FIELD CRITERIA FOR SURVIVAL OF ANCHOVY LARVAE: THE RELATION BETWEEN INSHORE CHLOROPHYLL MAXIMUM LAYERS AND SUCCESSFUL FIRST FEEDING[1]

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ABSTRACT

Northern anchovy larvae, *Engraulis mordax*, produced by laboratory-spawned fish, have been used to detect concentrations of larval fish food in situ along the California coast. First-feeding larval anchovies, whose development was controlled by temperature manipulation aboard ship, were placed in samples of Los Angeles Bight water taken from the surface and from chlorophyll maximum layers. Feeding by larvae in water from the surface was minimal in all experiments but extensive feeding occurred in water from the chlorophyll maximum layers when these contained phytoplankters having minimum diameters of approximately 40 μm and which occurred in densities of 20 to 40 particles/ml. In March and April 1974, the chlorophyll maximum layer along the California coast from Malibu to San Onofre (a distance of about 100 km) consisted chiefly of a bloom of the naked dinoflagellate *Gymnodinium splendens*, a food organism known to support growth in anchovy larvae. Copepod nauplii and nonliving particles were never in high enough concentration or of the proper size to be eaten by the larvae. A storm which caused extensive mixing of the top 20 m of water obliterated the chlorophyll maximum layer and effectively destroyed this feeding ground of the larval anchovy.

Probably the major problem confounding fishery scientists interested in rational management of fisheries is an inability to predict recruitment failure (Gulland 1973) despite the vast amount of laboratory and field work on food chain analysis leading to fish production which has occupied many workers in marine studies for the past two decades (Steele 1970). Gulland (1973) asks the most pressing question, "Can a study of stock and recruitment aid management decisions?" and in the same article answers "No." This pessimistic reply is given because, as he says, "there is no method which is likely to be generally successful, [because] the most promising depends on lengthy and costly collection of data, probably extending over a long period." The work reported in this paper suggests an approach which has not been previously used in fishery research as far as I am aware, and which, I believe, makes the answer Gulland has given somewhat less pessimistic than when he made it.

However, it is generally agreed among fishery biologists that large spawning populations of fish do not ensure subsequent large year classes, and conversely, small spawning populations occasionally give rise to exceptionally large classes (Hjort 1926). Hjort (1914) postulated that these variations in year class strength are probably due to differential mortality of the larvae. He believed, for example, that the larvae of the Norwegian herring, *Clupea harengus*, suffered huge mortalities resulting in small year classes when there was a lack of food for the first-feeding larvae. The attractiveness of this hypothesis has generated a number of laboratory studies (see, for example, Lasker et al. 1970) which have shown that the density of larval food must be higher than that usually found at sea in order to obtain even moderate larval growth and survival. For an in-depth discussion of the larval "critical period" as affected by food see May (1974), and for a review of laboratory attempts to rear fish larvae, refer to May (1971). The conclusion that the mean density of larval food organisms in the ocean is generally too low to support reasonable survival of fish larvae through metamorphosis, is also substantiated by data from field surveys (Beers and Stewart 1967, 1969). Thus, despite extensive efforts in quantitative marine food chain analysis, it is yet to be demonstrated whether, where, and to what extent there are rich feeding areas in the sea for larval fishes.

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As a new approach to this problem it is the purpose of this study to show how laboratory-spawned fish larvae can be used to detect larval feeding grounds at sea and to point out some of the ways this technique might be used to provide the link between marine food chain research and stock and recruitment predictions in fisheries; the latter by determining what the environmental conditions at sea must be with respect to larval fish food to result in a good or bad survival year for particular species of fish larvae.

Because it is essential to the general methodology of using larval fishes as assay organisms for the fitness of seawater as larval fish feeding grounds, in the following I describe some background information on maturation and spawning of anchovies in the laboratory; the methods used for feeding larval anchovies; and the laboratory-determined criteria for feeding already known for the larva of this species. A description of the field work is then given, concluding with a discussion of the criteria which can be used to judge the fitness of the larval anchovy's environment.

THE NORTHERN ANCHOVY

In the California Current, the major pelagic fish population at present is that of the clupeoid *Engraulis mordax*, the northern anchovy. This species is found from British Columbia, Canada to Cape San Lucas, Baja California and extending west about 600 km. Although the anchovy has a protracted spawning season from December to August, about three-quarters of its spawning occurs in the winter and spring months of January, February, March, and April. The factors affecting larval mortality of clupeoids have been investigated in a number of laboratories throughout the world (Holliday and Blaxter 1963) including my own. Recently, it has been possible to intensify laboratory research at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service because of the continuous availability of anchovy larvae. This has been made possible by inducing sexual maturation of adults in the laboratory resulting in daily spawning and fertilization of anchovy eggs throughout the year. Details of this maturation and spawning technique are given by Leong (1971) and Lasker (in press). The availability of first-feeding larvae hatched from laboratory-spawned eggs has made possible the development of a technique whereby specific areas of the ocean could be examined for their potential as larval feeding grounds, and criteria established to characterize parts of the ocean as good or bad areas for larval survival.

LABORATORY-DETERMINED CRITERIA FOR SUCCESSFUL LARVAL ANCHOVY FEEDING

A background of information on larval anchovy feeding is available from a number of studies and was used to guide this investigation.

1. *Particle size at first feeding appears to be critical.* First-feeding anchovy larvae (standard length 3.5 mm) have small mouths and require a food particle about 50 μm in diameter, although particles larger than 100 μm may be taken (Berner 1959). Smaller particles may not be visible to the larvae. Berner (1959) reported that anchovy larvae smaller than 4 mm long taken in plankton tows had eaten particles ranging in length from 24 to 186 μm. However, over 70% of the food in their intestines was between 60 and 80 μm long.

2. *The number of particles per unit volume in the anchovy larva's environment must be above a minimum concentration.* O'Connell and Raymond (1970), using natural plankton as food, showed that the survival of first-feeding anchovy larvae was dependent, in their experiments, on the number of micronauplii per unit volume available to the larvae. Successful first feeding, as pointed out by Hunter (1972), also depends on a sufficiently high density of food particles to compensate for the low capture efficiency (about 10%) exhibited by anchovy larvae when they begin to feed.

3. *The kind of food organism determines survival and growth.* Lasker et al. (1970) fed a variety of phytoplankters and zooplankters to first-feeding anchovy larvae. Only one phytoplankter of those tested, *Gymnodinium splendens*, supported growth and gave relatively good results in survival experiments when compared with larvae fed natural plankton. The rotifer *Brachionus plicatilis*, although not found in the anchovy's normal habitat, also could be used as a laboratory food for older anchovy larvae and a small proportion of first-feeding larvae (Theilacker and McMaster 1971; Hunter 1972).

4. *The greater the concentration of food particles, the more frequent are the feeding strikes made by anchovy larvae; consequently the greater the success in capturing food.* Although examination of field-caught anchovy larvae reveal very few with

any food in their intestine (Arthur 1956; Berner 1959), this seems to be a result of rough handling due to capture in a plankton net and subsequent preservation with Formalin[3] which causes almost all anchovy larvae to defecate (Kjelson et al. 1975). In the laboratory a high proportion of anchovy larvae which had never seen a food particle will strike at and ingest them provided there is a high enough concentration of the right size food particles. Hunter and Thomas (1974) have shown that the rate of larval anchovy feeding increases with increasing food density.

Despite the success of O'Connell and Raymond (1970) and Kramer and Zweifel (1970) who were able to rear anchovy larvae using micronauplii concentrated in wild plankton samples, the quantities needed by the larvae seemed inordinately higher than the concentration of nauplii reported by Beers and Stewart (1967) for the euphotic zone of the California Current. It was possible, of course, that concentrations of nauplii exist in dense aggregations. Beers and Stewart (1970a) reported that nauplii concentrate in or immediately above chlorophyll maximum layers off the California coast. However, no concentrations have been identified which are high enough to support anchovy larvae (e.g., 1/ml). On the other hand, Lasker et al. (1970) showed that anchovy larvae would feed and grow on a diet of the dinoflagellate *G. splendens*. The fact that blooms of a variety of phytoplankters are known to occur in the California Current, particularly in the spring, suggested that phytoplankton cells were more likely to provide the particle size and cell density essential to survival and growth of first-feeding anchovy larvae. For these reasons, inshore chlorophyll maximum layers were selected as possible fruitful areas to investigate for larval feeding.

METHODS

To determine areas in the sea where high concentrations of living particles might be present, a pump was used to bring water on board from known depths. The hose from the pump was lowered below the surface by means of a metered winch. The water was pumped through a Turner fluorometer in the ship's laboratory to measure chlorophyll *a* and other fluorescing substances. Chlorophyll *a* was extracted from water samples taken at each station from different depths and the fluorescence profile adjusted to reflect only chlorophyll *a* (Kiefer and Lasker 1975).

A school of approximately 700 sexually mature northern anchovies, maintained in the aquarium of the Southwest Fisheries Center, La Jolla Laboratory, produce about 1,000 fertilized eggs per day. The number of eggs can be increased by injections of gonadotrophins to stimulate massive spawning in individual fish (Leong 1971). With temperature control of development (Lasker 1964), larvae in first-feeding condition can be made available whenever desired. Thus, preliminary to a cruise, development of embryos and larvae can be accelerated or retarded by temperature manipulation to ensure that on each day of the cruise there will be at least several hundred larvae ready to feed.

Prior to each of the cruises described here, fertilized eggs at the same stage of development were sorted into liter jars containing seawater previously filtered through a 5-μm pore size Cuno Aquapure filter, and the jars were immersed in water baths at suitable temperatures. For transport to the ship insulated chests were used, and on board a temperature-controlled room was continually adjusted between 13° and 18°C to insure that feeding larvae would be available on specific days. Recent studies have shown that newly feeding larvae have only about 2½ days after the yolk sac is absorbed to get sufficient food or they will die (Lasker et al. 1970).

Experiments to determine if samples of seawater contained suitable food for anchovy larvae were done in cylindrical, 8-liter jars wrapped with dull black cardboard and set on black plastic. Above the jars a bank of four "daylight" fluorescent lights were suspended which illuminated the surface of the jars at approximately 2,152 lux. When a sample of seawater was brought into the ship's laboratory it was permitted to warm slowly to room temperature. Larvae were added to 5 liters of seawater by pouring them from the incubation jars. Dilution of the 5 liters by the larval incubation water was corrected by concentrating the contents of an additional liter of seawater to a few milliliters with fine mesh netting and by adding the concentrate to the whole.

A gentle air stream was directed onto the surface of the water in each experimental vessel to ensure mixing of the water. Control experiments on shipboard with cultured organisms indicated that this had little effect on the larvae.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Two cultured food organisms, *G. splendens* and *B. plicatilis*, were used aboard ship to determine if any particular batch of test larvae was in good condition and would feed. Details on the culture of these organisms are given by Thomas et al. (1973) for *G. splendens*, and Theilacker and McMaster (1971) for *B. plicatilis*. Usually a control 5-liter seawater sample was seeded with one or the other cultured organism and a feeding experiment with larvae run concurrently with samples of natural seawater.

Larvae were permitted to feed for 8 h then siphoned out and sucked down onto a membrane filter (pore size 0.8 μm) using a vacuum pump. This rapid removal of larvae from the experimental containers and their fast immobilization on the filters prevented defecation. After air drying, microscopic examination of the transparent larvae permitted counts to be made of larvae which had been feeding and those which had not. The relative proportion of feeding to nonfeeding larvae was subsequently correlated with sizes of the food particles, chlorophyll content, species composition, and the number of particles available to the larvae.

A 1-liter subsample of each seawater sample was preserved with Formalin (final concentration 5%) (Beers and Stewart 1970b). Later the particles in the preserved seawater were settled out and the species enumerated. The method of Utermöhl (as described by Lund et al. 1958) was used to concentrate organisms from known volumes of preserved seawater, usually 100 ml. At least 100 cells larger than 20 μm in diameter were counted from each settled water sample.

On a cruise of the NOAA RV *David Starr Jordan*, 18-21 March 1974, a 16-channel electronic particle counter with a 280-μm pore, Coulter Counter Model Ta, was used to determine the size distribution and numbers of sized particles in seawater samples used for feeding experiments. Only particles 20 μm and larger were counted. Very good agreement was obtained between the electronic counter particle counts and those obtained with the inverted microscope. A comparison is shown in Figure 1. The speed of counting and sizing particles makes the multichannel particle sizing instrument desirable for rapid field assessment of larval fish food organisms. Because the electronic counter was unavailable for two subsequent cruises. 8-12 and 22-23 April 1974, the results for these are given from microscope counts only.

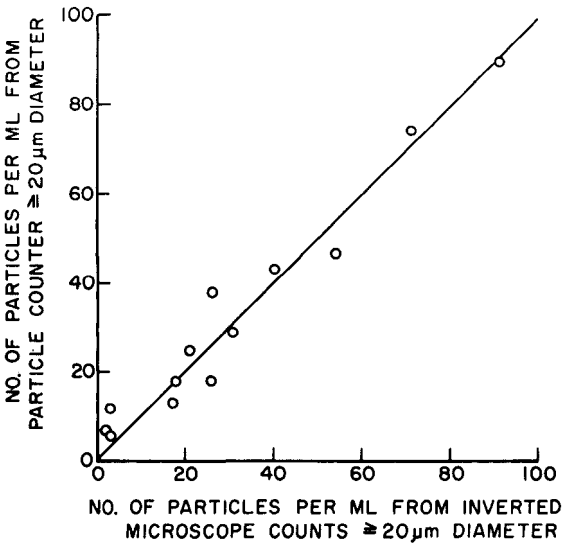

FIGURE 1.—Comparison between instantaneous particle counts per milliliter taken with Model Ta Coulter Counter and mean particle count per milliliter observed through an inverted microscope. A 100-ml sample was concentrated and at least 100 particles of the dominant organism were counted in any visual field. Only particles larger than 20 μm were counted.

To ascertain if anchovy larvae were present at particular depths, plankton tows were taken with a 0.333-mm mesh, 0.5-m mouth diameter net. Because an opening and closing net was unavailable for this work, an open net was dropped rapidly to the desired depth, towed for 10 min at a maintained wire angle of 45°, then pulled up rapidly. The total proportion of time the net spent in water other than in the desired stratum never exceeded 5% of the total towing time. All larvae captured were measured, sorted to species, and counted. Larval counts were corrected to a comparative volume of 1,000 m^3 (Kramer et al. 1972). A flowmeter in the mouth of the net provided a record of the volume of water filtered.

The shipboard experiments were ordinariy done at temperatures of between 15° and 19°C, whereas concentrations of larval fish food organisms and anchovy larvae were occasionally found between 14° and 15°C. It was desirable, therefore, to determine the feeding response of first-feeding anchovy larvae at different environmental temperatures. Experiments to determine this were identical to those done at sea except that the concentration of the cultured organism *G. splendens* was varied from 5 to 200 cells/ml, and the water temperature was controlled within ±0.2°C.

AREA OF STUDY

This investigation was conducted in the Los Angeles Bight along the southern California coastline from Malibu to San Onofre, between 18 and 21 March 1974. All the stations occupied were over the 20-fathom line except for the Laguna Beach station which was over the 270-fathom contour. Table 1 gives the coordinate positions and Figure 2 shows the relative location of the stations. The San Onofre station was reoccupied on 8 April 1974 to determine the persistence of the chlorophyll maximum layer which earlier had contained relatively large numbers of *G. splendens*. The station was occupied again on 10 April, after a violent wind storm and later on 22-23 April after a period of no storms.

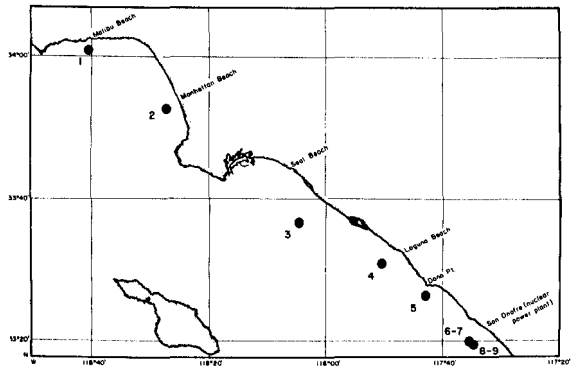

FIGURE 2.—Stations in the Los Angeles Bight.

RESULTS AND DISCUSSION

Shipboard Experiments with First-Feeding Anchovy Larvae

Table 1 provides a summary of the results of feeding experiments with first-feeding anchovy larvae in water from the surface and from the chlorophyll maximum layer or from a depth of about 15 m if no clear chlorophyll maximum was observed. The dominant phytoplankter in the chlorophyll maximum layers was *G. splendens*. For details about *G. splendens* blooms from Baja California, Mexico, and the Los Angeles Bight see Kiefer and Lasker (1975); as reported earlier, Lasker et al. (1970) had demonstrated that anchovy larvae will grow when fed on *G. splendens*.

Also given in Table 1 are the results of a feeding experiment at the San Onofre station on 8 April 1974, 18 days after a chlorophyll maximum layer containing *G. splendens* as the dominant phytoplankter was found. The chlorophyll maximum layer was still present and heavily populated with *G. splendens*. A violent wind storm on 9 April obliterated the chlorophyll maximum layer and no *G. splendens* were seen at this station when it was reoccupied on 10 and 11 April. A comparison of chlorophyll *a* profiles taken before and after the 9 April storm is shown in Figure 3. The results of control feeding experiments are given in Table 2.

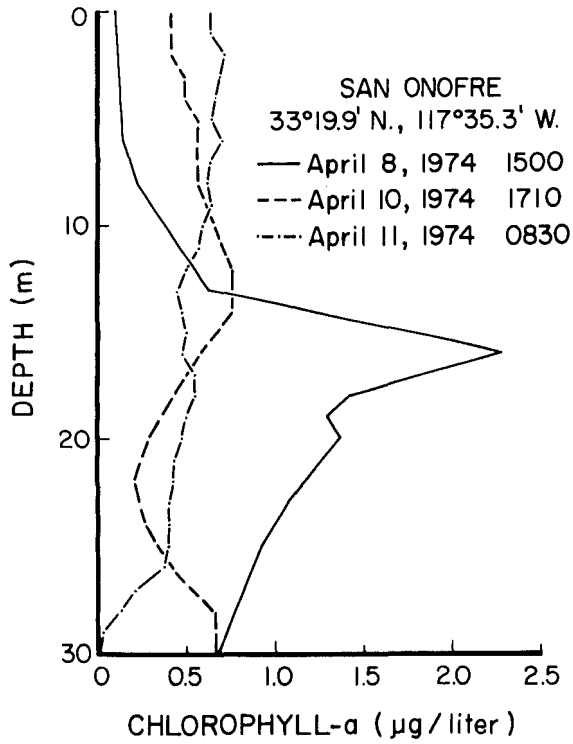

FIGURE 3.—Chlorophyll maximum layers before (8 April 1974) and after (10 and 11 April 1974) a violent wind storm near San Onofre, Calif.

Some anchovy larvae capture a few particles in any concentration of 20- to 100-μm particles over an 8-h period, but experience in the laboratory has shown that feeding on less than 1 particle/h will not sustain a first-feeding larva which becomes weak and dies. Thus, in Tables 1 and 2, two feeding categories are indicated: larvae observed with food organisms packed into the intestine, and

TABLE 1.–Summary of results of 8-h on-board feeding experiments with first-feeding anchovy larvae. *Gymnodinium splendens* appeared in the chlorophyll maximum layers (chl. max.) from Malibu to San Onofre, a distance of approximately 130 km. The subsurface bloom of *G. splendens* at San Onofre persisted until 8 April 1974 (see no. 7 below). A storm on 9 April obliterated the maximum and evidently dispersed the *G. splendens* by wind mixing (see Figure 3).

No.	Date and time A. Surf. temp. B. Chl. max., temp. and depth	Position (lat. N-long. W)	Total number particles/ml 23-37 μm diameter	 >37-299 μm diameter	μg Chl. *a* per liter	Feeding by anchovy larvae Percent of larvae with: ¼ to full gut	 1-8 particles in gut	Number of larvae per experiment
1	20 March 1974, 1250							
	A. 15°C	34°00.8′-118°40.6′	14.2	[1]4.1 (< 1)	[2]1.0	2	15	69
	B. 14.2°C, 12 m	(Malibu)	37.3	38.0 (12)	1.8	23	46	93
2	20 March 1974, 1745							
	A. 15.2°C	33°52.5′-118°27.0′	23.1	6.1 (6)	0.4	0	11	94
	B. 14.5°C, 13.5 m	(Manhattan Beach)	29.8	19.7 (12)	1.3	0	18	49
3	21 March 1974, 0900							
	A. 15.8°C	33°36.5′-118°04.3′	217.9	33.2 (< 1)	0.3	0	12	42
	B. 14.2°C, 16.5 m	(Seal Beach)	53.8	352.0 (380)	42.0	22	24	104
4	21 March 1974, 1340							
	A. -	33°30.8′-117°50.3′	34.0	9.0 (0)	0.6	0	10	20
	B. -, 15 m (no chl. max.)	(Laguna Beach)	29.0	5.7 (0)	0.7	0	11	46
5	21 March 1974, 1715							
	A. 15.5°C	33°26.3′-117°42.8′	18.7	5.9 (< 1)	0.5	[3]5	16	19
	B. -, 15 m	(Dana Point)	55.2	23.2 (5)	1.3	0	69	26
6	21 March 1974, 1900							
	A. 15.2°C	33°19.9′-117°35.3′	9.3	4.0 (< 1)	0.2	0	8	49
	B. -, 19.5 m	(San Onofre)	42.4	47.7 (34)	2.3	9	25	32
7	8 April 1974, 1500							
	A. 17.1°C	33°19.9′-117°35.3′	5.7	9.1 (< 1)	0.2	0	13	23
	B. 14.8°C, 16 m	(San Onofre)	14.0	81.3 (64)	2.3	9	40	58
8	10 April 1974, 1710							
	A. 14°C	33°19.4′-117°34.6′	8.4	14.1 (0)	–	0	12	33
	B. 13.5°C, 14 m (no chl. max.)	(San Onofre)	10.5	23.2 (0)	0.8	0	15	20
9	11 April 1974, 0915							
	A. 13.0°C, 5 m (no chl. max.)	33°19.5′-117°34.6′ (San Onofre)	6.4	10.5 (0)	0.6	0	4	50

[1]( ) = number of *G. splendens* per milliliter.
[2]Particles smaller than 20 μm may have contributed to the elevated chlorophyll *a* at this station.
[3]This 5% figure represents only one larva which filled its intestine ¼ full.

TABLE 2.–Controls for the experiments reported in Table 1. Surface water was seeded with *Gymnodinium splendens* or *Brachionus plicatilis*. In each instance the results showed that the larvae on shipboard were competent to feed. Feeding time was 8 h.

Date	Species seeded	Number particles/ml	Feeding by anchovy larvae Percent of larvae with: ¼ to full gut	 1-8 particles in gut	Number of larvae per experiment
20 March 1974	*B. plicatilis*	40	29	45	72
8 April 1974	*G. splendens*	100	27	13	30
10 April 1974	*G. splendens*	100	32	22	46

those with eight or fewer particles in the intestine after an 8-h feeding period. The largest proportion of larvae did not feed at all, a result common to laboratory experiments as well. The feeding intensity at Malibu, Seal Beach, and San Onofre is typical of first-feeding anchovy larvae in laboratory experiments seeded with a like number of suitable size particles, e.g., *G. splendens*.

The data presented in Table 1 show that the criteria for larval anchovy feeding determined by laboratory experiments are the same when freshly obtained seawater is tested as a source of larval anchovy food. Large numbers of particles smaller than 37 μm in diameter did not stimulate feeding in anchovy larvae. This was particularly apparent at Seal Beach on 21 March; surface water having 218 particles/ml smaller than 37 μm in diameter but with low chlorophyll *a* did not stimulate anchovy larvae to feed. Conversely, the bloom of *G. splendens* in the chlorophyll maximum layer produced heavy feeding larvae tested in shipboard experiments. Furthermore, even with particles

having the right diameter for feeding, a minimum concentration of perhaps between 25 and 50 cells/ml was needed.

The Effect of Temperature on Feeding

The chlorophyll maximum layers along the coast were characterized by temperatures between 14° and 15°C, which is lower than the optimum temperature for feeding and growth in anchovy larvae (16°C). Because shipboard experiments were done at temperatures higher than those found in the chlorophyll maximum layers it was desirable to determine if the minimum particle count at which first-feeding larvae were stimulated to feed was in any way reduced by lower temperatures. Figure 4 illustrates the results of experiments which show that at 14°C, the food particle count must be higher than 20 cells/ml before significant feeding can occur over an 8-h period. At the higher temperature tested, 18°-19°C, food particle counts of between 5 and 20 particles/ml may stimulate feeding. However,

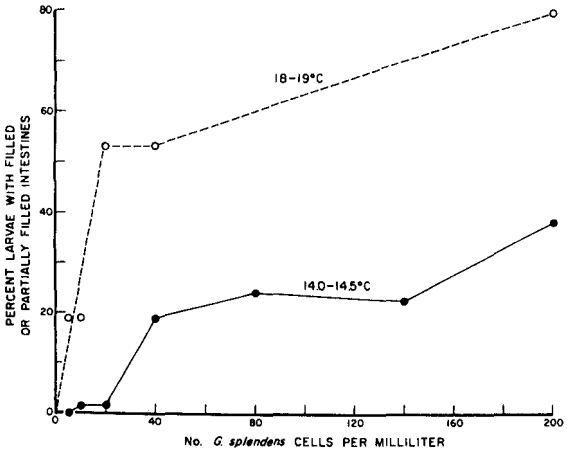

FIGURE 4.—The effect on larval anchovy feeding of different concentrations of food at two temperatures. Each experiment began with 100 larval anchovies which were in first-feeding condition and was terminated after 8 h. See text for details.

during the shipboard experiments, particle counts of 5-20 cells/ml did not stimulate larval feeding even at the higher temperatures (15°-19°C) of the ship's laboratory (Table 1). This discrepancy may be due to the different kinds of food particles available to the larvae, as well as to other factors related to a larva's inability to capture certain particles as opposed to others. For example, when *Chaetoceros* sp. was present in any of the samples, anchovy larvae did not feed on this phytoplankter, owing probably to the spiny nature of this chain-forming diatom, despite the considerable lengths (longer than 37 μm) of the chains. In the Seal Beach surface sample taken on 21 March 1974, *Chaetoceros* sp. and other chain-forming diatoms made up over 30% of the longer than 37-μm category. This result was confirmed at a station off Imperial Beach, Calif. (lat. 32°34.0′ N; long. 117°10.5′ W) on 11 April where a dense bloom dominated by *Thalassiosira* sp. (37 chains/ml) was found. Chlorophyll *a* at the surface was 4.8 μg/liter and slightly higher, 5.1 μg/liter, at a depth of 7 m. Feeding by anchovy larvae on this organism was virtually nil. Thus, the composition of the stock of phytoplankton appears to be an important factor in the initial feeding of anchovy larvae.

The observations described above indicate that chlorophyll measurements alone, and the indication of a strong chlorophyll maximum layer are not by themselves sufficient criteria for establishing the existence of good conditions for the feeding of anchovy larvae. A cruise of the RV *David Starr Jordan* was made back to the San Onofre station on 22 and 23 April 1974. A sharp chlorophyll maximum layer was discovered there once again and was found to extend seaward for at least 14 km (Figure 5), yet shipboard larval anchovy feeding was negative. Subsequent microscopic examination of the water from these layers indicated that cryptomonads of about 10 μm in diameter dominated the samples in concentrations of 3,400-7,200 cells/ml, a size too small to be fed upon by anchovy larvae.

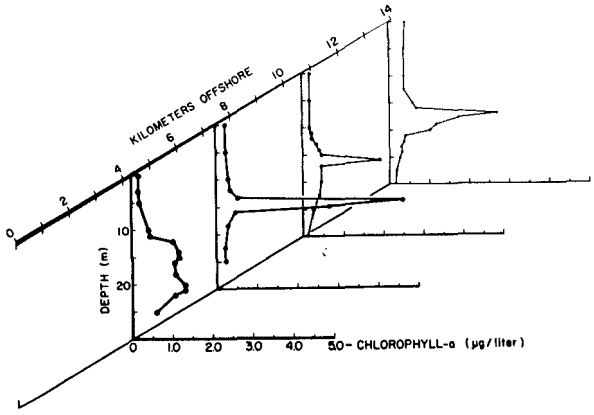

FIGURE 5.—Chlorophyll maximum layers off San Onofre, Calif., 22-23 April 1974.

Vertical Distribution of Anchovy Larvae

At San Onofre on 8 April the chlorophyll maximum layer was due, in part, to a high density of *G. splendens*. Larvae on board ship fed freely in the water from this layer. Judging from the larval feeding and the size and density of the food particles, this chlorophyll maximum layer should have been an ideal place for first-feeding larvae to be found. To test this, plankton tows were made at three depths: within the chlorophyll maximum layer at 16 m, just above the layer at 10 m, and at the surface (see Figure 3). The standard length of anchovy larvae from these tows was measured, and the degree of eye pigmentation noted (full pigmentation indicating a visually competent larva). The results, given in Table 3, show that there was a distinct difference in vertical distribution between the number of first-feeding larvae that could see as opposed to yolk-sac larvae which lack eye pigmentation and could not see.

The surface water contained 2,100 anchovy larve/1,000 m^3. Larvae without eye pigmentation outnumbered sighted larvae two to one. At the 10-m stratum above the chlorophyll maximum layer there were 40,000 anchovy larvae/1,000 m^3 with larvae capable of seeing outnumbered by eight to one. In the chlorophyll maximum layer 4,900 anchovy larvae/1,000 m^3 were present but larvae that could see were about as numerous as those which could not. Although it may be coincidental, the possibility that larvae were actively seeking out areas with food cannot be dismissed.

TABLE 3.—Distribution of anchovy eggs and larvae at three depths off San Onofre, Calif., 8 April 1974.

Stratum	Number of eggs or larvae per 1,000 m^3		
	Larvae with pigmented eyes	Larvae with unpigmented eyes	Eggs
Surface	756	1,344	67,200
10 m	4,610	35,804	151,965
16 m	2,004	2,941	60,034

Criteria for Successful First-Feeding by Anchovy Larvae

It is evident from the data presented in this report that the following environmental criteria must be met before first-feeding anchovy larvae can feed successfully in the ocean. Phytoplankton aggregations with over 20 cells/ml must be available at the same time or within 2½ days after the larvae are ready to feed. Individual phytoplankton cells must be about 40 μm in diameter. Successful feeding is dependent on food density so that the higher the concentration of cells, the better the feeding. Monotypic algal blooms are responsible for some chlorophyll maximum layers off the California coast and first-feeding anchovy larvae were found to be living within them. Only some phytoplankters stimulate feeding and support growth of anchovy larvae; for example *G. splendens* is known to support growth while anchovy larvae would not feed on *Chaetoceros* sp. or *Thalassiosira* sp., spiny and/or chain-forming diatoms. Finally, it could not be demonstrated that micronauplii or other microzooplankton contribute significantly to larval anchovy survival during the first week of larval life. Beers and Stewart (1967) reported that in December 1965, the inshore station off San Diego (their station I) contained a maximum of only 30 organisms/liter in the 35 to 103-μm size class. Of these organisms, copepod nauplii and post-nauplii together numbered 7-9/liter, two orders of magnitude lower than that required by anchovy larvae to survive, i.e., 1,000/liter (O'Connell and Raymond 1970). However, it is reasonable to assume that under special circumstances suitable concentrations of micronauplii might serve as a food source for first-feeding anchovy larvae. Nonliving particles larger than 37 μm were not seen and may be insignificant in the nutrition of first-feeding anchovy larvae because of their low concentration in anchovy spawning areas.

It is important to emphasize the transient nature of good feeding conditions. There was a large number of larvae present at depth at the San Onofre station on 8 April 1974, capable of taking advantage of the subsurface bloom of *Gymnodinium*. Furthermore, spawning had been extensive in the entire water column as indicated by the large number of anchovy eggs caught during the same tows (Table 3). Earlier I indicated that a wind storm obliterated the chlorophyll maximum layer at San Onofre on 9 April 1974, and that 8-h shipboard experiments showed the larvae were unable to capture enough food on 10 and 11 April to fill or partially fill their intestines. If my contention is correct, then a large proportion of the larvae which were present as eggs or yolk-sac larvae on 8 April were doomed to die from lack of food after the storm on 9 April because of the dilution and dispersion of suitable larval food organisms.

Although this investigation was confined to first-feeding anchovy larvae, the technique

described here, using laboratory-reared larvae for field tests of possible larval feeding areas, probably can be extended to older larvae and other species as well. An on-board electronic counter can give a rapid first evaluation of particle size and cell numbers. Microscopic examination of subsamples can be used to verify the shipboard counts and give additional information on species composition of phytoplankters. Chlorophyll profiles can be analyzed routinely on most oceanographic vessels. With information on the biology of the larvae being investigated, it may be possible to determine routinely the quality and extent of larval feeding grounds and with comprehensive temporal information on the food of the larvae, the degree of larval mortality due to inadequate food may be predictable.

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LITERATURE CITED

ARTHUR, D. K.
1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Ph.D. Thesis, Univ. California, Scripps Inst. Oceanogr., La Jolla, 231 p.

BEERS, J. R., AND G. L. STEWART.
1967. Micro-zooplankton in the euphotic zone at five locations across the California Current. J. Fish. Res. Board Can. 24:2053-2068.
1969. Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Mar. Biol. (Berl.) 4:182-189.
1970a. Numerical abundance and estimated biomass of microzooplankton. *In* J. D. H. Strickland (editor), The ecology of the plankton off La Jolla, California, in the period April through September, 1967, p. 67-87. Bull. Scripps Inst. Oceanogr. 17.
1970b. The preservation of acantharians in fixed plankton samples. Limnol. Oceanogr. 15:825-827.

BERNER, L., JR.
1959. The food of the larvae of the northern anchovy *Engraulis mordax*. Bull. Inter-Am. Trop. Tuna Comm. 4:1-22.

BLAXTER, J. H. S., AND F. G. T. HOLLIDAY.
1963. The behaviour and physiology of herring and other clupeids. Adv. Mar. Biol. 1:261-393.

GULLAND, J. A.
1973. Can a study of stock and recruitment aid management decisions? Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:368-372.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 20:1-228.
1926. Fluctuations in the year classes of important food fishes. J. Cons. 1:5-38.

HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.

HUNTER, J. R., AND G. L. THOMAS.
1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy *Engraulis mordax*. *In* J. H. S. Blaxter (editor), the early life history of fish, p. 559-574. Springer-Verlag, Berl.

KIEFER, D. A., AND R. LASKER.
1975. Two blooms of *Gymnodinium splendens*, an unarmored dinoflagellate. Fish. Bull., U.S. 73:675-678.

KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON.
1975. The general feeding ecology of postlarval fishes in the Newport River estuary. Fish. Bull., U.S. 73:137-144.

KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

KRAMER, D., M. J. KALIN, E. G. STEVENS, J. R. THRAILKILL, AND J. R. ZWEIFEL.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-370, 38 p.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.
In press. Induced maturation and spawning of marine fish at the Southwest Fisheries Center, La Jolla, California. Proc. 5th Annu. Workshop, World Mariculture Soc.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.

LUND, J. W. G., C. KIPLING, AND E. D. LECREN.
1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11:143-170.

MAY, R. C.
1971. An annotated bibliography of attempts to rear the larvae of marine fishes in the laboratory. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-632, 24 p.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, Berl.

O'CONNELL, C. P., AND L. P. RAYMOND.
1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

STEELE, J. H. (*editor*).
1970. Marine food chains. Univ. Calif. Press, Berkeley, 552 p.

THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. Mar. Biol. (Berl.) 10:183-188.

THOMAS, W. H., A. N. DODSON, AND C. A. LINDEN.
1973. Optimum light and temperature requirements for *Gymnodinium splendens*, a larval fish food organism. Fish. Bull., U.S. 71:599-601.