

# SWIMMING AND FEEDING BEHAVIOR OF LARVAL ANCHOVY *ENGRAULIS MORDAX*

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## ABSTRACT

The swimming and feeding behavior of laboratory-reared larval anchovy, *Engraulis mordax*, was described over the first 30 days of larval life. Estimates were made of cruising speed, proportion of time spent in rest, and burst speeds. Tail beat frequency, tail beat amplitude, and speed of swimming larvae were measured from cine photographs and the relationship between these variables determined. Complete and incomplete feeding sequences were described in detail from cine photographs and the frequency of feeding acts determined from visual observation. The extent of the reactive perceptive field for prey was measured from cine photographs and expressed as a function of larval length. Feeding success of larvae fed rotifers was determined for the first 21 days of larval life. These estimates were combined to estimate the volume of water searched by larvae per hour, and this estimate and others were used to calculate the density of food required by larvae to meet metabolic requirements. These calculations indicated that the density of food required by larvae just after yolk absorption was up to 37 times that required by older larvae.

In this report I describe the feeding and swimming behavior of the larval anchovy, *Engraulis mordax*, during the first 30 days of larval life. These observations will be combined with results of other studies in a model for estimation of the survival of larval anchovy in the sea. Similar studies of feeding and locomotor behavior have been made on other larval fishes (Blaxter, 1966; Braum, 1967; Rosenthal and Hempel, 1970), and the biology of larval fishes in general has been reviewed by Blaxter (1969).

## APPARATUS AND METHODS

Anchovy larvae were reared from the egg using techniques described by Lasker, Feder, Theilacker, and May (1970). The larvae were kept in 500-liter black, fiber glass tanks in non-circulated sea water at 17° to 18°C. They were illuminated by fluorescent lamps and were given a daily dark period of 10 hr with a half hour of dim light preceding and following the dark period. Larvae were fed a variety of organisms ranging from wild plankton to laboratory-cultured brine shrimp, *Artemia salina*, the dinoflag-

ellate, *Gymnodinium splendens*, the rotifer *Brachionus plicatilis*, and the veligers of various species of mollusks (Lasker et al., 1970; Theilacker and McMaster, 1971).

Most of the data in this report will be concerned with larvae younger than 30 days and 15 mm or less in length because larvae in this size range are more easily cultured than older ones. Metamorphosis of *Engraulis* occurs after about 50 to 60 days at 17° to 18°C when the larva is about 40 mm total length.

Visual observations of the feeding and swimming behavior of larvae were made in the 500-liter rearing tanks throughout the 13-hr day. A larva was chosen and all behavioral acts recorded continuously for 5 or more min. Behavioral acts were given a digital code, and the occurrence, duration of acts, and elapsed time were recorded on eight-channel paper tape by operation of a keyboard. The keyboard controlled a motorized paper-tape punch, and the perforated paper tape was computer-processed. Usually hundreds to thousands of larvae were present; thus a different larva was probably observed during each 5-min observation period and consequently each period was treated as an independent set of observations. A total of 447

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sets of observations was made of larvae ranging in age from 0 to 36 days.

Swimming and feeding behaviors were also recorded on motion picture film for subsequent

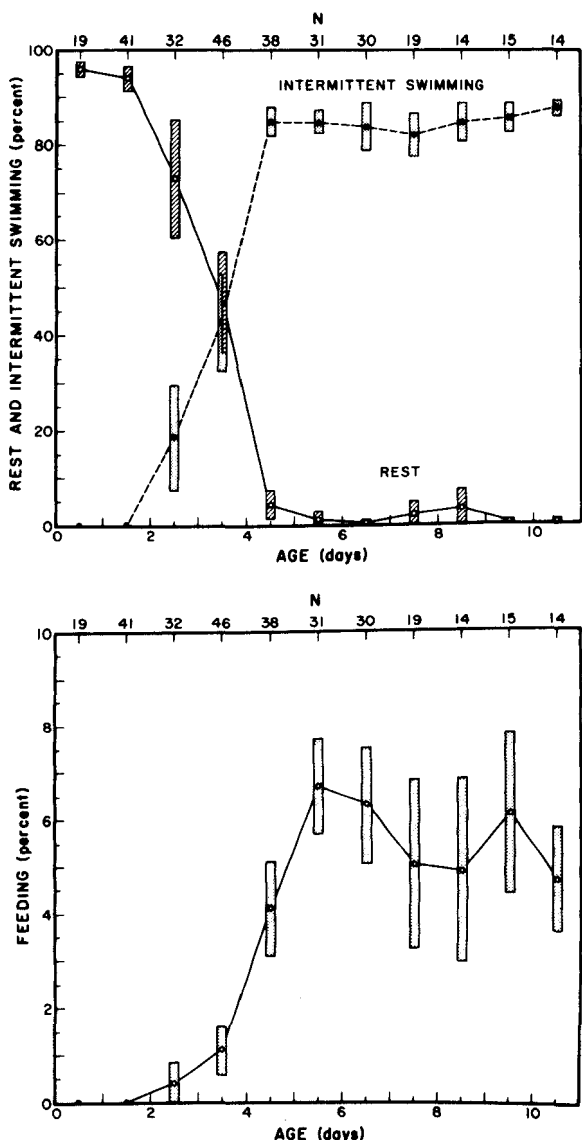


FIGURE 1.—Proportion of time spent in rest and intermittent swimming (top panel), and feeding (bottom panel) by anchovy larvae during the first 10 days of larval life. Points are mean percent  $\pm 2 \times SE$ , for each day; the number of observations ( $N$ ) is given at top of graphs.

analysis. For cine photography the larvae were placed in round plastic containers 1 cm deep and 8 to 25 cm diameter which had black opaque walls and a transparent bottom. The tank was illuminated from above by a reflector flood lamp operated below rated voltage. A water bath was inserted between the lamp and the tank to prevent heating the water. Light from the lamp was focused with a fresnel lens on the lens of the motion picture camera beneath the tank. The camera arrangement and lighting system was similar to the one used by Baylor (1959) for photographing transparent organisms with infrared radiation. From the position of the camera the subject was silhouetted against an intensely bright background because the light was focused directly on the camera lens. Thus, low sensitivity, high resolution, and high contrast film could be used. Swimming and feeding larval anchovy were photographed with a high-speed camera at 128 fps (frames per second) using AHU microfilm manufactured by the Eastman Kodak Company.<sup>2</sup> Photographic analysis of feeding was restricted to larvae that fed on food particles 100  $\mu$  or larger in diameter because I was not able to resolve smaller food particles and still maintain the larvae in a reasonably large photographic environment. Much slower camera speeds—1 to 2 fps—were used to estimate swimming activity.

## SWIMMING BEHAVIOR

### CHANGES IN THE TYPE OF SWIMMING WITH DEVELOPMENT

During the first 2 days of larval existence, anchovy larvae exhibited little locomotor activity. Over 90% of the time they floated motionless in the water (Figure 1). Usually the head was directed downward and often the motionless yolk-sac larvae were transported slowly by water currents. Occasionally, they executed a brief but intense burst of swimming. These bursts of swimming, which I called continuous swimming, occurred about once a minute and lasted

<sup>2</sup> Use of trade names does not imply endorsement by the National Marine Fisheries Service.

1 to 2 sec (Table 1). During a burst the tail and body beat continuously from side to side without interruption, and the larva accelerated and decelerated rapidly. Bursts of continuous swimming usually occurred in the absence of any observed stimulus although some bursts were stimulated by accidental contact with other larvae or the walls of the tank.

During the third day of larval life (age 2 days) a new swimming pattern appeared which was to become the dominant mode of locomotion throughout the rest of larval existence. The new mode of swimming was intermittent swimming, consisting of alternate periods of swimming and gliding; typically the larva executed one full tail beat, paused, and glided forward without beating the tail and then repeated the sequence of beating and gliding. The mean proportion of time devoted to intermittent swimming increased during the third and fourth days of larval life, more or less in proportion to the decrease in the time spent in rest (Figure 2). By the fifth day of larval life about 85% of the observation period was composed of intermittent swimming whereas the proportion of time devoted to rest during the day was nearly zero.

With the appearance of intermittent swimming the frequency and duration of continuous swimming decreased. Bursts of continuous swimming occurred once or twice per minute during the first 2 days of larval life whereas by the tenth day they occurred only once in 5 min, and the duration of the bursts also declined over the same period (Table 1). Bursts of contin-

TABLE 1.—Proportion of observation time spent in continuous swimming and the mean duration, and mean frequency, of bursts of continuous swimming during the first 10 days of anchovy larval life.

Age days	Percent of observation time Mean $\pm$ 2 $\times$ SE	Frequency of bursts/min Mean $\pm$ 2 $\times$ SE	Duration of bursts (sec) Mean $\pm$ 2 $\times$ SE	N
0	2.4 $\pm$ 0.86	0.85 $\pm$ 0.28	1.86 $\pm$ 0.50	20
1	5.2 $\pm$ 0.99	1.72 $\pm$ 0.32	1.72 $\pm$ 0.48	32
2	2.0 $\pm$ 0.58	1.38 $\pm$ 0.22	1.38 $\pm$ 0.52	28
3	3.4 $\pm$ 0.24	0.76 $\pm$ 0.78	0.76 $\pm$ 0.22	45
4	0.7 $\pm$ 0.10	0.33 $\pm$ 0.06	0.33 $\pm$ 0.16	37
5	0.12 $\pm$ 0.16	0.11 $\pm$ 0.12	0.37 $\pm$ 0.54	32
6	0.16 $\pm$ 0.12	0.10 $\pm$ 0.22	0.31 $\pm$ 0.22	27
7	0.22 $\pm$ 0.16	0.18 $\pm$ 0.06	0.41 $\pm$ 0.26	11
8	0.15 $\pm$ 0.18	0.13 $\pm$ 0.12	0.23 $\pm$ 0.24	13
9	0.29 $\pm$ 0.20	0.29 $\pm$ 0.18	0.30 $\pm$ 0.16	15
10	0.10 $\pm$ 0.08	0.20 $\pm$ 0.08	0.22 $\pm$ 0.14	14

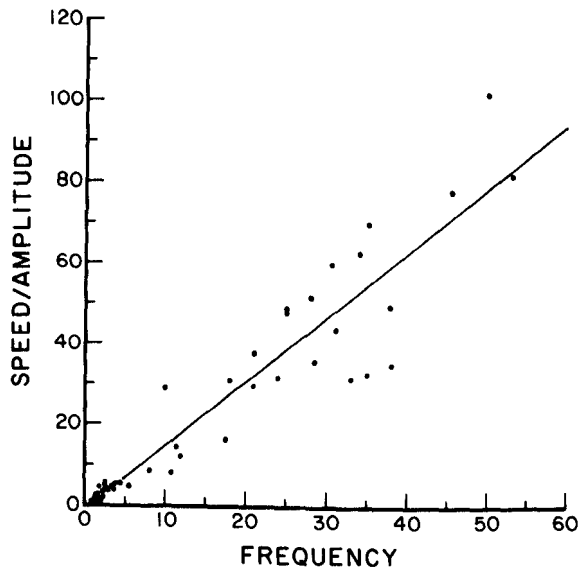


FIGURE 2.—Relationship between speed, tail beat frequency, and tail beat amplitude for anchovy larvae for all types of swimming. Equation for line is  $V/A = -1.11 + 1.59 F$  where  $V/A$  is speed (cm/sec) divided by tail beat amplitude (cm), and  $F$  is tail beat frequency (beats/sec).

uous swimming occurred at a low frequency throughout the rest of larval life.

The appearance of intermittent swimming coincided with the appearance of feeding behavior. Feeding behavior was closely associated with intermittent swimming; food was sighted during intermittent swimming and the larvae advanced on the prey using this mode of locomotion.

#### POSSIBLE SIGNIFICANCE OF SPONTANEOUS BURSTS OF SWIMMING IN YOLK-SAC LARVAE

The regularity of the bursts of continuous swimming of yolk-sac larvae (age 0-1 day) suggests that the bursts may have a respiratory function. Yolk-sac larvae have no functional gill filaments, and oxygen must be obtained through the integument. Thus the regular bursts of continuous swimming could be necessary for gas exchange. I conducted a short experiment to test this hypothesis.

I measured the duration and frequency of bursts of swimming of age 0 day and 1 day larvae in open 10-liter containers containing water

saturated with oxygen and in ones containing water below saturation at 17°C. In the tests below saturation the initial level was 30% of saturation, but it increased to 65% by the end of the observation period 7 hr later.

At oxygen concentrations below saturation, larvae of both ages swam more frequently than did the controls of the same age ( $P \leq 0.008$  Mann Whitney  $U$  Test, Siegel, 1956). Age 0 day larvae spent  $5.36 \pm 1.41\%$  ( $\pm 2 \times \text{SE}$ ,  $N = 15$ ) of the time swimming in water below saturation whereas they spent  $1.97 \pm 0.64\%$  ( $N = 10$ ) of the time swimming at saturation. Age 1 day larvae spent  $12.48 \pm 4.50\%$  ( $N = 5$ ) of the time swimming in water below saturation whereas the controls spent  $3.30 \pm 2.31\%$  ( $N = 5$ ). The proportion of time spent swimming by the controls in both tests did not differ from that given in Table 1 for larvae of the same age.

This experiment suggests that the regular bursts of swimming of yolk-sac anchovy larvae have a respiratory function. On the other hand, the increase in swimming could have been the result of stress induced by low oxygen concentrations and bear no relationship to behavior under normal conditions. I am not inclined to accept this explanation because except for the increase in the duration and frequency of swimming, the behavior of the larvae was normal. A different motor pattern, vigorous shaking of the head, appears at lethal or near lethal levels of oxygen, about 12% of saturation at 17°C.

#### STRUCTURE OF CONTINUOUS AND INTERMITTENT SWIMMING

To estimate the relationship between larval anchovy tail movement, size, and speed during continuous and intermittent swimming, 53 film sequences were analyzed frame by frame. They included sequences of artificially stimulated and spontaneous bursts of continuous swimming and of bouts of intermittent swimming. In each swimming sequence the mean tail beat amplitude, swimming speed, and tail beat frequency were measured by use of a coordinate reader and digitizer (Hunter and Zweifel, 1971). I assumed that the net course swam was equivalent to a path formed from the midpoints of the tail beat. If the course was straight, this esti-

mate was the same as a regression of the  $X$  and  $Y$  coordinates for the positions occupied by the head or about the same as a straight line fit by eye through frame by frame tracings of the larva. If the course was curved, the path formed by the midpoints provided a reasonable estimate of the net curvilinear path followed by the larva.

Typically intermittent swimming could be separated from continuous swimming at a glance, but when the tail beat frequency approached that of continuous swimming it was difficult to distinguish between the two types of swimming. Thus, to separate all data into one of the two classes of swimming it was necessary to determine the beat frequency at which larvae changed from intermittent to continuous swimming. This was accomplished by measuring the elapsed time between beats in the slower swimming sequences.

When the tail was beat at a frequency of 4.7 beats/sec or higher, the movement of the tail was continuous, that is, the interval of rest between beats was equal to or less than 0.0078 sec (1 frame at 128 fps). At tail beat frequencies at or below 4.4 beats/sec the movement of the tail was not continuous but rather pauses of 0.086 to 0.811 sec existed between beats. The mean of the duration of rest between beats was  $0.30 \pm 0.22$  sec ( $\pm 2 \times \text{SE}$ ) whereas the duration of a single beat was  $0.13 \pm 0.05$  sec. The duration of the pause or glide between beats was independent of larval size or swimming characteristics and was quite variable. The speed of tail movement was also independent of size but was about the same in all larvae. Thus, at beat frequencies below 4 beats/sec, larvae decreased speed by increasing the interval between beats but maintained about the same speed of tail movement.

Continuous and intermittent swimming data (Table 2) were analyzed separately to determine the relationship between tail beat amplitude, speed, length, and tail beat frequency. The general equation  $V/A = a + bF$ , where  $A$  is amplitude in cm,  $F$  is tail beat frequency,  $V$  is speed in cm/sec, and  $s_1$  is the standard deviation about the line, provided the best fit to continuous and intermittent data sets. The intercepts and slopes

for the two data sets were nearly the same, and consequently I combined the data and obtained the relationship of  $V/A = -1.11 + 1.59F, s_t = 8.311$  for all data (Figure 2).

The principal difference between the above equation and ones derived by Bainbridge (1958) or by Hunter and Zweifel (1971) for adult fishes was that amplitude was the estimator of size instead of length. Amplitude was required in the present study because during bursts of continuous swimming larvae modulated the amplitude of their tail beat. Inclusion of length in addition to amplitude and frequency did not improve the relationship. In the study by Hunter and Zweifel (1971) fish did not modulate the amplitude of the tail beat because they swam at a steady speed. Amplitude is known to change during acceleration (Gray, 1968), and the behavior of larvae during bursts of continuous swimming was no exception to this rule.

During intermittent swimming, amplitude was not modulated but was maintained at a minimum value of about one-fifth of a body length. The relationship between amplitude and length

during intermittent swimming was obtained by the equation  $A = 0.112 + 0.170 L$  where  $s_t = 0.066$  (Figure 3).

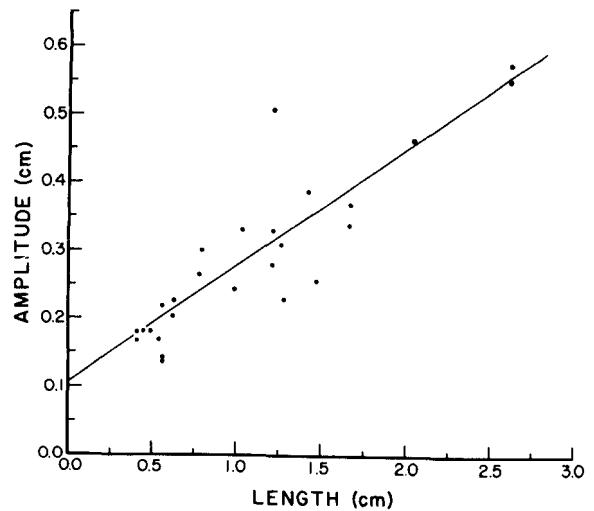


FIGURE 3.—Relationship between anchovy larval length (cm) and tail beat amplitude (cm) for intermittent swimming.

TABLE 2.—The speed, tail beat frequency, and tail beat amplitude for anchovy larvae of various lengths during continuous and intermittent swimming. Each value is a mean for a single swimming sequence swum by one larva.

Continuous swimming				Intermittent swimming			
Length	Speed	Tail beat frequency	Tail beat amplitude	Length	Speed	Tail beat frequency	Tail beat amplitude
cm	cm/sec	beats/sec	cm	cm	cm/sec	beats/sec	cm
0.34	4.71	38.1	0.133	0.41	0.31	2.3	0.169
0.37	4.59	33.3	0.142	0.41	0.30	2.0	0.182
0.38	0.75	5.5	0.143	0.45	0.33	2.4	0.183
0.39	10.68	45.5	0.137	0.49	0.20	2.3	0.181
0.41	1.22	10.9	0.150	0.54	0.64	3.8	0.170
0.42	1.08	4.7	0.194	0.56	0.44	2.1	0.221
0.42	8.05	35.3	0.115	0.57	0.73	4.5	0.138
0.42	11.63	50.0	0.114	0.57	0.37	2.7	0.142
0.42	3.86	17.9	0.124	0.62	0.17	1.1	0.205
0.43	7.28	30.5	0.121	0.63	1.01	2.8	0.229
0.43	8.92	34.5	0.140	0.78	0.63	1.3	0.267
0.43	7.91	28.2	0.152	0.79	0.52	1.5	0.302
0.43	7.48	38.5	0.147	0.98	0.20	1.4	0.245
0.44	12.18	53.3	0.148	1.03	1.61	3.1	0.333
0.44	4.89	35.3	0.148	1.21	1.23	2.8	0.514
0.50	9.61	24.7	0.200	1.21	1.35	2.3	0.278
0.56	2.52	17.5	0.150	1.21	1.52	2.6	0.332
0.72	1.75	8.0	0.206	1.27	1.18	2.7	0.310
0.72	2.17	11.4	0.150	1.28	1.27	2.6	0.231
0.93	4.28	10.2	0.148	1.42	1.02	2.1	0.390
1.00	11.22	28.6	0.311	1.47	1.26	3.2	0.257
1.00	15.91	20.7	0.422	1.66	1.02	1.7	0.340
1.24	31.26	31.6	0.716	1.66	0.78	1.7	0.372
1.24	9.08	12.0	0.718	2.04	1.68	2.2	0.468
1.24	23.16	21.0	0.777	2.62	2.50	1.9	0.581
1.32	21.16	24.0	0.664	2.62	3.02	2.9	0.555
1.42	26.85	25.0	0.545				

At intermittent swimming speeds tail movement was slow enough that the frequency of the beat could be counted by eye. If the length of the larva were known, intermittent swimming speed could be estimated from the general speed equation given above, the amplitude equation for intermittent speeds, and the tail beat frequency. Instead of the general speed equation it may be preferable to use one based on intermittent swimming data alone, which is  $V/A = 0.0466 + 1.308 F$  where  $s_t = 1.160$ .

### BURST SPEEDS

The speeds obtained by larval anchovy during bursts of fast continuous swimming are of interest because they may be a measure of the larva's ability to avoid predators or possibly plankton nets. Bursts of fast swimming were stimulated in larvae of mean length  $4.1 \pm 0.1$  mm (Table 2, continuous swimming, 0.34 to 0.44 cm larvae) and mean length  $12.1 \pm 1.2$  mm (Table 2, continuous swimming, 1.00 to 1.42 cm). Bursts were stimulated by moving a pin near a larva and photographing the larva at the film speed of 200 fps. Speeds were averaged for the entire duration of the burst, which lasted about 0.1 to 0.2 sec. The stimulated burst speed for larvae of mean length 4.1 mm was  $63 \pm 19$  mm/sec (mean  $\pm 2 \times$  SE) or about 15 body lengths/sec and that for the 12.1-mm larvae was  $198 \pm$  mm/sec or about 16 body lengths/sec. The maximum speed obtained by larvae in the 4.1 mm length class was swum by a 4.2-mm larva which swam 116 mm/sec (28 body lengths/sec) during a burst of 0.12 sec. The maximum speed for larvae in the 12.1 mm class was 313 mm/sec (25 body lengths/sec) swum by a 12.4-mm larva during a burst lasting 0.10 sec. In summary, larvae had a maximum speed capability of 25 body lengths/sec or faster for bursts lasting 0.1 to 0.2 sec, but the typical or average burst speeds were close to 15 body lengths/sec.

### ESTIMATES OF DAILY RATE OF SWIMMING

I shall consider only intermittent swimming in the estimates of daily swimming rate because only intermittent swimming was associated with food search, and because once feeding began,

continuous swimming was an insignificant proportion of daily activity (Figure 1 and Table 1). Two independent methods were used to estimate the rate of intermittent swimming. In the first method, larvae were photographed at 2 fps in a cylindrical chamber of 25 cm diameter, and swimming speed calculated from frame-by-frame analysis of the photographs. Five minutes of swimming were analyzed for each larva; swimming was divided into intermittent and continuous types; and periods of inactivity equal to or greater than 5 sec were tabulated as rest. In the second method, visual observations of larvae in the 500-liter rearing tanks were used to record the tail beat frequency of larvae during intermittent swimming and the frequency and duration of continuous swimming and rest. Larvae were observed three or more times a day. The speed of larvae during intermittent swimming was calculated from the tail beat frequency by use of the relationships between age, length, amplitude, tail beat frequency, and speed previously described.

The speed of intermittent swimming measured from photographs increased with larval length (Figure 4), and the regression of speed on length gave the relationship  $V = -0.215 + 1.038 L$  where  $s_t = 0.280$ . Visual measurements of tail beat frequency of intermittent swimming

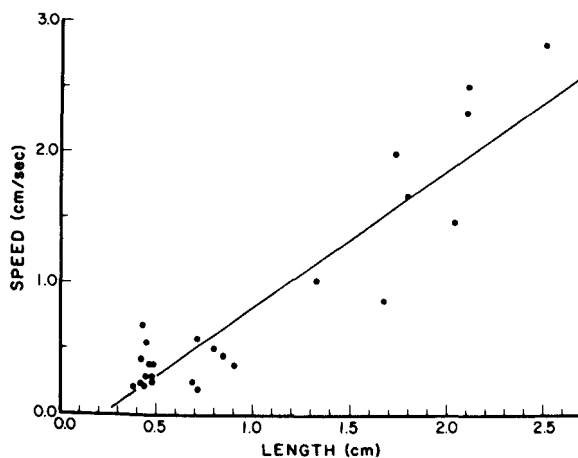


FIGURE 4.—Rate of movement during intermittent swimming (cm/sec) as a function of anchovy larval length (cm). Measurements taken from analysis of cine photographs. Equation for line is  $V = -0.215 + 1.038L$ .

TABLE 3.—Comparison of visual and photographic estimates of speed of intermittent swimming for anchovy larvae of three sizes.

Larval length (cm)	Tail beat amplitude <sup>1</sup> (cm)	Intermittent speed estimates (cm/sec)		Distance traveled <sup>4</sup> (m/hr)	
		Visual <sup>2</sup>	Photographic <sup>3</sup>	Visual	Photographic
0.5	0.197	0.414	0.304	12.3	9.0
1.0	0.282	0.592	0.823	17.6	24.5
1.5	0.367	0.771	1.342	22.9	39.9

<sup>1</sup> Estimated from  $A = 0.112 + 0.170L$ .

<sup>2</sup> Estimated from  $V/A = 0.047 + 1.308F$ , where  $F = 1.57$ .

<sup>3</sup> Estimated from  $V = -0.215 + 1.038L$ .

<sup>4</sup> When 82.6% time spent swimming.

did not change with age over the first 30 days of larval life. That tail beat frequency did not change implied that the interval of rest between beats, the principal determinant of frequency, was dependent on variables unrelated to size or development. The same conclusion was obtained from analysis of the structure of intermittent swimming in the preceding section. Thus, the change in speed associated with increased length or age may be a function of only the increase in tail beat amplitude with length.

The mean tail beat frequency for intermittent swimming,  $1.57 \pm 0.03$  beats/sec, was substituted into the speed equation for intermittent swimming. Speed of intermittent swimming could then be determined for larvae of any length by substitution of the appropriate tail beat amplitude into the equation. Speed estimates in which the above procedure was used and ones based on photographic analysis are compared in Table 3. The two sets of estimates are reasonably close for 0.5-cm larvae but they diverge for larger ones. No reason exists to disregard either set of estimates. It seems reasonable to assume that the true values lie somewhere between them.

The proportion of daylight hours devoted to intermittent swimming must be considered to estimate the distance traveled per hour. Visual observations are preferable for this purpose because of the greater number of observations (318) and because visual observations were systematically taken at different times of day. Between ages 4 and 30 days, no trend with age existed in the proportion of time devoted to swimming although time spent swimming decreased slightly on days of intensive feeding.

The mean proportion of time devoted to intermittent swimming was  $82.6 \pm 1.2\%$ . To arrive at this estimate I considered periods of inactivity longer than 5 sec as rest and periods equal to or less than 5 sec as a part of intermittent swimming bouts. Estimates of the distance traveled per hour, assuming 82.6% of the time is spent swimming, are shown in Table 3. These values will be combined with others to estimate rate of food search in a later section.

## FEEDING BEHAVIOR

### DESCRIPTION OF FEEDING BEHAVIOR

After a larva sighted a prey, the head turned toward it so that the prey was perpendicular to the tip of the snout and thus in about the center of the binocular field of the larva. Then, while keeping the prey in the center of the binocular field, the larva swam slowly toward the prey by executing one or more tail beats. After swimming ceased, the larva contracted its body into an S-shaped striking posture typical of the larval clupeoid fishes (Figure 5). During contraction of the body, the prey was maintained directly in front of the snout and small movements by the prey were compensated for by slight adjustments in the orientation of the head and larger movements by rotating the entire body with the pectoral fins. The larva continuously moved toward the prey while forming the strike posture by high frequency (50 to 60 beats/sec), low amplitude vibration of the finfold or caudal fin.

The order and rate at which portions of the body were contracted to form the S-strike posture were not fixed. The order appeared to be related to the initial orientation of the head and trunk. Frequently swimming movements were integrated into the beginning of the strike posture. The larva while approaching a prey often ceased swimming with the body partially bent, and the contractions to form the strike posture were carried onward from that point. Variations in the rate of contraction were related to movements of the prey. If the larva did not keep up with a moving prey, contraction of the body was often interrupted and the incomplete posture held for an extended period. The ampli-

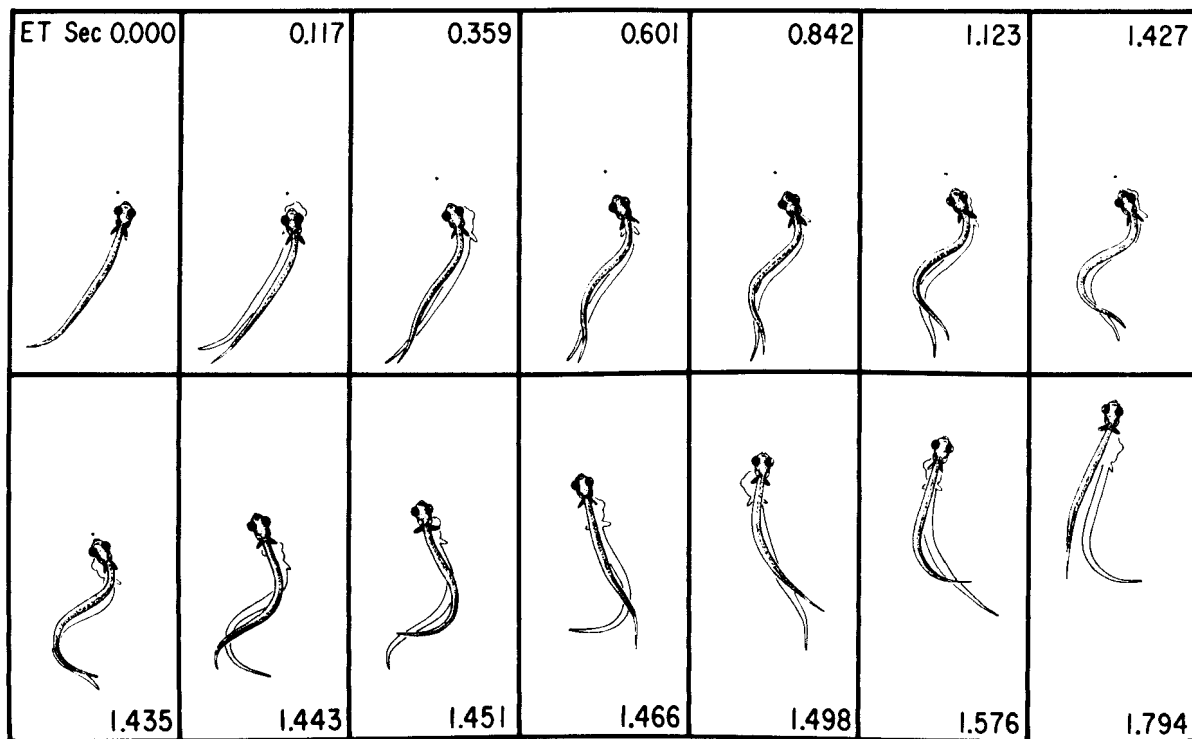


FIGURE 5.—Tracings of selected motion picture frames from a feeding sequence of an anchovy larva (8.9 mm, 21 days old) and a prey taken at 128 frames per second. Frame lines are fixed such that distance moved by larva is indicated by comparison of tracings; and unshaded image indicates position of larva in the preceding tracing. The following events are illustrated: elapsed time (ET) 0 sec, larva sights prey; ET 0-0.117 sec, larva orients head toward prey and swims toward it; ET 0.117-1.435 sec, larva forms s-shaped strike posture; ET 1.435-1.443 sec, strike begins and prey captured; and ET 1.451-1.794 sec, forward movement continues as tail returns to axis of progression.

tude of the posterior bend in the body reached a maximum just before the strike was begun.

The larva began the strike by drawing the tip of the tail rapidly anteriorly. It then thrust the tail backward, extended the head, opened the mouth, and the particle was taken or missed within 7.8 to 15.6 msec after the beginning of the backward thrust of the tail (one to two frames at 128 fps). The entire feeding sequence from sighting the prey to the strike lasted only 1 to 2 sec. The sequence of movements were so rapid that my first impression was that they were extremely stereotyped. Later, frame-by-frame analysis of film taken at 128 fps indicated that normal variance was associated with every characteristic that could be measured in the films.

Larvae of 15 to 20 mm formed the strike posture in less time than did one 5 to 15 mm long, and consequently, feeding sequences were shorter in larger larvae (Figure 6). On the other hand, the time used to approach the prey before forming the strike posture was about 0.6 sec in larvae of all sizes. Other characteristics increased directly in proportion to length, for example, the maximum amplitude of the body in the strike posture, the distance to the prey at the time of the strike, and the rate of movement toward the prey while in the strike posture. The speed of the strike also increased with length but the relationship appears to be nonlinear. The speed of the strike relative to length was less in the largest size class of larvae.



## INCOMPLETE FEEDING SEQUENCES

Feeding sequences often ended before they were completed by execution of the strike. The mean frequency of feeding strikes (the last act in the feeding sequence) for all visual observations for larvae of ages 4 to 27 days was  $1.28 \pm 0.14$  strikes/min ( $N = 325$ ) whereas that for the orientation movement of the head (the first act in the sequence) was  $3.22 \pm 0.30$ . Thus, about 40% of all feeding sequences were completed. The proportion of feeding sequences that were completed did not change with age, but there was some indication that the proportion of incomplete sequences increased when the larvae began to feed on *Artemia* nauplii. This increase in the proportion of incomplete sequences was caused by an increase in the proportion of sequences ended at the first act, the orientation movement of the head. The proportion of feeding sequences that were carried as far as bending the body was 52% and remained about the same regardless of age or food type.

In the film analysis I analyzed only incomplete feeding sequences that were continued beyond the head orientation movement and compared them with completed sequences. These measurements indicated that some feeding sequences ended at every stage up to and including the final strike posture, and the duration of incomplete sequences overlapped that of completed ones (Table 4). The only characteristic measured in the photographs that consistently separated incomplete from completed feeding sequences was that at the end of incomplete ones the prey was farther away from the larvae than it was in completed sequences. Thus, the principal cause

TABLE 4.—Comparison of characteristics of incomplete and complete feeding sequences for larval anchovy 5.1-10.0 mm.

Characteristic	Incomplete sequence <sup>1</sup> Mean $\pm 2 \times$ SE	Complete sequence <sup>2</sup> Mean $\pm 2 \times$ SE
Duration of S-posture (sec)	$0.82 \pm 0.26$	$1.11 \pm 0.16$
Duration entire sequence (sec)	$1.38 \pm 0.40$	$1.71 \pm 0.26$
Body amplitude (mm)	$1.03 \pm 0.40$	$1.52 \pm 0.20$
Distance to prey at end of sequence (mm)	$0.81 \pm 0.17$	$0.41 \pm 0.04$
S-posture forward movement (mm/sec)	$0.51 \pm 0.26$	$0.80 \pm 0.34$

<sup>1</sup>  $N = 19$ .

<sup>2</sup>  $N = 13$ .

of the failure to continue a feeding sequence was an inability to closely approach the prey while forming the strike posture.

To summarize, photographic analysis of incomplete and complete feeding sequences indi-

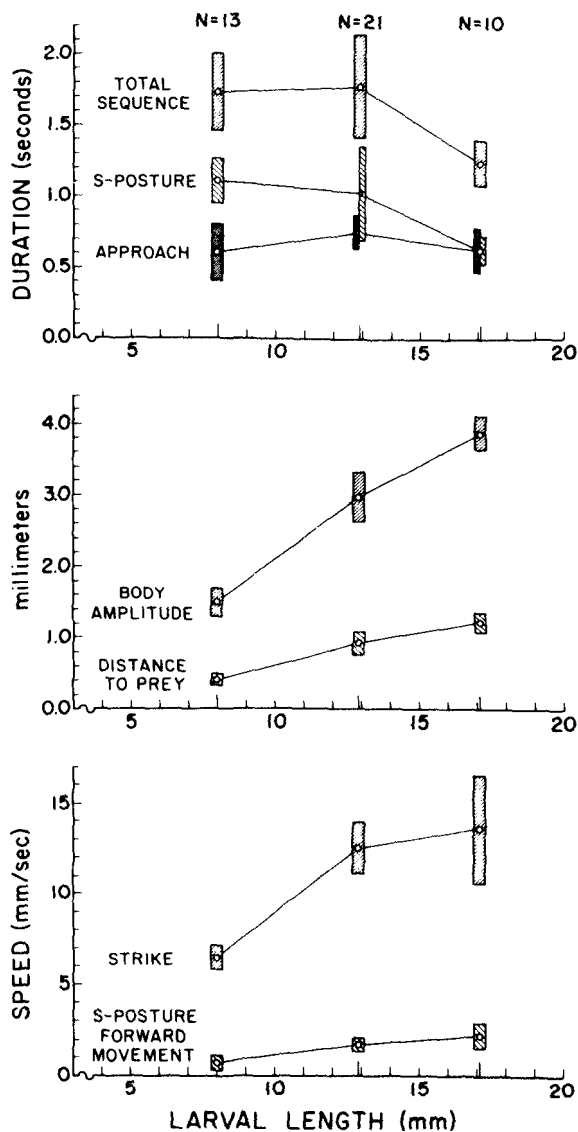


FIGURE 6.—Characteristics of complete feeding sequences of anchovy larvae taken from film analysis. Values are means  $\pm 2 \times$  SE for three size classes of larvae (5.1-10.0, 10.1-15.0, and 15.1-20.0) and are plotted at the mean length of the larvae in the class.

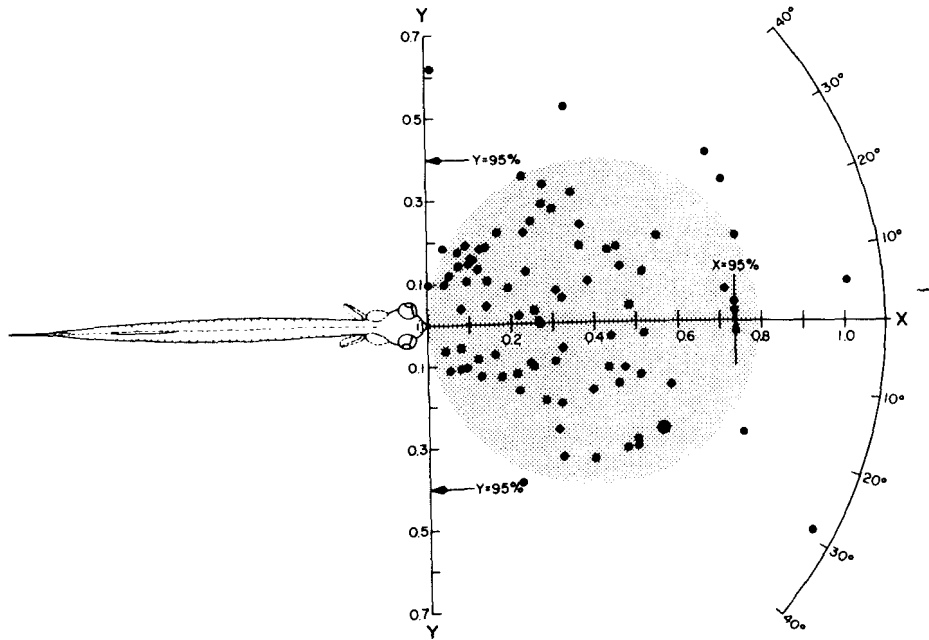


FIGURE 7.—Reactive perceptible field in the horizontal plane for anchovy larvae. Each point represents position of a prey in the horizontal plane at time larvae first reacted to it. Distances in  $X$  and  $Y$  axes were divided by the lengths of the larvae and expressed as proportions of larval length. Arrows indicate lines that would enclose 95% of prey sighted in each plane.

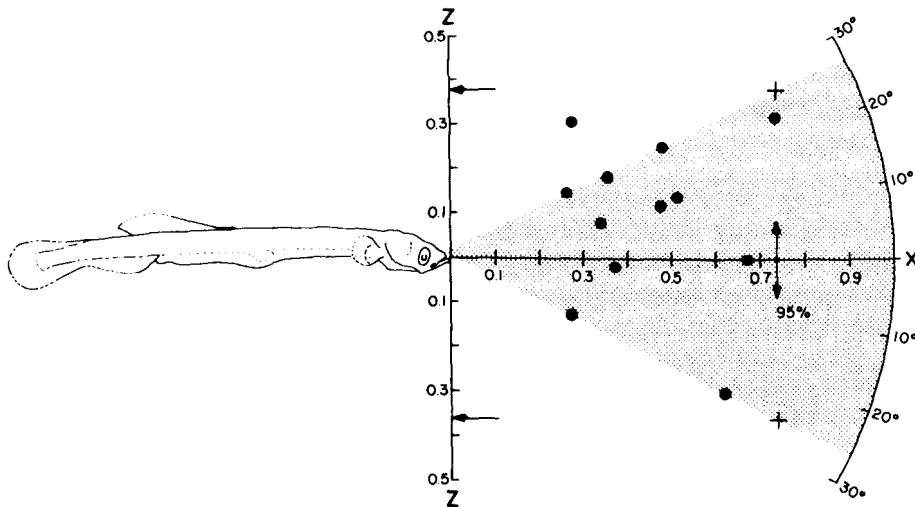


FIGURE 8.—Reactive perceptible field in the vertical plane for anchovy larvae. Distances on  $X$  and  $Z$  are expressed as a proportion of larvae length; points are position of prey when larvae first reacted to them; crosses indicate point of intersection of visual cone with  $Y = 95\%$  (the 95% limit of prey distribution in  $Y$  given in Figure 7); and arrows on  $Z$  indicate projected values of  $Z$  for intersection points.

cated that considerable flexibility exists in what appeared to be a highly stereotyped feeding pattern. Although a sequence was completed in only 1 to 2 sec, the larvae depend on feedback from the prey throughout the period. The larvae respond to the prey during the sequence by adjusting posture, speed, and direction of movement and by ending or continuing the sequence.

#### EXTENT OF REACTIVE PERCEPTIVE FIELD

The size of the predator's reactive perceptive field (Holling, 1965) is an essential element in the estimation of the rate of search for prey by a predator, that is, the extent of the area in which a predator will react to a prey. In studies on larval fishes the cross-sectional area of the perceptual field is multiplied by the speed of swimming to estimate the volume of water searched per unit of time. Estimates of this type have been made by Braum (1967), Rosenthal and Hempel (1970), and Blaxter (1966) and are summarized by Blaxter (1969).

To determine the position of prey when larvae first reacted to them feeding, larvae were filmed from below for horizontal measurements and separately from the side for measurements in the vertical plane. Seventy-one horizontal film sequences of larvae, 4.0 to 24.2-mm, and 12 vertical sequences of larvae, 7.0 to 24.7 mm, were analyzed frame by frame.

In the film analysis all measurements were made in reference to the body of the larvae;  $X$  signified measurements made in the axis of progression or swimming plane;  $Y$  those in the other horizontal axis; and  $Z$  those made along the vertical axis. Vertical measurements were made in relation to the orientation of the larvae and were not necessarily vertical in relation to the water surface. Searching behavior was independent of body orientation. Larvae reacted to prey when they swam upward, when they swam downward, as well as when they swam parallel to the water surface.

In each photographic sequence the angle and distance of the prey from the tip of the snout of the larva were measured 15 msec before the larva reacted to the prey by turning the head toward it (two frames at 128 fps). To correct for obvious length-dependent differences in field

size the distance to the prey was divided by laryal length and was expressed in body lengths ( $L$ ). Prey organisms included *Brachionus*, various veliger larvae, *Artemia* nauplii, and wild copepod nauplii of undetermined species.

In the horizontal plane larvae reacted only to prey ahead of them; prey at  $90^\circ$  or more from the tip of the snout were not selected, and most prey were less than  $60^\circ$  from the snout (Figure 7). The reactive perceptive field in horizontal cross section was roughly circular. A circle of radius  $0.4L$  with the center on the axis of progression or  $X$  axis enclosed 90% of all prey sighted (shaded area, Figure 7). In the vertical plane, larvae reacted to prey below as well as above the  $X$  axis. The maximum distance above and below the  $X$  axis at which prey were sighted in the vertical plane was  $0.3L$  and thus the maximum extent of  $Z$  was  $0.6L$  (Figure 8). The reactive perceptive field may be roughly triangular in vertical cross section, because a triangle with a central angle of  $53^\circ$  and altitude of  $0.74L$  enclosed all but one of the 12 observed values.

Maxima seem appropriate rather than averages to estimate the extent of the reactive perceptive field because only the exceptional larva survives in nature and because field size may change with feeding motivation. Considering the two axes in the horizontal plane separately, for 95% of all prey sighted the value  $Y$  for the position of prey was equal to or less than  $0.4L$  from the axis of progression ( $X$  axis), and for 95% of all prey the  $X$  values for prey position were equal to or less than  $0.74L$ . Ninety-five percent limits could not be used to estimate  $Z$  because the observations were too few to calculate percentages. The maximum observed  $Z$  value above and below the  $X$  axis was  $0.3L$ . This value could be used or alternatively  $Z$  could be estimated at a point on  $X$  by assuming the field is triangular in cross section as illustrated in Figure 8. Using the 95% limit for  $X$ ,  $0.74L$ , as the point to make the cross section, we obtain an estimate of  $Z = 0.36L$ . Thus, the estimate of the maximum extent of  $Z$  varied from 0.30 to  $0.36L$  depending on the assumptions used. Assuming an elliptical cross section where  $Y = 0.40L$  and  $Z = 0.36L$  the area of the ellipse is

equal to  $0.45L^2$  for a cross section at  $X = 0.74L$ . To estimate the volume search per unit time these areas need to be multiplied by the larval swimming speed. This aspect of the calculation will be considered in a subsequent section.

### FEEDING RATES

In all studies in this paper larvae were observed and maintained in tanks containing high and presumably optimum food densities (*Gymnodinium* 100 to 200/ml, *Brachionus* 10 to 20/ml, and *Artemia* nauplii 3 to 10/ml). It is unlikely that density limited the rate of feeding under these conditions. Thus, the rates recorded probably are near the maximum feeding rate that can be sustained by larval anchovy.

Records were kept of the frequency of feeding acts of larvae ages 4 to 27 days raised in the 500-liter rearing tanks. A total of 325 observations of 5-min duration was taken at three different times of day. No trend in the frequency of feeding strikes with time of day existed. The larvae fed actively throughout the day although their guts were filled after the first half hour of feeding each morning. The average frequency of feeding strikes for all data combined was  $1.28 \pm 0.144$  strikes/min. Some evidence existed that the rate may climb to 3 strikes/min for 2 to 3 days when *Artemia* nauplii were first introduced, but no direct cause and effect relationship could be established because other prey were also present in the tank.

Another estimate of feeding rate was obtained from the data on feeding success described in the next section. The larvae in that study had empty guts at the beginning of the observation period, and they were observed during their initial 10 min of feeding on a particular day, whereas the preceding data observations were begun about a half an hour after the larvae began feeding and continued throughout the day. The average feeding frequency for larvae studied in the feeding success experiments ( $N = 100$ ) was  $1.75 \pm 0.205$  strikes/min and the range was from 0.2 to 5.8 strikes/min. Thus, during the first 10 min of feeding, feeding rates were on the average somewhat higher than they were when averaged over the entire day. Feeding rates on *Artemia* were the same as those on *Brachionus*.

### FEEDING SUCCESS

Feeding success was estimated by counting the number of feeding acts completed in 10 min, removing the larvae from the container, and counting the number of prey in the gut. Larvae were kept in the dark for 12 or more hr before the test to insure that the gut was empty (anchovy larvae do not feed in the dark). I measured the feeding success of larvae fed *Brachionus* (density, 10 to 60/ml) from the first day of feeding (age 3 to 4 days) up to the 21st day of larval life. A separate experiment was run to determine the effect of a different prey on feeding success. At age 17 days the diets of some of the larvae were changed from one of only *Brachionus* to one of *Artemia* nauplii (density, 3 to 15/ml). Measurements of feeding success were made over the first week of feeding on *Artemia*. *Gymnodinium* was not used as a food for first feeding larvae because it was usually defecated before we were able to examine the contents of the gut. Two measurements of feeding success of larvae fed *Gymnodinium* fell within the scatter for *Brachionus* (Figure 9).

The success of larvae fed *Brachionus* rapidly increased over the first week of feeding (age 3 to 10 days), but thereafter the rate of increase of feeding success was much lower. The form of the relationship between age and success was that of a learning curve. A semilog transformation of the data provided an adequate correction for this curvilinear trend. The regression of feeding success in percent on the log of larval age gave the relationship, percent success =  $93.2 (\log \text{ age}) - 33.30$  where  $s_t = 20.14$ .

Seventeen-day-old larvae were less successful in capturing *Artemia* for the first time than they had been in capturing *Brachionus*. Only 37% of feeding acts were successful when larvae were fed *Artemia* nauplii for the first time at age 17 days whereas 81% were successful when the food was *Brachionus* (Figure 10). The initial level of feeding success for larvae fed *Artemia* was higher than that of larvae when they first began to feed at age 3 to 4 days, and less time was required to obtain a high level of success on *Artemia* than was required for first feeding larvae. By the third day of feeding on *Artemia*

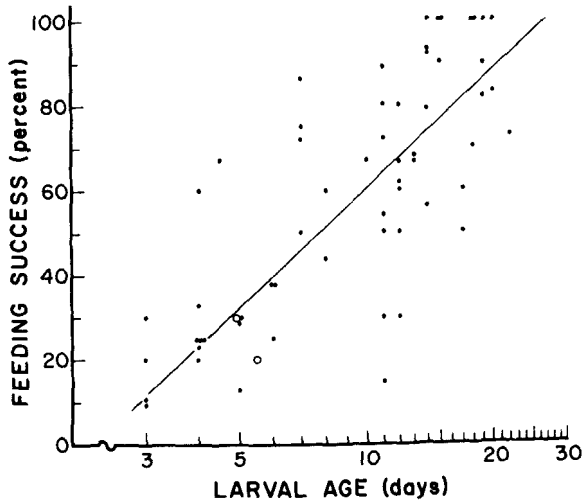


FIGURE 9.—Feeding success (percent of prey captured) of anchovy larvae of various ages fed *Brachionus*. Larval age is plotted on log scale, equation for line is percent success =  $93.2(\log \text{ age}) - 33.30$ . Two open circles, larvae fed *Gymnodinium*.

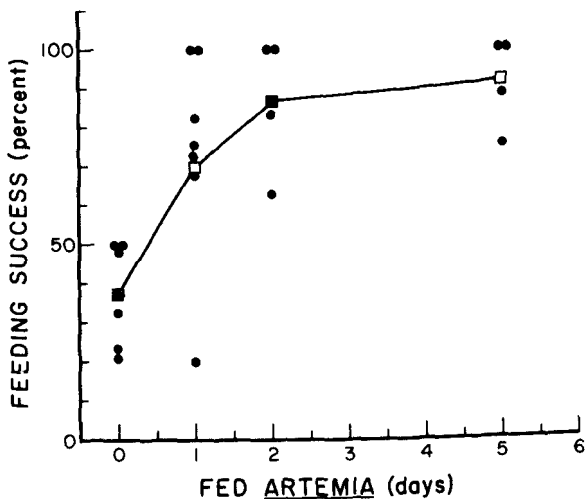


FIGURE 10.—Feeding success of anchovy larvae fed *Artemia* for the first time at age 17 days (0 days on abscissa) and for 5 additional days. The line connects mean values.

the level of success had reached the same level as it had after 2 weeks of feeding on *Brachionus*.

One interpretation of these results is that a considerable proportion of feeding experience on

one type of prey is transferable when larvae feed on a new prey. On the other hand, the surprisingly long period (about 2 weeks) required to achieve a high level of feeding success on *Brachionus* suggests that maturation of sensory and locomotor systems may also play a role in anchovy larval feeding behavior during the first 2 weeks of larval life.

### ESTIMATION OF VOLUME SEARCHED

In this section I combine the estimates made in the previous section to estimate the volume of water searched by larvae per hour and will use this estimate and others in a subsequent section to calculate the density of food required by larvae to meet metabolic requirements.

The volume of water searched per hour by larvae was calculated by multiplying the cross-sectional area of the reactive perceptive field by the distance traveled per hour by larvae. I made separate calculations for the photographic and the visual speed estimates given in Table 3. In both calculations the speed estimates were adjusted for the proportion of time spent swimming, 82.6%, and they were extended from distance/sec to distance/hr. In this and all subsequent calculations I have made larval age and length interchangeable by using the growth equation  $l_t = 3.24e^{0.0555t}$  given by Kramer and Zweifel (1970) who reared anchovy larvae at 17°C under conditions similar to those used in this study.

The estimate of the volume of water searched per hour increased exponentially with size (Figure 11). The two volume estimates were close for larvae less than 10 mm long but they diverged for larger ones. There was no reason to select one estimate over the other and, consequently, I chose to use the average of the two for future calculations. When the two estimates are averaged the outcome is nearly the same as the relationship, volume searched/hr =  $1,000L^3$ , where  $L$  is larval length in cm and volume is in  $\text{cm}^3$ , or simply, liters searched/hr =  $L^3$ . Examination of Figure 11 shows the line for  $L^3$  falls almost midway between the two estimates. I shall use the average estimate in the rest of the calculations, but  $L^3$  could be used with only a negligible difference. In the larger larvae  $L^3$

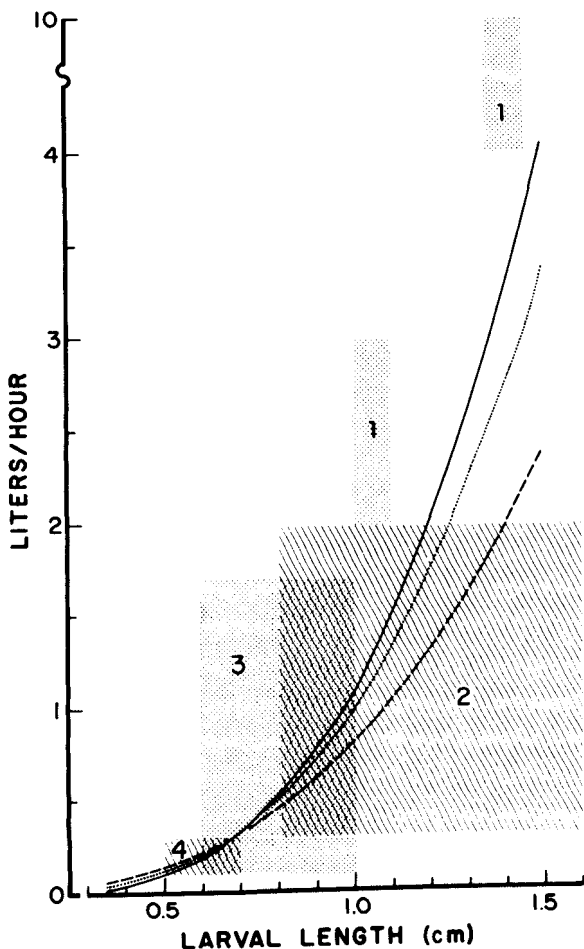


FIGURE 11.—Estimates of liters/hour searched by anchovy larvae 0.3-1.3 cm total length. Lines are based on average estimates and are not data points. Solid line is the volume searched when the photographic estimate of swimming activity was used; dashed line, the volume searched when visual estimate of swimming activity was used; and dotted line, the relationship, liters/hour =  $L^3$ , where  $L$  is total larval length (cm). Rectangles enclose estimates of search rates for other larval fishes from the literature: 1) *Clupea* (Rosenthal and Hempel, 1970); 2) *Clupea* (Blaxter, 1969); 3) *Pleuronectes* (Blaxter, 1969); and 4) *Sardina* (Blaxter, 1969).

yields a slightly higher estimate than the average estimate, but the difference does not exceed 5% even in the largest larva under consideration.

That the change in volume searched with length was nearly proportional to  $L^3$  could be

expected. The volume is the product of the speed and cross-sectional area of the perceptive field for prey. I assumed a length coefficient of one in the calculation of cross-sectional area (area =  $0.45L^2$ ), and the length coefficients for the two swimming speed estimates were close to one as is commonly the case in swimming speed studies (Bainbridge, 1958; Hunter and Zweifel, 1971). Thus the product of the length coefficient for speed and the one for area would be expected to be close to  $L^3$ . On the other hand, that the product of the various constants used in the calculation was close to 1,000 was simply chance.

The estimates of volume searched made for other larval fishes, shown as rectangles in the figure, are close to the two for anchovy, especially when the variance in such estimates is considered. How much of the difference between anchovy and other species can be attributed to specific differences and how much to differences in technique and assumptions is unknown. For example, differences in techniques of estimation of the distance of prey at the time of sighting could account for the differences between my results and others. The initial movement of the head toward the prey was easily detected in the films, but it is possible that a significant period elapsed between recognition and movement of the head. If this is true, I have underestimated the size of the perceptive field for prey. Perhaps some of the herring estimates are higher than the anchovy because the anchovy swims more slowly. Anchovy swim more slowly because unlike most pelagic fishes the anchovy swims intermittently; that is they glide between beats of the tail.

### ESTIMATION OF FOOD DENSITY

To fulfill their metabolic requirement larval anchovy must ingest about 686 rotifers/day/mg dry weight or the caloric equivalent. This estimate was derived from the following: 4.5  $\mu$ liter of  $O_2$ /mg dry wt/hr is consumed by anchovy larvae kept on a 14-10 hr light-dark cycle (Lasker, personal communication); 1  $\mu$ liter  $O_2$  = 0.005 cal; caloric value of the rotifer (*Brachionus*) =  $5,335 \pm 139$  cal/g (Theilacker and Mc-

Master, 1971); dry weight 1 rotifer = 0.16  $\mu\text{g}$  of which 92.2% is organic material (Theilacker and McMaster, 1971); and the assumption of 100% digestive efficiency. The estimate was converted from unit weight to length by the length-dry weight relationship of  $\log W = 3.3237 \log L - 3.8205$  given by Lasker et al. (1970).

The metabolic requirement given above was adjusted for feeding success by increasing it in proportion to the number of prey missed during feeding as predicted by the feeding success equation presented previously. The density of food required for survival was estimated by dividing the food requirement adjusted for feeding success by the volume of water searched in 10 hr. The average of the photographic and visual estimates of volume searched was used to calculate the volume searched by larvae. A 10-hr feeding period was chosen purely as a convenience because the actual duration of daily feeding periods is unknown.

The density of rotifers required to meet metabolic requirements decreased exponentially with size (Figure 12). First feeding larvae, 3 days old (3.5 mm) require 105 rotifers or the caloric equivalents/liter during a 10-hr feeding period whereas 10-day-old larvae (5.9 mm) require only 34 rotifers/liter. Older larvae require much lower food densities primarily because feeding success increases exponentially with age.

Density estimates based on rotifer equivalents probably underestimate the prey density required during the first few days of feeding because a smaller prey is needed by most anchovy larvae during this time. For example, Theilacker and McMaster (1971) found that only 12% of anchovy larvae survive to 19 days old when *Brachionus* was the only food, whereas 40 to 50% survived if in addition to *Brachionus* the dinoflagellate, *Gymnodinium*, was present during the first few days of feeding. To obtain a better estimate of food density required by larvae during the first days of feeding I estimated the caloric value of a single *Gymnodinium* cell and recalculated the density required in terms of dinoflagellate equivalents. The caloric value of a single *Gymnodinium* cell was estimated from the carbon content (Mullin and Brooks, 1970) and by assuming that the carbon content

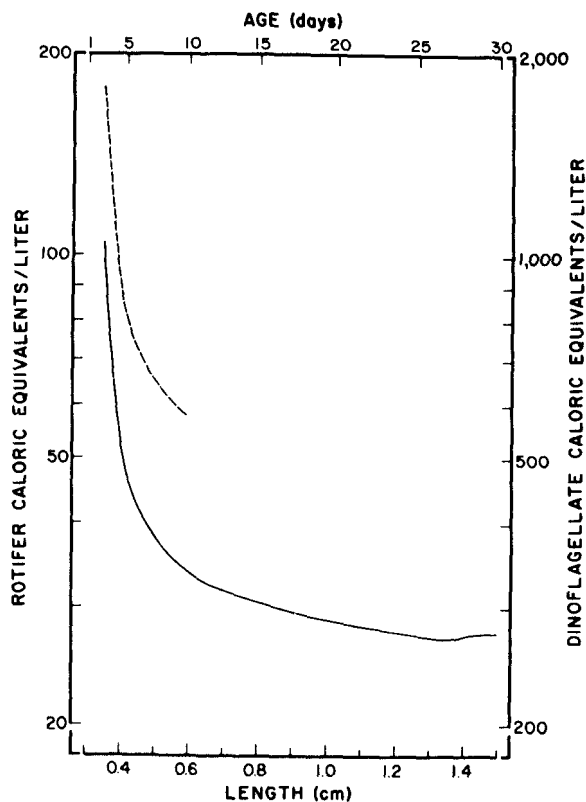


FIGURE 12.—Estimate of the density of prey in rotifer caloric equivalents/liter (left ordinate, solid line) and in dinoflagellate equivalents (right ordinate, dashed line) required to meet metabolic requirements of larval anchovy of 0.3-1.5 cm. Lines are based on average estimates. The shapes of the two curves are the same, but they differ in elevation by a constant factor of 17.

represented 40% of the organic material and that the caloric value of *Gymnodinium* was 5,000 cal/g of organic material. According to this calculation the caloric value of a single *Brachionus* is about 17 times that of a single *Gymnodinium* cell. Thus larvae feeding on dinoflagellates require about 17 times the prey density (dashed line Figure 12) than do those feeding on rotifers (solid line). Nearly all larvae are able to feed on *Brachionus* by age 5 days; thus, the food density requirement for the majority of the larvae shifts from 1,790 dinoflagellates/liter at age 3 days (the first day of feeding) to 48 rotifer equivalents/liter at age 5 days.

Although there are some differences, most of the assumptions and procedures I used were similar to those used by Rosenthal and Hempel (1970) to estimate food densities required by herring larvae. Rosenthal and Hempel estimated that the minimum food ration for herring larvae 10 to 11 mm was 4 to 8 nauplii/liter and the maximum was 21 to 42/liter. My minimum estimate based on metabolic considerations for a comparable size anchovy larvae was 29/liter. For the minimum density they assumed, as I have, that the larva struck at all prey that entered its perceptive field, but for the maximum density they assumed that only a part of the plankters perceived resulted in a completed feeding sequence. In the anchovy larvae feeding on food at high density, on the average only 40% of feeding sequences were completed. Thus, using a similar criterion for a maximum ration as Rosenthal and Hempel (1970), the maximum density required for anchovy larvae would be 2.5 times the minimum ration or for a 10- to 11-mm larva about 72 rotifer equivalents/liter. Considering specific differences and the differences in assumptions and procedures, the estimated food requirements of herring larvae by Rosenthal and Hempel (1970) do not differ much from the one calculated for an anchovy larva of comparable size.

In a survey of the literature given by Blaxter (1965) the densities of food for larval clupeoid fishes in the natural environment ranged from 1 to 68 items/liter. Arthur (1956) in a comprehensive study of the food of pelagic larvae in the California Current region found 1 or more nauplii/liter in 72% of his samples and 30 or more nauplii/liter in about 3% of his samples. Beers and Stewart (1967) measured the density of copepod and naupliar and post naupliar stages (35 to 103  $\mu$ ) in a 600-mile transect in an area of anchovy abundance and obtained densities ranging from 5 to 17 copepods/liter. Thus, food in the natural environment appears to be near or below the minimum concentration I estimated was required for older larvae but considerably below that for first feeding larvae.

Nearly every adjustment that could be made in my estimates of food requirements for anchovy larvae would sharpen the differences be-

tween early and late larval stages or elevate the overall food requirement. For example, natural prey would be of greater variety and could be more difficult to capture, thus causing a differential increase in food concentration required by younger larvae. In addition, older larvae are capable of feeding on a greater variety of food because they can feed on all food used by younger stages plus larger prey as well. I assumed a digestion efficiency of 100% but it must be less than that and this would also increase the overall food requirement. In short, an adjustment in the estimates would probably increase the difference between the estimated food density requirements taken from laboratory measurements and natural food densities.

Laboratory measurements indicated that larval anchovies are more vulnerable to death from starvation just after yolk absorption than at any other time during larval life. This conclusion agrees with those drawn from similar laboratory studies on the herring and other species. Whether or not the increased vulnerability to a starvation death just after yolk absorption is related to year class strength as contended by Hjort (1914) is still a debated question (Blaxter, 1969; Saville, 1971). The catch curves for larval anchovy over 10 years give no indication of an increase in mortality just after yolk absorption (Lenarz, 1972). Three explanations for the absence in the anchovy of an early critical period are: first, turbulence may generate random movement between fish larvae and prey and thereby considerably extend the search volume (Murphy, 1961); second, it may be that the mortality of larvae at all stages is so great because of starvation and other causes that the increased vulnerability at the youngest stages is not detectable; and third, food may not be limiting for early larvae because of patchy food distribution. The absolute number of prey required by early anchovy larvae is not great but a high concentration is required; hence, the patch size could be quite small. It would be of interest in this regard to determine the size, density, and distribution of food patches in the natural environment on a scale appropriate to fish larvae. It would also be of interest to determine the



extent larvae are adapted in their searching behavior to a patchy food distribution.

### SUMMARY

1. During the first 2 days of larval life (age 0-1 day) anchovy larvae spent 95% of the time resting. Rest was interrupted once a minute by a burst of continuous swimming lasting 1-2 sec. By age 4 days, yolk was completely absorbed; 85% of the time was spent in intermittent swimming, 7% in feeding, and only 4% in rest. The proportion of time spent in each of these activities remained about the same thereafter.

2. Intermittent swimming was associated with food search. It consisted of repeated sequences of a single tail beat followed by a glide. The speed of the tail was a constant; thus, tail beat frequency was a function of the glide duration. During intermittent swimming tail beat amplitude ( $A$ ) was the constant proportion of length ( $L$ ) expressed by the equation,  $A = 0.112 + 0.170L$ .

3. In continuous swimming, larvae executed a burst of swimming in which no pauses existed between tail beats. Both tail beat frequency and amplitude were modulated during the burst because the larvae accelerated and decelerated. Larvae had a burst speed capability in excess of  $25L/\text{sec}$  for bursts lasting 0.1-0.2 sec, but the typical or average burst speed was near  $15L/\text{sec}$ . The speed ( $V$ ), tail beat frequency ( $F$ ), and amplitude ( $A$ ) relationship for continuous and intermittent swimming were expressed by the equation,  $V/A = -1.11 + 1.59F$ .

4. The daily rate of movement of larvae excluding rest was estimated using visual and photographic techniques. Measurements taken from cine photographs gave the relationship  $V = -0.215 + 1.038L$ . Visual observations indicated that average tail beat frequency during intermittent swimming was a constant for larvae of different sizes, and this value was used to provide an additional estimate of the daily rate of movement.

5. The size of the reactive perceptive field for larval anchovy was determined from cine photographs taken in vertical and horizontal planes by plotting the position of prey when larvae first

reacted to them. The limits of the perceptive field were set to include 95% of the prey sighted. The field was elliptical, and increased with length and had a cross section proportional to  $0.45L^2$ .

6. Larvae first reacted to prey by turning the head toward the prey. The larvae then swam toward it, stopped swimming, coiled the body into an S-shape, and struck at the prey by thrusting the tail backward and extending the head. The total feeding sequence lasted only 1-2 sec. Throughout the sequence the larva adjusted its body to compensate for movements by the prey and slowly moved toward the prey by vibrating the finfold or caudal fin.

7. Only 40% of all feeding sequences were completed. Sequences were ended at all stages up to just before the strike began. The principal cause of failure to complete a feeding sequence after a larva began to form the S-shaped posture was the inability of the larva to close the distance between it and the prey.

8. Under conditions of high food density, larvae fed throughout the day. The average feeding rate for larvae 4 to 27 days old was 1.28 completed feeding sequences/min. During the initial filling of the gut in the morning the mean rate was to 1.75/min.

9. Feeding success of larvae fed *Brachionus* increased rapidly from 11% success on the first day of feeding (age 3 days) to 50% by age 8 days, but the rate of improvement was more gradual thereafter. The relationship between feeding success and age was expressed by the equation, % success =  $93.2 (\log \text{age}) - 33.30$ . Seventeen-day-old larvae were less successful in capturing *Artemia* for the first time than they had been in capturing *Brachionus*, but after 3 days of feeding experience on *Artemia* the larvae regained their former level of success.

10. The liters of water searched per hour by larval anchovy were estimated by combining the estimate of the reactive perceptive field with an estimate of sustained swimming activity. When the average of the two swimming activity estimates was used, the estimate of volume searched was nearly the same as the relationship, liters searched/hr =  $L^3$  where  $L$  is larval length in cm.

11. The density of rotifers and dinoflagellates required for larvae to meet metabolic needs was

calculated from caloric and respiration data, and estimates of volume searched and feeding success. These calculations indicated that anchovy larvae just after yolk absorption require up to 37 times the food density as older larvae. Thus, just after yolk absorption anchovy larvae are more vulnerable to death from starvation than at any other time during the larval stage.

### ACKNOWLEDGMENTS

David Holts assisted in all but the work on feeding success which Gary Thomas assisted. Alan Good wrote the program used to analyze the swimming behavior of larvae and the one used to analyze observational data collected on paper tape. James Zweifel fit various models to the swimming data.

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