *J. Oceanogr. Soc. Jap.* **23**: 10-17.
- , ———, AND O. D. KENNEDY. 1969. Production studies in the Strait of Georgia. Part 2. *J. Exp. Mar. Biol. Ecol.* **3**: 39-50.
- PETIPA, T. S. 1965. The food selectivity of *Calanus helgolandicus* (Claus), p. 102-110. In *Plankton investigations in the Black and Azov Seas* [transl. from Russian]. Akad. Nauk Ukr. SSR.
- REEVE, M. R. 1963. The filter-feeding of *Artemia*. 1. *J. Exp. Biol.* **40**: 195-221.
- RICHIAMAN, S., AND J. N. ROGERS. 1969. The feeding of *Calanus helgolandicus* on synchronously growing populations of the marine diatom *Ditylum brightwellii*. *Limnol. Oceanogr.* **14**: 701-709.
- STRATHMANN, R. R. 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnol. Oceanogr.* **12**: 411-418.