FOOD AND FEEDING OF LARVAE OF THREE FISHES OCCURRING IN THE CALIFORNIA CURRENT, *SARDINOPS SAGAX*, *ENGRAULIS MORDAX*, AND *TRACHURUS SYMMETRICUS*[1]

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ABSTRACT

The size, number, and types of food particles eaten by larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, were determined by an examination of gut contents of larvae captured in plankton samples from the California Current. Food particles found in larvae of the three fishes were predominantly the eggs, nauplii, and the copepodid stages of the smaller species of copepods. These increased in width as the larvae grew though not so uniformly for the anchovy as for sardine and jack mackerel. Particles ingested by anchovies at first feeding were slightly larger than were those ingested by sardines, while jack mackerel could eat particles three times wider than sardines of equal length. The smallest individuals of each species were the most euryphagous, especially anchovies. Feeding incidence of sardine and anchovy declined during the early larval period while that of jack mackerel increased. Sardine and anchovy larvae fed only during the day. The data were not analyzed for day-night feeding for jack mackerel.

The relative body depth and relative weight of laboratory-grown anchovy larvae increased throughout the larval periods examined, whereas, the relative body depth of most ocean-caught anchovy larvae decreased during the first half of this period, possibly as a result of the poorer ration obtainable in the ocean. The decline in relative body depth of ocean-caught anchovy larvae may be related to the decline in feeding incidence and to the apparent lack of increase in size of the food particles ingested.

Owing to the impending collapse of the Pacific sardine, *Sardinops sagax*, fishery, a biological-oceanographic survey program, which later became known as the California Cooperative Oceanic Fisheries Investigation (CalCOFI), was initiated in March 1949. Instrumental in initiating a program to study the food of the sardine larva was the concept developed by Hjort (1914) that the success of a year's spawning may be determined at the critical period when the fragile larvae must secure sufficient food from their environment. For a recent and thorough review of the literature concerning this subject, the reader is directed to May (1974).

To explore the possibilities proposed by Hjort (1914), 10,408 sardine larvae from 398 samples were examined. Food of two potential competitors, namely the northern anchovy (*Engraulis mordax*, 2,350 specimens, 69 samples) and the jack mackerel (*Trachurus symmetricus*, 750

specimens, 65 samples) was also investigated (Arthur 1956). Larvae of these three fishes were supplied to me by Elbert H. Ahlstrom and came from samples taken during early years of the CalCOFI program.

Sardines no longer support a viable fishery, but anchovies have increased in numbers to fill, in part, the ecologic if not economic void. Increasing attention, therefore, will be paid in this paper to this fish and to other species of the genus *Engraulis* which occupy coastal environments of many parts of the world (Reid 1967).

METHODS

Specimens were examined in glycerin because of its advantages over water. Its clearing qualities aid in the detection of food particles within the gut, and the greater viscosity of this medium dampens the movement of particles during dissection. Also, when in glycerin, larvae seem to be more pliable and the intestinal walls do not tend to fragment so readily.

At first the entire intestinal tract of each sardine larva was dissected from the body. This

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517

procedure proved to be difficult, unnecessary, and, at times, actually misleading. It was unnecessary because no food was ever found in the thin walled anterior intestine which forms about half of the total length of the digestive tract. Also, to view the anterior intestine, the liver which surrounds most of it must be carefully teased away resulting in the production of many fragments which may be confused with possible food particles. Schumann (1965) observed that food particles pass through this portion of the gut in about 25 s in laboratory-reared sardine larvae. The intestines of jack mackerel larvae are not as readily observable as in sardine or anchovy larvae because they are covered by well-developed pelvic fins and because of the earlier development of substantial body walls.

The presence of a single food particle in larval sardines or anchovies can usually be detected by a localized swelling of the surrounding gut wall. When several food particles are present, the posterior intestine may be highly expanded over its entire length. Food particles were dissected out of the gut by means of an instrument consisting of a pig's eyelash, bevelled cut to form a chisel point, and mounted in beeswax in one end of a glass tube. Food particles were identified to taxa as far as their condition allowed.

Each organism found in the intestine was measured as to the maximum cross section that the larva would have to encompass for ingestion. Herring larvae have been shown to ingest crustacean food particles "head on" by Hardy (1924), Bowers and Williamson (1951), and Blaxter (1965). This maximizes the ingestible size of the organism and positions appendages, spines, and setae to the rear of the food organism during its transit through the intestines.

To facilitate a consideration of changes in food with respect to growth, the size ranges of larvae of each of the three species of fishes being considered here have been subdivided into three length groups. The length intervals used in these subdivisions are based on the distribution of sizes in the collections rather than on any definite changes in the larvae with respect to age.

FOOD OF SARDINE LARVAE

Type of Food

The qualitative results of the examination of food material from intestines of larval sardines

TABLE 1.—Food of sardine larvae.

Food items	End of yolk-sac stage to 5.5 mm		6.0 to 9.5 mm		10.0 to 25 mm	
	No.	%	No.	%	No.	%
Copepod eggs	141	22.0	35	10.8	10	28.6
Copepod nauplii:						
Calanoid	40		18		3	
Cyclopoid	68		39		3	
Harpacticoid	62		42		2	
Unidentified	179		149		5	
Total nauplii	349	54.5	248	76.3	13	37.1
Copepodid stages:						
Calanoid			1		7	
Cyclopoid	2		7		3	
Harpacticoid			2		1	
Unidentified			1			
Total copepodids	2	0.3	11	3.4	11	31.4
Dinoflagellates	5	0.8				
Tintinnids	20	3.1				
Foraminifera	3	0.5				
Unidentified crustacean eggs					1	2.9
Unidentifiable material	120	18.8	31	9.5		
Total number of food particles	640		325		35	

are presented in Table 1. Length of sardine larvae at the end of the yolk-sac stage is variable. One as small as 3.4 mm contained food, others as long as 5.5 mm still had yolk, but no larva was observed containing both yolk and ingested food organisms. Eggs, nauplii, and juvenile stages of copepods composed almost all of the identifiable food. Copepodid stages in the diet increased in percentage by a factor of 100 through the successive size groups of the larvae. This is undoubtedly due to the severe size restrictions placed on the young larva by the small size of its mouth. As the larva increased in size, its mouth likewise increased in gape, and consequently a larger range of the size spectrum of plankton became available.

Size of Food

Although they are not always of the largest ingestible size, the food particles increased in size isometrically with the increased length of sardine larvae (Figure 1). A larva in doubling its length from 4 to 8 mm likewise doubled its maximum ingestible food size from 80 to 160 μm.

Feeding Incidence

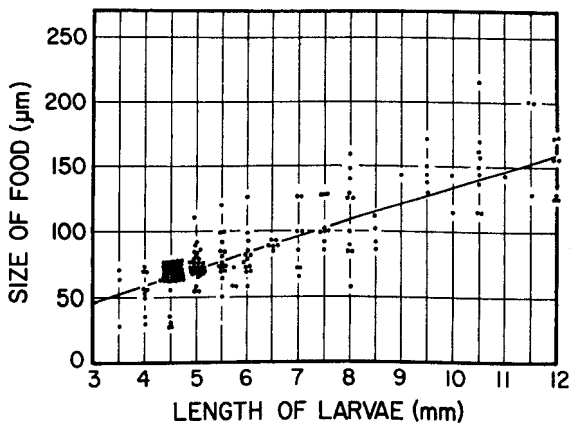The percentage of fish containing at least one food particle is termed the "feeding incidence" for

FIGURE 1.—Food size of Pacific sardine larvae. The line is a least squares fit to all data points and is expressed by the equation: $\hat{S}$ = 13.04L + 5.70, where $\hat{S}$ is width of food in microns and L is standard length of larvae in millimeters. The correlation coefficient r is 0.813 and the coefficient of determination r^2 implies that 66% of the variation in food size can be explained by larval size alone.

a particular sample and is considered a measure of a larva's ability to obtain food in the environmental circumstances at the time of sampling.

The available data permit an inspection of the average hour-by-hour series of trophic events for sardine larvae (Figure 2). The data were divided into 16 intervals composed of: the first half hour, the second half hour, the second hour, and the third hour both before and after sunrise, and both before and after sunset. There were also midday and midnight intervals which vary in length according to the season. Only those intervals in which at least 50 larvae from at least five samples were included. Feeding incidence of all three size groups increased throughout the day. This could have resulted from accumulation of food in the gut, or perhaps to the success of larvae in finding more suitable feeding conditions as the day progressed. The largest size group demonstrated the fastest return to a low feeding incidence at night which probably reflects faster digestive rates for older larvae, as has been shown for plaice larvae (Yasunaga 1971). The lower feeding incidence of older larvae may, therefore, be partly due to an increased digestive rate.

Figure 2 illustrates the diurnal nature of feeding which is due to the visual feeding sardine larva requiring light to detect its prey. (Schumann 1965). This results in diurnal changes of the intestine. The posterior intestine of larvae captured during the early morning is visibly striated.
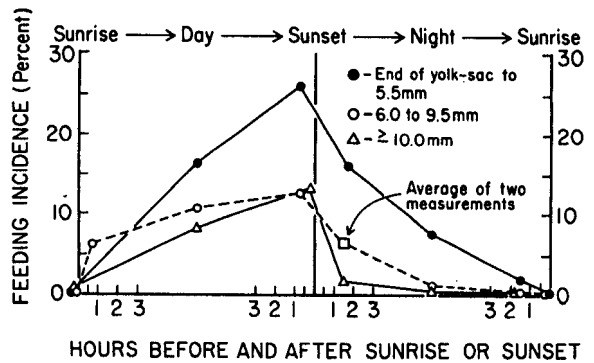

FIGURE 2.—Diurnality of feeding incidence of Pacific sardine larvae. Only those intervals in which at least 50 larvae coming from at least 5 samples are included.

In late afternoon and early evening, the posterior intestines of many larvae, especially the smaller ones, are expanded and have no visible striations. The intestinal wall contains large vacuoles of clear fluids. During this period of the day, it is common to capture larvae with greatly expanded intestines but with no identifiable food organisms. Often such larvae contain some granular material floating about in the intestinal lumen which is comparatively large due to the expansion of the surrounding wall. During the night, intestinal expansions disappear and by sunrise almost all of the larvae have returned to the compact, striated intestinal condition. This rhythm is most pronounced in the smallest size group where, as indicated in Figure 2, the amplitude of the diurnal feeding incidence is at a maximum.

FOOD OF ANCHOVY LARVAE

Type of Food

No larva was found containing both yolk and ingested food. The diet of anchovy larvae (Table 2) is very similar to that of the sardine. The most striking difference is that very young anchovies are more euryphagous. About 40% of their diet (by numbers) consists of noncrustacean food particles. A food category entitled "unidentified spheres" is represented by small (about 20 μm) objects, probably of plant origin. Copepod nauplii become increasingly important as anchovy larvae increase in length and compose the bulk of particulate food when all sizes of larvae are considered.

Copepod eggs and nauplii were found to be the most important element in the diet of larvae of

519

TABLE 2.—Food of northern anchovy larvae.

Food items	End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 9.0 mm	
	No.	%	No.	%	No.	%
Copepod eggs	15	15.3	4	14.3		
Copepod nauplii:						
Calanoid	10		6		3	
Cyclopoid	13		11		6	
Harpacticoid	4		1		1	
Unrecognizable	15		1			
Total nauplii	42	42.9	19	67.9	10	90.9
Copepod adults:						
Calanoid					1	9.1
Clam larvae	2	2.0				
Foraminifera	2	2.0				
Tintinnids	3	3.1				
Dinoflagellates	7	7.1	1	3.6		
Ciliates	2	2.0	2	7.1		
Coccolithophores	4	4.1				
Unidentified spheres	21	21.4	2	7.1		
TOTAL	98		28		11	

Engraulis mordax (Berner 1959), of *E. anchoita* (Ciechomski 1967), and *E. ringens* (Rojas de Mendiola 1974). Berner and Rojas de Mendiola found considerably more eggs than nauplii while Ciechomski reported about equal numbers.

An unusual example of feeding by both anchovy and sardine larvae was called to my attention by Elbert H. Ahlstrom because of the obvious gorged intestines of some of the larvae. This sample was taken about 38 km off the coast of central Baja California approximately 6 h after sunset and 1½ h after setting of a "first quarter" moon. Unusual aspects of the sample were that most of the larger larvae of the two species contained food at night and that they were literally crammed with the pteropod *Limacina bulminoides*. Of the larvae over 10 mm in length, the 26 feeding sardines averaged 24 pteropods per gut with a maximum of 54 in one 23-mm larva, and the 19 feeding anchovies averaged 18 per gut with a maximum of 26 in a 14-mm individual. Compared to the one or two food particles usually found in a feeding anchovy or sardine larva, the number of pteropods was surprising. The only other molluscs found in either sardine or anchovy larvae in this investigation were two bivalve larvae, one each in two very young anchovies. No molluscs were reported in the extensive investigations of the food of anchovy larvae by Berner (1959), Ciechomski (1967), or Rojas de Mendiola (1974). It cannot be determined whether the larvae found filled with *Limacina* reflected beneficial feeding conditions where they

were found, or a hazardous situation in which the larvae had ingested material they could not digest and void.

Because the number of pteropods found in this one sample is larger than the total number of food particles found in the larger sardine and anchovy larvae of all other samples examined, they were not included in the overall tabulations for these fish. The size of the pteropods was used to establish the upper ingestible size of food particles for older anchovies (Figure 3a).
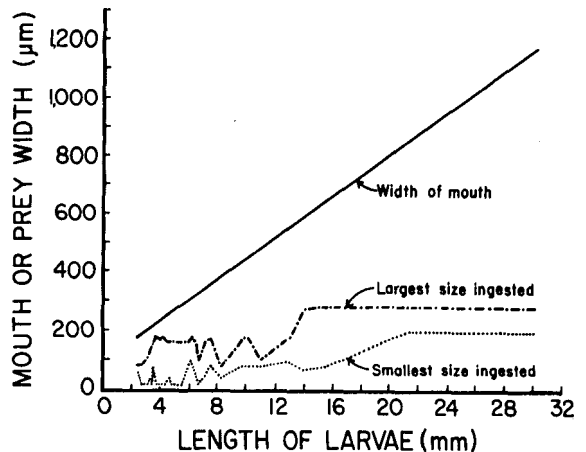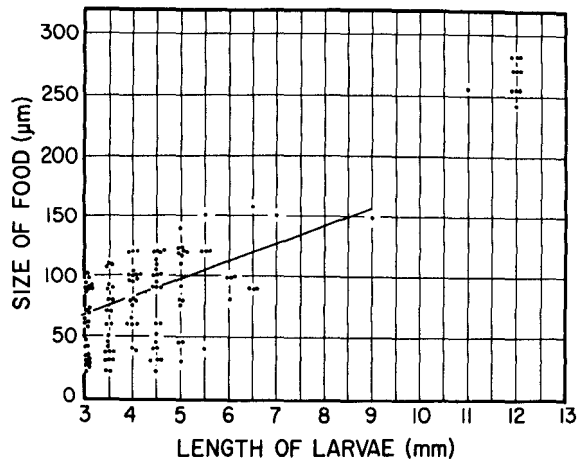

FIGURE 3.—(a) Food size of northern anchovy larvae. The line is a least square fit to all data points from 3 to 9 mm inclusive and is expressed by the equation: $S = 16.16L$, where S is width of food in microns and L is standard length of larvae in millimeters. The correlation coefficient r is 0.473 and the coefficient of the determination r^2 implies that 22% of the variation in food size can be explained by larval size alone. (b) Food size of anchoveta (*Engraulis ringens*) larvae. Adapted from Rojas de Mendiola (1974).

Size of Food

Food particles of young anchovy larvae are not selected from those near the largest ingestible size as are those of young sardine larvae, though there is a trend to increase particle size as larvae increase in length. The correlation coefficients (Figures 1, 3a) suggest that food size of sardines is more controlled by larval size (0.813^2 or 66% of variance explained) than of anchovies (0.473^2 or 22% of variance explained). The extensive data, including many older larvae, reported by Ciechomski (1967) and Rojas de Mendolia (1974) indicate a sharp increase in food size between the larval lengths of about 3 to 4 mm but relatively little increase for most of the remainder of the larval period. Rojas de Mendiola's data (Figure 3b), including food sizes of 2,088 feeding larvae 3.1 to 5.0 mm in length, are used to illustrate this important point. These data indicate that food size roughly doubles (from approximately 100 to 200 μm) while larvae grew from 4 to 16 mm. Assuming that both larvae and food particles increased in size isometrically, then their volumes increased by the cube of their increase in length or width. Food particles in doubling in width increased 8 times in volume, while larvae increasing 4 times in length increased 64 times in volume. Therefore, the nutritional equivalent of a 200-μm food particle to a 16-mm larva is only one-eight of that of a 100-μm particle to a 4-mm larva. Although Berner (1959) measured the length rather than the width of food particles and his data are not directly comparable, they do indicate that while anchovy larvae increased in length from 3 to 10 mm (an increase of 37 times in volume) their average food size increased from 68 to 128 μm (an increase of only 6% times in volume).

Feeding Incidence

Anchovy larvae also are daytime feeders (Figure 4). The disparity between night and day values for feeding incidence is greater for anchovies than for sardines during their youngest larval stages. This difference perhaps is due to a faster digestive rate for the anchovy.

FOOD OF JACK MACKERAL LARVAE

Type of Food

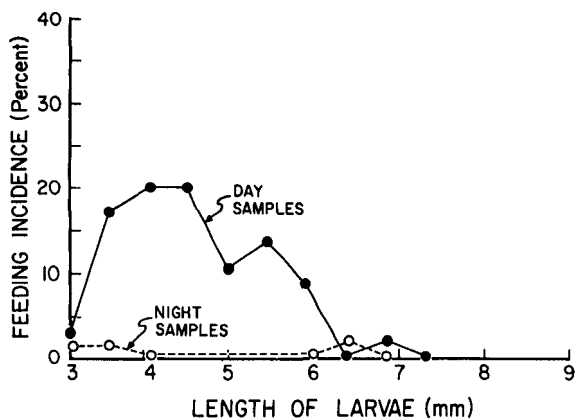The jack mackerel larva first starts to feed when

FIGURE 4.—Diurnality of feeding incidence of northern anchovy larvae.

it is about 3.25 mm long. By the end of the yolk-sac stage, the jack mackerel has attained a robustness which contrasts sharply with the slender early larval sardine or anchovy. Its body shape, in general, is more substantial and its mouth is proportionately larger. No jack mackerel larva was found with both yolk and ingested food organisms.

Just as for sardine and anchovy larvae, copepods contributed the greatest bulk of its food (Table 3). Eggs and naupliar stages, however, are much less important. The "egg sacs," appearing under the title of copepod eggs, were probably ingested attached to adult copepods and so represented a coincidental fraction of the food. Copepod nauplii seemed to be significant in numbers only in larvae of the smallest size group.

Copepodid stages of copepods make up the bulk of particulate food, increasingly so as the larva grows older. By the time the larva is 7.0 mm long, 96.0% (by number) of its food is composed of various species of copepods. The most significant feature of the diet is the very high percentage of occurrence of *Microsetella norvegica*, one of the few planktonic species of harpacticoid copepods. This probably represents a definite selection, as this species of copepod, though ubiquitous, never achieved numerical importance in our plankton hauls. Jack mackerel (*Trachurus trachurus*) larvae were reported by Sinyukova (1964) to have an "inborn ability" to select two species of copepods from the mass of plankton living in the Black Sea. On the other hand, the respective behavior of the early jack mackerel larvae and *M. norvegica* may cause the two species to be locally aggregated,

TABLE 3.—Food of jack mackerel larvae.

Food items	Size group					
	End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 10.5 mm	
	No.	%	No.	%	No.	%
Copepod eggs:						
Single eggs	5	4.3	9	4.4		
Egg sacs	1	0.9	4	2.0	1	0.6
Copepod nauplii:						
Calanoid	3		3			
Cyclopoid	5		2		1	
Harpacticoid	7		2			
Total nauplii	15	12.8	7	3.4	1	0.6
Copepod adults:						
Calanoid:						
Calanoid spp.	7		15		60	
Metridia sp.	1					
Candacia sp.					1	
Cyclopoid:						
Oithona sp.	1				3	
Corycaeus sp.	3		3		5	
Oncaea sp.	6		29		39	
Harpacticoid:						
Microsetella norvegica	46		130		56	
Microsetella rosea	1					
Clytemnestra rostrata					1	
Unidentified					4	
Total copepods	65	55.6	117	86.3	169	96.0
Euphausiid:						
Nauplii	1	0.9			2	1.1
Calyptopi			2	1.0	1	0.6
Cladocera			1	0.5		
Unrecognizable crustacean remains	10	8.5				
Pteropods	3	2.6	4	2.0	2	1.1
Tintinnids	16	13.7	1	0.5		
Foraminifera	1	0.9				
Total number of food particles	117		205		176	

perhaps at the surface, thereby allowing the larva a disproportionate chance of securing individuals of this copepod.

Jack mackerel larvae may perceive food organisms by their color, since *M. norvegica*, and species belonging to the genera *Corycaeus* and *Oncaea*, are among the most brightly colored or least transparent of copepods. Species of the two latter genera also enter into the diet of jack mackerel larvae. Calanoid copepods become more important in the diet of larger larvae, perhaps because of an increased visual acuity, or their larger mouths, or a change in their vertical distribution. Whereas each feeding sardine or anchovy larva normally contains only one or two food particles, feeding jack mackerel larvae usually contain more. Some intestines contained *M. norvegica* in numbers as high as a dozen with no other observable food items.

Size of Food

The relatively large mouth of jack mackerel larvae is reflected in the larger food particles ingested (Figure 5). The preponderance in numbers of particles at a size of 120 μm (greatest cross-sectional dimension) is due to the apparent selection of *M. norvegica*. The gape of the larva apparently increases isometrically with increasing length of the larva. At 3.5 mm long, it can ingest particles up to 225 μm in cross section. Doubling its length to 7.0 mm also doubles its ingesting capacity to particles of about 435 μm in cross section.
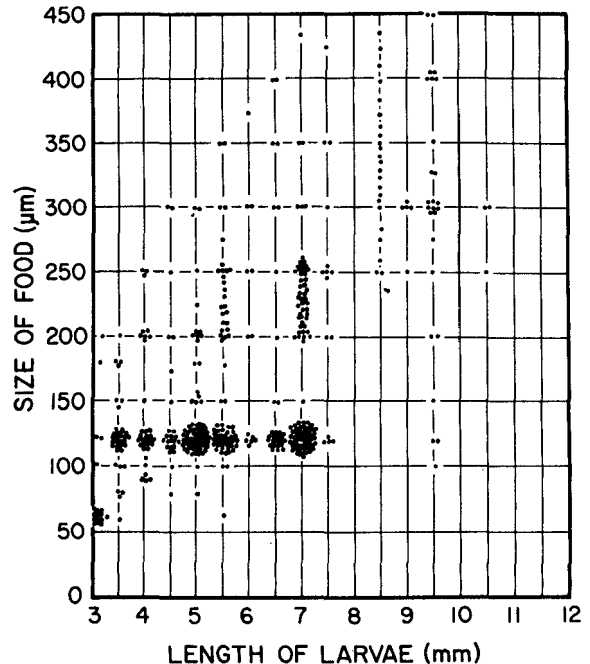

FIGURE 5.—Food size of jack mackerel larvae.

COMPARISONS

Type of Food

The three species may be characterized as primarily crustacean feeders as larvae (Table 4) and the youngest larvae are the most euryphagous. Crustacean food is predominant in all size groups of the larvae of all three species and, furthermore, becomes increasingly so as the larvae increase in size. Only in the smallest anchovies is noncrustacean food an important part of the diet.

TABLE 4.—Crustaceans as percentage of total number of identifiable food particles. Size groups of larvae—small = end of yolk-sac stage to 4.5 mm, middle = 5.0 to 6.5 mm, and large = 7.0 to 9.0 mm.

Species	Size group of larvae		
	Small (%)	Middle (%)	Large (%)
Sardine	96	100	100
Anchovy	58	82	100
Jack mackerel	83	98	99

Size of Food

Figure 6 compares the size ranges of food particles ingested by the three larvae. Because of their larger mouth, jack mackerel larvae can ingest particles about 3 times larger in diameter than can sardine larvae of the same length. This represents a difference in bulk of about 27 times between maximal ingestible sizes for the two larvae. The small anchovy can ingest particles about 40 to 50 μm larger than the maximum-sized particles of the sardine but does not appear to feed as frequently on organisms near to the maximum ingestible size as the sardine does.

Feeding Incidence and Its Relation to Type of Intestine

Feeding incidence increases with length in the jack mackerel but decreases with length in the anchovy and sardine (Figure 7). The high percentage of jack mackerel larvae containing food may indicate that either they are more voracious feeders, or their digestive rate is slower, or perhaps they are less apt to void their guts while being caught and preserved. Feeding incidence of larval fish appears to be associated with the morphology of the gut. The intestine of the sardine and anchovy remains long and straight with little observable differentiation until the larva is about 20 to 25 mm long. On the other hand, when the jack mackerel has attained a length of about 4.25 mm, a portion of its gut forms a loop. This loop divides the larval gut into definite functional parts. Based on a long-range study of feeding habits of fish in the Black Sea, Duka (1967) classified the larval gut into three types: long straight, short straight, and looped. Duka noted also that larvae with looped guts usually contained much more food than larvae with straight guts. Ciechomski and Weiss (1974) noted that the feeding incidence of E. anchoita larvae (0-28.0%) was much lower than of hake larvae (63.3-94.5%) taken in the
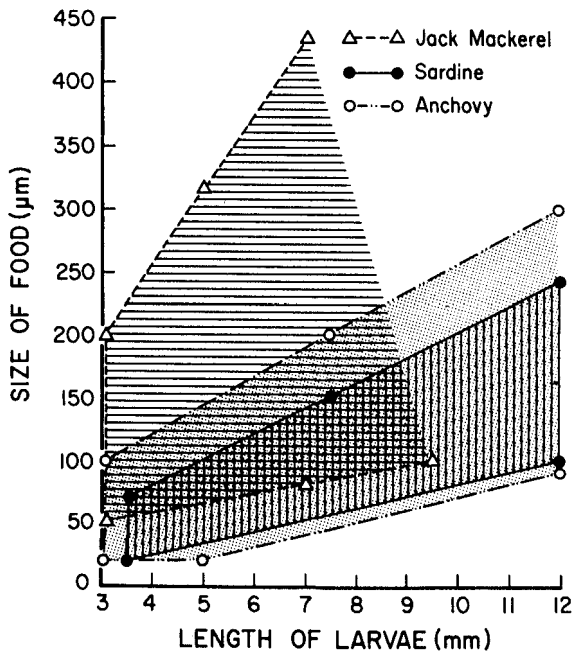

FIGURE 6.—Size range of food particles ingested by larvae of Pacific sardine, northern anchovy, and jack mackerel.
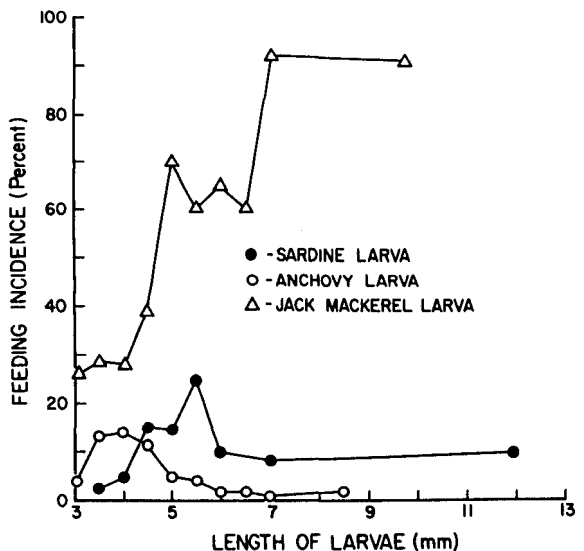

FIGURE 7.—Comparison of feeding incidence of Pacific sardine, northern anchovy, and jack mackerel larvae. Values for sardine and anchovy larvae are averages of day and night feeding incidences. Values for jack mackerel larvae are for all samples combined.

same plankton samples and that intestines of hake larvae are not straight but have several folds.

DISCUSSION

Significance of Feeding Incidence

For the past half century, there has been a discussion in progress concerning the significance of feeding incidence. Lebour (1921) called attention to the low feeding incidence of young clupeoids and attributed this to rapid digestion of food in the larval intestine. She was soon challenged by Hardy (1924) who, after observing herring larvae defecating after capture, assumed the low value to be an artifact produced by most larvae voiding their guts. The subject has attracted increasing interest recently. June and Carlson (1971) and Kjelson et al. (1975) observed older larvae of the menhaden, *Brevoortia tyrannus*, defecating after rough handling and fixation. Anchovy larvae have been observed defecating rotifers and *Gymnodinium* while being handled in the laboratory (John Hunter pers. commun.). *Gymnodinium* is eaten by *E. mordax* larvae in the laboratory (Lasker et al. 1970) and probably so in the ocean (Lasker 1975). Rotifers and the veligers of various species of molluscs in combination with *Gymnodinium* sustain anchovy larvae in the laboratory up to about 25 days of age (Lasker et al. 1970; Theilacker and McMaster 1971). Blaxter (1965), however, in attempts to assess the effect of Formalin [3] on food retention of herring larvae was able to demonstrate that only 10% of the larvae empty their guts due to Formalin fixation. Detwyler and Houde (1970) studying laboratory-grown larvae of scaled sardine *Harengula pensacolae*, and bay anchovy, *Anchoa, mitchilli*, found almost all of even the first feeding stages contained food after samples of them were taken from the plankton rich rearing tank and preserved in 5% Formalin. Feeding incidence of clupeoid larvae captured in plankton nets has been positively correlated with the availability of food by Pavlovskaia (1958), Nakai et al. (1966), Burdick (1969), Nakai et al. (1969), Bainbridge and Forsyth (1971), and Schnack (1974). Blaxter (1965) cited the wide variation and observed feeding incidence in the literature concerning herring larvae. I believe that much of the confusion has resulted from many authors failing to consider the time of day when larvae were caught (Figure 2) or the age of the larvae (Figure 4). When these variables are

taken into account, a series of observations of feeding incidence can reveal valuable insights into the tropho-dynamics of larvae. Feeding incidence must be viewed only as an indicator of feeding success because of the errors likely to be produced by defecation or to the difficulty in detecting soft bodied items such as *Gymnodinium*.

Comparison of the feeding incidence in four species of *Engraulis* (Figure 8) shows an increase in feeding incidence over larval lengths of 3 to 4 mm. Following this relatively high incidence at 4 mm, there is a drastic drop in this value until lengths of about 7 or 8 mm are reached. The mean feeding incidences for the four curves in this length range are 7 times higher for the 4-mm than for the 8-mm larvae. Feeding incidence remains low but relatively constant over the length range from 8 mm to about 14 mm at which point it begins to increase steadily over the remainder of the larval period. The value for the 20-mm length of *E. ringens* is based on only 12 specimens and, therefore, is not as reliable as values for other lengths.

The available data for sardine larvae suggest the same U-shaped curve. When the values for the sardine (Figure 7) are compared to Figure 8 it is seen that feeding incidence in relation to size falls roughly between *E. ringens* and *E. anchoita*, except that the decrease at intermediate sizes is not as precipitous. Yamashita (1955) reported the following feeding incidence values for larval *Sardinops melanosticta*: for about 14 mm = 8%, 21 to 30 mm = 56%, and 31 to 40 mm = 81% . The upward trend of these data is similar to those of larger anchovy larvae; however, the values are not comparable because the time of day of sampling was not reported. It seems significant that the shape of the curves of the four anchovy species (Figure 8) are so uniform in their relation to each other. *Engraulis ringens* is considerably higher than all others (except for the value at 20 mm). This probably is related to the rich plankton conditions of its habitat.

Clupeoid larvae visually detect prey, approach it, and then strike from a characteristic S-shaped posture. Proficiency of capture increases with age as observed in the laboratory for the larvae of herring and pilchard (Blaxter and Staines 1971), sardine (Schumann 1965), and anchovy (Hunter 1972). These investigators also noted that the volume of water searched increases with larval age. Feeding incidence should, therefore, increase markedly with age. Why, then, does the observed feeding incidence drop so drastically for anchovy

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
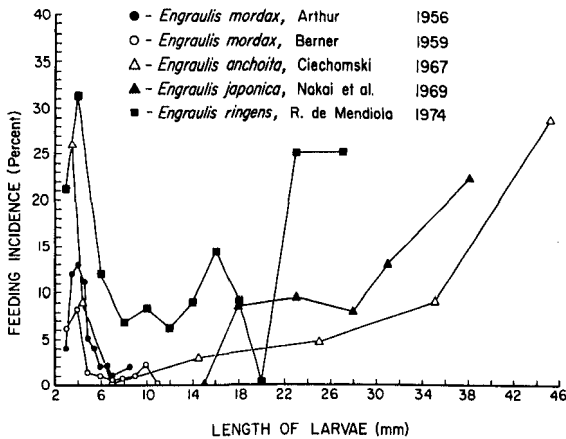
FIGURE 8.—Feeding incidence of larvae of various species of anchovy. Values are the average of day and night feeding (day values are divided by two because young anchovy larvae do not feed at night). Berner's data were recalculated to read "feeding incidence per length of larva" rather than "percent of feeding larvae occurring per length."

living in their natural environment? This could be partly a result of a faster digestive rate of older larvae as indicated for sardine larvae (Figure 2). It also could result if either the ambient food density decreases with time or the larval feeding activity decreases with age. There are reasons to suspect that both of these might occur and at the same time.

Decrease in Food Density

Sardine and anchovy larvae may initiate their first feeding in higher concentrations of food than they will experience several days later. Hand and Berner (1959) found that 74% of the food of adult sardines, when filter feeding at night, were small species of copepods, presumably the same species that produce the small nauplii so important in the diet of the sardine and anchovy larvae. Furthermore, they found that organisms in stomach contents had a high correlation with organisms in plankton samples taken at the same time and place. The adult anchovy, when feeding at night, is probably also a filter-feeding zooplanktivore although it does have more omnivorous tendencies (Loukashkin 1970), and the type of feeding, either biting or filtering, is controlled by the size of the food particles available (Leong and O'Connell 1969; O'Connell 1972). Both species also are selective feeders on larger organisms when visual conditions permit. As a consequence, filter-feed-

ing adults by actively searching for rich feeding conditions for themselves also prospect areas suitable for their larvae. More sardine and anchovy larvae were shown to occur in samples where both species were collected than in hauls where they occurred alone (Ahlstrom 1967); he concluded that these samples were collected near centers of heavier spawning for both species. It would appear that spawning adults of the two species were seeking out the same conditions. Sardines (Ahlstrom 1954), northern anchovies (Bolin 1936), and Argentine and other anchovies (Ciechomski 1965) spawn at night. Both spawning and filter feeding take place at night; therefore, the eggs may be laid near concentrations of suitably sized copepods (assuming spawning and feeding occur on the same night). However, as soon as the eggs have been spawned, they begin to be dispersed by water movement from each other and from organisms they will need for food several days hence. Sardine eggs are spawned in dense patches according to Smith (1973), who calculated that the horizontal mean distance between nearest neighbor eggs is of the order of 1 to 2 cm at spawning and changes to 15- to 20-cm mean distance for several-day-old larvae. These larvae may experience a diminution of their early feeding conditions as a result of diffusion as well as of grazing by the various predators. These ideas are presented to suggest how a general dilution of the co-occurrence of egg and plankton patches could occur in time. Lasker (1975) has recorded how rich larval feeding conditions can be destroyed overnight by a single storm.

Condition of Ocean-Caught and Laboratory-Grown Anchovy Larvae

There are differences in physical condition of the average ocean-caught and laboratory-grown anchovy larvae. These differences are probably a result of the available food.

Ahlstrom et al.[4] have presented a series of measurements of anchovy larvae and juveniles taken randomly from samples of the CalCOFI program. Figure 9 is a scatter diagram of relative body depths (body depth measured just anterior to pectoral fin base ÷ standard length) calculated from the above date. This diagram demonstrates that relative body depths of ocean-caught anchovy

[4]Ahlstrom, E. H., D. Kramer and R. C. Counts. Egg and larval development of the northern anchovy, *Engraulis mordax*. Unpubl. manusc.
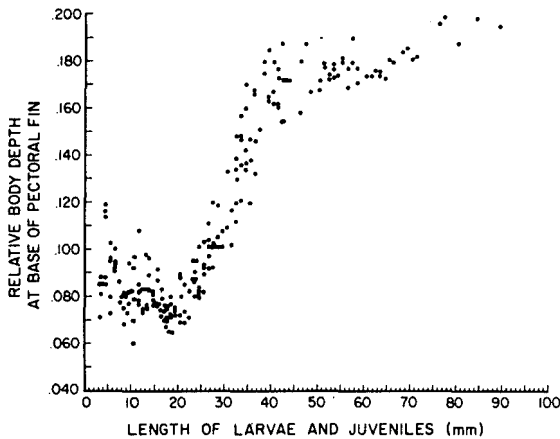
FIGURE 9.—Relative body depth of ocean caught northern anchovy larvae and juveniles calculated from Ahlstrom et al. (see text footnote 4).

larvae generally decrease until they are 17 to 18 mm long. Figure 10 compares relative body depth, averaged per millimeter of length, of the above ocean-caught anchovy larvae to that of larvae grown in the laboratory. These are larvae grown by Kramer and Zweifel (1970, experiment 17-II) at 17°C on a diet of wild plankton and with a feeding incidence described as "high." At the 10-mm length the two curves are different at the 0.05 sig-
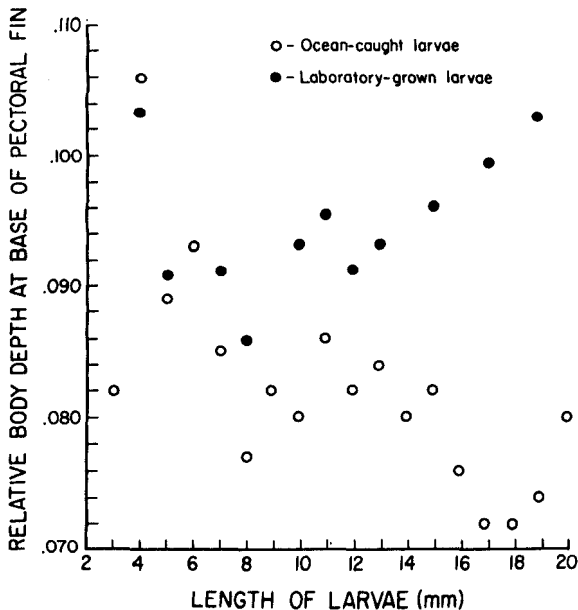

FIGURE 10.—Comparison of relative body depth of ocean caught and laboratory grown northern anchovy larvae. Each point represents an average of at least four larvae.

nificance level (*t*-test) and they differ with greater significance at increasing lengths.

Condition factor (weight ÷ length³) for laboratory-grown anchovies increases throughout the larval period as calculated from weight-length relationships presented by Lasker et al. (1970) and Hunter (1976).

Condition factor for ocean-caught *E. anchoita* larvae as calculated from wet weight data recorded by Ciechomski (1965) is at its lowest value between 15 and 20 mm.

The available data, therefore, indicate that relative body depths and weights of well-fed laboratory-grown anchovy larvae increase allometrically throughout the larval period, whereas these values for average ocean-caught larvae are at a low value at some midlarval period, followed by an increase through metamorphosis. This increase is probably related to the start of transformation to the juvenile stage but may also be accelerated by improving nutrition.

A relationship between gut thickness and feeding conditions was reported for ocean-caught larval sardine *Sardinops melanosticta* (Nakai 1960, 1962). The relationship of body depth to the nutritional level of fish larvae has been recorded for *E. japonicus* (Honjo et al. 1959; Nakai et al. 1969) together with relative body weight for herring larvae (Blaxter 1965, 1971). Blaxter attributed the low value of body weight for ocean-caught herring larvae to scarce plankton and to few feeding hours in the Clyde area at the time of sampling. The 14- to 15-mm long laboratory-grown herring larvae when deprived of food died at relative body weights that were higher than those of living ocean-caught individuals. This may be a result of the ocean-caught larvae having survived on suboptimal rations most of their existence whereas the laboratory-grown larvae had ample rations until the time they were suddenly deprived of food. The observed decrease in condition with size might also be an index of the increasing ability to resist starvation. The rich feeding conditions of successful laboratory-rearing experiments probably seldom obtain in the ocean (Lasker 1975; Hunter in press), and this may be reflected in the condition of the average ocean-caught larva.

The sardine larva initiates its first feeding activities in a nutritional deficit (Lasker 1962). This may also be indicated by the increasing thinness of the average ocean-caught *E. mordax*

larva until about midway through its larval existence. Further research is required to determine if the decline in relative physical condition indicates a state of serious malnutrition and, if so, how far from the well-fed state can the condition of the individual vary without resulting in mortality. It is also possible that laboratory-reared larvae have abnormally large relative body depths.

Food Size, Feeding Incidence, and Condition of Anchovy Larvae

The foregoing discussion points to three significant trophic features of the average ocean-caught anchovy larva. These features are:

1. A lack of increase in food particle size proportional to the increase in length for larvae larger than 4 mm (Figure 3b).
2. A steep decline in feeding incidence beginning at 4.5 mm followed by an increase in this value during the second half of the larval period (Figure 8).
3. A decline in relative morphological condition at lengths from at least 10 mm to 17 or 18 mm, followed by an abrupt increase (Figure 9).

Feature 1 must partly reflect the size spectrum of the available plankton. Arthur (1956) and Beers and Stewart (1970) have shown that there are far more food particles of the size taken by the first feeding larvae (50-100 μm) than there are of larger particles suitable for older larvae (i.e., 200 μm). Sardine and jack mackerel larvae, however, are able to secure increasingly larger food particles (Figures 1, 5). When features 1 and 2 are considered together, it would appear that the average oceanic anchovy larva does not sustain its original feeding intensity.

Growth of laboratory-grown anchovy larvae becomes asymptotic at 6 mm long when fed only *Gymnodinium* and at 20 mm when fed only a combination of *Gymnodinium* and rotifers. This was noted by Hunter (in press), who concluded that it is physically impossible for larvae to ingest enough prey in order to grow when the prey are below a certain size. Therefore, the decrease in relative body depth of the ocean-caught anchovy larva (feature 3) could be directly related to the insufficient increase in food particle size (feature 1).

Feeding intensity of clupeoid larvae decreases with malnutrition (Blaxter and Ehrlich 1974; Hunter in press). If the decline in relative body depth does denote a condition of malnutrition, then the decrease in feeding incidence (feature 2) is correlated with this decline, and might be the causative factor. This might also result in larvae spending a longer residence time at these lengths which would introduce a bias in mortality estimates.

It is important to keep in mind that we are considering larvae which have grown in the ocean and have also been caught by plankton nets. This is the reason that the expression "ocean-caught" rather than "ocean-grown" has been used herein. It might be reasoned that the decline in physical condition is a sampling artifact produced by the plankton net catching an increasing percentage of sick or malnourished specimens of the larger larvae as a result of the larger healthy larvae being more capable of dodging the net. The same reasoning could be applied to the decline in feeding incidence. An examination of the physical condition of over 5,000 sardine larvae (Arthur 1956) revealed that there is a higher percentage of larvae in poor shape (e.g., with liver deterioration) taken in day hauls when healthy larvae can avoid the plankton net. Such evidence led Isaacs (1964) to theorize that day-caught sardine and anchovy larvae represent an approximation of the percentage of the population removed by natural mortality. Assuming this sampling bias, however, it then becomes difficult to explain the increase in both relative body depth and feeding incidence of the older larvae taken by the same sampling methods. Burdick (1969), while examining Hawaiian anchovy (*Stolephorus purpureus*) larvae, observed no difference of feeding incidence or physical condition between samples taken concurrently with 1-m net and a plankton purse seine. Assuming the plankton purse seine captures all larvae, sick or well, he concluded that there is no bias produced by only the healthy larvae being able to avoid the 1-m net.

The average ocean-caught anchovy is significantly less robust at its midlarval lengths than its laboratory counterpart, owing presumably to differences in their respective rations. The first feeding (4-day-old) laboratory-reared anchovy larva spends 85% of the daytime in intermittent swimming, 7% in feeding, and 4% at rest (Hunter 1972). Perhaps the undernourished average ocean-caught larva, in response to the usual suboptimal

food densities, conserves its dwindling energy resources by increased resting and waiting for prey to appear within its range.

Hjort (1914, 1926) hypothesized that large-scale mortality will result if the proper food is not available in sufficient quantity at the "critical period" when newly hatched fish larvae require their first feeding, and that the numerical strength of a year class, therefore, might be determined at this time. The increasingly thin shape of young ocean-caught anchovy larvae suggests that feeding problems may exist for sometime into the larval period. Saville (1971) proposed that a "critical stage" might occur at any stage between hatching and metamorphosis and that the detection of same would allow one to specify the earliest stage at which reliable indices of year-class strength could be determined. The end of the decline in relative body depth of the average ocean-caught larva might mark the point in the larva's development when the danger of starvation has diminished and perhaps, as suggested by Saville, is the earliest stage at which estimates of recruitment might be made.

ACKNOWLEDGMENTS

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