

# LABORATORY STUDIES OF PREDATION BY MARINE COPEPODS ON FISH LARVAE

KURT LILLELUND<sup>1, 2</sup> AND REUBEN LASKER<sup>3</sup>

## ABSTRACT

A variety of marine copepods have been shown to fatally injure or capture and ingest young anchovy larvae in the laboratory. *Labidocera jollae*, *L. trispinosa*, and *Pontellopsis occidentalis* (family Pontellidae), species common to surface waters of the California Current, are effective predators of larval fish. The copepods can be attracted by the vibrations of the larval tail beat and react by biting or capturing the fish larvae. Cruising speeds for these copepods varies from 1.5 to 4 body lengths per second which, coupled with continuous swimming behavior, results in extensive searching by the copepod for prey. In laboratory experiments, when the ratio of larval fish prey to *L. jollae* female individuals was low (<10:1 in 3500 ml), all of the larvae were killed in 24 hr where "killing" refers to both capture-ingestion and biting resulting in a fatality. If the ratio was higher, killing increased but rarely reached 100% mortality of the larvae. *L. trispinosa* males and females never killed all the larvae offered to them in 24 hr in 3500 ml although more larvae were killed as the number offered was increased. Increased swimming and escape ability developed as anchovy larvae became older and were not caught or bitten as effectively as younger ones by copepods. However, killing of larvae by *P. occidentalis* was unaffected by the age of the larvae up to 3.5 days old.

When *Artemia salina* nauplii were substituted for larval fish as prey for *L. trispinosa*, the amount of grazing was proportional to the ratio of nauplii to copepods. If the number of *Artemia* nauplii was less than 11-14/liter per copepod in 3500 ml all the nauplii were killed in 24 hr. When the density of nauplii was increased, more were killed but never all of them. In experiments where nauplii and yolk-sac larvae were offered together as prey the mortality of the larvae due to predation declined in proportion to the increase in the number of nauplii provided.

Caloric requirements were calculated from oxygen consumption measurements and showed that only 1 to 4 anchovy larvae are required per day per copepod to satisfy the metabolic needs of *Labidocera*, depending on the species and the sex. This number is far less than can be killed or captured if the density of larvae is high enough.

In large (140 cm) vertical cylinders larvae and *L. trispinosa* were distributed within 25 cm of the surface in the dark. Data are presented which show that *L. trispinosa* and anchovy larvae also co-occur in the upper few meters under the surface of the sea. This is probably also true for *P. occidentalis* and *L. jollae*. No data are yet available on the relative density of predatory copepods and fish larvae where they co-occur or their possible predator-prey interactions in the sea.

Huge mortalities of larval fish are known to occur in the sea. From the time of Hjort (1914) these have been attributed mainly to the lack of the proper food when the larvae begin to feed (see review by Blaxter, 1969). Undoubtedly other biotic and abiotic factors are also involved

in larval fish mortality, but comparatively little work has been done to measure their effect. Among the possible causes of larval-fish mortality, predation by other zooplankters may be an important factor. Freshwater aquarists have known for some time that copepods must be eliminated from fish rearing tanks or high mortalities of young larvae or fry will occur (Davis, 1959). Lillelund (1967) reviewed the literature pertaining to predation by freshwater copepods on fish larvae and described the predatory behavior of cyclopoid copepods as he observed them

<sup>1</sup> Institut für Hydrobiologie und Fischereiwissenschaft der Universität Hamburg, 2 Hamburg 50, Olbersweg 24, Germany.

<sup>2</sup> This research was supported in part by a Grant from the Deutsche Forschungsgemeinschaft.

<sup>3</sup> National Marine Fisheries Service, Fishery-Oceanography Center, La Jolla, Calif. 92037.

in the laboratory. Zooplankters in general and copepods in particular have been seen to devour marine fish larvae. For example, in an early study on the rearing of marine fish, Garstang (1900) noted that the harpacticoid copepod *Idya furcata* (= *Tisbe furcata*) was a larval-fish predator. Subsequently Lebour (1925) from her examination of living marine plankton, concluded that a variety of zooplankters eat fish larvae and noted that "many jellyfishes and *Pleurobrachia* besides *Sagitta* and *Tomopteris* will readily eat small fishes." Lebour also illustrated the capture of an anglerfish larva (*Lophius piscatorius*) by the copepod *Anomalocera pattersoni* (family Pontellidae).

Despite this information on the predatory behavior of copepods, there is virtually no behavioral information available on the ability of marine copepods to capture and ingest or fatally injure fish larvae, although many marine copepods are known to be carnivorous (Gauld, 1966) and other incidental reports of copepods predatory on marine fish larvae have been made (Wickstead, 1965; Petipa, 1965). Furthermore, the possible importance of predation on fish larvae as it affects the determination of year class strength through larval fish mortality has been generally ignored, probably because of the lack of pertinent quantitative laboratory and field information.

In this study we present the results of experiments designed to measure quantitatively the ability of three pontellid marine copepods, *Labidocera trispinosa*, *L. jollae*, and *Pontellopsis occidentalis*, to capture or fatally injure larvae of the northern anchovy, *Engraulis mordax*, an important commercial fish of the California Current. The behavior of copepods and larvae which bears on the susceptibility of the latter to predation is also described in detail.

## METHODS

Copepods and anchovy eggs were captured with a 0.5-m-mouth-diameter plankton net (0.333-mm mesh) towed at the surface in coastal water off San Diego, Calif., between March and August 1970. The copepods were separated

from other plankton with a large bore pipette on shipboard, diluted with surface water in liter jars, and kept at sea water temperature (about 15° C) in an insulated chest until returned to the laboratory.

All experiments were performed in 3500-ml beakers in the dark because *Labidocera* were phototactic and attracted to the light source and *Pontellopsis* was inhibited in its attacks on larvae in the light. In an earlier study on freshwater cyclopoid copepods, Lillelund (1967) used a constant level, continuous flow device which we used also for maintaining marine copepods in good condition in the laboratory (Figure 1). However, it was more convenient to do all predation experiments in static water over a 20- to 24-hr period, since the copepods we investigated swim continuously throughout the small volume (3500 ml), obviating the need for continuously circulated water. A constant temperature of 18° C was maintained in the beakers by placing them in a running seawater bath.

Mortality of the larvae was measured by taking the difference between the number of larvae at the beginning of the experiment and those remaining alive at the end. Some mortality not associated with predation always occurred, hence control vessels containing larvae alone were always provided and the results of experiments corrected for larvae dead of other causes. In all experiments, this natural mortality never exceeded 10%.

Anchovy eggs were sorted in the laboratory according to their stage of development and newly hatched larvae were used as prey in the predation experiments. When older larvae were required they were reared according to the method of Lasker et al. (1970), except that the rotifer *Brachionus plicatilis* was substituted for snail veligers as larval-fish food (Theilacker and McMaster, in press).

Oxygen consumption measurements were made by Warburg manometry. Usually 18 to 22 copepods were put into 3 ml of seawater in a Warburg flask and oxygen uptake monitored for 8 hr at 18° C. Dry weight of individual copepods was measured with an electrobalance to  $\pm 2 \mu\text{g}$ .

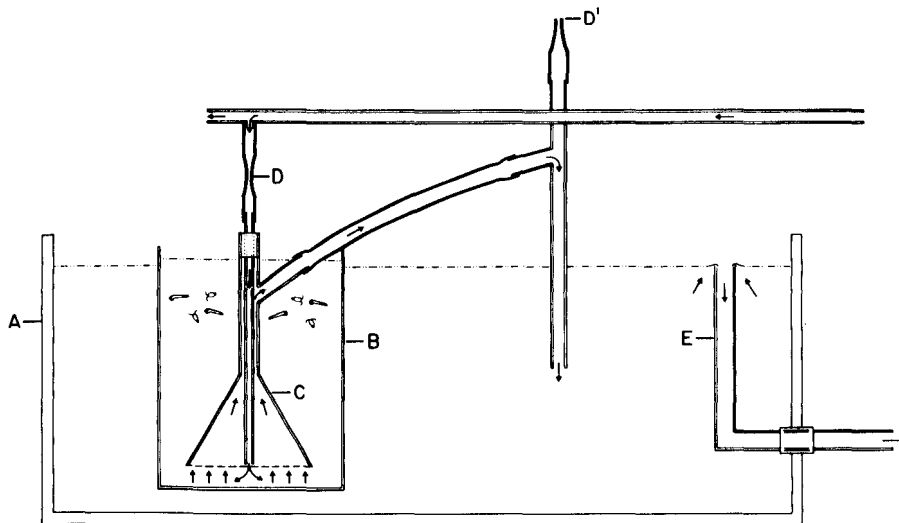


FIGURE 1.—Constant level device for maintaining copepods and fish larvae. The temperature of the 3500-ml beaker (B) was kept constant with running seawater in a water table (A) whose capacity was 610 liters. Plankton netting (0.333-mm mesh) was held over the mouth of the 500-ml funnel (C) with a section of bicycle tire tube. Rubber tubing showing constrictions as D and D' had screw-type clamps to regulate flow. E is the drain. Note that the level of seawater is higher in the beaker than in the bath. The drawing is not to scale.

### MARINE COPEPODS CAPABLE OF KILLING ANCHOVY LARVAE

Before choosing *Labidocera* and *Pontellopsis* for experimental work we tested a number of copepod species for their ability to capture or fatally injure newly hatched yolk-sac larvae of the northern anchovy. For each test, five fish larvae were isolated in 200 ml of seawater in a Petri dish at room temperature (20° C) usually with two or three copepods of a particular species to be tested. Of the local copepod species observed, the following fatally injured anchovy larvae by biting them or captured and ingested them:

*Acartia dana* and *A. tonsa*  
*Euchirella rostrata* and *E. sp.*  
*Labidocera jollae* and *L. trispinosa*  
*Pleuromamma borealis*  
*Pontellopsis occidentalis*  
*Euchaeta acuta*

*Euaetideus acutus*  
*Candacia bipinnata*

Because the two species of *Labidocera* listed above are common to waters adjacent to San Diego and were readily available, most of our experimental work was done with them. When *Pontellopsis occidentalis* became abundant, we also collected some information about its predatory behavior relative to fish larvae.

Although capture and ingestion of fish larvae was commonplace under laboratory conditions, it is rare to find a copepod with a captured fish larva in Formalin-preserved plankton. This may be the result of the Formalin preservation common on shipboard which, we have observed, usually causes copepods to drop larvae.<sup>4</sup>

<sup>4</sup> We have found that if a copepod has captured a larva it will retain the larva if both are transferred together to a slight melted depression in an ice cube with a pipette and preserved with a drop of 3% Formalin.

## SWIMMING AND FEEDING BEHAVIOR OF *Labidocera*

### REACTION TO THE LARVAL TAIL BEAT; BITING AND INGESTION OF LARVAE

We noted that individual *Labidocera* ignored motionless fish larvae or floating eggs. However, when a larva beat its tail in the close vicinity of a swimming labidoceran, the copepod swam immediately toward the beating tail and grasped the larva. The tail beat of the larva was often stimulated by the chance touch of a copepod's antenna. Figures 2a and 2b show a *L. jollae* female which caught a 3-day-old anchovy by the tail and partially ingested it. Figure 3 shows another larva caught behind the head

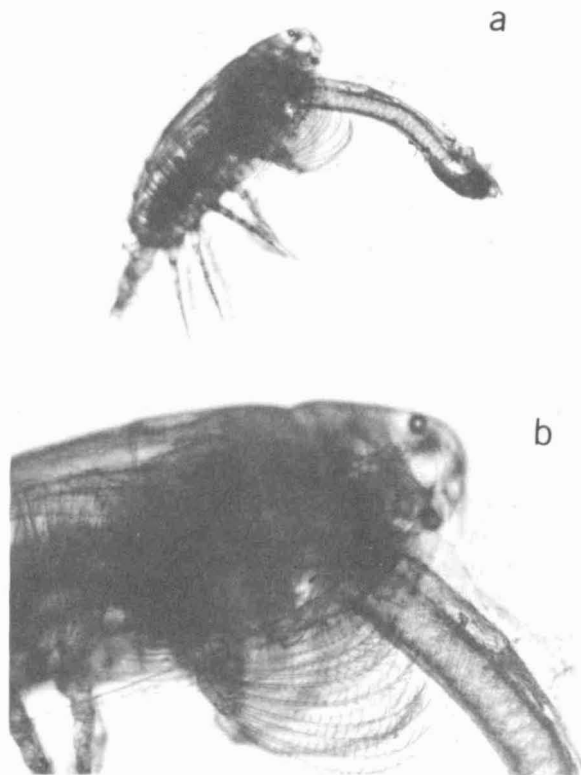


FIGURE 2.—(a) *Labidocera jollae* female, 3 mm long, and a 3-day-old anchovy larva 6 mm long which was captured by the tail and half ingested. (b) Enlargement of the head and setae of the copepod shown in 2a.



FIGURE 3.—The head of a *Labidocera jollae* female showing a newly captured 3-day-old anchovy larva caught behind the head.

by another female. Response to the larval tail beat is typical of all the copepods we have observed which attack fish larvae.

Often a copepod would capture, then drop a larva, inflicting a wound by biting the thin epithelium. The anchovy larval skin is only about 2 to 3  $\mu$  thick in the finfold and tail regions and appears to be easily injured. In every instance, a bite which damaged the larval skin resulted in the death of the larva. Therefore, in our experiments mortality due to a copepod was the result of either actual capture and ingestion of a larva or biting that resulted in damage fatal to the larva. Hence, the number of larvae reported as "killed" in an experiment is the sum of fatalities due to biting and the number of larvae actually ingested. For both sexes of each *Labidocera* species the time of ingestion of anchovy larvae varied between 6 and 25 min. In one instance an *L. trispinosa* male caught and completely consumed two larvae in 1 hr. If we increased the number of larvae to six or more in a 200-ml Petri dish containing two copepods, mortality through biting alone increased and the time during which a larva was held by a copepod varied from a few seconds to minutes. For example, an *L. jollae* female attacked six larvae in 50 min. The individual larvae were held only 10 to 60 sec and not ingested. All six larvae died subsequent to the attack.

### POSITIVE PHOTOTAXIS AND SWIMMING SPEED

*Labidocera jollae* and *L. trispinosa* are positively phototactic, and when confined to a beaker of seawater illuminated from above, concentrate at the water surface-beaker interface which is the brightest area. Copepods were induced to swim in the main body of water by wrapping the beaker with black paper with 1 cm lapped around the rim. This effectively eliminated the bright area and resulted in random swimming movements of the copepods near the surface.

Swimming distances of copepods were traced for 3 min in two dimensions on a clear acetate sheet laid over a glass plate on top of a 3.5-liter beaker. The distances were measured with a map measurer. Vertical movements were very slight, thus negligible, in these experiments because of the highly phototactic behavior of the individuals. Labidocerans can swim continually over relatively large areas in short periods of time (Vlymen, 1970). Comparative speeds for individuals are shown in Figure 4; on the aver-

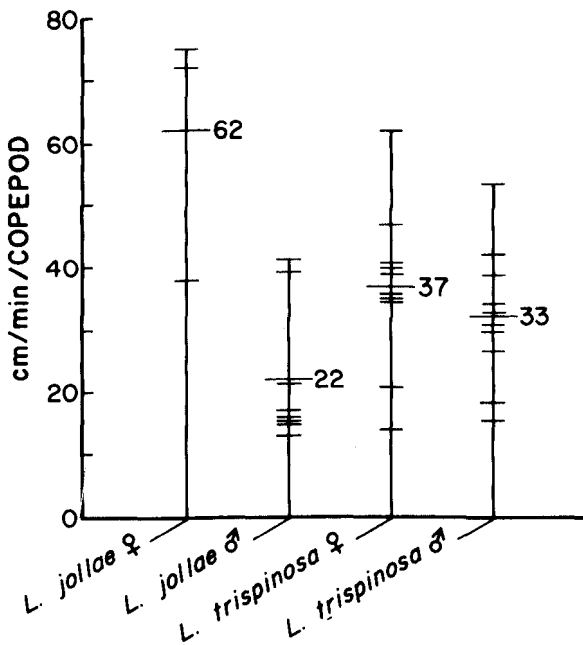


FIGURE 4.—Swimming speeds for individuals of *Labidocera*. Each small horizontal bar represents the speed of one animal; the large bar is the mean speed.

age a *L. jollae* female swims 62 cm/min (3-4 body lengths/sec) and the male swims 22 cm/min (1.5-2 body lengths/sec). Both sexes of *L. trispinosa* swim 33 to 37 cm/min (2-3 body lengths/sec). Although *L. jollae* females swim in a seemingly random pattern, the males usually swim in straight lines for a few seconds then swim in circles and cover a small area intensively.

### KILLING EFFICIENCY OF *Labidocera*

We discovered that if the ratio of anchovy larvae to *L. jollae* females was low (<10:1), all or almost all the larvae in 3500 ml would be killed within 20 to 24 hr in the dark. Two experiments were done which illustrate this. In the first, 30 anchovy larvae were confined with a variable number of *L. jollae* females (Figure 5) resulting in concentrations of larvae to copepods

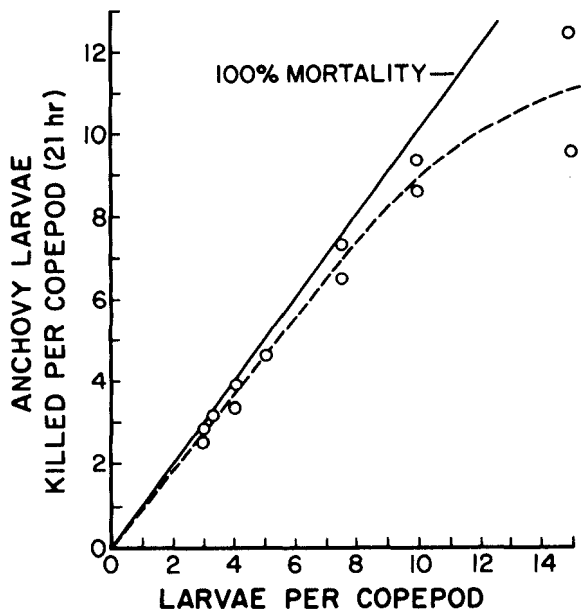


FIGURE 5.—Mortality of *Engraulis mordax* larvae, 0 to 1 day old, resulting from predation by different numbers of *Labidocera jollae* females. In each experiment 30 larvae were presented to 2 or more copepods in 3500 ml for 21 hr. Thus where 3 larvae per copepod is indicated on the abscissa, 30 larvae and 10 copepods were used; at the other extreme 15 larvae per copepod indicates 30 larvae and 2 copepods. The unbroken line is the theoretical 100% larval mortality curve.

of 3:1 to 15:1. In the other, only single *L. jollae* females were tested and the number of larvae varied to provide ratios of larvae to copepods of 5:1 to 40:1 (Figure 6). The results were

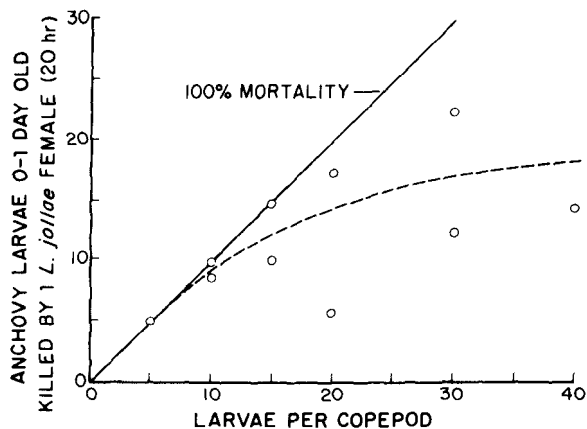


FIGURE 6.—Mortality of *Engraulis mordax* larvae, 0 to 1 day old, resulting from predation by single *Labidocera jollae* females. In each experiment 1 copepod was confined with 5 to 40 larvae in 3500 ml for 20 hr. The unbroken line is the theoretical 100% larval mortality curve.

similar in the two experiments; when the ratio was approximately 10:1 or less, it was usual for all larvae to be killed. When more than 10 larvae were available per copepod, more larvae were killed per copepod but the mortality dropped below 100%. In similar experiments two *L. trispinosa* females were tested with larvae to copepod ratios varying from 2:1 to 15:1. *L. trispinosa* females were much less efficient than *L. jollae* females and never killed all the larvae presented to them in 24 hr (Figure 7). Males of both species were similar in killing efficiency to *L. trispinosa* females. Based on these results, further predation experiments were performed over 20 to 24 hr using 30 larvae with two *L. jollae* females or five males; experiments performed with either sex of *L. trispinosa* had 30 larvae and 5 copepods. The comparative predatory ability of labidocerans is shown graphically in Figure 8. The mean number of anchovy larvae killed by *L. jollae* females was 15. *L. trispinosa* males and females had mean kills of 4 and 2

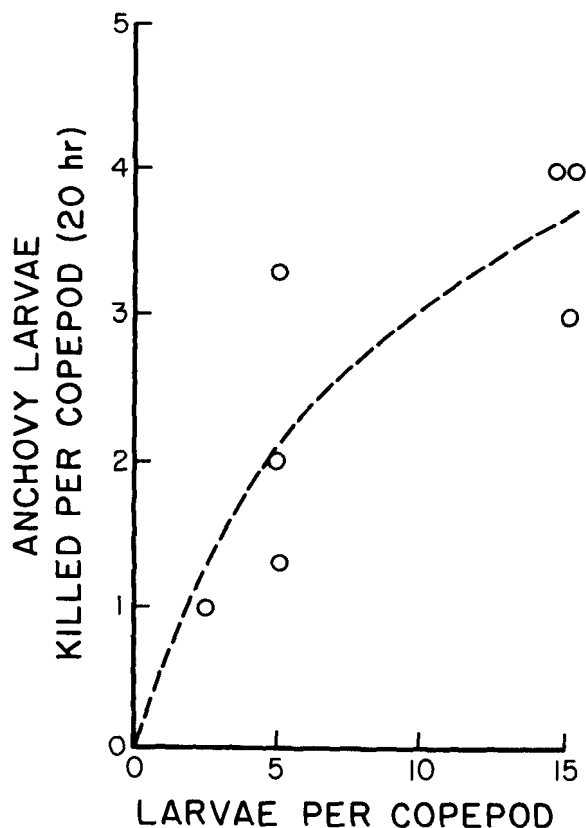


FIGURE 7.—The effect of increasing the density of larval anchovies on the predatory behavior of *Labidocera trispinosa* females. Each dot represents a separate experiment with 2 or 3 copepods and from 5 to 45 larvae.

larvae respectively in 24 hr, markedly less than *L. jollae* females. The high killing rate by *L. jollae* females reflects the longer distances and greater volume covered by them owing to their larger size. *L. jollae* females are approximately 0.2 mg dry weight, and males, 0.1 mg. Female *L. trispinosa* average about 0.1 mg dry weight; males, 0.09 mg.

#### EFFECT OF THE AGE OF THE LARVA ON PREDATION BY *Labidocera*

We noted in our experiments that *Labidocera* became less efficient in killing anchovy larvae as the larvae aged. The anchovy larva is 2.5 mm

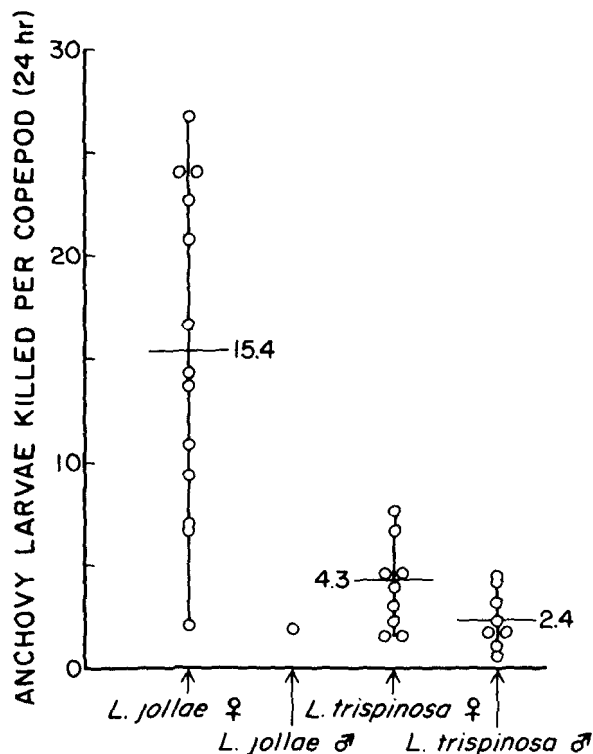


FIGURE 8.—Predation by individual *Labidocera jollae* and *L. trispinosa* under comparable prey density. Experiments were conducted in the dark for 24 hr in 3500 ml. Each circle represents the results of one experiment. The horizontal bar is the mean value for each series of experiments.

long when it hatches from the egg. Yolk-sac anchovy larvae have unpigmented eyes, lack a mouth and gills, and the yolk is invested with lipid (Bolin, 1936); when newly hatched the anchovy larva is very slightly buoyant. The newly hatched larva remains motionless most of the time at this stage and swims only sporadically. As it develops, swimming activity increases, occurring about 5% of the time at hatching to 25% on the second day and 50% by the third (John R. Hunter, personal communication). Figure 9 indicates a rapid decline in predation in the dark by *L. trispinosa* and *L. jollae* females as the larva grows older, presumably as a result of the latter's increased swimming and sensory ability. Effective predation is restricted therefore to yolk-sac larvae.

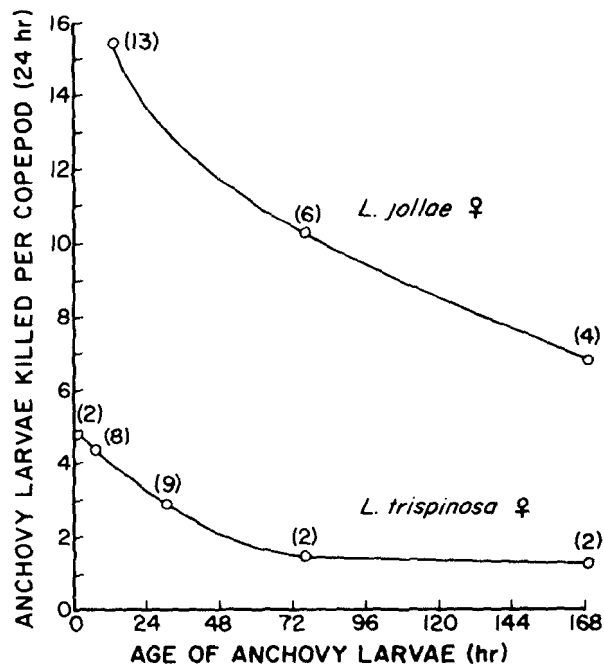


FIGURE 9.—The effect of the age of the anchovy larva on predation by *Labidocera jollae* and *L. trispinosa* females. Each open circle is the mean of the number of experiments shown in parentheses. The age of the larva at the beginning of each experiment is given on the abscissa.

#### EFFECT OF LARVAL ANCHOVY DENSITY ON *L. jollae* PREDATION

Given 2 to 3 days, single *L. jollae* females can kill by capture or biting all of 30 young anchovy larvae in 3500 ml. This is shown in a mortality curve (Figure 10) constructed from the results of a series of experiments, each of which had a number of newly hatched larvae (30 or less) at the start confined with a single *L. jollae* female. The density of larvae per unit volume (within the limits of these experiments) seemed to have little or no effect on the kill rate until there was only one larva remaining per 700 ml, when the rate due to predation by the copepod declined drastically. Our experience with predation experiments in 3500 ml volumes suggested that anchovy larvae were randomly distributed in this relatively small volume and that in the dark, at least, each *L. jollae* female could almost

### THE EFFECT OF AN ADDITIONAL PREY ON LARVAL PREDATION BY *Labidocera*

Recent experiments by Brooks (1970) with *Labidocera trispinosa* showed that this copepod selects *Artemia salina* nauplii over copepod nauplii from the plankton. She concluded that *Artemia* nauplii are selectively grazed because they are relatively less mobile, hence more easily captured.

We tested predation by *L. trispinosa* on *Artemia* nauplii and found that grazing corresponded roughly to the results we obtained when fish larvae alone were killed, i.e., up to a certain concentration all *Artemia* nauplii were killed in the experimental container in the dark over 24 hr. Survivors were found only if the number of nauplii exceeded 11-14 nauplii/liter/copepod. As the density of nauplii was increased more were killed. This result was the same whether experiments were performed in 3500-ml beakers or in 200-ml Petri dishes (Figure 11).

When *Artemia* nauplii in various concentrations and 30 anchovy larvae were offered together to five *L. jollae* males or five *L. trispinosa* males or females, larval mortality decreased in

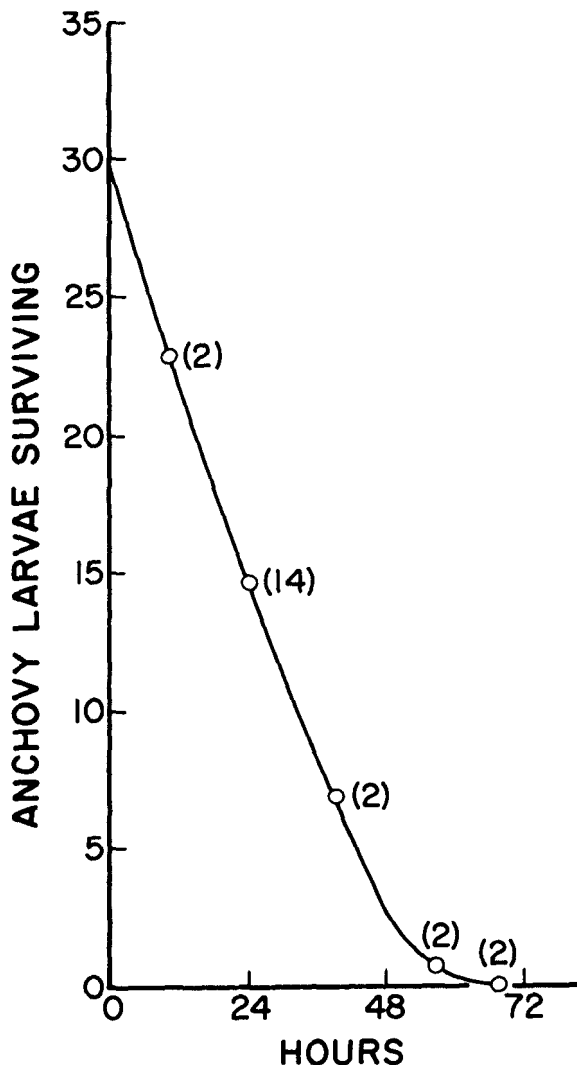


FIGURE 10.—Survival of 0- to 1-day-old anchovy larvae in the presence of a single *Labidocera jollae* female. The curve is a composite from a series of experiments in 3500 ml starting at different larval densities per copepod where the time was noted after the capture of a number of larvae. The numbers in parentheses indicate the number of experiments ending at each point.

completely search half this volume in 24 hr, resulting in continuing random contact with and killing of most, although not all, of the suspended larvae when two or more *L. jollae* females were present.

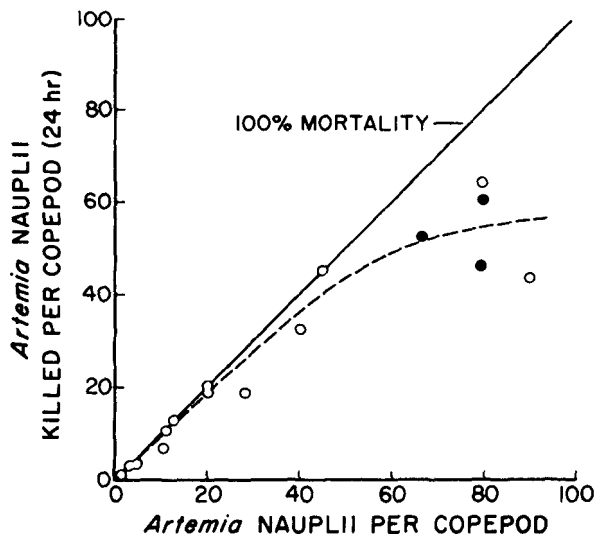


FIGURE 11.—Mortality of *Artemia* nauplii due to *Labidocera trispinosa* female predation at different densities of nauplii per copepod. Closed circles indicate experiments done in 200-ml Petri dishes.



proportion to the number of *Artemia* nauplii present. The results of these experiments are shown in Figure 12. There was a 50% decrease in mortality of larvae with *L. trispinosa* females, *L. jollae* males, and *L. trispinosa* males when the nauplii concentration was approximately 220, 150, and 100 nauplii/liter, respectively. The decrease in larval mortality is accentuated if *Artemia* nauplii are offered to *Labidocera* when older larvae are present. Fewer *Artemia* nauplii need to be present to depress the predation mortality on older larvae (Figure 13). The ease with which *Labidocera* can capture *Artemia* may make it less likely that fish larvae will be attacked. As the larvae age, this effect is compounded since it has become even more difficult to catch larvae and hence relatively less taxing for the copepod to take *Artemia* nauplii.

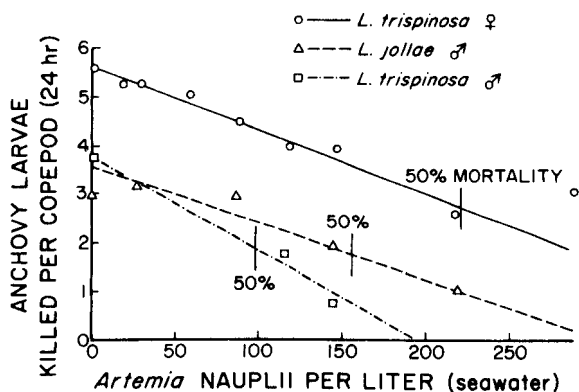


FIGURE 12.—Predation by *Labidocera jollae* males and both sexes of *L. trispinosa* on anchovy larvae when *Artemia* nauplii were also available to the copepods. Fifty percent reduction in larval mortality occurred when *Artemia* nauplii numbered 220/liter with *L. trispinosa* females, approximately 150/liter with *L. jollae* males and 100/liter with *L. trispinosa* males.

### CALORIC REQUIREMENT OF *L. jollae* AND *L. trispinosa*

We noted that the vigor of *Labidocera* individuals declined with time if they were not fed or fed only *Artemia* nauplii. For example, after 1 week in the laboratory the activity of copepods fed only *Artemia* was diminished so that a copepod's ability to capture larvae was about one-

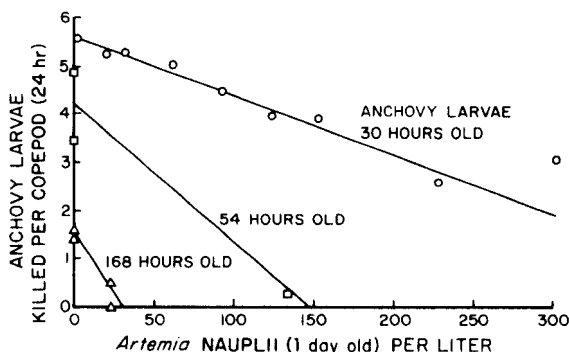


FIGURE 13.—The effect of the age of the anchovy larva and the addition of an extra prey (*Artemia* nauplii) on larval mortality due to predation by *Labidocera trispinosa* females.

half that of a newly caught copepod. *Labidocera* died after 2 or 3 days of starvation. This was preceded by a decrease in swimming activity which was reflected in a lower respiration rate and dry weight of individuals. In Figure 14 we give comparative respiration rates and dry weights for *L. jollae* females (a) newly caught, (b) larval-fish fed, and (c) starved for 2 days. These results show an enhanced respiratory rate for fed and presumably healthier animals and a drastic decline due to short term starvation.

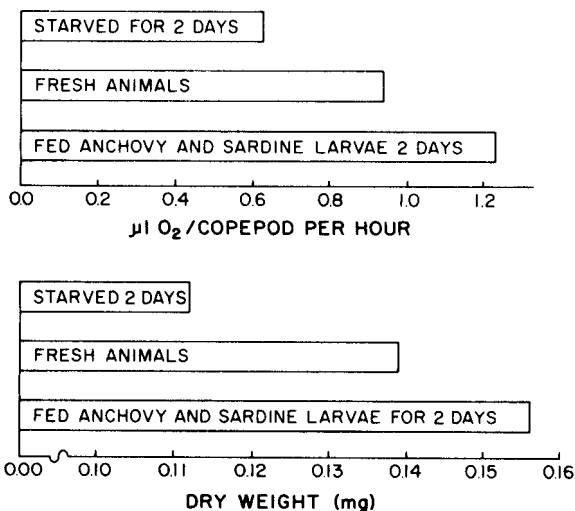


FIGURE 14.—Comparative oxygen consumption and individual dry weight measurements of *Labidocera jollae* females under starved and well-fed conditions at 18° C.

Further comparisons of respiration rates were made only between newly caught and larval-fish fed *L. jollae* females, males, and *L. trispinosa* males and females (Figure 15). In each instance there was an increase in respiratory rate after feeding on anchovy larvae. The caloric requirement of *Labidocera jollae* and *L. trispinosa* was calculated from oxygen con-

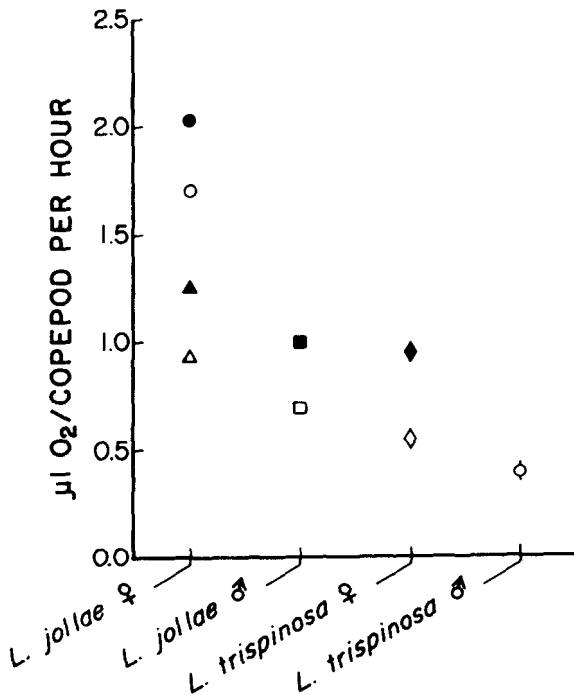


FIGURE 15.—Oxygen consumption by newly caught (open symbols) and larval-fish fed (closed symbols) labidocerans at 18° C.

sumption data to estimate the number of larvae which could sustain the copepod in a healthy condition at 18° C (Table 1). In spite of *Labidocera's* ability to kill large numbers of fish larvae or *Artemia* in a day, actual caloric requirements may be met by ingestion of only a few (1-4) larvae or nauplii (4-16).

#### PREDATION ON FISH LARVAE AND *Labidocera* BY *Pontellopsis occidentalis*

*Pontellopsis* adults and copepodites stages IV and V can kill by biting or capture and ingestion of anchovy larvae; older larvae (up to 3.5 days old in our test) were killed by this copepod as easily as yolk-sac larvae. Each stage V copepodite killed three larvae per day on the average and each adult female killed about 11 per day (Figure 16). We observed also that *Pontellopsis* attacked and ate *Labidocera* spp. when they were confined to the same beaker.

#### CO-OCCURRENCES OF PREDATORY COPEPODS AND FISH LARVAE IN THE SEA

In the laboratory we noted that 30 to 40% of the *Labidocera* individuals resided in the upper 5 to 25 cm of 140-cm-deep, 17.5-cm-diameter tanks—both in darkness and in the light. Yolk-sac anchovy larvae occupied a similar stratum because they are slightly buoyant. In the sea, spawning by anchovies occurs mostly in the upper 10 m but occasionally may occur relatively deeply (Ahlstrom, 1959). This prompted us to

TABLE 1.—Oxygen consumption and the calculated number of anchovy larvae required to sustain the respiratory requirements of *Labidocera jollae* and *L. trispinosa* per day at 18° C. The oxy-caloric equivalent of 1  $\mu$ liter of oxygen is 0.005 calorie. Yolk-sac anchovy larvae weigh 0.01 mg dry weight and contain 0.054 calorie. These data assume 100% digestive assimilation and an  $RQ = 0.8$  for each copepod. Approximately four *Artemia* nauplii are calorimetrically equivalent to one anchovy larva.

Species and sex	$Q_{O_2}$ $\mu$ liter/mg dry weight/hr	$O_2$ consumption $\mu$ liter/copepod/hr	Average dry weight per copepod (mg)	Anchovy larvae required/day
<i>Labidocera jollae</i> ♀	11	2.0	0.19	4
<i>L. jollae</i> ♂	11	1.0	0.095	2
<i>L. trispinosa</i> ♀	7.7	0.96	0.12	2
<i>L. trispinosa</i> ♂	4.3	0.40	0.092	1

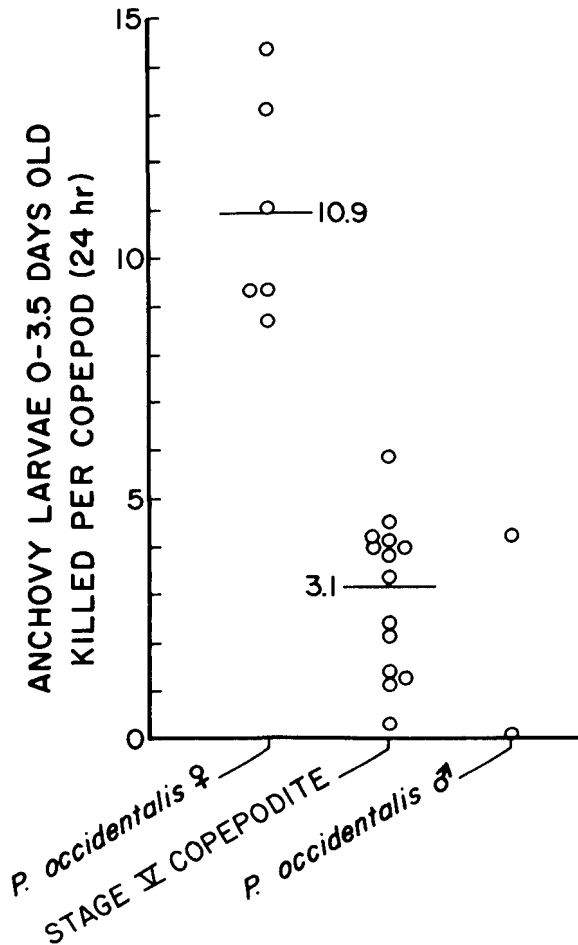


FIGURE 16.—Predation by *Pontellopsis occidentalis* on anchovy larvae 0 to 3.5 days old. Each horizontal line indicates the mean value of the experiments shown with open circles; 30 larvae were provided to 1 to 6 copepods in 3500 ml at the beginning of each experiment.

measure the rate of ascent of anchovy eggs to determine the maximum depth at which spawning could occur and yet insure the presence of yolk-sac larvae at the surface. In La Jolla seawater, salinity 33‰ and 17° C, anchovy eggs rise 5 cm/min or 3 m/hr. Thus, with time from spawning to hatching at 2 days, eggs spawned as deep as 144 m would hatch at or near the surface of the ocean, although spawning that deeply is rare (Ahlstrom, 1959). During development and, as they use up their yolk, an-

chovy larvae become almost neutrally buoyant and start to sink very slowly in laboratory containers. Even so, after 2 days of development, 50% of the laboratory-reared larvae were still above the 30 to 40 cm depth.

Ahlstrom (1959) reported closing-net captures of anchovy larvae at a variety of stations and depths in the California Current off California and Baja California. He has kindly provided us with length distributions of anchovy larvae taken at two stations, a night station, 5206-90.28, where over 500 larvae were taken, and a day station, 5504-120.50, where over 5000 larvae were captured. The length of the larva is roughly indicative of its age (Kramer and Zweifel, 1971), and we have tabulated the depth distribution of anchovy larvae at these stations by length and age (Table 2).

The depth distributions by age and length of anchovy larvae indicate that 50% or more of anchovy larvae up to 3 weeks old are above 10 m in depth. Fifty percent of the youngest class, 3 to 4.5 mm and 1 week old or less, were above 3.5 m during the day, and were slightly more than 2 m deep in the night. Ahlstrom's data also suggest that larvae of the Pacific sardine, *Sardinops caerulea*, Pacific mackerel, *Scomber japonicus*, and jack mackerel, *Trachurus symmetricus*, all pelagic fish of the California Current, may be similarly distributed.

Labidocerans are not diurnal vertical migrants and seem to be confined near the surface of the sea. Oblique tows with a plankton recorder (Longhurst et al., 1966) were taken in an area where *Labidocera trispinosa* and anchovy larvae are known to occur. The results are shown in our Table 3. The volume of each discrete sample at a particular depth was small (4-6 m<sup>3</sup>) and the zeros may simply indicate relatively low abundance below the surface. Both tows, taken a day apart in close proximity to one another, showed that *L. trispinosa* was mainly present above 10 m, as were anchovy larvae. Simultaneously 10-min neuston tows were taken which filtered 463 m<sup>3</sup> no deeper than 30 cm at the surface of the sea (Table 4). The large number of *Labidocera trispinosa* and anchovy larvae in these tows suggests that the upper 30 cm of the ocean

TABLE 2.—Depth distribution of anchovy larvae by age and length at two stations, 5504-120.50 (day) and 5206-90.28 (night); collected by Ahlstrom (1959).

Average depth of catch (m)	Length and age of larvae							
	3.0-4.5 mm 0-7 days old		5.0-7.5 mm 8-14 days old		8.0-11.0 mm 15-21 days old		11.5+ mm 21+ days old	
	no.	% of total	no.	% of total	no.	% of total	no.	% of total
Station 5504-120.50 (day)								
2	515	42	505	17	283	37	64	36
7	317	26	820	28	216	28	52	29
18	138	11	596	20	78	10	31	17
27	96	8	138	5	31	4	5	3
44	105	9	509	17	62	8	19	11
60	61	5	324	11	95	12	7	4
74	1	0	70	2	1	0	0	0
Total	1233		2962		766		178	
Station 5206-90.28 (night)								
2	65	50	52	40	44	20	35	36
7	54	42	48	37	73	34	25	26
17	10	8	15	15	50	23	14	14
27	0	0	15	12	49	23	23	24
Total	129		130		216		97	

TABLE 3.—Vertical distribution of *Labidocera trispinosa* adults and anchovy larvae at 32°55.1' (Station 1 at 0100) June 3, 1970, and 32°45.8' (Station 2 at 2340) June 3. Volume of water filtered for each discrete depth sample in oblique tows were: Station 1, 6 m<sup>3</sup>; Station 2, 4.35 m<sup>3</sup>. No *L. jollae* or *Pontellopsis occidentalis* individuals were caught in these samples.

Depth (m)	Number of <i>L. trispinosa</i> adults	Number of <i>Engraulis mordax</i> larvae
Station 1		
0-3	13	5 (7-11 mm long)
3-7	0	1
7-15	0	1
15-60	0	0
Station 2		
0-2	4	17 (7-10 mm long)
2-7	17	11 (9-10 mm long)
7-15	2	1
15-25	0	1
25-60	0	0

is the area which should be examined for further elucidation of this predator-prey relationship.

The observations presented in this paper indicate that marine copepods may be effective predators on larval fish, at least in the sense that a predator need not devour its prey but is equally effective if it injures it mortally. Young pelagic fish larvae are particularly susceptible to biting zooplankters because they have an extremely thin skin and are unable to survive once the skin is punctured. Pontellid copepods, in particular *Labidocera* spp., appear to have a well-developed

TABLE 4.—Numbers of *Labidocera jollae*, *L. trispinosa*, *Pontellopsis occidentalis*, and *Engraulis mordax* eggs and larvae taken in 463 m<sup>3</sup> within 30 cm of the surface simultaneously with the oblique tows described in Table 3.

Species	Station 1	Station 2
<i>L. trispinosa</i>	1152	6400
<i>L. jollae</i>	336	104
<i>P. occidentalis</i>	112	128
<i>E. mordax</i>	226	36
	(5-10 mm long)	(10-12 mm long)

vibration sense which serves to orient the copepod toward its swimming prey although this is preceded by random searching. A fish larva with its beating tail provides the right stimulus to the copepod to initiate an attack when the latter is close enough to detect the beat.

We have called attention to the vertical distribution of *Labidocera* in the sea and the apparent co-occurrence of larval anchovies in the same depth stratum. Unfortunately, quantitative data on the density of predatory copepods or other zooplankters as related to fish larvae have yet to be made. It is our opinion that pontellid copepods and fish larvae are concentrated in the upper few meters and probably the upper few centimeters of the sea and that observations of this oceanic fine structure may reveal densities of fish larvae to copepods which would implicate predatory copepods (and possibly other zooplankters) as important causes of larval fish mortality.

## ACKNOWLEDGMENTS

We thank James E. Smith and Donald L. Seibert of the Scripps Institution of Oceanography and Michael McMaster, Mrs. Gail Theilacker, and Raymond E. Shuey of the National Marine Fisheries Service, Fishery-Oceanography Center, for their generous assistance during this study.

## LITERATURE CITED

- 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.
- BLAXTER, J. H. S.  
1969. Development: Eggs and larvae. In W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 3, p. 177-252. Academic Press, New York.
- BOLIN, R. L.  
1936. Embryonic and early larval stages of the California anchovy. Calif. Fish Game 22: 314-321.
- 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, p. 56-74.
- DAVIS, C. C.  
1959. Damage to fish fry by cyclopid copepods. Ohio J. Sci. 59: 101-102.
- GARSTANG, W. R.  
1900. Preliminary experiments on the rearing of sea-fish larvae. J. Mar. Biol. Assoc. U.K. 6: 70-93.
- GAULD, D. T.  
1966. The swimming and feeding of planktonic copepods. In H. Barnes (editor), Some contemporary studies in marine science, p. 313-334. Allen and Unwin Ltd., London.
- HJORT, J.  
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Cons. Perm. Int. Explor. Mer, Rapp P.-V. Réun. 20: 1-228.
- KRAMER, D., AND J. R. ZWEIFEL.  
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest., Rep. 14: 84-87.
- LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.  
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5: 345-353.
- LEBOUR, M. V.  
1925. Young anglers in captivity and some of their enemies. A study in a plunger jar. J. Mar. Biol. Assoc. U.K. 13: 721-734.
- LILLELUND, K.  
1967. Experimentelle Untersuchungen über den Einfluss carnivorer Cyclopiden auf die Sterblichkeit der Fischbrut. Z. Fisch. Deren Hilfswiss. 15: 29-43.
- LONGHURST, A. R., A. D. REITH, R. E. BOWER, AND D. L. R. SEIBERT.  
1966. A new system for the collection of multiple serial plankton samples. Deep-Sea Res. Oceanogr. Abstr. 13: 213-222.
- 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. No. 72.
- THEILACKER, G. H., AND M. F. McMASTER.  
In press. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol.
- VLYMEN, W. J.  
1970. Energy expenditure of swimming copepods. Limnol. Oceanogr. 15: 348-356.
- WICKSTEAD, J. H.  
1965. An introduction to the study of tropical plankton. Hutchinson and Co., London, 160 p.