

Laboratory Studies of Predation by Euphausiid Shrimps on Fish Larvae

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INTRODUCTION

Despite a large literature on the vulnerability of marine fish larvae to changes in their physical and biotic environment, there is surprisingly little quantitative data available on organisms that eat fish larvae. There is ample evidence that huge mortalities of yolk-sac fish larvae occur (Ahlstrom, 1965); this is not due to lack of food, a factor implicated in the mortality of older larvae (Blaxter, 1969). Predation on yolk-sac larvae may be the most important cause of mortality during the early period in the life history of pelagic fish. There are a number of observations of zooplankters feeding on fish larvae (Garstang, 1900; Lebour, 1925; Wickstead, 1965; Petipa, 1965; Fraser, 1969); copepods, chaetognaths, ctenophores, and a variety of coelenterates have been seen to capture and ingest marine fish larvae. Recently Lillelund and Lasker (1971) quantified the predator-prey relationship between several species of marine copepods and larvae of the northern anchovy, *Engraulis mordax*, and described the behavioural responses involved in this interaction. They found, for example, that a variety of marine copepods (but particularly surface-dwelling pontellids) can capture and ingest or fatally injure young anchovy larvae under laboratory conditions.

Our experiments were designed to determine whether euphausiids could capture fish larvae, and if so, how many and under what conditions. We have combined our laboratory findings with the field data given by Brinton (1967 and unpublished) to estimate the mortality of northern anchovy larvae that may be caused by co-occurring *E. pacifica*.

Of the oceanic zooplankters which frequent the upper mixed layer of the sea where fish larvae are found in greatest abundance, the euphausiid shrimps are often dominant in biomass and number, particularly during the night hours when they migrate to the surface. Although neither Ponomareva (1963) nor Mauchline and Fisher (1969), in their respective monographs, mention fish larvae as a food of euphausiids, most euphausiids are known to be omnivorous and capable of capturing zooplankters, e.g. chaetognaths and copepods; therefore fish larvae may be captured too. The fragile nature of most fish larvae and the lack of hard parts would make recognition of the remains impossible in the euphausiid intestine even if they were an important part of their diet.

Brinton (1962 and unpublished) has estimated the distribution and density of several euphausiid species in the California Current over a number of years, *Euphausia pacifica* Hansen being one of the most abundant species. The general feeding habits and ubiquity of *E. pacifica* in the California Current, and the fact that it can be maintained in the laboratory (Lasker and Theilacker, 1965; Lasker, 1966) prompted us to investigate it as a possible predator of marine fish larvae, particularly of the northern anchovy (*Engraulis mordax* Girard), the dominant clupeid fish in the California Current and to estimate larval mortality from field data.

METHODS

We collected euphausiids by towing a 1-m (mouth-diameter, 0.505 mm mesh) plankton net or a 60 cm diameter Bongo net without bridles with the same mesh size (McGowan and Brown, 1966) in the Pacific Ocean near San Diego and Santa Catalina Island, California, during the spring and summer of 1971 and 1972. On board ship euphausiids were separated from other plankton immediately and after allowing for the initial mortality of damaged animals (10-12 h), the survivors were kept separately in individual containers. Detailed methods for collecting and maintaining euphausiids are given by Lasker and Theilacker (1965).

Juvenile *E. pacifica*, ranging in total length from 6-10 mm and 0.6 - 2.1 mg dry weight, were caught most frequently. Some euphausiids were used for predation experiments on shipboard while others were brought back to the Southwest Fisheries Center aquarium, and used for as long as 25 days. When an experiment was terminated, each animal was measured, rinsed in distilled water, dried at 60°C, and weighed. The anchovy larvae fed to euphausiids were hatched from eggs collected from a spawning school in our aquarium facilities or from hormone-injected anchovies (Leong, 1971). For shipboard experiments the eggs were transferred from the aquarium to the ship, thus eliminating the need for catching anchovy eggs in net tows and sorting the eggs from other plankton.

Temperature was maintained at 17°C, close to the sea-surface temperature at the time euphausiids were captured. *E. pacifica* follows a low intensity light level of about 1×10^{-4} $\mu\text{W}/\text{cm}^2$ (Clarke, 1966) during vertical migration; we therefore performed all of our experiments in the dark. Unless otherwise noted, each feeding test lasted for 22 h with a euphausiid in 3500 ml sea water filtered earlier through a Cuno® Aqua Pure Filter (pore size 5 μ). In all experiments the young anchovy larvae appeared to be randomly distributed in the feeding containers.

FEEDING BY ADULT, JUVENILE, AND LARVAL *E. PACIFICA* ON LARVAL ANCHOVIES

Experiments were performed to compare the relative ability of different growth stages of euphausiids to capture anchovy larvae. Larval *E. pacifica* weigh less than 0.6 mg dry weight and are less than 6 mm in total length. Juveniles range from 0.6 - 2.1 mg and from 6 mm to slightly less than 11 mm in length; adults are 11 mm or more long and greater than 2.1 mg in weight (lengths from Brinton, personal communication). In these experiments the smallest *E. pacifica* tested was 5 mm long (0.15 mg) and the largest 20 mm (13.2 mg). The length range of *E. pacifica* in the California Current is from 1-21 mm.

Sixteen larval, 30 juvenile, and 27 adult *E. pacifica* were tested individually to determine their ability to feed on yolk-sac anchovy larvae. Larval and juvenile euphausiids were offered 20 anchovy larvae a day and adults were given 50-80 larvae per day in 3500 ml. Larval euphausiids ate a median number of 2 larvae/day (range 1-5), juveniles ate a median of 7 larvae/day (range 1-19), and adults ate a median of 17 larvae/day (range 5-38) (Fig. 1).

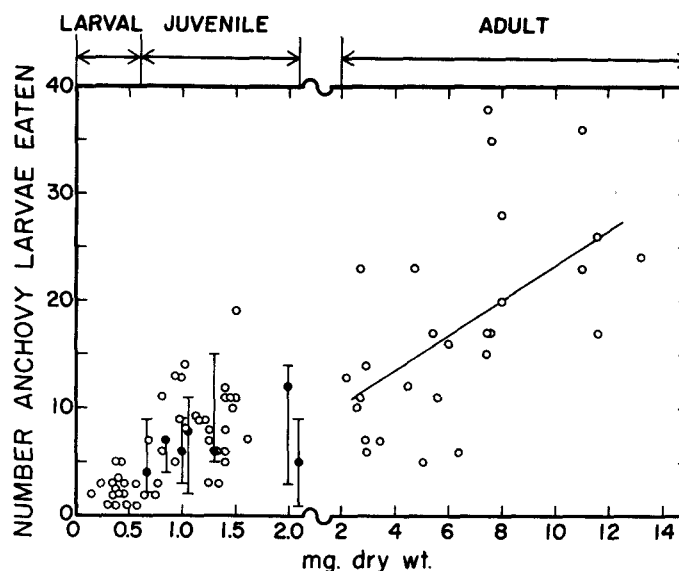


Fig. 1. Number of anchovy eaten per day by individual larval, juvenile, and adult *E. pacifica* (open circles). Closed circles indicate the median number of anchovy larvae eaten (with extremes given by the solid lines) when 7 individuals were fed daily for 5 consecutive days

No weight-specific feeding rate could be demonstrated within the juvenile size class (the slope [$b = 4.07$] does not differ significantly from zero [$p > 0.1$]). However, within the adult size group, feeding did increase with increasing animal size (Fig. 1). The slope ($b = 1.69$) of a least squares fit of the data differs significantly from zero ($p < 0.01$).

To test further the hypothesis that animal size, within the juvenile group, does not influence feeding, 7 juveniles were fed 20 anchovy larvae/day on each of 5 successive days. The euphausiids ranged from 7-11 mm (0.67 - 2.1 mg). The median number of anchovy larvae eaten per individual euphausiid/day ranged from 4-12 (Fig. 1). No significant difference in feeding could be demonstrated ($p > 0.20$) when the number of anchovy larvae eaten each day per animal was ranked and compared (Friedman two-way analysis of variance). All succeeding experiments were conducted with juvenile *E. pacifica*, since animal size did not influence feeding.

Lasker (1966) determined the carbon requirement at 10°C needed by various size groups of *E. pacifica* for growth, molting, respiration, and digestive inefficiency. From these data we calculated the necessary number of anchovy larvae which had to be consumed to satisfy the carbon requirement of larval, juvenile, and adult *E. pacifica*. Early anchovy larvae¹ weigh 22 μg and contain 42% carbon; therefore, one

¹Lillelund and Lasker (1971, p. 664) gave 10 μg for the dry weight of a yolk-sac anchovy larva. This figure should have been 22 μg .

larva provides about 9 μg of organic carbon. If no other food is available the carbon requirements of larval euphausiids at 10°C can be satisfied if each eats 1 anchovy larva/day; juveniles require 3-5 larvae/day, and adults from 7-28 larvae/day, depending on the euphausiid's weight.

At 17°C, the temperature of these experiments, the carbon requirements for growth, molting, and respiration would be greater than at 10°C. Respiratory carbon losses at 17°C are increased by 60% ($Q_{10} = 2$; Lasker, 1960) over the losses at 10°C and since respiration alone accounts for most of *E. pacifica*'s total carbon requirement (Lasker, 1966) we adjusted the above anchovy larval carbon equivalents by 60%. This increases the larval euphausiids daily requirement, see Table 1.

Table 1. The number of anchovy larvae/day needed by larval, juvenile, and adult *E. pacifica* to satisfy their daily carbon requirements at 17°C (based on Lasker, 1960, 1966) compared to the median and maximum number of anchovy larvae eaten by euphausiids in laboratory experiments

<i>E. pacifica</i>	Anchovy larvae required/day	Anchovy larvae eaten	
		Median	Maximum
Larval	1-2	2	5
Juvenile	5-8	7	19
Adult	11-45	17	38

FEEDING AT DIFFERENT PREY CONCENTRATIONS

The quantity of prey offered to juvenile euphausiids was varied from 1-80 anchovy larvae per 3500 ml/day. When 10 or less larvae were fed to juvenile euphausiids the maximum number eaten (Fig. 2) appears to be limited by the number fed and, probably, the searching capability of the euphausiid. Increasing the density further, offering more than 10 larvae, did not cause any differences in the median feeding rate. Feeding rates were compared statistically at 3 food concentrations (Fig. 2) 18-21, 29-32, and 40-50 larvae fed per container. The median number eaten per day increased from 6 at the lowest density (20 observations), to 8 at the next (9 experiments) and 10 at the highest density (6 experiments); however, no differences could be demonstrated between each paired comparison (Mann-Whitney U test, $p > 0.20$ for each pair tested).

From these experiments it appears that the average number of anchovy larvae juvenile euphausiids can process in a day - catching, eating, digesting, and excreting - is 10 or less. Increasing the prey concentration above this number had no effect on feeding in the volumes tested. This independence between feeding and food concentration has also been described for the crustacean *Daphnia* (Rigler, 1961) and the chaetognath, *Sagitta* (Reeve, 1964). Both authors found that above a critical food concentration the food-intake rate held constant as the food density continued to increase.

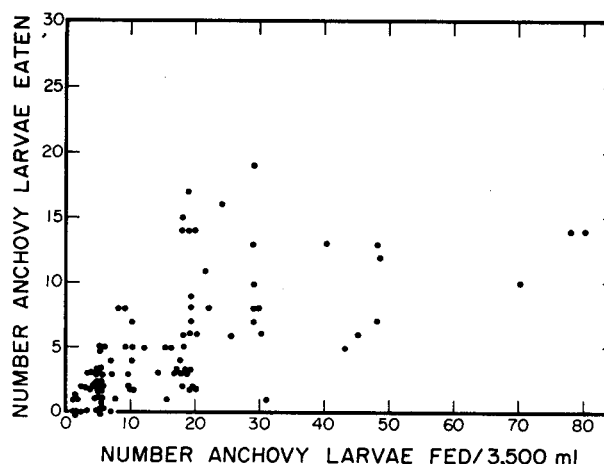


Fig. 2. Feeding of juvenile *E. pacifica* at different concentrations of anchovy larvae

FEEDING RATE

Fisher and Goldie (1959), studying the euphausiid *Meganyctiphanes norvegica*, did not find consistent differences in the amount of feeding between day and night samples taken in the North Sea. However, Ponomareva (1954) found that *E. pacifica* fed at a higher intensity during the evening and night in the Sea of Japan. Roger (1971) also observed a feeding rhythm for most of the 28 euphausiid species he studied in the field. He noted that the intensity of feeding usually increased before the nocturnal ascent, so that the rhythm was not, in most cases, synchronous with the day-night vertical migration.

Feeding intensity may be correlated only with the availability of food. To determine whether a periodicity in *E. pacifica* feeding could be demonstrated when food is not limiting, 11 juvenile euphausiids were fed anchovy larvae for 3 consecutive 12-h periods (midnight and noon were chosen as starting times to avoid any effect of a diel rhythm). Twenty larvae were offered to each euphausiid at the beginning of each 12-h experiment. At the end of the 36-h period, the animals were fed 20 larvae for 24 h. The median number of larvae eaten was 2 (Table 2) during the first 12 h (noon to midnight); 4 were eaten in the midnight-to-noon period and 2 in the second noon-to-midnight period. The median for the 24-h period was 5. No periodicity in feeding can be shown when the data were tested statistically. Feeding during the three 12-h periods was homogeneous when compared using Friedman's two-way analysis of variance by ranks ($p > 0.20$). Also, no differences could be demonstrated by comparing the 2 combined noon-midnight periods with the midnight-noon period (Mann-Whitney U, $p = 0.68$). The results suggest a constant feeding rate when food is not a limiting factor.

Table 2. The number of anchovy larvae eaten by 11 juvenile *E. pacifica* for each of 3 consecutive 12-h feeding periods followed by a 24-h period

Juvenile <i>E. pacifica</i> mg dry weight	Noon-midnight 12 h	Midnight-noon 12 h	Noon-midnight 12 h	24 h
2.00	8	4	8	3
2.10	5	0	2	1
0.52	0	6	6	5
1.28	1	4	3	5
1.23	2	5	3	7
0.67	3	4	6	4
0.56	0	2	0	1
0.82	3	2	2	7
1.00	2	4	1	6
0.84	1	0	0	4
1.02	1	2	2	5
Median number eaten	2	4	2	5

EFFECT OF TIME IN CAPTIVITY ON FEEDING BY JUVENILE *E. PACIFICA*

Twelve animals (0.5 - 2.1 mg dry weight) tested aboard ship on the first day of capture ate a median of 6.5 anchovy larvae when 18-20 were offered in 3500 ml, consuming between 2-13 larvae individually. Eight other juveniles (0.7 - 2.0 mg dry weight) were observed in the laboratory to determine whether or not feeding rate changed during captivity. Five days of feeding (7, 8, 13, 17, and 21 days after capture), when the density of larvae offered was the same as in the above shipboard experiments, were compared (Table 3). The number of larvae eaten per animal on each day was ranked. The sums of the daily ranks were compared and no significant difference in feeding rates was obtained (Friedman two-way analysis of variance by ranks, $0.1 < p < 0.2$). The number of larvae eaten by all animals varied from 1-15 per day; the individual medians for the 5 days of feeding ranged between 2 and 12 and the overall median number of larvae eaten was 6. Therefore, the daily feeding rate of juvenile *E. pacifica* does not appear to change with the time maintained in captivity.

Table 3. Feeding by 8 juvenile *E. pacifica* maintained on anchovy larvae in the laboratory for 3 weeks

Juvenile <i>E. pacifica</i>	Number of anchovy larvae eaten					
	Days after capture					Median
	7	8	13	17	21	
no. 1	5	5	8	15	6	6
2	12	3	14	4	14	12
3	7	1	8	3	9	7
4	6	4	2	3	9	4
5	4	7	5	7	7	7
6	1	4	3	1	2	2
7	4	6	3	9	9	6
8	3	5	11	8	8	8

THE EFFECT OF AN ALTERNATIVE PREY

Lillelund and Lasker (1971), in their study on the predation of anchovy larvae by the copepod *Labidocera trispinosa*, found that the addition of *Artemia* nauplii, as an alternate prey, decreased the feeding on larvae. The decrease in feeding rate was proportional to the density of the additional prey; at high nauplii densities fewer larvae were killed. *Euphausia pacifica* will also feed on *Artemia* nauplii, the number eaten determined by Lasker (1966) being 100-350/day for *E. pacifica* ranging in dry weight between 1.8 and 5.6 mg. Nine individual juvenile *E. pacifica* were offered 20 larvae daily for 5 consecutive days with *Artemia* nauplii as an alternative. Four of the experiments were conducted in 3500 ml and 5 in 700 ml containers. On the 2nd, 3rd, and 4th days *Artemia* nauplii were also given at densities of one nauplius per 5, 10, 20, and 40 ml. The median number of the larvae eaten in the 3500 ml containers was 5 when anchovy larvae only were offered, but 3 when *Artemia* nauplii were present with the larvae; in the 700 ml containers the median number eaten was 5 for each treatment. The data were tested statistically (the 2 container sizes tested separately) by comparing the ranked sum of the number of anchovy larvae eaten for the 3 days when *Artemia* were present to the number eaten during the 2 days when anchovy larvae alone were fed. The ratio of the sums of the ranks for the 2 treatments (with and without *Artemia* nauplii) was the same as the ratio of the number of observations (for both container volumes), so the null hypothesis must be accepted ($p > 0.20$, Mann-Whitney U Test).

The same data were rearranged to test the daily feeding on anchovy larvae as a function of *Artemia* density (Fig. 3). The data were homogeneous; feeding on larvae was the same at each *Artemia* density (Friedman's two-way analysis of variance by ranks, $p > 0.20$). Therefore, the presence of *Artemia* nauplii, even at a density of one per 5 ml, does not alter euphausiid feeding on anchovy larvae.

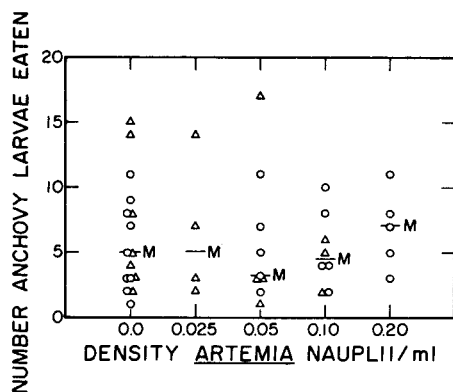


Fig. 3. Predation by *E. pacifica* on anchovy larvae with addition of *Artemia* nauplii as an alternative prey. o = 3500 ml container; Δ = 700 ml container; M = median number during control and at each *Artemia* density

In all of the experiments in which *Artemia* nauplii were offered, the number of nauplii eaten increased as the nauplii concentration was increased. Filtering rates (Gauld, 1951) calculated from the number of nauplii eaten at each density remained constant (Friedman's two-way analysis of variance by ranks, $p > 0.20$), indicating that the *Artemia* are filtered as a passive particle. Brooks (1970) concluded that particle-feeding copepods grazed on *Artemia* as a passive particle and that predatory copepods may feed on *Artemia* nauplii in preference to natural nauplii only because they are more easily captured and no active selection of the *Artemia* nauplii over the natural nauplii is involved.

STARVATION

Several juvenile euphausiids, 0.6 - 0.8 mg dry weight, were kept in the laboratory for 24 days without feeding. These animals commenced feeding on anchovy larvae and molted for 2 additional weeks when the experiment was terminated.

To determine whether or not periods of starvation cause a change in feeding rate, 8 individual juvenile *E. pacifica*, (0.70 - 2.00 mg dry weight) were either fed 20 larvae/day on consecutive days or starved from 2-3 days and then fed 20 larvae. Each individual (9-10 observations/animal) was tested separately, comparing the number of larvae eaten during a day of feeding when the animal had been fed the previous day to the number eaten when the animal had not been fed the previous day. One euphausiid ate less than usual after a period of starvation ($p < 0.05$); however, the other 7 animals showed no differences in the daily feeding patterns whether or not the euphausiids had fed the previous day (p values all > 0.20 , Mann-Whitney U Test). Therefore, under laboratory conditions, when food is not limiting, 2-3 days of previous starvation does not appear to have an effect on feeding.

MOLTING

Lasker (1966) found that molting of *E. pacifica* depressed the feeding on *Artemia* nauplii. To test for this effect, the data from all the

anchovy larvae feeding experiments were combined and the number eaten on days the euphausiids did and did not molt were compared. Juvenile euphausiids used in this comparison were fed more than 10 larvae/day and had molted at least once. The median number of larvae eaten for 99 animal-days when the euphausiid did not molt was 7 (range 1-19). There were only 11 molting days that fit the above requirements. The median number of larvae eaten during a molting day was 5 (range 1-14). No significant difference could be demonstrated between the 2 sets of data (Mann-Whitney U Test $p = 0.63$); hence molting does not appear to depress the feeding of *E. pacifica* on anchovy larvae.

The median intermolt period at 17°C for *E. pacifica* fed anchovy larvae (22 observations on 12 animals) was 4 days, the range was between 2 and 6 days; 91% of the observations were between 3 and 5 days. This is the same molting frequency observed by Lasker (1966) for *E. pacifica* fed *Artemia* nauplii at 15°C.

FEEDING ON OLDER ANCHOVY LARVAE

Lillelund and Lasker (1971) noted in their predation study that the ability of the copepod *Labidocera trispinosa* to capture anchovy larvae decreased as the larvae aged and became more active. A 1-day-old anchovy larva rests more than 95% of the time and 2-day-old larvae rest about 70% of the time; at 3 days of age the larva spends almost 50% of its time in intermittent swimming and the next day swims intermittently 85% of the time (Hunter, 1972). Increasing larval activity correlates well with the decreasing ability of *E. pacifica* to capture larval anchovies.

Day-1 (newly hatched) and 2-day-old larvae were fed to 10 individual juvenile euphausiids at a concentration of 1 larva/3500 ml. In this situation the euphausiids were 60% successful in capturing the single larva. Successful capture dropped to 17% when the larvae were 3 days old (12 experiments) and to 11% for 4-day-old larvae (9 experiments), all fed to the euphausiids at the same low density.

FEEDING ON ANCHOVY EGGS

E. pacifica will feed on anchovy eggs although the incidence of ingestion is very low in the laboratory. This is probably because the eggs are unavailable to the euphausiid, floating at the surface of the sea water since there was no water movement in the containers. In the open ocean, anchovy eggs are distributed in the upper 50 m of the water column (Ahlstrom, 1959).

Sixteen juvenile euphausiids were offered 20 anchovy eggs each in 700 ml. Only 3 animals ate eggs; the median number eaten was 5.

CO-OCCURRENCE OF *E. PACIFICA* AND ANCHOVY LARVAE IN THE CALIFORNIA CURRENT

Dr. Edward Brinton of SIO has kindly provided us with unpublished data on the abundance of *E. pacifica* in the California Current. The euphausiids were collected in standard (1-m net towed to 140 m depth) night CalCOFI tows (Kramer et al., 1972) between January 1953 and July 1955. The counts are given as numbers of individuals/1000 m³ of each mm size group, 1-21 mm, per station per month for 27 stations between Point Conception and San Diego (Fig. 4), an area of 30,000 square miles (8×10^{10} m²).

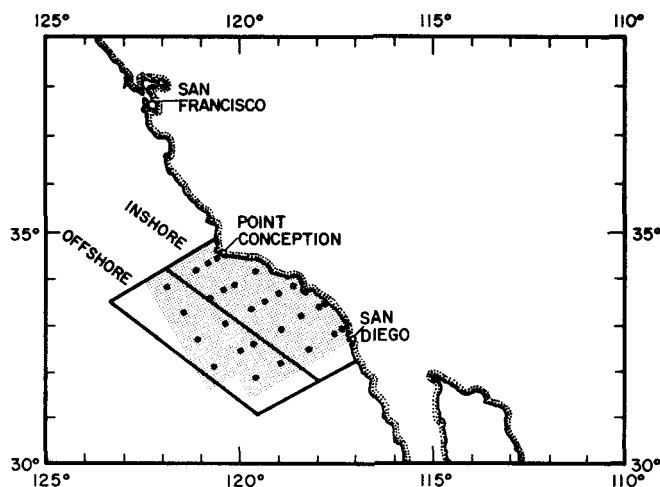


Fig. 4. Map showing anchovy (outlined) and euphausiid (shaded) surveys. • = euphausiid stations

The abundance of anchovy eggs and larvae in the California Current has been studied intensively since 1949. Data for the anchovy spawning season during 1953, 1954, and 1955 in the same area of the California Current as Brinton's euphausiid study are given by Smith (1972). The anchovy area extends 40 miles further south than the euphausiid area (Fig. 4). Spawning during the 1953-1954 season was between October 1953 and March 1954; in 1955 the major spawning was in the first quarter of the year and is given in numbers of anchovy larvae per m² sea surface per positive station in Table 4. There were more positive stations inshore (to 80 miles off the coast) than offshore (between 80 and 160 miles off the coast); the frequencies are given in Table 4. Although there is some spawning throughout the year, the number of larval anchovies is only one-tenth to one-fourth of the number obtained during peak spawning. During the spawning period 68% of the larvae sampled were 5.25 mm or less in length (Smith, personal communication), or between hatching and 1-week-old.

About 98% of the anchovy larvae occur above 56 m and 49% are above 8 m (Ahlstrom, 1959). The vertical distribution of each *E. pacifica* size group was calculated from data provided by Brinton (unpublished and 1967). The samples, taken at 25-m increments between 25 and 250 m

with a closing net, were collected at 4 night stations. Night catches indicate that an average of 87% of larval, juvenile, and adult *E. pacifica* are above 50 m. However, because of active vertical migration it is conceivable that all of the euphausiids may reach the surface some time during the night.

Table 4. The estimated number of anchovy larvae (<5.25 mm long) under 1 m² of sea surface during the peak spawning season in 1953, 1954, and 1955

Spawning season	Inshore		Offshore	
	No. larvae/m ²	No. positive stations	No. m ²	No. positive stations
1953	36	100	13	86
1954	59	100	11	83
1955	38	95	4	69

The average number of larval, juvenile, and adult *E. pacifica* under 1 m² of sea surface in the area of the California Current is tabulated in Table 5 for the months of peak anchovy spawning in 1953, 1954, and 1955 (9 months). At the median feeding rates on anchovy larvae determined in this study and the mean euphausiid densities calculated to include the number of euphausiids co-occurring with anchovy larvae, 831 anchovy larvae could be consumed/day/m². For the purpose of this discussion we assume that *E. pacifica* is in the upper 50 m of the water column for 10 h, an hour after sunset to an hour before sunrise. If the total water column *E. pacifica* frequents daily is considered, the *E. pacifica* (average of Brinton's 29-month survey) under 1 m² of sea surface could devour a total of 2847 fish larvae/day/m² (Table 5) regardless of other zooplankton being present.

Table 5. The average number of *E. pacifica* under 1 m² sea surface and the total number of fish larvae that could be consumed daily

	Larval	Juvenile	Adult	Total
No. of <i>E. pacifica</i> /m ² during peak anchovy spawning (9 mo. average)	314	118	38	470
No. of <i>E. pacifica</i> above 50 m at night	273	103	33	409
No. of fish larvae <i>E. pacifica</i> above 50 m can consume/10 h/m ²	248	328	255	831
<i>E. pacifica</i> /m ² (29 mo. average)	582	139	43	764
No. of fish larvae <i>E. pacifica</i> can consume/2 h/m ²	1,164	952	731	2,847

It is possible that the small number ($<60/m^2$) of anchovy larvae caught in plankton nets (Table 4) is a result of heavy predation. The abundance of euphausiids and other predators may be a factor in determining the patchiness of fish larvae.

SUMMARY

The abundant euphausiid in the California Current, *Euphausia pacifica*, may be an important predator of fish larvae. Laboratory experiments showed that when the number of yolk-sac anchovy larvae (*Engraulis mordax*) offered was not limiting (not less than one larva/350 ml) the median number eaten per day by larval *E. pacifica* was 2; juvenile euphausiids eat 7, and adults 17. The carbon requirements of *E. pacifica* for the 3 growth stages is approximately the amount of carbon provided by the median feeding rates. Within the adult euphausiid size group, feeding on fish larvae significantly increased with increasing animal size, but no size-specific feeding could be demonstrated for juvenile euphausiids. All replicate experiments with individual *E. pacifica* in this study were conducted with juveniles. These showed that the amount of feeding was not affected by the addition of another prey, imposed starvation, molting, or the length of time the euphausiids were in captivity. The amount of feeding increased as the prey density was increased from 1-10 larvae offered per 3.5 l/day; further increases had no effect. Feeding rate was constant regardless of time of day. The percent capture of fish larvae by euphausiids was lower than usual when older, more active anchovy larvae were offered. These studies are discussed in terms of field data collected in the area of the California Current where *E. pacifica* and anchovy larvae co-occur.

REFERENCES

- Ahlstrom, E.H., 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Wildl. Serv., Fish. Bull., 60, 107-146.
- Ahlstrom, E.H., 1965. A review of the effects of the environment of the Pacific sardine. ICNAF Spec. Publ., 6, 53-74.
- Blaxter, J.H.S., 1969. Development: eggs and larvae. In: W.S. Hoar and D.J. Randall (Eds.), Fish Physiol., 3. New York: Academic Press, 177-252 pp.
- Brinton, E., 1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif., 8, 51-270.
- Brinton, E., 1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr., 12, 451-483.
- Brooks, E.R., 1970. Selective feeding of some adult female copepods on an array of food including *Artemia* and naturally-occurring nauplii. U. Calif. Inst. Mar. Resour., Res. Mar. Food Chain Prog. Rep., July 1969-June 1970, Part 2, 56-74.
- Clarke, W.B., 1966. Bathyphotometric studies of the light regime of organisms of the deep scattering layers. AEC Res. Develop. Rep., SAN-548-1, UC-48 Biol. Med., TD-4500, 47 pp.
- Fisher, L.R. and Goldie, E.H., 1959. The food of *Meganyctiphanes norvegica* (M. Sars), with an assessment of the contributions of its components to the vitamin A reserves of the animal. J. Mar. Biol. Ass. U.K., 38, 291-312.

- Fraser, J.H., 1969. Experimental feeding of some medusae and chaetognaths. J. Fish. Res. Bd Can., 26, 1743-1762.
- Garstang, W.R., 1900. Preliminary experiments on the rearing of sea-fish larvae. J. Mar. Biol. Ass. U.K., 6, 70-93.
- Gauld, D.T., 1951. The grazing rate of planktonic copepods. J. Mar. Biol. Ass. U.K., 29, 695-706.
- Hunter, J.R., 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S., 70, 821-838.
- Kramer, D., Kalin, M.J., Stevens, E.G., Thrailkill, J.R. and Zweifel, J.R., 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA, Tech. Rep., NMFS Circ., 370, 38 pp.
- Lasker, R., 1960. Utilization of organic carbon by a marine crustacean: analysis with carbon-14. Science, 131, 1098-1100.
- Lasker, R., 1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. J. Fish. Res. Bd Can., 23, 1291-1317.
- Lasker, R. and Theilacker, G.H., 1965. Maintenance of euphausiid shrimps in the laboratory. Limnol. Oceanogr., 10, 287-288.
- Lebour, M.V., 1925. Young anglers in captivity and some of their enemies. A study in a plunger jar. J. Mar. Biol. Ass. U.K., 13, 721-734.
- Leong, R., 1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S., 69, 357-360.
- Lillelund, K. and Lasker, R., 1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull., U.S., 69, 655-667.
- Mauchline, J. and Fisher, L.R., 1969. The biology of euphausiids. Advan. Mar. Biol., 7, 1-454.
- McGowan, J.A. and Brown, D.M., 1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref., 66-23.
- Petipa, T.S., 1965. The food selectivity of *Calanus helgolandicus*. Invest. Plankton Black Sea, Sea of Azov. Akad. Sci. Ukrainian, SSR, 102-110. Ministry of Agriculture and Fisheries Trans. N.S., (72).
- Ponomareva, L.A., 1954. Euphausiids of the Sea of Japan feeding on the copepoda. Dokl. Acad. Sci. USSR (Zool.), 98, 153-154.
- Ponomareva, L.A., 1963. The euphausiids of the North Pacific, their distribution and mass species (in Russ., Engl. summary). Moscow, 142 p.
- Reeve, M.R., 1964. Feeding of zooplankton, with species reference to some experiments with *Sagitta*. Nature, 201, 211-213.
- Rigler, F.H., 1961. The relation between concentration of food and feeding rate of *Daphnia magna* Straus. Can. J. Zool., 39, 857-868.
- Roger, C., 1971. Euphausiids of the equatorial and south tropical Pacific Ocean: zoogeography, ecology, biology and trophic relationships. Thesis to be publ. in Mémoires Orstom.
- Smith, P.E., 1972. The increase in spawning biomass of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S., 70, 849-874.
- Wickstead, J.H., 1965. An introduction to the study of tropical plankton. Hutchinson and Co., London, 160 p.

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