

### I-3. Studies on the Northern Anchovy; Biology, Recruitment and Fishery Oceanography

Reuben LASKER\*

I would like to thank the Japanese Society of Fisheries Oceanography for this invitation to address the Society on the main subject studied in my laboratory, fishery oceanography of the Northern anchovy, *Engraulis mordax*. I am delighted to be in Japan and to have this opportunity to meet with my esteemed Japanese colleagues.

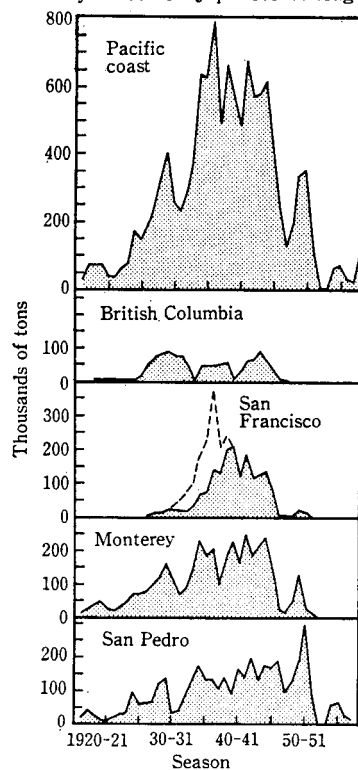


Fig. 1. Catch of the Pacific sardine, *Sardinops sagax*=*S. caerulea*, off California. The dotted line refers to catch processed in offshore floating canneries (after Marr, 1960).

\* Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, California, U. S. A.

#### Introduction

Before I discuss our work on the northern anchovy, I will describe briefly the events which led to our involvement in the study of sardines and anchovies. In 1949 a crisis occurred in the rich fishery for the Pacific sardine, *Sardinops sagax* off California. Catches fell off precipitously and the huge losses suffered by the fishermen and canners resulted in an extreme economic depression on Monterey's Cannery Row and elsewhere in the state of California. A graph of the sardine catch off the Pacific west coast from Canada to California is shown in Fig. 1.

The up-and-down nature of clupeoid catches is well-known throughout the world. The Peruvian anchoveta (Fig. 2) supported the largest fishery in the world in 1970, more than 12 million tons, and the collapse of that fishery also caused enormous economic hardship. Today the price of fish meal (\$280/mt in the U.S.) is very low because the traditional market for fish meal, the poultry and

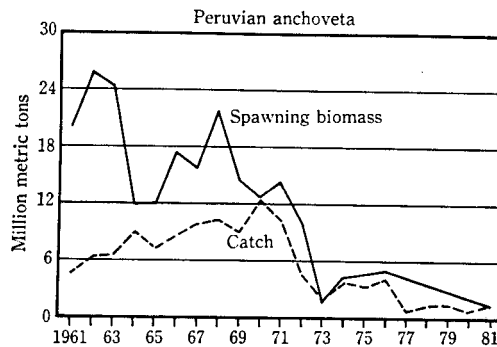


Fig. 2. Spawning biomass and catch of the Peruvian anchoveta, *Engraulis ringens* (after Tsukayama, 1982).

cattle food manufacturers, switched to soybeans during the anchoveta's collapse and fish meal has never fully recovered its market, even after 14 years.

Another good example of the crash of a clupeoid population is that of the Japanese sardine, *Sardinops melanosticta* (Fig.3).

This illustrates another phenomenon of sardine and anchovy populations, the ability to recover from apparent catastrophe and to produce enormous catches. Among the clupeoids the capacity to rebound from extremely low population sizes has also been seen in recent

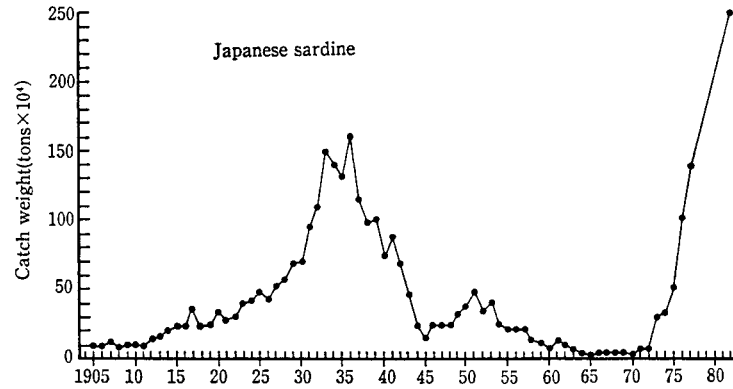


Fig. 3. Catch of the Japanese sardine, *Sardinops melanosticta* (after Kondo, 1980 and Tanaka, 1983).

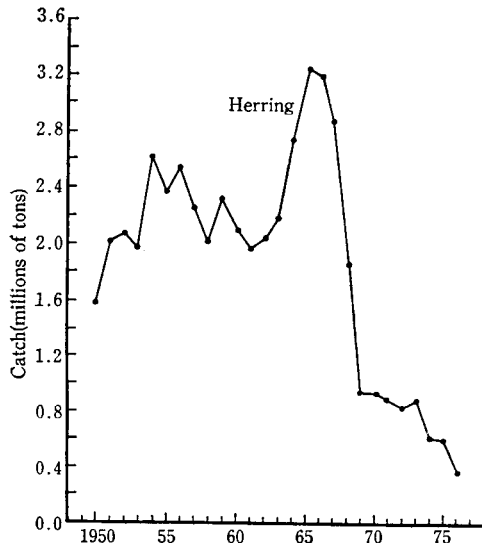


Fig. 4. Catch of the North Sea herring, *Clupea harengus* (after Schumacher, 1980).

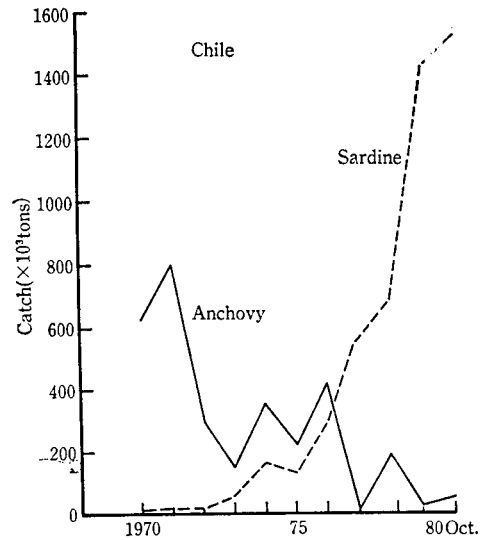


Fig. 5. Catch of the Peruvian anchoveta and the Chilean sardine by Chile (O. Rojas, Instituto de Fomento Pesquero, Santiago, Chile, Personal communication).

times in the Atlanto-Scandian herring (Fig. 4) and the Chilean sardine (Fig. 5). While this paper concerns clupeoids almost entirely, it should be understood that other fishes, such as the mackerels, cod and haddock also undergo similarly large fluctuations in population size.

The collapse of the sardine fishery off California was the major reason for the establishment of a U.S. Government research laboratory (now the Southwest Fisheries Center) to study the problem of fish population fluctuations. In the early 1950s a cooperative organization was set up in California which included the Southwest Fisheries Center, the Scripps Institution of Oceanography and the California Department of Fish and Game to find out what happened to the Pacific sardine. Today this organization is known as the California Cooperative Oceanic Fisheries Investigations, or CALCOFI. From the inception of the study, the scientists involved approached the problem from an *ecosystems* point of view. This meant that instead of just investigating the sardine, all the important fish of coastal California and the California Current were to be studied. The chief pioneer in these studies was Dr. Elbert H. Ahlstrom who began the unique surveys for ichthyoplankton off California and Mexico to answer the questions: 1) How is the sardine distributed? and 2) How is the population changing with time? From the first, one of the major hypotheses to be investigated was that year class strength may be determined environmentally (Sette, 1943).

While the sardine was disappearing from California waters, the northern anchovy was increasing in numbers. The fishery on sardines shifted to anchovies and the scientists also shifted their attention. We knew that both species ate the same kinds of food and that spawning overlapped in space and time. The anchovy was not new to us since studies on this species had been going on at the same time we were investigating the sardine, due to Dr. Ahlstrom's insistence on studying all the important fishes off California.

Because wide swings in population size are a

relatively periodic and unusual property of clupeoid populations, these fishes serve as excellent subjects for studying the causes of recruitment success or failure.

#### § 1. Is recruitment success of anchovies density dependent or density independent?

An examination of the events leading to the loss of the huge anchoveta fishery off Peru brought fishery experts to the conclusion that excessive fishing on the anchoveta parent stock reduced its reproductive potential below a level that could insure survival of a new year class and that fishing by man was the chief cause of recruitment failure (Murphy, 1974) but environmental effects were not ruled out (Fig. 6). In speculating about what happened to the Pacific sardine, Clark and Marr (1955), two of the scientists working on the California sardine program in the early 1950s, believed that there must be some minimum stock size to allow successful reproduction of the Pacific sardine although they could not say what the minimum was. Marr suggested that something in the environment caused the stock to be depressed below this minimum threshold level while Clark was certain that it was overfishing that prevented recovery of the population.

To a great extent this confusion exists today. The fishery biologist still has the task of trying to determine whether density dependent or density

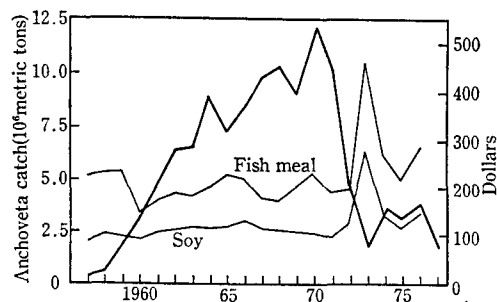


Fig. 6. Catch of the Peruvian anchoveta and the price of fish meal and soy beans from 1958 through 1977 (after Barber *et al.*, 1980).

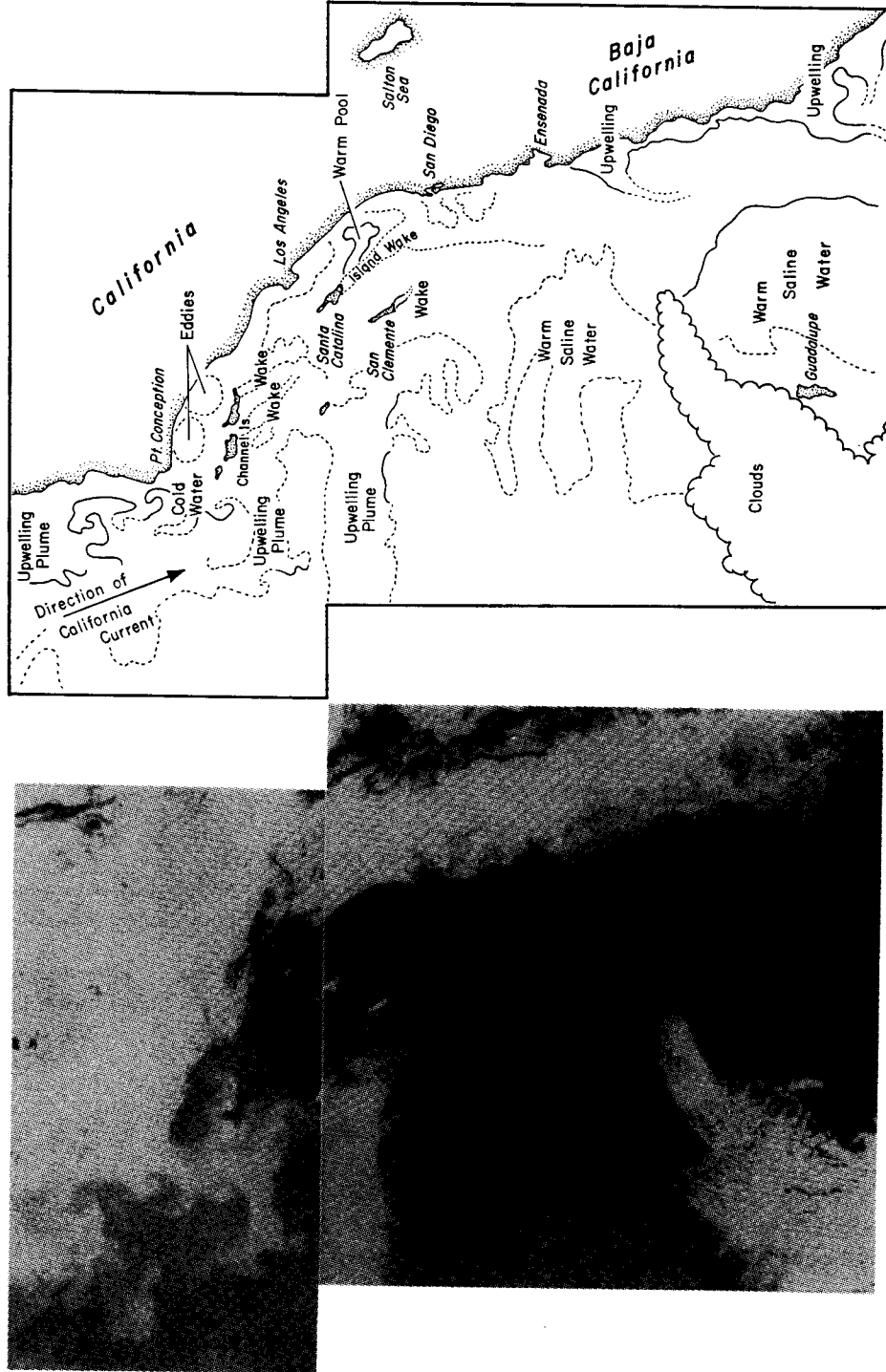


Fig. 7. Left panel: satellite image of sea surface temperatures, March 29, 1980, off the coast of California and Baja California; Right panel: line drawing indicating important oceanographic features seen in the satellite image (after Lasker *et al.*, 1981).

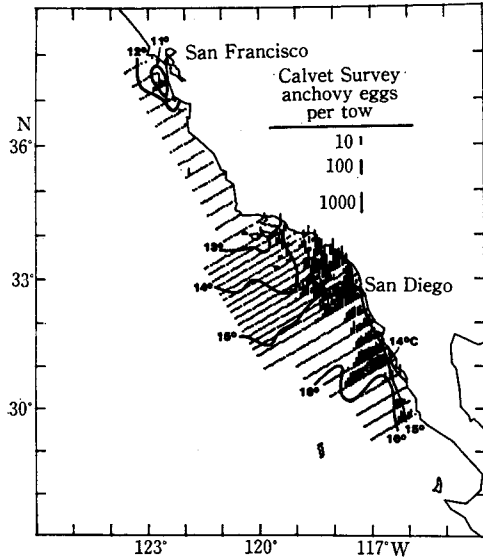


Fig. 8. Distribution of anchovy spawning off California in February 1982 as related to sea surface temperature (after Picquelle and Hewitt, 1983).

independent factors, or both, determine year class strength. Density dependency suggests that the size of the spawning stock and the number of eggs spawned has a direct relationship to the number of recruits while density independency implies that the causes of stock fluctuation are mainly environmental.

## § 2. The California current and the Southern California Bight

The satellite picture of the nearshore ocean off California illustrates some general features of the oceanography of the California coastal zone (Fig. 7). About 150 km off the coast is the California Current which is part of the large-scale, anticyclonic North Pacific gyre. The northern anchovy and the Pacific sardine are coastal fish whose main habitat is the Southern California Bight. The whole California coast is an active upwelling region but the Southern California Bight acts as a refuge because the shoreline curves inward and

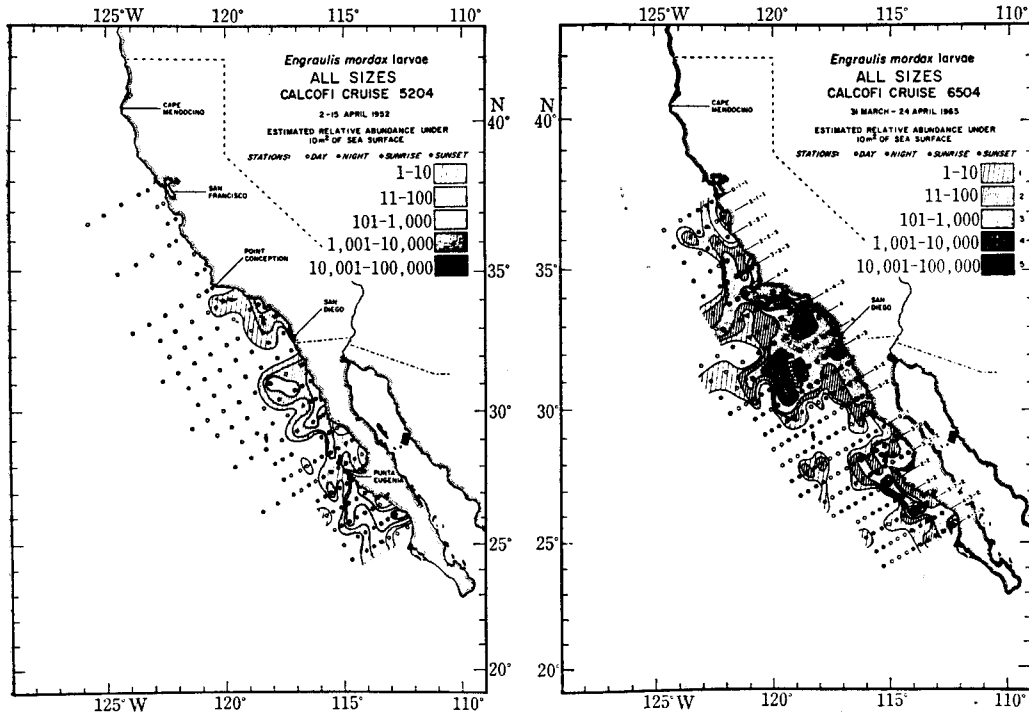


Fig. 9. Distribution of anchovy larvae off California in 1954 and 1962 (after Kramer and Ahlstrom, 1968).

the Bight is protected by the Channel Islands (Fig. 8). A distribution map (Fig. 9) of anchovies illustrates how this species uses the Bight as its essential habitat and ranges beyond it when its population exceeds the carrying capacity of the near shore habitat.

§ 3. The paleosedimentary record

Soutar and Isaacs (1974) working at the Scripps Institution of Oceanography examined cores taken in the anaerobic Santa Barbara Basin which is in the Southern California Bight, for evidence of anchovies, sardines and hake. Varves, as those cores are called, contain undisturbed sediments, thousands of years old. Fish scales falling to the bottom of the ocean became trapped in these sediments and are found in layers which can be accurately dated. By examining each layer of sediment for fish scales an index of anchovy, sardine and hake populations could be constructed. Fig. 10 shows data taken from their paper which illustrates the relative magnitude of these fish populations from 1800 when no fishery of any size existed on these populations.

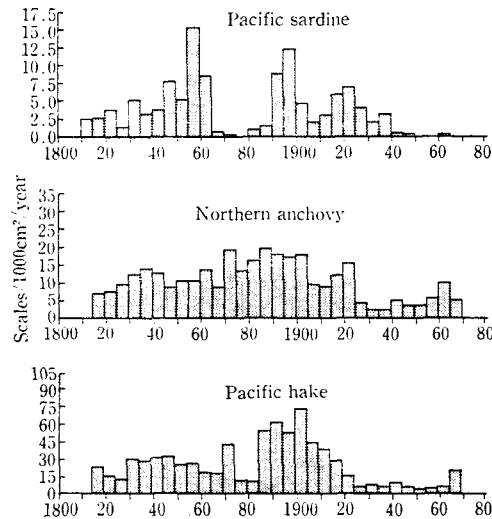


Fig. 10. The concentration of sardine, anchovy, and hake scales in anaerobic cores taken from the Santa Barbara Basin off California (modified after Soutar and Isaacs, 1974).

The results clearly show that the sardine and anchovy have fluctuated in population size even when no fishery was present. Exceptional sardine year classes occurred in 1855 and 1865 but this did not prevent the natural but sharp decline in the 1870s. The drastic decline in the 1940s which precipitated our investigations and was reflected in declining catches, was also seen in the Santa Barbara Basin varves.

§ 4. The Japanese sardine

*Sardinops melanosticta* is one of the more remarkable examples of the resiliency of the clupeoid's ability to recover if the conditions for survival are favorable. Resurgence from a virtually unfishable level to the current level of a 4.2 million metric ton catch off Japan in 1984 has been recorded. Kondo (1980) has written that the 1972 year class probably had extraordinarily good conditions for larval survival because of a change in the course of the Kuroshio Current. The importance of this example is that it shows that even very small populations of clupeoids are able to have unusually successful recruitment.

§ 5. The northern anchovy

In common with other clupeoids the northern anchovy is highly fecund, and each female spawns from 20 to 30 times during a span of about 4 months, a spawning season which extends from December through April in California and Baja California coastal waters. This frequency of spawning was discovered by my colleagues Dr. John Hunter and Dr. Steve Goldberg (1980) and constitutes an important contribution to our knowledge of pelagic fishes. It afforded us an opportunity to investigate whether recruitment is density dependent based on the number of fish spawning and the number of eggs spawned or density independent mechanisms under environmental control.

§ 6. The first-feeding larva and the critical period

Johan Hjort (1913, 1926) while working on the

Atlanto-Scandian herring suggested that if newly hatched larvae did not find suitable food as soon as they were ready to eat then they would die. This required that there has to be simultaneous development of the special plants and nauplii used for food when the larvae were ready to eat. Hjort suggested this hypothesis because the early culture work of the French scientists Fabre-Domergue and Biatrix (1905) showed that sole larvae (*Solea vulgaris*=*S. solea*) started to look for food even before the yolk-sac was absorbed, and if they did not find it right away, the larvae became "anaemic" and died of starvation. To Hjort this laboratory observation suggested an explanation for the fact that occasionally there appeared coincident good year classes of several different species of fish in the Norwegian fisheries; that is, when good larval food is available, it feeds many species. The idea that there is one stage in the early life history of a species whose ability or inability to capture food can account for the success or failure of a year class has been called the "critical period" hypothesis.

The critical period hypothesis provided the motivation for research into the mortality and survival of anchovy larvae in La Jolla. However, early in our work we recognized that there were two possible processes involved in larval fish mortality, starvation and predation. I shall discuss each of these in relation to the anchovy.

#### § 7. Experiments on mortality of first-feeding larvae

Our laboratory studies on the anchovy always indicated that the only way we could insure survival of *some* of the larvae, usually a very small percentage, was to provide food at very high densities. It seemed to us that this observation was incompatible with what we knew about the ocean. For example, we found that feeding and survival in the laboratory required about one nauplius per milliliter or 1000 per liter (O'Connell and Raymond, 1970) but the maximum found in California waters is only about 200 nauplii per liter (Beers and Stew-

art, 1967; Lasker, 1978). Other food organisms were found to support anchovy growth and survival but generally at even higher densities than nauplii. For example, the naked dinoflagellate *Gymnodinium splendens* was found to be good food at densities of about 30000 per liter or higher. The problem was to find where particles of the right size and in the right density occur in the ocean and to determine what affected their concentration and distribution. Once this was done, the intent was to predict from larval food availability whether larval survival would be good or bad and subsequently whether or not there would be a good year class.

#### § 8. Effects of storms and upwellings

A simple bioassay for larval anchovy food was devised in 1974 (Lasker, 1975) by spawning and hatching anchovy larvae in the laboratory, taking the first-feeding larvae to sea in laboratory containers, and by putting the larvae in natural concentrations of food organisms taken from various depths in the anchovy's habitat. The finding was unexpected; food organisms of the right size and of the right density (20 to 30 particles/ml or more) were mostly dinoflagellates and were generally located in stratified layers near the chlorophyll maximum (Table 1). Twenty to thirty particles per milliliter seemed to be a threshold quantity needed for successful first feeding. During this experiment at sea, a short (one day) storm arose which chased us into harbor. When I went back the next day, the stratified layers of larval food organisms were gone (Fig. 11). It was clear from this that wind-induced turbulence had diluted and disrupted the aggregation of food particles to below the threshold number needed by the anchovy first-feeding larva and this led me to hypothesize that turbulence might be correlated with larval anchovy survival and subsequent recruitment. In other words, stable ocean conditions favor the aggregation of suitably-sized food organisms so that above-threshold numbers of food particles become available to larvae.

Table 1. Results of a field experiment on the feeding of first-feeding anchovy larvae in relation to different concentrations of natural food, Numbers in ( ) refer to counts of the dinoflagellate *Gymnodinium splendens* at each depth. (after Lasker, 1975).

No.	Date and Time A. Surf. Temp. B. Chl. Max., Temp. and Depth	Position	Total number particles/ml		Feeding by Anchovy Larvae	
			23-37 um Diameter	>37-299 um Diameter	Percent of Larvae with:	
					1/4 to full gut	1-8 particles in gut
1.	3/20/74, 1250 A. 15°C B. 14.2°C, 12m.	Malibu	14.2	4.1 (<1)	2	15
			37.3	38.0 (12)	23	46
2.	3/20/74, 1745 A. 15.2°C. B. 14.5°C., 13.5m.	Manhattan Beach	23.1	6.1 (6)	0	11
			29.8	19.7 (12)	0	18
3.	3/21/74, 0900 A. 15.8°C. B. 14.2°C., 16.5m.	Seal Beach	217.9	33.2 (<1)	0	12
			53.8	352.0 (380)	22	24
4.	3/21/74, 1340 A. - B. -, 15m. (no chl. max.)	Laguna Beach	34.0	9.0 (0)	0	10
			29.0	5.7 (0)	0	11
5.	3/21/74, 1715 A. 15.5°C. B. -, 15m.	Dana Point	18.7	5.9 (<1)	5	16
			55.2	23.2 (5)	0	69
6.	3/21/74, 1900 A. 15.2°C. B. -, 19.5m.	San Onofre	9.3	4.0 (<1)	0	8
			42.4	47.7 (34)	9	25
7.	4/8/74, 1500 A. 17.1°C. B. 14.8°C., 16m.	San Onofre	5.7	9.1 (<1)	0	13
			14.0	81.3 (64)	9	40
8.	4/10/74, 1710 A. 14°C. B. 13.5°C., 14m. (no chl. max.)	San Onofre	8.4	14.1 (0)	0	12
			10.5	23.2 (0)	0	15
9.	4/11/74, 0915 A. 13.0°C., 5m. (no chl. max.)	San Onofre	6.4	10.5 (0)	0	4

The following year (1975) a full scale oceanographic survey was mounted to test the effect of wind on stratification of larval anchovy-sized food particles (Lasker, 1978). Nature once again performed an interesting experiment. Although the weather was calm and the ocean stable and stratified, a red tide composed of the thecate dinoflagellate *Gonyaulax polyedra* dominated the anchovy larva's environment for first half the spawning season. Earlier we had found that *Gonyaulax* in the laboratory was eaten avidly by first feeding anchovy larvae but that the larvae would not grow and soon died (Scura and Jerde, 1977). In the midst of the spawning season, there was an onset

of Northwesterly winds which normally cause upwelling off the coast of California. These winds were strong enough to induce massive upwelling which swept out *Gonyaulax* and brought in nutrient rich water resulting in a diatom bloom (Fig. 12). Our laboratory findings, however, showed that anchovy larvae do not eat diatoms. Thus, two poor phytoplankton food types were dominant in the larva's environment in 1975. The 1975 anchovy year class was the worst that had been recorded over a sixteen year recording period despite indicators to the contrary, such as an enormous spawning (Fig. 13), and great primary productivity (Fig. 14). My belief is that most of the larvae



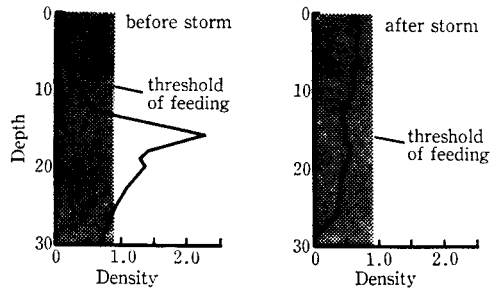


Fig. 11. The effect of a storm on the vertical distribution of larval food particles. The threshold for larval feeding was 30 particles per milliliter. The dark line indicates relative concentrations of food (dinoflagellates) with depth (after Lasker, 1975).

starved and were lost to the year class because the major food sources in their environment were unsuitable for growth and survival.

In 1978 I had another opportunity to study the habitat of the anchovy during its entire spawning season (Lasker, 1981). Early in the spawning season, December, 1977, a great storm occurred off the Pacific coast of the U.S. and was succeeded by frequent but less intense storms through March (Fig. 15). Precipitation in Southern California in the 1977-78 season set a 20 year record of 56 cm (100 year average = 25 cm). Furthermore, these storms covered a large geographic area,

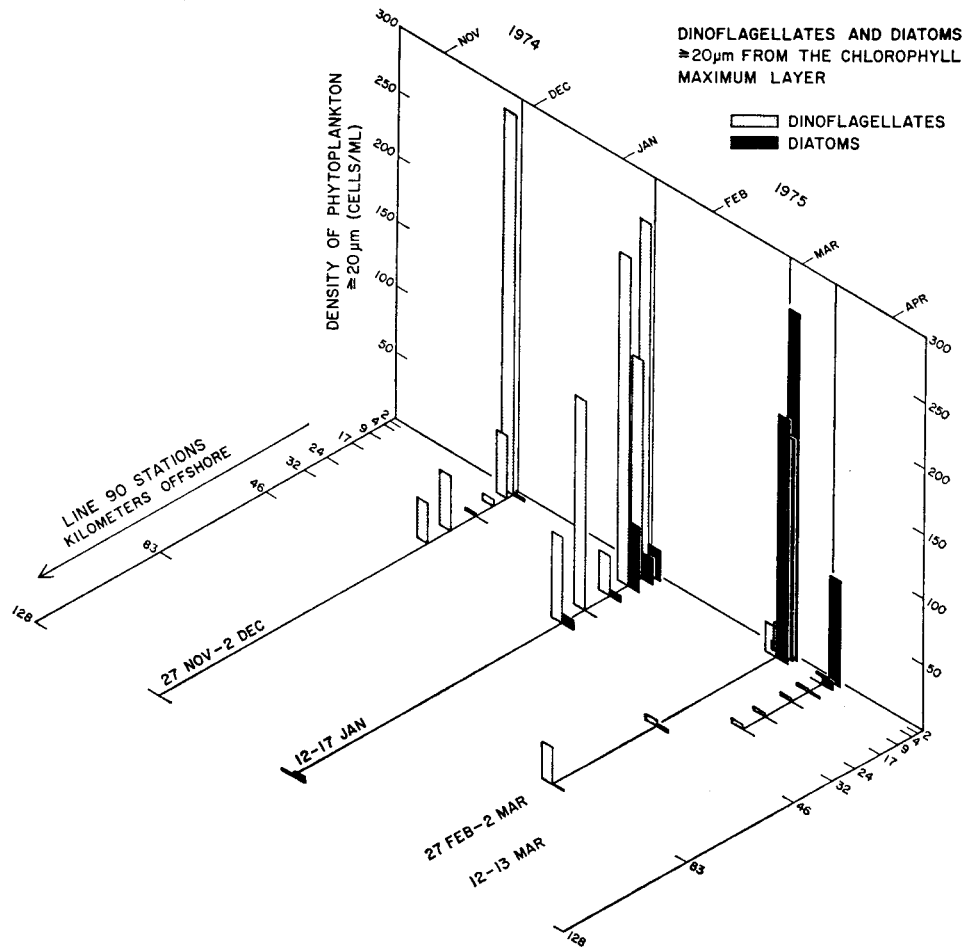


Fig. 12. Diatoms replace dinoflagellates as a result of an upwelling event in 1975 off California (from Lasker, 1978).

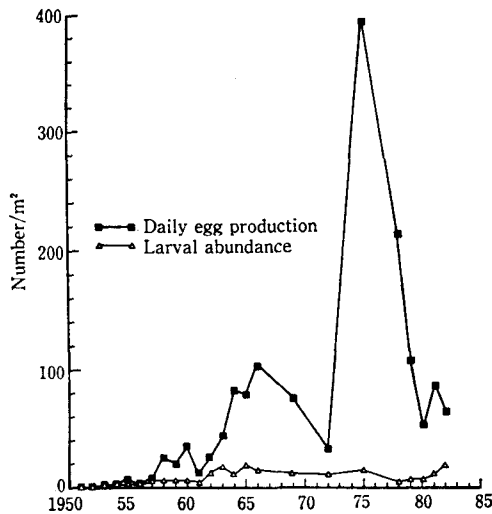


Fig. 13. Anchovy egg production off California from 1950 through 1982 (after Lo, 1984).

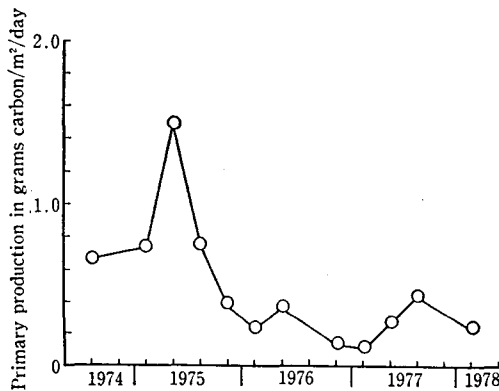


Fig. 14. Primary production in the Southern California Bight, 1974 through 1978 (modified from Smith and Eppley, 1982).

affecting virtually all of the anchovy spawning habitat.

Based on my earlier work I expected to find no aggregations of organisms suitable for first-feeding anchovies and did not find any, although anchovy spawning continued unabated through the stormy periods. In March the storms ceased, stable conditions were re-established and prevailed to the end of the spawning season, early May. Stratification of anchovy larval food organisms was evident in

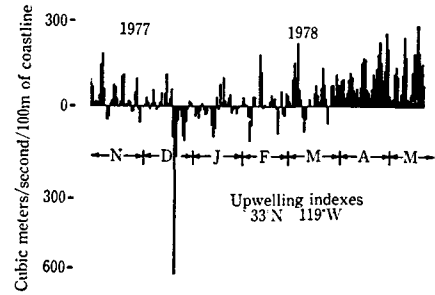


Fig. 15. Upwelling indexes 1977-1978, at San Clemente Island in the Southern California Bight (after Lasker, 1981). The values above the line indicate offshore flow; below the line, onshore flow.

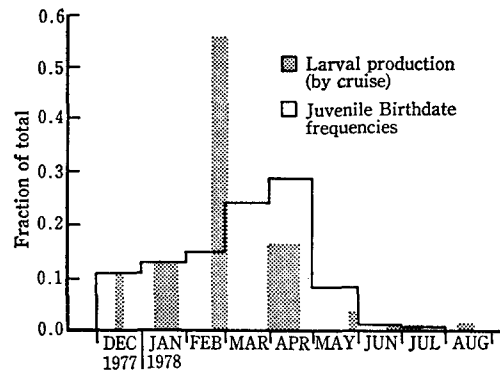


Fig. 16. Larval anchovy production compared to fractional survival of juveniles for the 1977-78 spawning season off California (after Methot, 1983).

mid-March and continued to the end of the spawning season.

I predicted that the 1978 year class would have very few survivors from the first half of the spawning season but that survival from mid-March to the end of spawning would be good to excellent. This prediction was confirmed by Methot (1983) who was able to show that the juvenile survivors of the 1978 year class had birthdate distributions which agreed with the prediction. A much larger number of survivors had been born from March to May than from December to March despite the fact that larval production was about equal in both halves of the spawning season (Fig. 16).

### § 9. Larval starvation

Because starvation in the sea may be an extremely important phenomenon, scientists at the Southwest Fisheries Center have tried to quantify

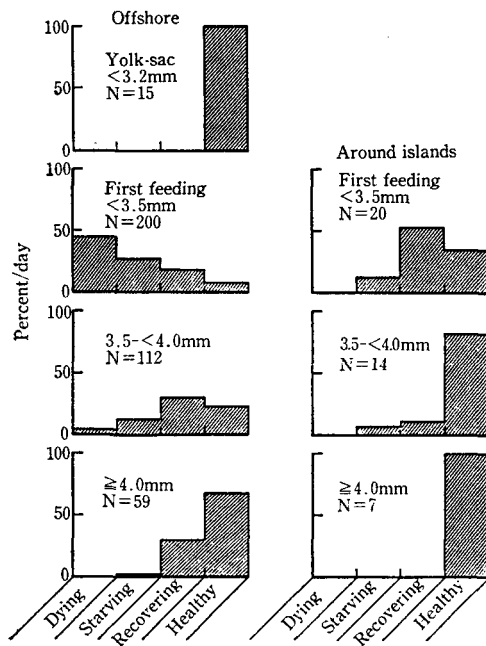


Fig. 17. Percent starvation in jack mackerel (*Trachurus symmetricus*) larvae in an offshore and an island environment (from Theilacker, 1986).

starvation by using morphometric and histological methods. O'Connell (1976, 1980) developed histological criteria to determine if a larva was starving. An examination of his data by Theilacker (1986) showed that appreciable numbers of anchovy larvae can be found starving each day when tested histologically. For example, in March 1977, 35 to 46% of anchovy larvae were shown to be dying from starvation each day. Theilacker has also shown with jack mackerel larvae, *Trachurus symmetricus*, that at first-feeding they are mostly starving in oligotrophic (offshore) parts of their spawning environment but are mostly well fed in eutrophic areas, e.g. close to islands (Fig. 17).

### § 10. Larval transport

Gyres, island wakes, fronts and upwelling plumes are the most prominent features of the California and Baja California coastal regime when viewed by infrared satellite (Lasker *et al.*, 1981) and by the Coastal Zone Color Scanner (Fiedler, 1983). The extent of water moving actively offshore was not really appreciated until satellite photos showed that there are "jets" of water streaming from the coast a hundred or more kilometers offshore in Eastern Boundary upwelling regions (Fig. 18). In

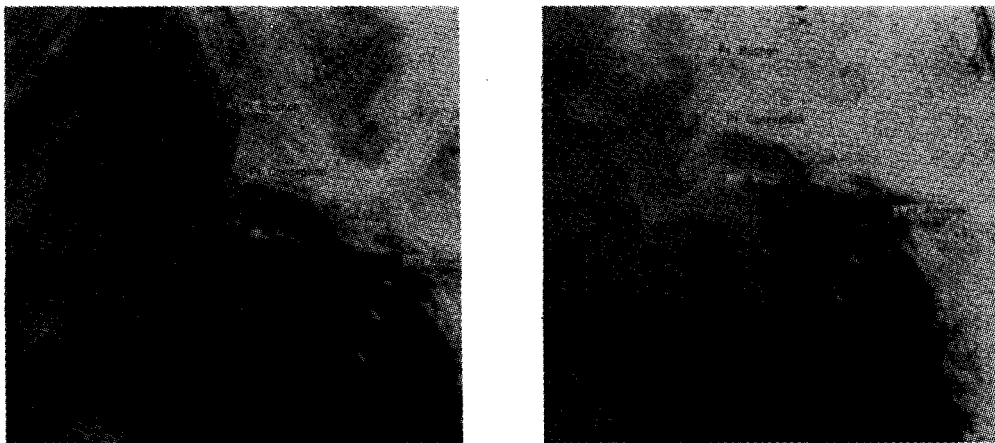


Fig. 18. Development of upwelling off the California Coast (left March 19, 1980; right: March 28, 1980 as) seen by an infrared satellite (after Lasker *et al.*, 1981).

recent studies at the SWFC we have shown that anchovy eggs and larvae, while usually confined to the Southern California Bight, occasionally are drawn far offshore into an extremely unfavorable habitat for larval survival. This kind of transport has been found to be associated with large gyres which induce water to flow strongly offshore (Fiedler, 1986).

Parrish *et al.* (1981) hypothesized that deviations from "normal" transport conditions could have profound detrimental effects on a year class by carrying eggs and larvae to areas where there is not enough food for the larvae to survive. Methot (1983) compared the 1978 and 1979 anchovy year classes and found that despite the relatively low survival in the first half of the spawning season, 1978 had one of the largest anchovy recruitments in years. Conversely, the 1979 year class had a very poor recruitment and he believed this difference could be explained by increased upwelling and larval transport of larvae into poor feeding areas offshore in 1979. In any event lack of food for larvae is still the basic hypothesis for poor year classes if offshore transport is invoked as a mechanism.

Although offshore transport is a possible mechanism that can be detrimental to the survival of a particular year class, over evolutionary time anchovies and sardines appear to have chosen the least energetic area (the Southern California Bight) and time (late Winter, early Spring) for spawning with respect to upwelling and offshore transport (Parrish *et al.* 1981). A comparison of wind mixing and stability indices for the major spawning regions of the three subpopulations of *Engraulis mordax* show that "peak spawning occurs during seasons and locations associated with stable stratification, relatively low rates of turbulent energy production, and weak offshore transport (upwelling)" (Husby and Nelson, 1982).

A comparison of the California and Peru Current anchovy stocks by Bakun and Parrish (1982) showed that there is "a consistent pattern of avoidance of centers of maximum upwelling, which are

characterized by intense turbulent mixing and offshore transport. Large stocks tend to occur in regions of low turbulent mixing, downstream of upwelling maxima."

#### § 11. Oceanographic explanations of differential recruitment

Several effects on larval anchovy survival by specific oceanographic events seem clear from the work we have done in California. First, upwelling can be either favorable or detrimental, depending on its timing and the biological response of anchovy larvae. For example, upwelling due to sustained northwest winds brings nutrients to the surface near shore and provides an excellent habitat for organisms that can be eaten by anchovy larvae, e.g. copepods. On the other hand, sustained and excessively strong upwelling, particularly during the anchovy's spawning season, can destroy the stratification needed to provide high enough concentrations of food for larval survival. Furthermore, it is also possible that with sustained upwelling larvae may be swept out to sea into unfavorable feeding environments. When the response to upwelling is the production of diatoms, anchovy larvae do not benefit directly and this may be particularly bad for first-feeding larvae, although older larvae benefit from the nauplii produced by copepods which are stimulated to reproduce by eating diatoms.

Storms can have enormous effects on larval survival by disrupting stratified larval food layers and by preventing restratification. My colleagues in La Jolla, Dr. Peterman and Mr. Bradford (1987) have analyzed 13 years of wind data where they correlated the average instantaneous mortality rate of northern anchovy larvae against the number of four day calm periods found in each month of the anchovy spawning season (Fig. 19). A highly significant correlation ( $r=0.81$ ) was found further supporting the idea that stability is a necessary prerequisite to larval survival in this species.

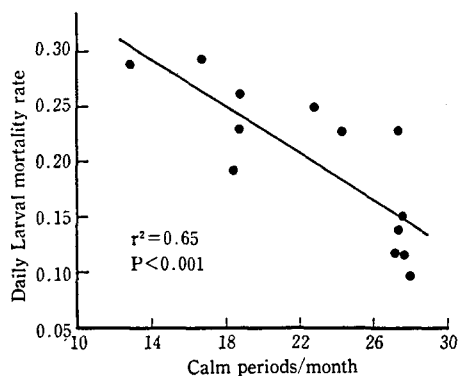


Fig. 19. Correlation between calm periods per month with daily anchovy (*Engraulis mordax*) larva mortality rate for a thirteen year data set (after Peterman and Bradford, 1987).

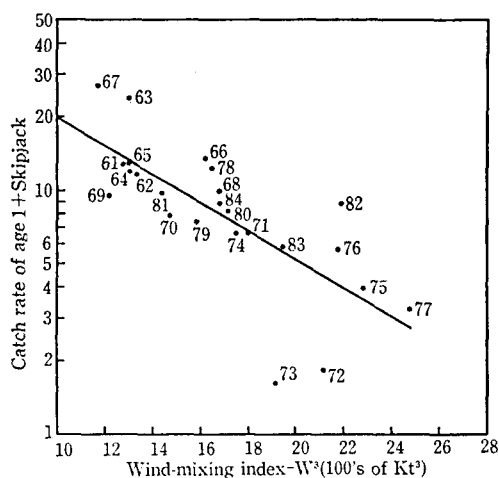


Fig. 20. Catch rate of age 1+ skipjack, *Katsuwonus pelamis* in thousands of fish per day in the equatorial Pacific Ocean correlated with wind speed cubed (after Forsbergh, 1986).

By analyzing 24 years of catch data, Forsbergh (In Press) has shown that there is a very good correlation between cube of the wind speed and the catch of one year old skipjack tuna over a large area of the Pacific Ocean (Fig. 20). Thus, the idea that stability is needed for the production of good year classes seems applicable to other fishes.

## §12. Older larvae and mortality curves

Hjort ignored older larvae in his hypothesis but many scientists believe that larval mortality over the entire larval period is more likely to determine recruitment than the heavy mortality seen in first-feeding larvae. This seems to be borne out by our inability to match up first-feeding larvae mortality rates with recruitment. The answer to the question of the involvement of any stage larva in determining recruitment is tied to our inability to determine the precise shape of the annual mortality curve. For anchovy our best mortality curves (Fig. 21) are derived from the number of eggs and larvae obtained over a 40 day period in the midst of the anchovy spawning season and from an area over thousands of square kilometers. Corrections are made for extrusions of eggs and larvae through the meshes of the plankton net, avoidance of the net as the larvae grow older, adjustment for individual growth rates and the application of two models, an age-independent instantaneous mortality rate for eggs and an age-dependent mortality rate (a) for larvae (Lo, 1986). The imprecision of these curves makes it difficult to interpret whether some particular time in the life cycle is a determinant of recruitment or not. Peterman *et al.* (1986), using sophisticated statistical techniques has shown first-feeding larval anchovy

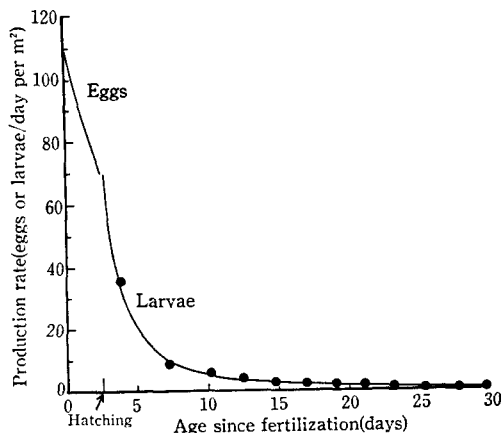


Fig. 21. Mortality curve of anchovy eggs and larvae (after Picquelle and Hewitt, 1983).

mortality and abundance are poor predictors of recruitment. Their data show that the entire larval period may have to be taken into account before significant correlations can be found with recruitment.

§13. Predation

In our attempt to assign causes to egg and larval mortality, the work in La Jolla has also centered around another hypothesis, that predation is the major cause of larval mortality. Since the paper by Lillelund and Lasker (1971) which implicated various copepods as possible consumers of first-feeding fish larvae, there have been a large number of studies on marine organisms consuming fish larvae, such as euphausiid shrimps (Theilacker and Lasker, 1974), ctenophores and coelenterates (Purcell, 1985; Bailey and Batty, 1984), chaetognaths (Alvaríño, 1985) and fishes (Hunter and Kimbrell, 1980). New work at the Southwest Fisheries Center by Theilacker and her associates (1986) has demonstrated the use of an immunoassay to detect euphausiid predation on yolk-sac anchovy larvae. However, the conclusion one must come to at present is that, like every organism in the sea, there is the possibility that an anchovy larva will be eaten, but thus far with an unknown probability.

§14. Density dependent regulation of populations

It is particularly difficult to assign density effects to the fluctuation of clupeoid populations. From the example of the Japanese sardine, there seems

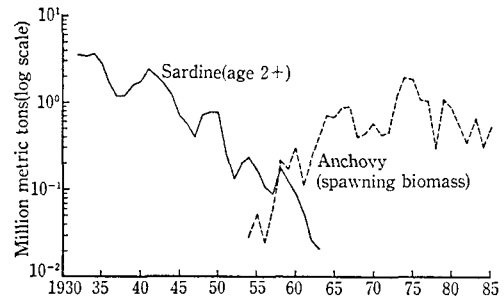


Fig. 22. Sardine and anchovy biomasses off the West Coast of the United States.

to be no minimum stock size which cannot give rise to a reasonable year class given that the conditions are right. There is, on the other hand, reasonable evidence to indicate that in some instances two species may interact in some way so that it appears as if one affects the other. In California, the rise of the anchovy population during the decline of the sardine (Fig. 22) suggests this possibility while in Peru and Chile the sardine population increased greatly when the anchovetta collapsed (Fig. 5). Mr. Butler of my laboratory has correlated sardine larval mortality coefficients against anchovy biomass and concludes that cannibalism by anchovies on sardine eggs and larvae was a highly probable cause of the sardine's demise off California (Butler, 1987).

In La Jolla, one of the important needs for managing the anchovy fishery was an accurate method for determining biomass. We devised an egg production method technique for doing so (Lasker, 1985) and now have 6 years of data on the egg

Table 2. Anchovy egg production, spawning biomass and other adult parameters measured with the egg production method of biomass assessment, 1980 through 1985; coefficients of variation are not shown (see Fiedler *et al.*, 1986).

YEAR	1980	1981	1982	1983	1984	1985
Spawning female weight, g	17.50	13.37	18.83	11.20	12.02	14.49
Female fraction	.475	.501	.472	.549	.582	.609
Batch fecundity for average female	7788	8208	10845	5297	5485	7343
Spawning incidence, per day	.145	.106	.120	.094	.160	.120
Specific fecundity, eggs/day-g	30.28	33.03	32.53	24.35	42.43	37.00
Egg production, 10 <sup>12</sup> eggs/day	26.34	20.96	13.51	17.25	12.98	16.95

Table 3. Effects of the 1983 El Niño on adult anchovies (from Fiedler *et al.*, 1986).

Year	1980	1981	1982	1983	1984	1985
Spawning biomass, in 10 <sup>3</sup> metric tons	870	635	415	652	306	458
Spawning female weight, g	17.5	13.4	18.8	11.2	12.0	14.5
Mean age in February, yrs	1.80	1.80	2.46	1.29	1.76	1.46
Year class size, 10 <sup>9</sup> fish	63	14	45	35	109	39

production and interannual fluctuation in spawning biomass. These data are given in Table 2. They show that the spawning biomass of anchovies has been increasing off California and that there is a reasonable consistency in the biological parameters of the anchovy (such as egg production, fecundity and frequency of spawning) but with changes brought on by an El Niño event which occurred in 1982-1983.

#### §15. El Niño

One of the most impressive environmental events affecting clupeoid populations is the massive warming of the eastern Pacific, known as El Niño. The El Niño conditions of 1982-1983 were the most impressive of the century and affected fisheries from Peru to California (Table 3). Both in California and Peru there is evidence that zooplankton production was far below normal. In Peru this resulted in great losses in body weight per fish (30% for anchovies; 15% sardines) and much lower egg production (Arntz, 1986). Our California data shows a similar loss in female weight in 1983, a lowered frequency of spawning and a low batch fecundity, but despite this, the number of eggs produced by the population was about average because the anchovy population was somewhat larger in 1983 than it was in 1982 and there were many first year spawners (a result of the warmer water) in contrast to previous years (Fiedler, *et al.* 1986). As far as this large El Niño event is concerned, the effect on fisheries, even in Peru, seems to be due to changes in the distribution of fishes and their availability rather than to changes in the size of the population or the number of eggs spawned.

#### §16. The sardine/anchovy recruitment project

The work I discussed earlier provides the basis for a study of recruitment that we have never been able to do before. We are now able to analyze events within a spawning season and to determine the effect of specific oceanographic events on monthly survival and mortality of larvae. In conjunction with cohort analyses we may be able to tell what determined the strength of a particular year class.

The Intergovernmental Oceanographic Commission (I.O.C.) and the Food and Agriculture Organization of the United Nations have endorsed a program encompassing this idea called SARP or the Sardine/Anchovy Recruitment Project. I wish to outline how such a program would be put together, what measurements need to be taken, what area needs to be sampled and what can be expected to be deduced from the data collected.

#### §17. Larval production

The basis for SARP is the comparison between the measured larval production by month and the survivorship by month as deduced from the birthdates of large larvae and juveniles (Methot, 1983). The development of the accurate ageing of fish larvae and juveniles by counting daily rings on the otoliths has provided the fishery biologist with a powerful tool for studying recruitment. We have calibrated the rings by counting the increments on otoliths taken from larvae of known age (Brothers *et al.*, 1976) and have proven them to be daily. Since then many fish species have been examined and have been seen to have daily increments.

Because the anchovy has a protracted spawning season from January through May, it is now possi-

ble to correlate environmental events occurring within the season with larval survival. It follows that most of the clupeoids can be studied in this way. For a complete analysis, additional information is important such as the number and strength of cohorts, the number of eggs spawned, the spawning biomass, the number and distribution of predators, larval production, the proportion of starving larvae, larval growth rates, mortality rates of all egg and larval stages, and an assessment of older larvae throughout the spawning season. The egg production method of anchovy biomass assessment that I mentioned earlier provides many of these parameters, while the fishery statistics gives the recruit and adult fish information.

Thus a minimum plan for recruitment studies was decided on by an I.O.C. working group.

- 1) A quantitative larval survey and an egg production method biomass survey must be done.
- 2) Large larvae and juveniles must be sampled sufficiently to determine birthdates by the otolith daily ring method.
- 3) Physical oceanographic measurements and monitoring must be done over the spawning season.
- 4) Meteorological measurements (especially winds) should be taken from ship and shore.
- 5) A quantitative analysis of year class strength must be done from fisheries statistics.

Sardines and anchovies are prime candidates for these studies because they meet all the criteria for success, such as a protracted spawning season, easy to read otoliths, multiple spawning behavior, discreet stocks, and a highly variable population. Furthermore these are fishes of commercial importance with adequate sampling and statistics collection already in place, and with a known geographical distribution.

#### References

- Alvariño, A. (1985): Predation in the plankton realm; mainly with reference to fish larvae. *Investigaciones Marinas CICIMAR*, 2, 1-122.
- Arntz, W. E. (1986): The two faces of El Niño 1982-83. *Meeresforsch.*, 31, 1-46.
- Bailey, K. M. and R. S. Batty (1984): Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. *Marine Biology*, 83, 287-291.
- Bakun, A. and R. H. Parrish (1982): Turbulence, transport, and pelagic fish in the California and Peru Current systems. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 23, 99-112.
- Barber, R. T., W. W. Kirby Smith and P. E. Parsley (1980): Wetland alteration for agriculture, p. 642-651. In P. E. Greeson, J. R. Clark and J. E. Clark (eds.), *Wetland Functions and Values*, Amer. Wat. Res. Assoc., Minneapolis, MN.
- Brothers, E. B., C. P. Mathews and R. Lasker (1976): Daily growth increments in otoliths from larva and adult fishes. *Fish. Bull. U. S.*, 74, 1-8.
- Butler, J. (1987): Comparison of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph. D. Thesis, U. C. S. D., San Diego, 242pp.
- Clark, F. N. and J. C. Marr (1955): Population dynamics of the Pacific sardine. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 4, 11-48.
- Fabre-Domergue and E. Biérix (1905): *Développement de la Sole (Solea vulgaris)*. Introduction à l'étude de la pisciculture marine. Travail du Laboratoire de Zoologie Maritime de Concarneau. Vuibert et Nony, Paris. 243pp.
- Fiedler, P. C. (1983): Satellite remote sensing of the habitat of spawning anchovy in the Southern California Bight. *Calif. Coop. Oceanic Fish. Invest. Rep.*, 24, 202-209.
- Fiedler, P. C. (1986): Offshore entrainment of anchovy spawning habitat, eggs, and larvae by a displaced eddy in 1985. *ibid.*, 27, 144-152.
- Fiedler, P. C., R. D. Methot and R. P. Hewitt (1986): Effects of California El Niño 1982-84 on the northern anchovy. *J. Mar. Res.*, 44, 317-338.
- Forsbergh, E. D. (1986): The influence of environmental variables on the apparent abundance of skipjack tuna (*Katsuwonus pelamis*) in the fisheries of the eastern Pacific Ocean. *Bull. Inter. Amer. Trop. Tuna Comm.* (in Press).
- Hjort, J. (1914): Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-V. des Réun. Cons. Perm. int. Explor. Mer*, 20, 1-228.
- Hjort, J. (1926): Fluctuations in the year class of important food fishes. *Jour. du Conseil*, 1, 5-39.
- Hunter, J. R. and S. R. Goldberg (1980): Spawning incidence and batch fecundity in northern anchovy,



- Engraulis mordax*. *Fish. Bull. U. S.*, **77**, 641-652.
- Hunter, J. R. and C. A. Kimbrell (1980): Egg cannibalism in the northern anchovy, *Engraulis mordax*. *Fish. Bull. U. S.*, **78**, 811-816.
- Husby, D. M. and C. S. Nelson (1982): Turbulence and vertical stability in the California Current. *Calif. Coop. Oceanic Fish. Invest.*, **23**, 113-129.
- Kondo, K. 1980: The recovery of the Japanese sardine—the biological basis of stock-size fluctuations. *Rapp. P.-V. Réun. Cons. int Explor. Mer.*, **177**, 332-354.
- Kramer, D. and E.H. Ahlstrom (1968): Distributional atlas of fish larvae in the California Current region: Northern anchovy, *Engraulis mordax* Girard, 1951 through 1965. *Calif. Coop. Oceanic Fish. Invest. Atlas*, **9**, 269 pp.
- Lasker, R. (1975): Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull. U. S.*, **73**, 453-462.
- Lasker, R. (1978): The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-V. Réun. Cons. int. Explor. Mer.*, **173**, 212-230.
- Lasker, R. (1981): Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: Contrasting years, 1975 through 1978. *ibid.*, **178**, 375-388.
- Lasker, R.(ed). 1985: An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. *Nat. Oceanic Atmos. Admin. Tech. Rep. NMFS*, **36**, 99pp.
- Lasker, R., J. Pelaez and R. M. Laurs (1981): The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). *Remote Sensing of Environment*, **11**, 439-453.
- Laurs, R. M., P. C. Fiedler and D. R. Montgomery (1984): Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Research*, **31**, 1085-1099.
- Laurs, R. M. and R. J. Lynn (1977): Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with transition zone waters. *Fish. Bull. U. S.*, **75**, 795-822.
- Lillelund, K. and R. Lasker (1971): Laboratory studies of predation by marine copepods on fish larvae. *ibid.*, **69**, 655-667.
- Lo, N.C.H. (1986): Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. *ibid.*, **84**, 395-407.
- Marr, J. C. (1960): The causes of major variations in the catch of the Pacific sardine *Sardinops caerulea* (Girard). *Proc. World Scientific Meeting on the Biology of sardines and related species*, **3**, 667-791.
- Methot, R. D. Jr., (1983): Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. *Fish. Bull., U. S.*, **81**, 741-750.
- Murphy, G. T. (Chairman) (1974): Report of the fourth session of the panel of experts on stock assessment on Peruvian anchoveta. *Instituto del Mar del Perú (Callao), Bol.*, **2**, 605-719.
- O'Connell, C. P. (1976): Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. *J. Exp. Mar. Biol. Ecol.*, **25**, 285-312.
- O'Connell, C. P. (1980): Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. *Fish. Bull.*, **78**, 475-489.
- 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.
- Parrish, R. H., C. S. Nelson and A. Bakun (1981): Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.*, **1**, 175-203.
- Peterman, R. M. and M. J. Bradford (1987): Wind speed index correlates with mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science*, **235**, 354-356.
- Peterman, R. M., M. J. Bradford, N. C. H. Lo and R. D. Methot (In Press): Contribution of early life stages to interannual variability in recruitment of northern anchovy, *Engraulis mordax*. *Can. J. Fish. Aquat. Sci.*
- Picquelle, S. J. and R. P. Hewitt (1983): The northern anchovy spawning biomass for the 1982-83 California fishing season. *Calif. Coop. Oceanic Fish. Invest. Rep.*, **24**, 16-28.
- Purcell, J. E. (1985): Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull. Mar. Sci.*, **37**, 739-755.
- Schumacher, A. (1980): Review of North Atlantic catch statistics. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer.*, **177**, 8-22.
- Scura, E. D. and C. W. Jerde (1977): Various species of phytoplankton as food for larval northern ancho-

- vy, *Engraulis mordax* and relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. *Fish. Bull. U. S.*, 75, 577-583.
- Sette, O. E. (1943): Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). Structure of a research program to determine how fishing affects the resource. *U. S. Dept. Interior, Spec. Sci. Rep.*, 19, 27pp.
- Smith, P. E. and R. W. Eppley (1982): Primary production and the anchovy population in the Southern California Bight: Comparison of time series. *Limnol. Oceanogr.*, 27, 1-17.
- Soutar, A. and J. D. Isaacs (1974): Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fish. Bull. U. S.*, 72, 257-273.
- Tanaka, S. (1983): Variation of pelagic fish stocks in waters around Japan. In G. D. Sharp and J. Csirke (eds.), Proc. of the Expert Consultation to Examine Changes in Abundance in Species Composition of Neritic Fish Resources. *FAO Fish. Rep.*, 291, Vol. 2, 17-36, Rome.
- Theilacker, G. H. (1986): Starvation induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. *Fish. Bull. U. S.*, 84, 1-17.
- Theilacker, G. H. and R. Lasker (1974): Laboratory studies of predation by euphausiid shrimps on fish larvae. *The Early Life History of Fish*, J. H. S. Blaxter, ed., Springer Verlag, Berlin, p. 287-299.
- Theilacker, G. H., A. S. Kimball and J. S. Trimmer (1986): Use of an ELISPOT immunoassay to detect euphausiid predation on larval anchovy. *Marine Ecology-Progress Series*, 30, 127-131.
- Tsukayama, I. (1982): Recursos pelagicos y sus pesquerias en Peru. Seminario Regional sobre Recursos Pelagicos y sus Pesquerias en el Pacifico Sudeste, Guayaquil, Ecuador, 25-26 Oct. 1982.

# I-4. R. Lasker 博士の「カリフォルニア沖カタクチイワシの研究—その生物学・資源加入と水産海洋学—」について

川口 弘一\*

1949年に始まるカリフォルニア沖マイワシ資源の急減とそれに伴う漁業と缶詰業界の不況は、カリフォルニア州内とその周辺地域に大きな経済停滞をもたらした。これが契機となって魚の資源量変動研究のための国立研究所が設立され、それが現在の南西水産研究所（ラホヤ）の基となった。そして1950年代始めにカリフォルニア沖イワシに何が起きたかを明らかにするために共同研究組織が作られ、この活動が現在の CalCOFI となって続いている。この共同研究は初期段階から、カリフォルニア沖を一つの生態系としてとらえ、単にイワシのみを対象とするのではなく、すべての重要種を関連づけて研究してきた。イワシが減少する一方で、カタクチイワシ資源が増加しつつあったので研究の焦点もマイワシからカタクチに移り現在に至っている。

## (1) 漁獲圧力のない時代の大きな資源変動

カタクチイワシの生息域であるサンタバーバラ海盆の無酸素状態の海底から得られるコア（Varves と呼ばれる）は、数千年間層目が乱されていないことが分かっており、層別に年代確定ができる。このコア中に含まれるカタクチイワシ類、マイワシ類、タラ類の鱗の数を層別に計数し、各種の各年別の相対資源量を出したところ、漁獲圧力のない1800年代にも資源量変動が存在したことが明らかになってきた。

## (2) カリフォルニア沖イワシの研究の始まり

カリフォルニアでは、産卵期が12月から4月にかけて4か月つづき、その間同一雌が20~30回産卵することが明らかとなった。この知見により資源加入量が産卵親魚の数や総産卵量に影響される密度依存タイプなのか、それとも環境要因に影響される密度独立タイプなのかを研究する方法が我々に与えられた。そして、Hjot が大西洋のニシンについて出した“critical period” hypo-

thesis に基づいてラホヤでの研究が進められた。しかし、初期の段階での仔魚の死因には飢餓だけでなく被捕食も重要であることが分かっている。

## (3) 飼育実験と野外実験

飼育実験の結果で最も注目すべきことは、仔魚の生残を確保するためには、実際の海で観測するよりもはるかに高密度の餌料を与えねばならないということであった。例えば、コペポダノープリウスでは1000個体/l以上の密度が必要だが、カリフォルニア沖では200個体/l程度しか存在しない。そこで問題は好適サイズの餌が最適な密度で何処に存在するか、その分布を規定する要因は何かということにしばられた。飼育した仔魚を船に乗せ、現場で各水深から採水を行い、その試水で仔魚を飼育することも行われた。その結果20~30個体/ml以上の密度を示した鞭毛藻類が餌として好適サイズで、好適密度に分布していることが分かった。この種は *Gymnodinium splendens* で、飼育実験でもよい餌料ということが確かめられている。

## (4) 時化（しけ）と湧昇

*G. splendens* はクロロフィル極大層に高密度に集中分布するが、シケによる海の成層の乱れにより容易に分散し、摂餌開始期の仔魚の生残に重要な必要最低餌量密度以下になってしまうことがわかった。この他湧昇によって起こる沖への流れ出しによって、餌密度の低い外洋へ運搬される仔魚の量も生き残りにとって重要な要因であることも分かってきた。これと並行して野外採集仔魚の飢餓状態を組織学的に判定する方法を開発し、35~46%の仔魚が毎日死亡しているという観測例も得られている。

## (5) 今後の展望

これまでの研究結果によれば、摂餌開始期の仔魚の生き残りだけから加入量を説明することは難しい。仔魚期全体を通じての生存率が加入量を決定していると考えら

\* 東京大学海洋研究所 Ocean Research Institute, University of Tokyo, Minamidai 1, Naka-ku, Tokyo, 164 Japan