Omnivory by *Euphausia pacifica:* the role of copepod prey

Mark D. Ohman*

School of Oceanography, WB-10, University of Washington, Seattle, Washington 98195, USA

ABSTRACT: Adult *Euphausia pacifica* obtain a maximum carbon-specific ration of 8.8 % d^{-1} from the centric diatom *Thalassiosira angstii* and 0.45 % d^{-1} from the copepod *Pseudocalanus* sp. *E. pacifica* exhibits a sigmoidal or 'stabilizing' functional response to diatoms but not to copepods. Adult copepods may be attacked and injured by *E. pacifica* but they are suboptimal prey item for this omnivore.

INTRODUCTION

Prediction of the impact of predation by euphausiid crustaceans on plankton assemblages requires an understanding of the responses of euphausiids to changes in prey abundance and composition. Based on analyses of dietary remains in stomachs of preserved euphausiids, most euphausiid species are thought to be omnivores (reviewed in Ponomareva, 1963; Mauchline and Fisher, 1969; Mauchline, 1980). However, little information is available to describe quantitatively the functional response of euphausiids to changes in concentration of different prey types. Particulary lacking are attack rates on natural zooplankton prey such as adult copepods, nauplii, or protozoans.

Previous experiments treating carnivory by euphausiids have been done with *Artemia* nauplii (Lasker, 1966; Gopalakrishnan, 1973; Sameoto, 1976; Pelymsky and Arashkevich, 1980; Ponomareva and Nikolayeva, 1981; Ikeda, 1984), *Artemia* juveniles (Fowler et al., 1971), or with fish larvae as prey (Theilacker and Lasker, 1974). *Artemia* nauplii are sluggish swimmers with limited escape responses and are captured by copepods (and presumably euphausiids) at different rates than natural prey such as copepod nauplii (Mullin and Brooks, 1967). In addition to these carnivory experiments, other approaches have provided some assessment of dietary breadth of different euphausiid species, including analyses of lipid class composition

(Falk-Petersen et al., 1981), digestive enzyme activity (Cox, 1981), and functional morphology (McClatchie and Boyd, 1983). However, these techniques do not yet permit measurement of ingestion rates or quantitative comparison of ingestion responses to different prey types such as copepods and diatoms.

Euphausia pacifica Hansen was selected for these experiments because it is the most abundant euphausiid species in eastern boundary currents of the northeast Pacific (Brinton, 1962; Brinton and Townsend, 1982) and in adjacent coastal fjords (Cooney, 1971; Harrison et al., 1983). Due to its abundance, high ingestion (Parsons et al., 1967) and growth rates (Ross, 1982), *E. pacifica* may have a significant grazing or predatory impact *in situ.*. The small copepod *Pseudocalanus* sp. (0.86 mm prosome length, adult female) was chosen as a prey item because it is the most numerous calanoid copepod over much of the northerly range of *E. pacifica* (Hebard, 1956; Peterson and Miller, 1977; Corkett and McLaren, 1978; Koeller et al., 1979); it is likely to experience frequent encounters with *E. pacifica* when not reverse migrating (Ohman et al., 1983); and is more likely than larger copepods to be captured by euphausiids. The diatom *Thalassiosira angstii* was used in grazing experiments due to its edibility by other suspension feeding zooplankton (e.g. Vidal, 1980). In addition to comparing the feeding behavior of *E. pacifica* on *Pseudocalanus* to that on diatoms, the incidence and patterns of injury of *Pseudocalanus* were examined to attempt to identify a signature of attack by *E. pacifica* for possible use in field studies.

---

* Present address: Friday Harbor Laboratories, Friday Harbor, Washington 98250, USA

METHODS

Zooplankton was collected in Puget Sound using nets with non-filtering cod ends and then transported to the laboratory in thermally insulated containers. Euphausiids were acclimated for at least 24 h to either diatoms *(Thalassiosira angstii)* or to a suspension of small copepods dominated by *Pseudocalanus* sp. For predation experiments euphausiids were then placed in filtered seawater for ca. 24 h prior to starting the experiment. Seawater was filtered with either Gelman A/E glass fiber filters or with a 1 μm Strainrite filter bag (AP1). All experiments were performed at 8 °C in the dark in 3.8 l jars. Two to 4 euphausiids and prey were added to experimental containers and rotated at ca. 1.5 rpm on a grazing wheel or roller mixing device.

Predation experiments were run for 24 h with 4 to 8 replicate jars containing *Pseudocalanus* sp. adult females in filtered seawater. Experiments were terminated by collecting prey remains on a fine mesh Nitex screen. The remaining *Pseudocalanus* were preserved immediately, then counted and examined closely for injuries with a dissecting microscope. Injuries in five body regions were scored according to the following criteria: I. Antennules – both missing; II. Mouthparts – more than 50 % missing; III. Prosome – exoskeleton torn; muscle fibers usually damaged; IV. Swimming legs – at least 2 pair damaged; V. Urosome – caudal rami and 1 to 4 segments of urosome missing. Predation rates were corrected for recovery of *Pseudocalanus* in controls (average 98.7 %).

In grazing experiments euphausiids were fed an exponentially growing suspension of the unicellular centric diatom *Thalassiosira angstii* (33.5 μm equivalent spherical diameter, ESD). Diatoms were cultured in f/2 medium at 15 °C under continuous illumination. The true cell diameter of *T. angstii* is closely approximated by the ESD determined with a Coulter Counter (Runge and Ohman, 1982). Control containers (usually 3 replicates) were run concurrently to correct for phytoplankton growth. Aliquots were withdrawn at 4 to 12 h intervals for counting on a model TAII Coulter counter and 5 to 8 replicate counts made per aliquot. No evidence of particle production was observed in the channels where *T. angstii* occurred; from Parsons and Seki's (1970) results newly formed particulate matter would be expected to occur in channels below 8 to 10 μm ESD. Grazing calculations were made using the equations of Frost (1972).

Following incubations, total length (mid-point of eye to tip of telson) was measured on live euphausiids. These were then rinsed briefly with distilled water and dried to constant weight at 55 to 60 °C. Individuals were weighed on a Cahn electrobalance. In predation experiments *Euphausia pacifica* averaged 19.56 ±

0.45 mm total length ($\bar{x}$, 95 %) and 8.43 ± 0.44 mg dry weight, equivalent to 3.38 mg carbon from the carbon-dry weight relation of Ross (1982). In grazing experiments *E. pacifica* averaged 21.14 ± 1.56 mm total length and 11.81 ± 1.01 mg dry weight, equivalent to 4.73 mg carbon. The carbon content of *Pseudocalanus* sp. females was approximated as 6.0 μg C, from a weight-length regression (Ohman, 1983) and from Vidal's (1980) result that carbon content averaged 46.0 % of dry weight for *Pseudocalanus* sp. The carbon content of *Thalassiosira angstii* was estimated from the equation for diatoms reported in Strathmann (1967). Carbon is used as currency for comparisons although consumers may be nitrogen-limited in the sea (e.g. Checkley, 1980). Curve-fitting was performed with a non-linear least squares algorithm using Marquardt's method.

RESULTS

Predation rates by mature *Euphausia pacifica* feeding on adult female *Pseudocalanus* sp. are shown in Fig. 1. The predation rate varies significantly with prey density (P < 0.001, Jonckheere's test for ordered alternatives). No significant dependence of clearance rate on prey density was detected (P > 0.50, Jonckheere's test). The mean clearance rate (± 95 %) for all treatments was 9.2 ± 5.0 ml euphausiid^{-1} h^{-1}. The ingestion rates fitted a Holling Type II relationship (Fig. 1)
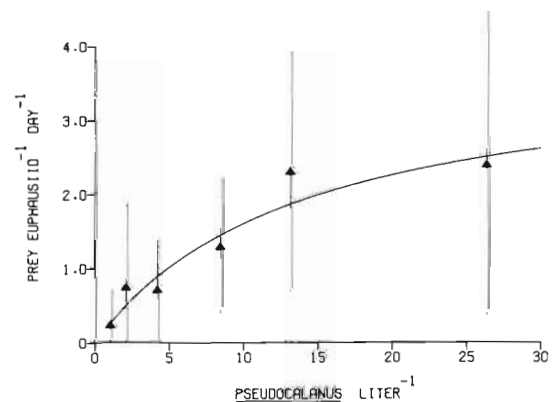

Fig. 1 *Euphausia pacifica.* Predation rate ($\bar{x}$, s) on adult female *Pseudocalanus* sp. as a function of prey concentration. Includes prey injured but not completely consumed.

$$Y = \frac{0.2800\ X}{1 + 0.0735\ X}$$

and an Ivlev curve, but did not fit a Type III relationship as well, based on the minimization of the sum of squared deviations between observed and fitted values.

The determinations in Fig. 1 include *Pseudocalanus* sp. that had been injured but not completely consumed (on average 22.3 % of the total of missing plus injured

prey). These injuries were not distributed with equal frequency in all prey body regions. The 5 major types of injury of *Pseudocalanus* females by *Euphausia pacifica* are illustrated in Fig. 2. A control individual subjected to the same collection and handling procedures is also shown. Attacked *Pseudocalanus* are clearly distinguishable from intact individuals and from those experiencing minor damage such as loss of
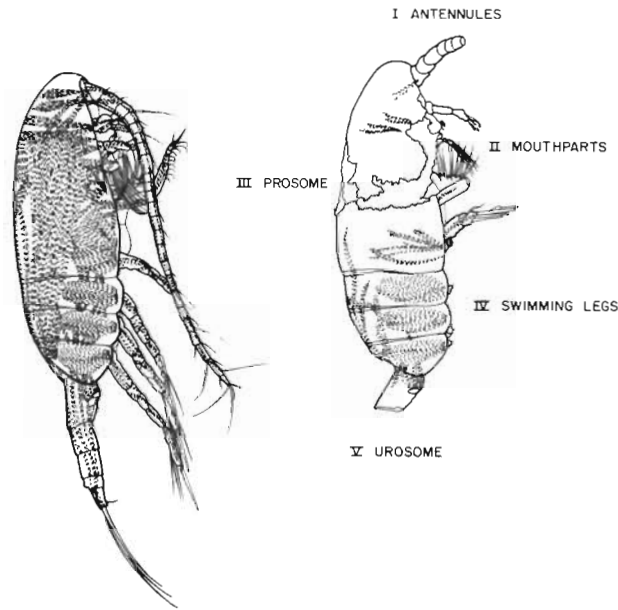

Fig. 2. *Pseudocalanus* sp. Females recovered from feeding experiments. Copepod from control treatment (left) and from experimental treatment with *Euphausia pacifica* (right). Five major sites of injury are identified

caudal setae, apical spines on swimming legs, or terminal segments of the antennules. The proportion of injuries inflicted upon *Pseudocalanus* in the 5 regions identified in Fig. 2 are shown in Table 1. Fewer injuries were found in the prosome and mouthpart region than the extended appendages (the antennules, urosome, and swimming legs; $P < 0.05$, proportion of injuries on extended appendages versus other injuries).

Euphausia pacifica exhibits a different functional

Table 1. *Pseudocalanus* sp. Distribution of injuries on females recovered from laboratory incubations with *Euphausia pacifica*. A total of 3291 *Pseudocalanus* was examined and 107 injuries identified

	Body region	Proportion of injuries
I	Antennules	0.318
II	Mouthparts	0.093
III	Prosome	0.122
IV	Swimming legs	0.243
V	Urosome	0.224

response to phytoplankton prey. Grazing rates for *E. pacifica* feeding on the diatom *Thalassiosira angstii* are illustrated in Fig. 3. Note the reduction in feeding effort at low cell concentrations, a sigmoidal or Type III functional response (Holling, 1959), which is particularly apparent in the clearance rate data. A Type III response provided a better statistical fit to the ingestion data than a Type II or Ivlev relationship. The sigmoidal response can be expressed as:

$$Y = \frac{a X^2}{1 + a T_h X^2} \quad (1)$$

where Y = ingestion rate; X = prey concentration; a = initial slope of the curve; T_h = handling time (derived from Holling, 1965; Hassell, 1978). Assuming handling time remains constant with changing densities of *T. angstii*, the handling time parameter obtained from the ingestion curve is 0.141 s cell^{-1}.
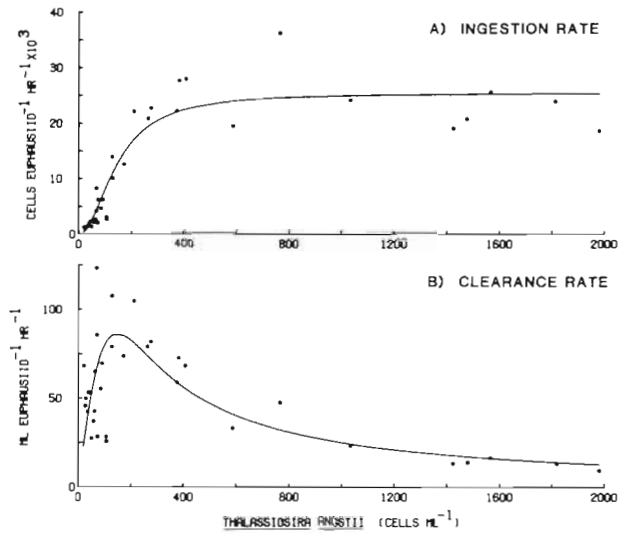

Fig. 3. *Euphausia pacifica*. (A) Ingestion rate and (B) clearance rate on the centric diatom *Thalassiosira · angstii*.

$$Y = \frac{1.1726 X^2}{1 + 0.0000459 X^2}$$

Comparative carbon-specific ingestion rates for *Euphausia pacifica* feeding on *Thalassiosira angstii* and on *Pseudocalanus* sp. females are shown in Fig. 4. The curves are derived from the fitted curves in Fig. 1 and 3 A. For this comparison it was assumed that all attacked *Pseudocalanus* were ingested completely. At a prey concentration of 158 µg C l^{-1}, the highest used in copepod prey experiments, *E. pacifica* could ingest 0.45 % of its body carbon daily from *Pseudocalanus* and 6.26 % of its body carbon from the centric diatom. *E. pacifica* daily ingests 7.8 % of its body carbon at the critical concentration of *T. angstii* (i.e. the prey concentration needed attain 90 % of the maximum ingestion rate, or 290 µg C l^{-1}; off scale in Fig. 4).
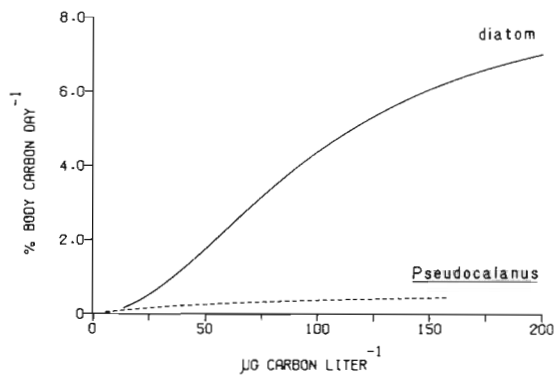
Fig. 4. *Euphausia pacifica*. Carbon-specific ingestion rate of individuals feeding on *Pseudocalanus* sp. females or the diatom *T. angstii*

The ingestion rates of *Euphausia pacifica* on a variety of prey types in pure culture are compared in Fig. 5. Ingestion rates were corrected to 8 °C (from 10 °C, Lasker, 1966, his Fig. 11; from 17 °C, Theilacker and Lasker, 1974, their Fig. 2; assuming $Q_{10} = 2.0$) and the functional responses described with fitted curves. *Artemia* nauplii were approximated as 0.55 µg C (Lasker, 1966) and anchovy larvae as 9 µg C (Theilacker and Lasker, 1974). Rates were converted to daily carbon ration rather than carbon-specific ingestion because the individual weight of the juvenile and adult euphausiids used by previous authors could not always be determined. Fig. 5 suggests that diatoms are
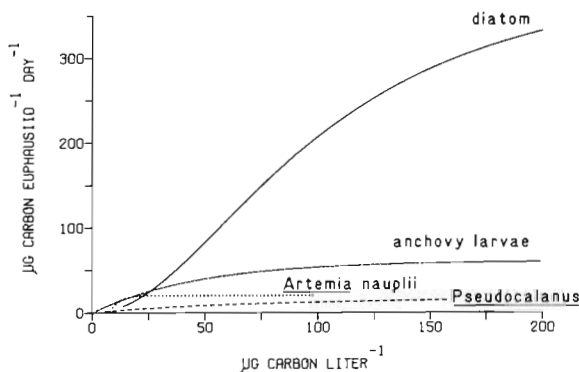

Fig. 5. *Euphausia pacifica*. Daily carbon ration of individuals feeding on a variety of prey. Curves summarize feeding rates from Lasker (1966; *Artemia* nauplii) and Theilacker and Lasker (1974; anchovy larvae) in addition to the prey used in the present experiments

the most suitable prey for *E. pacifica*, particularly when the prey concentration exceeds 30 µg C l^{-1}.

In experiments with natural particulate matter as prey for *Euphausia pacifica* Parsons et al. (1967) observed a maximum ingestion rate similar to that in Fig. 5 on diatoms but at a much higher food concentration (ca. 1000 µg C l^{-1}). This difference is probably

attributable to the presence of inedible detrital carbon in the natural particulate suspension.

The curves in Fig. 5 are not strictly comparable because previous authors apparently used smaller *Euphausia pacifica* than those used here, though the comparison is robust to these size differences. The effects of ingestion rate increasing with body size and weight-specific ingestion decreasing with size cancel. From Theilacker and Lasker (1974, their Fig. 1), for a case where body size is known, a large euphausiid of comparable body weight to those used here (11.8 mg) obtains a temperature-corrected ration of 125 µg C d^{-1} at a prey concentration of 450 to 720 µg C l^{-1}, which leads to a conclusion similar to that expressed in Fig. 5. *E. pacifica* attains a substantially greater ration from diatoms than from other prey.

DISCUSSION

The feeding behavior of *Euphausia pacifica* differs in both a qualitative and quantitative manner when offered the copepod *Pseudocalanus* sp. or the centric diatom *Thalassiosira angstii*. The low and variable predation rates, incomplete consumption of copepods, and low daily ration obtained suggest that adult *Pseudocalanus* sp. are suboptimal prey for *E. pacifica*. By contrast, when feeding on *T. angstii*, *E. pacifica* exhibits high a ingestion rate and a relatively rapid, non-linear increase in feeding rate with increasing cell concentrations.

The suitability of adult copepods and diatoms as prey for *Euphausia pacifica* can also be evaluated from estimates of the euphausiid's metabolic requirements. Using the relationship in Ross (1982) between respiration rate and body weight, the respiratory cost (apparently routine metabolism; see Torres and Childress, 1983) for *E. pacifica* at 8 °C is 3.08 % body carbon d^{-1} for the large euphausiids used in these experiments. While a daily ration meeting this cost was never attained when *Pseudocalanus* was offered as prey (maximum = 0.45 % d^{-1}), it was met when *E. pacifica* fed on *Thalassiosira angstii* at a prey concentration as low as 75 µg C l^{-1}. *E. pacifica* attained a relatively high maximum ration on diatoms (8.8 % body carbon daily) with a low critical concentration (290 µg C l^{-1}), further indicating the viability of diatoms as prey. Growth experiments, as well as these feeding data, support this conclusion: Ross (1982) observed that growth rates of *E. pacifica* on diatom prey were at least six times greater than growth rates observed earlier on *Artemia* nauplii (Lasker, 1966).

Low predation rates on *Pseudocalanus* sp. are not an effect of prey size alone. Newly hatched anchovy larvae (2.5 to 3.0 mm long) are more than twice the length

of *Pseudocalanus* females, yet anchovy larvae are captured at higher rates than copepods. The limited escape response and soft integument of anchovy larvae may make them more susceptible to euphausiid predation. Adult *Pseudocalanus* may be suboptimal prey due to their escape responses or to the difficulty for *Euphausia pacifica* of handling and macerating the copepod exoskeleton. By analogy, it is unlikely that *E. pacifica* can efficiently ingest adult stages of other species of calanoid copepods.

Injury analysis suggests that *Euphausia pacifica* ingests the extended appendages of a copepod first, then proceeds to other body regions if the prey has not escaped or been discarded. The encounter has fatal consequences for the prey and thus differs from those injuries reported by Murtaugh (1981) where a mysid non-lethally injures larger *Daphnia*. Predatory copepods may also ingest prey appendages before ingesting other body regions (Yen, 1983).

On those occasions when a euphausiid *does* successfully ingest muscle tissue and other internal body contents (Fig. 2) there may be few recognizable hard parts of prey in euphausiid guts. Ponomareva (1954) noted incomplete consumption of *Pseudocalanus* by the euphausiid *Thysanoessa inermis*, and Fowler et al. (1971) reported that *Meganyctiphanes norvegica* feeding upon large adult *Artemia* may kill the prey and remove only soft tissues. Often only soft internal tissues or appendages of crustaceans are consumed by the amphipod *Parathemisto gaudichaudi* (Sheader and Evans, 1975). These results suggest that the analysis of stomach contents of such predators or omnivores will give a poor indication of the ingestion of copepods or other zooplankton prey.

A decrease in feeding effort (measured as clearance rate) at low phytoplankton concentrations is consistent with theoretical predictions of the optimal foraging behavior of suspension-feeding zooplankton (Lam and Frost, 1976; Lehman, 1976). When the energetic return per unit foraging time is sufficiently diminished, the optimum behavior is to reduce the cost of feeding by decreasing feeding effort. A reduction in feeding effort at low food concentrations has been observed for copepods (Adams and Steele, 1966; Corner et al., 1972; Frost 1972, 1975; Reeve and Walter, 1977; Kiorboe et al., 1982; Frost et al., 1983) as well as for the euphausiids *Euphausia pacifica* (Parsons et al., 1967) and *E. superba* (Antezana et al., 1982). The copepod *Centropages typicus* also reduces swimming activity (usually correlated with feeding) in the absence of food (Cowles and Strickler, 1983). The present study provides further evidence for the occurrence of 'stabilizing' functional responses by planktonic suspension feeders.

The decrease in clearance rate at very high phytoplankton concentrations is commonly held to be due to a reduction in feeding effort. However, the clearance rate as measured experimentally actually includes the instantaneous rate of search plus the time spent handling prey (Holling, 1959; Cushing, 1968). If the cumulative time spent handling phytoplankton cells becomes sufficiently large, handling will decrease the time available for searching and thus lower the observed clearance rate, despite a constant instantaneous rate of search. For example, using the handling time value of 141 ms cell^{-1} for *Euphausia pacifica* feeding on *Thalassiosira angstii* and assuming a constant maximal 'searching' rate of 100 ml h^{-1} at high cell concentrations, then at a concentration of 1000 cells ml^{-1} the experimentally measured clearance rate would be reduced to 20.3 ml h^{-1}. This is not far from the observed reduction to 25.0 ml h^{-1}. Therefore the measured clearance rate can decrease even as instantaneous feeding effort remains constant. Handling time determined by an entirely different method (direct ciné observations; Paffenhöfer et al., 1982) for 2 species of the copepod *Eucalanus* ranged from 10 to 678 ms cell^{-1} for different phytoplankton species. These values are in the same range as the value deduced here indirectly from an ingestion curve, suggesting that the time spent capturing, manipulating, macerating, and ingesting cells may measureably alter the total time available for searching for food by suspension feeders.

The feeding rates reported here for *Euphausia pacifica* are averages determined over 4 to 24 h. This experimental time scale is useful for understanding the population consequences of omnivory for prey organisms but it cannot resolve the mechanisms of particle capture. High-speed ciné observations of the Antarctic krill *E. superba* suggest that this euphausiid species employs a quasi-raptorial mode of feeding on phytoplankton (Boyd and Heyraud, 1982). These observations are consistent with visual observations of periodic bolus formation and rejection by *E. superba* (Antezana et al., 1982). Hamner et al. (1983) also report evidence for discontinuous feeding by *E. superba*. *E. pacifica* and other omnivorous euphausiids probably exhibit a rich repertoire of behavioral responses in different prey suspensions, the details of which have yet to be fully studied.

LITERATURE CITED

Adams, J. A., Steele, J. H. (1966). Shipboard experiments on the feeding of *Calanus finmarchicus* (Gunnerus). In: Barnes, H. (ed.) Some contemporary studies in marine science. Allen and Unwin, London, p. 19–35

Antezana, T., Ray, K., Melo, C. (1982). Trophic behavior of *Euphausia superba* Dana in laboratory conditions. Polar Biol. 1: 77–82

Boyd, C. M., Heyraud, M. (1982). Feeding rates and mechanisms of the antarctic krill, *Euphausia superba*. EOS, Trans. Am. geophys. Un. (Abstract) 63: 939

Brinton, E. (1962). The distribution of the Pacific euphausiids. Bull. Scripps Instn Oceanogr. 8: 51–270

Brinton, E., Townsend, A. W. (1982). A comparison of euphausiid abundances from bongo and 1-m CalCOFI nets. Calif. Coop. Oceanic Fish. Inv. Rep. 22: 111–125

Checkley, D. M., Jr. (1980). The egg production of a marine planktonic copepod in relation to its food supply: laboratory studies. Limnol. Oceanogr. 25: 430–446

Cooney, R. T. (1971). Zooplankton and micronekton associated with a diffuse sound-scattering layer in Puget Sound, Washington. Ph. D. thesis, Univ. Washington

Corkett, C. J., McLaren, I. A. (1978). The biology of *Pseudocalanus*. Adv. mar. Biol. 15: 1–231

Corner, E. D. S., Head, R. N., Kilvington, C. C. (1972). On the nutrition and metabolism of zooplankton. VIII. The grazing of *Biddulphia* cells by *Calanus helgolandicus*. J. mar. biol. Ass. U.K. 52: 847–861

Cowles, T. J., Strickler, J. R. (1983). Characterization of feeding activity patterns in the planktonic copepod *Centropages typicus* Kroyer under various food conditions. Limnol. Oceanogr. 28: 106–115

Cox, J. L. (1981). Laminarinase induction in marine zooplankton and its variability in zooplankton samples. J. Plankton Res. 3: 345–356

Cushing, D. H. (1968). Grazing by herbivorous copepods in the sea. J. Cons. perm. int. Explor. Mer 32: 70–82

Falk-Petersen, S., Gatten, R. R., Sargent, J. R., Hopkins, C. C. E. (1981). Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: seasonal changes in the lipid class composition of *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa raschii* (M. Sars), and *T. inermis* (Kroyer). J. exp. mar. Biol. Ecol. 54: 209–224

Fowler, S. W., Benayoun, G., Small, L. F. (1971). Experimental studies on feeding, growth and assimilation in a Mediterranean euphausiid. Thalassia jugosl. 7: 35–47

Frost, B. W. (1972). Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17: 805–815

Frost, B. W. (1975). A threshold feeding behavior in *Calanus pacificus*. Limnol. Oceanogr. 20: 263–266

Frost, B. W., Landry, M. R., Hassett, R. P. (1983). Feeding behavior of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the subarctic Pacific Ocean. Deep Sea Res. 30: 1–13

Gopalakrishnan, K. (1973). Developmental and growth studies of the euphausiid *Nematoscelis difficilis* (Crustacea) based on rearing. Bull. Scripps Instn Oceanogr. 20: 1–87

Hamner, W. M., Hamner, P. P., Strand, S. W., Gilmer, R. W. (1983). Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. Science, N.Y. 220: 433–435

Harrison, P. J., Fulton, J. D., Taylor, F. J. R., Parsons, T. R.

(1983). Review of the biological oceanography of the Strait of Georgia: pelagic environment. Can. J. Fish. aquat. Sci. 40: 1064–1094

Hassell, M. P. (1978). The dynamics of arthropod predator-prey systems. Princeton Monogr Biol. 13: 1–237

Hebard, J. F. (1956). The seasonal variation of zooplankton in Puget Sound. M. S. thesis, Univ. Washington

Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entom. 31: 293–320

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entom. Soc. Can. 45: 3–60

Ikeda, T. (1984). Development of the larvae of the Antarctic krill (*Euphausia superba* Dana) observed in the laboratory. J. exp. mar. Biol. Ecol. 75: 107–117

Kiorboe, T., Mohlenberg, F., Nicolajsen, H. (1982). Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. Ophelia 21: 181–194

Koeller, P. A., Barwell-Clarke, J. E., Whitney, F., Takahashi, M. (1979). Winter condition of marine plankton populations in Saanich Inlet, B.C., Canada. III. Mesozooplankton. J. exp. mar. Biol. Ecol. 37: 161–174

Lam, R. K., Frost, B. W. (1976). Model of copepod filtering response to changes in size and concentration of food. Limnol. Oceanogr. 21: 490–500

Lasker, R. (1966). Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. J. Fish. Res. Bd Can. 23: 1291–1317

Lehman, J. T. (1976). The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. Limnol. Oceanogr. 21: 501–516

McClatchie, S., Boyd, C. M. (1983). Morphological study of sieve efficiencies and mandibular surfaces in the Antarctic krill, *Euphausia superba*. Can. J. Fish. aquat. Sci. 40: 955–967

Mauchline, J. (1980). The biology of mysids and euphausiids. Adv. mar. Biol. 18: 373–677

Mauchline, J., Fisher, L. (1969). The biology of euphausiids. Adv. mar. Biol. 7: 1–454

Mullin, M. M., Brooks, E. R. (1967). Laboratory culture, growth rate, and feeding behavior of a planktonic marine copepod. Limnol. Oceanogr. 12: 657–666

Murtaugh, P. A. (1981). Inferring properties of mysid predation from injuries to *Daphnia*. Limnol. Oceanogr. 26: 811–821

Ohman, M. D. (1983). The effects of predation and resource limitation on the copepod *Pseudocalanus* sp. in Dabob Bay, a temperate fjord. Ph. D. thesis, Univ. Washington

Ohman, M. D., Frost, B. W., Cohen, E. B. (1983). Reverse diel vertical migration: an escape from invertebrate predators. Science, N.Y. 220: 1404–1407

Paffenhöfer, G.-A., Strickler, J. R., Alcaraz, M. (1982). Suspension-feeding by herbivorous calanoid copepods: a cinematographic study. Mar. Biol. 67: 193–199

Parsons, T R., LeBrasseur, R. J., Fulton, J. D. (1967). Some observations of the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J. oceanogr. Soc. Japan 23: 10–17

Parsons, T. R., Seki, H. (1970). Importance and general implications of organic matter in aquatic environments. In: Hood, D. W. (ed.) Symposium on organic matter in natural waters. Univ. Alaska Mar. Sci. Occ. Publ. 1: 1–27

Pelymsky, A. G., Arashkevich, Ye. G. (1980). Quantitative characteristics of the feeding of euphausiids in the tropical part of the Pacific Ocean. Oceanology 20: 199–203

Peterson, W. T., Miller, C. B. (1977). Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fish. Bull. U.S. 75: 717–724

Ponomareva, L. A. (1954). Copepods in the diet of euphausiids of the Sea of Japan. Dokl. Akad. Nauk. SSSR 98: 153–154 (Translation)

Ponomareva, L. A. (1963). Euphausiids of the North Pacific, their distribution and ecology. Dokl. Akad. Nauk SSSR, 1963, p. 1–142 (Israel program for scientific translations, Jerusalem)

Ponomareva, L. A., Nikolayeva, G. G. (1981). Food and feeding of euphausiids in the Peruvian Current region. Oceanology 21: 91–94

Reeve, M. R., Walter, M. A. (1977). Observations on the existence of lower threshold and upper critical food concentrations for the copepod *Acartia tonsa* Dana. J. exp. mar. Biol. Ecol. 29: 211–221

Ross, R. M. (1982). Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. 68: 1–13

Runge, J. A., Ohman, M. D. (1982). Size fractionation of phytoplankton as an estimate of food available to herbivores. Limnol. Oceanogr. 27: 570–576

Sameoto, D. D. (1976). Respiration rates, energy budgets, and molting frequencies of 3 species of euphausiids found in the Gulf of St. Lawrence. J. Fish. Res. Bd Can. 33: 2568–2576

Sheader, M., Evans, F. (1975). Feeding and gut structure of *Parathemisto gaudichaudi* (Guerin) (Amphipoda, Hyperiidea). J. mar. biol. Ass. U.K. 55: 641–656

Strathmann, R. R. (1967). Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12: 411–418

Theilacker, G. H., Lasker, R. (1974). Laboratory studies of predation by euphausiid shrimps on fish larvae. In: Blaxter, J. H. S. (ed.) The early life history of fish. Springer, New York, p. 287–299

Torres, J. J., Childress, J. J. (1983). Relationship of oxygen consumption to swimming speed in *Euphausia pacifica* 1. Effects of temperature and pressure. Mar. Biol. 74: 79–86

Vidal, J. (1980). Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. 56: 111–134

Yen, J. (1983). Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. Mar. Biol. 75: 69–77