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.
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 (*Ei*) was computed as:

\[
E_i = \frac{1 - \text{number of prey carcasses}}{\text{number of prey attacked}} \times 100\%.
\]

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 *Ei*, 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 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 1⁻¹), predation rates were measured in 1-liter jars as described by Yen (1982a). At low food concentrations (less than 5 copepods 1⁻¹), large-volume experimental vessels were used; e.g. at 2 prey 1⁻¹, an 8-liter experimental volume was used; at 1 prey 1⁻¹, 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*:

\[
\frac{N_a}{P} = \frac{aNT}{1+aNT_h},
\]

where *Nₐ* = number of prey attacked, *N* = number of prey available, *P* = number of predators, *T* = experimental duration (= 1 d), *Tₜ* = 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 (*Tₜ*) and time spent exposed to prey (*T*). *Tₜ* encompasses several components of feeding including prey capture, handling, ingestion and digestive pause (Holling, 1965, 1966). The other time is spent searching. i.e., *Tₜ* = *T* - *Tₜ*: 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 *Tₜ* obtained here can be used only as a measure of relative differences in *Tₜ* 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, *Iₚₘ* = 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% *Iₚₘ*, 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*.

Prosome lengths of anesthetized live copepods were measured at 250 × and 500 × 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