BEHAVIOR AND SURVIVAL OF NORTHERN ANCHOVY
ENGRAULIS MORDAX LARVAE

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ABSTRACT
The object of this review was to provide an understanding of the behavioral factors that determine whether or not larvae of the northern anchovy, *Engraulis mordax* Girard, will starve. The swimming and feeding behavior of anchovy larvae is described and related to temperature, developmental stage, characteristics of the food and food distribution and to other variables. The principal sources of this information were published and unpublished observations of larvae cultured in the laboratory.

INTRODUCTION
Predation and starvation are considered by most specialists to be the dominant factors influencing survival of larval fishes. In the Southwest Fisheries Center (SWFC) of the National Marine Fisheries Service (NMFS), we have concentrated on the problem of starvation although some studies have been made on predation (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974). The object of this review is to provide an understanding of the behavioral factors that determine whether or not an anchovy larva will starve. The swimming and feeding behavior of anchovy larvae is described and related to temperature, developmental stage, characteristics of the food and food distribution, and to other variables. The principal source of this information is observations of larvae cultured in the laboratory. Experimental design will not be given where information is already published, but a brief description will be given for new data. For information on laboratory culture of northern anchovy, the reader should consult Lasker, Feder, and Theilacker (1970), Theilacker and McMaster (1971), and Hunter (1976).

EGGS AND YOLK-SAC LARVAE
In southern California the major spawnings of anchovy occur in February and March but some spawning continues throughout the year (Lasker and Smith, 1977). During the height of the spawning season, temperatures in the upper 10 m vary from about 13° to 16° C.

Eggs are transparent oblate spheroids about 1.34 mm long and 0.66 mm wide, and are neutrally buoyant. Larvae hatch in 89.8 hrs at 13° C and at 59.8 hrs at 16° C (Zweifel and Lasker, 1976). The larvae at hatching averages 2.86 ± 0.028 mm standard length and weigh 0.0246 ± 0.0014 mg dry weight, of which 53% is yolk. At hatching larvae are nearly transparent, have no functional eye or jaw but olfactory and lateral line organs are developed (C. O'Connell, National Marine Fisheries Service, La Jolla, pers. comm.). After hatching, larvae are inactive; over 90% of the time they float motionless in the water usually with head directed downward. About once a minute they execute a burst of intense swimming, lasting about 1 to 2 sec. These bursts of activity may have a respiratory function as they occur regularly and increase in frequency when oxygen concentrations are below saturation (Hunter, 1972). The larvae have no functional gill filaments at this time so movement could serve to increase the transport of gases across the integument.

Owing to their inactivity, small size, and lack of a functional visual system, it appears anchovies in the yolk sac stage must be extremely vulnerable to predation. Indeed, Lillelund and Lasker (1971) showed that the copepod *Labidocera trispinosa* were 60% successful in capturing 1 day old yolk-sac larvae whereas success decreased to 11% for larvae that had begun to feed (4 days old). These authors also point out that success of capture seems to be correlated with the degree of activity of the larvae.

Development of a functional visual system and jaw, and nearly complete absorption of yolk coincides with the onset of feeding and a major increase in locomotor activity. Typically, larvae average about 4.0 mm standard length (SL) at this time but means vary from 3.8 to 4.4 mm depending on average egg size. The mean size of anchovy eggs varies seasonally, with larger eggs being more common in the winter (February and March) and small eggs occurring more frequently during the summer months (Lenarz and Hunter, MS). This seasonal variation would be expected to produce a seasonal trend in average larval size at first feeding. A larger size at first feeding would probably be of greater adaptive advantage in the winter months when cold temperatures produce slower growth rates than in the summer when it is more rapid.

SWIMMING BEHAVIOR OF POST YOLK-SAC LARVAE
Knowledge of swimming abilities of larval fish is essential for an understanding of survival. For example, the cruising speed of a larva will determine the frequency it will encounter prey, and determines in part whether or not a larva will remain in areas

where prey are concentrated; also swimming accounts for most of the larva's energy expenditure. Burst speed capabilities determine in part the ability of a larva to avoid predation and plankton nets.

From the onset of feeding through adulthood, anchovy swimming consists of two types: continuously propagated caudally directed waves typical of most fishes that swim by caudal propulsion, and a series of bursts of motion consisting of a single tail beat followed by a rest or a glide. The beat and glide mode of swimming or intermittent swimming is used for cruising, whereas the other mode, continuous swimming, is used for high speed bursts. Nearly all swimming is intermittent in adult anchovy and in larvae after feeding begins. Continuous swimming in larvae is used for occasional bursts lasting usually less than a second and with a frequency of about 12 bursts/hour, less than 1% of the time devoted to swimming (Hunter, 1972).

Vlymen (1974) developed a model for energy expenditure of larval anchovy during intermittent swimming from theoretical considerations and analysis of cine photographs. He found that larvae of 14 mm standard length expended 5×10^{-3}cal/hr, and had a metabolic efficiency of 25%. This efficiency was high when compared to values obtained for larger fish and led Vlymen to speculate that this may have given anchovy larvae a competitive advantage over the Pacific sardine, *Sardinops caerulea*. It should be mentioned parenthetically, that although intermittent swimming may be more efficient, it is slow, and consequently the volume of water that can be searched for prey is less than that of a fish that swims in the continuous mode.

Swimming speeds of larval anchovy have been measured in various ways: plotting positions from cine photographs; counting tail beat frequencies; and visual approximation of larval position against a grid. For a temperature of 17° to 18° C the mean swimming speed of a 5 mm larval anchovy was 3.0 mm/sec using the photographic technique, 4.1 mm/sec using counts of tail beat frequency (Hunter, 1972); and 4.5 mm/sec when a grid was used (Hunter, unpublished data). These data set a range of cruising speeds of 0.6 to 0.9 body lengths/sec for anchovy larvae at 17° to 18°C. Maximum bursts of speed, on the other hand, appeared to be about 15 body lengths/sec but swimming in this case is continuous rather than intermittent and can be sustained for only brief periods (Hunter, 1972).

Although it is clear that larval size is a significant determinant of speed, the methods used to measure speeds of larvae, however, are not sufficiently accurate to establish the correct length coefficient. To do this larvae must be subject to known water speeds. Consequently, to adjust for size, the convention of dividing speed by length has been followed (Bainbridge, 1958), but it should be recognized that the true coefficient is probably less than unity (Brett, 1965). In addition to size, cruising

speeds are influenced by many other variables, thus the above averages can be considered only to be general estimates.

Temperature, age, food distribution, feeding activity, and condition of the larva all influence swimming speed. Speed declines in starving larvae until they remain almost motionless, floating head down in the water. Food distribution may have several effects on swimming speed. In dense patches of food (*Gymnodinium splendens*) speed declines by about 60%. On the other hand, at any given density the larvae that are feeding at the highest rate are generally the ones that are swimming the fastest (Hunter and Thomas, 1974). This latter effect might be caused by the physical state of the larvae. For example, within a given food density the healthy and presumably better fed larvae are the most active and feed most often.
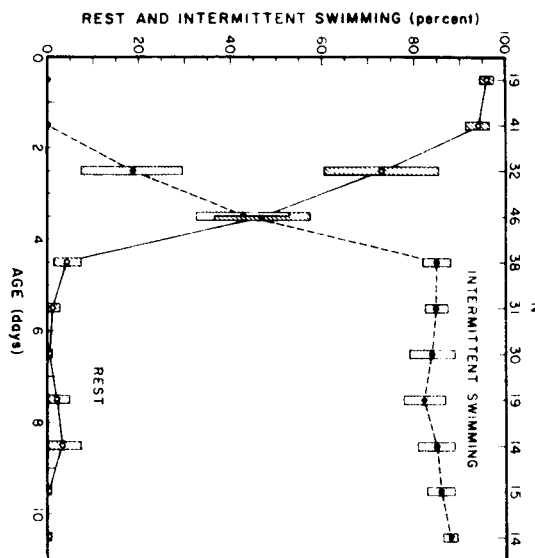

FIGURE 1. The proportion of time spent in rest and intermittent swimming by anchovy larvae during the first 10 days of larval life at 17° to 18° C (from Hunter, 1972). Points are the mean percent ± 2 X SE; the number of observations (N) is given at top of graph.

Temperature affects rate of development which, in turn, affects the age at which the transition occurs between occasional bursts of swimming typical of yolk-sac larvae to the almost continuous intermittent swimming typical of larval and adult anchovy. This transition is shown for the temperature range of 17° to 18° C, and indicates that by age 5 days the proportion of time spent in intermittent swimming becomes nearly constant (Figure 1). More recent data show how temperature determines the time at which this transition is made. The very low swimming speeds at 13° C (Figure 2) indicate that the transition did not begin at age 4 days, whereas

the transition had started in larvae in 14° C water, and was almost complete in 4 day larvae in 17.5° C water. By age 6 days, larvae at all temperatures have completed the transition. The data indicate a direct temperature effect on swimming behavior as well. At ages 8 to 12 days larvae reared at temperatures less than 16° C appear to swim at a slower speed than those above 16°C.
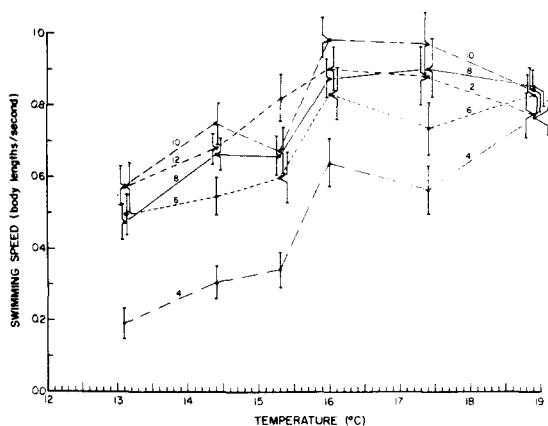

FIGURE 2. Swimming speed in body length/sec for anchovy larvae reared at five different temperatures. Speed was measured at ages 4, 6, 8, and 12 days by visual approximation of larvae against a grid; points are means ± 2 X SE (bars); numbers are age in days. All larvae were reared on *Gymnodinium splendens.*

In summary, size, temperature, food distribution, and starvation all influence cruising speeds. It is the complex interaction of these variables that determine whether or not a larva will find food and survive. Cooler temperatures cause a reduction in activity and therefore, in metabolic demand; on the other hand, cold temperatures result in slower growth and greater exposure to predation during the larval phase.

ENERGY SPARING MECHANISMS

Mechanisms that reduce activity and thereby conserve energy are probably important in the survival of larval fishes. Two possible mechanisms have been mentioned previously in this report: the reduction in activity associated with high food density; and the reduction in activity associated with colder water temperatures.

Another possible energy-sparing mechanism was proposed by Uotani (1973) for a Japanese anchovy and sardine, presumably *Engraulis japonica* and *Sardinops melanosticta.* Uotani found that net captured larvae of both species had expanded gas bladders at night and deflated ones in the day. He proposed that inflation at night was an energy sparing mechanism. He also suggested it might be effective in reduction of predation at night.

This behavior was examined for the northern anchovy, *Engraulis mordax,* in the laboratory by measuring the width of the gas bladder at night and during the day[1]. Larvae were maintained under a 12 hr light-12 hr dark cycle without a dawn or dusk transition in illumination. The width of the gas bladder of larvae collected in the dark and in the light was measured for nine, 0.5 mm length classes for larvae 8.5 to 15.4 mm SL and statistical comparisons were made between dark and light samples for each length class using the Mann-Whitney U test (Siegel, 1956). Larvae 8.5 to 9.4 mm showed no difference in gas bladder width in the dark from the light (P = 0.78) while larvae 9.5 to 10.4 mm differed at P = 0.035, and the remaining seven length classes differed at P 0.001. Thus, the threshold larval length for filling the bladder at night occurred between 9.5 and 10.4 mm corresponding to the intersections of the regression lines for bladder width on length for larvae in the dark and light (Figure 3). In this comparison, only data from larvae collected in the middle of the day were used because a transitional period of 2 to 4 hours occurs in the morning after the onset of the light (Figure 4). The change in light intensity would be expected to be much slower for larvae in the sea than in this laboratory experiment and thus deflation of the bladder is probably not a critical problem. In the dark, larvae with inflated bladders were suspended motionless, head downward, until disturbed by the light used to see them. The bladders were frequently so distended at night that they constricted the gut, a feature noted by Uotani (1973) in field caught larvae. The most tenable explanation of diel change in bladder size is that it permits the larva to adjust to neutral buoyancy at night and thus to conserve energy. It might also be useful if it enabled the larva to remain at about the same vertical position in the water column at night.
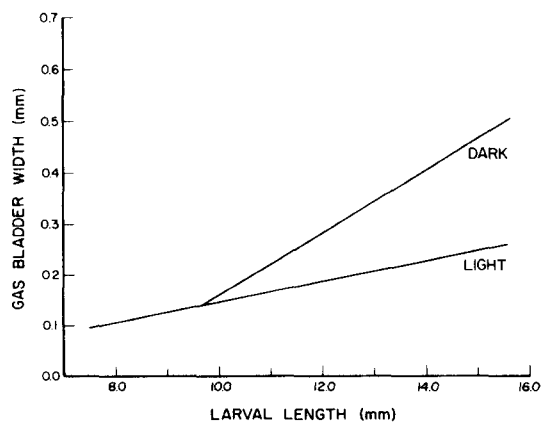
LARVAL LENGTH (mm)

FIGURE 3. Regression of width of gas bladder in the dark (Y) on larval length (X) is Y = 0.613 X —0.453 and standard error of the estimate, s_{yx} = 0.0785; the regression of width of gas bladder in light on larval length is Y = 0.203 X —0.0556 and s_{yx} = 0.038.
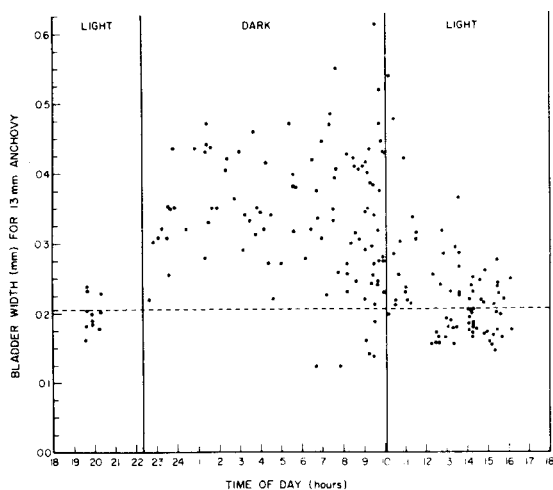
FIGURE 4. Diel change in width of gas bladder for anchovy larvae 13 mm SL. Larvae in sample ranged in length from 12.0 to 15.4 mm SL. Gas bladder width was adjusted to a common length, 13 mm, by using regression equations given in Figure 3.

FEEDING BEHAVIOR

Studies of the feeding behavior of larval anchovy provide insight into the conditions at sea that would favor starvation or growth. A complex of interacting variables determine if a larva will respond to a prey and whether or not it will find enough food to survive. Starvation, temperature, stage of development, time of day, larval size, prey size, feeding success, swimming speed, sighting range for prey, prey visibility, prey avoidance behavior, prey distribution and density may affect the amount of food ingested directly, and may affect it indirectly through interactions with other variables. Some information exists on the direct effects of some of these variables but little information exists on possible interactions.

Description of Feeding Behavior

On the average, larval anchovy first react to a prey when it is about 0.4 body length from the head of the larva. Upon sighting a prey the larva forms an S-shaped posture and advances toward the prey by sculling the pectoral fins and undulating the finfold, while maintaining the S-posture. When the prey is about 0.07 body length from its snout, the larva opens its mouth and straightens its body. This causes the body to drive forward, and the prey is ingested. The prey is maintained in the center of the binocular field while the fish is in the S-posture by slight adjustments in the position of the head and body. The entire act requires 1 to 2 seconds.

Time of Day and Satiation

Larval anchovy feed during the day and not at night, at least during the first half of larval life. Rods are not present in the retina in noticeable numbers (C. O'Connell, National Marine Fisheries Service, pers. comm.) until 20 days of age (11 mm SL). That larval anchovy feed only during the day is supported by my laboratory observations and also by field data described by Arthur (1956) who examined the stomach contents of sea-caught larvae 3 to 12 mm in length. In addition, stomach content analysis of adult anchovy also indicate that adults feed primarily during the day (Loukashkin, 1970).

In the laboratory, larval anchovy do not cease feeding once the gut is filled. Larvae with filled guts, sometimes with a fecal pellet protruding from the anus, can be seen feeding throughout the day. Thus satiation probably does not occur during the early portion of larval life, but it may occur after the larva reaches 18 to 20 mm and schooling begins. Satiation does occur in adult anchovy (Leong and O'Connell, 1969).

Starvation

Feeding declines with starvation until a point is reached where larvae are unable to feed sufficiently to maintain life although they may live a number of days after they reach this point. First feeding larvae reach this point 2.5 days after yolk absorption (Lasker, et al, 1970). At metamorphosis, on the other hand, anchovy are able to withstand starvation for over 2 weeks and survive when given food (Hunter, 1976). Thus, there exists a dramatic change in the ability to withstand starvation over the larval period ranging from 2.5 days for first feeding larvae to 2 weeks for newly metamorphosed anchovy (35 mm SL).

Temperature

The effect of temperature on feeding behavior in anchovy 4 to 12 days old was recently examined. For this survey I selected data on feeding behavior from rearing experiments conducted at a variety of temperatures in which the lengths of the larvae were about the same. Owing to different growth rates at different temperatures the ages of larvae are different but all were grown at high food densities in excess of 200 *Gymnodinium splendens* cells per ml. Only larvae greater than 4.5 mm or larger are considered because the stage of development influences feeding rate for smaller larvae and developmental stage is also a function of temperature. Feeding activity was measured by counting the number of feeding strikes executed by a larva in 5 minutes. Observations were made on 3 to 4 groups of larvae at each temperature and usually 15 observations per group per day. The data show that for larvae of similar length, and thus similar weight,

feeding rates are higher for higher temperatures (Table 1). Thus the effect of temperature on feeding coincides with that on activity, indicating increased metabolic demand at higher temperatures. The feeding rates observed are, in general, quite high at all temperatures. This is because the larvae were feeding on a prey, *Gymnodinium splendens*, that is less than optimal in size, a point I shall return to in more detail later.

TABLE 1

Average Feeding Strikes per Minute and Mean Length of Anchovy Larvae Reared on *Gymnodinium splendens* at Various Temperatures.

Temp. °C	Age (days)	Length mm ± 2 × SE *	Feeding strikes/min ± 2 × SE*	Age (days)	Length mm ± 2 × SE *	Feeding strikes/min ± 2 × SE*
13.1	12	4.7 ± 0.1	3.1 ± 0.6	—	—	—
14.4	10	4.6 ± 0.1	4.3 ± 0.8	12	5.0 ± 0.1	4.7 ± 0.6
15.3	10	4.6 ± 0.1	3.3 ± 0.6	12	5.0 ± 0.1	4.1 ± 0.7
16.0	8	4.8 ± 0.1	4.1 ± 0.8	10	5.0 ± 0.1	4.3 ± 0.9
17.4	6	4.5 ± 0.1	4.8 ± 1.0	8	5.0 ± 0.1	5.9 ± 0.9
18.9	6	4.8 ± 0.1	7.0 ± 1.0	8	4.9 ± 0.2	7.7 ± 1.3

* SE = Standard error.

Density and Distribution of Food

Larval anchovy feed less often at lower food densities than at higher ones. Food density, however, also alters the structure of the search pattern for food. Larvae that enter a dense patch of *Gymnodinium* reduce speed, and alter the directional characteristics of their search pattern. In a dense patch they swim directly ahead less frequently and make more 180° turns than they do when the density is lower. The result of these changes in search pattern is a reduction in the area covered while searching for food if the food is highly concentrated and an increase in area covered when it is not. In other words, larvae respond kinetically to a food distribution which results in the larvae remaining in areas where food is more dense (Hunter and Thomas, 1974).

Feeding Success

At the time of first feeding, larvae are much less successful in capturing prey than they are later in life. This pattern has been observed in herring and other larval fishes (Rosenthal and Hempel, 1970). Larval anchovy capture about 10% of the food at which they strike at the time of first feeding but this value increases to about 90% when they are 20 days old (Hunter, 1972). This observation suggests that larvae are more vulnerable to starvation at the time of first feeding than later in development.

Characteristics of Prey

The characteristics of the prey such as size, nutritional value, digestibility, visibility, avoidance behavior, and the presence of protective devices such as spines must be important elements in the survival of larval fishes. The importance of most of these characteristics to marine fish larvae have not been evaluated. There is some evidence that

digestibility may be important. For example, *Artemia salina* nauplii are ingested by herring and anchovy larvae but they fail to digest them completely and grow slowly or die when fed an exclusive diet of *Artemia* (Rosenthal, 1969; Hunter, 1976). Once a larval anchovy develops a differentiated gut, however, they are able to grow and survive on *Artemia* nauplii. In addition, evidence exists that first feeding anchovy larvae do not survive or grow slowly when fed some species of thecate algae whereas they are able to survive when fed unarmored dinoflagellates such as *Gymnodinium splendens* (Lasker et al., 1970). Thus, the straight tube gut, characteristic of young larval clupeoid fishes, may restrict these fishes to food that may be easily digested. Such potentially indigestible items as copepod eggs and diatoms which are found in guts of anchovy larvie (Arthur, 1956) may contribute little to growth or survival.

Prey size is the only other characteristic for which some evidence exists on the importance to larval survival. Culture techniques for all larval fishes require that prey size be increased as a larva grows. Most studies of foods ingested by larvae indicate that prey size increases with larval length. This has been shown for larval anchovy by Berner (1959) and Arthur (1956).
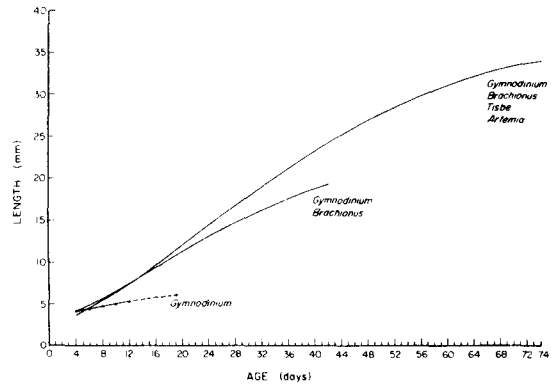

FIGURE 5. Growth of anchovy larvae fed different foods at 16° C. Foods used in rearing are given at end of each curve. Top, Laird-Gompertz growth curve for anchovy through metamorphosis and fed a graduated series of foods; middle, Laird-Gompertz growth curve for larvae fed only smaller foods (*Gymnodinium; Brachionus*); bottom, the curve connects mean lengths for ages 4 to 20 days for larvae fed only *Gymnodinium*. Densities for the same food are comparable in all experiments. Data and parameters for the first two curves are given by Hunter, (1976); data for the last curve are unpublished (n = 120 larval lengths per point; results are from eight rearing experiments; the last point, age 19 days, is from Lasker et al. (1970)).

The importance of increasing prey size with growth is illustrated by comparing growth rates of larval anchovy fed different foods (Figure 5). When larvae are fed *Gymnodinium* alone, growth becomes asymptotic at about 6 mm, whereas, when *Gymnodinium* and the rotifer *Brachionus plicatilis*

are used, growth becomes asymptotic at about 20 mm and few larvae survive. A heavy mortality occurs in larvae fed only *Brachionus* and *Gymnodinium;* survival drops from 46% at age 26 days to 6% at age 42 days. On the other hand, if larvae are given, in addition to these foods, copepodites and adults of *Tisbe* sp., and *Artemia* nauplii when the gut becomes differentiated, larvae can be grown through metamorphosis with a reasonable survival, 12.5% at age 74 days (Hunter, 1976). The most tenable explanation for this result is that it becomes physically impossible for larvae to ingest sufficient numbers of prey when the prey are below a certain size. To illustrate this point, I calculated the number of *Brachionus, Gymnodinium,* and *Artemia* needed for larvae of different sizes (Table 2). The calculation is based on oxygen consumption data of Lasker (unpublished data), and the caloric value for the different foods and does not include adjustments for success in feeding or digestive efficiency which would increase the numbers needed.

TABLE 2

Numbers of *Gymnodinium splendens*, *Brachionus pilicatilis* and *Artemia salina* Nauplii needed per day to meet metabolic requirements of anchovy of various sizes.

Larval length mm	Dry weight mg	Numbers needed per day *		
		Gymnodinium	*Brachionus*	*Artemia*
4	0.021	230	14	—
6	0.064	690	43	4
10	0.314	3,400	210	18
20	4.164	45,000	2,800	230

* Calculated from: A respiratory requirement of 0.54 cal/mg dry weight larval anchovy/day and the caloric value per organism of

    Gymnodinium = 0.00005 cal

    Brachionus = 0.0008 cal

    Artemia = 0.0096 cal

These calculations indicate that extremely high rates of ingestion must be maintained just to meet metabolic needs when the prey is small relative to the larva. Feeding activity would be considerably higher than the required ingestion rate since feeding success and digestive efficiency is not 100%, and many feeding acts are not completed. Other works suggest that a prey too small to support growth alone still may be beneficial as a supplement to the diet as long as larger organisms are also available (Hunter, 1976).

From the above considerations it seems obvious that it would be adaptive for an anchovy larvae to select as large a prey as possible. Shirota (1970) correlated the gape of the mouth of various larvae to the width of typical foods and found reasonable correspondence between 50 to 75% of gape and the width of typical prey organisms. Ambiguity exists, however, on the critical dimension of prey. For example, Arthur (1956) used the maximum prey width when studying the food of anchovy larvae, whereas Berner (1959) used the maximum dimension. This is not a trivial point since copepods,

the principal food of larval fishes, are oblong. Thus, to determine whether or not a copepod or a particular stage of copepod can be ingested one needs to know the critical dimension. To solve this problem and determine the relationship between feeding success and mouth size, the mouth size of larval anchovy was measured and compared to the feeding success of larvae fed freshly hatched *Artemia.* Anchovy larvae of various sizes were allowed to feed on *Artemia* nauplii (density 10 *Artemia* /ml), and their stomachs were examined 4 hours later. The larvae had no previous experience feeding on *Artemia.*

The mean size of the *Artemia* selected (0.236 mm wide x 0.433 mm long) was less than the mean size of the *Artemia* in the tank (0.260 x 0.525 mm). When the mouth width was equal to or less than the width of *Artemia* selected, no prey were taken, whereas, when the mouth was slightly larger than the width of *Artemia,* 25% of the larvae captured one or more *Artemia* (Figure 6). When the mouth size was 1.5 times the width of the prey (larval length 8.1 to 8.5 mm), all larvae ingested one or more *Artemia* in the 4 hour feeding period and the mean number eaten, 19 (N = 7), exceeded the numbers required to meet metabolic needs for an entire day. These results also indicate that all prey were ingested end on since the length of the *Artemia* exceeded the width of the mouth in all cases.

Thus, a reasonably close correspondence existed between the maximum width of prey that was ingested by larval anchovy and the width of the mouth. On the other hand, for ingestion of prey to be independent of mouth width, the width of the mouth must exceed that of the prey by about 1.5 times.

Estimates of Food Densities

Two approaches have been used to estimate the density of food needed for survival of larval anchovy. Survival can be determined for larvae reared in the laboratory at various food densities or alternately the required density can be calculated from a searching model based on estimates of daily ration and the volume of water searched by a larva per day.

O'Connell and Raymond (1970) using the first approach, determined that first feeding anchovy larvae need at least one copepod nauplius per ml to survive and four or more per ml to insure good survival (about 50% survival after 12 days at 17° C). Lasker (1975), in a series of density experiments, found that anchovy larvae need 20 to 40 *Gymnodinium splendens* cells/ml to fill their guts in 8 hours, and Lasker et al. (1970) found that 100 to 200 cells/ml were required to insure growth for the first week.

The searching model approach was employed by Hunter (1972) to estimate the food density requirements of anchovy larvae. The model is similar to models of Cushing and Harris (1973), Blaxter
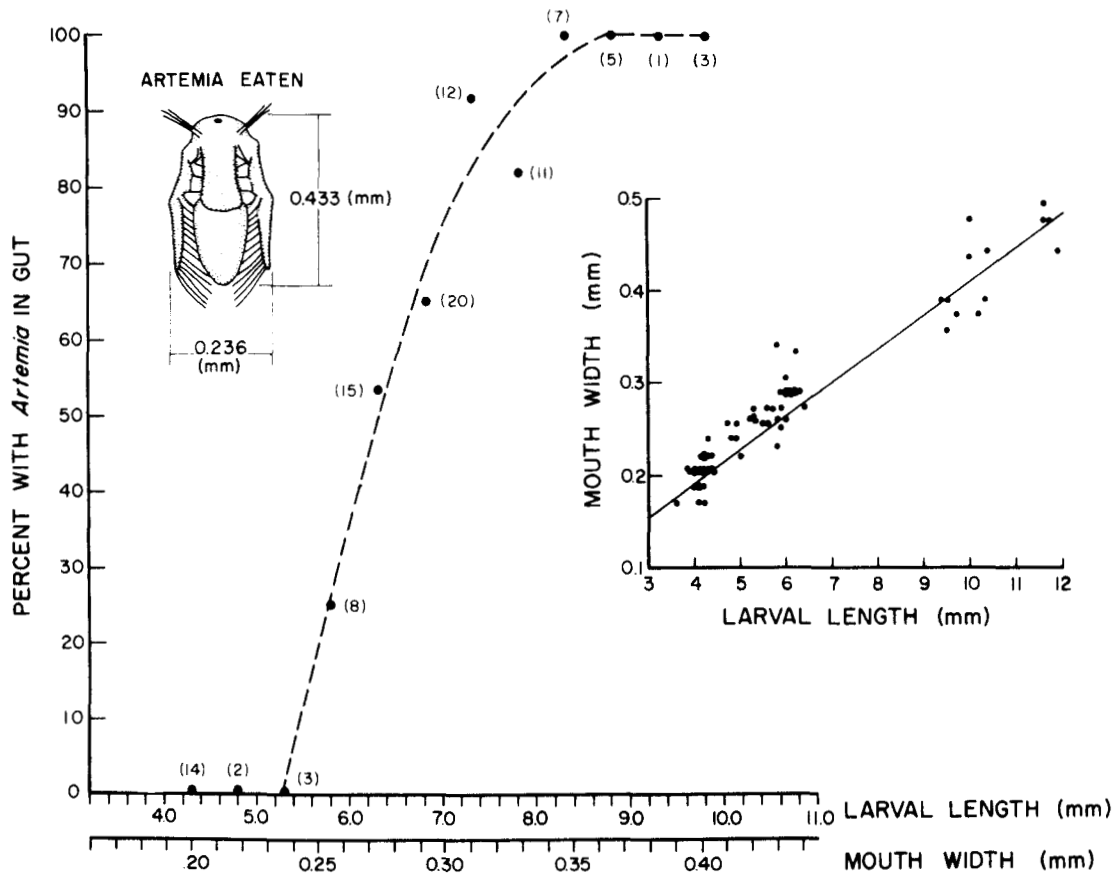
FIGURE 6.   Percent of anchovy larvae with one or more *Artemia* nauplii in stomachs after 4 hours of feeding. Percentages calculated for 0.5 cm length classes and plotted at the midpoint of each class; number of larvae per class is given in parentheses. In the upper left corner the mean dimensions of the nauplii ingested are given, drawn to show the position of appendages when measured. Upper right, regression of mouth width (Y) on larval length (X) where Y = 0.0431 + 0.0366X and s_{yx} = 0.0585; this regression was used to construct mouth width scale at the bottom of the figure.

(1969), and Rosenthal and Hempel (1970). It is an estimate of daily ration, adjusted for feeding success, divided by the volume of water searched by a larva per day. The volume searched per day is the product of cruising speed (assumed here to be 0.29 cm/sec for a 4 mm larva) and the cross sectional area of the reactive perceptive field for prey (the attack range of Cushing and Harris, 1970). When the 95% limits of the perceptive field for prey are used (0.36 body length to the sides, and 0.40 body length above and below the swimming plane), the volume searched in 10 hours is 622 ml (Hunter, 1972). On the other hand, if the mean distance at which prey are sighted (0.185 body length) is used the volume searched per day is only 148 ml (data recalculated from Hunter, 1972). The ration is calculated from metabolic

requirements for a 4 mm larva (Table 2), but is increased to account for digestive efficiency assumed here to be 80% (Lasker, 1965) and for feeding success which is 11% for first feeding larvae (Hunter, 1972). The ration adjusted in direct proportion to these percentages is 2,614 cells of *Gymnodinium*. Division of this ration by the two volume estimates gives 4 cells/ml when the 95% limits are used and 18 cells/ml when the average distance to prey is used. Despite the relatively large ration, the estimated densities are still below the densities of *Gymnodinium* required in laboratory tanks for larvae to survive.

The large difference between the estimate in which the mean perceptive field was used and the one in which the 95% limits was used, demonstrates

the extreme sensitivity of the model to assumptions regarding the size of the perceptive field. Probably one of the more serious problems in models of this type is the tacit assumption that a larva reacts to and attempts to capture every prey that enters its perceptive field. In the laboratory, larvae frequently pass without responding to many *Gymnodinium* cells which appear to be in their perceptive field. It is likely that a larva reacts only to one prey at a time; thus, the division of the ration by the , volume searched produces an unrealistically low food density requirement. The proportional increase in prey density to account for the prey attacked but not captured is probably also a source of error. In addition, search patterns of larval fish may have considerable redundancy (Hunter and Thomas, 1974). Clearly, more realistic models are required.

In summary, laboratory density experiments yield higher food density requirements for survival of anchovy larvae than simple searching models. The laboratory density experiments have the advantage that they measure density directly but they suffer from the possible existence of larval density dependent interactions, and a small tank volume which may limit the searching capacity of the larva. The searching model is not affected by these variables but is affected by errors in the parameters, and in the assumptions required by the model.

CONCLUSIONS

The average density of food in the sea is too low to support larval anchovy, regardless of whether one used laboratory density experiments or searching models. Lasker (1975) has recently shown that patches of dinoflagellates known to be nutritious to anchovy larvae exist in the sea in sufficient concentrations to support larval life during the first feeding stage. Laboratory studies reported here indicate that larvae have the ability to remain in patches of food once they find them. On the other hand, such patches may be ephemeral features, and even if they persisted for a reasonable period larvae would have to find other patches of larger prey to exist. Whether or not a larva will find a concentration of food organisms of the appropriate size and whether or not it will be able to survive until it finds another, involves a complex set of interacting variables including all of those described in this review. At present it is impossible to predict the outcome of such a series of interacting variables. Evaluation of this will require development of more complex models of larval feeding behavior and energetics than presently are available. I believe our understanding of the ecology of larval anchovy is at the point where such models could be constructed on a more realistic basis than has been possible in the past, and these models would expand our understanding of larval fish ecology.

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