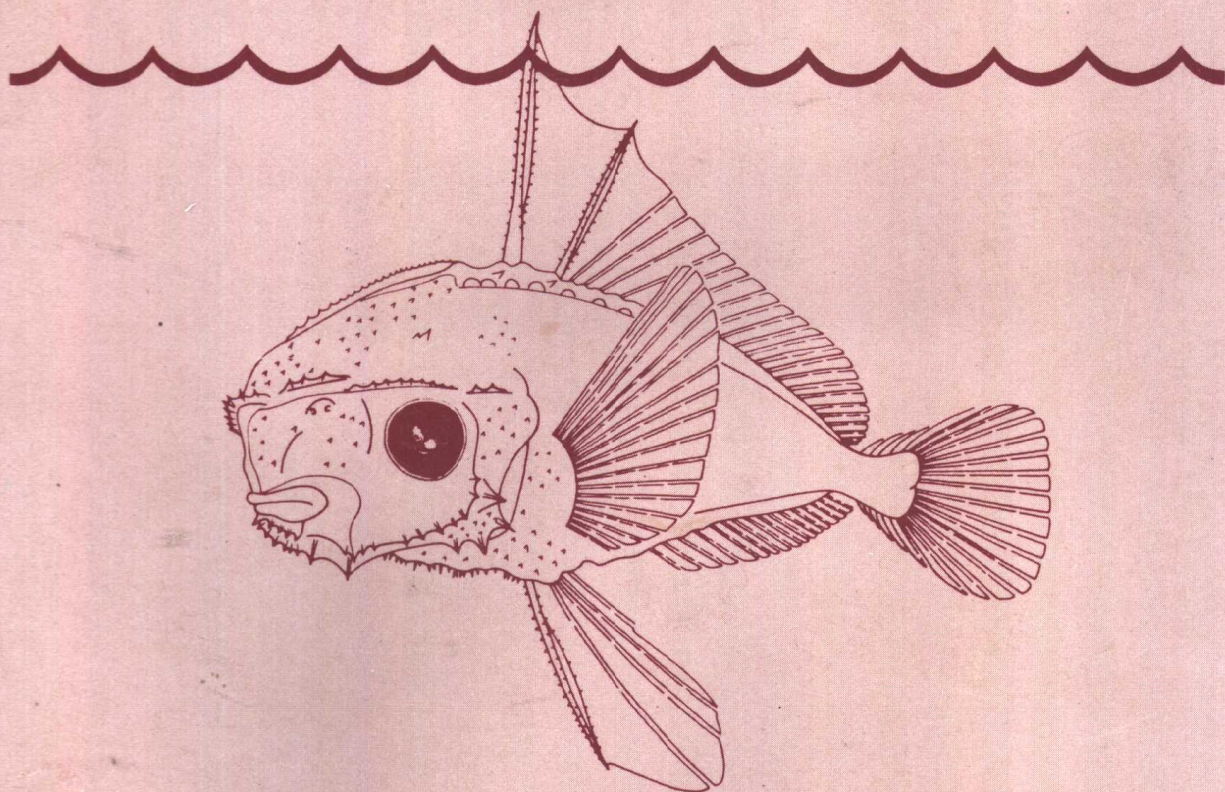


10<sup>th</sup> Annual

LARVAL FISH  
CONFERENCE



**American Fisheries Society**

**Symposium 2**



# **10th Annual Larval Fish Conference**

Edited by  
**Robert D. Hoyt**

Proceedings of a Conference Held in  
Miami, Florida, USA  
May 18–23, 1986

American Fisheries Society Symposium 2

Bethesda, Maryland  
1987

The American Fisheries Society Symposium series is a registered serial.  
Suggested citation formats follow.

*Entire book*

Hoyt, R. D., editor. 1987. 10th annual larval fish conference. American Fisheries Society Symposium 2.

*Article within the book*

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2:17-29.

© Copyright by the American Fisheries Society, 1987

Library of Congress Catalog Card Number: 87-072976

ISSN 0892-2284

ISBN 0-913235-45-8

*Address orders to*

American Fisheries Society  
5410 Grosvenor Lane, Suite 110  
Bethesda, Maryland 20814, USA

## **10th Annual Larval Fish Conference**

### **Conference Sponsors**

Cooperative Institute for Marine and Atmospheric Studies, University of Miami  
Southeast Fisheries Center, National Marine Fisheries Service

### **Conference Committee**

William Richards, Chair

James Bohnsack	Nancy Johnson
Elizabeth Clarke	Sharon Kelly-Fraga
Joseph Contillo	Kenneth Lindeman
Donald de Sylva	Michael McGowan
Lise Dowd	Thomas Potthoff
Randy Edwards	Richard Robins
Phyllis Fisher	Carol Stuka
Bruce Henderson	Jeffrey Tellock
Joaquin Javech	Patrick Walsh
Jacquelyn Johnson	Carol Wolf

### **Proceedings Sponsors**

Early Life History Section, American Fisheries Society

### **Editorial Board**

Robert Hoyt, Editor

Serge Doroshov	Arthur Kendall
Lee Fuiman	Kenneth Sherman
Robert Werner	

## DEDICATION



**SALLY LEONARD RICHARDSON**  
**1944-1986**

Dr. Sally L. Richardson (nee Sarah Leonard) passed away unexpectedly of cardiac failure on May 15, 1986, in Ocean Springs, Mississippi, while on her way to the 10th Annual Larval Fish Conference. Sally received her Bachelor of Science degree from Wilkes College in 1966 and her Doctor of Philosophy degree from the Virginia Institute of Marine Science in 1972. From 1971 to 1979, she was on the faculty of the School of Oceanography at Oregon State University, where she concentrated her efforts on ichthyoplankton ecology and the use of ontogenetic characters in elucidating systematic relationships of fishes. Her publications established her as a leader in these fields. From 1979 to 1985, Sally was Associate Ichthyologist at the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, where she continued her innovative early life history studies on the Gulf of Mexico fauna. In March 1985, she was a Visiting Scholar

at the Museum of Comparative Zoology, Harvard University, where, in less than 1 year, she transformed the large collection of over 90,000 unsorted larval fishes into a major archival collection. Sally was actively involved with the International Symposium on the Ontogeny and Systematics of Fishes, dedicated to the memory of Elbert Halvor Ahlstrom. She served on the symposium organizing committee, presented several papers, and was a member of the Editorial Committee for the symposium volume. Sally was a dedicated scientist and will be remembered for the outstanding contributions she made to the early life history studies of fishes. In recognition of Sally's efforts, the Planning Committee of the 10th Annual Larval Fish Conference in Miami dedicated that Conference to Sally's memory and established the Sally Richardson Award for the best paper presented at the 10th and subsequent conferences.

## PREFACE

### 10th Annual Larval Fish Conference

The 10th Annual Larval Fish Conference and Annual Meeting of the American Fisheries Society Early Life History Section were held in Miami, Florida, May 18–23, 1986. Plenary sessions opened and closed the conference. The first plenary session began with words of welcome from representatives of the conference cosponsors—Bradford E. Brown, Deputy Director of the National Marine Fisheries Service's Southeast Fisheries Center, and William W. Fox, Jr., Director of the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), University of Miami. This was the 10th anniversary of the annual Larval Fish Conferences, and an important goal of the Program Committee was to have the keynote and other plenary speakers review recent accomplishments in the various disciplines that deal with early life history of fishes, and explore trends and directions for future work. The speakers accomplished this goal admirably.

The keynote address, which appears in this volume, was delivered by Reuben Lasker of the National Marine Fisheries Service (NMFS), La Jolla, California, who addressed the "Use of Fish Eggs and Larvae in Probing Some Major Problems in Fisheries and Aquaculture." The first disciplinary review paper, on ecosystems research, was "California Current Fish Larvae in the Northeast Pacific Ecosystem: Environment, Regionality, and Time Series 1954–1960," prepared by Paul Smith, Geoffrey Moser, and Lawrence Eber of the NMFS, La Jolla. Ecology research was considered by Edward Houde of the University of Maryland's Chesapeake Biological Laboratory, Solomons; his paper, "Fish Early Life Dynamics and Recruitment Variability," also appears in this volume. Jean Dunn, NMFS, Seattle, dealt with systematics in a paper entitled "Ontogeny and Phylogeny: Perspectives Based on the Study of the Early Life History of Fishes." Finally, George Boehlert, NMFS, Honolulu, treated the "Behavior and Physiology of Larval Fishes in the Context of Ecological Field Studies."

A sad note of the opening session was struck by an announcement of the untimely and unexpected death of Sally L. Richardson on May 15. Sally was traveling to the conference to deliver a paper

when she suffered cardiovascular failure. After a moment of silence in her memory, an anonymous donor contributed \$150 toward a commemorative prize for the best contributed paper at the conference. A judging panel consisting of the plenary speakers gave the first Sally Richardson Award to John Olney and Douglas Markle for their paper "Ontogeny and Systematics of the Pearlfishes: Carapidae (Ophidiiformes)."

Following the first plenary session, concurrent sessions were held for invited and contributed papers over the next two days. Brenda Norcross convened a major workshop on "Techniques for Estimating Recruitment," at which 18 papers were given. Altogether, 100 oral and 13 poster papers were presented at the conference. Meeting registrants totaled 180, representing 29 of the United States and 9 other countries.

In the closing plenary session, which followed a business meeting of the Early Life History Section, authors of the first plenary papers briefly reviewed the results of the conference. They stressed the high quality of contributed and invited papers, which provided strong evidence that early life history events are extremely important in determining future populations sizes of fish stocks. Sound advances are being made in determining the causes of population fluctuations.

At the close of the conference, attendees visited the University of Miami's Rosenstiel School of Marine and Atmospheric Science and NMFS's Southeast Fisheries Center. Visits were made to the University's fish hatchery, the National Oceanic and Atmospheric Administration's recompression chamber and hyperbaric center, and the Southeast Fisheries Center's otolith- and scale-aging laboratory. A planned beach party was forced by rain into the Rosenstiel School's cafeteria (though the food still had to be cooked over an open beach fire), but dancing and socializing enthusiasms were undashed. During the next two days, field trips were made to the Everglades and to Biscayne National Park, and a scuba dive trip went to an artificial reef and a patch reef. In addition, a mini-workshop on identification of marine larval fish was held at the Southeast Fisheries Center.

As Conference Chair, I wish to thank members of the Local Committee for their untiring and

dedicated work on behalf of the conference. They include, from the University of Miami, Nancy Anderson, Liz Clarke, Don de Sylva, Lise Dowd, Randy Edwards, Bruce Henderson, Jackie Johnson, Mike McGowan, Dick Robins, Carol Stuka, Jeff Tellock, and Pat Walsh and, from the Southeast Fisheries Center, Jim Bohnsack, Joe Contillo, Phyllis Fisher, Jack Javech, Sharon Kelly-Fraga, Ken Lindeman, Tom Potthoff, and Carol Wolf. William Fox, Director of CIMAS, and Richard Berry, Director of the Southeast Fisher-

ies Center, were extremely helpful and supportive cosponsors of the conference. On behalf of the sponsors and the local committee, I thank all those who attended and presented such a large number of fine papers.

WILLIAM J. RICHARDS, *Conference Chair*  
*Southeast Fisheries Center*  
*National Marine Fisheries Service*  
*75 Virginia Beach Drive*  
*Miami, Florida 33149*

### Editorial Acknowledgments

Participants in Larval Fish Conferences are invited to submit their papers for publication in the annual proceedings, but they are neither required nor pressured to do so. Submitted papers undergo stiff peer review; as a result, some are

declined for publication and others undergo substantial revision. The Editorial Board for the 10th Conference thanks the following manuscript reviewers for their contributions to these proceedings.

Nancy A. Auer  
 Kevin M. Bailey  
 Fred P. Binkowski  
 Larry J. Birchfield  
 Stephen B. Brandt  
 Ernest L. Brannon  
 Howard I. Browman  
 Carl R. Brown  
 Christopher L. Brown  
 C. Fred Bryan  
 Lawrence J. Buckley  
 Randall K. Buddington  
 Joseph J. Cech, Jr.  
 Daniel J. Faber

Neal R. Foster  
 Kenneth T. Frank  
 Russell Kappenman  
 Arthur Kendall, Jr.  
 Grace Klein-MacPhee  
 C. Douglas Knechtel  
 William C. Leggett  
 Douglas F. Markle  
 F. Douglas Martin  
 Michael F. McGowan  
 Peter B. Moyle  
 Robert T. Muth  
 David L. Noakes  
 George Noguchi  
 Allyn B. Powell

James H. Power  
 Dennis Powers  
 William J. Richards  
 Neil H. Ringler  
 Saul B. Saila  
 Carl B. Schreck  
 James Schumacher  
 Mike Sinclair  
 Michael P. Sissenwine  
 Wallace Smith  
 Gail Theilacker  
 David W. Townsend  
 Gordon T. Waring  
 Steven Yeo

# CONTENTS

<b>Dedication.....</b>	vii
<b>Preface</b>	
William J. Richards .....	ix
<b>Keynote Address</b>	
<b>Use of Fish Eggs and Larvae in Probing Some Major Problems in Fisheries and Aquaculture</b>	
Reuben Lasker.....	1
<b>Recruitment</b>	
<b>Fish Early Life Dynamics and Recruitment Variability</b>	
Edward D. Houde.....	17
<b>Precision of Estimates of Abundance of Coastal Fish Larvae</b>	
Andrew E. Jahn.....	30
<b>Transport Processes Affecting the Survival of Pelagic Fish Stocks in the California Current</b>	
James J. Simpson .....	39
<b>Recruitment Mechanisms of 2-Year-Old Atlantic Herring to the Maine Fishery: The Larval Stage</b>	
Joseph J. Graham and Keith M. Sherman .....	61
<b>Effects of Climatic and Density-Dependent Factors on Intra-annual Mortality of Larval American Shad</b>	
Victor Crecco and Thomas Savoy .....	69
<b>Growth and Survival of the Larvae of Three Species of Temperate Marine Fishes Reared at Discrete Prey Densities</b>	
L. J. Buckley, T. A. Halavik, A. S. Smigielski, and G. C. Laurence .....	82
<b>Field Evaluation of Barriers to Walleye Egg and Larva Survival in the Lower Fox River, Wisconsin</b>	
Nancy A. Auer and Martin T. Auer .....	93
<b>Factors Associated with the Dynamics of Grass Carp Larvae in the Lower Mississippi River Valley</b>	
Steven P. Zimpfer, C. Fred Bryan, and C. H. Pennington .....	102
<b>Nutrition</b>	
<b>Nutritional State Analysis and Its Use in Predicting Striped Bass Recruitment: Laboratory Calibration</b>	
F. Douglas Martin and David A. Wright.....	109
<b>Analysis of Nutritional Condition and Its Use in Predicting Striped Bass Recruitment: Field Studies</b>	
Eileen M. Setzler-Hamilton, David A. Wright, F. Douglas Martin, Catherine V. Millsaps, and Sallie I. Whitlow.....	115
<b>Lipid Class and Fatty Acid Composition As Indicators of the Nutritional Condition of Larval Atlantic Herring</b>	
A. J. Fraser, J. R. Sargent, J. C. Gamble, and P. MacLachlan .....	129



**Development**

<b>Occurrence of Thyroid Hormones in Early Developmental Stages of Teleost Fish</b> Christopher L. Brown, Craig V. Sullivan, Howard A. Bern, and Walton W. Dickhoff .....	144
<b>Effects of Light on Movement of Rainbow Trout Embryos within, and on Their Emergence from, Artificial Redds</b> Christopher P. Nunan and D. L. G. Noakes .....	151
<b>Influences of Acclimation Temperature and Development Stage on Behavioral Responses of Lake Chubsuckers to Temperature Gradients</b> Mary T. Negus, John M. Aho, and Charles S. Anderson .....	157
<b>Factors Influencing Initial Swim Bladder Inflation by Striped Bass</b> Carl G. Hadley, Michael B. Rust, Joel P. Van Eenennaam, and Serge I. Doroshov .....	164
<b>Inducement of Cranial Anomalies in Freshwater Larval Fish during Collection and Fixation</b> Larry J. Birchfield .....	170

**Distribution**

<b>Distribution of Larval Gizzard Shad in the Upper Cape Fear River, North Carolina</b> David R. Sager .....	174
---	-----

**Taxonomy**

<b>Descriptions of Protolarvae of Seven Species of the Subgenus <i>Nothonotus</i> (Percidae: Etheostomatini) with Comments on Intrasubgeneric Characteristics</b> Thomas P. Simon, Robert Wallus, and Keith B. Floyd .....	179
---	-----

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

REUBEN LASKER

*National Marine Fisheries Service, Southwest Fisheries Center  
La Jolla, California 92038, USA*

**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.

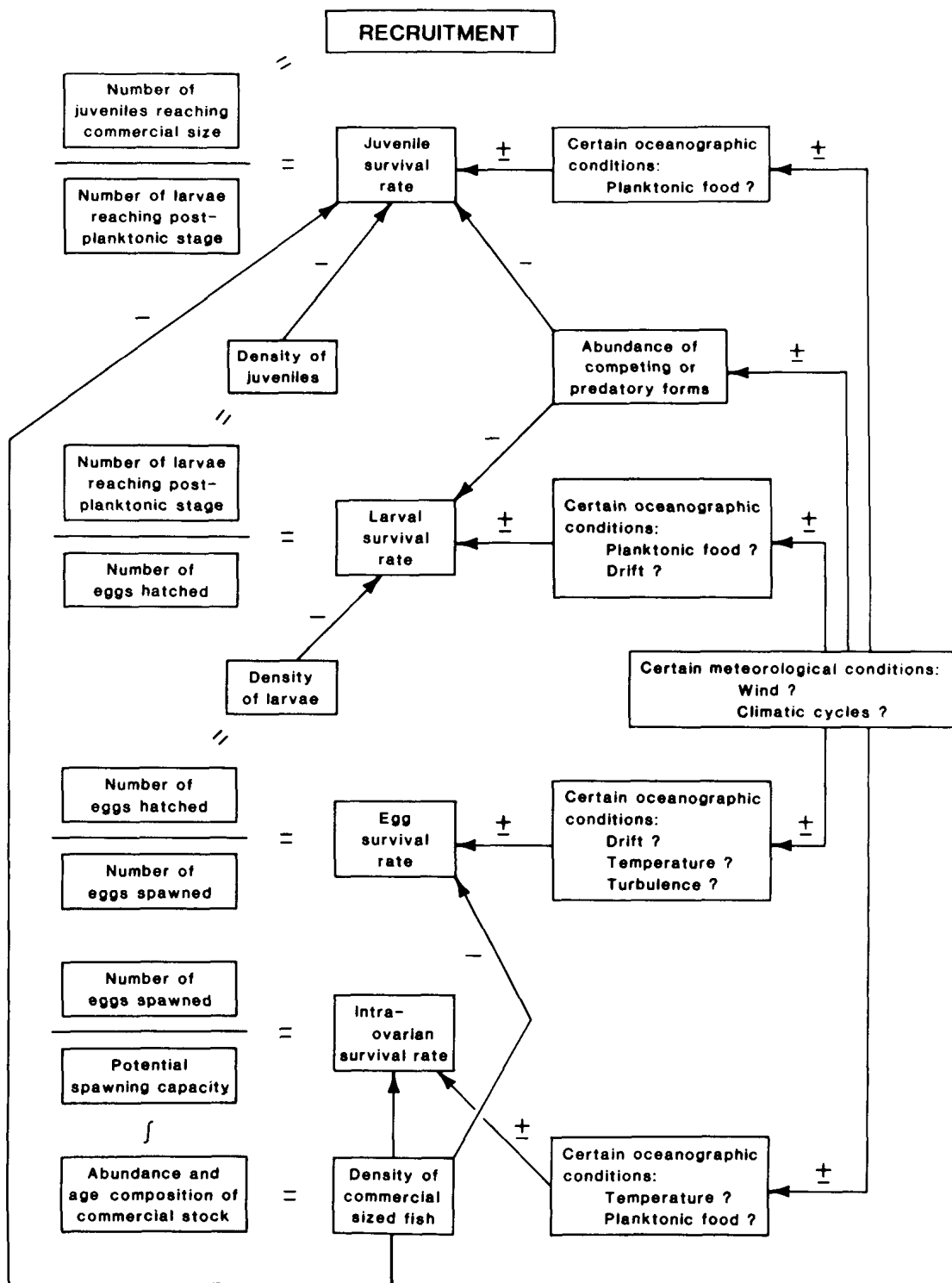


FIGURE 3.—Sette's plan to study recruitment of the Pacific sardine, 1943.

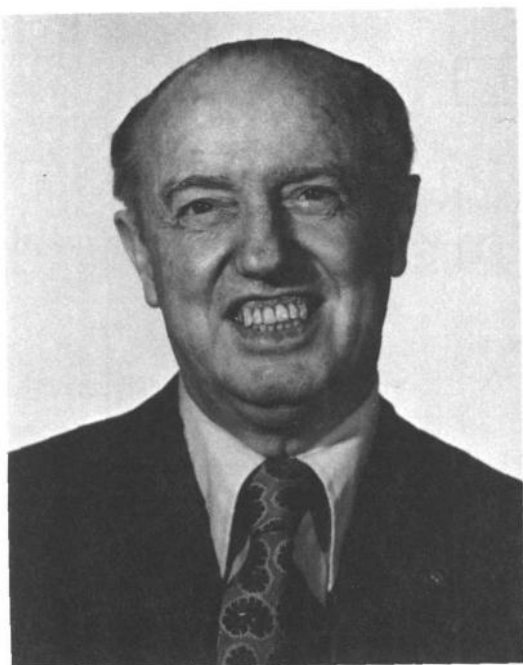


FIGURE 4.—Elbert H. Ahlstrom, about 1969.

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

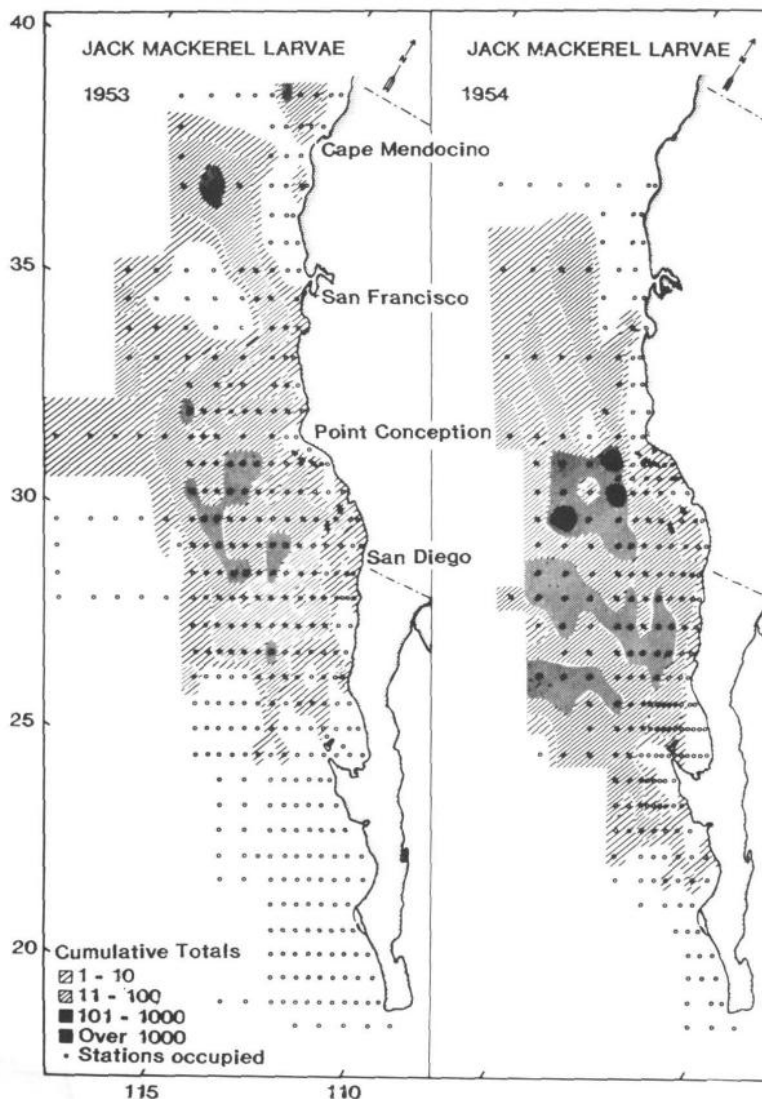


FIGURE 6.—Distribution of larval jack mackerel *Trachurus symmetricus* off California, 1953 and 1954. Data are larvae per standard tow.

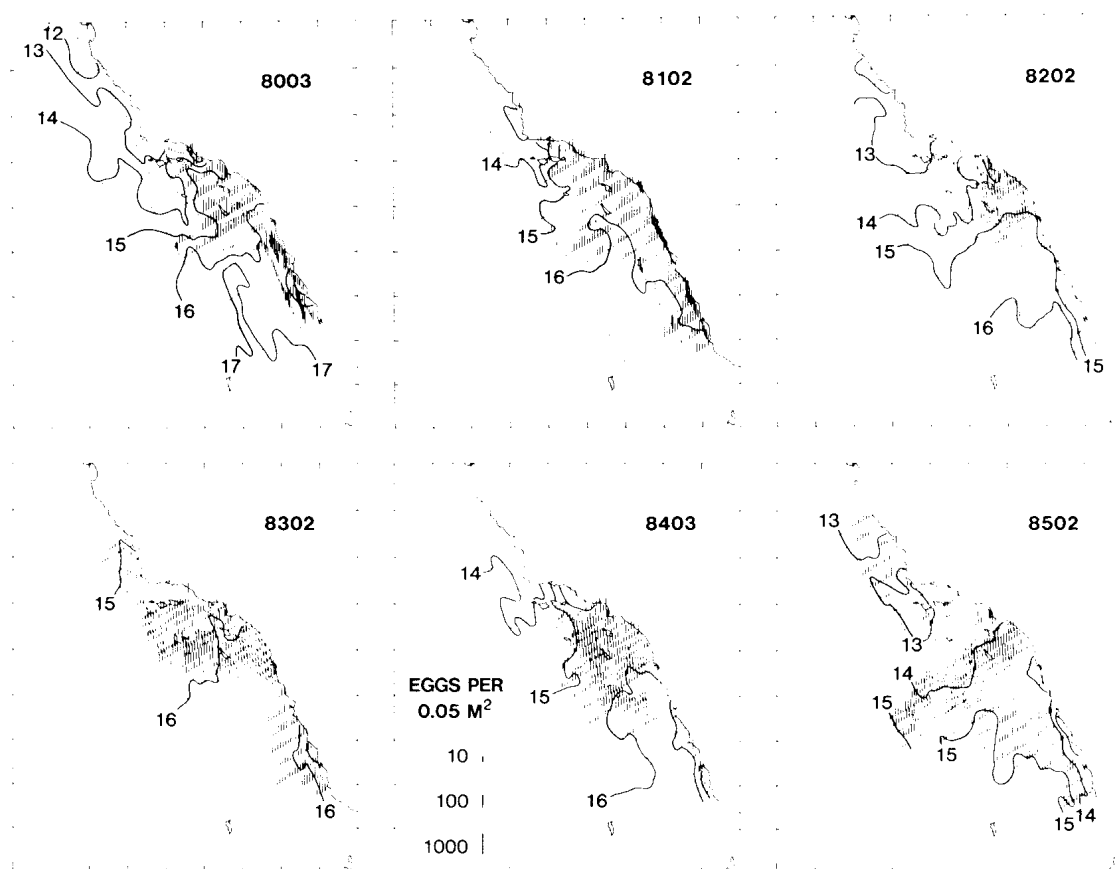


FIGURE 7.—Egg distributions for northern anchovy *Engraulis mordax* off California during February (02) or March (03) 1980–1985. Dots represent sampling stations; surface isotherms are in °C. (From Fiedler et al. 1986.)

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

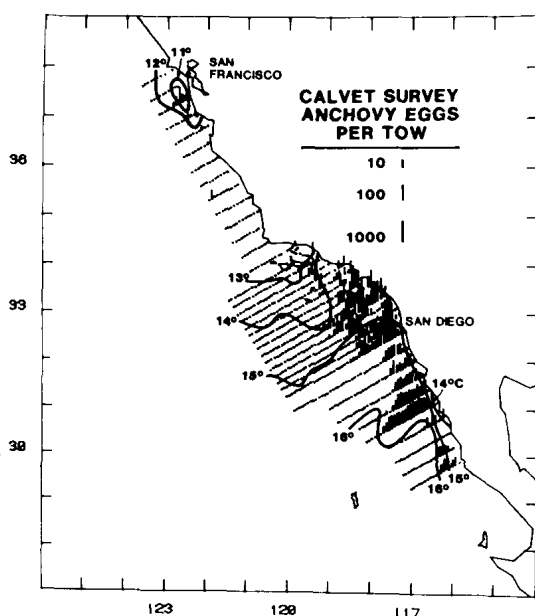


FIGURE 8.—An egg survey for northern anchovy biomass assessment off California in 1982. Surface isotherms (°C) are superimposed on the egg distribution. (From Picquelle and Hewitt 1983.)

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 Biétreix (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 Biétreix 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

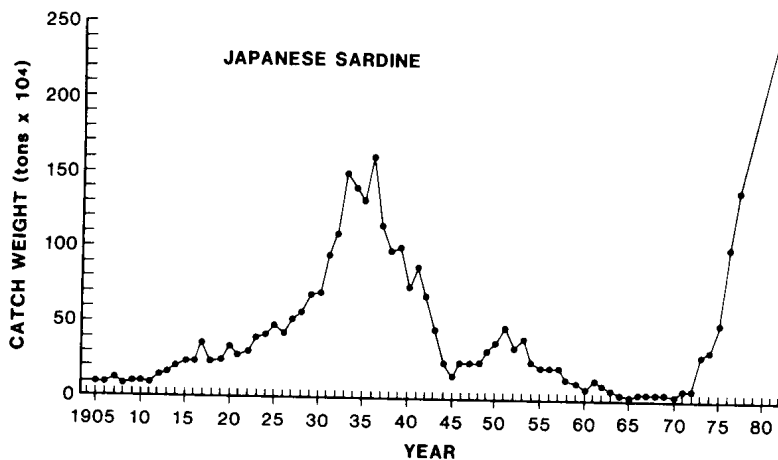


FIGURE 10.—Catches of Pacific sardine off Japan, 1905–1981. The 1984 catch was  $420 \times 10^4$  tonnes.