

## SOME ASPECTS OF BEHAVIOR IN CLUPEID LARVAE

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One of the most interesting phases of my project of rearing larvae of pelagic fishes has been the opportunity to investigate some aspects of theories proposed to explain peculiarities of feeding and high mortality among clupeid larvae. Owing to the marked decline of Pacific sardine (*Sardinops caerulea*) populations off the coast of California, particular emphasis has been placed on studying the larval history of this fish.

Sardine larvae can be placed into a natural assemblage of fish larvae possessing non-functional optic, oral, digestive and excretory systems at hatching. Food reserves in the form of egg-yolk are generally small in this group, and the larvae also seem to be exceedingly sensitive to largely undetermined environmental factors affecting survival during early larval life. In addition to pelagic larvae this group includes some larvae originating from demersal eggs of marine and freshwater species as well.

### LARVAL MORTALITY

One of the primary considerations in studies of clupeoid fishes, and particularly in studies on the Pacific sardine has been the elucidation of factors responsible for mortality of larvae during a period up to and including metamorphosis of larvae to the adult body form. As in all fish spawning large numbers of eggs, an enormous reduction in numbers of individuals occurs between the egg and adult. Although it was known long ago that mortality must be highest in the earlier life stages, it is only recently that anyone has attempted to learn just when and where in time this took place.

Early attempts at rearing the pelagic young of some marine fishes were for the most part futile, even though a quite comprehensive hatchery technology had been developed for rearing many species of freshwater fishes. Two of the earliest investigators of pelagic marine fish larvae, Fabre-Domergue and Biéatrix (1897), noted that small marine fish larvae being reared in aquaria died soon after the yolk-sac was absorbed and the tiny larvae became dependent upon the environment for nourishment. Because mortality was low or absent during embryonic, and the pro-larval stages, and high when the yolk reserve was exhausted and the larva began to search for food, some significance was attached to rate of survival during the first days of active life. This time of apparent extreme sensitivity to the environment was termed a "critical period." Later Hjort (1914, 1926) discussed a critical period concept whereby in general fish larvae were thought to have sensitive periods particularly in relation to their food supply.

Specifically, a "critical period" is thought to be a time when larvae are prone to markedly increased mortality over a short time span. "Short time" in this context may be a matter of several days to several weeks depending upon the species of fish and period in the life history. For instance, a "critical period" for sardine larvae reared in aquaria (although not definitely established for larvae in nature) may occupy a time interval of between several hours to several days, may occur more than once during larval life.

Attempts to study the rate of survival of various species of fish larvae in nature have proven difficult. Although much of our still inadequate information concerning survival has been drawn from studies of economically important freshwater fish populations, our knowledge of the details affecting survival of fish from the time of hatching to some early juvenile stage is fragmentary even for the most intensely studied and easily accessible freshwater fish species. It is not surprising, therefore, that although special interest and studies concerning the fate of pelagic eggs and larvae of various marine fishes took shape some 60 years ago, very little factual information is at hand on details concerning survival of larvae in the open sea.

One of the most informative studies on the survival of sardine eggs and larvae over the major portion of the distributional range, has been that of Ahlstrom (1954), whose Figure 32 (p. 138) is reproduced here as Figure 1. It may be seen that losses seem to be quite high between the final egg stage (hatching) and larvae of 3.25 and even 5.75 mm in length.

It would be of considerable importance to know precisely when losses took place because if mortality were actually high during a limited period of time, a few days after the yolk was absorbed, for instance, then the term "critical period" might have special biological significance. The factors causing mortality might then be sought in the physiology and particular food relations of larvae during the short time when they become wholly dependent upon external sources of nutrition and first subject to the stresses of an active life.

On the other hand, if losses were of a high but decreasing intensity over the first weeks of life, no one period could logically be considered as potentially more hazardous for sardine larvae than any other period. Mortality would then be a form of continuous environmental attrition removing a percentage of the larval population. Factors causing mortality might then be expected to be any or all normal dangers of life such as disease, predation, food supply and the like.

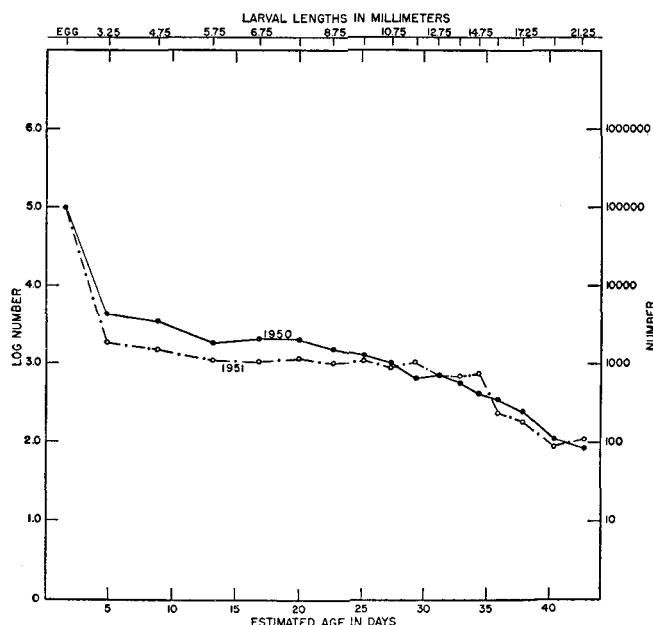


FIGURE 1. Survival of sardine larvae in the sea based on numbers of larvae in net samples (after Ahlstrom, 1954).

In discussing his Figure 32, Ahlstrom points out that although there seems to be an abrupt decline in numbers of larvae during the yolk-sac stages of development (when larvae are independent of external sources of nourishment), it is more likely the loss is an artifact resulting from the escape of very small larvae through the meshes of the net. Marr (1956), in discussing the significance of this loss (p. 167), mentions that evidence suggests only one-tenth of 3.25 mm sardine larvae encompassed by the net used by Ahlstrom were retained by the meshes. Figure 1 shows that rate of survival seems fairly constant from about the 5.75 mm stage of growth to at least 12.0 mm, therefore it may be assumed that the net had reasonably good retention of larvae from at least the end of the yolk stage, or by the onset of feeding (5.0–5.5 mm) in sardine larvae. If this assumption is reasonable then the numbers of larvae reported by Ahlstrom to be present at the 5.75 mm stage of growth may have represented the actual situation, while numbers reported present in the 3.25 to 4.75 (or 5.0) mm stage may in actuality have been far higher at one stage or another, meaning after Marr, that the magnitude of increase could be nine fold at any point. In other words, escapement may mask when any sudden reduction in numbers may occur and the severity of such reduction. In any event, there seems little reason to doubt that quite rapid decline in numbers does take place in sardine larval populations between two fairly reliable points of population estimation i.e., the egg and 5.75 mm stage. The recent paper by Isaacs (1964) and the discussion elsewhere in this symposium show that when all data are considered (70,000 sardine larvae from 10,000 plankton hauls over the years 1950 to 1957) there is a steep mortality curve for sardine larvae ending at approximately 5.75 mm–6.75 mm.

It is not the purpose of this paper to enter too deeply at this time into the specific question of whether or not "critical periods" do actually exist in nature during larval development, but rather to present some facets of larval behavior occurring during the first weeks of active life. On the other hand, some interesting though tentative observations on survival rate of "populations" of sardine larvae in large aquaria seem worth mentioning here, particularly in relation to Figure 1. A curve describing the mode of survival of 200 sardine eggs, pro-larvae and larvae up to 12 mm in length (Fig. 2) very closely approximates the curves in Figure 1.

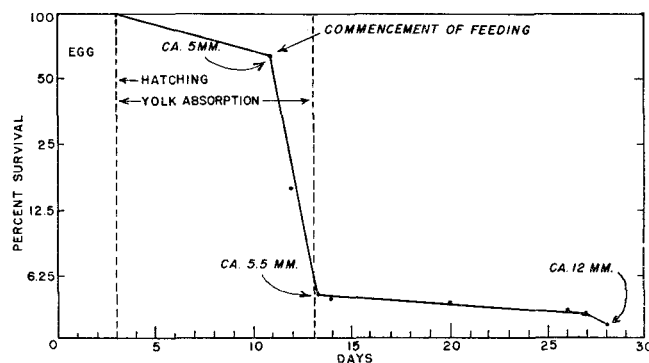


FIGURE 2. Aquarium experiment. Pattern of survival of 200 sardines at various stages of development.

In these aquarium experiments 200 sardine eggs of the same stage of development were allowed to hatch and a record maintained of daily losses in all stages of growth. Losses were very low or absent during the embryonic period; tests included a number of experiments with eggs collected at an early stage of development thus requiring about  $2\frac{1}{2}$  days to hatch (at  $16^\circ$ ), and eggs held for longer periods at low temperatures. Losses were also low or absent during the pro-larval stage (7 days), while nutrition was obtained from the yolk supply. Approximately at the point, however, when larvae began actively searching for food (5.0–5.5 mm) while existing on stored energy and body tissue, losses began to mount rapidly. Only in exceptional cases was survival during the next three days better than 10 out of about 200 pro-larvae. In several separate instances, after 5 or 10 larvae had survived to a size of approximately 5.5 to 6.0 mm in length, no further losses were experienced until about the 11–12.0 mm stage of growth (about 30 days after hatching), and a time when larvae seemed to be changing their feeding habits, when losses again were high.

Rearing experiments by Blaxter (1962) with herring larvae seem to indicate a pattern of survival comparable to that found for the Pacific sardine. After an initially high mortality upon complete yolk absorption, surviving herring larvae had a low mortality until a later period in development when mortality was again high. Blaxter's Figure 5, reproduced here as Figure 3, is particularly interesting in that the overall pattern of survival in each experiment changed little although the actual number of larvae surviving subsequent to hatching varied from 10 to 50 percent.

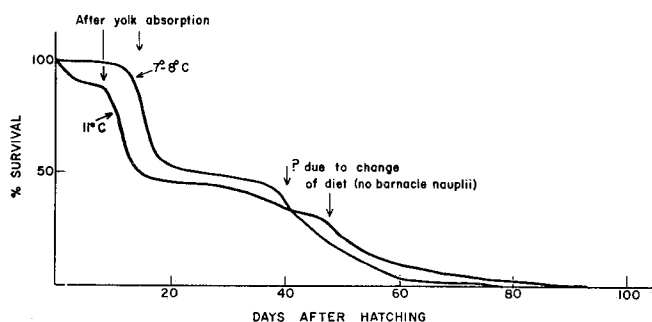


FIGURE 3. Aquarium experiments on survival of herring larvae at different temperatures (after Blaxter, 1962).

Ahlstrom's interpretation (p. 136-137) of his Figure 32 chooses between the seeming alternatives of a "critical period," or an artifact of net selectivity, to explain the abrupt decline between terminal egg and yolk-sac stages. Ahlstrom favored the latter explanation, but it seems at least possible, in light of the experimental results outlined above, that both conditions might apply. In other words, nets are not sampling the earliest larval stages accurately enough to detect a period of increased larval mortality just prior to the 5.75 mm stage of development, if, following Marr's (1961) conclusion that nine-tenths of the very earliest larval sardine stages escape through the meshes.

The curves showing survival in Figure 1, level off somewhat in the section reporting abundance of larvae between 5.75 and 11.75 mm in length, the 1950 curve not showing quite as pronounced a flat section. In commenting upon the more or less level sections in the curves, Ahlstrom noted that "this means, interpreted literally, that mortality during this period of life was negligible, after having been precipitous immediately following hatching. This does not seem reasonable. Net selectivity severest on newly hatched larvae [i.e., 5-5.75 mm larvae] and becoming progressively less severe with increase in larvae size, could produce a flat section of the curve." One might well ask why this type of survival is unreasonable, particularly in light of a similar "flat section" occurring in the rate of survival of clupeid larvae being reared under experimental conditions where predation of larvae was absent and the presumed main condition for larval survival was adequate quantities of food of the correct size and type.

Survival curves drawn from sampling at sea, and efforts at rearing sardine larvae are at present too incomplete to offer more than interesting parallels. However, it is in the small details of larval ecology and behavior—particularly the relation between the larva and its food organisms—that experimental rearing of pelagic fish larvae can aid studies on the same species of larvae in nature. For the period when feeding of larvae is governed by innate behavior, at least, it seems likely that normal behavior will be expressed whether the microcosm occupied by the larva be in the sea, or in an aquarium where it can be observed.

### INCIDENCE OF FEEDING

Examination of various species of clupeoid larvae seems to indicate that incidence of feeding is very

low (Lebour, 1921; Soleim, 1942; Arthur, 1956), in contrast to that of some flatfish (Scott, 1922), Cod, (Wiborg, 1948), and mackerel, (Lebour, 1920; Arthur, 1956). Theories on low incidence of feeding presume a number of factors being responsible for few clupeid larvae containing food in samples containing hundreds or thousands of specimens. The magnitude of the proportions—i.e. larvae containing food to those not containing food—as judged from tow net samples, is enormous in some species. For example, Berner (1959) found that in a sample of 13,620 anchovy larvae (*Engraulis mordax*) captured in the year 1954, only 211 contained food.

The chief artificial factor proposed to explain the low food content of captured larvae is that nets tend to selectively capture dead or dying larvae in disproportionate numbers, therefore low incidence of feeding may be an artifact of sampling (Arthur, 1956; Berner, 1959; Soleim, 1942). On the other hand, no one seems to have proposed an explanation of the cause underlying the natural occurrence of such quantities of dead or dying larvae in the plankton; Marr (1956) noted that poorly washed nets may have been contributory to such (artificial) occurrences in some cases.

Another possibility to which apparent low incidence of feeding could be ascribed, is that the majority of clupeoid larvae investigated come from samples taken at night when larvae are thought not to feed. It is possible that this objection is valid. However, Arthur (1956) noted that young sardine larvae of 5 to 6 mm in length contained about as much food at night as they did during the day, whereas older larvae containing food occurred only in samples collected during the day. This note is all the more interesting in light of observations of my own which suggest anchovy larvae of about 4 to 5 mm in length, hatched and reared out of doors in a 50 gallon aquarium, feed during the night or at least under very low light intensities. The larval hind-gut and frequently the mid-gut of the fish was filled with food organisms by 5:30 in the morning. The observed feeding frequency (the act of striking at food) indicated that the gut could not have been filled to the observed extent in the short period between dawn and time of observation.

As a general rule, however, we may assume that the majority of particulate feeding fish larvae will exhibit diurnal feeding habits, or at least have a higher food intake during the day than at night, and we may further assume that regardless of species more clupeid larvae will be collected at night than during the day. This also would hold true for most pelagic species, but even so, clupeid larvae seem to be noteworthy for the low number of individuals captured containing food.

Other theories accept low incidence of feeding among clupeoid larvae as a natural occurrence. Factors affecting low incidence of feeding include the possibility that food must be quickly digested and excreted because its presence in the gut would tend to make a transparent larva conspicuous and thus more subject to predation (Lebour, 1921). It is pre-

sumed that food is taken at long intervals and rapidly passed through the gut. Since the rate of digestion and gut clearance of sardine larvae has been established by Arthur (1956) at approximately 11 hours for 5.5 mm larvae and 3 hours for 10 to 25 mm larvae, the survival value theses of rapid digestion seems questionable, at least for sardine larvae. My experiments tend to confirm Arthur's data on the rate of gut clearance, although the rate of digestion of *Artemia* by sardine and anchovy (*Engraulis mordax*) larvae may vary from that for natural marine plankters. I have observed that an average of only 25 seconds is required by larvae of 15 mm in length or larger to pass an *Artemia* nauplius from the mouth to approximately one-half the length of the digestive tract (to a point just under the air bladder). Progress of a food particle (*Artemia*) through the remainder of the gut is much slower, with an average of two minutes required for food to reach the end of the gut and form a food plug.

The food of the jack mackerel (*Trachurus symmetricus*) has been found by Arthur (1956) to be substantially the same as that of sardine and anchovy larvae, but the ontogeny of the two body types and food capacities are very dissimilar. When they emerge from the egg, the jack mackerel is about 2 mm long and the sardine about 3 mm. Neither fish has functional eyes, mouth, or digestive system. Soon after the onset of feeding, (about 3.5 mm) the jack mackerel has developed a large head and capacious mouth. The sardine larva at this time is about 5.0-5.5 mm long and has a small head and mouth. The relative capabilities of the two types of oral apparatus may be seen in the progressive increase in food consumed by the jack mackerel larvae as compared to the anchovy, the latter being morphologically very similar to sardine larvae. Arthur notes (p. 95) that "at a length of 4.5 mm, the jack mackerel might contain about .004 cc of food. Assuming that the volume of the jack mackerel increases roughly by the cube of its length, then doubling its length would result in a body-volume increase of eight times; the volume of food, however, has increased about 200 times. The anchovy, while increasing in length from 4.0 to 7.0 mm theoretically increases in bulk by a factor of about 5.4 times. Its average food volume increases during this growth only by a factor of 1.25 times." It would seem, on the basis of these calculations, that low food intake may be a normal occurrence among clupeoid larvae, although low consumption does not rule out the possibility that the conversion of food to energy may be very high. Presumably the energy expended in hunting food is roughly similar in the two types, at least during early larval stages.

At onset of feeding, sardine larvae have been observed to spend only an average of 25 minutes per hour in motion, when food is captured, and an average of 35 minutes resting motionless in the water. The duration of each individual active or quiescent period lasted from roughly 30 seconds to 10 minutes, with a number of alternating active and quiescent periods occurring in one hour. It appears that there is a correlation between the length of time a larva had been

active and length of the succeeding quiescent period, i.e. the longer (or more energetic) the active period was, the longer the duration of the following quiescent period. Several explanations for this behavior seem feasible. The most intriguing conjecture concerns the effect of the metabolite level which presumably increases during activity and which must be reduced—possibly by diffusion—as the larva rests motionless in the water. Small (5-7 mm) larvae do not show evidence of a well developed vascular system. Thus it may be assumed that waste products of metabolism, along with oxygen, pass through the skin by simple diffusion. It is interesting to note, in this context, that erythrocytes or at least hemoglobin, indicating an increased role of the blood in oxygen transport develop first in the larva at metamorphosis when the skin becomes covered by scales and thus presumably impermeable to diffusion. The motionless-drift period may also be a time when food is digested and absorbed and energy is conserved.

The yolk is exhausted at the 4.5-5.0 mm stage of development and larvae exist on their own tissue and whatever food they capture. An average of two units of effort (a striking motion) per 25 minute active period, to capture food is the observed situation at onset of feeding for sardine larvae held in aquaria. It is not known, in every instance, whether or not larvae are successful at every attempt at feeding. A deficit may be acquired during the 25 minute average active period of one hour, which may be rectified by a double success in a succeeding active period. It should be pointed out, in any case, that the margin between life and death in sardine larvae at onset of feeding seems exceedingly narrow (Lasker, 1962).

This type of alternating active and resting behavior, which limits food intake of sardine larvae, but conserves energy, contrasts with feeding behavior of some other pelagic fish larvae equal or smaller in size to the sardine larva at onset of feeding. Various species of 2-3 mm flatfish larvae, for instance have been observed to move slowly but constantly through the water feeding at short intervals on organisms in their path. Presumably flatfish larvae acquire more food when rich aggregations are encountered, but expend more energy than do sardine larvae when food is widely dispersed. The young of the California flying fish (*Cypselurus californicus*), which hatch with an abundant food reserve, have been observed to swim continuously from the moment of hatching and to capture food (*Artemia*) while some yolk remained unabsorbed. Food is located by this fish, as in the large group of larvae from demersally spawned eggs, by traveling long distances in proportion to the body length. Most of the larvae in this group are physically, and probably physiologically, well developed at birth and rely less on chance—as does the sardine larvae at onset of feeding—to bring them into contact with food, than on their own swimming abilities.

One very interesting report concerning incidence of feeding raises some questions which observation on living material has been able to at least partially answer. Arthur (1956) states "Feeding incidence, when high, obviously implies . . . that a large percentage of

the fish larvae [in a net-tow sample] have been able to secure food. In other words, there is a relation between feeding incidence and the number of food particles per feeding fish, and the number of particles found in a larva should be related to its probability of securing a food particle during the digestive period. In one sample, 279 sardine larvae were captured, of which 200 had completed yolk absorption. Of these 200 potentially feeding larvae, 14 contained food and a total of 30 food particles were found in these 14 larvae. Using a Poisson type distribution for 30 particles scattered among 300 individuals, the expected number of larvae containing 0, 1, 2, and 3 particles was calculated. The expected number of particles becomes insignificantly low for 4 or more particles. The difference between the observed and the expected frequency distributions is that the actual larvae with food were fewer than the number calculated on the basis of chance, whereas the larvae with three or more particles were more numerous than calculated." Arthur goes on to say that "this may be explained by assuming that a larva that has captured one food particle has an increased probability of catching another within a unit length of time. Such a situation would follow if the larva is somehow conditioned by the first particle thereby increasing its efforts or ability to obtain a second or third particle." A second explanation of the disparity between the observed and the expected values within a sample was also discussed. The gist of Arthur's explanation is that it would be possible to capture with the same net, portions of two or more larval concentrations which had been living with dissimilar local plankton aggregations. This situation obviously implies a marked heterogeneity of plankton distribution within a small area.

Among the items of interest brought out by the above are 1) conditioning of feeding behavior, and 2) the problem of plankton dispersal, more specifically, the availability of food for sardine larvae.

### CONDITIONING OF FEEDING BEHAVIOR

In the first instance, if sardine larvae can be conditioned to further efforts by the capture of food, presumably they would also be liable to frustration upon repeated failure. Both premises are valid for some species of adult fish at least. Soleim (1942) described a conditioning of non-feeding behavior in herring (*Clupea harengus*), whereby the larva having failed to capture food after several attempts, gives up and ultimately dies. I have observed this behavior to occur at onset of feeding in sardine larvae, however, it is not entirely clear whether the fish experiences a loss of motivation, or simply exhausts its limited energy reserve, and in either case starves. Perhaps the stimulus provided by the act of capturing prey, or by food in the gut, engenders—or permits—further food getting activity.

A second assumption is that the larva increases its ability to obtain a second or third food particle; in other words, the larva learns to feed, becoming more proficient at recognizing, stalking and striking food organisms. Although learning undoubtedly occurs in

later larval stages it seems probable that for the earliest larval stages feeding behavior is a reflection of ontogenetic development of inherited instinctive behavior patterns.

Limited observations of sardine and anchovy larvae indicate the presence of behavior patterns which probably have some influence on larvae finding food. One such pattern was observed most often after a sardine larva (6-7 mm) had captured food, or had attempted to capture food. The larva seemed to engage in a pattern of "search" in which after moving a distance in one direction, a 90° turn to the right or left was made and an equal distance covered before turning 90° again in the same direction. Some larvae were observed to turn six times, though the usual number of turns seemed to be three or four. Anchovy larvae also appear to stay within an area where they have been successful in obtaining food, but a distinct "search" pattern has not been observed in larvae of 4-5 mm in length which had been reared in aquaria.

It seems possible that the presence of a "search" behavior in sardine larvae may account for Arthur's (1956) observation that among larvae containing food, each individual contained more food organisms than could be accounted for by chance. In other words, a larva that has captured one food particle would stand an increased probability of catching another if instinct caused it to hunt in the same area where food organisms were aggregated. This seems to be the case rather than the sardine larva being a randomly oriented predator operating on a randomly dispersed food supply.

The feeding reflex of sardine larvae, conditionable or not, does not begin immediately after the yolk sac is absorbed. The transition from yolk nutrition to feeding upon other organisms seems to be interspersed with a short period in which larvae subsist on the energy derived from body tissue. This is indicated by slight shrinkage in the length of the body. Presumably an adjustment is necessary in the visual, or some other organ system, because during this period a larva will move about periodically with slow undulations of the body, pausing now and then when it perceives small organisms nearby. Visual perception is assumed because a larva would occasionally recoil slightly and the head and eyes would move although no attempt would be made to feed. Usually the larva drifted motionless in the water for several minutes before becoming active again. The first active interest in food is seen when a larva apparently tries to focus on a particle in the water. The body is slightly drawn into an S-shaped position and the head is jockeyed back and forth in what seems to be an attempt to keep a moving particle within a very critical point of focus. Apparently the stimulus to feed is not always high enough at this period to cause the larva to strike at whatever it is that it perceives. Presumably the larva and the particle drift apart and visual contact is lost, or the feeding instinct is latent and there is a loss of interest in the particle. The larva may abruptly break off its inspection and lapse into motionless drifting, or move away. In following periods the sinuous position of the body becomes more pronounced, the head moves rap-

idly back and forth, and the first attempt to capture a particle is made. Only one lunge is made at a particle at onset of feeding.

Sardine larvae which are successful in their first attempts at feeding develop in later stages an obvious proficiency at capturing food. A food particle is sighted and struck in rapid succession. After the larva has reached 7 mm in length the broad swimming undulations are followed by short, rapid undulations as food is sighted. The head of the larva moves from side to side and the eyes are in constant motion as the body is drawn into a pronounced S-shape and a rapid strike is made. Each of these acts progress smoothly and the hesitancy seen during the first attempts at capturing food is no longer observed. One has the distinct impression that visual acuity is improving and that the larva can perceive movement of food organisms at a greater distance—presumably the head must still be brought very close to an organism, however, before it can be recognized as “edible”. As the larva grows in length, the rest periods become shorter and at about 9 mm the larva is in almost constant motion.

When *Artemia* ranging in size from newly hatched nauplii to several mm in length are introduced into a tank containing advanced sardine or anchovy larvae, it is at once apparent that larvae of about 15 mm in length obtain proportionally less food than larvae of 30 mm in length during the first few minutes of feeding. It is not primarily a question of fewer optimum sized *Artemia* being present that limits the food intake of the smaller fish, but it seems that smaller larvae still retain the early larval behavior of inspecting each food particle before eating or rejecting it. The larger larvae are at the point of metamorphosing to the adult body form and are possibly at the threshold of true filter feeding.

### HOMOGENEITY OF PLANKTON DISPERSAL

The second item of interest noted under “incidence of feeding” concerned the relation between the sardine larva and the distribution of plankton in the larva’s environment, and whether the potential food is uniformly dispersed or occurs in patches. This question is directly related to the availability of food, as opposed to the physical quantity present in a given volume of sea water. Present sampling methods tend to indicate the volume or mass of plankton present in a volume of water, but provide little information on micro-aggregations of organisms. In general, papers speculating on dynamics of larval marine fish populations equate numbers of invertebrate plankters with their availability as food, or, to put it another way, show that the ratio of larvae to food-mass is low, and therefore food is not of major significance to survival of larvae.

It seems evident from a perusal of the literature that the large volume of food organisms frequently associated with larvae in the contents of tow-net samples seems irreconcilable to the thesis that sardine, or other fish larvae may starve in the sea. The ratio of sardine larvae to potential food organisms has been calculated by Arthur (1956) who found a distinct

“surplus” of food organisms. Arthur calculated the distance between food organisms on the basis of numbers caught per volume of water sieved by the tow-net, and gave a mean distance between food organisms as 10 cm or less at 70 percent of his stations, and 7 cm or less at 50 percent of his stations. This would seem to lend credibility to the notion that food for larvae is abundant in the sea, or that, as observed by Murphy (1961) “because of motion of food and larvae, only a short time need pass before a [sardine] larva has a food organism within easy reach.” Random distribution of food is obviously assumed in this statement, because if an aggregation of food organisms were separated from a larva by only 20 cm, a great deal of time might pass before a 5 mm larva would find food within easy reach. The relative rates of drift for plankton aggregation and larva, in this circumstance, would be the same and even if the larva was disposed to swim four times its body length in one direction, there probably would be no clue as to the direction it must take to reach food. There is reason to believe, in fact, that 5 to 7 mm larvae are not capable of perceiving, or at least recognizing food organisms if they are more than a fraction of a millimeter distant. This statement is based upon many hours of observing larvae when they first attempt to feed.

During early stages of growth the larval sardine is incapable of much directed movement, thus if “chance of random encounter”, produced by macro- or micro-currents in the sea, was the sole, or major means of sardine larvae obtaining food, any biological or physical phenomena which hindered random distribution presumably would in like degree hinder or prevent larval fish from feeding. The real problem then, is to establish what the true conditions are in the sea; i.e. not whether mixing of sea water takes place but whether such mixing has any effect on the spatial distribution of organisms. We are again subject to the limitation of not having very much information on just how small crustacea and other potential food organisms react to various physical influences which would tend to disperse them. Numerous studies of predator-prey relationships, among other pertinent studies have pointed up the fact that randomness of distribution of either predator or prey is exceedingly rare in nature and regardless of the physical conditions imposed upon a population of organisms—whether bacteria or crustacea nauplii—aggregation rather than dispersal is the general rule. Although the sea may present a somewhat more uniform aspect than land, distribution of pelagic organisms is known not to be uniform with depth and, after a number of investigators, has also been found not to be uniform in a horizontal plane. Barnes and Marshall (1951) for instance, concluded that various copepod nauplii, lamellibranch larvae, and unidentified eggs were not distributed at random, except at low population densities, but had a contagious distribution. It is interesting to note that although copepod nauplii and lamellibranch larvae would be able to resist dispersal by

micro-currents, the unidentified eggs being non-motile, would not. Conceivably micro-currents, or convergences in the sea may be more liable to concentrate organisms or particles than they would be to disperse such material. Phenomena such as foam-lines and slicks, denoting concentrating rather than dispersing action, are frequent at sea.

At this point we are confronted by a very incongruous set of data. On the one hand a low incidence of feeding among clupeoid larvae seems to be well documented from many parts of the world. On the other hand, calculations of the ratio of plankters to larvae—indicate an abundance of food in the sea. In both cases, however, the contents of tow-nets were assessed to obtain the data.

A third incongruity is provided by observation of larvae held in aquaria under experimental conditions. Sardine and anchovy larvae ranging in size from 15 to 17 mm in length have been found to feed continuously on *Artemia* when these organisms are offered as food. Both species have been observed to completely fill the gut in about ten minutes and to have an initial mean feeding interval of 17 seconds, i.e. a strike by a larva at an *Artemia* nauplius was observed to result in its capture. When the gut is filled and some digestion has taken place, after about 30 minutes, feeding slows down to approximately one *Artemia* per minute as long as food is present. Larvae larger than 17 mm fill the gut in less time and capture food much more rapidly by gulping one or more *Artemia* in continuous feeding.

One may well wonder, however, if this is "normal" behavior, and whether it is representative of feeding behavior of larvae in the sea under comparable conditions of high food concentration. If it is natural for clupeoid, or at least sardine and anchovy larvae to eat as much as they can hold when food is readily available, then a re-evaluation of our methods of estimating the abundance of the available larval fish food biomass is in order.

Very little information is on hand to judge the actual availability of food organisms to larvae under natural conditions, but one important study points up the necessity of further investigation on this question. In his study of the relation between larval fish and food organisms, Arthur (1956) observed an unusual natural occurrence of sardine and anchovy larvae behaving like the larvae held under the experimental conditions noted above. In this instance Arthur reported (p. 96) that "approximately 36 sardine and 264 anchovy larvae were in this haul. Twenty-seven of the sardine and 41 of the anchovy larvae were 10.0 mm or longer. The *unusual* (italics mine) aspect of the sample is that most of the larger larvae of each species were literally crammed with pteropods." This sample was omitted from the list of food eaten, as Arthur reported "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. . ." In my opinion, the sample should have been retained as a rare natural example of food aggregation and larval

feeding behavior. The natural biomass (pteropods) had, in this instance, very likely the same relative availability as the *Artemia* in the feeding experiments previously described, and the larvae which found themselves in this aggregation of pteropods ate to capacity.

The behavior of sardine and anchovy larvae, when one considers all aspects, seems intimately correlated to the behavior of the food organisms, indicating copepod behavior studies must be considered in conjunction with studies of larval fish ecology. Calculations of mean distances between food organisms may well represent only mathematical probabilities rather than biological actualities. The factors which influence fish populations cannot be viewed from the standpoint of all-encompassing equations, but rather must be studied as a series of minutiae which affect each individual step in the life history of fish from the egg to spawning adult. Each growth period or phase in the larval stage alone presents to the individual larva a new range of potentialities for success or disaster. My observations, limited as they are, indicate changes of survival tend to increase after the individual sardine has passed through one critical period at onset of feeding and very likely another period at about 11 to 12 mm in length. Thus agreeing in general with Marr's (1956) hypothesis that survival rate of sardine larvae increases at a nearly constant rate. Concomitant improvement in vision, the ability to range further in search of food, increased experience in capturing food, and the phasing in and out of certain behavior patterns throughout larval life all serve, to point up the large element of chance that determines life or death for sardine larvae at the critical onset of feeding. Probably at no other time in its life is the sardine so dependent upon the capture of food and so inadequately equipped to obtain it.

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