

Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata**

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Abstract

Adult females of the large carnivorous copepod *Euchaeta elongata* Esterly were collected from 1977 to 1980 in Port Susan, Washington, USA. Predation rates of the adult females increased with increasing prey abundance when fed the following 4 sizes of copepods: adult females of *Calanus pacificus* (average prosome length [PL] of 2 650 μm), adults of *Aetideus divergens* (PL of 1 560 μm), adult females of *Pseudocalanus* spp. (PL of 1 060 μm), and nauplii of *C. pacificus* (PL of 410 μm). Saturation feeding levels were reached when adult females of the predator were fed the small adult copepod, *Pseudocalanus* spp. Maximum biomass ingested of this small copepod was more than the maximum amount ingested of the larger copepods. Predation rates of the predatory copepodids at Stages IV and V also increased with increasing concentration of the 1 060 μm (PL) prey. High feeding rates exhibited by both adults and copepodids at Stage V of the predator indicate their importance as sources of mortality on populations of small copepods. Ingestion efficiency E_i (prey wholly consumed [prey attacked]⁻¹) varied as follows: adults of *E. elongata* were more efficient than copepodids of *E. elongata*; adults were more efficient than copepodids when ingesting smaller prey; starved adults were more efficient than fed ones; and both adults and copepodids were more efficient at low food concentrations. For adults of *E. elongata*, there were no marked seasonal variations in predation or respiratory rates that would represent acclimatory responses; however, small adults obtained during winter were more efficient at ingesting prey than were the larger adults gathered in summer. This seasonal variation in the efficiency of ingestion may be a

useful indicator of physiological state: high E_i values could indicate that predators are starving in winter, and low E_i values could indicate that predators are satiated in summer.

Introduction

Predation rates of marine copepods generally increase as prey concentration increases (Ambler and Frost, 1974; Reeve and Walter, 1977; Robertson and Frost, 1977; Lampitt, 1978). This relationship between prey concentration and ingestion rates defines a functional response (Holling, 1959). However, prey concentration is not the only factor affecting ingestion rates. Prey or predator size and predator hunger influence feeding by planktivorous fish (Ware, 1972), insects (Hassel *et al.*, 1976), particle-grazing copepods (Frost, 1972; Runge, 1980), predatory chaetognaths (Pearre, 1980) and predatory copepods (Ambler and Frost, 1974). It is clear that these factors are important to planktonic consumers, since seasonal variations occur in the size, species, and stage composition of both planktonic prey and predator. Predatory copepods may also experience hunger not only due to long-term seasonal changes, but also during vertical migrations (Runge, 1980) or because of prey patchiness (Dagg, 1977).

Mortality due to predation by marine copepods influences the population abundance and species composition of zooplankton communities. Recent marine ecosystem models (Steele and Frost, 1977; Steele and Henderson, 1981) have generalized predation by invertebrates as a removal of a certain fraction of the overall prey population. For multispecies models of plankton dynamics it is necessary to understand how each of the above factors influences the response. This relationship between predation rates and prey concentrations can be used in models to define the rate of prey mortality and the specific rations of the predators. Feeding rates comprising the functional response can be measured over short time intervals. This

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response, therefore, is useful in assessing the immediate impact of predators on a plankton community.

In the present study, I describe the functional response of the planktonic carnivorous marine copepod *Euchaeta elongata* Esterly and how the response is affected by prey size, predator size (life history stage), predator starvation, and season. An additional objective of this study was to examine changes in ingestion efficiency of the predator in response to variations in prey concentration, prey and predator size, predator hunger state, and season.

Materials and methods

Euchaeta elongata Esterly were collected from 1977 to 1980 in Port Susan, Washington, USA. Further details of copepod collection and experimental procedure for measuring predation rates and respiratory rates of *E. elongata* have been described by Yen (1982a). Clearance rate, defined for predators as the volume effectively searched, was computed as prescribed by Frost (1972). Ingestion efficiency (E_i) was computed as:

$$E_i = \left(1 - \frac{\text{number of prey carcasses}}{\text{number of prey attacked}} \right) \times 100\%.$$

The number attacked was the difference between the number of prey added to experimental containers and the number left alive after 24 h incubation with predators. Carcasses were prey which were left more than half uneaten by the predator. Therefore, a minimum estimate of the predator's ingestion rate was the attack rate multiplied by E_i , while attack rates gave a maximum estimate.

The functional response of adult females copepods to 4 prey types was determined. For each prey type, rates at all concentrations tested were measured simultaneously for predators collected from the same area and day to assure that predator preconditioning would be similar. Only copepods collected in good condition with undamaged antennal and urosomal setae were used as prey and predators.

The functional responses of copepodids at Stages IV and V and adults of *Euchaeta elongata* were also determined for one prey type. Rates at most prey concentrations were obtained simultaneously; some of the low concentrations were tested on separate dates. At high food concentrations (greater than 20 copepods l^{-1}), predation rates were measured in 1-liter jars as described by Yen (1982a). At low food concentrations (less than 5 copepods l^{-1}), large-volume experimental vessels were used; e.g. at 2 prey l^{-1} , an 8-liter experimental volume was used; at 1 prey l^{-1} , a 20-liter experimental volume was used. These large vessels were not placed on a mixing device.

The Holling disc equation (Type II invertebrate response; Holling, 1959) was chosen as one model of the functional response of *Euchaeta elongata*:

$$\frac{N_a}{P} = \frac{aN_T}{1 + aNT_h},$$

where N_a = number of prey attacked, N = number of prey available, P = number of predators, T = experimental duration (= 1 d), T_h = prey "handling" time, and a = attack coefficient or the instantaneous rates of discovery of prey by the predator. In this type of functional response, it is assumed that the predator spends time capturing and ingesting its prey so that the predator's search rate declines with increasing food concentration. Time is divided into only two parts: time spent "handling" prey (T_h) and time spent exposed to prey (T). T_h encompasses several components of feeding including prey capture, handling, ingestion and digestive pause (Holling, 1965, 1966). The other time is spent searching, i.e., $T - T_h$: all times when the predator is not in contact with its victims. Here I have assumed that the total exposure time (T) or time spent with each of the 4 prey types is equal to 1 d, which was the actual experimental duration. It was observed that *E. elongata* feeds primarily at night (Yen, 1982a), and therefore exposure time (T) for this calculation could be reduced to 12 h. Within the 12 h, the predator may feed for an even shorter, but unknown, amount of time. In any case, the value of T_h obtained here can be used only as a measure of relative differences in T_h of *E. elongata* feeding on different-sized food items.

The Ivlev (1961) equation served as another functional response model in order to estimate the maximum ingestion rate:

$$I = I_{mx} (1 - e^{-\delta P}),$$

where I = ingestion rate, I_{mx} = maximum ingestion rate, P = prey concentration, and δ = proportionality constant specifying the rate of change of I with respect to P . The prey concentration resulting in 50% I_{mx} , analogous to the half-saturation constant of a Michaelis-Menten fit, was computed by this model. Both the Holling equation and the Ivlev equation were fitted to the data using the SPSS nonlinear least-squares regression procedure (University of Washington Academic Computer Center, Announcement 26).

Prey types in these single-species experiments were either adult females of *Calanus pacificus* Brodsky (available from March–October in Puget Sound, Washington), adults of *Aetideus divergens* Bradford (available all-year round), adult females of *Pseudocalanus* spp. (3 species, not differing in prosome lengths by more than 100 μm , were available in spring and early summer), or nauplii of *C. pacificus*. Nauplii, cultured by methods described by Vidal (1980), were hatched from eggs at 12 °C, fed on *Dunaliella tertiolecta* for 6 d, and acclimated to 8 °C for 1 d before use in experiments. All of the copepods co-occur with *Euchaeta elongata*.

Prosomal lengths of anesthetized live copepods were measured at 250 \times and 500 \times using an ocular micrometer on a dissecting microscope. Dry weights (single specimens of large copepods; 5 to 10 specimens of small copepods) were determined with the CAHN Electrobalance (Model G-2 and Model 25). Carbon contents of single adult females of *Euchaeta elongata* were determined with a

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Predation rate
(No. of prey attacked predator⁻¹d⁻¹)

CARLO Erba Elemental analyzer. Egg development times of *E. elongata* were determined by methods described by Burgis (1970), where ovigerous females were placed in filtered seawater at 8 °C.

The vertical distributions of ovigerous and non-ovigerous adult females of *Euchaeta elongata* were determined in Dabob Bay, a deep (190 m) basin in Puget Sound, Washington where this copepod is abundant (Damkaer, 1964). Four months of the year were analyzed from a series of vertically stratified samples taken in 1973 with a 1 m diam closing net equipped with a 216 μm mesh (King, 1979). When less than 50 adult females of *E. elongata* were present, the entire sample was analyzed. Otherwise, the sample was subdivided with a Folsom plankton splitter to gain 2 or 3 aliquots, each containing at least 15 females; each aliquot was analyzed for the number of females and the number of egg sacs, free or attached.

Results

Functional response of adult females of *Euchaeta elongata* to 4 sizes of copepod prey

The rate of predation by adult females (average prosome length [PL]=4.2 mm) was tested on 4 species of copepod prey ranging in prosome lengths from 410 to 2 650 μm . Predation rates increased with increasing concentration of all 4 prey types (Fig. 1). Rates were plotted against initial prey concentration to indicate how much the predator would consume given these initial levels. Although the Type II model (Holling, 1959) adequately described the trend between rates and concentration, a Type III sigmoid response (Holling, 1965) may be a better fit to the functional responses to the large copepods *Calanus pacificus* or *Aetideus divergens*.

The Ivlev equation fitted to the data produced curves that were often similar to or exactly the same as curves drawn from the Holling equation at the tested food levels. With increasing prey density, rates on all prey approached

asymptotic values. However, saturation was convincingly attained only when adult females of *Euchaeta elongata* fed on *Pseudocalanus* spp. (Fig. 1C), with 50% I_{mx} occurring at 7.9 prey l^{-1} (Table 1).

Predation rates may be compared at a single concentration for the 4 prey types. At 10 items l^{-1} , the predation rate on the small copepod, adult females of *Pseudocalanus* spp. (1 060 μm PL), was 9.4 copepods d^{-1} . This rate was higher than those obtained on larger copepods, adult females of *Calanus pacificus* (2 650 μm PL) and adults of *Aetideus divergens* (1 560 μm PL), of 0.46 and 1.3 d^{-1} , respectively, or the rates on the smaller prey, nauplii of *C. pacificus* (410 μm PL), of 1.0 d^{-1} . Data replotted on the basis of the common unit of dry weight also show that highest rates were on adult females of *Pseudocalanus* spp. (Fig. 2). Even though the available dry weight of the large copepod was 10 times greater than that of this smaller adult copepod, the maximum biomass ingested as large prey was still much less than the biomass ingested as *Pseudocalanus* spp., as determined from the number of prey attacked.

When a copepod was captured by *Euchaeta elongata*, it was held perpendicular to the body between the predator's maxillipeds. Moving parts of the copepod, such as the first antennae and/or urosome, generally were eaten first. The prey was then repositioned parallel to the body and held lengthwise between the second basipodal segments of the maxillipeds of the predator for further consumption. During the repositioning, it is possible that *E. elongata* could drop its victims: often, copepod carcasses lacking antennae or urosome were found, indicating inefficient ingestion. In fact, the average ingestion efficiency (E_i) declined with increasing prey size (Table 1). Handling time (T_h) increased exponentially with increasing prey size (Table 1), possibly explaining the observed decline in E_i . Maximum ration for *E. elongata*, assuming complete prey consumption of *Pseudocalanus* spp., was 17.1% of the predator's body weight and minimum estimates, taking into account E_i , reduced the proportion to 12.9%.

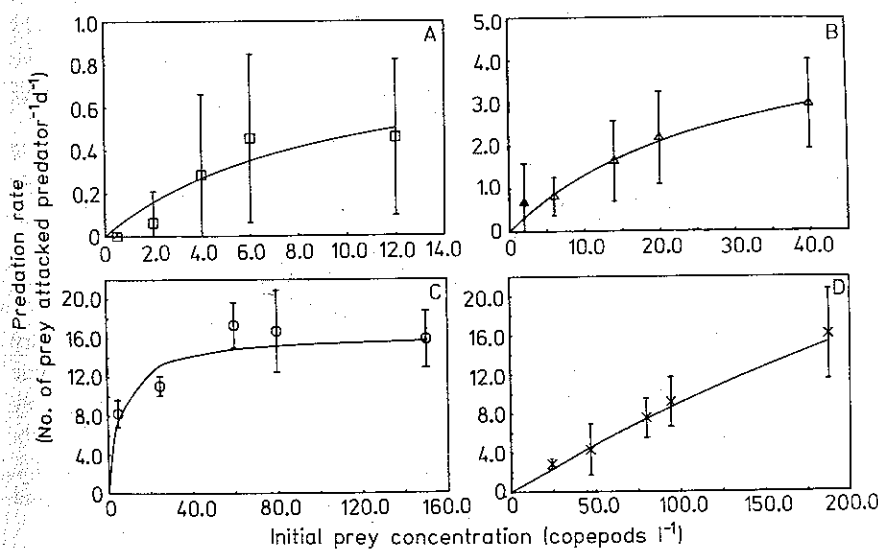


Fig. 1. *Euchaeta elongata*. Functional response of adult females feeding on 4 types of prey. (A) adult female *Calanus pacificus*, 2 646.1 ± 41.1 (95% confidence interval) μm prosome length; (B) adult *Aetideus divergens*, 1 559.1 ± 18.5 μm ; (C) adult female *Pseudocalanus* spp., 1 056.1 ± 100.3 μm ; (D) nauplii of *C. pacificus*, 407.1 ± 86.1 μm . Data points with error bars represent mean of 8 replicates with their 95% confidence interval. Rates at all concentrations were measured simultaneously for each prey type. Curves represent the fitted Holling disc equations (see Table 1 for coefficients of equations)

Table 1. *Euchaeta elongata*. Characteristics of functional response (using models of Holling, 1959, and Ivlev, 1961) of adult females (1.4 mg dry wt) to 4 species of copepod prey

	Prey species			
	<i>Calanus pacificus</i> (adult ♀)	<i>Aetideus divergens</i> (adults)	<i>Pseudocalanus</i> spp. (adult ♀)	<i>Calanus pacificus</i> (nauplii)
Prosome length (μm):	2 650	1 560	1 060	410
Dry wt (μg):	184	45.6	15.6	1.4
Holling values				
T_h (h)	27.3	4.56	1.47	0.033
a (d ⁻¹)	0.0978	0.172	2.78	0.104
Ivlev values				
δ	0.167	0.048	0.088	0.0025
I_{mx} : prey d ⁻¹	0.572	3.47	16.0	40.5
I_{mx} : μg dr. wt d ⁻¹	105.2	158.2	249.6	56.7
$P_{50\% I_{mx}}$: prey l ⁻¹	4.15	14.4	7.88	277.4
E_i (av %)	18	33	75	100
% body wt ingested	6.43	10	17.1	1.43
% body wt × E_i	1.16	3.3	12.9	1.43
Clearance rate ^a (liter predator ⁻¹ d ⁻¹)	0.01	0.42	3.5	0.11

^a At initial prey concentration of 100 μg l⁻¹

Clearance rates at an initial prey concentration of 100 μg l⁻¹ were also greatest on the small adult copepod (Table 1). At this biomass of prey, *Euchaeta elongata* can effectively search 3.5 liters d⁻¹. This high clearance rate during the experimental period reduced the prey concentration of *Pseudocalanus* spp. to a geometric mean of 37 μg, which gives an estimated ingestion rate of 130 μg d⁻¹.

Effect of predator life history stage

The functional responses of *Euchaeta elongata* were measured for adult females, copepodids at Stage IV (CIV) and

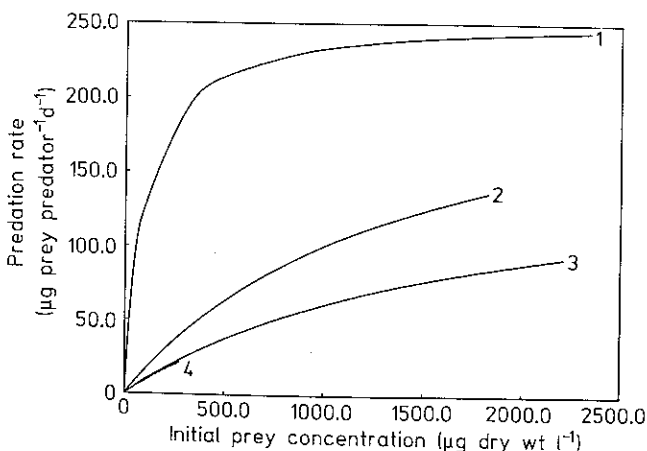


Fig. 2. *Euchaeta elongata*. Functional response of adult females feeding on 4 types of copepod prey: 1, adult female *Pseudocalanus* spp. (15.6 μg dry wt); 2, adult *Aetideus divergens* (45.6 μg dry wt); 3, adult female *Calanus pacificus* (184 μg dry wt); 4, nauplii of *C. pacificus* (1.4 μg dry wt). Curves of Fig. 1 were redrawn with quantity of prey converted to dry wt

Stage V (CV); each predator was exposed to one prey type, adult females of *Pseudocalanus* spp. The results again indicated that predation rates increased with increasing prey concentration (Fig. 3, Table 2).

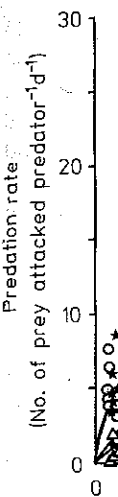
Fifty percent of I_{mx} , determined from the Ivlev model, occurred at 10.1, 7.6, and 18.2 prey l⁻¹ for adult females, and Stages CIV and CV of the predators, respectively ($P_{50\% I_{mx}}$; Table 2). At all concentrations, adult females exhibited higher predation rates than Stage CV. Even at the low food concentration of 1 copepod l⁻¹, adult females of *Euchaeta elongata* were able to capture and ingest 5.6 prey predator⁻¹ d⁻¹. Copepodids at Stage V, in turn, ingested more prey than those at Stage IV. Weight-specific ratios of CV were higher than rates obtained for CIV and adults.

Ingestion efficiency, determined from the number of carcasses, decreased with increasing prey concentration. Also, the smaller stage, CIV, was less efficient than the larger one (Fig. 4). Handling time (T_h) increased as predator size decreased (Table 2) which may explain this decline in E_i .

As an independent check of the value of the predation rates, respiratory rates were measured and converted to μg C catabolized:

$$\frac{\mu\text{l O}_2 \text{ respired}}{\text{copepod} \cdot \text{h}} \times 24 \times \frac{12}{22.4} \times \text{RQ} = \mu\text{g C catabolized d}^{-1}.$$

RQ was chosen as 0.75 (Parsons *et al.*, 1979). The dry weight of *Euchaeta elongata* was 1.4 mg and the organic carbon content was 0.74 mg. The carbon content of prey was estimated as 40% of their dry weight (Mullin, 1969). The 3 stages of *E. elongata* respired between 9.2 and 21.0% of their daily ingested ration (I_{mx}) and between 3.3 and 4.9% of their body weight (Table 2).



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Table 2. *Euchaeta elongata* at Stage IV and Copepod

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I_{mx} : prey
I_{mx} : μg dr
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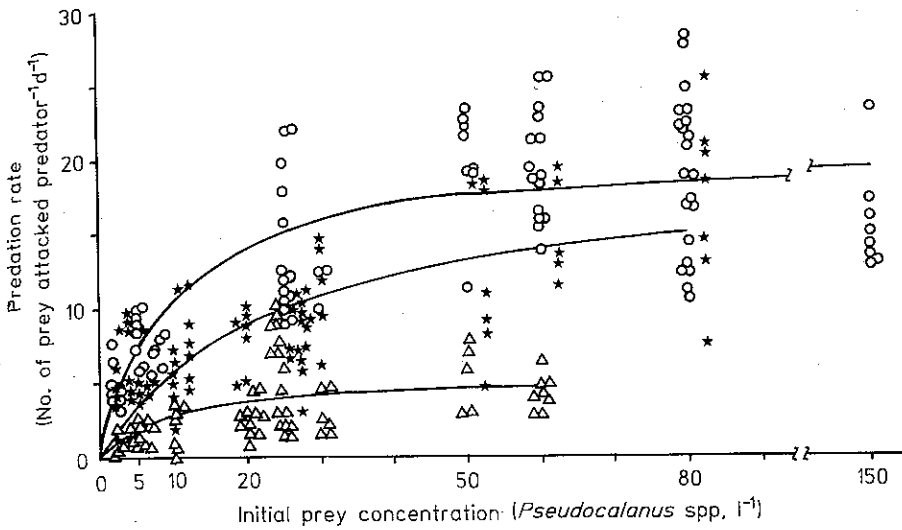


Fig. 3. *Euchaeta elongata*. Functional response of adult females (○), Copepodid Stage IV (△), and Copepodid Stage V (*) feeding on adult female *Pseudocalanus* spp. Curves are Holling disc equation fitted to the data (see Table 2 for coefficients of equations)

Effect of starvation

Starvation may occur during seasons when suitable prey are not available or in areas where the spatial distribution of prey and predator do not overlap. Analyses of the vertical distribution of adult females of *Euchaeta elongata* indicated that ovigerous females stay at depth during the day and night (Fig. 5). During this time, these females may be in a starved condition, since most small copepod prey are abundant primarily near the surface (Damkaer, 1964; Yen, 1982 b). To estimate the potential length of time females do not feed, the egg development time was measured. Ovigerous females carry their eggs for a period of 18.8 d (Fig. 6).

To determine the effect starvation has on predation, attack rates of individuals collected from the same area and on the same date were measured within 1 d after capture. They then were divided into two groups: one was kept in filtered seawater without food and the other was fed on small copepods at medium concentrations (10 to 20 prey l⁻¹). After 6 or 7 d, predation rates of starved and fed predators were compared to the initial rates.

Below the saturation level for ingestion on *Aetideus divergens*, starved predators were able to consume twice as many prey items as fed predators (Table 3). In fact, at 40 *A. divergens* l⁻¹, starved *Euchaeta elongata* consumed the same dry weight (280 μg d⁻¹) as when *E. elongata* fed on the smaller copepod *Pseudocalanus* spp. at the saturation

Table 2. *Euchaeta elongata*. Characteristics of functional response of adult females, Copepodid Stage IV and Copepodid Stage V. Prey items were adult females of *Pseudocalanus* spp. (15.6 μg dry wt)

	Predator stage		
	CVI	CIV	CV
Prosome length (μm):	4 200	2 600	3 600
Weight (mg dr. wt):	1.4	0.191	0.373
Weight (μg C):	740 ^a	101 ^b	197 ^b
Holling values			
<i>T_h</i> (h)	1.16	4.37	1.23
<i>a</i> (d ⁻¹)	2.21	0.551	0.844
Ivlev values			
<i>δ</i>	0.069	0.091	0.038
<i>I_{mx}</i> : prey d ⁻¹	18.7	4.52	16.1
<i>I_{mx}</i> : μg dr. wt d ⁻¹	291.7	70.5	251.2
<i>I_{mx}</i> : μg C d ⁻¹ (40% dr. wt)	116.7	28.2	100.5
<i>I_{mx}</i> : μg prey μg predator ⁻¹ d ⁻¹	208.4	369.1	673.5
<i>P_{50%}</i> <i>I_{mx}</i> : prey l ⁻¹	10.1	7.62	18.2
Respiration rate (μl O ₂ h ⁻¹)	2.23 ± 0.34	0.51 ± 0.18	0.96 ± 0.19
Respiration rate (μg C d ⁻¹)	24.5	4.9	9.2
% <i>I_{mx}</i> respired	21.0	17.4	9.2
% body wt respired	3.3	4.9	4.7

^a Measured

^b Computed as 52.9% dr. wt

Table 3. *Euchaeta elongata*. Predation rates of starved and fed adult females feeding on adult *Aetideus divergens* and adult female *Pseudocalanus* spp. CI: confidence interval

Prey concentration (No. per liter)	Predation rate (No. of prey predator ⁻¹ d ⁻¹ ± 95% CI; n=8)		
	initial	starved	fed
<i>A. divergens</i>			
20	2.50 ± 1.07	4.25 ± 1.14	2.06 ± 0.91
40	4.06 ± 1.27	6.13 ± 1.09	3.94 ± 0.82
<i>Pseudocalanus</i> spp.			
50	20.0 ± 6.2	ND	ND
80	23.9 ± 11.2	18.9 ± 5.5	22.6 ± 8.0

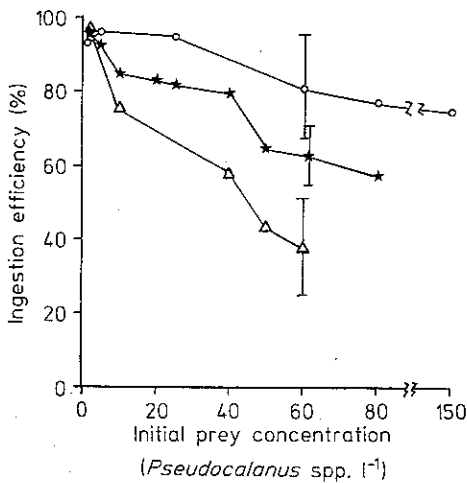


Fig. 4. *Euchaeta elongata*. Ingestion efficiency of adult females (O). Copepodid Stage IV (Δ) and Copepodid Stage V (*), at different concentrations of adult females of *Pseudocalanus* spp. Data points represent means of 5 to 8 replicates and error bars represent 95% confidence intervals

level (295 μg d⁻¹). Higher rates might have been obtained had rates been measured for exposure times of less than 1 d. Above the saturation level on *Pseudocalanus* spp., starved and fed predators ate the same number of prey.

Although at high food concentrations there was no difference in feeding rates by starved and fed predators, starved predators consumed prey more efficiently than fed predators: *E_i* at 80 prey l⁻¹ was initially 76.1 ± 10.5% (95% confidence interval); after 6 d, *E_i* was 79.5 ± 5.9% for starved predators and 56.8 ± 10.9% for fed predators.

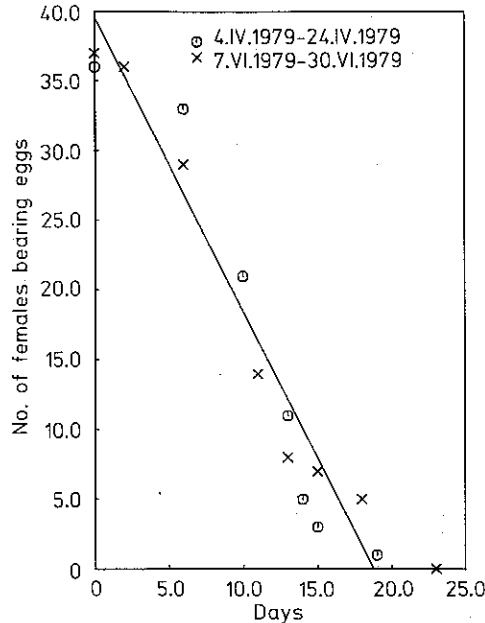


Fig. 6. *Euchaeta elongata*. Egg development time estimated from X-intercept of the linear regression of the number of *E. elongata* bearing eggs vs time: 18.8 ± 1.65 (95% confidence interval) days at 8 °C

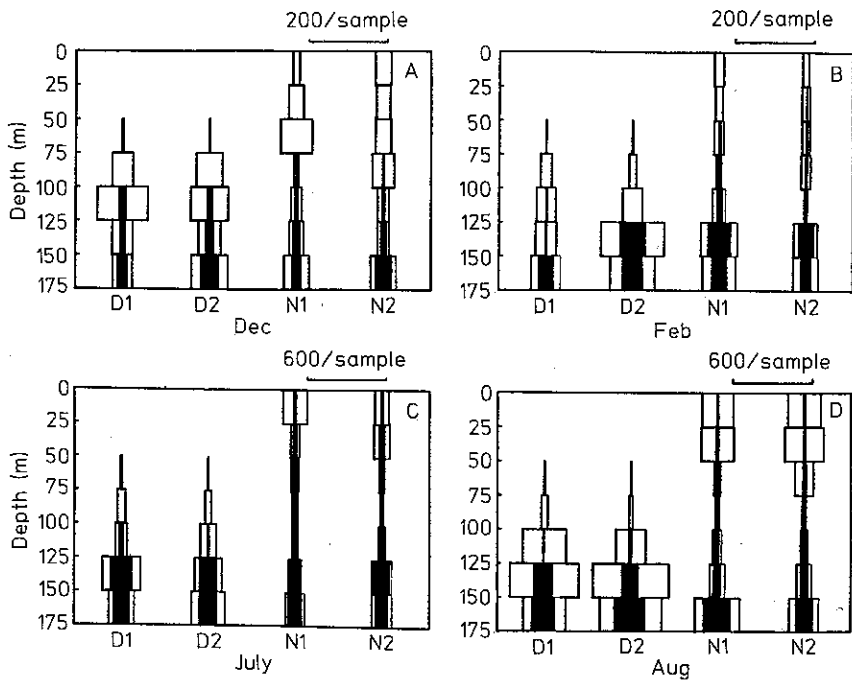


Fig. 5. *Euchaeta elongata*. Vertical distribution of ovigerous (shaded portions) and non-ovigerous (open portions) adult females during day (D) and night (N) in Dabob Bay, Washington, USA. (A) 16. XII. 1972, 10.50 hrs (D1); 16. XII. 1972, 12.05 hrs (D2); 15. XII. 1972, 22.30 hrs (N1); 16. XII. 1972, 00.15 hrs (N2). (B) 19. II. 1973, 09.05 hrs (D1); 19. II. 1973, 10.35 hrs (D2); 18. II. 1973, 21.25 hrs (N1); 18. II. 1973, 22.40 hrs (N2). (C) 21. VII. 1973, 15.55 hrs (D1); 21. VII. 1973, 17.25 hrs (D2); 21. VII. 1973, 22.50 hrs (N1); 22. VII. 1973, 00.07 hrs (N2). (D) 4. VIII. 1973, 11.04 hrs (D1); 4. VIII. 1973, 12.35 hrs (D2); 3. VIII. 1973, 23.12 hrs (N1); 4. VIII. 1973, 00.30 hrs (N2) (B. Frost, unpublished data; J. Hughes, unpublished data). Bar lines represent numbers of adult females per sample taken with a 1 m diam closing net over a 25 m depth interval

No. of prey attacked predator⁻¹ d⁻¹
μl O₂ (predator h)⁻¹
Micrometer
Percent

Fig. 7. *Euchaeta elongata*. (A) feeding rates, (B) respiration rates, (C) ingestion efficiency, (D) oxygen consumption, (E) percent of prey ingested, (F) percent of prey respiration, (G) percent of prey oxygen consumption, (H) percent of prey ingested and respiration, (I) percent of prey oxygen consumption and respiration, (J) percent of prey ingested, respiration and oxygen consumption

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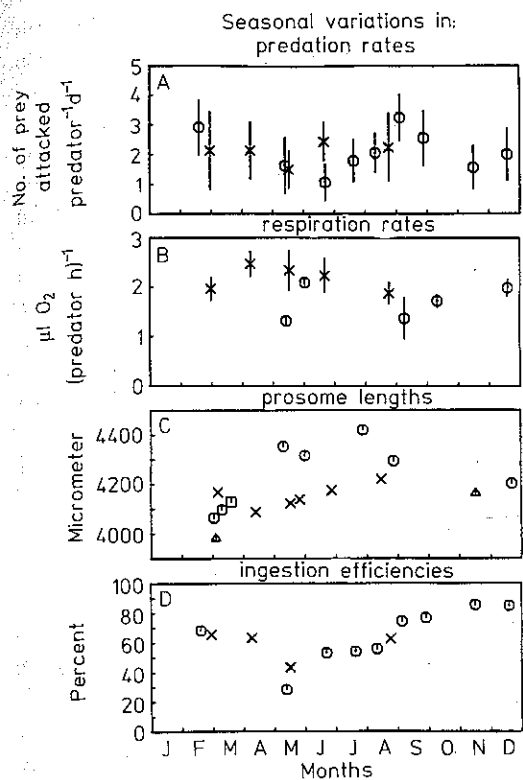


Fig. 7. *Euchaeta elongata*. Seasonal variations in (A) predation rates, (B) respiration rates, (C) prosome lengths, and (D) average ingestion efficiencies of adult females during 1977 (\square), 1978 (Δ), 1979 (\circ), and 1980 (\times). Points with error bars in (A) and (B) represent means of 8 replicates and their 95% confidence intervals. Average coefficient of variation in prosome lengths was 2.7%. Prey was *Aetideus divergens*.

Effect of season

Predation rates of adult females of *Euchaeta elongata* at 14 *Aetideus divergens* l⁻¹ (below saturation levels of this prey) and respiratory rates in filtered seawater were measured at various times over a 4 yr period (1977–1980). *A. divergens* was used as prey because it is available throughout the year, whereas *Pseudocalanus* spp. are available only in summer. These rates were measured within 1 d of capture at 8°C after an acclimation of 12 to 24 h. Temperatures ranging from 8° to 12°C have little effect on predation or respiratory rates (Yen, 1982 a). No marked seasonal trends were observed in these rates (Fig. 7A, B). Average rates of adult females were approximately 2 *A. divergens* d⁻¹ and 2 μ l O₂ h⁻¹.

Prosome lengths of adult female predators and ingestion efficiencies did vary with season (Fig. 7C, D). Maximum length occurred in summer. Minimum ingestion efficiencies (less than 65%) occurred in spring–summer (February–August), and highest efficiencies (greater than 75%) were observed during winter (September–January).

Discussion

Whereas other studies have demonstrated the ability of small raptorial copepods to feed at high rates on the

naupliar stage of copepods (Ambler and Frost, 1974; Landry, 1978; Lonsdale *et al.*, 1979), few studies have shown that predatory copepods may feed on adult copepods (Mullin, 1979). In this study of a large carnivorous copepod, *Euchaeta elongata*, both the adult female (4.2 mm prosome length [PL], 1.4 mg dry wt) and copepodid at Stage V (3.6 mm PL, 0.37 mg dry wt) exhibit high predation rates on adult females of the small copepod *Pseudocalanus* spp. (1 060 μ m PL, 15.6 μ g dry wt). Maximum ingestion rates on *Pseudocalanus* spp. for these two life-history stages of the predator were 18.7 prey predator⁻¹ d⁻¹ and 16.1 prey predator⁻¹ d⁻¹, respectively. Maximum rates were lower when adult female predators were fed nauplii of *Calanus pacificus* (410 μ m PL, 1.4 μ g dry wt) and also when larger copepods were offered as prey: adults of *Aetideus divergens* (1 560 μ m PL, 45.6 μ g dry wt) or adult females of *C. pacificus* (2 650 μ m, 18.4 μ g dry wt). Maximum predation rates were 16 prey predator⁻¹ d⁻¹, 2.5 prey predator⁻¹ d⁻¹, and 0.45 prey predator⁻¹ d⁻¹, respectively. The difference in rations obtained on the small copepod *Pseudocalanus* spp. and large prey was further accentuated by the decline of ingestion efficiency on large copepods, similar to that observed for a carnivorous amphipod (Dagg, 1974).

Besides size of prey, size of the predator also influenced predation rates of *Euchaeta elongata*. When fed adult females of *Pseudocalanus* spp., the larger adult females and copepodids at Stage V ingested more prey than the smaller copepodids at Stage IV. Furthermore, ingestion efficiency was low for the smaller predators compared to adults. From the consideration of relative handling time, large predators (adults) appeared better able to handle *Pseudocalanus* spp. compared with small predators (copepodids at Stage IV). However, it will be interesting to determine if small predators are able to handle small prey, such as nauplii, more effectively than large predators.

Saturation of predation rates was convincingly attained for adult females of *Euchaeta elongata* ingesting adults of *Pseudocalanus* spp. Saturation probably occurs as a function of handling time, gut capacity, and gut passage time. Although saturation feeding has been obtained for other copepods (Frost, 1972; Ambler and Frost, 1974; O'Connors *et al.*, 1980), some studies (Mayzaud and Poulet, 1978; Conover and Huntley, 1980) indicate that this saturation level has a seasonal component where the maximum feeding rate reflects the ambient concentrations of prey due to acclimation by consumers; enzyme levels and feeding rates evidently change according to seasonal availability of food. In this study, *E. elongata* did not seem to acclimate because there was little variation in predation rates from one season to another and the same saturation feeding rate was maintained by predators that had been acclimated for 6 d to high food levels or starved for 6 d. The lack of an acclimatory response may be a strategy evolved for vertical migrators, such as *E. elongata*, which enter and exit patches or discrete bands of prey. Such rapid changes in prey concentrations leave little time for

acclimation. Nonmigrating copepods experience the seasonal change in prey concentration and thus have more time to physiologically adjust to the new food levels.

Concentrations of food at which high feeding rates were observed may occur in nature. Although integrated net hauls rarely show prey concentrations of over 30 liter⁻¹, observations by SCUBA (Reeve, 1975) and submersible (Yen, personal observations) have noted small copepods aggregated in bands of 1 to 5 m at approximately 10⁵ liter⁻¹. Therefore, the ability of *Euchaeta elongata* to feed at high rates can be a useful response to prey patchiness.

At low prey concentrations, predation rates of *Euchaeta elongata* can double if predators are starved. Runge (1980) reported that grazing rates increased by 1.5 to 3 times when *Calanus pacificus* are starved. He postulated that copepods do not graze continuously, but rather pause intermittently to digest food already captured (Holling, 1966); a hungry copepod can elevate its feeding rate by increasing the number of feeding "bouts". This starvation response may be exhibited by ovigerous females which appear to migrate only occasionally to the surface. With elevated rates, a ration can be obtained at the surface which permits the females to remain longer in the food-poor near-bottom layers. By not migrating, these conspicuous copepods can reduce their mortality loss to visual or surface-dwelling predators.

An increase in the efficiency of ingestion (E_i) was discovered to be another component of the starvation response. Considering that later developmental stages of *Euchaeta elongata* were more efficient than early stages in these laboratory experiments, I expected that, in winter, when prosome lengths of adult females were shortest, E_i should have been lowest. However, the small adult predators were more efficient during winter than the larger summertime predators. These experiments also indicated that E_i decreased as prey concentration increased, which may be of overriding importance compared to predator size. When food concentrations are high during summer, the predatory copepods apparently are satiated and need not be efficient feeders. During winter when prey are less abundant, predators are hungry and exhibit high E_i . Thus ingestion efficiency may be a useful indicator of the hunger state for this predatory copepod.

Patterns in ingestion efficiency may explain the occurrence of a large number of copepod carcasses (16 to 28% of total copepods) that was observed by Weikert (1977) in the transition zone between freshly upwelled and older upwelled waters off North-West Africa. This area was marked by a high abundance of small copepods where *Euchaeta marina* was a dominant carnivore. It is possible that the carcasses in these transition waters resulted from inefficient ingestion by planktivores feeding at high prey concentrations.

The ability of both adult females of *Euchaeta elongata* and the copepodids at Stage V to feed at high rates on small copepods and the abundance of the predators in marine systems like Dabob Bay, present a potentially significant source of mortality on populations of small

copepods. Laboratory experiments such as those in this study are important for estimating ingestion rates at specific prey concentrations and for determining what factors may influence these rates. However, before these studies can be used for quantitative measures of mortality due to predation in nature, better estimates of natural concentrations of plankton and the size and permanence of patches are necessary.

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Literature cited

- Ambler, J. and B. W. Frost: The feeding behavior of a predatory planktonic copepod, *Tortanus discaudatus*. *Limnol. Oceanogr.* 19, 446-451 (1974)
- Burgis, M.: The effect of temperature on the developmental time of *Thermocyclops* sp., a tropical cyclopoid copepod from Lake George, Uganda. *Limnol. Oceanogr.* 15, 742-747 (1970)
- Conover, R. J. and M. E. Huntley: General rules of grazing in pelagic ecosystems. In: Primary productivity in the sea, pp 461-485. Ed. by P. G. Falkowski. New York: Plenum Press 1980
- Dagg, M. J.: Loss of prey body contents during feeding by an aquatic predator. *Ecology* 55, 903-906 (1974)
- Dagg, M. J.: Some effects of patchy food environments on copepods. *Limnol. Oceanogr.* 22, 99-107 (1977)
- Damkaer, D. M.: Vertical distribution of copepods in Dabob Bay, December 1960, 84 pp. M. S. thesis, University of Washington, Seattle 1964
- Frost, B. W.: Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 17, 805-815 (1972)
- Hassell, M. P., J. H. Lawton and J. R. Beddington: The components of arthropod predation I. The prey death rate. *J. Anim. Ecol.* 45, 135-164 (1976)
- Holling, C. S.: Some characteristics of simple types of predation and parasitism. *Can. Ent.* 91, 395-398 (1959)
- Holling, C. S.: The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. ent. Soc. Can.* 45, 1-60 (1965)
- Holling, C. S.: The functional response of invertebrate predators to prey density. *Mem. ent. Soc. Can.* 48, 1-86 (1966)
- Ivlev, V. S.: Experimental ecology and feeding of fishes, 302 pp. New Haven: Yale University Press 1961. [Translation by D. Scott]
- King, K. R.: The life history and vertical distribution of the chaetognath, *Sagitta elegans*, in Dabob Bay, Washington. *J. Plankton Res.* 1, 153-167 (1979)
- Lampitt, R. S.: Carnivorous feeding by a small marine copepod. *Limnol. Oceanogr.* 23, 1228-1230 (1978)
- Landry, M. R.: Predatory feeding behavior of a marine copepod, *Labidocera trispinosa*. *Limnol. Oceanogr.* 23, 1103-1113 (1978)
- Lonsdale, D. J., D. R. Heinle and C. Siegfried: Carnivorous feeding behavior of the adult calanoid copepod *Acartia tonsa* Dana. *J. exp. mar. Biol. Ecol.* 36, 235-248 (1979)
- Mayzaud, P. and S. A. Poulet: The importance of the time factor in the response of zooplankton to varying concentrations of

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Mullin, M. M.
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Biol. Ecol

- naturally occurring particulate matter. *Limnol. Oceanogr.* 23, 1144-1153 (1978)
- Mullin, M. M.: Production of zooplankton in the ocean. The present status and problems. *Oceanogr. mar. Biol. A. Rev.* 7, 293-314 (1969)
- Mullin, M. M.: Differential predation by the carnivorous marine copepod, *Tortanus discaudatus*. *Limnol. Oceanogr.* 24, 774-777 (1979)
- O'Connors, H. B., Jr., D. C. Biggs and D. V. Ninivaggi: Particle-size-dependent maximum grazing rates of *Temora longicornis* fed natural particle assemblages. *Mar. Biol.* 56, 65-70 (1980)
- Parsons, T. R., M. Takahashi and B. Hargrave: *Biological oceanographic processes*. 2nd ed. 332 pp. New York: Pergamon Press 1979
- Pearre, S., Jr.: Feeding by Chaetognatha: the relation of prey size to predator size in several species. *Mar. Ecol. Prog. Ser.* 3, 125-134 (1980)
- Reeve, M. R.: The ecological significance of the zooplankton in the shallow subtropical waters of South Florida. In: *Estuarine research*, Vol. 1. pp 352-371. Ed. by L. E. Cronin. New York: Academic Press 1975
- Reeve, M. R. and M. A. Walter: Observations on the existence of lower thresholds and upper critical food concentrations for the copepod *Acartia tonsa* Dana. *J. expl. mar. Biol. Ecol.* 29, 211-221 (1977)
- Robertson, S. B. and B. W. Frost: Feeding by an omnivorous planktonic copepod *Aetideus divergens* Bradford. *J. exp. mar. Biol. Ecol.* 29, 231-244 (1977)
- Runge, J. A.: Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnol. Oceanogr.* 25, 134-145 (1980)
- Steele, J. H. and B. W. Frost: The structure of plankton communities. *Phil. Trans. R. Soc.* 280, 485-534 (1977)
- Steele, J. H. and E. W. Henderson: A simple plankton model. *Am. Nat.* 117, 676-691 (1981)
- Vidal, J.: Physioecology of zooplankton. I. Effects of phytoplankton, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. *Mar. Biol.* 56, 111-134 (1980)
- Ware, D. M.: Predation by rainbow trout (*Salmo gairdneri*). The influence of hunger, prey density, and prey size. *J. Fish. Res. Bd. Can.* 29, 1193-1201 (1972)
- Weikert, H.: Copepod carcasses in the upwelling region south of Cape Blanc, N. W. Africa. *Mar. Biol.* 42, 351-355 (1977)
- Yen, J.: Sources of variability in attack rates of *Euchaeta elongata* Esterly, a carnivorous marine copepod. *J. exp. mar. Biol. Ecol.* 63, 105-117 (1982 a)
- Yen, J.: *Predatory feeding ecology of Euchaeta elongata* Esterly, a marine planktonic copepod, 130 pp. Ph.D. thesis, University of Washington, Seattle 1982 b

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