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The feeding response of copepods from the Peru upwelling system: Food size selection

by Timothy J. Cowles[1,2]

ABSTRACT

Two cruises to the Peru upwelling in 1976 and 1977 provided the opportunity to examine the feeding response of *Centropages brachiatus, Calanus chilensis,* and *Eucalanus inermis.* The shipboard experiments with naturally occurring particulate matter were designed to test two hypotheses: 1) that food size selectivity by a copepod is a function of overall food concentration, and 2) that a copepod varies the range of food sizes ingested as a function of food concentration and available food size. The results indicate that all three copepod species examined were size selective feeders at high food concentrations, but showed decreased selectivity as total food abundance decreased. At low phytoplankton food abundance the range of food size ingested was significantly wider than at higher food abundances (P <.01). An additional particle capture mechanism must supplement the "sieve" mechanism to account for these data.

1. Introduction

High frequency temporal and spatial variability in phytoplankton abundance is common in coastal marine environments (Platt, 1975), such that an individual copepod may encounter a wide range of food sizes, species, and abundances during its lifetime. The experimental analysis of copepod feeding response to the naturally occurring range of food variability has proceeded slowly because of the inherent difficulty in obtaining this range of natural variability within the time constraints of an experimental feeding study. As a result, the first generation of experimental feeding studies of copepods have used single species of phytoplankton in their determinations of zooplankton feeding rates (Conover, 1956; Mullin, 1963; Paffenhöfer, 1970; Frost, 1972, 1975). Two major generalizations have emerged from these single-species laboratory studies. First, copepods ingest food at a rate directly proportional to its abundance, up to a critical concentration at which the ingestion rate reaches a plateau. Second, copepods ingest large phytoplankton cells at a faster rate than small cells. These two components of the generalized feeding response of

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copepods interact to produce complex results when naturally occurring particulate matter is used as the experimental food. For example, does an exclusive increase in the biomass of large phytoplankton cells increase the ingestion rate in the same manner as a biomass increase across all available cell sizes? Are the effects of total particle abundance on ingestion rates independent of the effects of relative abundance of particle size classes within the total particulate size-frequency distribution? The adaptation of electronic particle counting to marine science applications (Sheldon and Parsons, 1967) has made it possible to determine the particle size-frequency distribution and biomass (as particle volume) within each size category measured, so that the combined effects of food size distribution and abundance can be examined with higher precision than is possible with microscopic techniques.

Copepods that have been fed natural phytoplankton assemblages with a mixture of cell sizes have displayed complex feeding behavior. Poulet (1973, 1974) found that *Pseudocalanus minutus,* a small neritic copepod, could ingest a wide range of particle sizes, and it shifted its maximum effort to those size classes with greatest relative abundance. Poulet (1978) has recently reported that *Oithona similis, Eurytemora herdmani,* and *Temora longicornis* display opportunistic feeding behavior which parallels that found in *P. minutus.* A recent study by Richman *et al.* (1977) has provided results similar to Poulet's for three estuarine copepods, *Eurytemora affinis, Acartis tonsa,* and *Acartia clausi.* Each species had highest ingestion rates on those size classes with greatest relative abundance, with both species of *Acartia* also selectively ingesting particles slightly larger than those within the biomass peak.

The studies of Poulet (1973, 1974, 1978), Richman *et al.* (1977), and Wilson (1973) demonstrate that the size selection mechanism of copepods is not fixed and may be under behavioral control. However, these studies did not specifically address the question of the combined effects of particle abundance and size frequency distribution on copepod feeding rates and selectivity. Two oceanographic cruises to the Peru upwelling system (Fig. 1) provided the opportunity to test this interaction with shipboard experiments using naturally occurring particulate matter. The phytoplankton concentration and production in an upwelling area such as Peru is a function of a suite of hydrographic, chemical, and biological interactions (Huntsman and Barber, 1977; Walsh, 1975) which vary widely on time scales of days and spatial scales of miles. This heterogeneity of the phytoplankton in time and space provided an easily obtainable range of food levels and food size distributions for these experiments. The experiments were designed to test 1) if a species responds to a food level increase by decreasing the range of food sizes ingested; 2) if a species becomes less "selective" of "preferred" size classes as total food abundance decreases.

2. Methods

Adult, female *Centropages brachiatus, Calanus chilensis,* and *Eucalanus inermis* were chosen as experimental animals based upon their relative body sizes as well as
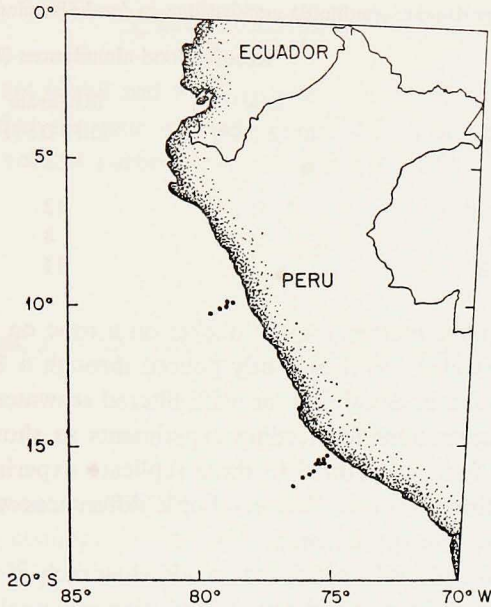
Figure 1. Area of Peru coast in which copepod feeding studies were conducted. Filled circles denote regions in which experiments were conducted.

their relative abundance within the plankton. Samples were collected with nets hauled vertically from approximately 100 meters depth to the surface. Collected animals were healthy and active (based upon pipette avoidance response) if the net retrieval rate was no greater than 20 meters per minute, and if the end of the net was a nonfiltering cup rather than an open mesh. Contents of the net were distributed into several large beakers of unfiltered surface water. Each beaker was then examined, and adult females of the appropriate copepod species were isolated with a hand-held, large volume pipette. In order to minimize handling prior to experimentation, animals were identified and sorted to species level without use of a microscope. As a result, occasional errors in identification of species and sex occurred, but these errors were noted during the microscopic identification done following the experiment.

Animals were maintained within 1°-2°C of water temperature at capture (18°-20°C) before and during experimentation. In an effort to reduce the effects of previous feeding history on the experimental design, animals were maintained under experimental food conditions for 4-6 hours before initiation of a feeding experiment. The precise time course of feeding rate "acclimation" has not been quantified, therefore 4-6 hours was chosen as a best estimate given the experimental conditions.

To establish initial food conditions for the animals, I collected surface water con-

Table 1. Number of experiments conducted under different food abundances.

Relative food abundances ($10^6 \mu m^3 \cdot ml^{-1}$)

Range	Low (0.12-0.49)	Moderate (0.50-0.99)	High (>1.00)
Species			
Centropages brachiatus	15	12	14
Calanus chilensis	14	8	6
Eucalanus inermis	7	11	10

taining natural particulate matter, using a bucket on a rope on a messenger-tripped sampling bottle. The water was then gently poured through a 223 μm mesh net to remove larger zooplankton. Serial dilution with filtered seawater was used to obtain a range of food concentrations for feeding experiments as shown in Table 1. The water containing the food was added to three replicate experimental bottles (250-1000 ml) plus up to three controls. Between bottle differences were always less than 5% at the beginning of an experiment.

One to four adult females of a species were added to each of the replicate feeding chambers which contained the experimental food. Experimental replicates plus controls were kept in the dark at environmental temperatures (18°-20°C) for twenty-four hours, with the particulate food kept in suspension by rotation of the bottles at 1-2 rpm. Triplicate electronic particle counts were made before and after each experiment, using a Coulter™ counter model TAII equipped with a population accessory. Particle counts were made with a 280 μm aperture, calibrated with polystyrene spheres (18.04 μm) so that fourteen volumetric size channels ranged from particles with apparent average diameters of 5.67 μm (channel 2) to 114.1 μm (channel 15). Channel 1 was not used due to noise problems. Counts recorded in channel 16 (all particles with apparent diameters larger than 114.1 μm) were discarded as well. The Coulter counter was used in the TIME mode in order to count particles in larger volumes than is possible in the MANOMETER mode. Gardner (1977) has pointed out the potential errors in using the TIME mode during shipboard experiments, but I relied on triplicate counts of each sample to indicate when excessive ship's motion had affected the flow rate through the aperture tube. For each particle spectrum determination, 50 to 75 ml of sample was counted in order to insure precision at low particle abundances. Comparison of counts of serial dilutions of the same initial particle distribution indicated that the precision in determining the particle distribution did not change with decreasing total particle abundance.

Ingestion rates were calculated for each size class (Coulter channel) using the equations of Frost (1972). Size class frequency distributions of ingested food were compared to the distribution of available food sizes, in which the "available" food concentration, $\bar{C}$, is determined by

$$\bar{C} = \frac{C_2^* - C_1^*}{(t_2 - t_1)(k - g)}$$

where C_1^* and C_2^* are initial and final particle concentrations in the experimental grazing chamber during the time interval $t_2 - t_1$. The algal growth constant, k, is calculated from the control particle concentrations, C_1 and C_2 at times t_1 and t_2, such that

$$k = \frac{\ln C_2 - \ln C_1}{t_2 - t_1}$$

The grazing coefficient, g, is calculated for each experimental grazing chamber from the equation

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

The available food concentration, $\bar{C}$, thus reflects the particle growth rate and the grazing rate. On the assumption that grazing rates are constant during the experimental time interval, $\bar{C}$ provides the best estimate of what the copepods "see" during the experiment.

An operational definition of selective feeding is needed before reporting the results, since "selective" feeding has had numerous connotations in the literature. The chi-square (χ^2) goodness-of-fit test (Sokal and Rohlf, 1969) tests the similarity of two distributions. This test has been used to compare the frequency distribution of phytoplankton particle size classes in the copepod's diet to the frequency distribution of those size classes in the available food. Selective feeding is defined as having occurred if the two distributions are significantly different according to the χ^2 test, that is, if some size classes are ingested out of proportion to their relative abundance in the available food.

The chi-square goodness-of-fit test was used instead of an electivity index (Ivlev, 1961) since statistics cannot be done on electivity indices, and since electivities are relevant only for individual size classes, not the entire distribution. The Komolgorov-Smirnov test can also be used to compare discrete distributions, but it is relatively insensitive when used with a limited number of size classes. Relative frequency distributions were calculated for both the available particle distributions and the ingested particles by summing the particle volumes across all size classes, then plotting the relative proportion each size class volume contributed to the total. In this way the "diet" composition can be easily compared to the available food distribution.

It has been demonstrated that particles produced by copepods grazing on natural particulate matter can occasionally bias experimental results (O'Connors et al., 1976). In none of the experiments reported here did particle production via grazing increase particle biomass in the small size-classes ($<10~\mu m$) more than 15% above control biomass in those same size classes.
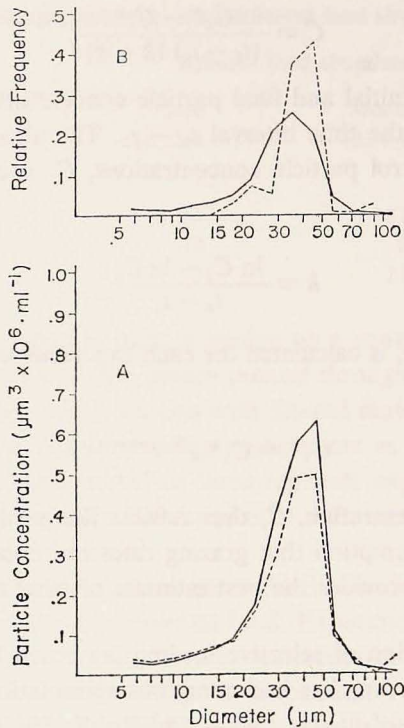
Figure 2. Grazing of *Centropages brachiatus* on a natural phytoplankton distribution which has high total particle volume, with greatest relative abundance in large size-classes. A. Comparison of particle distributions at the end of a twenty-four hour feeding experiment. Solid line = control, dashed line = experimental. B. Frequency distributions of size-classes in the available food (solid line) and in the diet (dashed line). $\chi^2 = 75.98$, $P < .005$.

3. Results

The figures which follow have been selected to illustrate each species feeding across the particle size range under different conditions of relative and total size class abundance. The feeding data are discussed in terms of high, moderate, and low total particle abundance as defined in Table 1. Within each of these categories, the feeding results are discussed in terms of the relative abundance of size classes within the available particle volume-frequency distribution. The results are representative of those found in over 90 shipboard feeding experiments.

Centropages brachiatus, Calanus chilensis, Eucalanus inermis display similar abilities to consume a wide range of particle sizes (Figs. 2-16). Each figure illustrates the differences in the particle distributions of the control and experimental bottles after a twenty-four hour experiment. In addition, the relative frequencies of each size class are plotted for the available food and for the food ingested by the copepod.
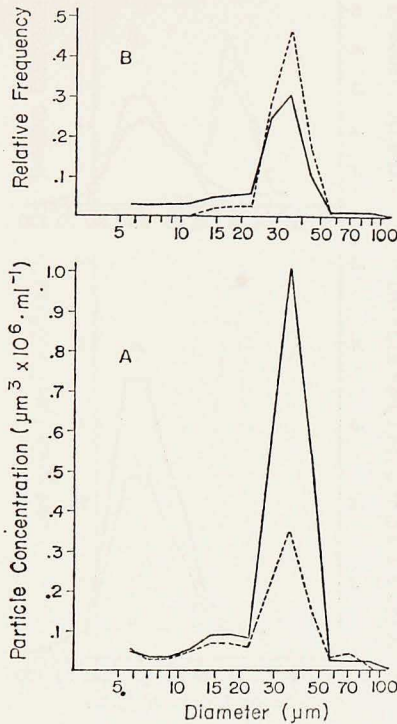
Figure 3. Grazing of *Calanus chilensis* on a natural phytoplankton distribution which has high total particle volume, with greatest relative abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 26.72$, $P < .005$.

The χ^2 goodness-of-fit statistic is included with each figure, giving the level of significance if the two distributions differ.

At high total particle abundance, with large size classes predominating, *Centropages brachiatus, Calanus chilensis, Eucalanus inermis* disproportionately ingest those size classes with greatest relative abundance (Figs. 2, 3, and 4). All the diet vs. available particle frequency distributions were significantly different ($P < .005$) under these food conditions, with the maximum contribution to the χ^2 statistic coming from the size class with greatest relative abundance.

The pattern of size-selectivity changes as the particle size frequency distribution shifts to medium size-class predominance at high food levels. *Calanus chilensis* feeds disproportionately on the size class with greatest relative abundance (Fig. 5) even though the particles in this size class are 20 μm smaller than the peak size class in Figure 3. This result suggests considerable flexibility in size-selectivity at high food levels. *Centropages brachiatus* and *Eucalanus inermis*, on the other hand, continue
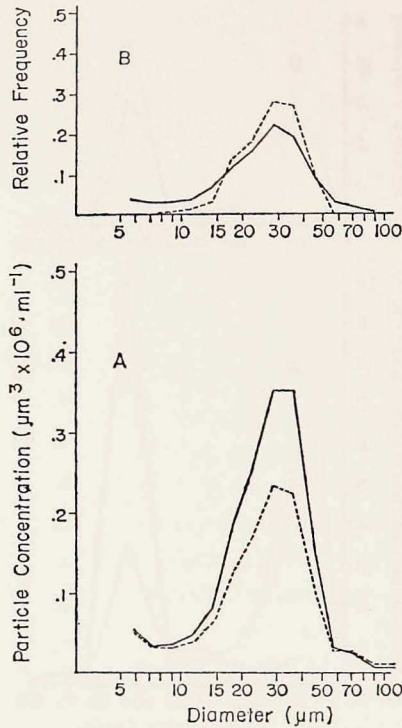
Figure 4. Grazing of *Eucalanus inermis* on a natural phytoplankton distribution which has high total particle volume, with greatest relative abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 16.024$, $P < .005$.

to select larger size classes disproportionately when the peak relative abundance is between 10 μm and 20 μm particle diameter (Figs. 6 and 7).

At moderate total particle abundance, the three species of copepods continue to select the size classes with greatest relative abundance (Figs. 8, 9, and 10) when large particles predominate. *C. brachiatus* selects the same range of food sizes at this food abundance as at high abundances as the relative abundance maxima shifts to smaller size classes (Fig. 11). *E. inermis* ingested a wide size range of particles when the available particle distribution showed no large peaks in relative abundance (Fig. 12).

At low food levels, *C. chilensis* and *C. brachiatus* frequently did not demonstrate selective feeding, i.e., the size distribution of particles in the diet was often not significantly different from the size distribution in the available food. The particle size ingestion by *C. chilensis* under low food conditions is shown in Figures 13 and 14. The size-frequency distributions of the diet are more similar to the available food (χ^2 goodness-of-fit test: not significant) than at higher food levels. The same result
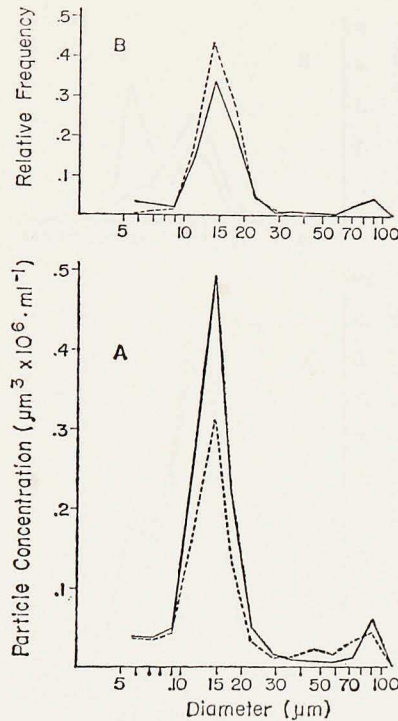
Figure 5. Grazing of *Calanus chilensis* on a natural phytoplankton distribution which has high total particle volume, with greatest relative abundance in medium size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 13.113$, $P < .005$.

was obtained for *C. brachiatus* at low food levels (Figs. 15 and 16, χ^2 goodness-of-fit test: not significant). The experiments done with *E. inermis* at low food levels did not reveal any consistent pattern of selectivity or nonselectivity.

The above results suggest that *C. brachiatus* and *C. chilensis* modify their mechanism of particle selection as total food abundance decreases to low levels. A shift from specialized to generalized size-class ingestion is apparent from a comparison of Figures 2-11 with Figures 12-16. Minimum and maximum food sizes ingested may also characterize the feeding behavior at any given food abundance. Minimum and maximum size class are operationally defined as those extremes which have at least 5% of the total volume ingested during an experiment. Size categories have been labeled 1 through 12, rather than in terms of particle diameter, in order to avoid confusion with transformation of the logarithmic particle size scale. *C. chilensis* extends the minimum size class in its diet from a mean of 6.25 to a mean of 4.55 when food abundance decreases ($t = 2.619$, $P < .05$, $df = 32$). No change in maximum size class occurs ($t = 1.44$, NS). *Centropages* also expands the range of size classes
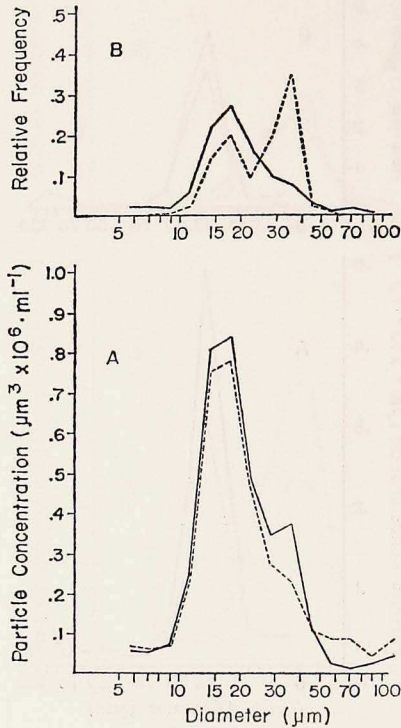
Figure 6. Grazing of *Centropages brachiatus* on a natural phytoplankton distribution which has high total particle volume, with greatest relative abundance in medium size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 140.45, P < .005.$

ingested as food abundance decreases ($t = 3.298, P < .01, df = 23$) (Table 2). The size class extremes in the diet do not differ between *C. chilensis* and *C. brachiatus* at either high or low food abundance (Table 2). *E. inermis* also broadens its diet as food abundance decreases, with significant differences between high and low food levels at both minimum and maximum size classes.

4. Discussion

Copepods have been recognized as "selective" feeders since Harvey (1937) reported that *Calanus finmarchicus* disproportionately ingested the largest cell size in a mixture of three phytoplankton species. Evidence for large-particle selectivity has been accumulated for a variety of copepod species feeding upon mixtures of phytoplankton (Mullin, 1963, 1966; Richman and Rogers, 1969). Comparisons of ingestion rates for copepods fed single food species indicate that the highest rates occur
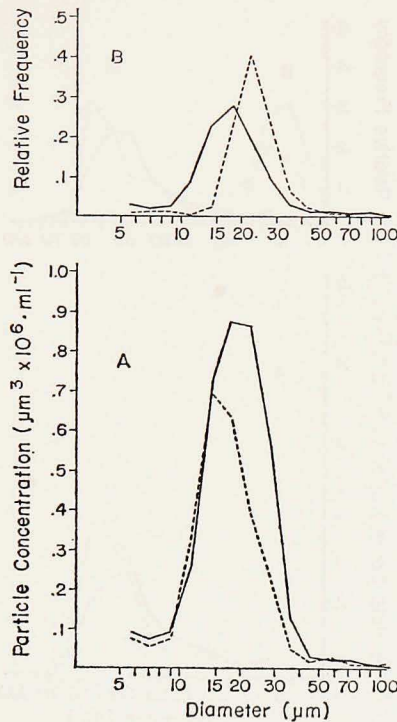
Figure 7. Grazing of *Eucalanus inermis* on a natural phytoplankton distribution which has high total particle volume, with greatest relative abundance in medium size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 68.91$, $P < .005$.

Table 2. The range of food sizes ingested under conditions of low and high food abundance.

			Species			
	Centropages brachiatus		*Calanus chilensis*		*Eucalanus inermis*	
Food levels	lower*	upper*	lower	upper	lower	upper
High	5.93†	10.21	6.25	9.94	5.89	9.3
Low	3.73	10.0	4.55	10.61	2.8	10.8
Significance‡	P<.01	NS	P<.01	NS	P<.01	P<.01

* operationally defined as that size class representing at least 5% of the total volume ingested.
‡ based upon *t*-test.
† size classes correspond to particle diameter according to the following:

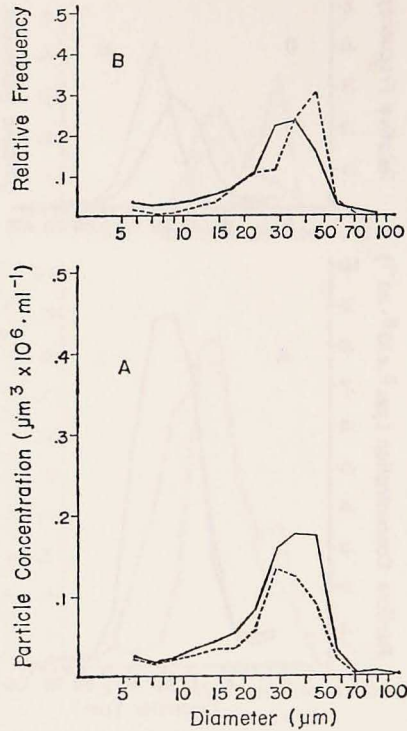| Size class	1	2	3	4	5	6	7	8	9	10	11
mean particle diam (μm)	5.67	7.13	8.98	11.31	14.25	17.96	22.6	28.5	35.9	45.3	57.0

Figure 8. Grazing of *Centropages brachiatus* on a natural phytoplankton distribution which has moderate total particle volume, with greatest abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 7.664$, NS.

when large phytoplankton cells are offered (Frost, 1972; Paffenhöfer, 1971). The few feeding studies which used natural particle distributions found that highest size-class specific feeding rates occurred on large size classes which had the greatest relative abundance (Gamble, 1978; Parsons *et al.*, 1967, 1969; Poulet, 1973, 1974, 1978; Richman *et al.*, 1977). In none of these studies, however, was the distinction made between particle selectivity and total particle abundance, since the majority of experiments used high food levels in order to achieve near maximal feeding rates.

The results of this study provide clear evidence that copepods alter their size-selectivity as a function of total food abundance. At high food levels, all of the copepod species examined selectively ingested particles that had the greatest relative abundance (Figs. 2, 3, and 4), or selectively ingested particles slightly larger in size than those with greatest relative abundance (Figs. 5, 7, and 11). As total food levels decreased, however, disproportionate feeding decreased (Figs. 13-16).

Decreased selectivity as food levels decrease has also been found in fish (Ivlev, 1961), birds (Lack and Owen, 1955; Orians, 1966) and *Conus* molluscs (Kohn,
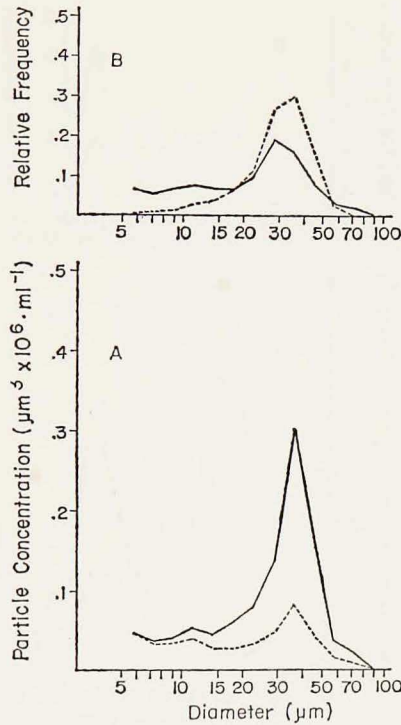
Figure 9. Grazing of *Calanus chilensis* on a natural phytoplankton distribution which has moderate total particle volume, with greatest relative abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 38.215$, $P < .005$.

1968). These results correspond with the most general prediction of optimal foraging theory that the range of food types in the diet will increase and the diet will be less specialized as food abundance decreases (MacArthur and Pianka, 1966; Emlen, 1966; Schoener, 1971; Pyke *et al.*, 1977). While no direct evidence is available to suggest that copepods possess "optimal diets", the results of this study indicate that copepods must modify their mechanism of food capture as food abundance decreases to low levels.

Examination of the morphology of copepod mouth parts, and particularly the setulation of the filtering appendages, has led to the widely-held view that particles are removed from the water by "sieving" mechanism (Marshall and Orr, 1955; Nival and Nival, 1976; Boyd, 1976). By such a mechanism, phytoplankton particles larger than the average "mesh" size of the copepod's filter (the second maxillae) are caught with 100% efficiency, while particles smaller than the smallest mesh size pass through without being captured. Nival and Nival (1973, 1976) described the mesh size of the second maxillae in terms of a normal distribution, with the upper and
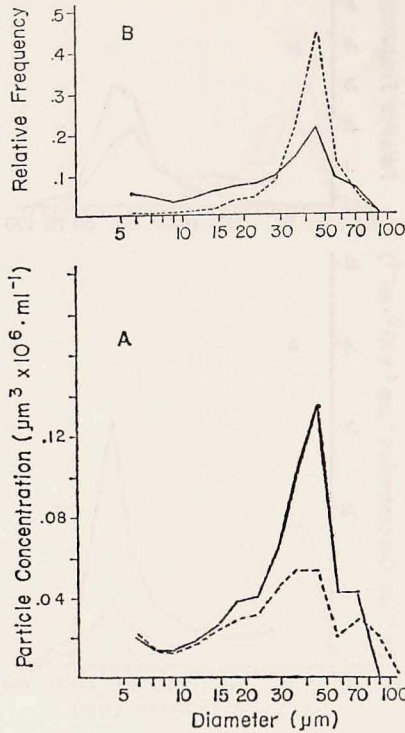
Figure 10. Grazing of *Eucalanus inermis* on a natural phytoplankton distribution which has moderate total particle volume, with greatest relative abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 68.042$, $P < .005$.

lower lobes of the second maxillae possessing different mean mesh sizes, with different associated variances. Lehman (1976) and Boyd (1976) have incorporated the findings of Nival and Nival (1976) into the "sieve" mechanism, and predict that copepods will show selective feeding on large cells regardless of the size distribution of the phytoplankton cells. Results of Poulet (1973, 1974), Wilson (1973), and Richman *et al.*, (1977) indicate that the particle size with greatest relative abundance is removed with greatest selectivity. Wilson (1973) and Lehman (1976) explain these results on the assumption that the copepod is capable of varying the "mean mesh size" of its filtering appendages.

If copepods remove particles with a passive sieving mechanism as described by Boyd (1976), the peak size-selectivity will occur on those size-classes of food which are larger than the average mesh size of the copepod's "sieve". Incorporation of an "adjustable" sieve (Lehman, 1976) also results in maximum size-selectivity on those size classes larger than the size class with greatest relative abundance, and allows the copepod to more closely "track" the peaks of greatest relative abundance.
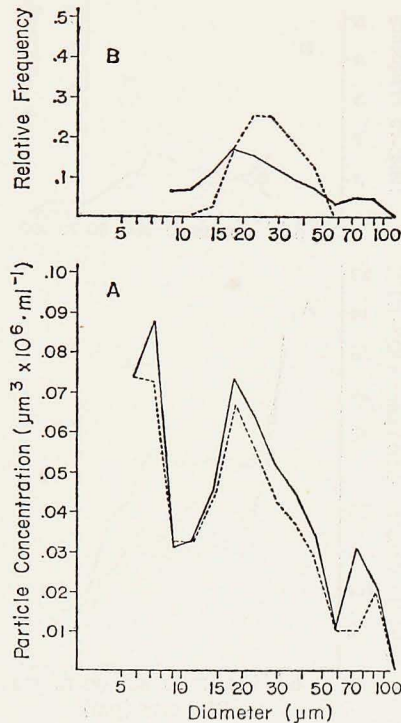
Figure 11. Grazing of *Centropages brachiatus* on a natural phytoplankton distribution which has moderate total particle volume, with greatest relative abundance in medium size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 41.53$, $P < .005$.

While the sieve mechanism appears to adequately account for the size-selective results with *C. brachiatus, C. chilensis,* and *E. inermis* at high food abundances, it does not adequately explain the decreased selectivity and diet expansion found at low food levels. The most parsimonious explanation of the feeding response would invoke a supplemental mechanism which operates primarily at low food levels.

Such a supplemental filter-feeding mechanism has been presented by Rubenstein and Koehl (1977). They have incorporated the theory of particle motion in fluid flow (at low Reynolds number) to describe particle capture by filters. Capture is a function of particle diameter, particle mass, velocity and viscosity of the fluid, diameter of the filter fiber, and filter pore size. One of the predictions which results from the application of filtration theory to biological filters is that small particles can be captured with greater efficiency as fluid velocity through the filter increases.

Copepods may have two mechanisms which can vary the velocity at which water passes through the particle capturing appendages. Morphological evidence found by Friedman (1977) indicates that the second maxillae of a copepod has the neces-
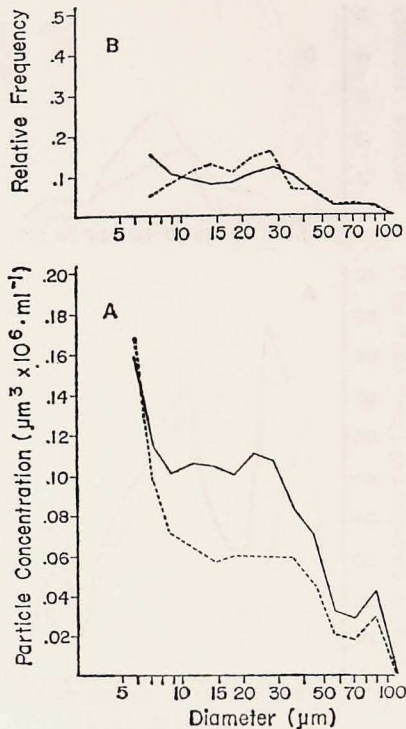
Figure 12. Grazing of *Eucalanus inermis* on a natural phytoplankton distribution which has moderate total particle volume, with relatively even distribution of abundance across size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 14.135$, NS.

sary internal musculature to move the upper and lower lobes apart as shown in Figure 17. If the feeding appendages direct a *constant* velocity current toward the mouthparts, the effective velocity across the particle capturing appendages could possibly be changed by altering the gap between the upper and lower lobes of the second maxillae.

A copepod could also increase fluid velocity across its second maxillae by moving its second antennae and first maxillae at a faster rate, these appendages being the principal elements of the filtering current (Gauld, 1966). High-speed films of appendage movement indicate that appendages move at a frequency of about 60 Hz (Friedman, pers. comm.). Small particles may be captured with higher efficiency if a *variable* appendage movement rate can increase the effective fluid velocity at the particle capturing appendages.

It must be said, at this point, that any proposed supplemental particle capturing mechanism will remain a "proposed" mechanism until more is understood about the
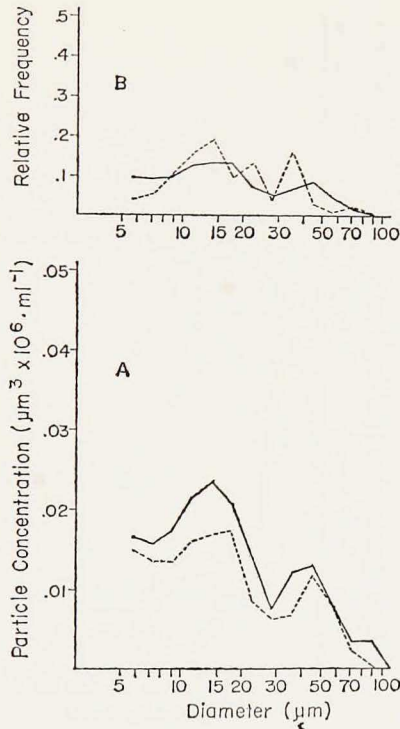
Figure 13. Grazing of *Calanus chilensis* on a natural phytoplankton distribution which has low total particle volume, with greatest relative abundance in small and medium size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 12.11$, NS.

hydrodynamics of the feeding appendages of copepods. The low Reynolds number environment of phytoplankton places constraints upon any consideration of inertial forces within the viscous medium of seawater. Rubenstein and Koehl (1977) have provided a theoretical framework for additional work in this area.

Frost (1977) presents convincing evidence for a passive, i.e., simply mechanical, mechanism of particle capture by filter-feeding copepods. Large particles are "selectively" ingested as a result of the greater capture efficiency of the filter mesh for large phytoplankton cells. The results reported here are in agreement with Frost (1977) for those experiments with moderate to high food levels. At low food levels, however, my results indicate that copepods may supplement the passive, mechanical, particle capturing mechanism in order to increase the number of food particles captured.

The experimental results reported here have not addressed the chemosensory aspect of food capture. The role of "taste" in food selection by crustaceans may be
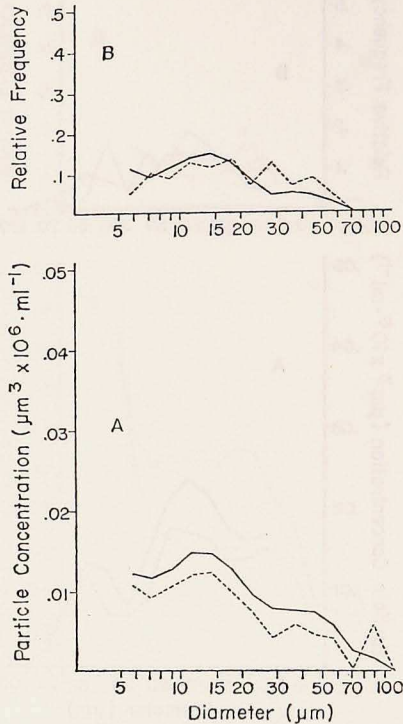
Figure 14. Grazing of *Calanus chilensis* on a natural phytoplankton distribution which has low total particle volume, with greatest abundance in small size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 13.18$, NS.

just as important as the selection of food on the basis of size (Hamner and Hamner, 1977; Poulet and Marsot, 1978) thereby reinforcing the need for additional behavioral studies of the feeding process.

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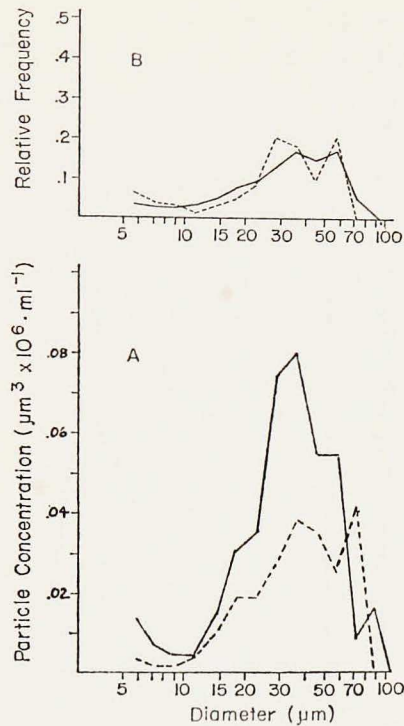
Figure 15. Grazing of *Centropages brachiatus* on a natural phytoplankton distribution which has low total particle volume, with greatest relative abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 10.03$, NS.

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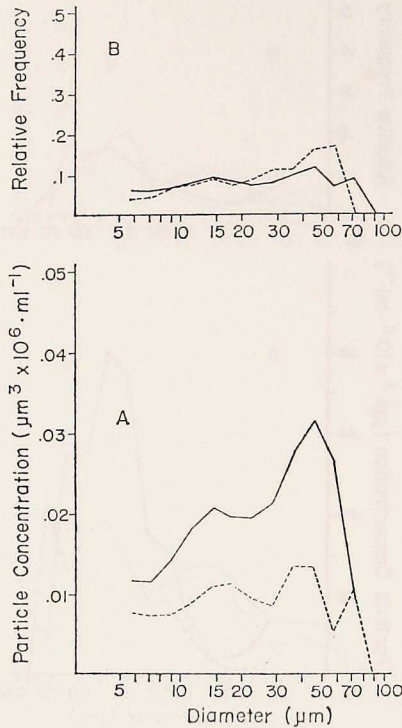
Figure 16. Grazing of *Centropages brachiatus* on a natural phytoplankton distribution which has low total particle volume, with greatest relative abundance in large size-classes. A and B. Symbols as in Figure 2. $\chi^2 = 6.58$, NS.

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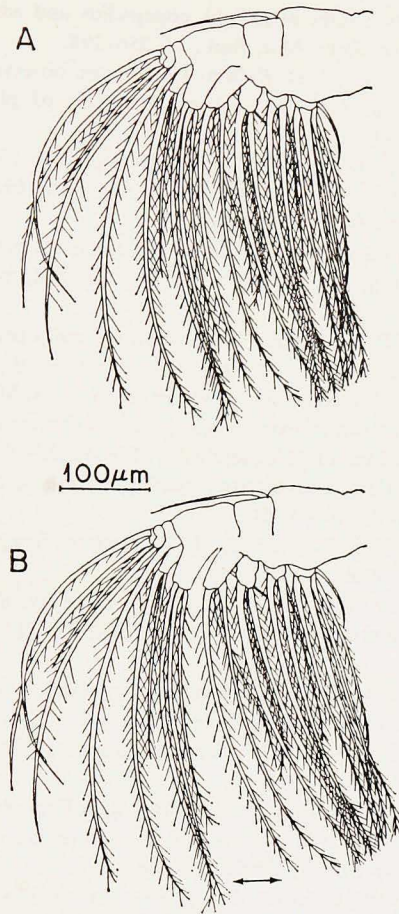
Figure 17. Change in the particle capturing appendage resulting from separation of the upper and lower lobes of the second maxillae. A. Lobes in the closed position. B. Lobes in the open position. (Figure modified from Frost, 1977).

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