

**SOURCES OF VARIABILITY IN ATTACK RATES
OF *EUCHAETA ELONGATA* Esterly,
A CARNIVOROUS MARINE COPEPOD¹**

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Abstract: An accurate and precise measure of ingestion is important for understanding trophic interactions in the plankton. This paper describes effects on the ingestion rate of the carnivorous marine copepod *Euchaeta elongata* Esterly of several biotic and abiotic factors operating in the pelagic environment. Sources of variability in the attack rate included, in order of decreasing influence: (1) light, (2) prey activity (live vs. heat killed), (3) predator condition (with and without antennae), (4) prey type, (5) time of day, (6) prey density, and (7) mixing regime. While these responses were observed in the laboratory, they are consistent with *E. elongata*'s behavior in the field. No significant changes were noted in the attack rate in response to the presence of prey exudate, number of predators per experiment duration, container size, reproductive state of predator, or temperature. The adult female copepods were exclusively carnivorous. An experimental method based on these results is described for use in further investigations on the predatory feeding ecology of *E. elongata*.

INTRODUCTION

Copepods adjust their feeding rates in response to diverse stimuli in the aquatic environment. Prey size and concentration modify the predation rate of carnivorous marine copepods (Lampitt, 1978; Landry, 1978; Mullin, 1979) while a variety of factors have been observed to affect the ingestion rate of particle grazing copepods – temperature (Vidal, 1980), time of day (Boyd *et al.*, 1980), chemical cues (Poulet & Marsot, 1978), and species and developmental stage (Mullin, 1963). However, there has been no study that has systematically investigated the effects of all these variables on the feeding rate of a single planktonic predator.

The purpose of this study is to show if certain factors affect predation rates of the marine calanoid copepod *Euchaeta elongata* Esterly. *E. elongata* is a large (4 mm prosome length, 1.5 mg dry wt) non-visual predator which in the copepodid stages seems to feed chiefly on crustaceans (Gauld, 1966). I seek to establish a method which will give an accurate and precise measure of predation by this copepod so that subsequent experiments can study in detail its feeding response to varying intensities of selected factors. Understanding the response to these variables may explain aspects of the observed patterns in copepod feeding behavior.

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Before attempting to ascertain the regulatory influence a predator may have on the structure of the prey community, it is necessary to examine the predator and the sources of variability in its activity. In this study, I examine predation rates of *E. elongata* feeding on copepod prey that co-occur with the predator while varying certain factors that were identified from a consideration of the ecology of *E. elongata*. For example, *E. elongata* is a tactile predator and is likely to respond to slight modifications of the hydrodynamics of its surroundings. Therefore, I studied the effects on the feeding rate of several important components influencing the hydrodynamic regime, including prey movement, mixing conditions, and container volume. Since non-visual predators also may rely on chemosensory detection of prey (Griffiths & Frost, 1976), the response of *E. elongata* to the presence of prey exudate was monitored. In addition, non-ovigerous adult female copepods undergo a diel vertical migration: ascent at dusk and descent at dawn. Ovigerous females migrate to a lesser extent (Hughes, 1974; Morioka, 1975). Light levels, detected by a non-image forming light-sensitive organ (Campbell, 1934), and time of day (diel cycle) – cues important in regulating vertical distribution of copepods – were examined for their effects on feeding rates. Since reproductive state appears to dictate what fraction of the population migrates to the surface where prey are abundant, I compared predation rates of ovigerous, non-ovigerous, and ripe females. To check for omnivory or exclusive carnivory in the species, observations were made of the copepod's ability to graze phytoplankton. I documented the variability in individual vs. average rates by changing the number of predators per duration of experiment. Standard factors of prey density, prey size, and temperature, previously shown to significantly influence copepod ingestion rates, were also investigated.

METHODS

Euchaeta elongata were collected at stations in Dabob Bay (170 m) and Port Susan (120 m), Washington. Dense populations of *E. elongata* are found in these deep basins of Puget Sound, Washington (Damkaer, 1964, Frost, unpubl.) and the species ranges widely over the subarctic Pacific (Littlepage & Dagg, 1972; Morioka, 1975). Oblique hauls from the bottom to the surface were taken with a 571- μ m mesh 1-m diameter ring net having a cod-end adapted for obtaining live specimens. Groups of *E. elongata* were sorted immediately into gallon jars containing sea water from 30-m depth (7 to 12 °C), maintained between 7 and 12 °C while on shipboard (8–24 h), and brought to the laboratory. The copepods were placed into 8-l stock cultures (20 to 40 animals per container), fed with small copepods, and kept at 8 °C. Half of the water was changed twice weekly. Only *E. elongata* kept in the laboratory in the dark for <2 wk were used in predation experiments, although preliminary experiments on feeding rates of animals maintained in the laboratory showed little change for >1 month. Even after 1 month in captivity, adult females continued to produce eggs.

Prey copepods were collected in oblique net hauls from areas and at times when

certain copepods are abundant in Puget Sound. Nets of mesh sizes appropriate to the desired prey size (73 to 571 μm meshes) were used. The catch was gently diluted in gallon jars filled with sea water pumped from 30-m depth and kept in the laboratory at 8 °C. A mixture of phytoplankton species was added to feed the zooplankton.

Depending on prey size and swimming speed, the copepods were sometimes anesthetized with m-aminobenzoic acid ethyl ester methanesulfonate (MS-222, CalBiochem; 8–10 drops/50 ml of a 2% solution) so that they could be sorted quickly. If MS-222 was used, prey were allowed one day recovery before experiments were begun. Landry (1978) noted no effect of MS-222 on prey mortality. The desired number of prey per experimental container were placed into small beakers. These groups of prey were transferred randomly into experimental containers prefilled with filtered sea water. Natural prey mortality and accuracy of sorting the desired number of prey were determined from predator-free controls.

To initiate an experiment, *E. elongata* were added to the experimental containers. The containers were then placed on a continuously rotating mixing device. Unless otherwise specified, experiments were normally run in darkness. After 24 h, predators were removed and the remaining live prey and carcasses counted. Calculation of the attack rate was based on equations from Frost (1972), where k , the prey mortality coefficient, usually equaled zero ($99.3 \pm 1.5\%$ recovery of prey in controls as averaged from 44 experiments). The number of prey attacked included all prey missing and uneaten carcasses, representing the loss in the prey population due to predatory feeding by *E. elongata*. Five to eight replicates with predators and two controls were analyzed per treatment condition. Confidence intervals (95% C.I.) about the mean were calculated. Significant differences in rates were noted when the 95% C.I. did not overlap.

Each treatment involved testing two or three conditions of one factor, such as three temperatures. Unless otherwise stated, for each treatment: (1) all conditions of a treatment were investigated simultaneously; (2) experiments were done in 1-l jars; (3) predators, at experimental concentrations of 2/l, were obtained from the same stock cultures and therefore were collected on the same date from the same place and pre-fed on the same mixture of small copepods; and (4) prey copepods, at experimental concentrations of 10–20/l, were either adult *Aetideus divergens* (1440 μm prosome length; available year around in Puget Sound), adult female *Pseudocalanus* spp. (950 μm ; spring–summer), adult female *Paracalanus parvus* (650 μm ; late summer), or adult female *Oithona similis* (430 μm ; autumn). *Artemia nauplii* were used once.

Respiration rates were measured by placing two to three predators without prey in a 30-ml stoppered bottle filled with filtered sea water and incubating the bottles at the desired temperature for 9–12 h. The concentration of O_2 was measured with the micro-Winkler technique (Carritt & Carpenter, 1966; Dagg, 1976).

RESULTS

FACTORS HAVING INSIGNIFICANT EFFECTS ON ATTACK RATES OF *EUCHAETA ELONGATA*

When fed two sizes of single-celled diatoms, *E. elongata* in late developmental stages (at 6/l) showed no grazing over a period of 5–12 h, as determined by changes in algal concentration measured with the Model TAI Coulter Counter (Table I). No fecal pellets were produced by starved adult female copepods kept in a suspension of chain-forming diatoms.

The attack rate is the rate that this predatory copepod kills and effectively removes prey from the population, which includes all prey completely and partially ingested. The attack rates of predators feeding on *Aetideus divergens* with and without prey exudate

TABLE I

Factors having insignificant effects on attack rates of *Euchaeta elongata*: *A.d.*, *Aetideus divergens*.

Treatment	Condition	Prey concn. (number/l)	Attack rate (prey · predator ⁻¹ · day ⁻¹ ± 95% C.I.)
Phytoplankton	<i>Thalassiosira weisflogii</i> (19 µm) and <i>T. angustii</i> (30 µm)	200 µg C of each species	No grazing on mixture of single-celled diatoms by copepodid IV, V, VI males, VI females
	<i>Chaetoceros gracilis</i> , <i>C. danicus</i> , <i>Skeletonema costatum</i>	Thick suspension	No fecal pellets formed in mixture of chain-forming diatoms by starved adult females
Prey exudate	with	20 <i>A.d.</i>	3.18 ± 1.05*
	without		2.96 ± 0.88
No. of predators; duration	1 predator; 3 days	20 <i>A.d.</i>	1.19 ± 0.72
	3 predators; 1 day		1.52 ± 0.68
	6 predators; overnight		1.82 ± 0.88
	6 predators; overday		1.02 ± 0.37
Container size	1 l w; 2 predators/l	7 <i>A.d.</i>	1.56 ± 0.57
	4 l w; 2 predators/l	20 <i>A.d.</i>	1.71 ± 0.67
	1 l w; 2 predators/jar		1.74 ± 0.51
	4 l w; 2 predators/jar	10 <i>A.d.</i>	2.74 ± 1.04
	1 l w; 3 predators/jar		1.24 ± 0.54
	4 l w; 3 predators/jar	1.71 ± 1.21	
Reproductive state	non-ovigerous	20 <i>A.d.</i>	1.41 ± 0.50
	ovigerous		0.67 ± 0.53
	non-ovigerous	10 <i>A.d.</i>	1.24 ± 0.54
	ovigerous		1.04 ± 0.38
	non-ovigerous	14 <i>A.d.</i>	1.81 ± 0.86
	ovigerous		2.69 ± 0.67
ripe		2.88 ± 0.54	

* Following rates are of adult female *E. elongata*.

were compared. Prey exudate was made by crushing *A. divergens* prey copepods and filtering out the large particles. No significant increase or decrease in rates due to this chemical addition were detected (Table I).

No significant difference was noted in attack rate when the concentration of predators was increased from 1/1 to 6/1 and the experimental duration reduced from 3 days to 12 h (Table I). Any interference between predators at high densities was not detected in this treatment. A slight reduction in variability occurred when the concentration of predators was increased.

There was no effect of container size on rates of predators feeding within 1-l vs. 4-l jars, if relative densities of prey and predator were constant with respect to container volume (Table I).

Adult female *Euchaeta elongata* can be separated easily into three reproductive states: non-ovigerous (no egg sac present), ovigerous (carrying an egg sac), and ripe (oviducts obviously packed with blue eggs). Egg sacs may increase drag and packed oviducts may inhibit further filling of gut cavity with food. However, these differences were not reflected in their attack rates (Table I).

TABLE II

Respiration and attack rates on 14 *Aetideus divergens* per l of adult female *Euchaeta elongata* acclimated to three temperatures.

Temp. (°C)	Respiration rate ($\mu\text{l O}_2 \cdot \text{copepod}^{-1} \cdot \text{h}^{-1}$)	Attack rate (prey predator ⁻¹ · day ⁻¹ ± 95% C.I.)	
	4-day acclimation	4-day acclimation	1-day acclimation
8	1.37 ± 0.41	2.18 ± 0.50	2.06 ± 0.65
12	1.78 ± 0.25	2.94 ± 0.79	0.69 ± 0.22
15	1.73 ± 0.13	2.28 ± 0.88	1.69 ± 1.02

Predators were acclimated to three temperatures: 8, 12, 15 °C, over 1 and 4 days. After acclimation, attack and respiration rates were measured. No significant difference was noted between these rates within the small range of temperatures tested (Table II).

FACTORS HAVING SIGNIFICANT EFFECTS ON ATTACK RATES OF *E. ELONGATA*

Mixing type, prey movement, intact first antennae

Factors potentially influencing the characteristics of the hydrodynamic regime significantly affected predatory feeding by *E. elongata*. These included mixing type (Fig. 1), prey movement (Fig. 2), and the predator's possession of intact first antennae (Fig. 3). Rates of attack in containers placed in three different mixing apparatuses were compared. The "ferris" wheel turns the containers end-over-end. The rates obtained in containers on this mixer were one-half the rates obtained in beakers that were not mixed

(Fig. 1A). This result discouraged the use of the "ferris" wheel in other experiments. However, unmixed beakers did not keep the prey evenly distributed; on several occasions, I found prey congregated near the bottom of the beaker. To maintain a more homogeneous distribution of prey, another mixing device, the "roller", was tested which gently rotates the jars on their sides. Rates obtained from experimental containers placed on this mixer were not significantly different from rates in unmixed beakers (Fig. 1B). This mixing device was used in all other experiments.

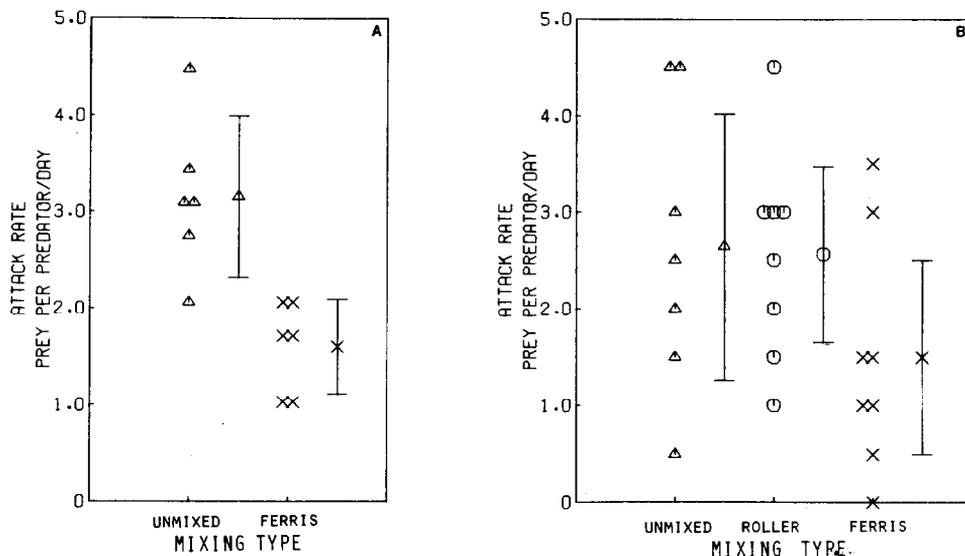


Fig. 1. A, attack rates of *Euchaeta elongata* in unmixed beakers (Δ) and on the ferris wheel (\times) at 20 *Aetideus divergens*/l; B, attack rates of *Euchaeta elongata* in unmixed beakers (Δ), on the roller (\circ), and on the ferris wheel (\times) at 14 *Aetideus divergens*/l; in all figures, individual points represent rates obtained from each experimental container with two adult female predators; point with error bars is the mean with its 95% confidence intervals.

The importance of prey movement was disclosed by comparing feeding rates on live vs. heat-killed copepods (Fig. 2A). Direct observations showed that dead prey did not sink out of suspension when containers were rotated. Attack rates on heat-killed prey were near zero, while high rates on live prey of the same species and density were maintained. The effect was observed with two types of prey (Fig. 2B).

Antennae were gently pinched off anesthetized *E. elongata*. The copepods were allowed to recover for 2 days before experimentation. Antennaless predators attacked seven times fewer copepod prey than predators with intact antennae (Fig. 3A). This effect was also observed on *Artemia* nauplii (Fig. 3B). Since *Euchaeta elongata* does not ingest phytoplankton, I could not check whether the copepod was functioning normally by grazing as Landry (1980) did for *Calanus pacificus*. Instead, I monitored the survival of starved predators with and without antennae and found no difference in their survival.

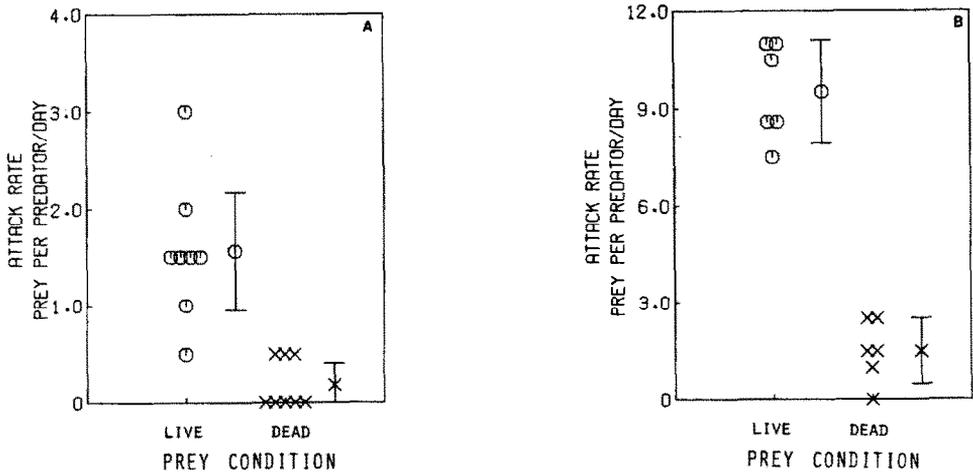


Fig. 2. Attack rates of *Euchaeta elongata* on live prey (○) and heat-killed prey (×) at prey concentrations of: A, 14 *Aetideus divergens*/l, and B, 25 *Paracalanus parvus*/l.

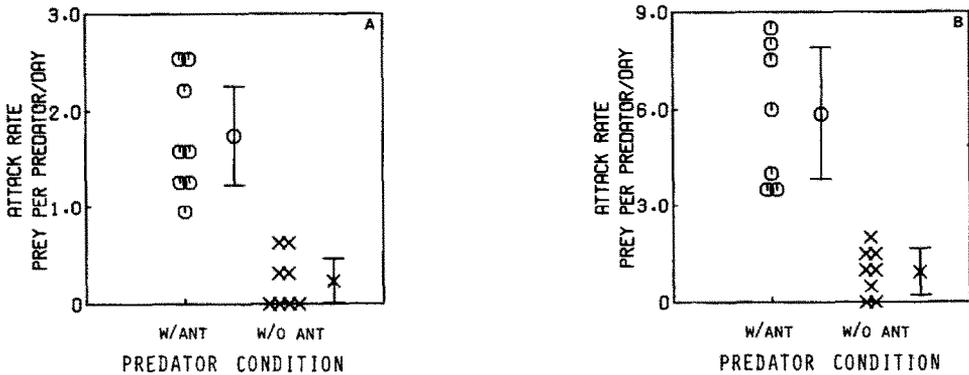


Fig. 3. Attack rates of *Euchaeta elongata* with intact first antennae (○) and without antennae (×) on: A, *Aetideus divergens* at 14/l and B, *Artemia salina* at 25/l (7-day-old nauplii).

Diel periodicity, light level

To investigate feeding periodicity, feeding rates at a specified prey concentration were measured in complete darkness over two 12-h intervals per day: 0900–2100 and 2100–0900. Rates measured on the first day after capture showed that when predators were offered a continuous supply of food they ingested more prey at night (Fig. 4). Even after *Euchaeta elongata* had been kept in the laboratory for 6 days in the dark and fed small copepods at low concentrations, they continued to show the same periodicity of higher rates at night.

To study the effect of light, clear and black plastic-covered experimental containers

were strapped onto a roller-type wheel and exposed to a low light intensity of $5 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Jars were rotated into and out of direct exposure to the light at a rate of 1.2 rpm. Predators attacked 19 times more prey in continuous dark than in inter-

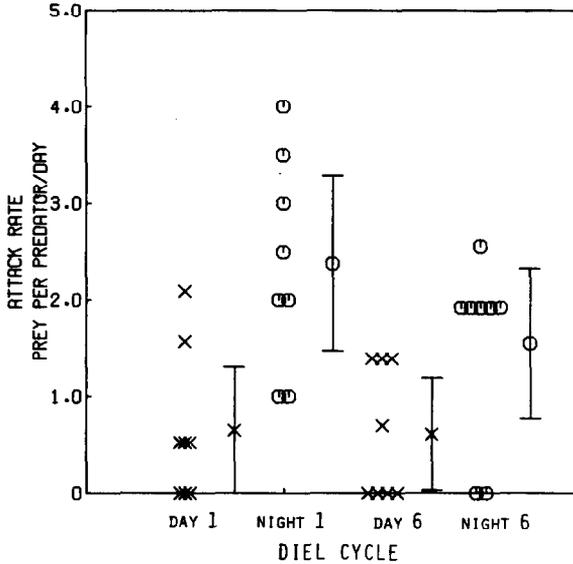


Fig. 4. Attack rates of *Euchaeta elongata* during Day 1 (x) and Night 1 (O) at 20 *Aetideus divergens*/l, and during Day 6 (x) and Night 6 (O) at 10 *A. divergens*/l.

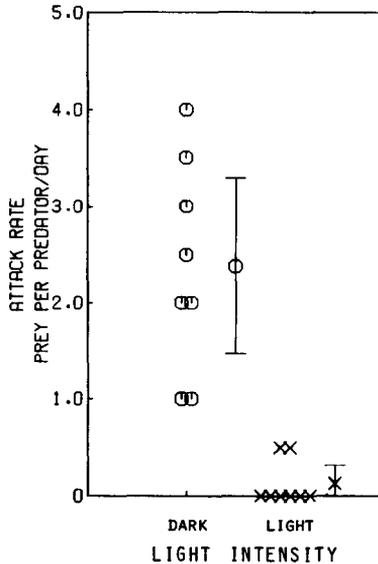


Fig. 5. Attack rates of *Euchaeta elongata* in the dark (O) and in the light (x) of intensity $5 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, at 20 *Aetideus divergens*/l.

mittent light (Fig. 5). When *E. elongata* were exposed to light, they stopped swimming and sank passively.

Prey type; prey density

Prey type and density significantly modified attack rates. Moderate rates were measured for *E. elongata* feeding at 25 prey/l on small prey (*Oithona similis*: 430 μm prosome length) and large prey (*Aetideus divergens*: 1440 μm), while high rates were measured for predators feeding on the intermediate-sized prey (*Pseudocalanus* spp.: 950 μm) (Fig. 6). Feeding rates on the apparent "preferred" prey, *Pseudocalanus* spp.,

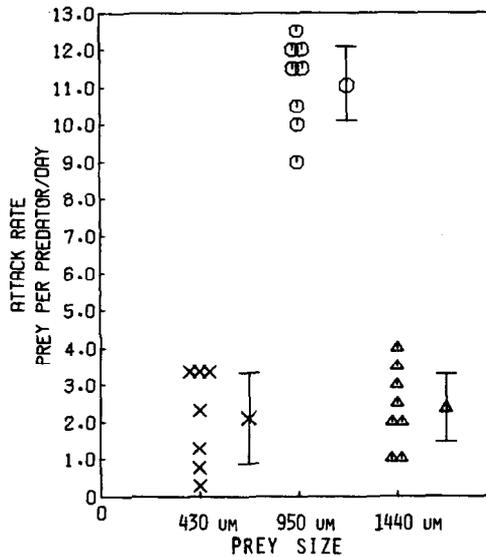


Fig. 6. Attack rates of *Euchaeta elongata* on *Oithona similis*: 430 μm prosome length (x), *Pseudocalanus* spp.: 950 μm prosome length (o), and *Aetideus divergens*: 1440 μm prosome length (Δ) in single species experiments at 25 prey/l.

at 60 prey/l were two times higher than at 5 prey/l, indicating an effect of density on rates (Fig. 7). Adult male *Euchaeta elongata*, incubated with this prey type at 25/l, did not ingest any *Pseudocalanus* spp.

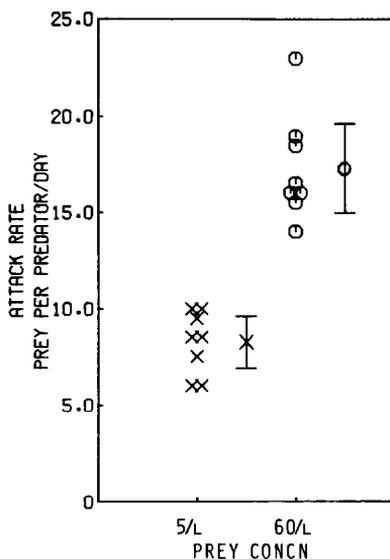


Fig. 7. Attack rates of *Euchaeta elongata* on *Pseudocalanus* spp. at 5 prey/l (x) and 60 prey/l (O).

DISCUSSION

Predatory feeding of *Euchaeta elongata* was significantly influenced by changes in several biotic and abiotic factors. These sources of variability included: (1) light: *E. elongata* attacked 19 times more prey in the dark than in the light; (2) prey activity: *E. elongata* attacked seven times more live prey than heat-killed prey; (3) predator condition: attack rates of copepods with intact first antennae were seven times greater than rates of antennaless predators; (4) prey type: *E. elongata* attacked five times more of the intermediate-sized type prey (950 μm prosome length) than either of the larger or smaller prey copepods; (5) time of day: nighttime feeding rates were three times higher than daytime rates; (6) prey density: attack rates at 60 prey/l were two times greater than rates at 5 prey/l; and (7) mixing type: *E. elongata* attacked two times more prey in the gentle "roller" mixing type than in the "ferris" wheel.

Adult female *E. elongata* were found to be exclusively carnivorous. Copepodid stages IV and V did not graze small single-celled diatoms. Copepodid stage VI males have atrophied mouth parts (Campbell, 1934) and so did not feed on either small copepod prey or phytoplankton. Factors which did not significantly influence attack rates were presence of prey exudate, number of predators per experiment duration, container size, reproductive state of predator, and a narrow range of temperatures.

From these results, an experimental method can be derived to reduce variability and obtain accurate rates under conditions similar to what the animal experiences in nature. (a) To obtain average daily rates of predation, experiments should be run for 24 h with

two to three predators per container. Rates measured only overnight would give higher-than-natural estimates of daily predatory activity if extrapolated to 24 h. (b) Experiments should be run in the dark. In Dabob Bay, *E. elongata* migrate up at night and down during the day. The entire population remains below 60 m during the day, far below the $5 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ light level which corresponds to 8–30 m in Puget Sound (N. Welschmeyer, pers. comm.). (c) Experiments should be run at 8 °C. *E. elongata* usually remain below the thermocline in Dabob Bay (5–15 m) where temperatures vary little between 7–9 °C (Collias *et al.*, 1974). (d) Container volume should be chosen to maintain equitable absolute numbers of prey available for predation. Large-volume (2–4 l) jars should be used at low prey densities, and 1-l jars can be used at high prey densities. (e) Predators maintained in stock cultures should be fed small copepods at low densities. Phytoplankton can be added to experimental containers to prevent starvation of prey copepods. Homogeneous prey distribution should be maintained by placing experimental jars on the gentle “roller” mixer. (f) The attack rates, as calculated from the number of missing prey and carcasses, is accurate since *E. elongata* do not scavenge dead copepod carcasses.

E. elongata appears to detect prey primarily by mechanical or tactile reception rather than visual or chemosensory detection. This conclusion is supported by several results reported in this study. Active movement of live prey was necessary for prey detection by *E. elongata* whereas light depressed its predation rates. Turbulence created in the end-over-end mixing of experimental containers disturbed *E. elongata*'s ability to mechanically detect and ingest prey while the “roller” maintained prey homogeneity and kept a quiet hydrodynamic regime which did not affect predation rates. Sensory receptors, sensitive to pressure changes in the surrounding medium, have been found on copepod cuticle (Strickler & Bal, 1973). Removal of the first antennae, an important sense organ, impaired predatory ability, as has been found for *Calanus pacificus* (Landry, 1980) and *Rhincalanus nasutus* (Mullin & Brooks, 1967). Unlike *Euchaeta elongata*, *Rhincalanus nasutus* feeds at high rates on *Artemia* nauplii and dead copepod nauplii, but not on live copepods. These copepods appear to detect and capture prey in different ways. The addition of prey exudate did not arouse *Euchaeta elongata* into a feeding frenzy nor did it confuse the predator. Evidently, *E. elongata* did not need to separate chemical trails from the high ambient concentration of prey exudate to find and ingest its prey.

When offered three species of copepods, *E. elongata* ingests more prey of an intermediate size. This response can be caused by several size-related effects. Large prey swim faster and may be better able to evade capture. The predator may be inefficient in handling large prey or could satiate itself with fewer of them. Movements of *Oithona*, the small prey, may not be detected by *Euchaeta elongata*. In fact, *Oithona* remains motionless much of the time, with short bursts of movement, while *Aetideus*, the large prey, swims more continuously on a horizontal plane, turning often, with their prosome nearly perpendicular to the direction of motion. *Pseudocalanus* moves continuously and smoothly with the prosome parallel to the direction of movement. Hence, the three prey

types differ in their behavior which, in addition to size, may influence their susceptibility of perception and capture by *E. elongata*.

These results also bear on some aspects of the field behavior of *E. elongata*. In earlier observations at Dabob Bay (Aug. 1973, Aug. 1978), four times more *E. elongata* with material in their gut were collected at night than during the day. This field observation can now be explained by laboratory findings that a periodicity in rates exists with higher nighttime feeding rates and inhibition of feeding in the light. These diel variations in feeding activity are also well coupled to the migratory habits of adult female *E. elongata*. At night, non-ovigerous female predators migrate up to feed in surface layers where prey are abundant.

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