

## Predation by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific hake, *Merluccius productus*

K.M. Bailey<sup>1\*</sup> and J. Yen<sup>2</sup>

<sup>1</sup>School of Fisheries and <sup>2</sup>School of Oceanography, College of Ocean and Fishery Sciences, University of Washington, Seattle, WA 98195, USA

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**Abstract.** The predatory behavior of the carnivorous marine copepod, adult female *Euchaeta elongata* Esterly, feeding on eggs and larvae of the Pacific hake, *Merluccius productus*, was examined in the laboratory and in a natural setting. *E. elongata* did not feed on eggs. Predation on larvae is believed to depend on larval swimming behavior: (1) predation rates were low on early stage yolk-sac larvae which are inactive swimmers and are relatively undetected by the predator; (2) rates were high on middle stage yolk-sac larvae which are more active swimmers yet have a poorly developed escape response; and (3) rates were low on larger larvae which are able to escape the predator effectively. Starved hake larvae were more vulnerable to predation due to a poor escape ability although they were less active and not easily detected. The presence of naturally occurring alternative prey, *Pseudocalanus* sp., depressed the rate of *E. elongata* predation on hake larvae. In an analysis of field data, hake larvae and *E. elongata* were found to occupy the same depths in Dabob Bay. A high percentage of *E. elongata* collected had apparently been feeding on hake larvae, as indicated by the presence of pigments in their guts. Survival of hake larvae in late spring appears to be relatively poor compared with early spring; poorer survival in late spring may be due partly to an increase in the abundance of invertebrate predators, such as *E. elongata*.

### Introduction

Predation on fish eggs and larvae is one of the most critical, but least understood, factors affecting the recruitment of marine fishes (Hunter, 1976). Pioneering experimental studies by Theilacker and Lasker (1974), Lillelund and Lasker (1971), von Westerhagen and Rosenthal (1976) and Kuhlman (1977) demonstrated that several invertebrate predators are able to consume significant numbers of larvae. Furthermore, several field investigations also indicated that invertebrate predators eat many fish larvae (Purcell, 1981; Möller, 1980); however, few studies have attempted to link laboratory and field observations.

In this research we have examined feeding by a carnivorous marine copepod, *Euchaeta elongata* Esterly, on eggs and larvae of the Pacific hake, *Merluccius productus* in the laboratory and in nature. Variations in feeding rates due to the developmental stage of larvae, prey density, availability of alternative natural prey and starvation of larvae were measured in the laboratory. In addition, since previous research indicated that the feeding selectivity of *E. elongata* is related, in part, to the swimming characteristics of its copepod prey (Yen, 1982a), we hypothesized that differences in the swimming behavior of larvae would cause

\*Current address: Northwest and Alaska Fisheries Center, 2725 Montlake Blvd, Seattle, WA 98112, USA.

differences in *E. elongata*'s predation response. We examined this hypothesis by comparing *E. elongata*'s predation rates on different stages of hake larvae with concurrent measurements of the relative swimming characteristics of the larvae. Field observations are presented which indicate that feeding on larvae does occur in nature, and these observations are combined with laboratory analyses to examine how the numerical abundance of *E. elongata* may affect larval survival in a field setting.

Adult female *E. elongata* (4 mm prosome length) have enlarged maxillipeds well suited for capture of small copepods and fish larvae. *E. elongata* was selected as a model predator for these experiments because of previously gained knowledge of its feeding behavior (Yen, 1982a). Furthermore, at the site of the field sampling, Dabob Bay, Washington, *E. elongata* is an important predator and ranks third in total biomass of 19 major copepods there (Damkaer, 1964). Eggs and larvae of the Pacific hake are also very abundant in Dabob Bay and are present there from January until June.

### Methods

Live hake eggs and adult female *E. elongata* were collected simultaneously with a 571  $\mu$ m mesh, 1 m diameter net in the winter and spring months at Pt. Susan and at Dabob Bay in Puget Sound, and were returned to the laboratory. Yolk-sac larvae were separated from hake eggs. Eggs were hatched at 12–15°C and maintained at 12°C in 4 l jars until the first feeding stage. We were not successful at rearing larvae much beyond the expected starvation date. Instead, larger larvae used in these experiments were collected from the field with a slowly towed plankton net that was equipped with a jar-type codend adapted for obtaining live specimens. These larger larvae were fed *Artemia* and maintained in the laboratory for 36 h before experiments to insure that they were not damaged. The copepod, *E. elongata*, was maintained at 8°C in 10 l containers, and was fed with mixtures of copepods, small hake larvae and *Artemia* nauplii.

Twenty-four hours prior to each experiment, larvae were sorted and acclimated to 8°C. Since both *E. elongata* and hake eggs and larvae are found below the mixed layer (>20 m) in Dabob Bay, all experiments were run in total darkness at 8°C, the temperature below the mixed layer (Collias *et al.*, 1974). Larvae were counted into 1–4 l jars and one *E. elongata* was added to each experimental jar. No *Euchaeta* were added to control jars. For most experiments, there were 5 experimental replicates and 3–5 control replicates. Jars were placed on a mixing device that gently rolled the jars about the long axis and effectively kept predators and prey evenly distributed (see Yen, 1982b, for more detailed methods). After 24 h, the number of live larvae and dead carcasses were compared with the initial number of live larvae added, to determine the number of larvae missing. Consumption rates were calculated from the number of larvae missing, i.e., the number of larvae totally consumed. Attack rates were determined from the number of remaining live larvae and from the instantaneous rate of handling and natural mortality as determined from the controls using the equation:

$$N = N_0 e^{-(m + p)t}$$

where  $N$  is the number of larvae alive after the experiment,  $N_0$  is the number of larvae at the beginning of the experiment,  $m$  is the natural and handling mortality rate determined from the controls,  $p$  is the predation or attack rate and  $t$  is the duration of the experiment (24 h). The number of larvae attacked,  $A$ , was thus:

$$A = pN_0 \left( 1 - e^{-(m + p)t} \right) / (m + p)$$

To determine the relative changes in activity as the larvae developed, the swimming behavior of larvae was monitored in dim light (same lighting conditions for all tests) at 8°C. Three larvae were placed in a Petri dish and the number of swimming burst activities in 2 min intervals was recorded. At least 5 replicate sets were observed. The relative escape ability of larvae as they developed was measured simply by attempting to capture larvae with a pipette (5.5 mm bore, taking in 1.2 ml of water with each capture attempt). Larvae were placed in a graduated cylinder and the percentage of successful captures at different distances from the larvae was recorded. At least 20 capture attempts were made at each distance.

The vertical distribution of hake larvae and of *E. elongata* was determined from a series of vertically-stratified zooplankton samples taken with a 216  $\mu$ m mesh, 1 m diameter closing net in Dabob Bay in 1973. Details of the sampling design are described in King (1979). These samples were made available by B.W. Frost, School of Oceanography, College of Ocean and Fishery Sciences, University of Washington. Vertical tows sampling the entire water column (0–175 m) were taken every 2–3 weeks in Dabob Bay in 1973 with the 216  $\mu$ m, 1 m diameter net. This provided a time series of egg and larvae abundances. Samples were enumerated by taking two or four 10 ml subsamples with a Stempel pipette from each plankton sample. Depending on the density of plankton, these samples had been previously made up to a volume of 100–300 ml. Two samples from each sample period were analyzed.

Gut contents of adult female *E. elongata* from samples taken in February, 1980 in Dabob Bay and in March, 1981 in Pt. Susan, WA, were examined. Specimens preserved in formalin were placed in lactic acid to render the tissues transparent. The presence of material in the distended guts was noted. Specimens with full guts were dissected to remove their stomach and intestine which were then mounted in glycerin and squashed beneath a cover slip prior to examination under a compound microscope.

### Results

#### Laboratory studies

**Factors affecting laboratory predation rates.** Rates of predation by *E. elongata* on different developmental stages of hake larvae were examined in 2-l jars at densities of 5 larvae  $l^{-1}$  and with 1 *E. elongata* per jar. *E. elongata* did not feed on hake eggs, while consumption rates and attack rates were highest on middle yolk-sac stage larvae (Figure 1). Lower rates were observed on early yolk-sac and post yolk-sac stage larvae.

Since *E. elongata* depends on prey motion for detection, the relative dif-

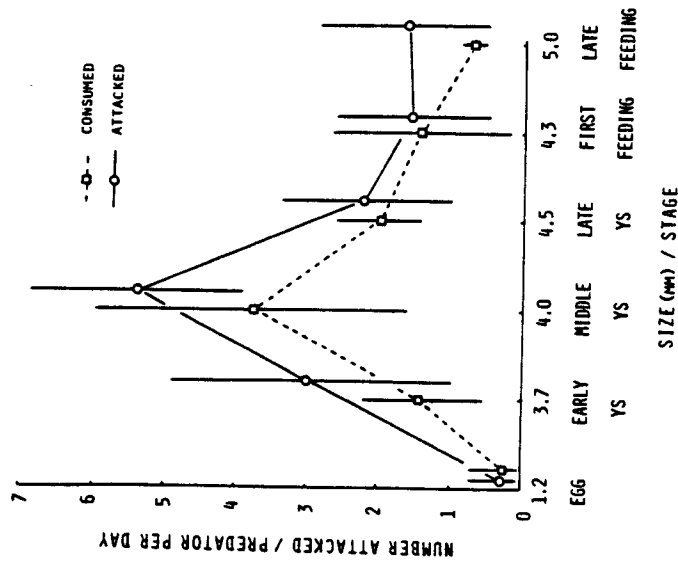


Fig. 1. Predation rates by *E. elongata* on Pacific hake eggs and on different developmental stages of larvae. Means are shown  $\pm$  1 standard deviation. Initial densities were 10 larvae  $2\text{ l}^{-1}$  and 1 *E. elongata*  $2\text{ l}^{-1}$ ; experiments were run for 24 h.

ferences in the swimming behavior of different developmental stages of hake larvae were examined to explain the observed differences in predation rates. Swimming burst activity and relative escape ability of larvae were the two components of larval swimming we observed. Since *E. elongata* feeds only in darkness (Yen, 1982b), it was not possible to examine directly the interactions between larval activity and predation by *E. elongata* with the equipment available to us. Hake larvae were monitored in dim light without the predator present. Small containers (50 ml) were used which may have restricted movement; however, relative levels of activity could be compared.

Hake larvae were intermittent swimmers with activity periods occurring over 1–3 s. Early yolk-sac stage larvae were inactive, only engaging in short and infrequent burst swimming activities; middle yolk-sac stage larvae are ~60% more active (Figure 2). Swimming activity increased considerably with development through feeding stages. Starvation decreased activity; larvae starved for 3–4 days at 15°C were 78% less active compared with first-feeding larvae.

Attempts to capture larvae with a pipette were used simply as a measure of the relative reactive ability of larvae to a physical disturbance. The distance at which 50% of the capture attempts were successful was determined by linear interpolation from the relationship of distance versus the percent capture success, and is shown in Figure 3. Ability of larvae to avoid capture increased with progressing larval development. Starved hake larvae were relatively less able to avoid capture compared with first-feeding larvae.

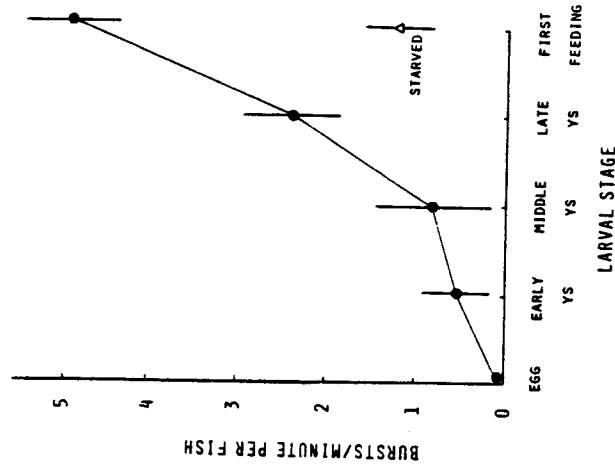


Fig. 2. The burst activity of Pacific hake larvae as related to developmental stage. Means are shown  $\pm$  1 standard deviation.

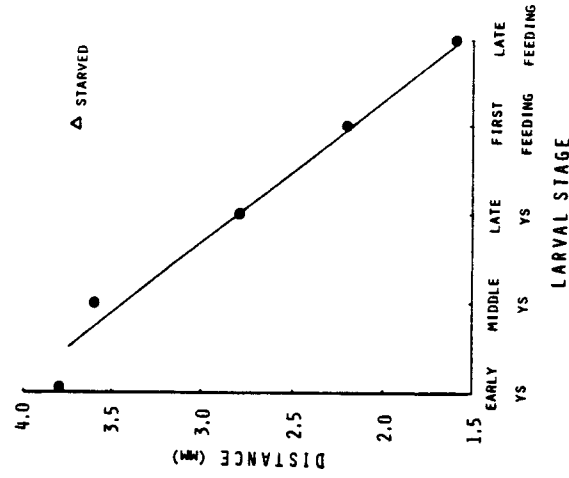


Fig. 3. The distance at which 50% of attempts to capture Pacific hake larvae with a pipette are successful related to developmental stage.

The functional response of *E. elongata* feeding on different densities of the preferred stage, middle yolk-sac larvae, was examined. The Ivlev (1961) equation was used to estimate the maximum predation rate:

$$P = P_{mx}(1 - e^{-aN})$$

where P is the predation (attack) rate,  $P_{mx}$  is the maximum predation rate, N is the initial prey concentration and a is a proportionality constant relating the rate of change of P with N. The resulting parameters were estimated as  $a = 0.46$  and  $P_{mx} = 3.21$ . The nonlinear Ivlev equation was a significantly better model than a linear model (residual sum of squares: 125.0 versus 129.6), indicating that predation rates approach a maxima (Figure 4).

Predation rates were measured on larvae that had just entered the post yolk-sac stage but had not yet started feeding, i.e., the first-feeding stage. These rates were compared with rates obtained for *E. elongata* fed starved first-feeding larvae which were post yolk-sac stage that had been starved for 3–4 d at 15°C (mean time to starvation death at 15°C is 6 d; Bailey, in press). Although lengths of the starved larvae (4.2 mm) and unstarved larvae (4.3 mm) were about the same, the bodies of starved larvae were emaciated and swimming was noticeably impaired. Predation rates on starved larvae were 70% greater than on first-feeding larvae (Table I).

*Pseudocalanus* sp. was used to examine the effect of an alternative prey on

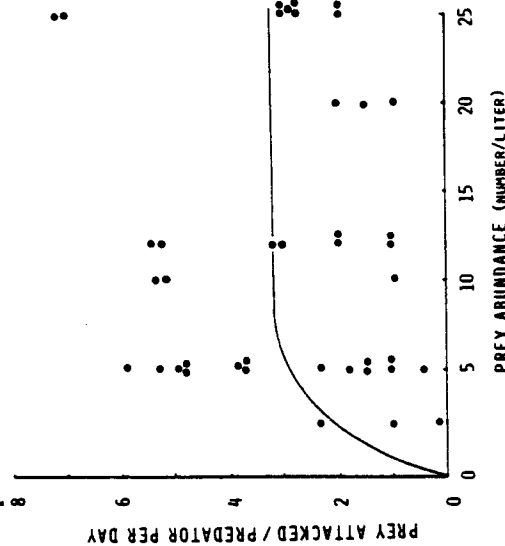


Fig. 4. The effect of prey density on predation rates by *E. elongata* on middle stage yolk-sac hake larvae. The data were fitted with an Ivlev model.

Table I. Comparison of daily predation rates of *E. elongata* on first feeding and starved first-feeding larvae of Pacific hake.

Prey condition	Mean length (mm)	Number replicates	Mean number attacked	s.d.
Non-starved	4.32	5	1.64	0.72
Starved	4.16	4	2.79	0.83

*E. elongata* predation on hake larvae; *Pseudocalanus* sp. is among the preferred prey of *E. elongata* (Yen, 1982a). At equal densities of copepod and fish larvae prey, the availability of *Pseudocalanus* depressed the predation rate on middle yolk-sac stage larvae by 60% compared with rates on larvae without alternative prey present (2.12 larvae attacked  $\text{d}^{-1}$  per predator versus 5.35 larvae attacked  $\text{d}^{-1}$  per predator; larval density =  $5 \text{ l}^{-1}$ , duration of experiments = 1 d).

*Other predators on hake eggs and larvae.* The ability of several co-occurring types of invertebrate predators to eat hake eggs and larvae was tested. These experiments were conducted in standing seawater in 500 ml beakers for 24 h (12 h light, 12 h dark). Hake eggs were eaten in 4 of 14 tests (Table II). Medusae and ctenophores appeared to be especially able to feed on hake eggs. The only crustacean to feed significantly on hake eggs was the amphipod, *Calliopius* sp. Yolk-sac larvae were more vulnerable to a wider range of predators. Crab larvae, *Calliopius* sp., *Parathemisto* sp. and medusae were all active predators on larvae. All larvae present in the beaker with *Sarsia*, were dead, but not eaten. *Sarsia* may excrete a toxin or could fatally sting, but not capture or ingest larvae.

#### Field studies

The vertical distributions of *E. elongata* and of hake larvae were examined to determine the extent of their spatial overlap. In Dabob Bay, adult female *E. elongata* migrate upward from depths of 150–175 m in daytime to depths of 25–75 m at night (Yen, 1982a). Hake eggs and yolk-sac larvae do not appear to migrate vertically and are distributed primarily between 150 and 175 m (Figure 5). Feeding stage larvae (<5 mm) do appear to migrate out of the bottom layer and towards the surface in daytime. No larvae >5 mm were captured in this

Table II. Results of tests to determine the ability of invertebrate animals to feed on eggs and larvae of Pacific hake. Experiments were run for 24 h at 8°C in 500 ml beakers.

Predator	Predators added	Eggs added	Eggs recovered	Larvae added	Larvae recovered
<i>Euphausia pacifica</i>	1	5	5	5	2
<i>Parathemisto</i> sp. (large)	1	5	5	5	4
<i>Parathemisto</i> sp. (small)	2	10	10	5	1
<i>Calliopius</i> sp.	1	5	0	5	0
<i>Cyphocaris</i> sp.	1	10	10	5	4
Shrimp larvae	1	5	5	5	5
Crab larvae (large)	1	5	5	5	0
Crab larvae (small)	2	10	10	5	5
Chaetognath	2	10	10	5	4
<i>Corycaeus</i> sp.	4	10	10	5	5
<i>Phialidium</i> sp.	1	5	1	5	0
<i>Pleurobrachia</i> sp.	1	5	1	5	5
<i>Cyanea</i> sp.	1	—	—	5	0
<i>Sarsia</i> sp.	2	5	2 (dead)	5	4 (dead)

series of tows. Hake eggs and small larvae at Pt. Susan, WA (110 m depth) are also distributed in the near bottom layer (Bailey, in press), and hake larvae > 5 mm in Pt. Susan are primarily distributed between 40 and 75 m.

In plankton tows taken in Pt. Susan and Dabob Bay during periods when hake larvae are abundant, we observed a high percentage of *E. elongata* adults with black guts. These black guts are not observed at other times of the year when hake larvae are not present; during these other seasons guts are normally clear or light brown. *E. elongata* that were fed hake larvae in the laboratory were also observed to have black guts. Black guts from the field that were dissected contained an amorphous material, whereas brown guts that were dissected contained copepod body parts. We believe that the gut-blackness of field caught *E. elongata* is due to the ingestion of body and eye pigments of hake larvae. Fish larvae of other species were not abundant in any of our samples.

Some quantitative observations were made on the percent of *E. elongata* that had been feeding on hake larvae in the field. In March 1981, 76 *E. elongata* from Pt. Susan were examined; 46% had food in their guts and of those with food, 93% had black guts. In February 1980, 75 *E. elongata* from Dabob Bay were examined; 41% had food in their guts and of those with food, 74% had black guts. These results indicate that when hake larvae are abundant, from 30 to 40% of the adult *E. elongata* appear to feed on hake each day.

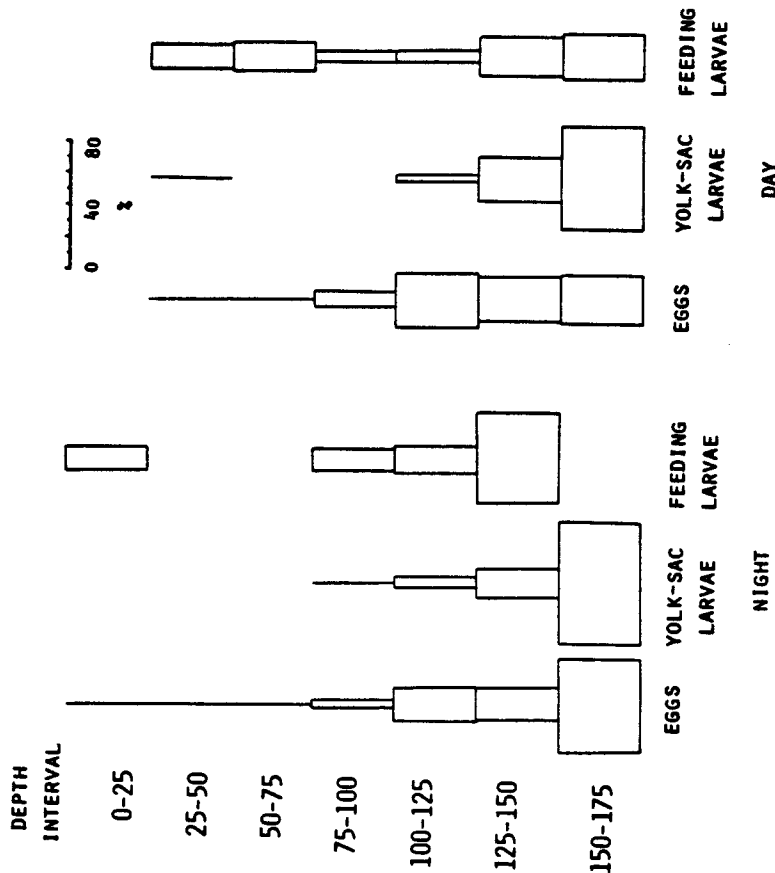


Fig. 5. The vertical distribution of hake eggs and larvae in Dabob Bay, April 1973, showing the percent of the total number of each stage at each depth interval.

From tows taken every 2-3 weeks in Dabob Bay, it was possible to compare changes in abundance of hake eggs and larvae with changes in the abundance of *E. elongata* (Figure 6). The sampling was not designed to study the population dynamics of hake and the period between sampling dates was too long to assess mortality rates (at 8°C the duration of the egg stage is 6.5 d and the yolk-sac stage is ~12 d; Bailey, in press). However, the peak in abundance of hake eggs in the late February-early March period appeared to give rise to peaks in abundance of yolk-sac and feeding larvae (< 5 mm) in the late March-early April period. In contrast, a great abundance of eggs produced in the mid April-mid May period did not result in high numbers of yolk-sac or feeding larvae. Since transport out of Dabob Bay does not appear to be a factor in the dynamics of plankton during this period (King, 1979), this decline is apparently due to poor survival. Larval mortality could be related to the abundance of adult CVI *E. elongata* which rose dramatically in April from an average monthly abundance of 242  $m^{-2}$  in March to 444  $m^{-2}$  in April and 1015  $m^{-2}$  in May. To explore the impact *E. elongata* could exert on the standing stock of yolk-sac larvae, the theoretical percent con-

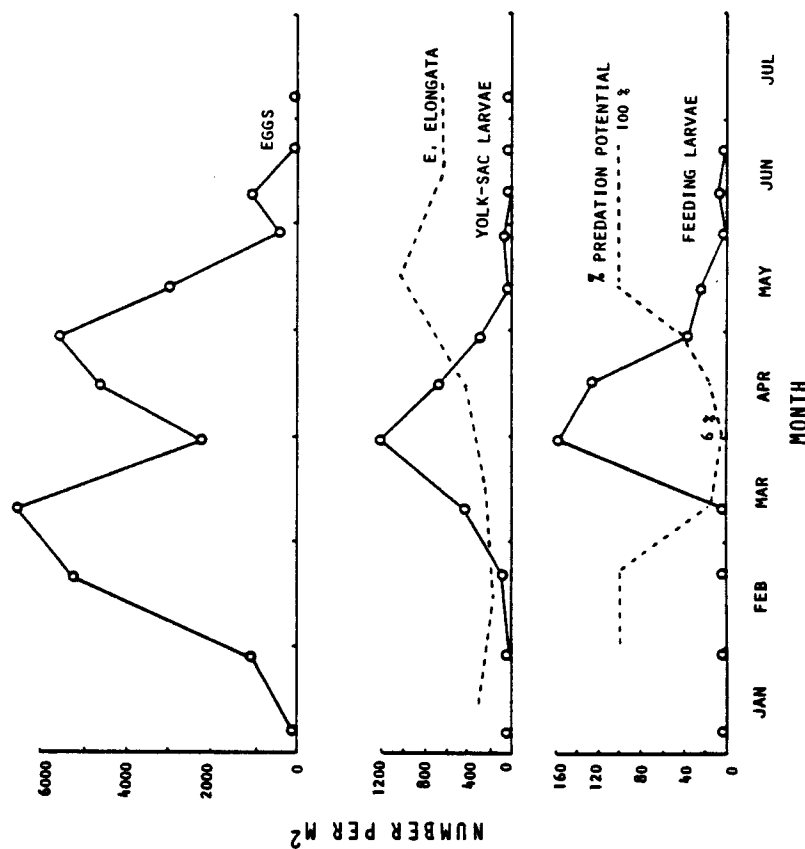


Fig. 6. The mean abundance of Pacific hake eggs (top), yolk-sac larvae (middle) and feeding larvae (bottom) at different sampling periods in Dabob Bay, 1973. The mean monthly abundance of adult female *E. elongata* (dotted line, middle figure) and the percent of the standing stock of yolk-sac larvae potentially eaten by *E. elongata* (dotted line, bottom figure) are also shown.

sumed by the carnivorous copepod was estimated (Figure 6). This percentage was calculated as the product of the average monthly number of *E. elongata*, the percent of the predator population feeding on hake larvae (estimated at 35% from the black guts noted above), and the predation rate of *E. elongata* on larvae (estimated from Ivlev model as one larvae eaten per day at low prey densities). Fish pigments in the guts of the predators from the 1973 series could not be examined because pigments had bleached with age (8 years). When the percentage of the standing crop of yolk-sac larvae consumed by *E. elongata* is overlaid against the abundance of feeding larvae, we noted that a high abundance of surviving feeding larvae appear when the percentage of yolk-sac larvae consumed is lowest. Eggs produced in late spring do not survive the feeding larvae stage, possibly due to increased potential predation pressure. In the samples we also noted, but did not enumerate, that other potential predators on hake eggs and larvae, especially medusae and euphausiids, were more abundant in late spring compared with the earlier period.

#### Discussion

Many reviews state that invertebrate predators have a great impact on the survival of fish eggs and larvae, yet only recently had studies actually demonstrated the magnitude of their impact. Möller (1980) estimated that the scyphomedusa, *Aurelia aurita*, daily consumed 2–5% of the standing stock of yolk-sac herring larvae in the Baltic Sea. In another study, Purcell (1981) estimated that the siphonophore, *Rhizophysa eysenhardti*, daily ate 28% of the standing stock of fish larvae in the Gulf of California. Purcell noted that this estimate may be somewhat high. In our study we have attempted to demonstrate how the potential predation pressure by *E. elongata* could influence larval survival.

Our analyses included laboratory work to determine maximum rates of predation and stage vulnerability, which were combined with a time series of field data that was available opportunistically, to estimate potential predation pressure. We demonstrated that *E. elongata* does consume hake larvae in the laboratory, even in the presence of its preferred copepod prey, and that guts of *E. elongata* that had eaten fish larvae were black with melanin pigments. In Dabob Bay, WA, *E. elongata* and hake larvae occupy the same habitat, and when hake larvae are abundant, a high percentage of *E. elongata* have melanin in their guts. Finally, we have attempted to relate the survival of larvae to the abundance of *E. elongata*. An increase in the abundance of *E. elongata* occurring in April appears to accompany an apparent decrease in survival of larvae where predation pressure can be attributed primarily to the feeding activity of *E. elongata*. We have also presented results indicating that other invertebrates are potentially capable of feeding on eggs and larvae; these predators must also have an important impact on the survival of early life history stages of hake. Further field studies are suggested by our analyses of the field data; this field sampling should be designed with spatial and temporal adequacy to enable estimates of mortality related to predation pressure.

Apparent stage selective predation on fish larvae was exhibited by adult female *E. elongata*; in the laboratory, predation rates on middle yolk-sac stage larvae

were high compared with earlier and later stages. The results are similar to *E. elongata*'s feeding behavior on copepod prey where predation rates are highest on intermediate sized copepods compared with smaller and larger animals. Size selectivity, also found in feeding by other predatory copepods (Ambler and Frost, 1974; Landry, 1978), may result from handling of the prey, among other factors. The observed differences in predation rates by *E. elongata* on developmental stages of hake larvae cannot be explained on the basis of size alone because hake yolk-sac larvae change very little in size during development. Here, two aspects of the swimming behavior of larvae, activity and escape ability, seem to account for the observed patterns in selectivity, since *Euchaeta* is a nonvisual feeder and depends on mechanical stimuli for prey detection (Yen, 1982b). Predation rates are low on early yolk-sac stage larvae because they are relatively inactive and difficult to detect. Older larvae become more active and are easily detected, but as larvae become older they also develop an improved escape ability. Similar, but undocumented, observations were made for chaetognaths feeding on fish larvae (Kuhlman, 1977).

The presence of a naturally occurring alternative prey, *Pseudocalanus* sp., also depressed the predation of *E. elongata* on hake larvae. However, even though *Pseudocalanus* is in the preferred prey size range of copepods, there is no evidence of strong positive selection for *Pseudocalanus* over hake larvae in our results. This result differs from that found for chaetognaths, which appear to strongly select for copepods when offered a mixture of copepods and fish larvae (Kuhlman, 1977). This aspect of predation on fish larvae needs further investigation.

Other factors including prey starvation and activity were demonstrated to significantly influence predation on hake larvae by *E. elongata*. Starvation of larvae has generally been considered to be a significant but untested factor in mortality due to invertebrate predation (Hunter, 1976). Our findings do not disprove this hypothesis; starved larvae demonstrate an impaired escape response and are more often killed by *E. elongata* than nonstarved larvae of equal size. However, predation by *E. elongata* is not so great as expected simply from the escape response. Starved larvae are less active swimmers which may lower the probability of being detected. The effect of starvation may be most important via the effect of slowed growth, resulting in an extended period when larvae are in those stages vulnerable to predation.

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