

## Use of Fish Eggs and Larvae in Probing Some Major Problems in Fisheries and Aquaculture

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**Abstract.**—Studies of the early life history of marine fishes have progressed greatly in the quarter century since the pioneering work of Sette, Ahlstrom, and others. A brief history of this recent era points out the many ways in which eggs and larvae have been used to address central problems of fishery dynamics, management, and culture. Challenges and opportunities await early life historians in the areas of fish distribution, biomass estimation, species identification, recruitment, species interactions, aquaculture, enhancement, pollution assessment, definition of subpopulations, and production. Early life history studies have acquired considerable relevance to society as well as to science.

I was pleased and flattered to be asked to be the keynote speaker to this meeting of the Early Life History section of the American Fisheries Society. The papers of this meeting are very impressive and comprehensive, much more so than those of the very first Larval Fish Conference in the United States, which was held at Lake Arrowhead, California, in October 1963. The proceedings of that early conference appeared in volume X of the California Cooperative Oceanic Fisheries Investigations Reports of 1965. Figure 1 is a photograph of the conference contributors.

In 1963, although we had some data which showed that fish eggs and larvae could be important tools in the study of fish populations, we still had much to prove. Now, many of the papers being given at this 1986 conference are proof of this early premise. This paper is a personal perspective on studies of early life history of fish. It is intended to give a historical view of some of the reasons fishery scientists find the subject interesting and to suggest what the future may hold for those of us who continue with it. Although I cannot possibly cover every aspect of the early life history of fishes, I hope to make the point that fisheries science has benefited a great deal from the subject.

The need for fisheries management is one good reason to bring us together and I would like to aim my remarks towards that end, recognizing, of course, that foremost we are biologists trying to answer the important basic question of how fish eggs and larvae survive in natural waters.

### Sette, Ahlstrom, and Schaefer

In California, I was able to meet and associate with some of the pioneers in the study of fish eggs

and larvae. These people are becoming fewer and those with an early vision of the importance of this field to fisheries science are no longer with us. I am referring to scientists like Elbert H. Ahlstrom, Milner B. Schaefer, and Oscar Elton Sette, each of whom would have made a better speaker than I. However, I did have substantial contact with each of them and I would like to start this talk with a few anecdotes which should give you an impression of how important they were to the study of the early life history of fishes in relation to fisheries.

Sette (Figure 2) was a fishery biologist for the U.S. Fish and Wildlife Service who believed that an understanding of fish eggs and larvae and what affected them in the sea would lead us to an ability to predict the size of incoming year classes. When the population of Pacific sardine *Sardinops sagax* (then known as *S. caerulea*) suffered from its now famous collapse in the 1940s, he was sent by the federal government to set up a U.S. initiative to find out what happened. Figure 3 is from his 1943 paper (Sette 1943b) on setting up a research program to determine how fishing affected the sardine resource. In it you can see all the elements for determining what factors affect an incoming year class to a fishery. In particular, the importance of fish eggs and larvae is clearly pointed out.

Ahlstrom (Figure 4) was Sette's collaborator, and it was he who was given the day-to-day responsibility to carry out systematic ichthyoplankton surveys. This was the origin of the now unique larval fish time series of California and Baja California species which began in 1939. Ahlstrom believed that at least two important questions could be answered with these surveys: How is the Pacific sardine distributed? and How is



FIGURE 1.—Participants in the first conference on the early life history of fishes, Lake Arrowhead, California, October 1963. Left to right: George O. Schumann (La Jolla), Wilhelm Einsele (Austria), Fred Holliday (Aberdeen), John Isaacs (La Jolla), Horst Schwassman (La Jolla), James E. Shelbourne (Lowestoft), John Blaxter (Aberdeen), Elbert H. Ahlstrom (La Jolla), Reuben Lasker (La Jolla), Gotthilf Hempel (Hamburg).

the Pacific sardine population changing with time? To our everlasting benefit, Ahlstrom chose not

only to look for Pacific sardine eggs but, because of his deep interest in systematics and ontogeny, set out to name and identify all of the eggs and larvae that were caught by the plankton nets deployed for Pacific sardine.

In a less complicated world where direct contact with Washington for assistance was possible, funds were always ample for these surveys. Joining with the Fish and Wildlife Service was the Scripps Institution of Oceanography, headed in the 1950s by Roger Revelle, who saw the enormous value in such surveys not only for monitoring fish populations but for describing the oceanography and ecology of the California Current system. The California State Legislature provided funds for the Marine Life Research Group at Scripps Institution of Oceanography at the request of a former director, Harald Sverdrup, and it continues today as a partner in what is known as the California Cooperative Oceanic Fisheries Investigations or CalCOFI. From the surveys we learned that the collection and identification of fish eggs and larvae can tell us where fish reside, when they spawn, and how they are related to each other numerically and ontogenetically.

Schaefer (Figure 5) was one of the original Pacific sardine investigation scientists with Sette



FIGURE 2.—Oscar Elton Sette, about 1949.

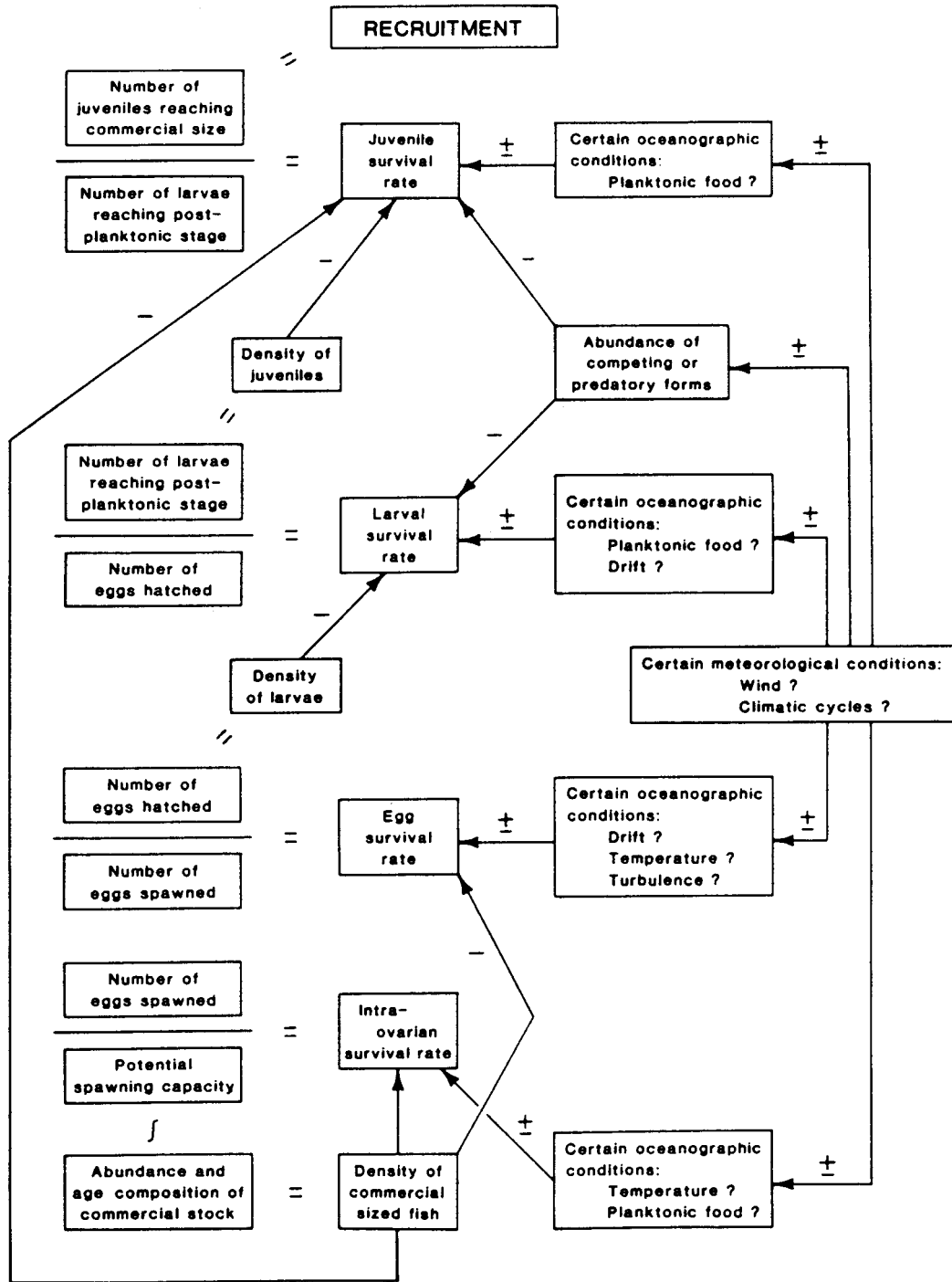


FIGURE 3.—Sette's plan to study recruitment of the Pacific sardine, 1943.



FIGURE 4.—Elbert H. Ahlstrom, about 1969.

in 1946 but, to my knowledge, he never worked on fish eggs or larvae. Why then, do I include him in this essay? The reason, quite simply, is that he had the major role in writing the section on fisheries for the National Academy of Sciences report on "Oceanography in the 1960s." The post-Sputnik era promised increased money for science and it was Schaefer who pointed out the potential importance of the study of fish eggs and larvae to aquatic science and fisheries in particular. We probably all owe a debt to him.

I make no claim that the following is an exhaustive survey of who has done what in this remarkable field. Rather, I have chosen to talk about the attempts made at solving some major problems in fisheries science by studying fish eggs and larvae. Examples are taken mostly from the west coast of the USA with which I am personally familiar.

#### Some Major Problems in Fisheries Science

The major scientific problems in fisheries science today, by my definition, are those which fishery scientists agree need to be solved to facilitate rational management of fisheries throughout the world. I have listed those which I believe are the most pressing; attempts to solve them have involved fish eggs and larvae. It is surely not an exhaustive list.

- (1) *Distribution*: Where are the fish?
- (2) *Biomass estimation*: How many fish are in the sea?
- (3) *Species identification*: What fish are there?
- (4) *Recruitment*: How many fish will be available to a fishery next year? This question subsumes others. Can the magnitude of recruitment be predicted? What are the biotic and abiotic factors affecting recruitment? To what extent can we fish a population without endangering successive year classes? How and why do populations fluctuate?
- (5) *Species interactions*: Does the presence of one species hinder or enhance the survival or reproduction of another species?
- (6) *Aquaculture*: Can we insure domesticated crops of desired species?
- (7) *Enhancement*: Can we release fish eggs and larvae into the sea and thereby increase stocks?
- (8) *Pollution*: Do pollutants affect fish populations through their effects on fish eggs and larvae?
- (9) *Subpopulations*: Do more than one stock contribute to a fishery?
- (10) *Production*: How many fish can a body of water produce and support?



FIGURE 5.—Milner B. Schaefer, about 1970.

*Distribution*

Sette did one of the first, if not the first, comprehensive ichthyoplankton surveys off the U.S. east coast to study the Atlantic mackerel *Scomber scombrus*. His plan for the Pacific sardine, in modified and extended form, has been continued for 40 years. Figure 6 indicates the use of the ichthyoplankton survey off California and Baja California to assess the distribution of a population and how it changes with time. In recent years, the Southwest Fisheries Center has done a finely spaced egg survey which gives an

even clearer idea of how spawning ranges change, sometimes coincident with a major environmental event like the 1983 El Niño, a warming of the Pacific over a vast area (Figure 7). Charts of these distributions in California waters have been published in atlases (Kramer and Ahlstrom 1968; Ahlstrom 1969; Kramer 1970; Ahlstrom and Moser 1975) and in many other publications. We know now that when the Pacific sardine population was on the brink of collapse, the remainder of the population retreated into the Southern California Bight, making the remnants even more

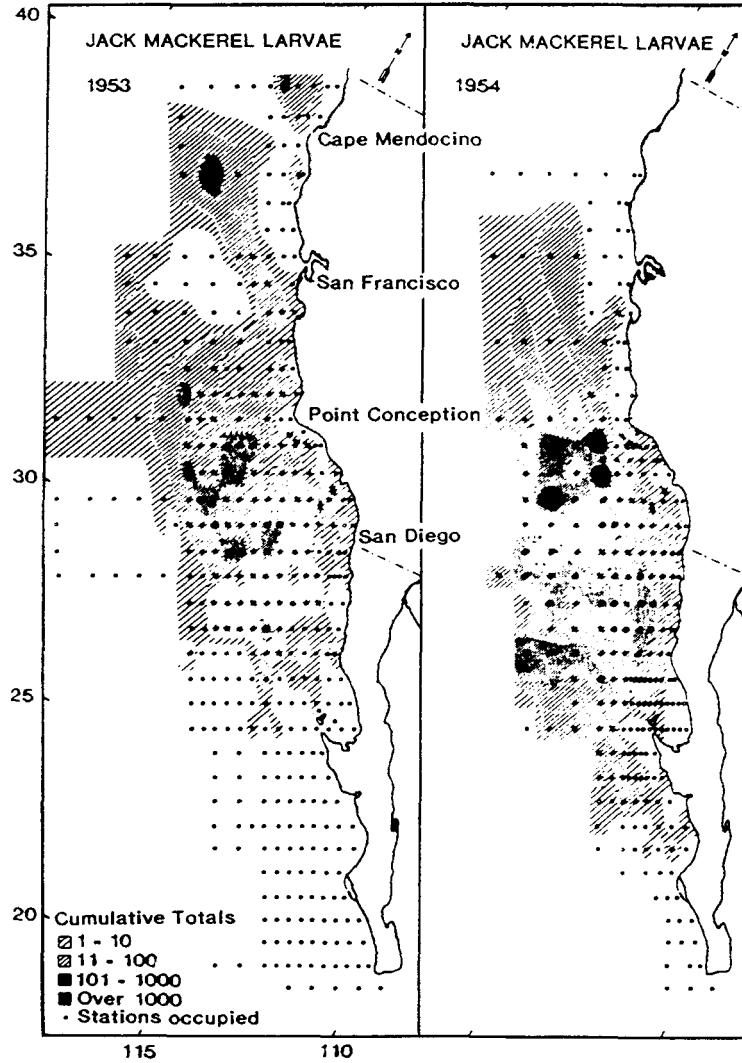


FIGURE 6.—Distribution of larval jack mackerel *Trachurus symmetricus* off California, 1953 and 1954. Data are larvae per standard tow.

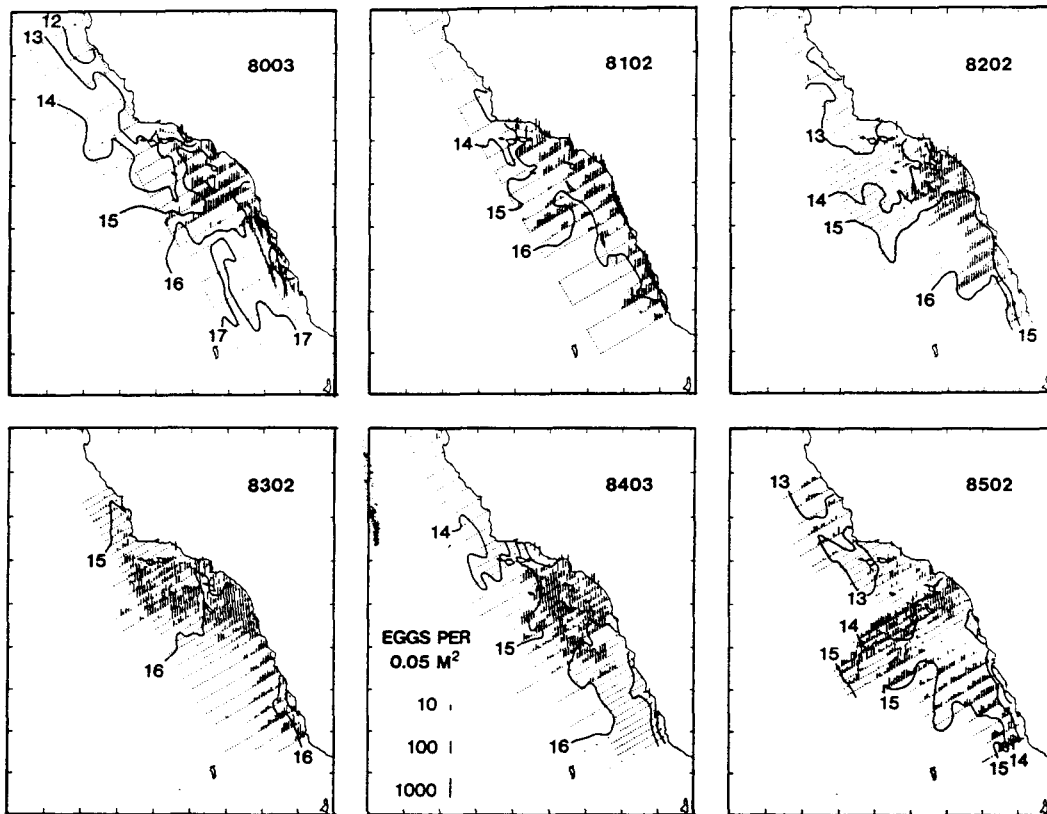


FIGURE 7.—Egg distributions for northern anchovy *Engraulis mordax* off California during February (02) or March (03) 1980–1985. Dots represent sampling stations; surface isotherms are in °C. (From Fiedler et al. 1986.)

vulnerable to fishing (Murphy 1977). The Peruvian anchovy anchovetta *Engraulis ringens* exhibited this same behavior just prior to its collapse (Valdivia 1978).

Paul Smith, Geoffrey Moser and Larry Eber are taking the distribution information much further. Using CalCOFI data from 7 years of intensive sampling, they have analyzed changes in the distribution and abundance of major components of the larval fish assemblage off California and Baja California in response to dramatic changes in oceanographic conditions.

#### Biomass Estimation

Several marine scientists have used the number of fish eggs or larvae to estimate the spawning biomass of commercial species in the sea (e.g., Saville 1964). The difficulty has always been with the assumption that the number of larvae or eggs is proportional to the abundance of females spawning them. In our laboratory, in common

with other fisheries laboratories, we have sought an ichthyoplankton method which would be more precise and with which we could assign errors to every biological parameter. We devised such a method for the northern anchovy, which we call an egg production method (Lasker 1985). Briefly, the idea is to encompass the spawning habitat of the population and to sample about 1,000 times within the habitat with a small, rapidly retrieved plankton net (Figure 8). The eggs caught are then related to female fecundity and the frequency of spawning (Figure 9). That is an all-too-brief characterization of a method that takes 40 d of ship time, retrieval of anchovy eggs from plankton samples, staging and aging of the eggs in the laboratory, histological preparation and examination of the female gonads, and mathematical analysis of the data. The advantages of the method are that no assumptions are made about the biology of the fish and it takes 100 fewer days of ship time than our normal larval survey. This technique is

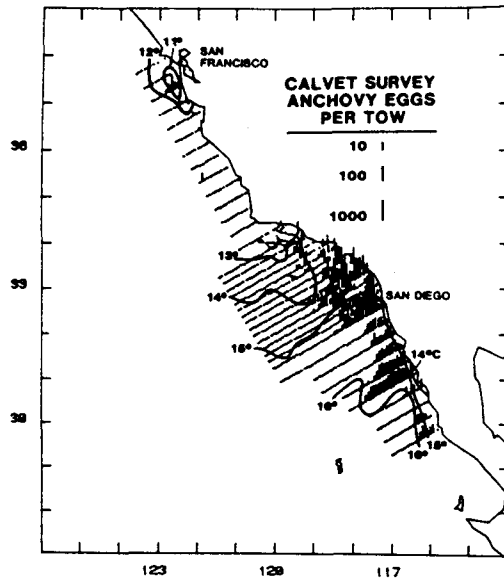


FIGURE 8.—An egg survey for northern anchovy biomass assessment off California in 1982. Surface isotherms (°C) are superimposed on the egg distribution. (From Picquelle and Hewitt 1983.)

now being applied to a variety of fish stocks including the Peruvian anchovetta, the North Sea sprat *Clupea sprattus*, the *Sardinella* off Brazil, and the Pacific sardine, and a program is planned for the Spanish sardine *Sardina pilchardus*.

#### Species Identification

The ichthyoplankton survey had its origin in the work of the Norwegians, English, and Germans at the end of the 19th century. Notable in using plankton nets for determining what plankton were present were Hensen (1895), Schmidt (1909), and Buchanan-Wollaston (1911). In the United States, Sette (1943a) used the survey technique to study the occurrence of Atlantic mackerel off New England from 1927 to 1932. As I have said, it was Sette who outlined the survey program for California, but it was Ahlstrom who honed it to such a degree that the California Current now is one of the best characterized for fish species in the world. These studies were unique for their time because the surveys covered the habitat of an entire population (the Pacific sardine) and have told us what species were associated with it. From monthly cruises over a 10-year-span, the spawning seasons of the Pacific sardine and many other species were delineated. The other species were identified by the construction of life histories

$$B = \frac{k^1 k^2 P W}{RFE}$$

- B SPAWNING BIOMASS  
 k<sup>1</sup> SURFACE AREA OF OCEAN OVER WHICH P IS ESTIMATED (units of 0.05 m<sup>2</sup>)  
 k<sup>2</sup> CONVERSION FACTOR FOR GRAMS TO SHORT TONS  
 P DAILY EGG PRODUCTION (eggs per 0.05 m<sup>2</sup>)  
 W AVERAGE WEIGHT OF MATURE FEMALES (grams)  
 R SEX RATIO (fraction females based on weight)  
 F SPAWNING FRACTION (fraction of mature females that are day-1 post-ovulatory)  
 E BATCH FECUNDITY (eggs per mature female)

FIGURE 9.—Equation and parameters for the egg production method of estimating the biomass of spawners (Lasker 1985).

through the technique of demonstrating morphological similarities between growth stages. In the last decade, sophisticated rearing techniques have permitted identification of larvae heretofore unidentifiable. Over 200 species of larvae have been identified in the California Current to date, and another 60 or so have been named to family. Numerous publications on the identification and developmental life stages have appeared from the Ahlstrom-Moser laboratory; recently, the volume "Ontogeny and Systematics of Fishes" was produced by Ahlstrom's colleagues and dedicated to his memory (Moser et al. 1984). The ichthyoplankton survey in the Ahlstrom style has been adopted as a scientific tool throughout the world.

#### Recruitment

As a fishery problem, the prediction of recruitment is foremost in the minds of fishery scientists. Fishery theory has it that if we could accurately predict recruitment a year in advance for most commercial fishes, management would be that much more precise and risks by the fisherman and processors would be greatly reduced. I leave the economics of that to the economists but I would like to comment on the hypotheses about recruitment, specifically on those that involve the survival of fish eggs and larvae.

Hjort (1926) suggested the "critical period" hypothesis: "... those individuals which at the very moment of their being hatched did not succeed in finding the very special food they wanted would die from hunger. . . . in other words the origin of a rich year-class would require the contemporary hatching of the eggs and the development of the special sort of plants or nauplii which the newly hatched larva needs for its nourishment." Hjort

suggested this hypothesis because the early culture work of the French scientists Fabre-Domergue and Biérix (1905) showed that larvae of sole *Solea vulgaris* (= *Solea solea*) started to look for food even before their yolk sacs were absorbed; if they did not find food right away, they became "anaemic" (as they called it) and died of starvation. This experimental result, when coupled with the observation that good year classes of several different species of fish sometimes coincided in the Norwegian fisheries, suggested the "critical period" concept to Hjort (1914).

Sette's work did not support the critical-period concept for first-feeding Atlantic mackerel larvae. He found that the greatest mortality occurred late in the larval period, when the animals were about 9 mm long or about 1 month old. But laboratory work on sardine, anchovy, and herring larvae seemed to give results similar to what Fabre-Domergue and Biérix found with sole larvae, and the testing of the Hjort hypothesis continues to this day.

Fishery scientists are convinced that at least two processes must prevent fish from surviving to a fishable size: starvation and predation. A lot of effort has been expended in recent years trying to decide which is more important and whether the conditions that cause one or the other can be predicted. As an example, my own work showed that food for first-feeding northern anchovy larvae was highly variable in the environment, and, at least in the Southern California Bight, was restricted to nearshore areas (Lasker 1975). Laboratory experiments by my colleagues (Scura and Jerde 1977) indicated that these larvae could not or would not eat diatoms or microflagellates and relied on dinoflagellates or microneuplii in their

immediate environment. Furthermore, as aquaculturists know, even foods which are readily ingested do not necessarily support growth and survival. Work off California showed that there was also a threshold number of food particles which had to be in the larva's immediate surroundings before it could be assured a meal. When these facts about the first-feeding larva's needs and behavior are considered, prediction of survival becomes a much more complicated matter because the measurement of all of these factors over a spawning season is a formidable task.

The argument about density-dependent and density-independent recruitment has also occupied fishery biologists. Those believing in density dependency say that we have to take into consideration the number of fish in the population, the number of eggs spawned, and how these numbers have an effect on the number of fish that finally survive. Those convinced that density-independent effects are the most important have ample evidence to show that even unfished populations undergo wide variation in population size, hence recruitment. Hjort also recognized that sometimes very small fish populations could give rise to very strong year classes and in, recent times, we have the examples of the Japanese and Chilean subspecies of Pacific sardine, the North Sea Herring *Clupea harengus harengus*, the chub mackerel *Scomber japonicus* in California, and many others (Figures 10, 11).

The environment seems to regulate the food available for first-feeding northern anchovy larvae. Stable ocean conditions favor aggregation of suitably sized food organisms so that above-threshold numbers of food particles become available to the larvae. I found that when a strong

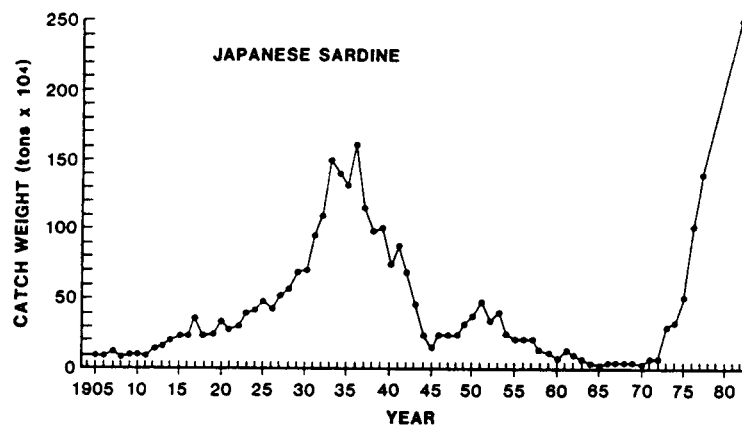


FIGURE 10.—Catches of Pacific sardine off Japan, 1905–1981. The 1984 catch was  $420 \times 10^4$  tonnes.



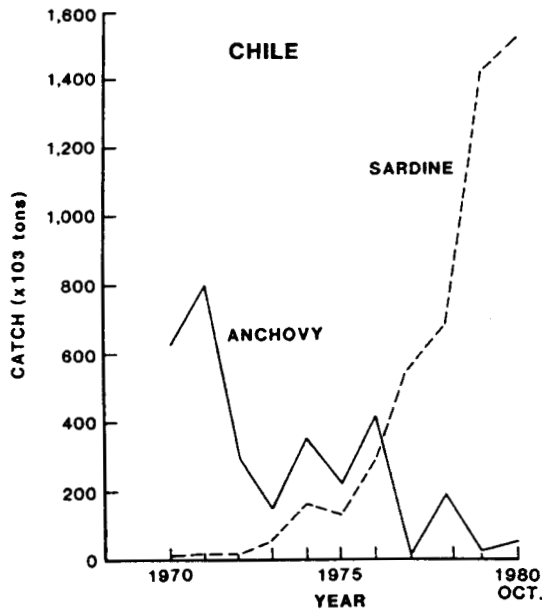


FIGURE 11.—Catches of Pacific sardine and anchovetta off Chile, 1975–1980.

storm or strong upwelling came along, food for the larvae would be dissipated and diluted, making it impossible for first-feeding larvae to find enough food to survive (Figure 12) (Lasker 1981). O'Connell (1976) developed histological criteria by which he could detect starvation of northern anchovy larvae, and he applied these criteria to the estimation of starvation of larvae in the ocean (O'Connell 1980). A reexamination of his data by Theilacker (1987) showed that 35–46% of the first-feeding northern anchovy larvae died from

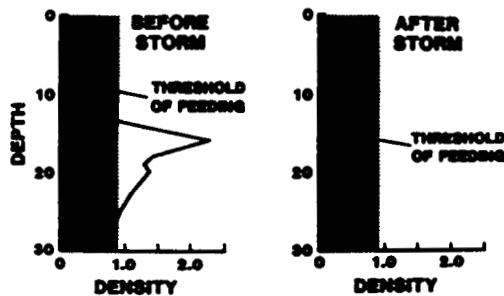


FIGURE 12.—Effect of a storm on the vertical density of particles needed by first-feeding northern anchovy larvae. (From Lasker 1975.)

starvation each day. Theilacker (1986) also showed histologically and morphologically that first-feeding jack mackerel are mostly starving in an oligotrophic part of the species' spawning habitat (Figure 13). Close to islands, evidence of starvation drops off considerably; in this case, we must invoke predation as the main cause of mortality (see also Hewitt et al. 1985).

As far as northern anchovies off California are concerned, it is clear that the kind of food available is of paramount importance too. We have demonstrated that a particular dinoflagellate, *Gonyaulax polyedra*, was the dominant food available to first-feeding larvae in 1975 but, in the laboratory, the larvae could not survive on it (Lasker 1981). That year was an interesting one. Primary production in 1975 was far higher than in any previous or subsequent year but it produced one of the worst year classes of 20 consecutive ones measured. Upwelling brought in diatoms after sweeping out the bloom of *Gonyaulax polyedra*, but diatoms are not eaten by northern anchovy larvae.

The starvation idea also is supported by a modeling study (Lasker and Zweifel 1978) and an energetics study with northern anchovy larvae by Theilacker (1987). Both indicated that the density of food organisms in the sea must be higher than the usual density of nauplii, so the smaller, more dense aggregation of particles (e.g., dinoflagellates) must be the main supply of food for these fragile larvae. When the environment does not cooperate, a poor year class seems inevitable.

The importance of starvation in larval recruitment seems to vary among taxa, however. Houde (1987, this volume) distinguished between anchovy-like species and cod-like species and concluded that the mechanisms for survival and recruitment are different for each group. May (1971b) discovered that larvae of California grunion *Leuresthes tenuis* could withstand up to 20 d of food deprivation after hatching, and concluded that starvation could not be a factor in their mortality in the sea. Recruitment thus depends on a species' behavioral and physiological response to the biotic and abiotic environment, and that generalities with respect to recruitment mechanisms cannot be made. Each species (or species group) needs to be examined separately, and undoubtedly different mechanisms will be found that determine recruitment.

The predation aspect continues to be an intriguing one. Can we get some quantitative fix on recruitment if we know the number and kinds of

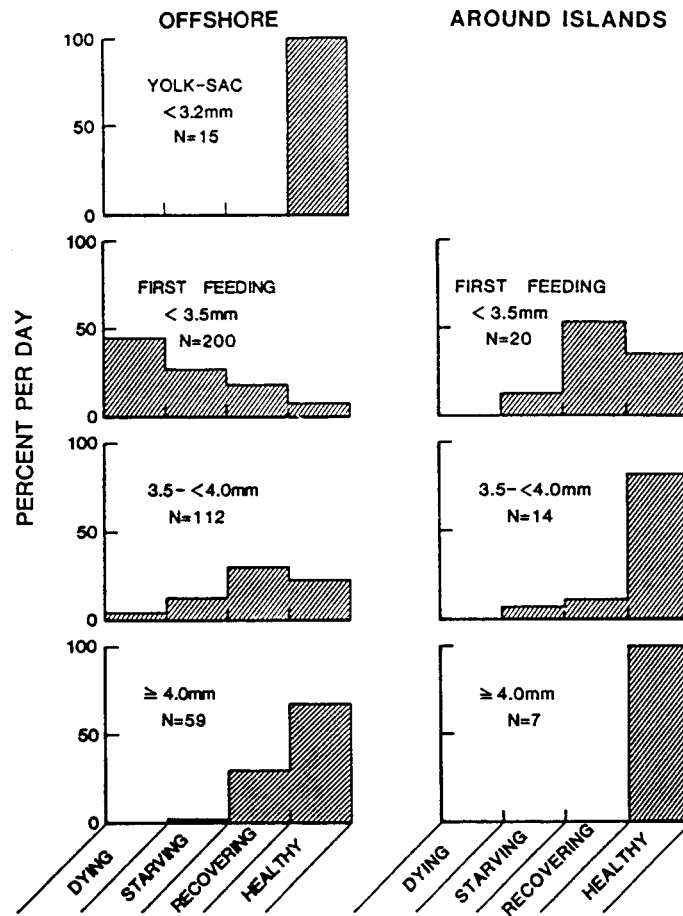


FIGURE 13.—Mortality, starvation, and survival of developing jack mackerel larvae off California. (From Theilacker 1986.)

predators on fish eggs and larvae? Hunter and Kimbrell (1980) have shown that adult northern anchovies feed on northern anchovy eggs and probably the larvae as well. Many other authors have shown how vulnerable fish larvae are to invertebrate predators (Lillelund and Lasker 1971; Theilacker and Lasker 1974; Bailey 1984; Purcell 1985) but we have no tool yet that would allow us to quantify the effect of these predators. An immunoassay technique to detect the degree of euphausiid shrimp predation on yolk-sac larvae has just been developed by Theilacker et al. (1986). The field data are very promising, and this may be what we need to solve the quantitative aspect of predation. Something like this approach is certainly needed now for postyolk-sac larvae.

Our growing expertise in calibrating and reading the ages of larvae and juveniles from the daily

rings on otoliths has opened some new avenues to study recruitment of larvae. The important paper by Methot (1983) showed us how we might correlate survival and mortality of larvae with environmental changes. In essence, Methot showed that monthly larval production over a spawning season could be compared to the birthdate frequency of juveniles, i.e., the surviving recruits. For those months in which most survivors had hatched, correlations can be sought with specific events in the environment (Figures 14, 15). It is the first time we have been able to analyze events within a spawning season, rather than averaging variables over an entire spawning season. This idea forms the basis of an international program called SARP, the sardine-anchovy recruitment project, an initiative of the Intergovernmental Oceanographic Commission and the United Nations Food

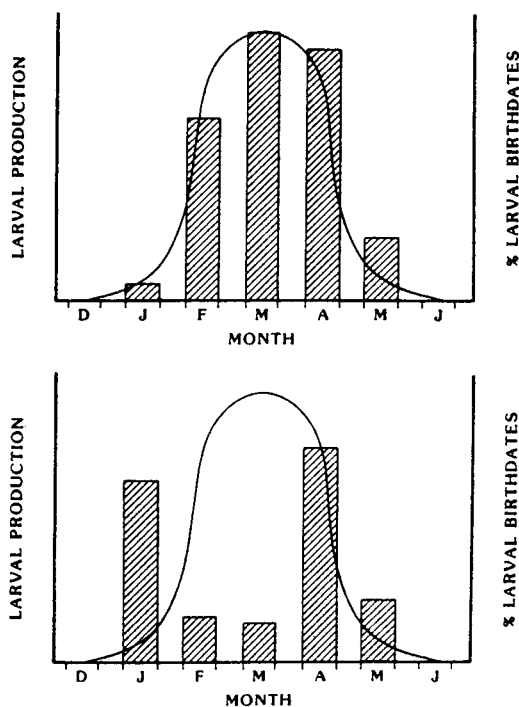


FIGURE 14.—Generalized curves of northern anchovy larval production over a spawning season off California, and distributions (bars) of birthdates of surviving juveniles. The top panel shows the birthdate distribution that would occur if there were no major environmental perturbations during the spawning season. The lower panel shows the distribution that might occur if environmental factors affected survival at various times during the spawning season.

and Agriculture Organization under the International Recruitment Program (IREP).

To summarize this recruitment section, it seems to me that we are on the threshold of making great strides in understanding how fish larvae are controlled by their physical and biotic environment and to quantify the roles that environmental factors play in recruitment. I think Hjort would be pleased with the progress made in the last 15 years, but he would also admonish us because the definitive test of the critical period hypothesis has not yet been made. At the very least the SARP initiative may be the way to accept or reject the "critical period" hypothesis for anchovies and sardines. We have a very long way to go to do the same for the other important commercial species.

*Species Interactions*

Competition is extremely difficult to observe in pelagic and benthic systems. We know that there

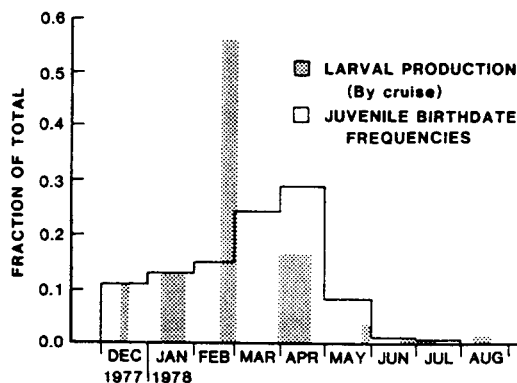


FIGURE 15.—Methot's (1983) actual data for larval production and birthdates of juvenile northern anchovies during the 1977-1978 spawning season off California.

is a body of literature on competition for habitat among adult fish, particularly on coral reefs, but how can fish eggs and larvae help us decide whether and to what degree competition occurs? First, one has to have some indication that there is a reciprocal relationship between species; then one can proceed to an analysis of causal mechanisms. As an example, MacCall (in Lasker and MacCall 1983) studied Pacific sardine and northern anchovy scales in anaerobic sediment cores collected from the Santa Barbara Basin, California. He found that northern anchovy scales were smaller when sardine populations were large and larger when sardine populations were small. This kind of presumptive evidence suggests a competition for food among the adults. Does such a competition between species occur in the larval stages?

The CalCOFI data base lists and enumerates the fish larvae of myctophid species, some of which spend their entire lives in the dark and are by necessity carnivorous. Some of these populations are enormous by number if not by biomass and must exert great predation pressure on pelagic fish larvae of all kinds. Some fish larvae, e.g., those of chub mackerel, can eat northern anchovy larvae handily in laboratory tank environments. Competition between individuals of different species for food somehow seems unlikely because fish larvae are usually such a small component of the plankton, but what do we really know? Not much. I think it is clear that this is an area of research that requires much more attention and may have very important implications for multispecies management of commercial species.

### Aquaculture

I think the evidence is very good now that aquaculture is a proven technology for a variety of organisms and is paying off in real money for various carps and tilapias, striped mullet *Mugil cephalus*, madai *Pagrus major*, black porgy *Acanthopagrus schlegeli*, European bass *Morone labrax*, and a host of others, but there are many species which have defied propagation and culture. It is interesting to read the journals devoted to aquaculture. Papers on fish larvae abound, and techniques for raising particular larvae are outlined in great detail. The challenge to early life history scientists is to reduce mortality and insure rapid growth of the egg and larval stages of those species that are desirable for human food and commerce.

The use of the rotifer *Brachionus plicatilis* for larval food was introduced in Japan in 1965 and was a breakthrough for fish rearing, although the species originally was considered a noxious zooplankton in eel culture ponds (Hirano 1969; Hirata 1979). *Brachionus plicatilis* has succeeded almost everywhere it has been tried with marine species. In La Jolla, we have used a clone isolated from the highly saline inland Salton Sea (Theilacker and McMaster 1971) to rear northern anchovy larvae; nauplii of the euryhaline crustacean *Artemia salina* have probably been used even more as a larval fish food and also with notable success (May 1971a). Copepods are very desirable for this purpose but culturing them in appropriate quantities is a more formidable problem.

Aquaculturists would be the first to say that their task is not easy and that the road to success is filled with obstacles, but we have seen remarkable progress in fish rearing during the last three decades. This has been accomplished in great part by academic and applied scientists who have had an interest in determining the behavior and the fastidious environmental and food requirements of fish larvae in freshwater and marine systems. I was an early skeptic, but I am convinced now that the culture of marine fishes has seen, and will continue to see, some real successes such as we have had with freshwater species.

### Enhancement

One of those areas of rearing that needs particular attention is the trend toward enhancement of natural stocks. This leads us back in time to the work of the first Administrator of the U.S. Commission of Fish and Fisheries, Spencer F. Baird



FIGURE 16.—Spencer F. Baird, first U.S. Commissioner of Fisheries. (From Allard 1978.)

(Figure 16). In 1871, Baird persuaded Congress to create the commission and then willingly accepted the charge of countering the decline of fish off southern New England. The next year, he was given the charge of artificially propagating fish to replenish and restock depleted freshwater and marine areas. There were some successes with, for example, various salmonids and common carp *Cyprinus carpio*, and, in 1878, a major program was started with marine species. Baird did not think that there would be much success in the open sea but he was convinced that there would be some impact in local coastal areas, such as from the several million larvae of Atlantic cod *Gadus morhua* that were released into Gloucester harbor, Massachusetts. There was little evidence of any effect, however. I am not sure we have yet learned the important lesson, now over 100 years old, that any attempt to enhance natural systems requires us also to determine what proportion of stocked animals survives. The failure to do this was really the undoing of the marine enhancement program Baird had so laboriously erected (Allard 1978).

In the early years of the Fish Commission, Baird was an active participant in the American

Fish Cultural Association, which, after 1884, was known as the American Fisheries Society. Thus the Early Life History Section of the American Fisheries Society has important historical roots.

#### *Pollution*

Surprisingly, we do not yet have a larval fish analog of the laboratory white rat. With all the rearing of larvae going on at present, one would have expected that some larval fish would have made the perfect test organism for pollutants. In 1965, when the Santa Barbara, California, oil spill occurred, I used northern anchovy larvae as test organisms in the laboratory to see if the dispersant used by the oil companies was in any way toxic. It was no surprise that the dispersant was highly toxic to larvae in concentrations as low as 2 mg/L (Anonymous 1969). I then received funds to see if northern anchovy larvae could be used to evaluate other pollutants. The work resulting from that program showed that the larvae take up chlorinated biphenyls directly from sea water (Scura and Theilacker 1977). My own agency considered this work a very low priority at that time, however, and it was terminated.

Granmo (1981) reviewed some of the reasons for using fish eggs and larvae in pollution studies, and listed the following. (1) Fish are economically important. (2) Fish eggs and larvae are sensitive to pollutants. (3) It is relatively inexpensive, quick, and easy to run toxicity tests on fish larvae. (4) We know a lot about fishes. In my opinion, there is another reason: fish eggs and larvae may be the key stages in determining the magnitude of fish populations.

What has eluded fishery scientists is some determination of how populations of fish are affected by pollutants. This question should be central to most of the work going on in lakes and the sea, but few studies are aimed in that direction. Currently, in my own laboratory, Michael Prager and Alec MacCall are looking for correlations between historical trends in fish stocks (as indicated by collections of fish eggs and larvae) and contaminant inputs into California coastal waters. To what extent the mortality of fish eggs and larvae might be involved in these correlations requires field experiments no one is really ready to do, yet it is most likely that it is these sensitive stages of development which bear the brunt of ocean and lake pollution.

#### *Subpopulations*

Fishery managers always want to know whether a fishery is based on one stock or several.

What can fish eggs and larvae tell us about contiguous populations which are close to one another but genetically separate? Does it make sense to use these developmental stages when the adults are available for analysis? I think not, but the ease of capturing the spawn provides genetic material when it is virtually impossible to capture the adults—for example, before a fishery is initiated on a species whose adults live in deep waters but whose eggs and larvae occur at or near the surface.

In 1962, I had the opportunity to work with Blaxter and Holliday on larvae of Atlantic herring. My introduction to this species was in Kiel, where Gotthilf Hempel had arranged for me to collect some larvae. I was astonished to find that newly hatched Atlantic herring larvae were only about one third the size at Kiel that they were in the North Sea. Clearly, this species has evolved remarkably different subpopulations within a few hundred kilometers of each other.

The use of larvae in subpopulation studies deserves much more attention.

#### *Production*

I have spent a great deal of my professional life pursuing an understanding of fisheries production, trying to evaluate the steps in the marine food chain leading to harvestable fish. It took me about 20 years to realize that this is much more difficult than I had naively thought. It will take many more years and much more effort to come to any real conclusions about production dynamics.

In 1969, Ryther published a harvest prediction for marine fisheries. With admittedly rough calculations, incorporating what we knew at that time about primary and secondary production in the sea, the efficiency of transfer through trophic levels, and the productive areas of the world's oceans, he concluded that the potential sustained yield of fish to humans would not exceed 100 million tonnes (Ryther 1969). Eighteen years later, we find that Ryther (considered by fishery scientists the pessimist of his time) gave us a figure which seems grossly optimistic. Today the harvest is barely 70 million tons and increasing at an infinitesimal rate (Figure 17). One must conclude that we have been doing something wrong or that the assumptions we have made, e.g., that the efficiency of nutrient transfer seen in the laboratory can be extrapolated to the sea, are incorrect. My own work has shown that the magnitude of primary production may have little relation to the size of a resultant fish year class

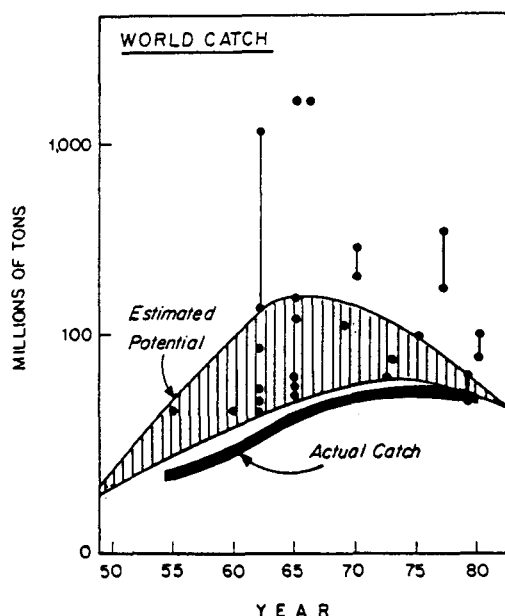


FIGURE 17.—Actual and predicted world fish harvests. (From Darr and Hennemuth 1985.)

(Lasker 1981) and that this discrepancy may be rooted in the behavior and physiology of the larvae. We do not know enough about the inner workings of the larvae of most commercial fish, nor do we know much about how primary production is partitioned among groups of organisms. We now know that most euphausiids (Lasker 1966) and copepods (Cowles and Strickler 1983; Price et al. 1983; Koehl 1984; Strickler 1984) are preferentially carnivores or at least selective feeders just like fish larvae, yet most food chain models are based on their empirically derived filtering rates. Notwithstanding the problems we have with measuring primary production, we have to conclude that the measurement of secondary production is in a very dire condition and requires new insights, new techniques, and a fresh look.

#### Conclusions

At a student's exam at Scripps Institution, Russ Doolittle, a biochemist, asked if the problem the student had chosen for a doctoral project was a *significant* one. Doolittle explained that, as a student himself, he had worked for professors who seemed to be wrapped up in trivia, trying to find out more and more about less and less. The lesson he was trying to convey was that there are many important problems to be worked on which

are just as much fun as any other but carry the added benefit of being important to society as a whole.

In early life history studies of fish we have that added benefit: our work is relevant to fisheries and aquaculture. I have tried to point out some of the significant problems that our laboratory and field studies can address. The papers being given at this meeting illustrate broad recognition of these points. This was not the case 25 years ago, however, and we needed the pioneers I mentioned who had the foresight to persevere with early life history studies. Without them, our work would have been of academic interest only and might never have shown its potential in solving some of society's most pressing aquatic resource questions.

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