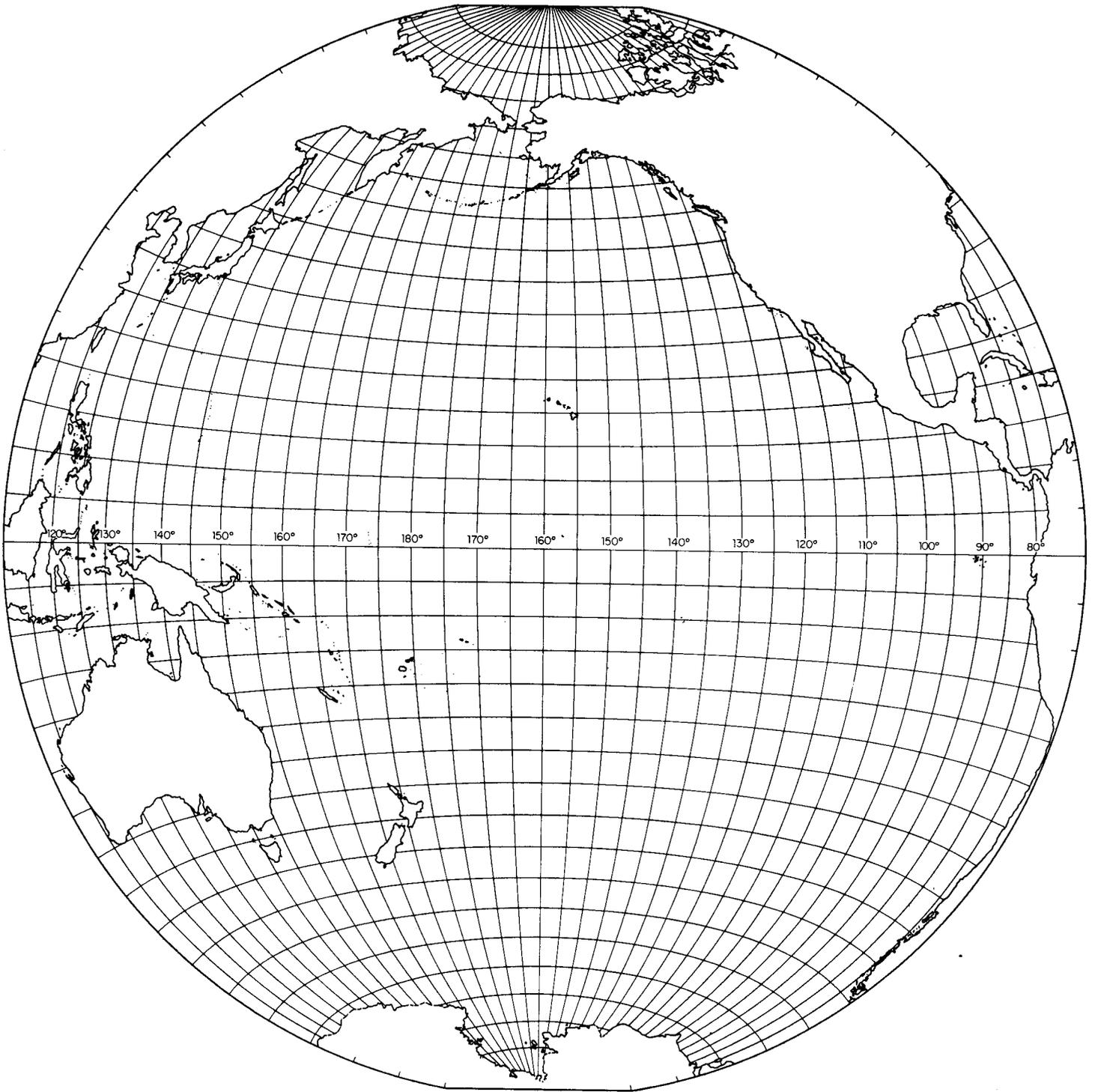


STATE OF CALIFORNIA
MARINE RESEARCH COMMITTEE



CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

VOLUME XI
JANUARY 1967

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STATE OF CALIFORNIA
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CALIFORNIA
COOPERATIVE
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Reports

Volume XI

1 July 1963 to 30 June 1966

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1 January 1967



This volume is dedicated to JULIAN G. BURNETTE, Member of the Marine Research Committee since its inception in 1948 and Chairman, 1948-1967.

The work reported upon in this volume and all those preceding it was done during the period of his leadership.

Much of the credit for the scientific advances that we have made belongs to him. His continued interest, wholehearted support, early understanding of the necessity for a broad examination of the ocean environment, and, particularly, his farseeing insight into the delicate balance between freedom and obligation in research, created an almost unprecedented rapport between men of science and of practice; an intellectual environment in which both basic scientific progress and practical results became possible; and a high goal for future research programs.

LETTER OF TRANSMITTAL

January 1, 1967

RONALD REAGAN
Governor of the State of California
Sacramento, California

Dear Sir: We respectfully submit the eleventh report on the work of the California Cooperative Oceanic Fisheries Investigations.

The report consists of three sections. The first contains a review of the administrative and research activities during the period July 1, 1963 to June 30, 1966, a description of the fisheries, and a list of publications arising from the programs. The second section is comprised of papers prepared for a special symposium on anchovy biology. The third is comprised of original scientific contributions which are either a direct result of CalCOFI research programs, or represent research directly pertinent to resource development in the pelagic realm of California.

Respectfully,

THE MARINE RESEARCH COMMITTEE
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CONTENTS

	Page
I. Review of Activities	
1. Review of Activities July 1, 1963–June 30, 1966	5
2. Review of the Pelagic Wet Fisheries for the 1963–64, 1964–65, 1965–66 Seasons	21
3. Publications	22
II. Symposium on Anchovies, Genus <i>Engraulis</i>	
<i>John L. Baxter, Editor</i>	27
1. Oceanic Environments of the Genus <i>Engraulis</i> around the World	
<i>Joseph L. Reid, Jr.</i>	29
2. Synopsis of Biological Information on the Australian Anchovy <i>Engraulis australis</i> (White)	
<i>Maurice Blackburn</i>	34
3. A Note on the Biology and Fishery of the Japanese Anchovy <i>Engraulis japonica</i> (Houttuyn)	
<i>Sigeiti Hayasi</i>	44
4. Present State of the Investigations on the Argentine Anchovy <i>Engraulis anchoita</i> (Hubbs, Marini)	
<i>Janina Dz. de Ciechomski</i>	58
5. Influence of Some Environmental Factors upon the Embryonic Development of the Argentine Anchovy <i>Engraulis anchoita</i> (Hubbs, Marini)	
<i>Janina Dz. de Ciechomski</i>	67
6. Investigations of Food and Feeding Habits of Larvae and Juveniles of the Argentine Anchovy <i>Engraulis anchoita</i>	
<i>Janina Dz. de Ciechomski</i>	72
7. A Brief Description of Peruvian Fisheries	
<i>W. F. Doucet and H. Einarsson</i>	82
8. Preliminary Results of Studies on the Present Status of the Peruvian Stock of Anchovy (<i>Engraulis ringens</i> Jenyns)	
<i>G. Saetersdal, J. Valdivia, I. Tsukayama, and B. Alegre</i>	88
9. An Attempt to Estimate Annual Spawning Intensity of the Anchovy (<i>Engraulis ringens</i> Jenyns) by Means of Regional Egg and Larval Surveys during 1961–1964	
<i>H. Einarsson and B. Rojas de Mendiola</i>	96
10. The Predation of Guano Birds on the Peruvian Anchovy (<i>Engraulis ringens</i> Jenyns)	
<i>Rómulo Jordán</i>	105
11. Summary of Biological Information on the Northern Anchovy <i>Engraulis mordax</i> Girard	
<i>John L. Baxter</i>	110
12. Co-occurrences of Sardine and Anchovy Larvae in the California Current Region off California and Baja California	
<i>Elbert H. Ahlstrom</i>	117
13. The Accumulation of Fish Debris in Certain California Coastal Sediments	
<i>Andrew Soutar</i>	136
III. Scientific Contributions	
1. The Pelagic Phase of <i>Pleuoncodes planipes</i> Stimpson (Crustacea, Galatheidae) in the California Current	
<i>Alan R. Longhurst</i>	142
2. Summary of Thermal Conditions and Phytoplankton Volumes Measured in Monterey Bay, California 1961–1966	
<i>Donald P. Abbott and Richard Albee</i>	155
3. Seasonal Variation of Temperature and Salinity at 10 Meters in the California Current	
<i>Ronald J. Lynn</i>	157

PART I

REVIEW OF ACTIVITIES

July 1, 1963—June 30, 1966

REPORT OF THE CALCOFI COMMITTEE

INTRODUCTION

It has become increasingly apparent that the policy of the CalCOFI has been a valid and valuable one—that the intensive long-term study of the California Current has constituted a nucleus and *raison d'être* of an expanding research and technology of greater depth, field and compass in the North Pacific. The nature of these expanded portions of the program are discussed later in the reports of agencies.

The CalCOFI Committee is deeply involved with its fundamental objectives and with reappraisal of the direction that the CalCOFI should now take. This reappraisal is necessitated by the delineation of unutilized fish resources of the eastern North Pacific and the initiation of a fishery one of these—the anchovy.

The philosophical, scientific, and politico-economic factors pertinent to this reappraisal cannot be competently discussed here. However, the crucial questions can be reasonably well formulated as follows:

Are the long-term needs of the state, society, and mankind best served at this juncture by a concentration of research on the anchovy and its fishery or by a continued expansion of the research into the total environment?

The resolution of this problem depends upon a valid understanding of the evolving position of California; its changing responsibilities to its people and to its challenges and opportunities; and the present and potential contribution of the CalCOFI to the State.

On the one hand, as a result of CalCOFI research, we have the opportunity of reestablishing a reduction fishery of some magnitude. On the other hand, we have the demonstrated, suspected, and as yet unrecognized opportunities and implications of the Pacific and of the expanding research into it, of which the anchovy fishery is an early product.

Clearly the rational solution to these mutually exclusive extremes is an optimum attention to each—a *juste milieu* in which the anchovy fishery is substantially documented and studied and, at the same time, the research continues to be directed toward a broad-scale inquiry into the eastern North Pacific, its oceanography, zoogeography, history and fish populations.

BACKGROUND

The CalCOFI program, thus, plans a thorough coverage of the California Current system each three

years (1969 next), and a continuing expansion of the several programs, descriptions of which follow.

Early in 1966 the CalCOFI Committee, in a letter to the Chairman of the Marine Research Committee, outlined the history, accomplishments, and status of the CalCOFI research program in simple, brief, factual terms. The 13 points, to which we referred as “a few of the many unshakeable pillars of certainty”, were:

- (1) The CalCOFI program was established as a broad and thoughtful inquiry into the environment and the biology of the California Current system.
- (2) An object of the program was to clarify the nature of the decline of sardine abundance and to understand the nature of the other organisms associated with the sardine in the California Current system.
- (3) Organizationally, the CalCOFI is established as a group of cooperative research programs responsible to these objectives and subject to the review of their progress by the Marine Research Committee, a highly selected group of interested, practical men.
- (4) As will be enumerated below, this arrangement has proven to be extremely successful and rewarding. The rapport between men of scientific and practical bents has, we believe, been unique. There has been neither constraint, on the one hand, nor lack of direction, on the other but rather an almost wholly unprecedented balance between the two where the scientist has been able to work with “responsible freedom” and where he, the MRC and the public have been highly rewarded.
- (5) The oceanography, the biology of the California Current system, and the variations in these are now the best documented and best understood of any oceanic area in the world.
- (6) The understanding of fish populations, biology and resource potential through studies of eggs, larval and adults of pelagic fishes are the most highly advanced of any.
- (7) Wholly new technologies of studies of pelagic fish have been developed and are of far-reaching, world-wide import.
- (8) Entrees into the pre-fishery history of the pelagic fish populations and environments have been developed and are of great local and world-wide significance.
- (9) The populations of a large group of pelagic fish have been determined, studied, and understood to a degree that far surpasses any similar studies in the world.
- (10) The interrelations between competing species of pelagic fishes have been characterized for the first time in history.
- (11) Possibility of a pelagic fishery has been pointed out and the fishery has been established, in which there is a far greater fund of scientific understanding and knowledge available at its outset than for any other pelagic fishery in the history of man.
- (12) A program exists that is ably discharging its full responsibilities both present and future in cooperative research.

- (13) These responsibilities include the study of the effects of the present fishery and the inquiries essential to future development and understanding of other and extensive resources.

The above are overly simplified statements of a part of a large and important program. We believe the results of this program can be characterized by stating that new and important concepts in the uses of our living oceanic resources have been evolved. These, together with the resources at our door, have put California on the threshold of increasing her wealth, and perhaps more importantly, of assuming world leadership in the scientific use of pelagic fish resources. This may, in the long run, be a far more valuable asset to Californians than the economic yield of the resources themselves.

It was on the basis of the research program described in the above letter that we had prepared for the Marine Research Committee, 2 years earlier, an outline of one possible way to enter this new era. This proposal was presented to MRC in March, 1964 by the CalCOFI Committee which at that time was composed of G. I. Murphy, J. D. Isaacs, J. L. Baxter, and E. H. Ahlstrom and appears as Document XII of the minutes of that meeting. It seems appropriate at this time to publish the proposal for all to study, evaluate, and comment upon. In the following it is quoted essentially verbatim.

REQUIREMENTS FOR UNDERSTANDING THE IMPACT OF A NEW FISHERY IN THE CALIFORNIA CURRENT SYSTEM

Our philosophical guide in preparing this discussion has been simple. We have asked ourselves, "How should a fishery be conducted, and what investigations should be initiated to give the public guidance of maximum value from marine science?" We would like to regard a new fishery on the sardine-anchovy system as a careful scientific experiment, in which the effect of a controlled harvest of the anchovy and sardine populations is explored. We believe this is a new and stimulating point of departure. While we do not propose it to you as a necessary course of action, we hope you will examine it thoughtfully and decide for yourselves the extent to which the scientific requirements for such an experiment are compatible with the broad needs of society.

Background Résumé

The results of over 40 years of study, including 14 years of very intensive inquiry can be succinctly summarized as follows: After many years of intensive selective fishing for sardines, the sardine population declined. This decline was accompanied by a dramatic upsurge of an ecologically similar species, the anchovy. The decline of the sardine was apparently the result of an intensive fishery together with a series of years in which the environmental regime was unfavorable to the sardine. The rise of the anchovy is apparently the result of a series of favorable years for that species, and man's removal of sardines which created more living space for anchovies. The evidence does not allow us to arrive at a consensus as to whether or not the anchovies aggressively drove down the sardine population, but biological interaction between these ecologically similar species is strongly indicated now by the failure of the sardine to respond to a recent spectrum of oceanographic conditions that should have been favorable, and conversely unfavorable to the anchovy.

In any event results of all these studies show that there is now a large unused population of anchovies. They also infer that there is a real chance that simultaneously reducing the pressure on sardines and imposing pressure on anchovies will reverse the present equilibrium and assist in bringing back the more valuable sardine. This constitutes an exciting opportunity for marine science to assist society in meeting its complex needs.

Requirements for the Fishery

In developing this section three factors have been paramount.

1. The basis for the suggested experiment while the most complete ever achieved still is not precise enough to foresee exactly how many anchovies and sardines should ultimately be taken. A careful, stepwise, approach such as was used in South Africa is the only defensible experiment.

2. There are time lags in the response of fish populations to new factors. With respect to sardines and anchovies, their life histories suggest that at least 3 years would be required for the responses of the populations to be detected, even in a regime of favorable environments.

3. There are also time lags in scientific analysis, these are especially significant when dealing with a new problem. Thus it is necessary to carry out measurements that can follow events closely, and which will yield results that are readily interpreted. With these factors in mind the approach below is divided into phases. We believe that three years is a minimum for each phase.

Phase 1. The objective is to initiate a conservative fishery on anchovies and reduce sardine fishing just sufficiently to produce an observable change in the system, and just enough to improve our preliminary appraisal of the magnitude of the anchovy resource. During this phase a limit of 200,000 tons should be placed on the anchovy fishery and the sardine fishery should be limited to 10,000 tons. Thirty-five percent of both of these limits should be taken off California and 65 percent off Baja California.¹ From the viewpoint of conducting a controlled experiment, it would not be desirable to place a complete moratorium on sardines for two reasons. The fishery is a primary tool for detecting responses in the sardine population. Were the fishery terminated this tool would be lost, and we would have to rely entirely on our surveys. Secondly, a complete moratorium would complicate the experiment by introducing two variables at the same time. The limit suggested for the sardine relieves these problems by keeping our "window" on the sardine population open, and by approximating the average rate of exploitation prevailing over the past years. If both the sardine fishery and competition from anchovies are affecting the sardine population, the chances of bringing back the sardine in the shortest possible time can be maximized by fishing for anchovies and not fishing for sardines. If this is the objective it might be desirable to have a moratorium on sardine fishing. The recommendations of this report are based on the viewpoint of conducting as careful an experiment as possible to determine the factors affecting both sardines and anchovies.

Phase 2. The amounts to be removed during Phase 2 and the areal distribution of the limits on each species must await the results of Phase 1. We can hazard a guess that during this Phase the anchovy quota might be raised about 50 percent providing that the results of Phase 1 are not widely different from our preliminary expectations.

Phase 3. This cannot be specified at all beyond indicating the ultimate objective. This is to restore the pre-decline balance between sardines and anchovies, and maximize the harvests consistent with all uses, i.e., food, recreation, etc.

Comment: It is beyond our scope to determine how such an advanced system of management on an international resource may be achieved. We do feel strongly that conservative managerial flexibility is essential.

RECENT DEVELOPMENTS

The 1964 proposal also outlined the basic programs which should be implemented if a fishery were initiated. At that time no fishery for anchovies existed, except for the limited (5,000-6,000 tons) fishery for

¹ At the 21 May, 1964 meeting of the Marine Research Committee, CalCOFI recorded the following emendation: "Our recommendation for Phase 1 included a provision to distribute the catch between Alta and Baja California. For the purposes of this provision we specify 31°N latitude, as this is a natural oceanographic and faunal boundary."

live bait. As a direct result of the CalCOFI proposal, the California Fish and Game Commission authorized an experimental anchovy reduction fishery on November 12, 1965. The 75,000 ton quota allowed is approximately of the magnitude recommended for California waters by CalCOFI. This fishery has continued to the present time (1967).

In March, 1966, with the fishery underway, E. H. Ahlstrom updated the 1964 proposal to point up the breadth and pertinence of CalCOFI research to present and long-range problems. The following is his outline of the programs implemented:

STUDIES ON THE FISHERY

Important information can be gained from the fishery about the quantity of fish landed, size and age composition of landings, and catch per unit of effort. Other kinds of information that can be derived from systematic sampling include growth rate, age at first maturity, longevity, yield per recruit, mortality estimates, etc. These are "conventional" investigations, involving fairly standardized techniques. A fishery carried out at a low level of intensity furnishes only limited data for determining vital statistics of the population being fished. Such studies are of greatest value in determining vital population parameters when carried out over different levels of fishing intensity.

Total Landings by Area

California Fishery: Landings statistics now obtained by the State cover tonnage landed, area of capture, and fishing effort. Accurate weights are reported on market and cannery receipts as required by law. Area of catch is determined from fishing logs, required of each boat skipper, whereby each day's fishing is plotted on a map-type log.

Baja California Fishery: Plant operators in Baja California cooperate by giving us access to landing records. Our primary source of information about area of capture of fish is personal interview.

Size and Age Composition by Area

Data concerning size and age composition are obtained by systematically sampling commercial landings from all ports of landing in California and Baja California. Sampling of commercial landings in California is carried out by the California Department of Fish and Game. Sampling of commercial landings in Baja California is carried out by the Bureau of Commercial Fisheries by means of a contract with the California Academy of Sciences. Samples of whole, adult fish will be retained for unforeseeable research. Age determinations are done cooperatively by California Department of Fish and Game and Bureau of Commercial Fisheries scientists. Cooperative aging of sardines by these two organizations dates from 1941; cooperative aging of anchovies from the early 1950's.

In the past, scales have been "read" to determine the age of both sardines and anchovies. Presently, evaluation is being made of the scale method for determining age versus use of ear bones (otoliths). Anchovy scales are highly deciduous, with the result that it is difficult to obtain adequate scale samples from some loads of fish. Sampling can be carried out more systematically if based on otoliths.

Catch Per Unit of Effort by Area

California has instituted a logbook system to obtain information concerning each commercial landings of anchovies. This is in addition to information obtained by interviews, whenever a load of fish is sampled.

It presently is not feasible to try to institute a logbook system for Baja California fishermen. We are able to obtain records of individual deliveries, and to supplement this by interviews.

STUDIES ON THE POPULATIONS

One of the major reasons for establishing CalCOFI was to obtain information about many aspects of the population dynamics of the sardine that could not be wrung out of catch and effort data. Methods independent of the fishery were developed to determine population size, population structure, factors underlying marked fluctuations in the survival of year-classes, shifts in distribution of the population with respect to the area of the fishery (availability), etc. What was not fully appreciated was the complexity resulting from competition between species of a trophic level (i.e. between sardine and anchovy).

We must continue to investigate the interaction between competing species. This requires more sophisticated research than is possible from studies on the fishery alone.

Tagging Experiment—Anchovy

The State has already initiated a tagging experiment in southern California waters. They had tagged about 100,000 anchovies by November, 1966, in areas off northern Baja California, southern California (inshore and offshore) and the Monterey Bay area. Eventually a tagging experiment should permit a determination of the extent of migrations and intermingling of fish from various parts of the anchovies' range—California, Baja California or the Pacific Northwest. Tagging experiments should be combined with genetic studies. Tagging on a broader scale may provide information about population parameters such as population size, fishing mortality, and natural mortality.

One of the initial problems we have to elucidate is the extent and rate of replenishment of stocks from other areas. Will fish move up from Baja California for example, to replenish stocks reduced by fishing off southern California?

A very successful tagging experiment was carried out on the Pacific sardine (1936-41), mostly by the California Department of Fish and Game. The Department will be chiefly responsible for the tagging experiment on the anchovy. The Bureau of Commercial Fisheries is cooperating, especially in developing techniques that will result in low tagging mortality; also in evaluating this mortality.

Genetic Studies

These are necessary to determine whether one or several stocks are being fished. We now know, for example, that the sardine fishery off southern California depended upon two genetic stocks (northern and southern subpopulations) with differing availability. Is the anchovy population in the Pacific off California and Baja California similarly made up of several genetically distinct stocks? In point of fact, a tagging experiment would be conducted quite differently if we definitely knew that the anchovy population consisted of a single intermingling stock rather than several genetically distinct stocks.

BCF's genetics program has been working on the problem of "genetic" stocks of anchovies, so far with inconclusive results. The Department of Fish and Game will conduct experiments with eye lens proteins as a means of differentiating possible genetic stocks.

Egg and Larva Surveys

To date this has been our prime instrument for evaluating the interaction between the sardine and anchovy populations. These studies furnish information on many other fishes—hake, rockfish, jack mackerel, Pacific mackerel, flatfishes, etc. There is no question about the need of their continuance, although this must be at a more modest scale than in the 1950's. Anchovy population can be adequately monitored with about one-half of the effort (ship time) expended in the 1950's.

We do not have to measure changes in the sardine population with the same degree of precision as changes in the anchovy. We have set a limit of $\pm 20\%$ as the acceptable level of variability for our estimates of abundance of anchovy larvae. For sardines, an order of magnitude would be acceptable. We are interested in major changes in the abundance of sardines, a small change would have little significance.

Fish Surveys

Surveys designed to assess the abundance of adult populations of sardines and anchovies should be given high priority. It is hoped that such surveys essentially will become as sensitive a measure of abundance as are the egg and larva censuses.

Both California Fish and Game and the Bureau of Commercial Fisheries have increased their research in this area. The California Department of Fish and Game is utilizing funds obtained under the Commercial Fisheries Research and Development Act (Bartlett Bill) to increase the coverage of their surveys of juvenile and adult fish. Their surveys will investigate fish populations farther to sea and at more frequent intervals than has been possible in the past. The Bureau of Commercial Fisheries has installed a Simrad research sonar on their new vessel, the *David Starr Jordan*. This gear should permit an assay of the distribution and abundance of schools of adult fishes. Cooperative cruises are planned by all three agencies for developing techniques for "Identification of acoustic targets and pelagic fish census."

ESSENTIAL BACKGROUND STUDIES

These are given in essentially the same form as in the March 1964 proposal.

Physical Oceanography

a. Monitoring program through buoys, shore stations, hydrographic cruises as needed, etc. (this should be a burden jointly shared with other interests).

b. Analytical program: Basic studies of dynamic processes affecting the California Current system with particular attention to factors affecting anchovies and sardines and the biota in general.

Biological Oceanography

This should be a broadly based background program. The organisms in the California Current system must be examined as an interacting community.

a. Studies of filter feeding fish, trophic level: (Including food habits, predators, natural mortality rates, etc.). This is a huge area, one in which many scientists could lose themselves for many years. Therefore, we recommend that sardines and anchovies be a starting point and that studies radiate out from them! One of the major pragmatic objectives of this program is to test the validity of the two species system. For example, if we lower the anchovy population some species other than the sardine may pop up. Other projects, e.g., the egg surveys, fish surveys, and the historical survey contribute to this study.

b. Historical: Study sediments to ascertain "recent" oceanographic history and changes of major biological components of the California Current system, including fluctuations in sardine-anchovy abundance. This history probably can be developed to cover the last 2,000 years, possibly on a year by year basis.

Fishery Biology

a. Age specific fecundity, mortality, etc., of important species, i.e., the biological properties of sardines and anchovies, etc., that underline their inherent rates of increase, and interpretation of egg surveys.

These studies are critical and must receive early emphasis.

b. Adult and larval physiology and behavior: These are essential to achieve understanding of the effects of environmental changes on the dynamics of the community. Initial focus should be on the sardine and anchovy.

Final Comment

Obviously this list is not complete (for example, the basic productivity studies underway are quite pertinent). We believe it incorporates the most essential investigations that offer attainable goals. It is impossible to foresee what will seem essential and attainable in the future. The only thing that can be done about this is to foster a group of scientists who are responsible with respect to vital and

attainable goals, and who are also responsive to new problems, new opportunities, and to advances in the marine sciences generally.

On February 27, 1967, the CalCOFI Committee updated the recommendations to the Marine Research Committee on the development of the experimental anchovy fishery. It finds that the basic rationale expressed in that document remains valid. However, the values expressed in Phase 1 of the proposed experimental fishery have been revised on the basis of data for eggs and larvae in the additional years.

Phase 1 had as its objective "to initiate a conservative fishery on anchovies and reduce sardine fishing just sufficiently to produce an observable change in the system, and just enough to improve our preliminary appraisal of the magnitude of the anchovy resource." This called for a 200,000 ton annual quota, 35% of which was to be taken off "California" (north of 31°N. lat.) and the balance off Mexico (south of 31°). It called for a concurrent sardine fishery at a 10,000 ton level. The anchovy quota was based on egg and larva data for the years 1951-59 which indicated a total anchovy biomass of about 2,000,000 tons. Since that time, egg and larva data through 1965 have been analyzed and considerable information is available for 1966. These data show that the population level for the period 1962-66 was two to two and one-half times as great as it was in 1958-59. At the same time, the center of distribution of the population has altered, so that about half is now found north of 31°N.

Using the conservative 2x increase and taking note of the northward change of the population center, the total quota becomes 400,000 tons, with an approximate take north of 31° of 200,000 tons. The total anchovy biomass is now of the order of 4-5 million tons. The recommended take, 10% of the minimum, is extremely conservative but is sufficient to serve the purpose of Phase 1.

CalCOFI now recommends a complete moratorium for at least 2 years on the take of sardines because of the extremely low population level. We believe that a moratorium will not have an adverse effect on the experiment. A moratorium was not originally recommended for two reasons: (1) So that conditions of only one component of the experiment (i.e. the anchovy) were changed and (2) so that appropriate samples of the adult sardine were obtained for study. However, the continued reduction of the sardine population already constitutes a significant and inescapable alteration of the conditions, and sufficient samples of sardines can be obtained from mixed catches, lift net samples, etc. Thus, neither of these earlier objections to a moratorium on the sardine remains valid and a moratorium is now recommended.

The CalCOFI Committee believes that the program should now progress in the following manner:

1. The anchovy and sardine populations should be carefully monitored and studied, following, in general, our previous recommendations for research on such a fishery. Research should include

the appropriate egg and larva studies, catch records, tagging, fecundity, and food studies, etc.

2. Data should be analyzed and published with all possible expedition. Back data should be given high priority.
3. The populations, distribution and biology of the total pelagic fishes of the eastern north Pacific must be much better quantified. The areas of limited biological knowledge for each important species must be clearly delineated and resolved.

Examples for such limitations are:

Jack mackerel—area of distribution—population size—fecundity.

Hake—distribution of adults, food.

Squid—population size, distribution, food.

These are conspicuous deficiencies of the previous data. In addition, the previous data that are pertinent to the problem must be further studied and analyzed for the important and necessary insight they provide into the population of these and other pelagic fishes.

4. The nature and mechanisms of oceanographic and marine biological variation must be extended further into the source waters of the California Current. New methods and new programs will now allow us to do this.

DISCUSSION OF RECOMMENDATIONS

Clearly the direction of research that CalCOFI recommends is far from a single-minded inquiry into the anchovy. We believe that we would be serving neither science nor the state were we to adopt the anchovy fishery as a single object of study. Rather we are recommending an adequate continuing and defensible study of the anchovy and sardine and an expansion of the broad studies of the pelagic environment, which have paid off so handsomely. In this we believe that we are choosing a multilane highway into the future, which not only coincides with the scientific objectives, but serves the statutory objectives of the State and the MRC, in manifold ways.

For example, if (or, perhaps, when) the State is called upon to defend its high seas fishery resources against the encroachment of foreign fleets, it would indeed present a sorry argument were it to possess a plethora of data on the anchovy and negligible quantitative data on the saury, hake, jack mackerel and squid, for these species also are in great abundance and clearly attractive to international exploitation.

This has been pointed out before, along with other reasons to broaden the program at this time. For example, a monolithic approach to the anchovy could, of course, result in a *cul-de-sac* of empty answers were the anchovy fishery to fail for economic or statutory reasons.—*E. H. Ahlstrom, J. L. Baxter, J. D. Isaacs, and P. M. Roedel.*

AGENCY ACTIVITIES

California Academy of Sciences

The experimental studies of responses of the northern anchovy (*Engraulis mordax*) to light stimuli were

extended into 1964 for additional tests with application of ultra-violet and infrared radiation, and concluded by the end of the same year. These studies revealed a few important factors that are related to behavior. These are as follows:

1. The anchovy is a phototactic animal.
2. It is capable of discriminating qualitatively between monochromatic (green, blue, red) and white lights.
3. It is able to distinguish green light from blue.
4. It shows a preference for the green and blue lights over white.
5. It proved to be strongly negative in reaction to red light (however, the fish tolerated this type of illumination as an alternative to total darkness).
6. It is capable of reacting differently to different intensities of white light.

The results of these studies were published in the Proceedings of the California Academy of Sciences on January 15, 1965 (Vol. XXXI, No. 24, pp. 631–692) under the title "Behavior and Natural Reactions of the Northern Anchovy, *Engraulis mordax* Girard, Under the Influence of Light of Different Wave Lengths and Intensities and Total Darkness," by Anatole S. Loukashkin and Norman Grant.

The investigation of food habits and feeding behavior of the northern anchovy in California and Mexican waters was initiated on July 1, 1965, and continued in 1966. By the end of the 1965–66 fiscal year, 592 anchovy stomachs had been collected in Baja California, southern and central California, mostly by Anatole S. Loukashkin. Preliminary analysis of the stomach contents shows that the northern anchovy is an omnivorous feeder. It feeds on both zooplankton and phytoplankton. From the scant material at hand it is difficult to determine the degree of preference for one type of food over the other. It seems that the anchovy feeds on the available supply, regardless of kind. The stomachs collected contained either zooplankton exclusively or phytoplanktonic ones, or both. However, the bulk of food found in the stomachs was zooplanktonic organisms, such as euphausiids, copepods and amphipods. The euphausiids were the dominant food item. Among the diatoms consumed by the anchovy, *Chaetoceros* was found to be a dominant form. In some cases it contributed to 99% of the contents in bulging stomachs (Monterey Bay).

As to the method of feeding, the anchovy is both a filter feeder, and a particulate feeder. During the reported period field observations under natural conditions were carried on during routine cruises of the California Fish and Game M/V ALASKA by Anatole S. Loukashkin. These observations include records of school patterns, feeding behavior, school maneuverability, and reactions to artificial light sources and fishing gear, of the sardine, anchovy, mackerels and other pelagic fishes.

**California Department of Fish and Game
Pelagic Fish Investigations**

The Department's portion of the CalCOFI Program is conducted by its Pelagic Fish Investigations. The primary responsibilities are: (i) basic monitoring of the pelagic wet fisheries, particularly Pacific sardine, Pacific mackerel, jack mackerel, and northern anchovy, and (ii) conducting research vessel surveys of the pelagic and bathypelagic fishery resources of the California Current system.

Studies of the wet fisheries include: (i) sampling of commercial and live-bait catches to determine the age and length composition; sardine and anchovy age determinations are made in cooperation with the U.S. Bureau of Commercial Fisheries; (ii) interviewing fishermen and collecting logbook data to measure fishing effort and determine catch localities; and (iii) determining the amounts of fish landed and insuring the accuracy of source documents in cooperation with the Department's biostatistical unit.

Good progress was made with respect to the large backlog of age composition and fishery data on jack mackerel. This information, some dating back to 1947, has been processed and the analysis of data and preparation of manuscripts is in progress. The analysis should reveal whether the jack mackerel fishery depends upon highly available year-classes and, if such is the case, possibly explain fluctuations in fishing success experienced in recent years.

High priority is being placed on analysing all age composition and fishery data relating to Pacific mackerel with the objective of determining various aspects of the population dynamics of the species. Such information has been only partially presented in the past and this work will aid materially in understanding recent changes in the status of Pacific mackerel.

In November, 1965, the California Fish and Game Commission authorized an experimental anchovy fishery for reduction with a quota of 75,000 tons. To do the research required to monitor the effects of the fishery, an expanded anchovy research project was established by the Department. Concurrent with the inception of a reduction fishery new or revised sampling and monitoring procedures were needed. Previously the anchovy fishery was quite small and sampling consisted of 50-fish samples, selected at random and as convenient, and skipper interviews. This sampling procedure continued through the 1965-66 season.

Beginning November, 1965, a logbook system was inaugurated to obtain catch, effort, gear and fishing area data. The chart-type logbook devised prior to the 1965-66 reduction season proved successful in fulfilling its intended purpose and with minor modification will continue to be used. Initial problems with the logbooks were lack of consistency among fishermen in recording scouting time and inaccuracy of the fishermen's estimate of catch size. Both problems decreased as the fishermen gained experience. Data recorded in these logbooks are coded, key punched, and machine processed to facilitate analysis.

At the start of the second anchovy reduction season, sampling procedures were changed rather extensively.

Changes were based on the knowledge gained during the first season and will probably be modified as the fishery increases and as we increase sampling efficiency. Briefly our southern California sampling plan required obtaining 20 random samples for every 5,000 tons of fish landed. The ton (within the 5,000) to be sampled is determined from a table of random numbers as is the port and the load to be sampled. Samples are by weight and consist of two 1-pound clusters. Each cluster is divided into equal parts. All the fish in one part are measured only, from the remainder we obtain length, weight, sex, maturity, and scales and otoliths for age determination. Maturity is determined by a method defined by Hjort.²

Central California sampling procedures differ from those in southern California in that one 4-pound sample is taken each day from alternate reduction plants in Monterey Bay. The sample is divided into two parts, $\frac{2}{3}$ are measured and the remainder of the sample is processed as in southern California.

As part of the expanded anchovy research program, the Department has tagged more than 100,000 northern anchovies since March, 1966. These fish have been tagged and released in areas along the coast from Cape Colnett, Baja California to San Francisco Bay. The tagging method is that developed by Vrooman, Paloma, and Jordán,³ in which an internal stainless-steel-alloy tag is used. Numerous problems were encountered and solved during the past months of tagging. The most serious potential problem was predation on tagged fish at the time of release. To avoid this problem all the fish tagged (3,000-4,000) during 1 day are released as a group. These fish were mixed with a greater number of untagged fish and released over an anchovy school whenever possible.

By February, 1967, about 350 tags had been recovered by magnets in the meal lines of the processing plants. Preliminary returns have shown movements of anchovies from southern California to Ensenada, Baja California, and to Monterey, California. Fish have also moved between inshore waters and offshore waters around the southern California Channel Islands. The large majority of the returns came from near the area which the tagged fish were released.

With funds obtained through Public Law 88-309, the Federal Aid for Commercial Fisheries Research and Development Act (Bartlett Bill), the Department has greatly expanded its oceanic surveys of adult and juvenile fishery resources. The scope of the surveys was changed from a survey of the inshore area during the fall months to a year-around survey of all pelagic and bathypelagic fishery resources. The survey covers the area from Oregon to Magdalena Bay, Baja California.

A calendar-year survey consists of 10 cruises each of 20 days duration. Eight are echo-sounder surveys, one each to southern Baja California and northern California and three each to central and southern

² Hjort, Johan. 1910. Report on herring investigations until January, 1910. *Cons. Perm. Int. Explor. Mer., Publ. Circumstance*, (53): 35.

³ Vrooman, Andrew M., Pedro A. Paloma, and Romulo Jordán. 1966. Experimental tagging of the northern anchovy, *Engraulis mordax*. *Calif. Fish and Game*, 52(4): 228-239.

California including northern Baja California. Followup cruises in southern and central California serve as both gear research cruises and intensive sampling surveys.

The first phase of the expanded survey, in fiscal 1965-66, was designed to provide continuity with cruises conducted during the past and to develop the following survey techniques, which have been in effect since June, 1966. An echo sounder is operated continuously during the day over predetermined transect lines that extend perpendicularly from shore for at least 35 miles or until the 1000-fathom depth contour is reached. These lines are spaced 15-30 miles apart and average about 50 miles in length. Hourly fixes are obtained and the number of schools appearing on the echo sounder are recorded for each hour of running time. Identification of species is accomplished by echo trace characteristics and by fishing a small, 30-foot midwater trawl. The trawl is also fished at regular 10-mile intervals during the night as the vessel returns inshore over the outbound transect lines. A record is kept of all visually observed surface schools and indications of fish during both day and night. Catch records include species, numbers, sizes and sex. Scale or otolith samples are obtained from the important species for determining age composition. Limited oceanographic observations pertaining to fish distribution are regularly obtained. These include bathythermograph casts, water turbidities, temperatures, and weather conditions.

We have now completed five cruises of this new type; two to central California, two off southern California which includes northern Baja California and one in southern Baja California. Anchovies have been the dominant species in all areas. Since these surveys were initiated some important seasonal distribution and behavioral aspects have been determined for anchovies. During spring the anchovy population was composed of thousands of very small schools distributed over large areas extending at least 50 to 80 miles offshore. These schools were located near the surface in clear, deep water and normally contained less than 2 tons of fish. All were adults in advanced spawning stages. Large compact schools, suitable for purse-seine fishing, were scarce and found only in a few localized areas. Juvenile fish were generally found close to shore in water shallower than 50 fathoms. During summer and fall all sizes of anchovies were found much closer to shore, at greater depths, and in larger but fewer schools. Decreases in school numbers from spring to fall in the southern California area exceeded 80 percent. These results indicate that, in general, the fish spread over a large area in spring to spawn and concentrate in small coastal areas during summer and fall. The most opportune time to estimate population size appears to be spring. With the large number of schools and extensive distribution, echo sounding surveying is much more effective. Schools size and identification are also more easily determined. Fall and summer distributions, with fewer and large schools, decrease the effectiveness of the echo sounder in probability of de-

tection, species identification and school size determination. This type of distribution and behavior should be more favorable for commercial fishing.

School types and behavior patterns were also observed. Small numbers of horizontal-layer school types 80 to 100 fathoms below the surface and more numerous plumes located 20-50 fathoms deep were the predominant schools in northern Baja California and central California. The southern California region contained these types plus plume-type schools at shallower depths. At nightfall all school types came to the surface where almost all dispersed into surface scatter or loose detached school segments. Only a very few remained compact enough to be visible as a bioluminescent spot or register as an echo trace.

The night behavior of anchovies appears closely associated with the upper extremity of the scattering layer that comes toward the surface after dark. The after dark rise and surface dispersal of schools suggests a feeding behavior as evidenced by the large numbers of recently ingested food organisms observed in stomachs of night-caught fish. A very high percentage of these organisms were euphausiids, which are an important constituent of the upper scattering layer.

Quantities of sardines were present only in the southern part of Sebastian Vizcaino Bay. Adults of the fall spawning sub-population overwhelmingly predominated the samples taken. This group is now apparently the strongest remnant of the whole population. Incoming juvenile year-classes were practically nil. Other species surveyed were minor in importance compared to anchovies. Juvenile jack mackerel, mostly of the 1966 year-class, were widely distributed in small scattered schools. Trawl catches usually ranged from 1 to 50 individuals, they rarely exceeded 100 specimens.

Hake were locally abundant in July off San Francisco. Many schools were found associated with white-bait smelt. Both species were in close association with each other, the hake were 1 to 3 fathoms off the bottom with the smelt 3-4 fathoms above them. The hake appeared as small groups, 20 to 50 yards apart. A series of these groups was counted as a school. One such school was over a mile across. Those sampled were large adults, 20-25 inches. Only minor traces of hake were noted in southern California in October and no concentrations were seen in November off central California.

The Department continued to issue data reports on past-year cruises (since 1950). The material is coded onto IBM cards, organized into tables by an electronic computer, and printed directly by a photographic process. The data are printed in the California Co-operative Oceanic Fisheries Investigations (CalCOFI) Data Report series.

Eight reports, covering the 9 years from 1950 through 1958, were printed and distributed while two more reports (9 and 10) for 1959 and 1960 were completed and ready for printing. Data for the several additional years were partially processed and will be printed as they are ready.

Hopkins Marine Station

The Hopkins Marine Station of Stanford University at Pacific Grove, California, conducts studies on the environment and organisms of the coastal waters of central California. Under the CalCOFI Program the marine station monitors the marine climate and phytoplankton of Monterey Bay. Approximately weekly cruises to six stations are made on Monterey Bay, and daily shore temperatures are reported from Pacific Grove and Santa Cruz. The data collected are compiled and distributed to interested agencies and individuals in the form of mimeographed quarterly and annual reports. A short paper summarizing some of the results obtained appears elsewhere in this report.

Scripps Institution of Oceanography Marine Life Research Program

The Marine Life Research Program includes that portion of the research of the California Cooperative Fisheries Investigation that is conducted by the Scripps Institution of the University of California. This program has been principally concerned with the ecology of the California Current system—that is, its currents and countercurrents, temperatures and temperature fluctuations, and its chemistry, plankton, climatology, etc.

The Marine Life Research Program (MLRP) has also expanded its scope considerably through a series of contracts and grants from the Office of Naval Research, the Atomic Energy Commission, the National Science Foundation, The Marine Research Committee and others. It also has expanded by informal cooperation with the Navy, the Coast and Geodetic Survey, other research programs of the University, etc.

In addition to the broadened research into the eastern North Pacific, the MLR also is carrying on its responsibilities for the monitoring of the California Current and the anchovy fishery, as discussed in the CalCOFI Statement.

The MLRP thus plans a thorough coverage of the California Current System each three years (1969 next), and a continuing expansion of the several programs, descriptions of which follow.

Atlases. The reduction of the load of routine data collections, has allowed an acceleration of the analysis and publication of the data taken over the period of intense inquiry. The last several years have thus seen the publication of a number of atlases on the distribution and distributional changes of the principal planktonic organisms of the eastern North Pacific. The atlases now published or in press include the Copepods of the California Current, Vol. I; the Euphausiids; the Dynamic Heights; and 10 Meter Temperatures. Other atlases in late stages of preparation are: Copepods, Vol. II; Biomass of Zooplankton (see below); Chaetognaths; Molluscs; Anchovy Larvae.

Within the next year there thus will be in published form the most extensive biological and physical oceanographic documentation of any oceanic region on earth. The atlases are published with particular attention to the requirements of an interdisciplinary cooperative program, so that scholars in a number of

different disciplines can compare distributions and check their hypotheses of interaction and dependency. The atlases are thus precursors of much added discovery.

Biomass Analysis. In the last several years the problems of arriving at a meaningful measure of zooplankton have been resolved. The purpose of the biomass analysis was to develop a measure and methodology for the zooplankton that would typify it as a functional component of the organic milieu. This is in distinction from a strict taxonomic breakdown. The nineteen functional groups are measured in volume in each sample. Thus the data from each cruise can be presented as the actual organic component of the water represented by each of the groups. The variations between years is striking and is related to the varying oceanographic conditions.

As the zooplankton are the vital food for most of the small pelagic fishes, these fluctuations are particularly important to the CalCOFI objectives.

Biomass analysis of the zooplankton have now been completed for a number of years and the first atlas will soon be published.

Varved Sediment Study. As previously reported, the sediments in certain basins are apparently laid down in annual layers and subsequently undisturbed. These sediments thus contain a "record" of almost annual resolution of the oceanographic and marine biological conditions of the overlying waters for at least the last several thousand years.

We are thus able to reconstruct the range of conditions to which the region has been subjected with a greatly enhanced insight. The conditions during recent studies can be placed in an extremely important perspective.

Sediments of this type have now been found in about six locations along the Pacific Coast from southern California to central Peru.

Fish scales are abundant and extremely well preserved in these sediments. The initial findings in southern California sediments are that the sardine scales are only twice abundant in these sediments. The recent period of about seventy years was a period of abundance and there was a similar period about eight hundred years ago. At other times sardine scales are rare. On the other hand the scales of the anchovy and the hake are in high abundance throughout the entire period except for short periods of time. Anchovy scales were rare in the recent period. The recent period appears to be typified by a weak California Current.

The importance of the local and world-wide implications of this sediment work can scarcely be exaggerated. It is an unexpected, unprecedented and potentially powerful entree into a very broad understanding of the distribution and variations of pelagic fishes and the related oceanographic conditions.

Sediment Collections. Not unrelated to the findings of the sediments, the MLRP has recently developed a collector that can be placed on the bottom of the deep ocean, and which will collect coarse particles of sediment that are precipitating from the water

column. Although only a few experimental sets have been made, from the data collected have been made the first direct estimates of the natural generation time of some planktonic marine organisms. It may be that this approach can yield much fundamental understanding of the economy of the sea that has avoided other efforts.

Planetary Food Potential. Included in the MLR program is a continuing study of the position of marine productivity in the food potential of this planet. This study is, of course, highly approximate. Nevertheless it aids in placing fishery development in perspective. Figure 1 compares the productivity of the land and sea and the related harvest by man. The potential harvest of the sea is seen to be several orders of magnitude greater than the present, or enough animal protein for more than 60 billion people. It is clear from this study that such a harvest can be achieved only by the capture of rather primitively feeding fish, such as the anchovies and sardines.

In addition, the probable efficacy of such interventions as artificial upwelling can be evaluated in such a perspective matrix. It appears that the heat rejection required to produce the world's power requirement from atomic sources can incidentally increase the ocean productivity in an amount approximately sufficient to supply a quarter of the needed protein.

Details of these and other such considerations can be found in several of the listed publications.

Sardine Parasites. An investigation into the stomach contents of sardines indicates that the sardine population off California was increasingly parasitized by two species of trematodes during the period 1925 to 1955. In later years the infestations were very heavy. There is even some evidence of competition between the two species of trematodes within the sardine stomachs. Such competition would be almost certain evidence that the infestation was damaging to the sardine.

Neither the sardine below Sebastian Viscaino nor the anchovy were subject to such infestations.

Whether or not this infection contributed to the decrease of sardine stocks cannot be definitely ascertained.

Sea Surface Temperature Anomalies. The Years of Change 1957-58, brought to our attention the fact that variations in oceanic conditions were not of local origin but rather involve the entire North Pacific, if not the entire planet. We now know that non-periodic departures from normal sea surface temperatures are common throughout the oceans. In the North Pacific these anomalous conditions are often large scale and of long persistence (ca. $\frac{1}{4}$ the width of the Pacific and of 2 years duration). These anomalies are associated with changes in weather conditions, the distribution of marine organisms, circulation, etc. We are now planning a large-scale study of these anomalies and their associated conditions utilizing a large number of unmanned instrument stations over a major part of the North Pacific.

In preparation for this research, a pilot study has been carried out. This study has revealed a number of high intriguing characteristics of these events that will require explanation. Among these findings are: A dependency of anomalies on the local spatial temperature gradient over one-half of the year; a relatively smaller variation in spatial and temporal temperature gradients in the regions of high anomalies than in the regions of "normal" conditions; an anisotropy of the heating-cooling cycle; and others.

In addition, the first long-term records from unmanned stations have been obtained. These have shown several important features including astronomic periodicities of temperature fluctuations.

This planned study of the North Pacific should result in better insight and input into North hemispheric meteorological and oceanographic prediction.

Some of these deep moored stations will be installed in the CalCOFI area and will result in almost continuous offshore data.

Deep Benthic Conditions. The oceanographic studies of the eastern North Pacific have been extended into deep water. The findings have been most significant.

Many of the conditions of the deep ocean bottom are virtually unexplored. The near-bottom currents are very poorly known, and little is known of the active creatures of the deep ocean floor. The development of autonomous instruments at Scripps has allowed

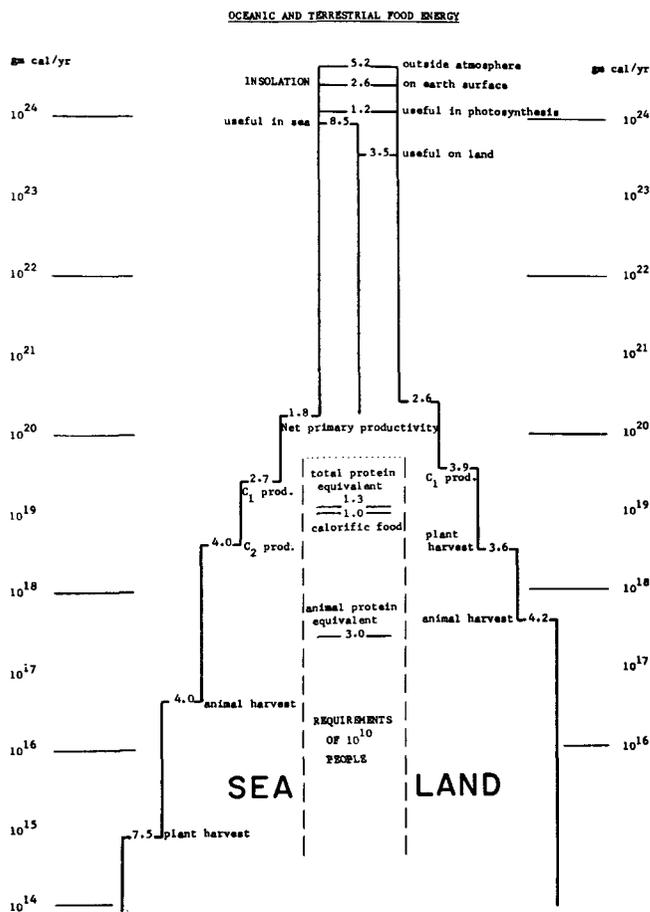


FIGURE 1. Diagram of total energy cascade into the food of the marine and terrestrial realms.—prepared by W. Schmitt.

us to add some insight into these conditions. Deep currents in the eastern North Pacific have been found to be low but of somewhat higher velocity than anticipated (ca. 3 cm/sec), and the fluctuating component has been found to result principally from the lunar semi-diurnal surface tide. We have also demonstrated the presence of unexpectedly large fish populations (see Figure 3) including very large climax predators, whose presence on the deep ocean bottom is an environmental condition of importance.

Instrument Development. Recent instrument development in the MLRP has been remarkably successful. All recent deep moorings have remained in operation at least six months in the open sea and one remained for 23 months. Long period records are now available that greatly increase our understanding of ocean conditions and are allowing the greatly increased program.

The autonomous instruments are valuable for research of the deep bottom.

The new Isaacs-Brown Opening-Closing Midwater Trawl is yielding much needed data on the vertical distribution of marine organisms.

New instruments under development include new sensors for deep moored stations, an acoustic release for autonomous instruments, isotherm following floats, etc.

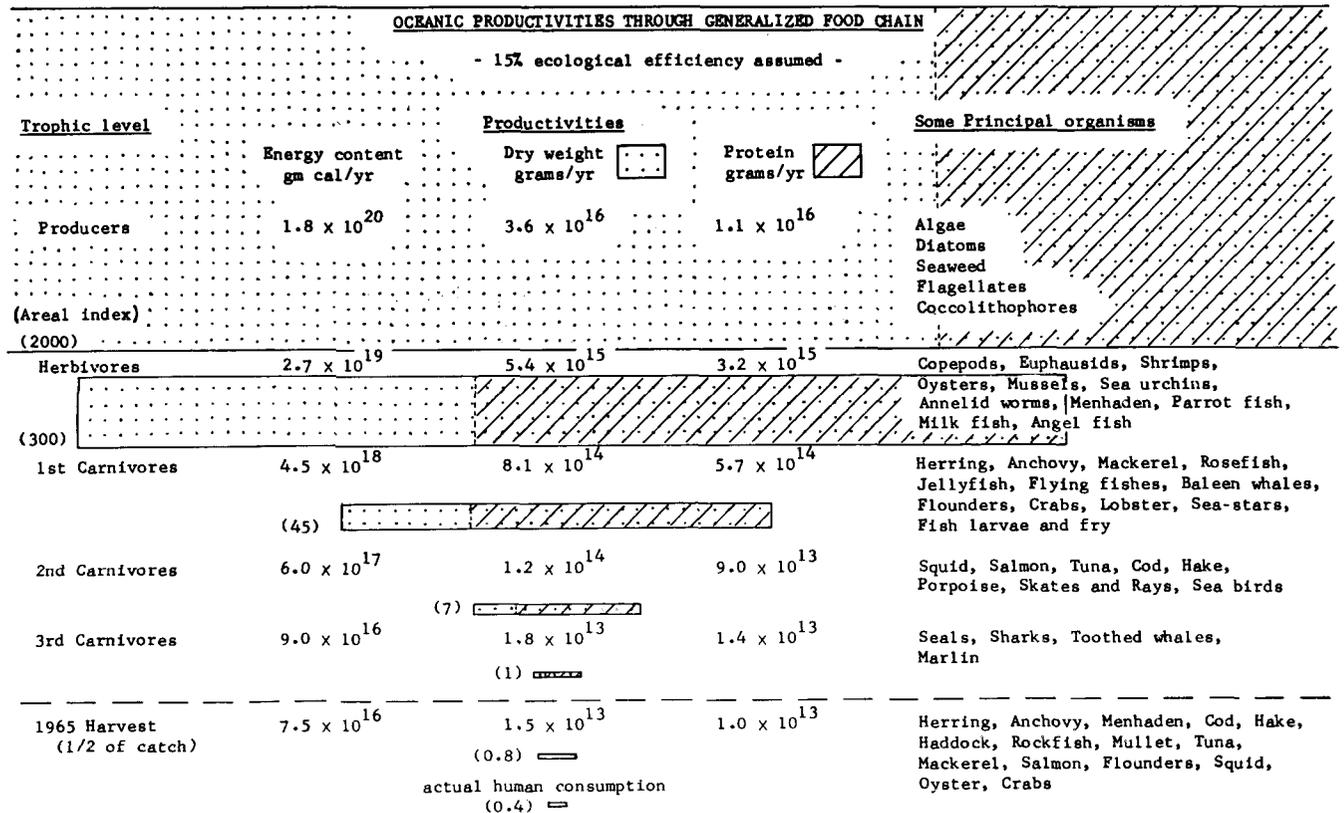
Special Cruises. The special cruises of the MLRP have been directed toward: (1) instrument development, (2) exploration of deep benthic conditions including the varved sediments, (3) cruises to explore and further delineate biological and oceanographic conditions in the North Pacific. Three such cruises were carried out in the period.

Summary. In summary, the MLR program over the recent period has greatly expanded its competency, range of interest, and findings. This expansion has been spatially into the North Pacific, vertically to the sea bottom, and temporally into the past range of conditions of the California Current.

This expansion is dependent upon and additive to the knowledge and insight that the CalCOFI program has created which is serving as a precious foundation for an expansion of research and the opportunities of California—and vindicating the prediction of the generators of the CalCOFI program that the Pacific can represent a freedom to the State of California rather than a barrier.

**U.S. Bureau of Commercial Fisheries
California Current Resources Laboratory**

The former La Jolla Biological Laboratory, the oldest Bureau of Commercial Fisheries Laboratory in California, was renamed the California Current Re-



Note: The food chain should more accurately be thought of as a food web, in which most organisms feed on more than one trophic level, changing diet with their age (especially when young) and the availability of food.

FIGURE 2. Diagram showing the total marine food web. Hatched areas show total food and total protein food at each step.—prepared by W. Schmitt.



FIGURE 3. Grenadiers, hagfish, migrating tube worms and other creatures attracted to a bait and photographed by an untethered automatic camera at 1200 fathoms off Baja California.—(field view is about 9' x 12').

sources Laboratory in 1964, and in September of that year moved from the old, frame building on the Scripps campus, where it had been housed since 1954, to the newly built Fishery-Oceanography Center on a cliff site overlooking the ocean, $\frac{1}{2}$ -mile north of the old location.

The Center is a strikingly modern laboratory, built of prestressed concrete and includes four multi-story buildings around a center courtyard. Noteworthy features of the Center are research laboratories grouped into functional complexes for studies of physiology, fish taxonomy, behavior, culturing of marine organisms, radiobiology, population ecology, and chemical and physical oceanography. An experimental seawater aquarium which delivers 200 gallons per minute, via epoxy-lined asbestos concrete and polyvinyl pipe lines from the Scripps Institution of Oceanography pier, is the focus for rearing and behavior experiments and physiological studies on fish and other marine organisms. These excellent facilities have made possible some of the results discussed later, as for example, the successful rearing of pelagic marine fish larvae and the maintenance of euphausiid shrimp in captivity.

The California Current Resources Laboratory carries out a broadly based research program, emphasizing

the study of pelagic fishes, exclusive of the temperate tunas, in the California Current region. The ocean survey program is carried out cooperatively with the Scripps Institution of Oceanography's Marine Life Research Group. With the California Department of Fish and Game, the California Current Resources Laboratory investigates the age and size composition of commercial landings of sardines and anchovies, and contracts with the California Academy of Sciences to sample the sardine and anchovy fisheries of Baja California.

We have tried to achieve a balance in the California Current Resources Laboratory between basic and applied research. The laboratory has pioneered in several important areas of ocean research, including the taxonomy of pelagic marine fish eggs and larvae, the use of systematic egg and larva surveys of oceanic areas for evaluating fish resources, the use of blood genetics for establishing the existence of genetic stocks (subpopulations) within the Pacific sardine populations, the rearing of pelagic fishes from eggs through larval stages to juveniles, and the gaining of an understanding of the hydrodynamics and performance of plankton sampling gear.

Bio-oceanographic Surveys. Sixteen bio-oceanographic surveys were made on the CalCOFI pattern

from July 1963 through June 1966. Coverage was on a quarterly basis through 1965 and then on a monthly basis in 1966.

The research vessel, *Black Douglas*, which was used almost exclusively for CalCOFI surveys, was retired after the last cruise in 1965 and replaced by the new research vessel, *David Starr Jordan*, which began its work in January, 1966. *Jordan* was designed specifically for oceanographic and biological research. It is of steel construction, 171 feet long, with a cruising speed of 12 knots, fuel capacity for 40 days, and a range of 12,000 miles. Special features include a bow thruster, underwater observation ports, biological, chemical, and hydrographic laboratories, research sonar, radar and navigational equipment.

Certain changes were made in coverage and methods of sampling during these years. In January and July 1964, a special grid of 80+ stations was occupied off Pt. Arguello to determine more fully the areal distribution and seasonal changes in abundance of fish larvae in that area. In all of the 1965 cruises, two samples were taken at most stations, one with the standard 1-m net and the other with a fine mesh (0.27 mm) 1-m net hauled together with or consecutively after the standard net. This was done in order to obtain information regarding the kind and degree of under-sampling by the standard net of anchovy eggs and of very small fish larvae. In 1966 almost all collections with the standard net were made in assembly with a newly-designed $\frac{1}{2}$ -m "anchovy egg net" (0.33 mm mesh).

In calendar 1966, monthly coverage, the first since 1960, was re-instituted in order to obtain data for a base year for studies of the anchovy population, in keeping with the opening of an experimental reduction fishery. Adequate coverage of the pattern from San Francisco to southern Baja California usually requires at least two ships. Since it was not always possible to have two for each month, surveys for one ship were planned always to include the pattern off southern California from Point Conception to San Diego and either to work north to San Francisco or south near Magdalena Bay.

The monthly surveys of 1966 will permit us to obtain current estimates of abundance of other important fishery resources in the CalCOFI area in addition to the northern anchovy—particularly Pacific hake, jack mackerel, sardine, and rockfishes.

Cooperative Hake Surveys. During the period of this report, three cooperative hake cruises were made, usually employing the *Black Douglas* of this laboratory and the *John N. Cobb* of the Exploratory Fishing and Gear Research Base, Seattle, Washington. The purpose of the cooperative cruise was to determine the location and extent of spawning concentrations of adult hake off California and Baja California and the quantities that could be captured per hour of trawling. All of the cruises were made in February-March, the months of peak spawning of hake.

In order to locate concentrations of spawning hake, the *Black Douglas* scouted for high concentrations of newly-spawned hake eggs by means of a systematic

program of plankton sampling and examination of samples immediately after collection. When high concentrations of eggs were found, the information was radioed to the *Cobb*, which moved to the area, located the position of spawning adults with its echo-sounding equipment and then lowered its large pelagic trawl to appropriate depths. Using this method a direct relation was found between areas of high egg concentration and the presence of spawning adults. Several such areas of adult hake abundance were surveyed off southern California and northern Baja California. One of the concentrations was estimated to extend over 23 square miles. The largest catches were obtained offshore from San Diego (in the vicinity of CalCOFI station 97.35). A catch of 20,000 pounds was obtained in one of the 1-hour sets. The location of spawning concentrations changed from year to year. Hake were encountered at depths of 80 to 225 fathoms with the fish occupying the shallower depths at night.

Males predominated in most catches, often contributing 90 to 95 percent of the fish caught. Males appeared to be more permanent residents of spawning schools than the females. The latter appeared to enter the spawning schools for a brief period, spawn their eggs, and then leave.

Anchovies were taken in more than half the trawl hauls made by the *Cobb* during the cooperative cruise of 1964. The most interesting phenomenon relating to these fish was their consistent occurrence during the day at depths of about 125 fathoms, and on one occasion at a depth of 185 fathoms. At dusk the echograms showed the schools rising to the surface.

Distribution of Schooling Fish as Determined by Sonar. With the commissioning of the *David Starr Jordan* in January 1966, the Behavior program started a field study of the distribution, movements and abundance of schools of anchovies and other pelagic species. The Simrad sonar installation will be the primary tool in this project. To date four surveys have been carried out in conjunction with monthly egg and larva cruises. Analysis of the sonar records has revealed that a few large aggregations of fish schools occurred on each cruise. In half a dozen cases the peak counts were higher than 100 schools per 10 miles and in one case as high as 200. These aggregations, furthermore, were extended over distances of 20 to 40 miles, some along the coast and some on station lines extending offshore, and a number of them were identified as anchovies by underwater observation. Targets of a biological nature also occur frequently in the outer portions of the survey pattern but so far these have been scattered and usually weak in signal strength. Trawling gear, which will be used to obtain samples for identification and life history information, has been tested but not yet used routinely.

The potential of sonar for ecological surveys and resource evaluation is evident not only in the high rate of target registration, but also in the way the limited sonar data already taken relates to other kinds of information collected. A major shift in distribution of anchovy concentrations within a period of 4

weeks, for instance, appeared to be associated with a marked shift in surface temperature distribution. Also, simultaneous depth sounder records indicate that some of the variation in distances at which school groups are detected from the vessel is probably related to the depth of the groups. On one occasion schools were observed to move vertically in close coordination with the deep scattering layer. The accumulation of such information, along with studies based on tracking schools, an operation already attempted with moderate success, should provide valuable field information for understanding the behavior of these fishes in relation to features of their environment, and perhaps also for estimating their seasonal and regional abundance, at least in a relative sense.

Resource Evaluation. Perhaps the prime accomplishment of the California Current Resources Laboratory has been the demonstration that systematic surveys of fish eggs and larvae constitute one of the best means available for evaluating fish resources. These surveys have shown that there are a number of important fish resources in the California Current region that are underutilized or not fished at all. The most abundant of these is the anchovy, which has shown a 10-fold increase during the 16 years of CalCOFI surveys. Second only in abundance to anchovy larvae are those of the Pacific hake. Jack mackerel larvae are less abundant in the area surveyed but more widely distributed. This species spawns throughout the CalCOFI area, but eggs and larvae are more

common in the outer half of the CalCOFI pattern; the offshore extent of spawning of jack mackerel seldom is completely delimited by CalCOFI surveys.

Of more importance is the documentation of the interaction between the sardine and anchovy populations. The anchovy population increased in abundance as the sardine decreased. Competition, coupled with a selective fishery for the sardine, gradually allowed the anchovy to become predominant in its trophic level. We are vitally interested in whether the action is reversible. Can the abundance of the sardine population gradually be increased by applying differential fishing pressure to the anchovy resource?

Rearing Pelagic Marine Fishes. The program for rearing pelagic marine fish larvae has the basic objective of developing techniques and equipment by which marine fishes may be cultured under laboratory conditions from the egg stage through the larval and metamorphic stages to the juvenile and eventually adult stage. Many scientists have attempted to rear pelagic marine fishes during the past century because of the wide scientific and commercial applications inherent in this accomplishment. Rearing pelagic fish larvae under laboratory conditions opens many avenues of scientific inquiry and provides new areas of specific studies on larval fish survival, taxonomy, embryology, physiology, and behavior.

Progress during the past 3 years of experiments in rearing pelagic fish larvae at this laboratory has culminated in outstanding success in multiple rearings



FIGURE 4. School of Pacific mackerel, reared from eggs by Dr. George Schumann.—photo by George Mattson.

of northern anchovy, Pacific sardine, and Pacific mackerel. Many hundreds of individuals of these valuable commercial species were reared from their eggs to the juvenile stage in the laboratory. At the same time approximately 18 other species of marine fish were successfully carried from hatching through metamorphosis to the juvenile form.

Success in rearing may have resulted from the combination of a suitable environment and a good food supply. Observations on newly-hatched larvae indicated the need for large volumes of sea water because of its stability of temperature, salinity, and biotic factors. Large aquaria provide room for swimming without frequent contact of walls, one of the major causes of mortality of laboratory-reared fishes.

At first feeding, sardine and anchovy larvae require high densities of food in their immediate environment. Live plankton has been provided, which has been obtained by filtering large volumes of sea water to obtain sufficient numbers of minute plankton organisms of sizes that can be ingested by newly-feeding larvae (organisms no larger than 0.08 mm in diameter). As the larvae grew, larger food organisms were supplied in high densities.

Sardine and anchovy larvae, at first feeding, can swim only limited distances. Their swimming ability requires that the entire volume of a 500-gallon aquarium must contain uniform distribution of food organisms at a density not less than 4 per cubic centimeter of water, regardless of whether only one larvae or a thousand are being cultured. This problem was solved by restricting the space for the larvae with use of thin-walled plastic bags floated in the aquarium. The thin plastic permitted gas exchange to take place between the waters inside and outside of the bag, while the soft material offered very little resistance when struck by a swimming larva. When larvae become able to hunt food over greater distances, the bags were silt open and the growing fish allowed the freedom of the larger container.

Life History Studies of Rockfish. A major goal of the Life History and Taxonomy program is to prepare complete descriptions of the life history stages of the fishes that contribute eggs and larvae to the plankton of the California Current region. A major study is being made of rockfishes (*Sebastes* spp.).

The large number of rockfish species (more than 50) pose an immense problem in attempting to identify rockfish larvae collected in plankton. The problem is simplified by the fact that rockfish are live bearers that retain their young to the larval stage. Such early larvae of 17 species have been obtained from identified females and have served as a means for identifying the later larval stages in our collections.

The complete series of developmental stages from the developing embryo to the adult, have been described for *Sebastes paucispinis*. It was found that young of this rockfish species spend the first several months of their life as epipelagic larvae and transform into juveniles at 30 mm length. Juveniles are found in shallow coastal waters over rocky bottoms in association with algae (*Macrocystis*, *Laminaria*, and

Egregia) or over sand bottom in association with eel grass (*Zostera*). Juveniles remain in waters shallower than 20 meters during their first year of life, then move into deeper water. Most of the adults collected were found in depths of 80 to 300 meters during the investigation.

Plankton Dynamics. Since the start of the work on quantitative sampling of fish eggs and larvae in 1939, the California Current Resources Laboratory has been involved in problems of quality control of plankton collection. In 1963 the diverse plankton-sampling studies were united under one program. The work of the Plankton Dynamics program is divided into four areas: plankton sampler design and operation, plankton behavior, microdistribution, and measures of amount of zooplankton (biomass).

It was our judgment in starting the plankton program that two major problems were inhibiting the improvement of precision and accuracy in quantitative zooplankton sampling. One problem area was that of plankton behavior, of the responses of organisms to sampling gear. The other was an inadequate understanding of the operation of plankton sampling gear. As anticipated, the description of the performance of sampling gear has proceeded at a faster pace than the study of the biological problems.

Comprehensive tests of hydrodynamics of plankton sampling devices were carried out at the David Taylor Model Basin near Washington, D.C. Eighteen persons participated in or were actively associated with these tests, including personnel from five BCF laboratories and from several university and industry groups.

The tests showed that in "clean" water at the model basin, the amount of effective straining area rather than the size of the mesh apertures was the predominant consideration. As long as the ratio of mesh aperture area to mouth area was at least 4 to 1, little difference was observed in filtering efficiencies of fine or coarse-meshed Nitex nets in "clean" water at towing speeds of 1½ to 3 knots. All had filtering efficiencies of 90 percent or more when new (less if the net previously had been used at sea).

The tests also showed that bridles and tow cables cause major accelerations and turbulence in the water ahead of nets. Although these disturbances have little effect upon the actual filtering efficiencies of large nets, they provide cues to which animals may respond to avoid capture.

Following the studies of plankton net performance under controlled model basin conditions, the nets were taken to sea, in order to study the effects of clogging on plankton net performance. The telemetering flow measuring devices used for the model basin tests were adapted for use at sea. Clogging was monitored in several phytoplankton rich areas, usually near shore, as well as in clear waters, 250 miles seaward of Pt. Conception. The rate of clogging was found to be markedly dependent upon the composition of the plankton community. When a series of nets were tested in plankton-rich waters at the same locality, the rate of clogging was found to be affected by mesh aperture size, mesh aperture amount and net form

(whether cylindrical, conical, or cylindrical-conical)—listed in order of importance.

Mesh aperture sizes markedly affected the rate of clogging. The smaller mesh sizes clogged at a rate which was related to the area of the individual mesh aperture. We concluded that the finest mesh practical for the usual survey tows should be 0.3 mm mesh aperture width but that even in such a net the combined areas of the apertures would have to be at least 8 times the mouth area to get sustained filtration for 15 minutes at 2 knots.

It was found that mesh aperture amount also affected clogging strongly. For instance, in a given body of water a 20 percent increase in reserve filtering area would allow a net to filter twice the amount of water before filtration efficiency was adversely affected. Our studies of the effect of net form on clogging rate showed that cylindercone nets clog more slowly than conical nets.

An important finding of the research on plankton gear is that the basic filtration characteristics of a towed plankton net in the field may be effectively predicted by establishing the proportions of mesh aperture area necessary for each size of plankton mesh. We have applied these data to the design of a small mesh net to retain the eggs of the northern anchovy. Since January, 1966, this net has performed with the predicted efficiency in more than 1,000 tows in all areas of the survey region of the California coast.

Experimental Tagging of Anchovies. Before the beginning of the anchovy fishery, it was understood that a tagging program would be needed to aid in the studies of the population structure, movements, and abundance of these fish, as well as to measure the effects of fishing pressures. Anchovies are extremely delicate and susceptible to injury when handled, therefore experiments were made to determine whether tagging was feasible and practical.

Since tags were to be recovered from magnets in fish canneries, steel internal tags were chosen for marking the fish. It was found that the same type of internal tag (13 x 3 x $\frac{1}{2}$ mm), used successfully on the Pacific sardine, herring, mackerel, and anchoveta, could also be used on the anchovy. Mortality was decreased by coating the tags with 5 percent tetracycline paste and inserting them posteriorly through an incision cut just dorsal to the tip of the pectoral fin. Contrary to expectations, greater mortality was found to occur among fish that had been anesthetized before tagging than among those tagged without anesthetic. Better survival occurred in freshly-caught anchovies than in fish that had been held in live bait tanks for several days.

The California Department of Fish and Game has successfully used these methods to tag many thousands of anchovies off the coasts of California and Baja California during 1966.

Since the metal internal tag is not visible and even the incision scar is completely indiscernible after 2 or 3 weeks, we have been unable to get tag returns from the bait fishery. Several methods of externally

marking the tagged fish have been tested. The most promising mark is created by injecting a red fluorescent pigment just under the skin of the opercle. This mark is readily visible in live or dead fish, is not injurious to the fish, and, when properly injected, does not fade.

Genetic Studies. Serology, which was successfully employed in distinguishing the three subpopulations of sardines, is also being applied in the search for northern anchovy subpopulations. In order to find blood groups that may be used in characterizing anchovy subpopulations, it was necessary to produce new blood-typing reagents. We have developed some new techniques that have enabled us to collect relatively large volumes of high titer reagents from immunized fish. These reagents produced in fish show a greater degree of specificity than reagents that were formerly produced in warm-blooded animals.

Electrophoresis of tissue proteins from anchovies has also been tried. The electrophoretic patterns produced in polyacrylamide gel from the soluble proteins of the eye lenses showed no differences in anchovies sampled from southern Baja California to San Francisco. The most promising proteins now appear to be the transferrins, a specific group of iron-carrying proteins found in the blood sera. Transferrins labeled with radioactive iron and electrophoresed on starch gel show polymorphism, which appears to be controlled by a 3-allele genetic system. The frequency of occurrence of these genes in anchovies taken from various areas can be used in looking for subpopulations.

Behavior Studies on Anchovies. One of the major endeavors of the Behavior Program during the past several years has been to develop a quantitative description of anchovy feeding: to discover what its food preferences are, how it captures different kinds of organisms, and how the rate at which it removes food from the water depends on the amount present, the size of the fish and its state of hunger.

Experiments have shown that predation is by filtering on organisms less than 1 mm in length and by particulate biting on organisms a few mm or more in length. It has been shown also that the larger organisms are preferred, but that the filtering attack directed at the smaller organisms is not abandoned in favor of biting unless the larger organisms are abundant enough to provide a greater rate of caloric intake.

Other experiments have shown that the rate of intake on both sizes of food organisms, when they are present in surplus quantity, increases with growth of the fish up to a weight of about 4.0 grams, beyond which it tapers off steadily toward an asymptotic level. Though this relation between size and feeding rate has the same pattern for the two sizes of food organisms, the rates are higher for the larger items, indicating that an anchovy at any size is able to consume more in weight and hence in calories of the large organisms than of the small organisms. Another set of experiments has shown that for an anchovy of any

given size the rate of intake by weight on small food organisms is constant for as long as 1 hour after the start of feeding, whereas the rate of intake on large organisms starts at a much higher level and declines rapidly. In less than an hour it is at a lower level than the constant rate on small organisms. Such information, along with the answers to a number of related questions, the effect of light intensity and temperature on feeding rates, for example, will lead to an understanding of what variations in plankton abundance means to the fish in terms of food availability.

Feeding, Growth, Respiration, and Carbon Utilization of Euphausiid Shrimp. An experimental study was made of the biology of the euphausiid shrimp, *Euphausia pacifica*, describing growth, feeding, respiration, molting, and the efficiency with which it incorporates carbon from its food into body tissue.

Among planktonic organisms in the food web of the oceans, euphausiid crustaceans rank high in abundance and importance. They are food for a variety of fishes, ranging from sardine and jack mackerel to tunas and salmon, and are the chief food of baleen whales.

The experimental studies were dependent upon successful maintenance of euphausiids in the laboratory. Techniques were developed that permitted normal growth and development of euphausiids in the laboratory; some experimental animals were kept for over one year.

The euphausiid shrimp studied, *E. pacifica*, is an omnivorous feeder, utilizing both algae and small zooplankton animals. In the laboratory, crustacean nauplii seemed to be preferred food over unicellular algae, but both were eaten when available.

Growth in euphausiids, as in all crustaceans, is accompanied by molting. Euphausiids kept in the laboratory at temperatures similar to those at which the animal lives in the sea (9–15°C) were observed to molt on the average every 5 days. The dry weight of each molt is approximately 10 percent (range 4–14 percent) of the dry weight of the animal which produced it. Molts contained approximately 46 percent ash, 17 percent organic carbon, and 2.5 percent organic nitrogen. Each molt contained about 4 percent of the organism's carbon, 2 percent of its nitrogen.

Assimilation of ingested carbon (digestion) appeared to be high, usually over 80 percent, as judged from tracer experiments with carbon-14. Respiration accounted for the major portion of the assimilated carbon—62 to 87 percent. The long term loss of carbon due to molting ranged from 6 to 11 percent. The fraction of assimilated carbon calculated to appear in eggs was 9 percent. In young individuals with rapid growth, incorporation of assimilated carbon into body tissue was as high as 30 percent, in older individuals with slower growth it was as low as 6 percent. Calculations from an oceanic population gave 9 percent as level of incorporation of organic carbon into tissue (excluding eggs and molts) over the life span of the animal.

REVIEW OF THE PELAGIC WET FISHERIES FOR THE 1963-64, 1964-65, 1965-66 SEASONS

During the past 20 years the Pacific mackerel, jack mackerel and sardine fisheries have been major contributors to California's pelagic wet-fish landings. In the same period the northern anchovy fishery was considerably less important, being relegated primarily to fresh fish and live-bait landings. In recent years the sardine population has declined drastically and the anchovy has taken on new significance with the authorization of a fishery for reduction in 1965 (Table 1).

TABLE 1
**LANDINGS OF PELAGIC WET-FISHES
IN CALIFORNIA IN TONS, 1962-1966**

Year	Sar- dines	An- chovies	Pacific mackerel	Jack mackerel	Herring	Squid	Total
1962-----	7,682	1,382	24,289	44,990	653	4,684	83,680
1963-----	3,566	2,285	20,121	47,721	315	5,780	79,788
1964-----	6,569	2,488	13,414	44,846	175	8,217	75,709
1965-----	962	2,866	3,525	33,333	258	9,310	50,254
1966*-----	450	31,089	2,004	20,580	120	8,798	63,041

* Preliminary.

The vessels harvesting these species consist primarily of purse seiners, lampara boats and scoop boats. During the past 4 years, vessels have continued to leave the fishery; the fleet declining from 69 vessels in 1963 to 54 in 1966. Most of the loss was in the large purse seine group (over 60 feet) which decreased from 38 to 29 vessels.

The fleet operating from Baja California ports during the period 1963 through 1966 remained fairly stable, between 30 and 32 boats.

The demand for wet-fish was good during the past 4 years with cannery imposed vessel limits generally 50 tons or more. Concomitantly there was a gradual increase in the price paid to the fishermen with sardines increasing from \$60 to \$75 per ton and jack mackerel and Pacific mackerel rising from \$42.50 to \$75 per ton.

SARDINES

1963-64 Period (June through May)

For the second consecutive year, cannery season landings dropped to an all-time-low. Central California landings (August 1, 1963 to March 1, 1964) amounted to only 943 tons. Southern California landings (September 1, 1963 to March 1, 1964) were slightly higher at 1,089 tons. Samples from both areas indicated 62 percent of the catch was produced by the 1958 and 1959 year-classes. Statewide landings for the 1963-64 period were 2,942 tons.

In central California, primary areas of catch were Monterey Bay and the coastal areas from Point Sur to

Point Lopez. The southern California catch came principally from Santa Catalina Island, with smaller quantities taken at Horseshoe Kelp, San Nicolas Island and between Santa Cruz and Anacapa Islands.

TABLE 2
**SARDINE CATCH IN TONS, 1962-63 THROUGH 1965-66
(Period June Through The Following May)**

Year	California	Baja California	Total
1962-63-----	4,172	14,620	18,792
1963-64-----	2,942	18,384	21,326
1964-65-----	6,103	27,120	33,223
1965-66*-----	719	22,247	22,966

* Preliminary.

Baja California landings from September 1, 1963 to March 1, 1964 were approximately 6,880 tons; more than three times the landings in California. About 58 percent of the catch was from the 1958 and 1959 year-classes. Total catch for the period (June through May) was 18,384 tons. Sardine demand was good and most of the fish were canned. The fishermen received from \$32 to \$42 per ton.

1964-65 Period

The southern California cannery season opened on September 1, 1964. Approximately 2,600 tons of sardines were taken near San Nicolas Island during the first night of fishing. Many of the large purse seiners caught 100 tons or more. After the exceptional catches of the first night, landings deteriorated throughout the rest of the season. The statewide catch during the cannery season was about 5,200 tons, with nearly 4,000 tons from San Nicolas Island. About 80 percent of the fish taken for age determinations were from 3 to 5 years old (1958 to 1960 year-classes).

The total statewide catch during the 1964-65 period was 6,103 tons, with central California contributing only about 50 tons.

Baja California landings increased to more than 27,000 tons for the period June, 1964 through May, 1965. Landings during the southern California cannery season amounted to approximately 12,000 tons. The age distribution of the fish sampled was essentially the same as that for California, about 87 percent were from the 1958-59 and 1960 year classes. The price to the fishermen varied between \$32 and \$42 per ton.

1965-66 Period

Statewide landings during the cannery season were 363 tons for the poorest catch on record. Landings for central and southern California were 69 and 294 tons respectively, with no fish younger than the 1962 year-class present in the age samples. The statewide

catch during the 1965-66 period was approximately 719 tons with most of the fish going to the fresh fish markets, where the fishermen received from \$200 to \$400 per ton. The primary areas of catch were Santa Catalina Island and the Horseshoe Kelp area.

Landings in Baja California dropped to approximately 22,000 tons for the period June, 1965 through May, 1966. Landings from September 1, 1965 to March 1, 1966 amounted to nearly 7,400 tons. The demand for sardines was good; 32 purse seiners were kept busy supplying 10 canneries with fish. The price to the fishermen remained fairly stable at \$40 per ton.

ANCHOVY

In 1963 and 1964 anchovy catches were used in canning, as fresh fish and as live-bait. In November, 1965, the California Fish and Game Commission authorized the use of 75,000 tons of anchovies for reduction into fish meal. In late-November, 1965, the experimental anchovy fishery for reduction opened. Landings were negligible through the end of 1965, but began picking up in February of 1966, and by the end of the season (April 30, 1966) over 16,000 tons of anchovies had been landed. The Horseshoe Kelp area produced about 75 percent of the fish taken.

TABLE 3
COMMERCIAL LANDINGS AND LIVE-BAIT CATCH
OF ANCHOVIES IN TONS, 1962-1966

Year	Commercial Landings	Live-Bait	Total
1962.....	1,382	6,167	7,549
1963.....	2,285	4,442	6,727
1964.....	2,488	5,191	7,679
1965.....	2,866	6,148	9,014
1966*.....	31,089	6,636	37,725

* Preliminary.

Los Angeles-Long Beach Harbor provided most of the fish for the live-bait fishery during the period from 1963 to 1965.

The age composition of the 1963-64 live-bait catch at Port Hueneme, San Pedro and Newport were similar. Zero's, one's, and two's constituted between 80 and 90 percent of the fish sampled. The most

prominent group was the 1962 year-class (one-year-old fish). At Port Hueneme, 46 percent of the fish sampled were from the 1962 year-class; at San Pedro, 54 percent and at Newport, 45 percent.

In 1964-65, the one's (1963 year-class) were again dominant in the live-bait samples. At Port Hueneme the 1963 year-class made up 45 percent of the fish sampled; 37 percent at San Pedro and 67 percent at Newport.

MACKEREL (May-April)

Pacific mackerel landings have dropped steadily since 1962-63 when about 23,000 tons were taken. During the 1965-66 season the catch fell to 3,788 tons (Table 4), and the outlook for the next 2 seasons is not encouraging. The primary areas of catch during the past 3 seasons were Cortes and Tanner Banks, San Nicolas, Santa Catalina, and San Clemente Islands.

Jack mackerel landings have been on the decline since the 1961-62 season, when 54,706 tons were landed. The catch dropped to 33,837 tons for the 1965-66 season (Table 4). Major areas of catch for the 3 seasons 1963-64 through 1965-66 were Santa Cruz, Santa Barbara, Anacapa, Santa Catalina, San

TABLE 4
JACK AND PACIFIC MACKEREL CATCH IN TONS,
1962-63 THROUGH 1965-66
(Period May through April)

Year	Jack Mackerel	Pacific Mackerel
1962-63.....	48,422	22,627
1963-64.....	42,038	17,105
1964-65.....	39,548	12,437
1965-66*.....	33,837	3,788

* Preliminary.

Clemente, San Nicolas Islands and Cortes and Tanner Banks. In 1963-64 these areas produced approximately 50 percent of the statewide catch; in 1964-65 they accounted for 65 percent of the catch and in 1965-66, 75 percent of the catch came from these areas. *Kenneth D. Aasen, California Department of Fish and Game.*

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PART II
SYMPOSIUM ON ANCHOVIES, GENUS *ENGRAULIS*

JOHN L. BAXTER, Editor

Lake Arrowhead, California

November 23–24, 1964

INTRODUCTION

Anchovies, genus *Engraulis*, comprise major fishery resources in all temperate seas except the northwest Atlantic Ocean. One species supports the world's largest single-species fishery, that of Peru, while others support major fisheries in Japan and Europe. Fisheries for anchovies are also developing in Argentina, South Africa and California where they comprise sizeable resources. Because of the worldwide interest in anchovies, this symposium was organized so that scientists with similar problems could present papers, exchange data and discuss research programs. The meeting was held at Lake Arrowhead, California on November 23 and 24, 1964 as part of the annual California Cooperative Oceanic Fisheries Investigations (CalCOFI) Conference and was organized by the California Department of Fish and Game.

Foreign scientists who were able to attend included: Herman Einarsson and Rómulo Jordán from Peru; and Sigeiti Hayasi from Japan. Janina Dz. de Ciechomski of Argentina, although unable to attend, submitted valuable contributions. Maurice Blackburn, now at Scripps Institution of Oceanography, participated and presented a paper on the Australian anchovy. The remaining papers were presented by scientists from CalCOFI agencies.

A stimulating and productive session resulted and most of the papers presented are made available by publication in this Report. I hope this fine collection will prove valuable to scientists everywhere.

I am particularly indebted to Gertrude M. Cutler who graciously served as Conference hostess, assisted in assembling papers, drafted illustrations, and helped wherever needed. Her assistance made a monumental task considerably easier.

Donald R. Johnson, U.S. Bureau of Commercial Fisheries, was particularly helpful in helping to contact foreign scientists and solicit their interest in the symposium.

Patricia Powell, Marine Resources Operations librarian, performed the difficult task of checking and standardizing references with her usual competence.

I am also grateful to the secretarial staff at the California State Fisheries Laboratory for the many hours spent typing and proofreading, particularly Kathleen O'Rear and Micaela Wolfe.

JOHN L. BAXTER, Editor

OCEANIC ENVIRONMENTS OF THE GENUS *ENGRAULIS* AROUND THE WORLD

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THE GENERAL AREA INHABITED BY *ENGRAULIS*

The areas where the genus *Engraulis* is known to occur are shown approximately in Figure 1. It is seen to be limited to coastal areas in general. Dr. Ahlstrom has reported spawning of *Engraulis* as far as 200 miles offshore in the California Current. This is in a particular region off southern California where the currents are such that the eggs and larvae will subsequently be brought much closer to the coast, along northern Baja California. Although eggs have been found as far as 1000 miles offshore from Japan it seems likely that these have been swept away from Japan by the Kuroshio and have little chance of surviving long enough to return to the ordinary Japanese habitat.

The genus has been found to extend to latitudes as high as 60°N and 43°S at least in summer. It is

found in all of the eastern boundary currents (California, Peru, Canary, and Benguela currents, and off western Australia) in three of the western boundary currents (Kuroshio, East Australia, and Brazil), though not in the Gulf Stream or Agulhas Current. It occurs also in the Sea of Japan, the area south of Australia, around the northern part of New Zealand, and in the Mediterranean and Black Sea. In summer it extends into the North Sea, the Baltic, and the Sea of Azov, but retreats from these areas when they become extremely cold in winter, though it does remain in the Black Sea throughout the year.

CHARACTERISTICS OF THE DIFFERENT AREAS

The eastern boundary current areas are cooler and lower in salinity than the central ocean waters at the same latitude. They are usually characterized by up-

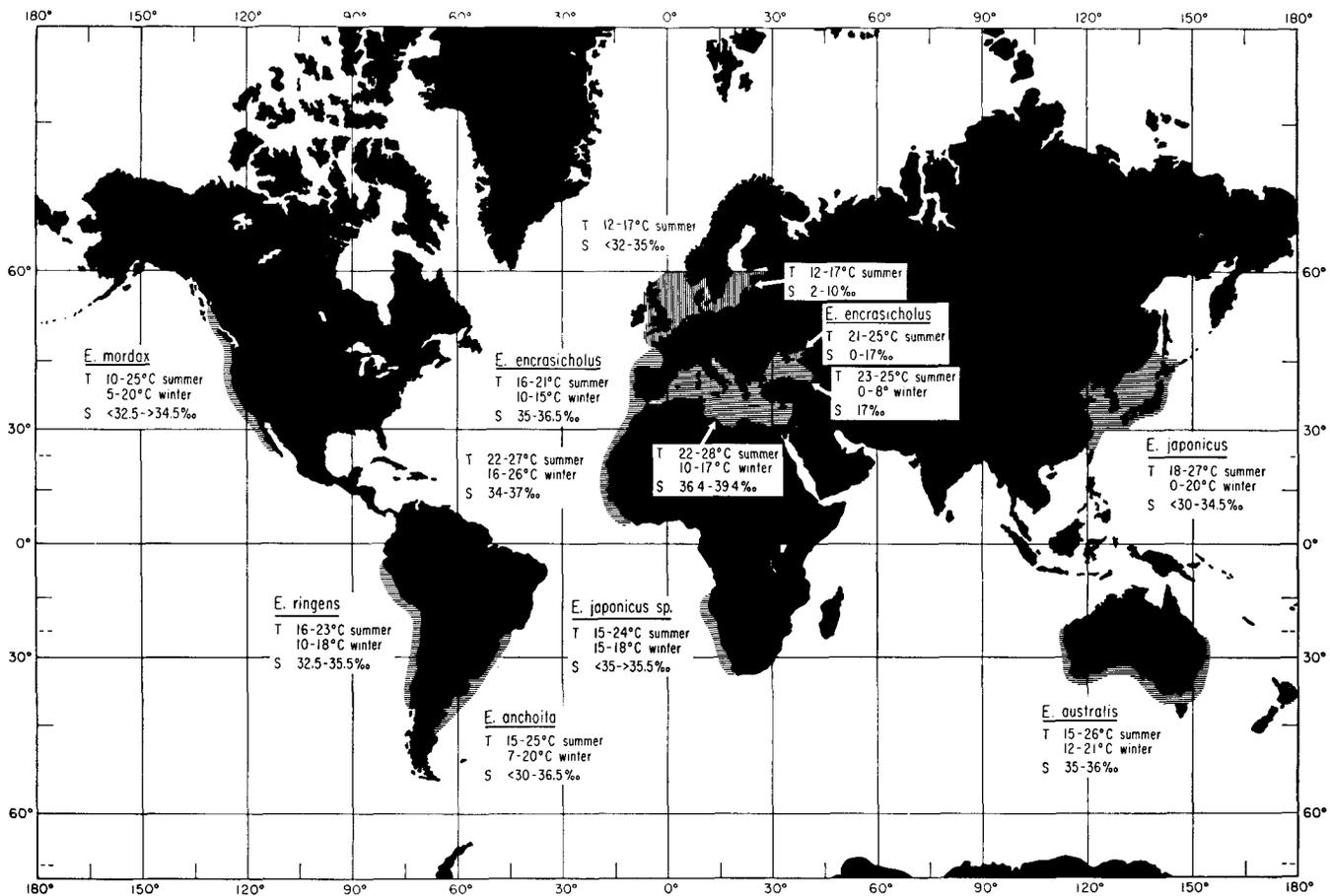


FIGURE 1. Areas inhabited by *Engraulis*.

welling in temperate latitudes and are richer in nutrients and higher in productivity and zooplankton volume than the central ocean waters. In temperate latitudes the depth of the mixed layer is notably shallower in the eastern boundary currents than further offshore.

The western boundary current areas in temperate latitudes are warmer than the central water masses. They are not so rich as the eastern boundary currents but are richer than the central ocean. Zooplankton volume is moderate. The mixed layer is much thicker than in the eastern boundary currents.

The North Sea is a tolerable environment in spite of its high latitude only because it receives some water from the south via the North Atlantic Current and the Gulf Stream: it is therefore much warmer than any other water at this latitude. It is shallow, much of it less than 100 m in depth, and fairly well mixed, so that it does not offer a wide range of properties, though the vertical mixing and advection render it fairly productive.

The Baltic is still shallower and much fresher, the salinity of the surface water decreasing almost to zero in the upper reaches and even the few deeper basins contain water of only about 12‰ at the bottom.

THE RANGE OF TEMPERATURE AND SALINITY IN THE HABITAT OF *ENGRAULIS*

The Mediterranean is a much more nearly homogeneous body of water than is the adjacent part of the Atlantic. Salinity is everywhere quite close to 38.5‰ and the temperature, except for the thin summer-warmed layer, is near to 13°C. Because of the extreme evaporation over the area the water is very saline and dense, and overturn to the bottom occurs in part of the Mediterranean. Exchange with the Atlantic occurs by outflow of saline water to the deeper part of the Atlantic, and inflow of surface water from the Atlantic. For this reason the nutrient concentration in the Mediterranean is low and productivity is generally low.

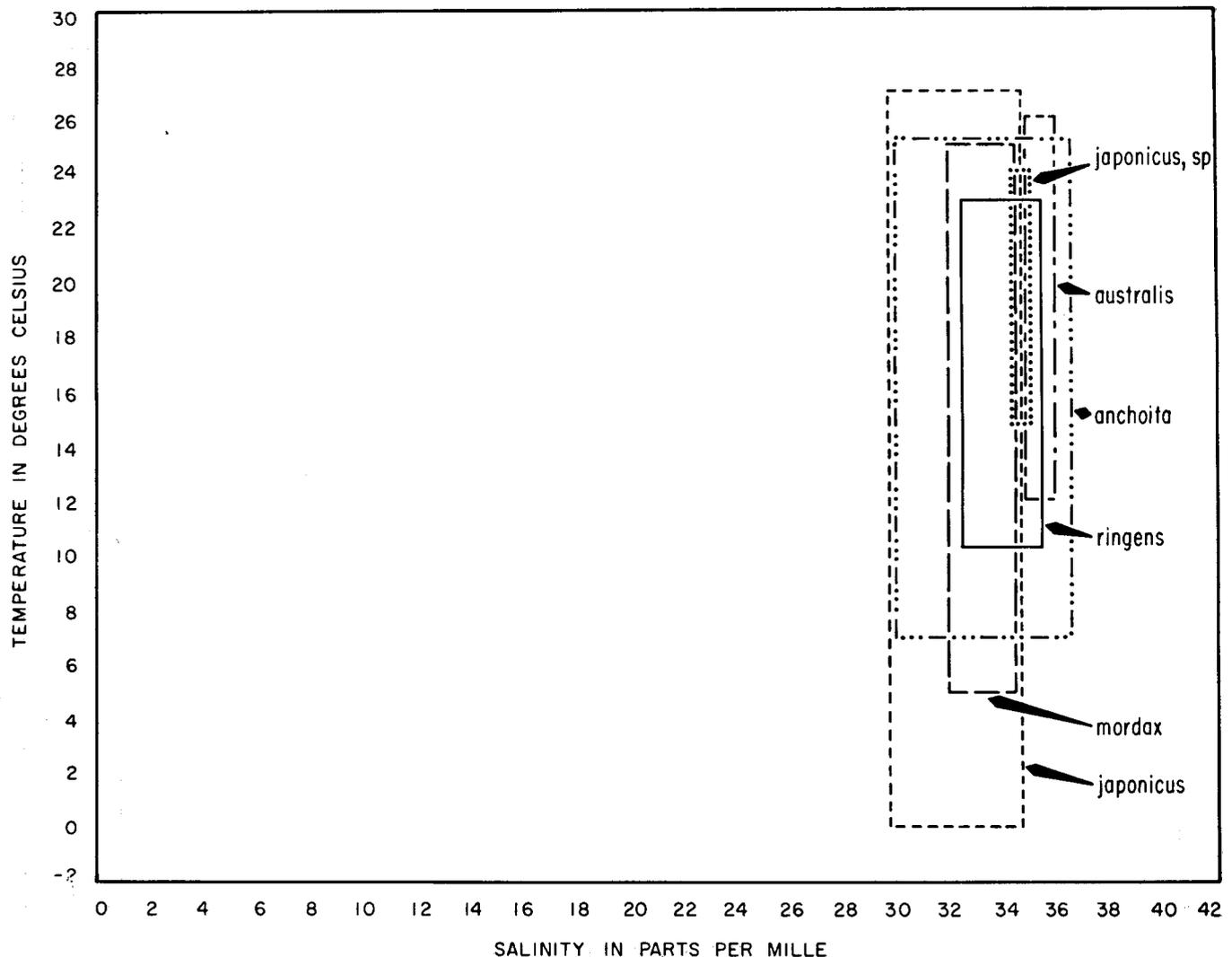


FIGURE 2. Temperature and salinity ranges of areas inhabited by *Engraulis*.

The Black Sea is the most curious habitat of *Engraulis*. Surface waters are maintained at such a low salinity that overturn to the bottom does not occur in the Black Sea, and exchange of the deeper waters with the Mediterranean is limited by the intervening sill. As a result the deeper water of the Black Sea is but slowly renewed and is devoid of oxygen below about 200 m depth: large concentrations of hydrogen sulphide are found beneath this level. *Engraulis* is therefore confined to a shallow level that is not enriched by overturn to great depth.

The Sea of Japan is fed by a flow from the south of relatively warm and saline water: this flows up the eastern boundary of the Sea, is cooled and diluted, and returns as much colder and less saline water. This and the effect of season give the Japan Sea a wide range of properties, from the freezing point in the northwestern region in winter to the warm values of the Kuroshio in the southeast in summer.

The areas inhabited by *Engraulis* include not only the oceanic areas roughly indicated in Figure 1, but

include also the very shallow inshore waters and bays, lagoons, and estuaries. The values of temperature and salinity that are shown on Figure 1 represent only the oceanic part of *Engraulis*' habitat: somewhat higher and very much lower values of salinity and temperature would appear if the inshore, non-oceanic habitats were included. Note also that for the Baltic, North, and Azov seas only the summer values are shown: apparently *Engraulis* retreats from these areas when they become very cold in winter. Surface temperatures in the Baltic are between 0 and 2°C in winter, in the North Sea between 2 and 7°C, and in the Azov Sea between 2 and 3°C. It is also noteworthy that *Engraulis* remains in the Black Sea throughout the winter when surface temperature is about 8°C.

Those figures do not take into account in any complete way the migrations, either horizontal or vertical, that *Engraulis* may make in response to seasonal changes in the environment. Therefore the values undoubtedly include a somewhat wider range

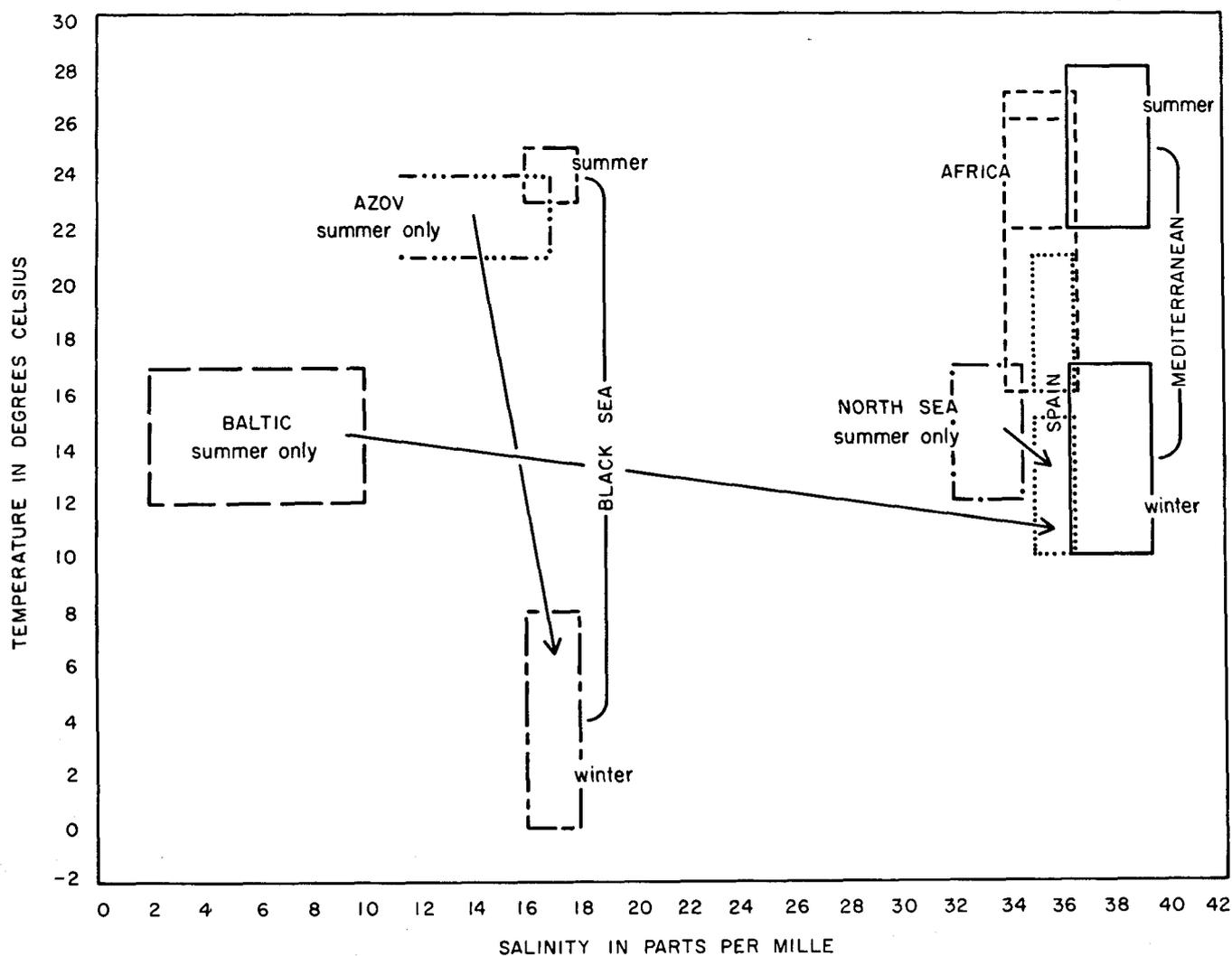


FIGURE 3. Temperature and salinity ranges of areas inhabited by *Engraulis encrasicolus*.

of temperature than the animal actually experiences. One conspicuous example of how misleading such a simple diagram might be is found in the Mediterranean. Summer surface temperatures are from 22° to 28°C and winter values are from about 10°C to 17°C. There is no overlap. On the other hand, we know that these very high surface temperatures in summer are restricted to the upper few meters, and that by being as little as 15 m beneath the surface the fish might easily find temperatures less than 22°C everywhere, even in August. This may apply in many of the other areas as well in summer, so that the upper limit of surface water temperature may not represent the temperature the fishes experience. Likewise, Dr. Hayasi reports, the fish avoid the extremely low water temperatures of the northern Sea of Japan in winter by staying in the southern area, which is much warmer. On the other hand, in some areas the winter temperatures are inescapable. Fishes in the Black Sea in winter must undergo temperatures of about 8°C: there is no warmer water anywhere in the Black Sea at that time.

On Figures 2 and 3 these open-ocean ranges of surface temperature in winter and summer are shown as rectangles with temperature as the vertical scale and salinity as the horizontal scale. In both cases the entire range of oceanic values of temperature and salinity is shown in order to emphasize the proportion of these ranges that *Engraulis* occupies. All except one of the species are included on Figure 2: *E. encrasicolus*' range is much wider and is shown separately on Figure 3.

Figure 2 would seem to indicate that the oceanic habitat of *Engraulis* comprises almost the entire range of temperature in the ocean but only a small part of the salinity range. This would be a very wrong inference indeed. Baxter (p. 110) and others have shown that *Engraulis* retreats to offshore and deeper water to avoid some extremes of temperatures; the total range, which includes extreme summer surface temperatures that the fishes may avoid by a slight submergence, and the extreme winter temperatures in the northern part of the Sea of Japan that the fish may avoid by moving a short distance to the south, may be quite misleading. On the other hand, it has also been shown that the fish do move into the quite brackish waters of bays and estuaries when the temperature is not too extreme. Therefore, all of these rectangles should extend an uncertain distance to the left on the graph to include, at least during some part of the year, waters of very low salinity indeed. This is emphasized in Figure 3 by the ranges of *E. encrasicolus*. The open-ocean values from the North Sea southward past Spain to western North Africa look very much like the ranges on Figure 2 of the other *Engraulis* species. But the ranges in the Baltic, the Mediterranean, the Black Sea and the Sea of Azov emphasize the real capability of *encrasicolus* to endure almost-fresh as well as extremely saline water and very cold water. It is apparently the seasonal change in temperature that causes them to leave the Baltic, North and Azov seas, since the salinity does not change very much with season.

Looking again at Figure 2, some of the open-ocean salinity ranges appear to be very narrow. This signifies that the total range of offshore salinity values in the *Engraulis* habitat is small, not that *Engraulis* is limited to a narrow range of salinity, since we know that it occurs in brackish waters. It appears that *Engraulis* can endure the total range of salinity encountered in the open sea, including the Mediterranean values above 39‰, but may be limited to only part of the temperature range. Various investigators who are better informed may correct me, but it seems possible that *Engraulis* may actually not experience temperatures much below 7 or 8°C, though it may experience these in many areas besides the Black Sea. Resident populations of *E. mordax* near Vancouver Island will experience 7 or 8° in winter and if *E. anchoita* and *E. encrasicolus* do not retreat completely from the Falkland Current and North Sea areas some of the individuals will undergo values of about 8°C or less.

In winter *E. encrasicolus* is found only at temperatures less than 18° and it may by a slight submergence in summer avoid temperatures more than 22°C.

Blackburn (this symposium) has shown that *E. australis* occurs only between about 10°C and 20°C, and Ahlstrom (1956) has said that most of the eggs and larvae of *E. mordax* have been taken in about that range, though some have been taken at more than 23°C. The total range of the area occupied by *E. ringens* is from about 10°C to 23°C, and this includes north to south and winter and summer: slight migrations might reduce this appreciably.

E. japonicus capensis simply has no opportunity to endure cold water: about 15°C is the lowest surface temperature he may encounter at the tip of Africa, which is only about lat. 35°S. Likewise, a population of *E. encrasicolus* that remains in the Mediterranean may not find water colder than 10°C at any time of year.

CONDITIONS LIMITING ENGRAULIS

We may speculate, then, that *Engraulis* is not limited by the salinity values encountered in the ocean or in estuaries: it not only occurs but spawns in regions of very low as well as very high salinity. We may speculate also, at least until the other speakers correct me, that *Engraulis* is limited by temperature, since it does not appear in either the coldest or the warmest oceanic conditions. Perhaps a range from 6°C to 22 or 23°C would include all, or nearly all, of its actual occurrences. This would account for its limited latitudinal range and for its most striking migrations from the Baltic, North, and Azov seas, whereas salinity variations would not.

This really does not add very much to what most of you know already, and it does not by any means specify the habitat of *Engraulis*. By this I mean to say that there is a vast area of ocean with surface temperature between 6°C and 22°C—about $\frac{2}{3}$ of the world ocean, in fact—but that *Engraulis* inhabits, so far as we know, less than $\frac{1}{10}$ of this area. Therefore temperature alone cannot define the habitat of *Engraulis*.

What are some of the other quantities that might be important to *Engraulis*, and that might explain their absence from other areas that seem to have the proper temperature and salinity?

First, it appears to be a coastal genus. Such information as I have got so far indicates that although eggs and larvae are sometimes found some hundreds of miles offshore they are definitely tied to a coastal population—that is, they do not appear in areas separated from the coast. I do not know how to interpret this. I have consulted several biologists and have concluded that there is no single, generally accepted explanation as to what there is about coasts that appeals to some nekton.

It is true that most coastal regions are somewhat more productive than the offshore temperate-zone areas, but the genus can inhabit the Mediterranean, where productivity is fairly low. The region near the equator and at some distance west of South America fits the temperature requirements of *Engraulis* and is extremely productive, yet *Engraulis* does not appear to be found any great distance offshore there. Likewise there are other offshore temperate-zone areas of relatively high productivity such as the region around lat. 45°N in the Pacific that *Engraulis* does not inhabit. Therefore temperature and productivity are not enough for *Engraulis*: there has to be a coast nearby—perhaps some place where the bays, lagoons or estuaries or the inshore countercurrents and tur-

bulence may provide a firm foothold for a population, so that it is not swept entirely away by the prevailing currents, as it might be in the truly pelagic areas.

Having accepted coasts and a particular temperature range as requirements for *Engraulis*, whether we can explain the relation or not, we have eliminated most of the ocean as habitable areas for *Engraulis*. We find that what is left, that is, coastal waters with temperature ranges between about 6° and 22°C, is in fact inhabited by *Engraulis* except for one conspicuous omission: the eastern coast of North America. In August the temperature range from 6° to 22°C is found between Labrador and New York, in February between New York and Cape Hatteras. The area of overlap is small but so is it in some of the other habitats: a minor amount of seasonal migration could keep *Engraulis* at optimum temperatures throughout the year in this general region. If inshore habitats are required this coast has plenty of estuaries and sounds that would seem to compare favorably with those of the other coastal areas inhabited by *Engraulis*; I cannot offer any speculation as to why *Engraulis* does not inhabit this area.

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SYNOPSIS OF BIOLOGICAL INFORMATION ON THE AUSTRALIAN ANCHOVY *ENGRAULIS AUSTRALIS* (WHITE)

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INTRODUCTION

Engraulis australis (White), sometimes known as the Australian anchovy, was investigated by the writer in Australia at various times and places between 1937 and 1948. The work was done as opportunities offered in the course of other duties. It was generally hard to obtain material because the annual commercial catch is only 50 to 100 tons, although it could be much higher if a good demand existed for the fish.

Most of the information was published in two papers (Blackburn 1941, and especially Blackburn 1950a).

The present paper summarizes the facts and interpretations presented in the former papers, and the very few observations on *E. australis* in Australia that have been published since 1950, and adds a little new information. There appear to have been no detailed studies of occurrences of the same species in New Zealand.

IDENTITY

The adult *E. australis* was well described and figured by McCulloch (1920), who listed most prior references. Blackburn described the eggs and larvae

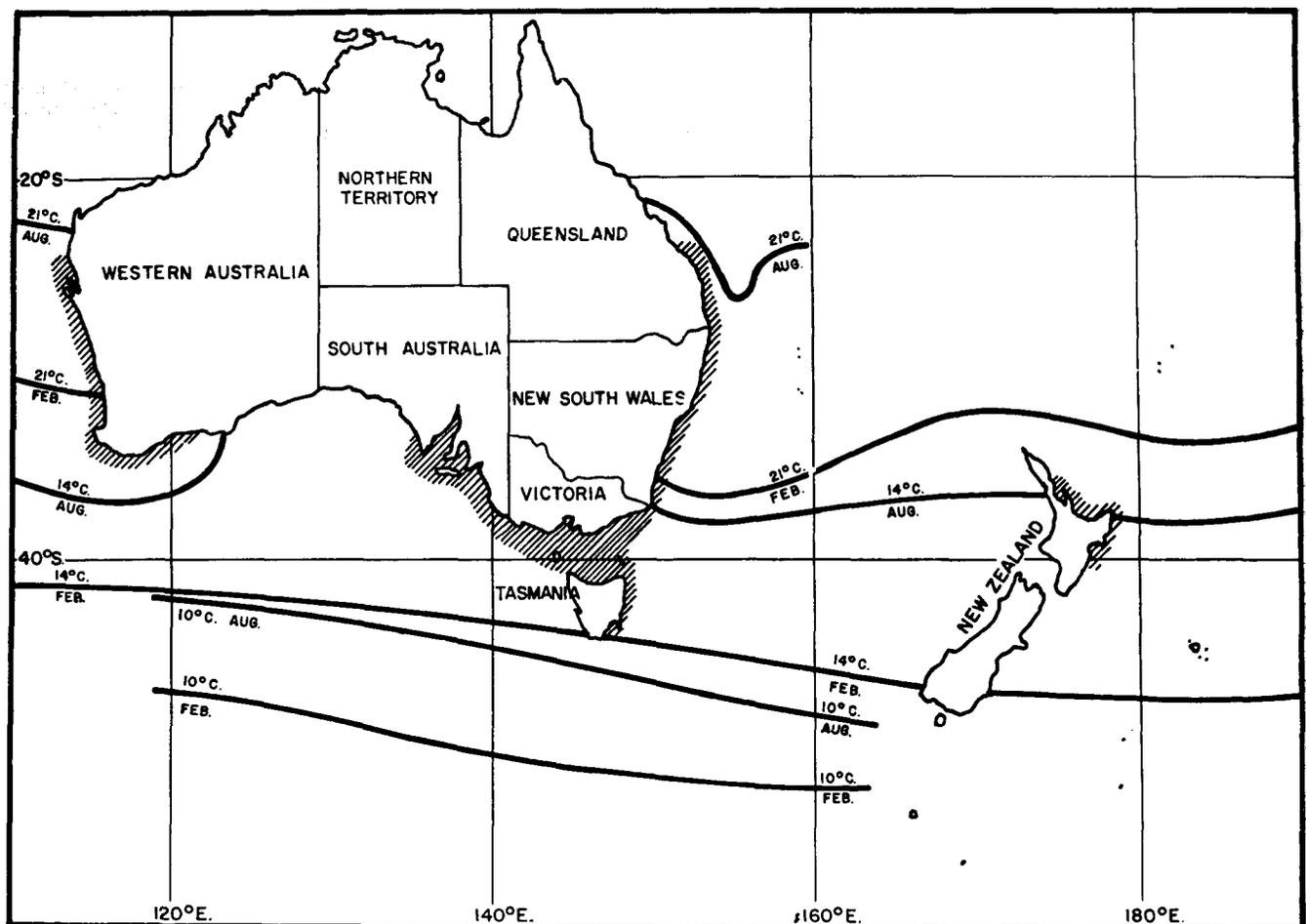


FIGURE 1. Known range of *Engraulis australis* (hatched areas), and mean positions of certain surface isotherms in February and August, in waters near Australia and New Zealand.

(1941) and listed additional references (1941, 1950a). The species falls in the genus *Engraulis* as defined by Jordan and Seale (1926) and Hildebrand (1943). It is the only engraulid species known to occur in Australian waters south of 28° S. latitude, and the only one in New Zealand waters; it is not known from tropical Australian waters, although several species of other engraulid genera occur there, or from any of the smaller islands near Australia and New Zealand.

SPATIAL DISTRIBUTION

E. australis has been found along most sections of the Australian coast south of the Tropic of Capricorn (Blackburn 1950 a), as shown in Figure 1. The range

in latitude is from 23° to 43° S. The species is unrecorded from the west coast of Tasmania and from a section of coastline near the South Australia-Western Australia border, but this probably reflects the comparative lack of human settlement, fishing, and marine investigations in those regions, rather than absence of the fish. For similar reasons, the distribution along the coast of New Zealand is probably more extensive than that recorded in the literature (Blackburn 1941) and shown in Figure 1.

Along the coasts where it occurs, *E. australis* inhabits estuaries, bays, and open waters over the generally narrow continental shelf; a few larvae have been taken in plankton hauls over the continental slope, and nothing is known of any occurrences

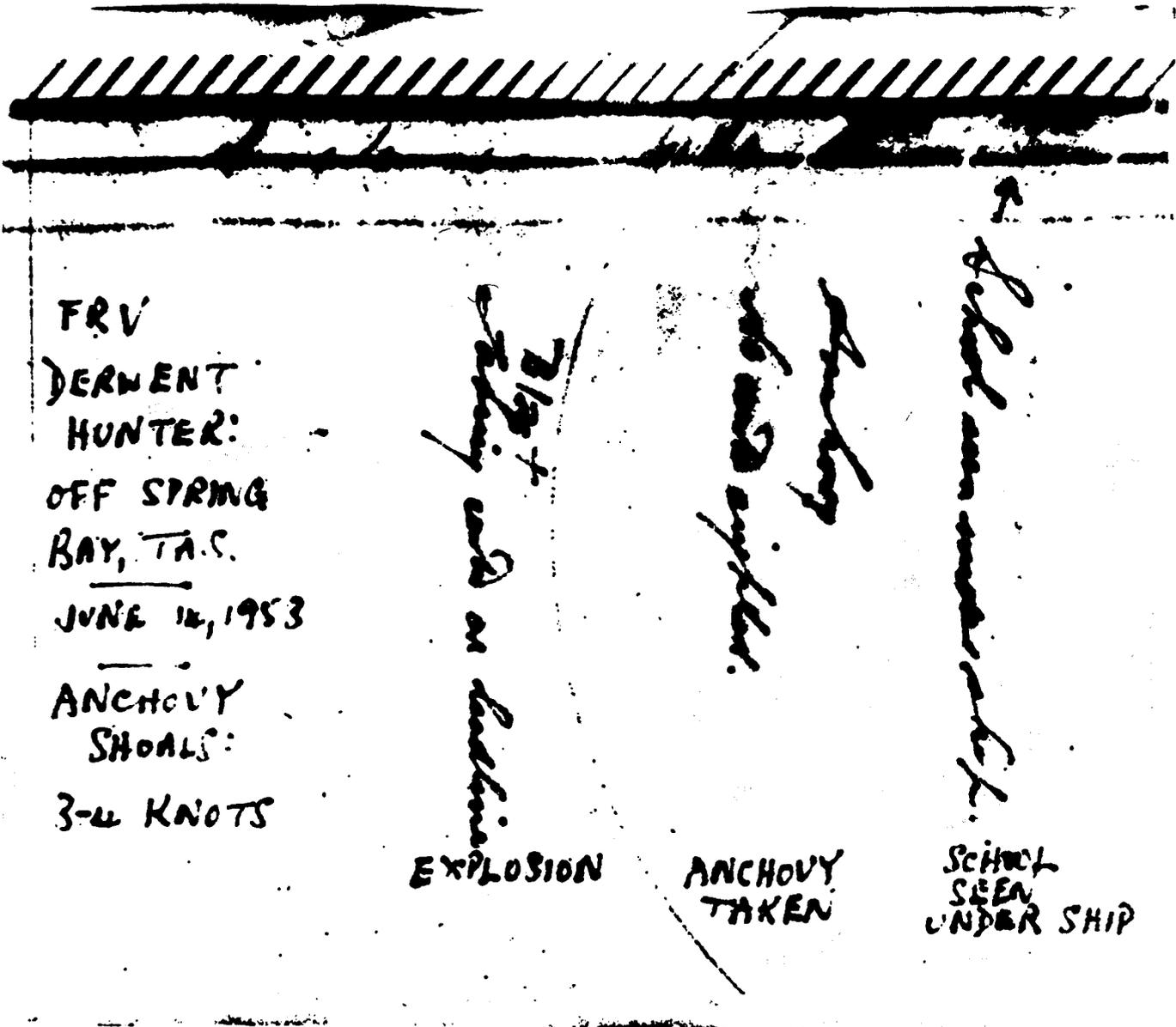


FIGURE 2. Echogram of schools of *E. australis* in 20 m of water off Spring Bay, Tasmania. Time scale across top is in minutes; ship speed was 3 to 4 knots; identification was made from fish killed by exploding TNT in the school.

further offshore (Blackburn 1941, 1950 a). There is no reliable information about the vertical distribution of *E. australis* in the sea. It is found frequently in the stomachs of large scombriform fish hooked at the sea surface (Blackburn 1950 a), but not at all in the stomachs of *Neoplatycephalus macrodon*, which is one of the most abundant and active demersal fishes of continental shelf waters over 50 m (Fairbridge 1951); this suggests that it is much commoner near the surface than near the bottom, in those waters. In shallower waters, such as 20 m, echograms show that the species can occur from top to bottom (Figure 2).

Charts of surface temperature and salinity from various sources (Schott 1935; U.S. Navy Hydrographic Office 1944; U.S.S.R. Ministry of Defense 1953; Muromtsev 1958; Rochford 1962) have been compared with the general spatial distribution of *E. australis* (Figure 1) and the seasonal changes that occur in it. This showed that the species tolerates temperatures at least from 10 to 21° C.; it may encounter temperatures up to 25° C. if it occurs in surface waters as far north in summer as it does in winter, but this is not certain; it probably encounters 9° C. in certain inshore waters in winter, but this also is not certain. The same comparison shows a tolerance of salinities from about 35.1 to 35.8‰, but data obtained from various inshore waters, at times and places where anchovies occurred, indicate that the range is actually from about 2 to 37‰ (Blackburn 1950 a, Gippsland Lakes rivers; Rochford 1957, St. Vincent's Gulf). The range of breeding temperature was investigated by comparing seasonal temperature data (including those for bays and estuaries in various volumes of the Australian "Oceanographical Station List") with information on spawning places and seasons; this range is at least 14 to 20° C. and possibly includes 13° C.

The above-mentioned temperature ranges for *E. australis* are almost the same as those for the Australian sardine, *Sardinops neopilchardus*, which has an almost identical distribution along the Australian coast (Blackburn 1960 and references). The sardine is not known to occur in waters of salinity below about 33.5‰, however, and thus it is not estuarine, whereas the anchovy is. Another difference in spatial distribution between the two species is obvious when their relative abundances are compared within different parts of their common total range of distribution (including saline bays and gulfs where both species occur); to the north of about 37° S. latitude the sardine is more abundant than the anchovy (shown mainly by differences in numbers of larvae, as there are no good data for eggs or adults of the anchovy; Blackburn 1941); to the south of 37° S. the anchovy is more abundant than the sardine (shown by differences in numbers of eggs and larvae, and general scarcity of adult sardines; Blackburn 1950 a, 1950 b, 1957).

INTRASPECIFIC POPULATIONS

Blackburn (1950 a) presented and analyzed the total vertebral counts, including urostyle, of 5,804 *E.*

australis from 21 localities around the Australian coast. Analysis of variance indicated that significant differences existed between vertebral count means for certain localities, and the variability was further investigated by the graphical method of Hubbs and Perlmutter (1942).

Figures 3 and 4, from Blackburn (1950 a), show the result. The localities listed in Figure 3 appear in the order in which they occur around the Australian coast, from north-east (top) to south-west (bottom). With one exception (Gippsland Lakes rivers, discussed below) the means fall clearly into eastern, southern, and western groups which were given subspecific names (*E. a. australis*, *E. a. antipodum*, and *E. a. fraseri*, respectively). The locality-means in the eastern group show a cline with means increasing from north to south (28 to 36° S. latitude, 43.1 to 44.0 vertebrae). Means in the western group are numerically similar to those of the eastern group at similar latitudes, and suggest a similar cline. The existence of clines, whether north-south or east-west, is doubtful in the means of the southern group; these means are all at least one vertebra higher (45.1 to 45.8 vertebrae) than any of the means of the other two groups, and this difference is statistically highly significant. Some of the differences between means within each group are significant.

The Gippsland Lakes are situated on the east coast of the state of Victoria. As shown in Figure 5 (left inset), this is a system of three rivers entering a coastal lagoon or lake which is permanently open to the sea. *E. australis* occurs in the sea outside the entrance, at the entrance, in the lake, and in the rivers (Blackburn 1950 a). Samples sufficient for vertebral count study were available only from the entrance (salinity about 35.5‰) and the rivers (salinity about 2‰), and these two localities are distinguished in Figure 3. The river fish have a mean about two-thirds of a vertebra lower than the mean for the entrance, a highly significant difference. This finding resembles that of Hubbs (1925) for *Engraulis mordax* in San Francisco Bay, California.

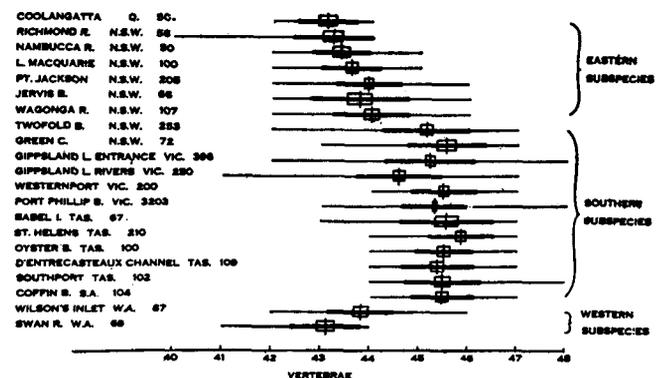


FIGURE 3. Summary of data on vertebral counts of *E. australis*. Numbers at the left are numbers of counts from different localities. The horizontal line for each sample is the range, the vertical cross-bar is the mean, the thickened portion of the line is one standard deviation on each side of the mean, and the hollow rectangle is twice the standard error on each side of the mean (from Blackburn 1950a).

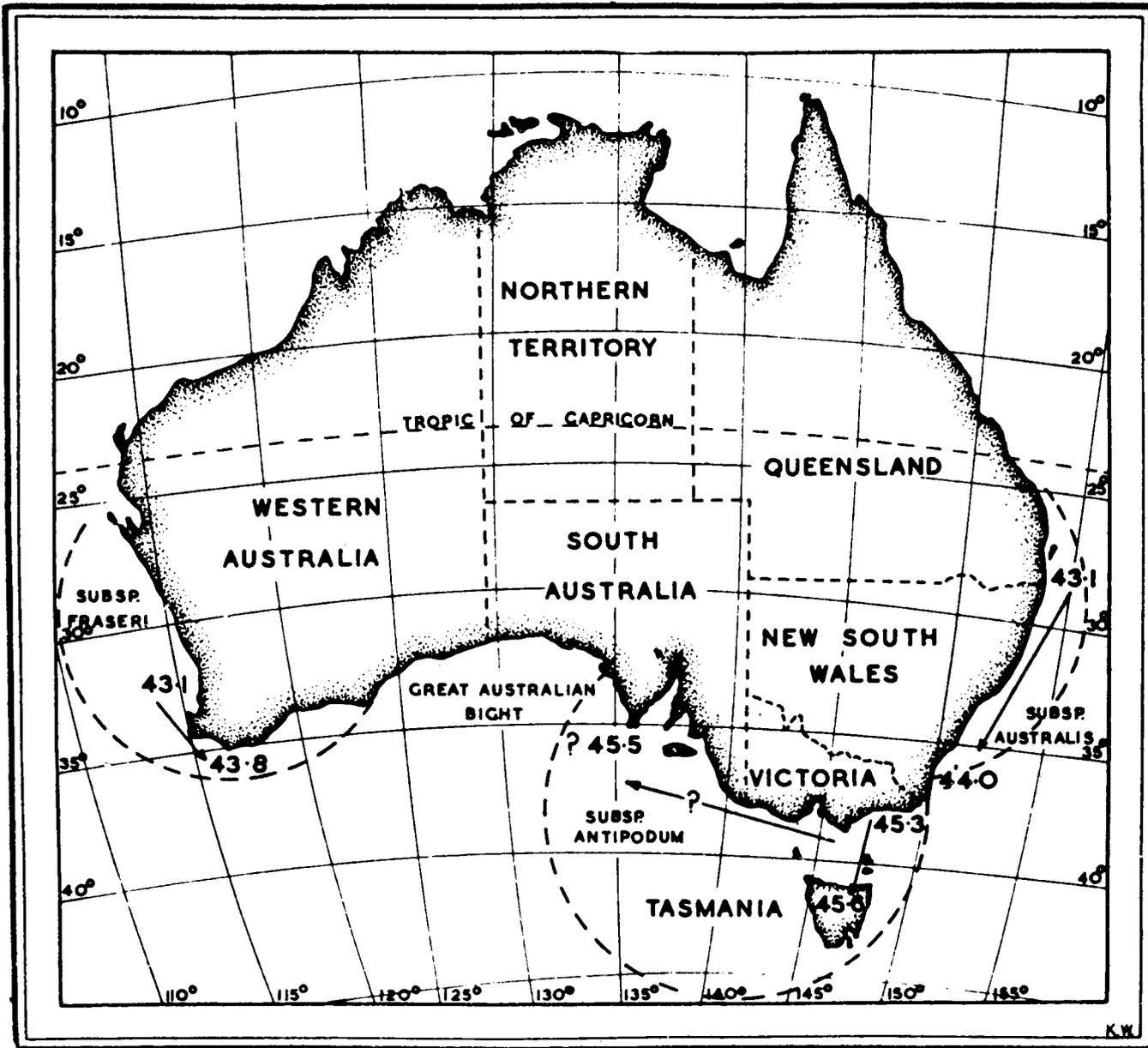


FIGURE 4. Approximate disposition of subspecies of *E. australis* in Australian waters, based on data in Figure 3. Arrows indicate clines in mean vertebra numbers (from Blackburn 1950a).

Although these various differences in mean vertebra number may be phenotypic rather than genotypic, their size and geographical distribution (and, for some well-studied localities, their consistency over many years) indicate that *E. australis* is a complex of different local, at least partly segregated, groups. There are three major groups (two of them morphologically similar, but separated geographically by a third which is morphologically different); within these, minor, less well differentiated, groups occur.

GROWTH

Growth in length was investigated by scale-reading and inspection of length frequency distributions

(Blackburn 1950 a). These studies were reasonably adequate only for Victorian fish (members of the southern subspecies), for which about 21,000 length measurements, and scales from 450 fish, were available and useful. Samples from the other five states yielded scales from 314 fish, and about 12,000 lengths which were obtained too irregularly to be useful for length-frequency studies. The deciduous nature of the scales limited the amount of scale material available, especially for small fish.

About three scales, all taken from the flank in the region of the dorsal fin, were usually read for each fish. The appearance of scales from this region is shown in Figures 6, 7, 8, and 9 (from Blackburn

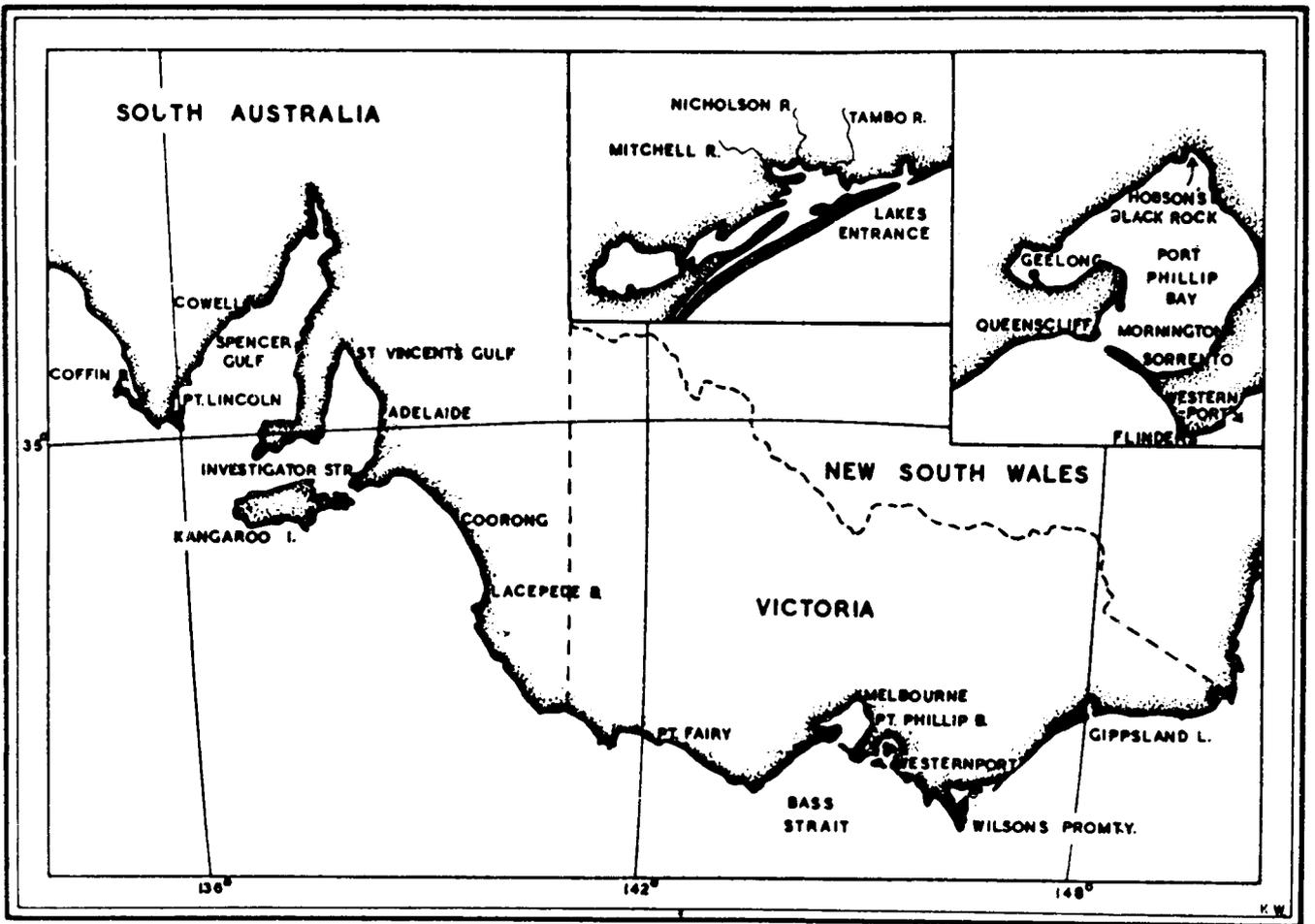


FIGURE 5. Map showing localities mentioned in the text, with Gippsland Lakes and Port Phillip Bay in insets (from Blackburn 1950a).

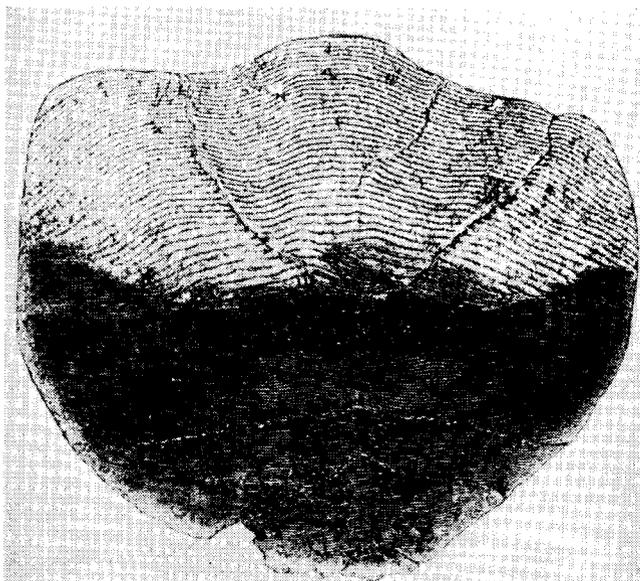


FIGURE 6. Scale from *E. australis* of standard length 64 mm taken in March, with first zone of crowded striae forming at the anterior edge (from Blackburn 1950a).

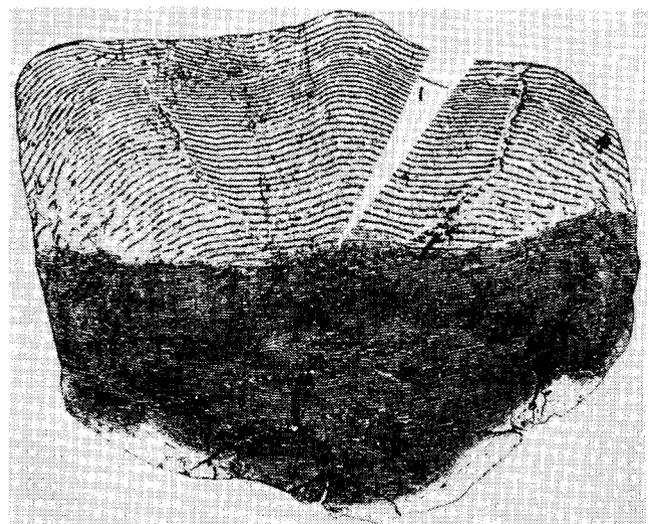


FIGURE 7. Scale from *E. australis* of standard length 64 mm taken in November, with first zone of crowded striae completely formed and succeeded by a zone of more widely spaced striae (from Blackburn 1950a).

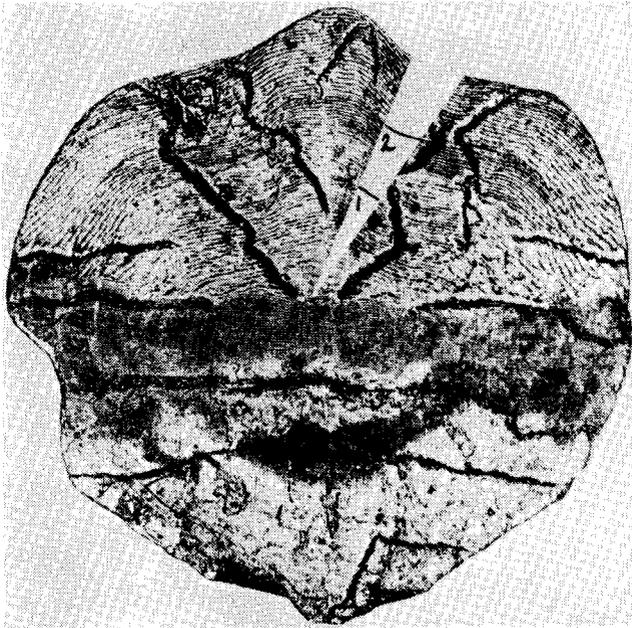


FIGURE 8. Scale from *E. australis* of standard length 75 mm taken in June, with third zone of crowded striae forming at the anterior edge (from Blackburn 1950a).

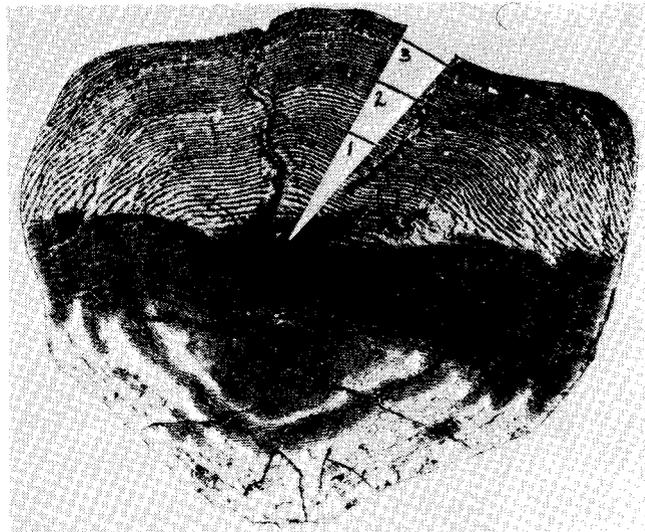


FIGURE 9. Scale from *E. australis* of standard length 81 mm taken in October, with third zone of crowded striae completely formed and succeeded by a zone of more widely spaced striae (from Blackburn 1950a).

1950 a); the embedded anterior portion is shown uppermost. The striae on the anterior portion are semi-concentric; they run parallel to the anterior edge of the scale and obliquely towards the lateral edges. In the region where they lie parallel to the edge, bands of widely spaced striae alternate with bands of narrowly spaced striae, in a way reminiscent of a salmonoid scale pattern.

It can be shown that this pattern is annual, and that the period at which the striae become most crowded is in winter. For instance, Figure 6 shows a March scale on which the striae are becoming crowded along the anterior edge, and Figure 7 shows a November scale on which a similar zone of crowded striae has been succeeded by one of widely spaced striae. A similar comparison may be made for the outermost zone of crowded striae in Figure 8 (June) and Figure 9 (October). Further information was given by Blackburn (1950 a). Each zone of crowded striae was therefore considered to represent one winter of life, with very few exceptions. Other apparently periodic features of the scale pattern might have been used, but were not, to indicate the age (e.g., the zones of interrupted, branched, or fragmented striae which occur more or less parallel to the scale sides).

Table 1, from Blackburn (1950 a), shows the frequency of occurrence of different numbers of winter "rings" (zones of crowded striae) in successive length-groups of fish; the lengths are standard lengths, snout tip to end of body excluding caudal fin (this applies to all lengths mentioned in this paper); 4.5 cm means 45 to 49 mm inclusive, and other length-groups likewise. Table 1 gives a general idea of the growth-rate of the Victorian *E. australis*;

TABLE 1

ENGRAULIS AUSTRALIS, VICTORIAN SPECIMENS, RECORDED BY NUMBER OF ANNUAL (WINTER) SCALE-RINGS AND STANDARD LENGTH OF FISH; FOR FURTHER EXPLANATION SEE TEXT. (FROM BLACKBURN 1950a).

Length-group (cm.)	0 Rings	1 Ring	2 Rings	3 Rings	4 Rings	5 Rings	6 Rings	Uncertain	Total
4.5	3	--	--	--	--	--	--	--	3
5.0	2	5	--	--	--	--	--	--	7
5.5	--	13	4	--	--	--	--	--	17
6.0	--	25	21	--	--	--	--	1	47
6.5	--	8	35	4	--	--	--	1	48
7.0	--	2	34	10	--	--	--	--	46
7.5	--	3	37	11	1	--	--	1	53
8.0	--	--	10	9	6	--	--	2	27
8.5	--	1	6	16	1	--	--	3	27
9.0	--	--	2	14	8	2	--	--	26
9.5	--	--	1	16	15	4	--	10	46
10.0	--	--	--	8	15	2	--	15	40
10.5	--	--	--	1	13	7	--	16	37
11.0	--	--	--	--	5	8	--	9	22
11.5	--	--	--	--	1	--	1	2	4
								Total	450

it is shown below that the fish are hatched in summer, so they are about 0.5 year old at the first ring, 1.5 years at the second, etc.

More precise information was obtained by calculating the successive intermediate lengths of the fish (L_1 , L_2 , etc.) at the times when the successive zones of crowded striae (first, second, etc.) were completed. Such calculations required knowledge of the relationship between the fish-length and the radius of the scale selected for measurement, which was investigated empirically as shown in Figure 10. Fish-length and scale-radius increase in direct proportion only above a fish-length of 60 mm; at fish-lengths between 35 and 60 mm the scales, which may have one or two complete winter zones, grow faster than the fish. The calculations of L_1 , L_2 , etc., were described by

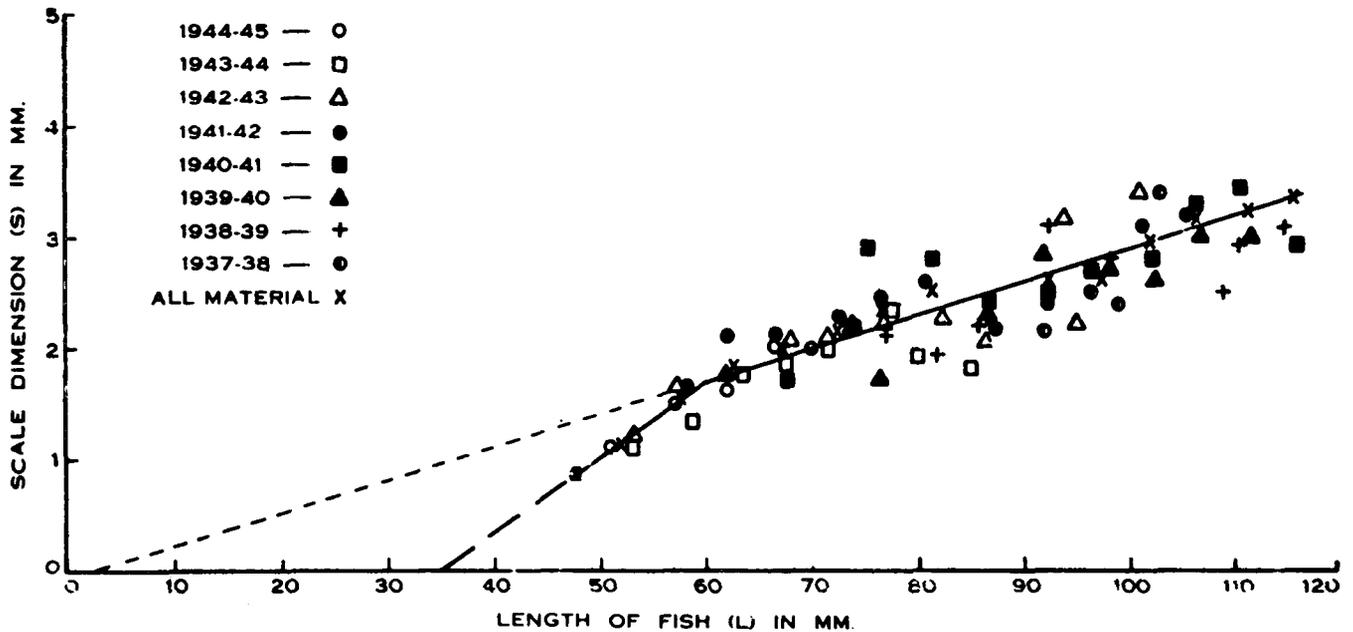


FIGURE 10. Relationship between standard length of fish and scale radius in Victorian specimens of *E. australis*. All scales were taken from the same part of the fish and measured in the same way. Regression lines are based on the material of all year-classes combined. For further explanation see text (from Blackburn 1950a).

Blackburn (1950 a), who analyzed the values in various ways exemplified by Table 2 (where L is actual fish-length at capture).

Table 2 shows that intermediate lengths are consistently higher in younger age-groups than in older; it is believed that this is a result of over-representation of comparatively large fish in the samples of the younger age-groups from which scales were available, because scales are more deciduous in small fish than in large; consequently, it is believed that the L_n means from the older age-groups are the most reliable. The best available estimates of mean $L_1, L_2, L_3, L_4,$ and L_5 are therefore 53, 65, 77, 93, and 104 mm for Gippsland Lakes fish; $L_1, L_2,$ and L_3 are slightly lower (50, 62, and 74 mm) for fish of Port Phillip, which is a saline bay about 170 miles west along the Victorian coast

from Gippsland Lakes. These data are quantitatively meager but qualitatively very good. They may be combined to give the following estimates of mean length of Victorian anchovies at successive ages:

- 0.5 years— 50 mm
- 1.5 years— 62 mm
- 2.5 years— 75 mm
- 3.5 years— 90 mm
- 4.5 years—102 mm

No estimate is given for 5.5 years because only one fish of that age, and none that were certainly older, was found. The greatest length recorded for *E. australis* is 136 mm, so older fish may well exist.

These findings agree fairly well with those of Table 1, in which allowance must be made for growth in

TABLE 2

***E. AUSTRALIS*, VICTORIAN LOCALITIES: MEANS OF CALCULATED INTERMEDIATE LENGTHS ($L_1, L_2,$ ETC.) FOR SUCCESSIVE AGE-GROUPS, WHERE n IS NUMBER OF FISH AND L IS THEIR MEAN LENGTH AT CAPTURE; FOR FURTHER EXPLANATION SEE TEXT. (FROM BLACKBURN 1950a).**

Age Group	L_1			L_2			L_3			L_4			L_5		
	Mean L_1	Mean L	n	Mean L_2	Mean L	n	Mean L_3	Mean L	n	Mean L_4	Mean L	n	Mean L_5	Mean L	n
A. Port Phillip Bay	1	55.87	61.40	32	--	--	--	--	--	--	--	--	--	--	--
	2	54.07	71.60	101	70.42	75.11	43	--	--	--	--	--	--	--	--
	3	52.23	78.23	26	65.60	78.24	25	75.67	79.00	6	--	--	--	--	--
	4	49.91	86.73	11	61.91	86.73	11	73.82	86.73	11	101.00	103.00	1	--	--
B. Gippsland Lakes	1	53.00	68.00	1	--	--	--	--	--	--	--	--	--	--	--
	2	56.21	83.14	14	72.00	83.25	12	--	--	--	--	--	--	--	--
	3	53.35	92.35	46	68.65	92.25	48	85.04	93.46	30	--	--	--	--	--
	4	53.23	100.48	48	66.50	100.71	44	84.91	100.76	46	96.59	103.00	22	--	--
	5	53.00	104.58	17	64.93	104.40	15	77.27	103.60	15	92.82	104.31	16	104.20	110.00

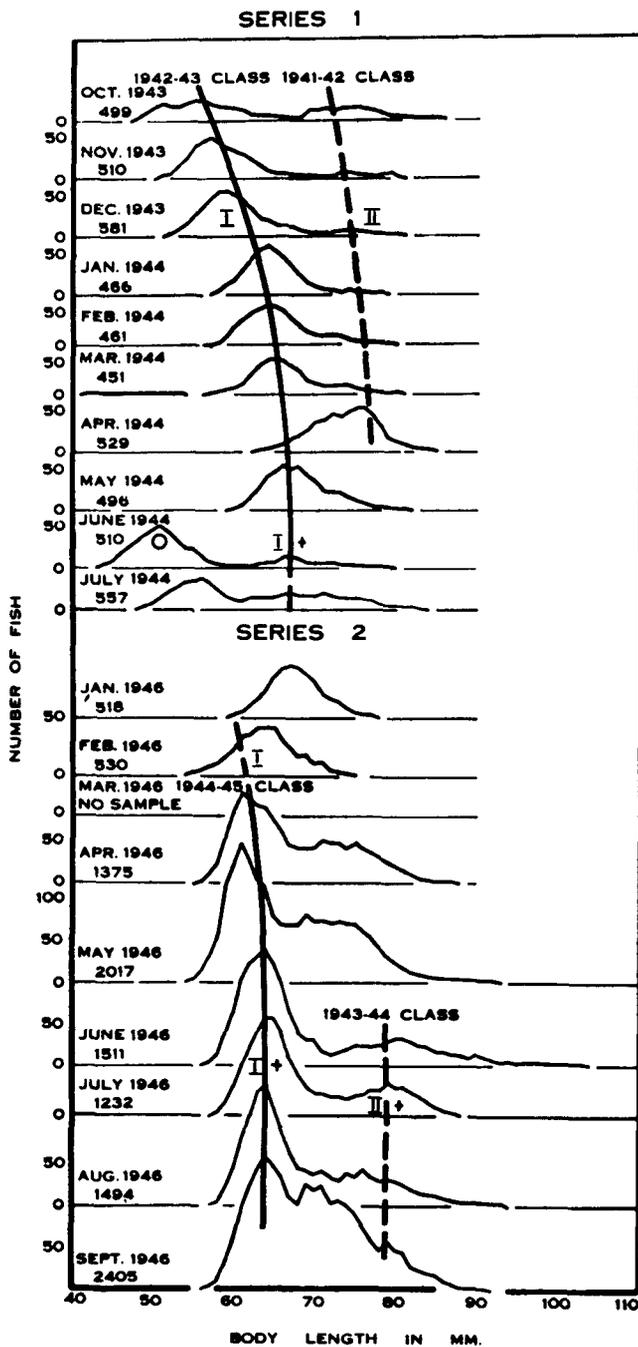


FIGURE 11. Length frequency polygons by months, two series for *E. australis* from Port Phillip Bay, Victoria. All samples in series 1 are from the head of the bay; in series 2 the January and February fish, and those from the younger age-group in later months, are from the head of the bay, and the others are from localities closer to the sea (from Blackburn 1950a).

length subsequent to "ring" formation on the scales. They also agree with length frequency data from Port Phillip, which are mainly for fish under three years of age, and some of which are shown in Figure 11 (Blackburn 1950 a). Figure 11 shows that most growth occurs in spring and summer, and none in winter. Scales read from anchovies obtained from

other Australian states gave results which were less reliable, but on the whole consistent with the findings for Victoria.

REPRODUCTION

Gonad maturity stages of *E. australis* were described by Blackburn (1950 a). The running ripe stage was not found, so estimates of length at first maturity were based on frequency of occurrence of "full", "spent", and "recovering" gonads in fish of successive length-groups. This showed that virtually all fish of both sexes become sexually mature at one year of age (about 6 cm) in Victoria. Data from Tasmania were consistent with this result, and those from other states were too scanty to justify a conclusion.

Spawning seasons and areas were identified by studying the distribution of advanced gonad stages in samples of fish old enough to be mature, and the distribution of eggs and larvae in plankton catches. The results (Blackburn 1941, 1950 a; Kott 1955) may be summarized as follows.

Southern subspecies.—Spawning occurs from October through April with a peak in summer, mostly in bays and estuaries and to a much less extent in open sea waters over the continental shelf.

Eastern subspecies.—The data are not nearly as good as for the southern subspecies. The peak spawning season in the southernmost part of the range is the summer, like that for the adjacent southern subspecies, but it appears to become progressively earlier, through spring and probably into late winter, in successively more northern areas. In the southern part of the range there is some spawning both in inlets and in the open sea, as with the southern subspecies; it is difficult to say which of these habitats is the more important for spawning in that region, but farther north, especially in Queensland, the inlets appear to be quite unimportant as spawning places compared with the sea.

Western subspecies.—The information is very scanty; all of it concerns gonad stages in inlet fish from the southern end of the range, and points to a summer peak of spawning.

CHANGES IN DISTRIBUTION WITH AGE AND SEASON

The following observations (Blackburn 1950 a, 1957) have been made on the southern subspecies, for which the best data on occurrence, growth, and reproduction are available.

1. In Port Phillip, anchovies under two years of age are most common at the head of the bay and older fish are most common closer to its mouth (e.g., Figure 11). No similarly detailed studies of distribution of age-groups were made in any other bays or estuaries.

2. Along the Victorian and Tasmanian coasts, anchovies of various sizes, but mainly large enough to be two and a half years or older, occur in the sea outside the inlets in the winter months. They are much less

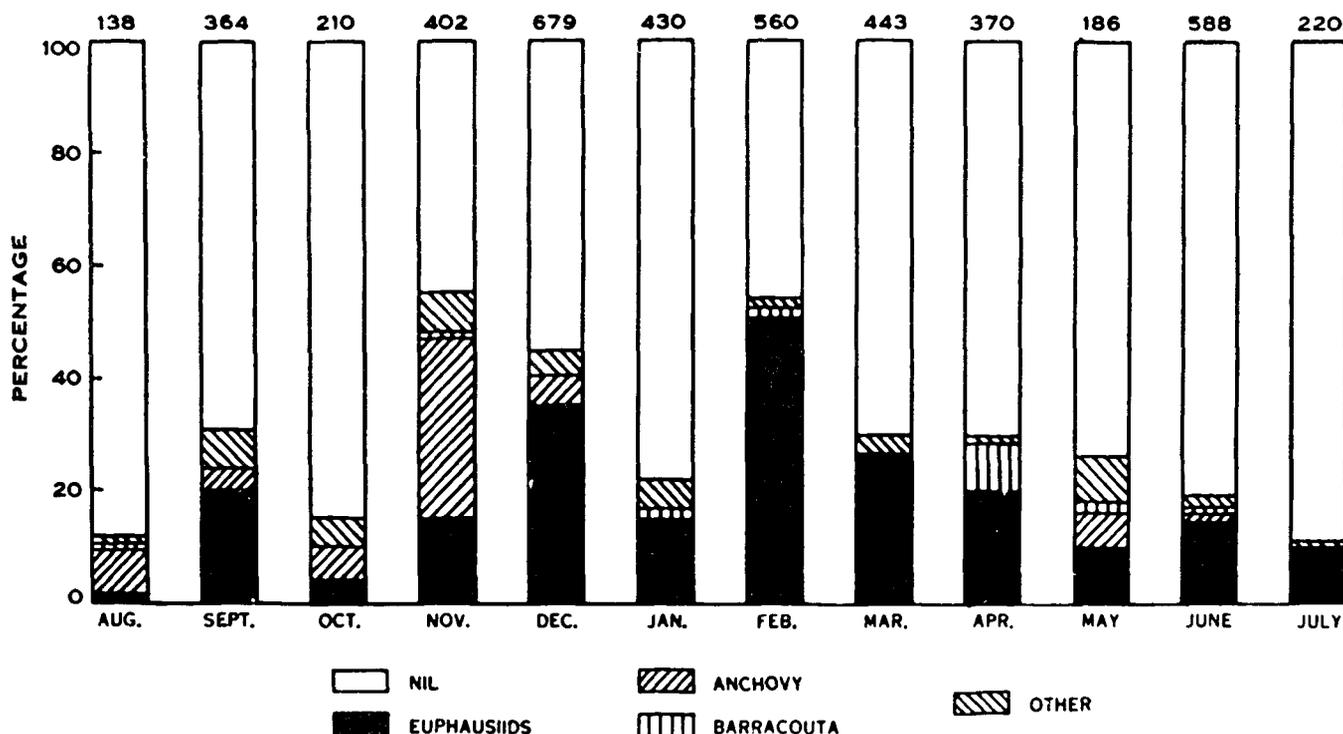


FIGURE 12. Percentage classification, according to contents, of stomachs of the gempylid fish *Thyrsites atun* taken along the south coast of Victoria in different months. Numbers of stomachs are above the columns. Anchovy means *E. australis*. For further explanation see text (from Blackburn 1957).

common there in summer. The best evidence for this statement is the seasonally changing representation of *E. australis* in the diet of the gempylid fish *Thyrsites atun*, which was studied by Blackburn (1957 and references there). This species occurs and is fished along the coasts close to land, but is not common at fishable sizes in bays. Figure 12 shows, for a section of the Victorian coast on to which Port Phillip and other inlet waters open, that *T. atun* feeds on *E. australis* from May through December, but not from January through April. Reports of anchovy schools at sea, by fishermen, indicate a similar pattern of seasonal change.

3. Schools of *E. australis*, of the sizes mentioned in the preceding paragraph, have been seen approaching and going through the entrances of Gippsland Lakes, Port Phillip, and Westernport (Victoria), from the sea, in the spring months. Records of similar schools going out to sea are lacking, however.

4. Anchovies of the sizes just mentioned are much more abundant in bays than in the sea in the summer, which is the spawning period. Some fish of these sizes remain in the bays in winter.

These observations reveal a tendency, increasing with age, for some *E. australis* of the southern subspecies to move each year from the inlets to the sea (probably in autumn) and back again (in spring). The inlets become colder than the sea in autumn and warmer than the sea in spring (e.g., Garner 1954, Port Phillip). The older anchovies may therefore be displaying positive thermotaxis.

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A NOTE ON THE BIOLOGY AND FISHERY OF THE JAPANESE ANCHOVY *ENGRAULIS JAPONICA* (HOULTUYN)

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INTRODUCTION

One of the most prolific groups of fishes in the Japanese fisheries has been *iwasi* which comprises three clupeoid species including the sardine, *Sardinops melanosticta* (Temminck & Schlegel), round herring, *Etrumeus micropus* (Temminck & Schlegel), and anchovy. These three species have been caught by various types of fishing methods in almost all of the coastal waters around Japan, not only at stages after metamorphosis but also at postlarval stages under a commercial name of *sirasu*, in combination with a few related fishes (Hayasi 1961). The total catch of *iwasi* reached 1,130,000 metric tons, or 42 percent of the total fish landings in Japan during 1929 through 1938 (Nakai 1962b). Even though the catch of *iwasi*, including *sirasu*, has decreased since the 1940's, the landings in 1962 still measured 511,000 tons, comprising 12 percent of all the fishes landed by the Japanese fleet based at domestic ports (Statistics & Survey Division, MAF 1963).

The anchovy comprised only a few percent of the *iwasi* during the prosperous period (Nakai *et al.* 1955, Kurita and Tanaka 1956). The catch of this small fish has increased since the drastic decrease of the sardine in the early 1940's, comprising about nine percent of the total fish landings, or 67 percent of *iwasi* for the recent 5 years from 1958 through 1962 (Statistics & Survey Division, MAF 1959-63). Furthermore, the anchovy is regarded to be of great consequence in the biological production of the ocean as a major source of food for many important fishes.

In 1949, a nation-wide research program, the Cooperative *Iwasi* Resources Investigations (renamed the Cooperative Investigations on the Important Neritic-Pelagic Fisheries Resources in Japan in 1955), started with the primary aim of elucidating reasons for fluctuations in the sardine population. Consequently, biological information has been obtained so as to permit biologists to present opinions regarding regulation and prediction not only of the sardine but also of the anchovy as shown in the progress reports of the programs (Nakai *et al.* 1955, Murakami and Hayano 1955, Yokota and Asami 1956, Yamanaka and Ito 1957, Ishigaki *et al.* 1959, Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1961-63). The Conference of the Fisheries Agency, Japanese Government, for Fisheries Resources Investigations that was founded in 1962 will continue to publish the

progress of the investigations. In addition, several individual biologists have presented comprehensive papers on the Japanese anchovy, mainly in the prosperous fishing areas. Hayasi (1961), Asami (1962) and Takao (1964) discussed the investigations and management of the species and fisheries on the Pacific coasts of Honsyu, Sikoku and Kyusyu, and in the Seto Inland Sea, respectively. Kubo (1961) has given a review of works on the species under discussion.

In spite of a number of investigations, however, it is still difficult to assess and forecast the anchovy population. Such deficit is noticed not only in the anchovy study but in the fishery biology of various species (Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan, 1961-63, Sato 1961, 1964). The present author has attempted to abstract the recent fishery investigations in Japan and introduce a new methodology through compiling this note that comprises (i) a brief description of fisheries, (ii) a remark on the cooperative investigation programs and (iii) biological information on the Japanese anchovy.

A BRIEF DESCRIPTION OF FISHERIES

Hayasi (1961) outlined fluctuations in the amount of the anchovy catch and its regional distribution in Japan for 53 years between 1905 and 1957 as well as major fishing gear, fishing seasons and size composition of the catch on the basis of the catch statistics compiled by the Statistics & Survey Division, MAF, and information reported by workers who dealt with fisheries for *iwasi*. The following descriptions are mainly taken from this paper. Details of the history of development, construction and methods of operation of the fishing gear are summarized by Miyazaki (1960).

History of Landings

Examinations of shell mounds, historical documents and literary works indicate that *iwasi*, including the anchovy, sardine and round herring, had been exploited by some kinds of nets, and that commercial fisheries have existed since the tenth century in various parts of Japan (Kishinouye 1908, 1911, Tagawa 1903, Fukuyo 1947, Yamaguchi 1947, Uda 1952, Yokota 1953, Nakai 1960, 1962b, Hayasi 1961). According to preliminary investigations of fisheries in Japan, the anchovy was one of the most abundant fishes around 1890 (Agriculture Bureau, MAC, 1891-93).

In 1894 the Statistics and Survey Division, MAF, commenced to publish a series of statistical year books

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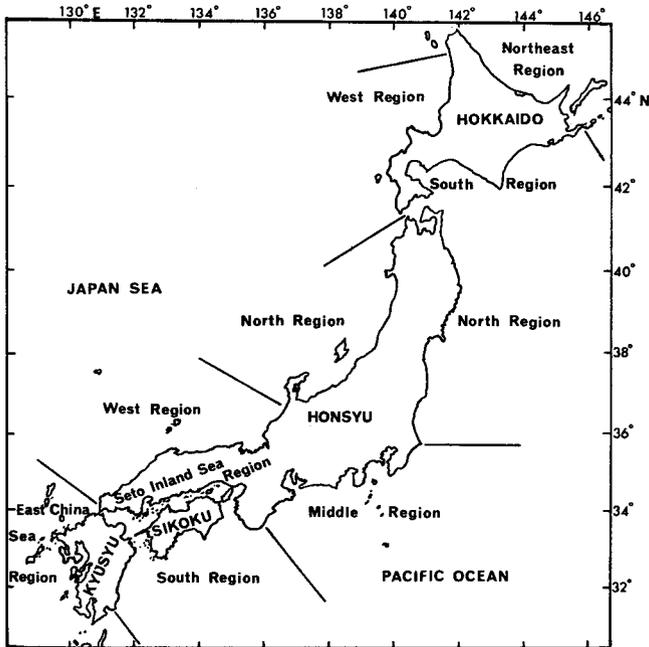


FIGURE 1. Division of the coast of Japan by Statistics and Survey Division, MAF. Division by Fisheries Agency is compared to that by Statistics and Survey Division as follows:

Fisheries Agency	Statistics and Survey Division
Hokkaido Region	North-East, South and West Regions of Hokkaido
Tohoku Region	North Pacific Region
Tokai Region	Middle Pacific Region
Nankai Region	South Pacific Region
Japan Sea Region	North and West Regions of Japan Sea
Seikai Region	East China Sea Region
Naikai Region	Seto Inland Sea Region

called *Nosyomu Tokai* (renamed *Norin Tokai* in 1925). Records of the anchovy catch, partly together with the sardine and round herring, have been given since 1905. On the basis of the catch statistics up to 1957, Hayasi (1961) summarized the fluctuations in amount of the anchovy catch as follows:

“The history of fluctuation in the anchovy catch (in Japan) are distinguished into four groups of years; early increase from 1905 to 1912, succeeding years of irregular fluctuation up to 1930, early part of the 1930’s of decrease, and following years of increase. The early increase might be caused by rapid development of fisheries. For the later three periods, it is noted that the anchovy catch has fluctuated reversely with the sardine catch. Investigation of published information indicates that the fluctuation in the anchovy catch has depended mainly on change in the population size rather than on change in species preference of fishermen, both of which might be largely due to the remarkable fluctuation in the sardine population. The geographic distribution* of the anchovy catch has been consistent for the last half century. The Pacific waters have produced 60 percent

* Two systems are used to divide the coast of Japan, one by the Fisheries Agency and the other by the Statistics and Survey Division of Ministry of Agriculture and Forestry. They are identical to each other except for the names and subdivision of the regions (Figure 1).

of the nation’s total. The landings in the Seto Inland Sea, coastal waters swept by the Tusima Current and seas surrounding Hokkaido have comprised 20, 15 and 5 percent of total, respectively.”

For the recent 5 years, up to 1962, total landings of anchovies and *sirasu*, mostly postlarval anchovy, showed no further increase (Figure 2). The major fishing grounds were still located in the Pacific waters and the Seto Inland Sea (Table 1).

TABLE 1
REGIONAL CATCH OF ANCHOVY AND SIRASU IN JAPAN, 1962.
UNIT: 1,000 METRIC TONS

	Anchovy	<i>Sirasu</i>
Total.....	349.5 (100.0 %)	26.3 (100.0 %)
Hokkaido.....	1.5 (0.4)	-- (--)
Pacific.....		
{North.....	38.3 (11.0)	2.7 (10.1)
{Middle.....	107.1 (30.6)	10.5 (39.8)
{South.....	36.4 (10.4)	4.6 (17.7)
Japan Sea.....		
{North.....	2.3 (0.7)	0.1 (0.2)
{West.....	20.8 (6.0)	0.3 (1.2)
East China Sea.....	66.8 (19.1)	1.2 (4.4)
Seto Inland Sea.....	76.2 (21.8)	7.0 (26.5)

Data from Statistics & Survey Division, MAF (1963).

Prospectus of Recent Fisheries

According to Hayasi (1961), the major types of fishing are with two-boat purse seines that produce 60 percent of the total anchovy catch, and boat seines of several varieties that catch 20 percent of the anchovies and 75 percent of *sirasu*. Two-boat purse seines and boat seines are chiefly operated for anchovies at various stages of their life, but the fishermen engaging in these fisheries often change their objects depending on the stock sizes and prices of the species within their fishing grounds. These fisheries have been best developed on the Pacific coast off Honshu and in the Seto Inland Sea, which comprise the major anchovy fishing grounds inclusive of the postlarval forms. In recent years these types of fisheries have continued to take the most important role in producing anchovies (Table 2).

Anchovies, including *sirasu*, are caught throughout the year in Japan as a whole. The amount of catch increases in the later half of a year with two peaks, one in the summer and the other in the winter. The fishing season is limited in the northern areas; *i.e.* in the autumn in the Hokkaido and North Pacific Regions, and in spring and autumn in the Japan Sea, while it lasts throughout the year in the central and southern areas of Japan. Fishing activities for both anchovies and *sirasu* move from the open coast to the bays and inlets during spring and summer, and then shift toward the open coast during autumn and winter (Asami 1958, Hayasi 1961).

The anchovy catch comprises various sized fish from postlarvae of 13 mm in total length to large individuals over 16 cm in body length. The fish over

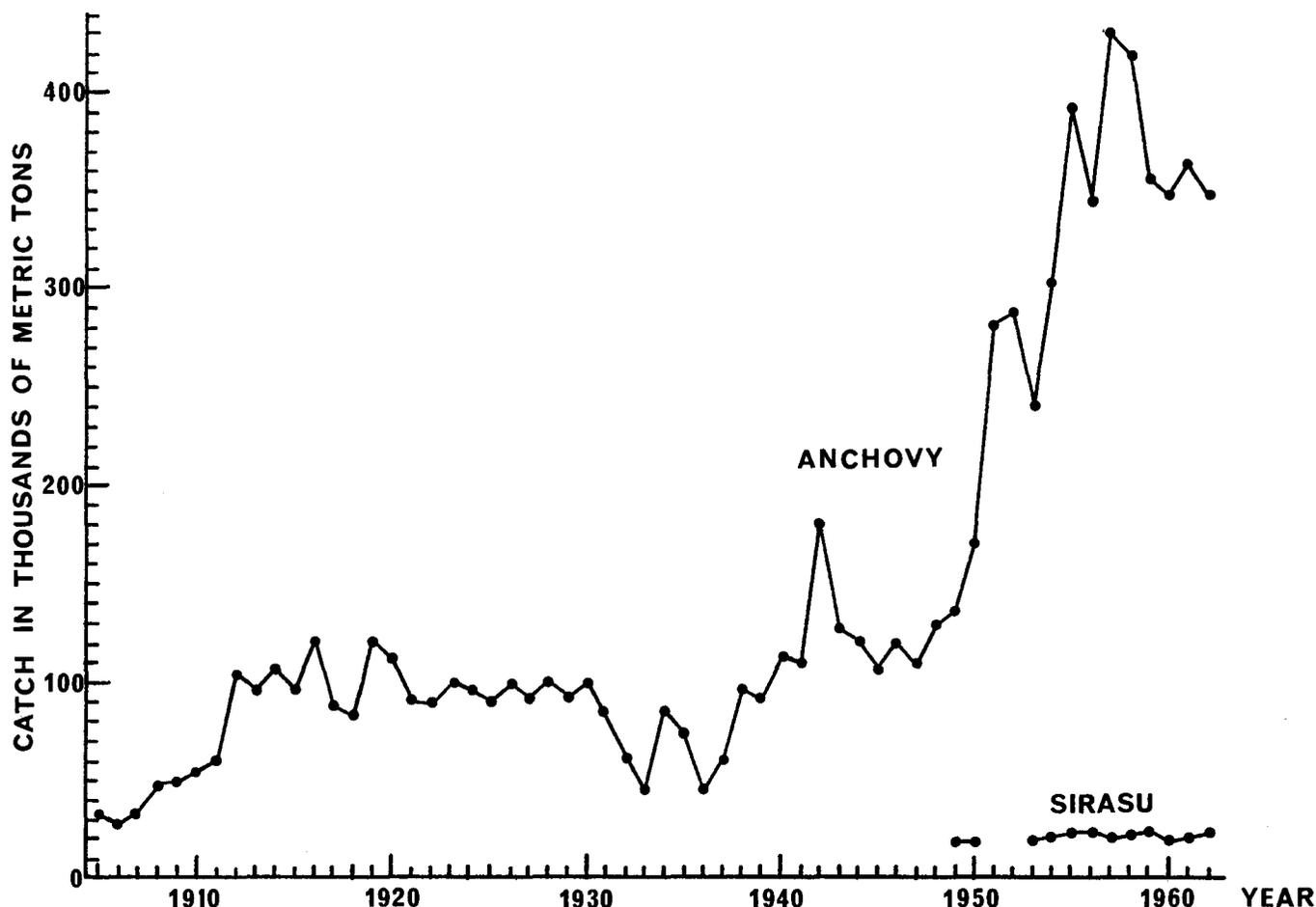


FIGURE 2. Annual landings of the anchovy (1905-62) and *sirasu* (1949, 1950 and 1953-62). Data for 1905-25 and for 1951-62 from Statistics and Survey Division, MAF (1906-26 and 1952-63), those for 1926-31 and for 1933-48 from Kurita and Tanaka (1956), those for 1932 from Statistics and Survey Division, MAF (1933) and Takayama and Sakai (1936), those for 1949 and 1950 from unpublished record taken by Tokai Regional Fisheries Research Laboratory. The figure for 1941 is corrected according to Nakai (1960).

TABLE 2
ANCHOVY AND SIRASU CATCH BY METHOD OF FISHING IN
JAPAN, 1962.
UNIT: 1,000 METRIC TONS

	Anchovy	<i>Sirasu</i>
Total.....	349.5 (100.0 %)	26.3 (100.0 %)
{ Subtotal.....	203.2 (58.1)	0.1 (0.3)
{ Two-boat		
{ purse seine.....	157.8 (45.2)	0.0 (0.1)
{ Others.....	45.4 (13.0)	0.0 (0.1)
Lift nets.....	18.2 (5.2)	2.2 (8.2)
Set nets.....	9.6 (2.8)	0.0 (0.0)
{ Subtotal.....	102.8 (29.4)	21.5 (81.6)
{ Boat seine		
{ group.....		
{ { <i>Patti-ami</i>	54.2 (15.5)	6.4 (24.4)
{ { Boat seine.....	48.7 (13.9)	15.1 (57.3)
Beach seine.....	14.8 (4.2)	2.5 (9.7)
Other methods.....	1.7 (0.5)	0.0 (0.1)

Data from Statistics & Survey Division, MAF (1963).

14 cm in body length are scarce in the commercial catch. All the sizes appear in both Pacific and Japan Sea sides. Generally, the length composition data show three modes, (i) postlarvae around 25 mm mainly caught by boat seine, (ii) immature around 6-8 cm in body length by *patti-ami* and (iii) adults over 10 cm in body length by two-boat purse seines. It is also noted that the mean length is usually larger in the northern areas than in the southern areas (Yokota and Asami 1956, Yamanaka and Ito 1957, Hayasi 1961, Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1961-63, Asami 1962, Takao 1964).

A REMARK ON THE COOPERATIVE INVESTIGATIONS

The life history of the Japanese anchovy has not been investigated thoroughly enough to promote advance in the studies for forecasting and assessing the population up to the early 1950's. Since the cooperative investigations started in 1949, the biological information of the fish, including the amount and composition of the commercial catch, the number of eggs and larvae in the sea, and the environmental condi-

tions have been collected through systematic surveys, which almost all fisheries experimental stations of prefectural governments facing on the sea and the seven regional fisheries research laboratories have engaged in. Another investigation program was started in 1964 with the aim of forecasting fish stocks, inclusive of anchovy, as well as oceanographic conditions.

As far as the neritic-pelagic fishes are concerned, these two investigation programs are conducted as almost one project. The following description covers (i) social demands on the fishery research agencies, (ii) development of methodology and (iii) scale of the investigations.

At the start of the cooperative investigations, major efforts were laid upon the sardine, the decrease of which caused serious economic and social problems in Japan (Nakai *et al.* 1955). Since the middle 1950's, anchovies have exceeded sardines in amount of the commercial catch and more extensive information has been necessitated for predicting and regulating the anchovy stock to increase the economic productivity of fisheries, especially the two-boat purse seine and the boat seines on the Pacific waters along Honsyu, Sikoku and Kyusyu, and on the Seto Inland Sea.

At the initial stage of the cooperative investigations, the most urgent project was to collect information on the life history of the species in order to advance the study of population dynamics (Hayasi 1961). However, the biological information thus collected has led many fishery biologists to think that the numerical analysis of the fish populations shows only limited aspects of nature (for instance, Tanaka 1960, Hayasi 1961, Nakai (1962b)). An alternative methodology, in which a species is treated as a member of the community (Yokota and Asami 1956, Yokota *et al.* 1962), is regarded fruitless unless the elemental species are sufficiently understood. Recently, Sato (1961, 1964) proposed a methodology of fishery biology, through investigations of the king crab, *Paralithodes camtschaticus* (Tilesius), which necessitates the logical system of scientific conceptions. A more detailed explanation of his proposal is given in the following sections.

During April 1949 through March 1950 the cooperative investigations covered collection of catch statistics, surveys on the age and length composition and morphometric characters of the commercial catch, and the distribution and abundance of eggs and larvae as well as oceanographic conditions. The morphometric characters surveyed were body length, body weight, sex, gonad weight, diameter of ova, stomach contents, vertebral counts and scale rings. The eggs and larvae were collected by standardized nets (Nakai 1962a).

Engaged in the investigations during the first year were 47 prefectural fisheries experimental stations and 68 research boats of 34 prefectures, five regional fisheries research laboratories and four research vessels of the Fisheries Agency. Consequently, eggs and larvae were collected at 5,035 observatory stations (Nakai and Hattori 1962), and morphometric characters were determined for 14,202 anchovies taken at 82 landing ports (Nakai *et al.* 1955). Since 1951, more

efforts have been laid on the length composition survey in order to improve the accuracy of the estimates of population characteristics (Nakai *et al.* 1955). For the later years, almost the same amount of data have been collected annually. In addition, daily reports have been taken from some of purse seiners operating on major fishing grounds (Hirakawa 1955, Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1961-63). Since 1964, the boat survey has been conducted routinely, and the number of regular oceanographic stations has been increased as much as twice that in the preceding years.

BIOLOGICAL INFORMATION

It is axiomatic that fishery biologists working on any project attempt to approach not only the aspect of their interest but also the mechanisms regulating biological production of the organisms. For instance, a biologist researches the growth of the fish in order to determine how the species population changes in size, distribution or migratory route in the natural waters. Unless the position and role of any research project are *subjectively* determined, however, the investigations may not indicate the true nature of the organisms, because all the aspects are *unified* in the real life of organisms, which essentially changes from step to step during the course of ontogenesis. This makes it necessary to consider methods to systematize biological information on any species.

In the course of fishery biology, most phenomena are observed through the commercial fisheries. This fact means that one can see only compounds of three factors, fishes and environments in nature, and productive power of the human society. Accordingly, it is necessary to establish three systems of sciences corresponding to these factors. In the case of the anchovy investigations, the scientific systems are (i) biology, especially ecology, (ii) oceanography, and (iii) technology and economics. The biological features of the anchovy will be described *subjectively* with the use of *categories* particular to biology, which must be drawn on the bases of the following three features of organisms.

First, the living resources are retained and develop through their two major functions, individual maintenance and species maintenance, that are results of interactions between organisms. This fact shows that the *species* is the most comprehensive category in biology.

Second, the species has differentiated in the course of evolution. This fact makes the species and the subspecies two conceptions mutually defining one another (Darwin 1917). Eventually, it is concluded that a species population comprises subspecies that have both *universality* of the species and *peculiarity* of the subspecies. Systematic fractions of a species population, *e.g.* subpopulation defined by Marr (1957), must comprise the same nature. Therefore, the *systematic fraction* is to be considered as one of the major categories, being defined on the basis of the substantial knowledge of life of the species population.

Third, form and function of an individual essentially change depending upon the *developmental*

stages (or etap) from egg to adult, and upon the yearly cycle of life inclusive of spawning and shoaling cycles as suggested by Steven (1948). Even the same environmental factors may have different effects upon two individuals at different stages or cycles. From the above discussion it may be readily accepted that the systematic fractions must be distinguished by difference of occurrence of the developmental stages and the maturation phases.

For these reasons, the biological information must be systematized on the basis of developmental stages and yearly cycles for each species. The system obtained as such may provide hypotheses of the systematic structure and assessment of any fish populations. Accordingly the present section is divided into three parts: (i) biological notes of the fish at each developmental stage or maturation phase, (ii) systematic fractions, and (iii) assessment of the population.

The developmental stages and yearly cycle of life are to be defined through the whole body of knowledge, and will be modified if those categories are found to contradict observations made by succeeding investigations. At present, we can assume that the anchovy passes through the developmental stages defined by Hubbs (1943), and that two yearly cycles repeatedly appear every year at the adult stage. The developmental stages and yearly cycles adopted here are listed below. The substance of the stage or cycle was obtained by unifying existing knowledge on all aspects of the stage or phase in question.

Developmental stage	Yearly cycle of life
Egg.....	--
Larva (before absorption of yolk).....	--
Postlarva (before completing metamorphosis).....	--
Juvenile (before reaching adult form).....	--
Immature (before sexual maturation).....	--
Adult.....	Shoaling Spawning

Geographical Distribution

The Japanese anchovy is actually widely distributed in the temperate zone of the Far East, extending from southern Sakhaline to Formosa, but the fisheries on this species have been concentrated in the waters around Japan and Korea (Hayasi 1961). Almost all the coastal waters surrounding Japan produce this species, except south of the Kuroshio Current (Matsubara 1955, Hayasi 1961). Most previous descriptions are given only in terms of the species.

Egg and larval stages. The spawning activities of anchovies have been determined through systematic plankton net collections conducted since 1949 (Nakai *et al.* 1955, Yokota and Asami 1956, Yamanaka and Ito 1957, Ex. Com., Conf., Invest. Neritic-Pelagic Fisher. Japan 1961-63). According to these studies, the species actually spawns over a wide extent of the waters between Hokkaido and Kyusyu, from the inlets to the high seas to a distance of around 1,000 nautical

miles from the coast. The spawning activities are distributed more abundantly over the middle and southern Pacific coast of Japan, and around the edge of continental shelf than in any other part of the sea. The spawning season lasts throughout a year in south of the middle Pacific and west Japan sea regions. The heaviest spawning activities occur during winter and early spring in the southern areas around Kyusyu and Sikoku, or in spring and in autumn in central Pacific waters such as between the Kii and Boso Peninsulas. Within an area the spawning proceeds with the passage of time from the outer coastal waters to the bays and inlets (Hayasi 1961; Asami 1958a, 1958b, 1962). The eggs are often transported by currents, and then the distribution pattern changes depending upon age of the eggs (Yokota 1953). The anchovy larvae have the same distribution as the eggs (Nakai *et al.* 1955, Yokota and Asami 1956, Yamanaka and Ito 1957).

Postlarval and juvenile stages. It is difficult to estimate, with the use of plankton nets, distribution and abundance of the postlarvae and juveniles that have gained enough swimming activity to avoid the nets. Some of the postlarval stocks are concentrated in the coastal waters, and are exploited by boat seines and other commercial fisheries operating within 5 miles from the coast and 20 m from the surface. The major fishing grounds for postlarval anchovies are located within the general areas comprising the spawning grounds. Representative fishing grounds are: The coast of Ensyu Nada and Hyuga Nada on the Pacific, and various parts of the Seto Inland Sea. Minor fishing grounds for postlarvae are found on the coast south of Kasima Nada on the Pacific and in Toyama Bay on the Japan Sea (Hayasi 1961). The postlarvae are abundantly distributed out of the fishing grounds (Nakai *et al.* 1962). Dense shoals are often found on *siome* in the waters off eastern coast of Honsyu (Odate 1957). The juveniles, less lucrative than the postlarvae, are caught just after the major fishing season for *sirasu* (Tanaka 1956).

Immature stage. Anchovies leave the nursery grounds by the time they reach the immature stage, and some are exploited by commercial fisheries mainly in the bays and inlets (Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1961-63, Hayasi 1961, Asami 1962, Takao 1964).

Adult stage. The adult anchovy is exploited in all areas. Generally speaking, the ratio of the adults among the total anchovy catch is higher in the outer coastal waters than in the bays and inlets, and is higher in the northern area than in the south (Yamanaka and Ito 1957, Hayasi 1961).

a. **Shoaling cycle.** Almost all the anchovies caught in the areas south of middle Pacific region are in the shoaling cycle (Hayasi 1961, Usami and Sugiyama 1962).

b. **Spawning cycle.** The spawning areas are identical with the distribution areas of the spawning adults. The set nets in the northern areas catch the

“ripe” fish just before they discharge the ova or sperm in early summer (Usami and Sugiyama 1962).

Abiotic Factors of the Habitat

The anchovy is regarded to be an eurythermal and euryhaline species (Kubo 1961), because of the wide space-time extent of appearance of exploitable shoals and spawning. The fish are easily transported across the Kuroshio Current alive in live-cars of fishing vessels even though no report was obtained from isolated islands south of the current (Matsubara 1955, Hayasi 1961).

Egg and larval stages. The eggs are found in areas, where surface temperatures range between 11 and 29°C (Naki *et al.* 1955, Kubo 1961). Generally speaking, the surface temperature of the spawning grounds is high in the southern area and low in the northern area (Table 3).

TABLE 3

SURFACE TEMPERATURE OF SOME SPAWNING GROUNDS OF JAPANESE ANCHOVY (AFTER YAMANAKA AND ITO 1957)

Locality	Surface temperature (°C)	
	Range	Major spring season
Southern tip of Kyusyu.....	15-29	15-25
Hyuganada east coast of Kyushu.....	15-29	15-26
Bungo Suido, east coast of Kyusyu.....	15-29	15-29
Suho Nada, Seto Inland Sea.....	11-29	15-25
Ise Bay, Pacific coast of Honsyu.....	13-27	15-26
Boso, Pacific coast of Honsyu.....	14-27	16-19
Amakusa Nada, west coast of Kyushu.....	16-27	16-21
Wakasa Bay, Japan Sea.....	11-27	14-25
Isikari Bay, Hokkaido.....	14-23	14-18
Okhotsk coast of Hokkaido.....	11-15	--

Chlorinity in areas where the anchovy eggs are found range between 14.8 and 19.5 per mil, most frequently 18.4-19.3 per mil (Nakai *et al.* 1955, Kubo 1961). According to Nishikawa (1901), the eggs normally develop under a wide range of specific gravity between 1.012 and 1.033.

The eggs occur most abundantly in the sea area over the continental shelf and extending 10 miles more offshore (Nakai *et al.* 1955, Kubo 1961). Most of the eggs are distributed at a depth less than 30 m from the sea surface (Kubo 1961). Nishikawa (1901) recorded the eggs from the deeper layer between 45 and 83 m. The larvae may live at almost the same abiotic conditions with the eggs.

Postlarval stage. Postlarval anchovies are widely distributed from coast to offshore. Major fishing grounds are located in areas with sand or mud bottom, under influence of river water.

Juvenile through adult stages. Adults definitely select the open sea, while immature fish are distributed in bays and inlets as well as the open sea. The spawners may require abiotic conditions that differ from those of adults during the shoaling cycle.

Although not defining which developmental stage, Kubo (1961) outlined the relationships between the

anchovy, seemingly at the juvenile through adult stages, and abiotic factors as follows:

“The anchovy is an eurythermal species, because the fish are caught throughout a year in some particular fishing grounds. Yamanaka and Ito (1957) estimated that the temperature of habitat ranges from 8 to 30°C, through the field observation on catch and spawning. Suehiro (1936) determined the heat tolerance of the anchovy under rearing condition. According to his experiment, it was found that 11° and 31° are the lowest and highest survivable ranges of the anchovy taken from the waters of 22-23°C. Compared with the sardine experimented under the same time, it is found that optimum temperature is higher for the anchovy than for the sardine. In the same experiment, Suehiro (1936) determined that the anchovy died when the oxygen content of the water decreased to slightly less than 2 c.c./l. Distribution depth is found to differ by time of a day, size or age of fish, area, season and weather (Inoue and Ogura 1958).

Suehiro *et al.* (1957) reported that the anchovy are frightened by sounds of military cannons. Imamura and Takeuchi (1960) found that the anchovy are attracted by light of 30-40 lux. through rearing examination.”

Relation With Systematically or Ecologically Related Fishes

Hayasi (1961) summarized the distribution of fishes systematically related with the Japanese anchovy as follows:

“The fishes of the genus *Engraulis* are widely distributed throughout the temperate zones of the world except for the Atlantic coast of North America, where a closely related genus *Anchoa* occurs. Many of these two genera have supported fisheries at various significance within the area in which they occur.

In the temperate zone of the Far East, three other genera of Stolephorinae are known to occur in addition to the genus *Engraulis*, and some of them were fairly important for the local fisheries in Korea.”

It is well known that in Japan the sardine and the round herring have been ecologically and commercially related with the anchovy (Nakai *et al.* 1955, Yokota 1953, Ito 1961, Hayasi 1961). In addition, the mackerels, *Scomber japonicus* Houttuyn and *S. tapeinocephalus* Bleeker, and jack mackerel, *Trachurus japonicus* (Temminck & Schlegel), occupy almost the same habitat as the anchovy (Yokota *et al.* 1961).

Postlarval stage. Postlarval anchovy are often caught incidentally with postlarval sardine. The white fish, *Salangithys microdon* Bleeker, and postlarval and juvenile sand lance, *Ammodytes personatus* Girard, are caught in more coastal area than the postlarval anchovy. Postlarvae of a systematically related fish, *Stolephorus zollingeri* Bleeker,² occur in the fish-

² A recent paper has reported: “Records of *Stolephorus zollingeri* from Japanese waters (Hayashi and Tadokoro 1962) are clearly based on another Hawaiian engraulid, *S. buccaneeri* Strasburg (Whitehead, P. J. P., M. Boesman, and A. C. Sheeler 1966. The types of Bleeker's Indo-Pacific elopoid and clupeoid fishes, *Zool. Verhand., Nat. Hist. Leiden*, (84): 159 pp).

ing grounds of sirasu, especially on the southern Pacific coast of Japan. These two species of Stolephorinae are distinguished from one another by meristic counts at a stage of 19 mm in total length (Hayasi and Tadokoro 1962).

Juvenile stage. Competition of the postlarval anchovy with those of the mackerels and jack mackerels affect the stock size of the anchovy in the south Pacific region (Yokota *et al.* 1961). The above rare species of Stolephorinae is easily distinguished from the anchovy by shape of head at a stage over 26 mm TL although these two species are caught incidentally (Hayasi and Tadokoro 1962).

Juvenile through adult stages. Anchovies compete with or are consumed by the fishes listed in the introductory part.

Feeding

The investigation covers the form of digestive organs and the food species of the Japanese anchovy. These works are summarized as follows (Kubo 1961):

"The gill rakers are fine and numerous. The intestine length increases more rapidly than the body length with growth of fish. The copepods comprises major food of the fish throughout the life span. Size of food is linearly correlated with size of the fish."

Postlarval stage. Nakai *et al.* (1962) investigated feeding habit of the Japanese anchovy as well as sardine in the Pacific waters of Honsyu. The results are summarized as follows:

"Postlarvae of less than 5 mm TL just after absorbing yolk take mainly nauplii and eggs of copepoda. Only a few of them were found with protozoa, small mollusca and diatom in their digestive tracts. Postlarvae of 5-10 mm TL still mainly eat nauplii of copepods, but copepodid larvae increase in number from before. Generally, sizes of postlarvae and food organisms are correlated with each other. Number of postlarvae with food in the digestive tract occupy less than 20 percent on the average. They take the food most actively in the day time. The copepod eggs and larvae are more abundantly distributed in the coastal waters than in the offshore."

Juvenile through adult stages. Copepods comprises major food of the anchovy. Other food organisms are diatoms, and various types of small crustacea, larvae of mollusca, Chaetognatha and other small animals. The adults eat eggs and larvae of fishes including the anchovy (Nakai *et al.* 1955, Kubo 1961).

Migration

No systematic knowledges have been obtained on migration of the anchovy. The following review covers fragmental information.

Egg and larval stages. It is shown that some amount of eggs are carried by the Kuroshio Current from southern Kyusyu to the Pacific coast along Honsyu (Hayasi 1961, Asami 1962).

Postlarval stage. Some postlarval anchovy assemble in the coastal waters (Yokota 1953, Tanaka 1956, Hayasi 1961).

Juvenile through adult stages. It is widely accepted that some of anchovy stocks enter into and leave from bays and inlets during spring through summer and during autumn, respectively (Kubo 1961). Most of sexually matured fish move from the coastal waters to the edge of continental shelves (Hayasi 1961).

Shoaling

The anchovy swim near the sea surface as schools throughout their life span.

Egg and larval stages. Since eggs and larvae are dispersed by currents after they are discharged, their geometrical distribution pattern changes depending upon age (Yokota 1953).

Postlarval stage. The postlarval anchovy actively forms schools so densely as to support commercial fisheries.

Juvenile through adult stages. In the live car, the anchovy tend to swim clockwise rather than counter-clockwise (Suehiro 1947). The fish can swim at a speed of 10-12 cm/sec. (Kimura 1934). Three swimming manners have been noticed in the fishing grounds (Inoue and Ogura 1958). As mentioned in abiotic factors, the species reacts sensitively against sound and light.

Spawning cycle. The anchovy discharge ova and sperm at a duration of time between sunset and midnight (Nakai *et al.* 1955, Yamanaka and Ito 1957, Kubo 1961).

Reproduction and Recruitment

Two problems are left unsolved about fecundity of the anchovy: (1) How many times an individual spawns in a year, and (2) how many times a group of the fish having occurred at a spawning season in a spawning ground spawn in a year. In addition, it is not yet confirmed whether or not the anchovy in offshore, extending 1,000 nautical miles from the coast, are recruited to the fishing grounds.

Larval and postlarval stages. The minimal size of the anchovy caught by commercial fisheries is 13 mm in total length. Recruitment to the boat seine is completed during the postlarval stage of 23 mm in total length (Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1961-63, Hayasi 1961).

Juvenile and immature stages. Juveniles of 3 cm in body length are taken by the fisheries that mainly exploit the immature anchovy. The fish are completely recruited at 7-8 cm to the stocks for these fisheries (Asami 1962, Hayasi and Kondo 1957, Hayasi 1961, 1962a). Immature fish over 6 cm in body length are taken by the large sized two-boat purse seines that mainly exploit the adult fish (Hayasi and Kondo 1957, 1959, Hayasi 1961, 1962a). Immature fish over 5 cm in body length are often distinguished by sex (Kubo 1961).

Adult stage. Examination of ovum frequency indicates that anchovies discharge their ova or sperm one or more times in a spawning season (Kubo 1961). Number of ova discharged by a female has been esti-

mated between 1,000 and 60,000 (Kubo 1961, Usami and Sugiyama 1962). The minimal size of matured fish was 5cm in body length, but the biological minimal size differs depending upon season and locality (Kubo 1961).

Growth and Life Span

Age determination was regarded one of the most important projects since the population dynamics was the major methodology of the investigations. The embryonic growth rate was investigated in order to determine the abundance of egg and larval stocks.

Egg stage. The eggs hatch out about 30 hours after fertilization at a temperature between 20° and 25°C (Nishikawa 1901, Uchida *et al.* 1958), or about 48 hours at 18°C (Kaymiya 1916).

Larval stage. The anchovy larvae just after hatching out range between 3.2 and 3.6 mm TL (Kamiya 1916, Uchida *et al.* 1958).

Postlarval stage. It is estimated through examination of meristic characters and abiotic factors that the postlarvae between 25 and 40 mm TL are 1 to 2 months old on the average (Hayasi and Suzuki 1957, Hayasi 1961).

Juvenile through adult stages. There are a number of works on the growth rate of the anchovy after the postlarval stage. Technically, these works were advanced through three steps: (1) analysis of length composition, (2) analyses of length composition and vertebral counts, and (3) analyses of length composition, vertebral counts and scale rings. Estimates of the growth rate of the fish differ depending upon workers. Examination of these investigations lead Hayasi and Kondo (1957) and Hyasi (1961, 1962b) to the following conclusions.

- “1. One may estimate the season of hatching of the fish in the first year of life through analyses of length frequency and vertebral counts.
2. The age of fish can be determined by scale readings since most fish form the scale annuli once a year during late autumn through early spring. To determine the age of a few fish, however, the date of catch, length and vertebral counts as well as the scale readings must be considered.
3. The anchovy grow 5-11 cm and 11-14 cm in body length by the end of the first and second years of life, respectively. Most fish leave the fishing ground by the summer of the third year when they attain 12-15 cm. As only a few fish were found to exceed 16 cm, the life span of the species is concluded to be two years.”

The following formulae approximate the growth of fish taken on the Pacific coast of Honsyu (Hayasi and Kondo 1957).

Fish spawned in spring;

$$14.82(1 - 0.9153e^{-0.0142t}) \text{ cm,}$$

Fish spawned in autumn;

$$15.23(1 - 0.9442e^{-0.084t}) \text{ cm,}$$

where, t is age in term of month.

Yokota and Furukawa (1952) and many other workers adopted the exponential curve for approximating the growth of the anchovy, and Yasumura *et al.* (1956), the logistic curve (Kubo 1961).

The immature and adult fish show different seasonal changes of their condition coefficients from one another (Hayasi and Kondo 1962a).

Mortality

The anchovy are consumed not only by commercial fisheries but also by various animals with large stocks such as the mackerels, skip jack, tunas, yellow tail, and squids. However, no attempt succeeded to estimate reliable mortality rates of the anchovy in the exploited phase. Investigation of plankton samples showed tremendously high mortality at the beginning of postlarval stage (Nakai *et al.* 1955, Yokota *et al.* 1961).

Egg stage. The mortality rate of the eggs was estimated as about 30 percent from fertilization to hatching out. The eggs are taken by many animals including the adult anchovy. *Noctiluca* also eat the anchovy eggs (Nakai *et al.* 1955, Enomoto 1956, Hattori 1962).

Larval and postlarval stages. About 10,000-20,000 tons of postlarval anchovy are commercially landed mainly by boat seiners. The larval and postlarval anchovy comprise one of the most common food organisms of various marine animals (Yokota *et al.* 1961). The mortality rate just after yolk absorption is quite high, and then the mortality rate from fertilization to larval stage of 5 mm TL reaches about 99 percent (Nakai *et al.* 1955). Known causes of the high mortality from larval to postlarval stages include starvation and predation (Nakai *et al.* 1962, Yokota *et al.* 1961). Monthly mortality coefficients were calculated to be about three for the postlarvae exploited in a major fishing ground along the Pacific coast of Honsyu (Tanaka 1960).

Juvenile through adult stages. More than 300,000 tons of anchovy have been landed every recent year. The fish are also eaten by various species (Yokota *et al.* 1961). The annual survival rate was calculated as 0.26 (Yoshihara 1962). Monthly mortality coefficients were calculated as 0.115 by the fishing and 0.136 by the natural causes for the local group in the southern Pacific waters (Asami 1962).

Morphometric Variation

A number of works on the vertebral counts of the anchovy were conducted for discriminating the fish having occurred in different seasons of a year in different places, as reviewed by Asami and Hanaoka (1957), Asami (1958), Hayasi and Kondo (1957), Hayasi and Suzuki (1957, 1959), Hayasi (1961, 1962a), Kubo (1961) and Takao (1964). Eventually, it was concluded that the systematic fractions of the anchovy population are not distinguished by one or a few morphological characters (Hayasi 1961).

Egg stage. Asami (1953) showed seasonal variation in size and shape of the anchovy eggs taken from the eastern coast of Kyusyu.

Postlarval stage. Comprehensive notes are given on variations of the vertebral counts of the anchovy at postlarval through adult stages by Kubo (1961) and Hayasi (1961, 1962a). Major features in variations of vertebral, and dorsal and anal fin ray counts of the postlarval anchovy are summarized as follows (Hayasi 1961):

1. The adult numbers of vertebrae (43-47), and dorsal and anal fin rays (13-17 and 15-20, respectively) are fixed by the time the fish reaches 19 mm TL.
2. On the basis of meristic variation, the fish spawned in the early half of the year can be segregated from those spawned in the later half.
3. The meristic characters differ depending upon the hatching place, but usually the actual differences are too small to make the meristic variation practically useful in segregating local groups.

Kubo (1961) showed that many workers indicated that the mean vertebral counts are reversely correlated with temperature at hatching place (Figure 3).

The postlarvae taken in the coastal waters have larger body depth than those taken offshore (Nakai *et al.* 1962).

Juvenile through adult stages. Through a number of investigations, it has been found that the vertebral counts differ depending upon size of fish at the juvenile through immature stages but not at the adult. The locality of habitat is not as significant a source of the vertebral variation as size of fish or season of sampling (Kubo 1961, Hayasi 1961).

Systematic Fractions of Population

The wide space-time extent of spawning and short life span imply that the anchovy population comprises fractions at various steps of differentiation. Hayasi (1961) defined two of such steps as follows:

Local group: A local group is a fraction of a population regarded to consist of fish inhabiting a general locality, such as the Pacific waters along Honsyu. A local group includes several space-time groups.

Space-time group: A space-time group consists of fish that are spawned in a particular area during a particular season of the year. Because the spawning activities continue to some extent spatially and seasonally, if the amount is disregarded, a space-time group is referred to a group of fish spawned to such an extent as in the western Pacific area of Honsyu during spring months.

The systematic fractions segregate most completely at the spawning phase. Examination of the distributions of eggs as well as several characters of commercial catch indicates major local groups chiefly propagating in four different localities: (1) between Hyuga Nada and Tosa Bay and (2) Kii Peninsula and Boso Peninsula in the Pacific waters, and (3) between western Kyusyu and western Honsyu and (4) Wakasa Bay and Toyama Bay in the Japan Sea. The stocks in the Seto Inland Sea comprise immigrants from Hyuga Nada and Tosa Bay as well as the indigenous group. In addition to these major groups, there are

a number of minor local groups that may intermingle with each other and with the major groups. The eggs and larvae of the group inhabiting the southern Pacific region, major spawning area of which extends between Hyuga Nada and Tosa Bay, are transported, especially in the early spring, to the middle Pacific region, in which large egg stocks are observed in the waters between Kii Peninsula and Boso Peninsula (Hayasi 1961, Asami 1962, Takao 1964).

For each of the local groups, several space-time groups are segregated. In the middle Pacific region, the spawning activity reaches to the highest peak during March through June, and the second peak appears sometime in autumn. The landings of *sirasu* are the most numerous in spring and early summer, and the second peak of catch appears in autumn. Thus, there are two major time groups, spring and autumn groups. In the waters, the anchovy are observed at four developmental stages; eggs by the spawning surveys, and postlarvae, immatures and adults of two age groups by the commercial fisheries. Examination of the growth, morphological characters, stock sizes, and seasons of their appearance indicate the following features of life history of the local group inhabiting the waters under discussion (Hayasi 1961, 1962b).

Most of the anchovies in the Pacific waters along Honsyu occur in the waters between Kii Peninsula and Boso Peninsula. The eggs are chiefly produced by the fish in their second year of life (I-age). The mortality rates at postlarval through adult stages did not remarkably change for most of about ten year classes up to 1960. A portion of them moves into the coastal area at postlarval, immature and adult stages except the spawning cycles. A few eggs and larvae may drift to the high sea along the Kuroshio current. Most fish may die within two and half years after birth.

The spring group mainly occurs in the outer coastal waters, and intermingles with eggs and larvae that immigrated from the southern waters in spring. After juvenile stage, many of the fish spawned in spring enter into the bays during the warmer months of the first year of life. The autumn groups occur not only in the outer waters but in bays. They also appear in the coastal waters in their first autumn, but their stock size is smaller than that of the spring groups. These two time-groups are discriminated by body length, meristic characters and distribution at the stages just before sexual maturation, and then intermingle with each other (Hayasi 1961, 1962b).

The anchovy inhabiting the southern Pacific region are closely related with those in the Seto Inland Sea (Asami 1958 a, b, c, 1962, Takao 1964). The major spawning season shifts from the outer coastal waters to the bays and inland sea during spring and summer, and then reversely during autumn and winter. The major fishing grounds of each space-time group are located in the waters near the spawning grounds. Most fish leave the fishing grounds by one and half years after birth. The fish having occurred in the spring are liable to move toward the middle Pacific region at the egg and larval stages, but most of the other groups stay within the region under discussion.

Assessment of Population

Even though many estimates have been made of the characteristics inherent to the population dynamics (Yokota 1953, Yokota and Asami 1956, Hayasi and Kondo 1957, Hatanaka 1960, Tanaka 1960, Hayasi 1961, Yoshihara 1962, Asami 1962, Beverton 1963), it has been concluded that the anchovy is one of the most typical organisms indicating limitations of the present system of the population dynamics (Tanaka 1960, Hayasi 1961). The most comprehensively accepted opinion on the effects of fisheries upon the stock is that the fisheries may not seriously damage the anchovy stocks, because of the short life span and vigorous reproduction of that species, even if increase of amount of fishing efforts often causes decrease of the catch per unit effort (Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1962). Techniques of forecasting the anchovy stock size have succeeded in limited areas, where the life history of the fish is understood (Ex. Com., Conf. Invest. Neritic-Pelagic Fisher. Japan 1963).

Hayasi (1961) summarized a general belief among fishery biologists engaging in the Cooperative Investigations on effect of fisheries upon the anchovy population as follows:

“One of the most important biological features of the Japanese anchovy is the short life span, practically about two years in duration. Another important feature is the wide-temporal and areal extent of the spawning activities.

Deduced on the basis of these features are the following two general conclusions on fluctuation in the size and distribution of the population. Firstly, the environmental change in the early stage of life of a space-time group may not exert any serious effect on the amount of recruitment for the year, because the population consists of a number of such groups. The wide-extended spawning indicates that the species can propagate under various environmental conditions. Secondly, the natural mortality rate is regarded to be high because the anchovy, being small in size, represents the major prey of diverse fishes, and because the life span of two years is much shorter than that of other neritic-pelagic species such as the sardine, many of which live for five or more years (Nakai and Hayasi 1962). Therefore, changes of the mortality rate by natural causes, especially those based on predation and competition, may play more important roles than the changes of the fishing intensity in determining the population size of the anchovy. The consistent regional distribution of catch suggests that the well-developed fisheries in the Pacific waters and the Seto Inland Sea have not seriously depleted the stocks therein.”

In the Pacific waters along Honsyu, it is possible to estimate sizes of large stocks at five developmental stages; (1) eggs in offshore, (2) postlarvae on the fishing grounds of *sirasu* fisheries on the outer coast, (3) immatures in the fishing grounds in the bays, (4) adults at the end of their first year of life and (5) adults at the early half of their third year of life on the fishing grounds along the Boso Peninsula and north. The egg stock must be proportionate with

the stock of parents, mainly I-age fish. Hayasi (1961, 1962b) compared the stock sizes at these five stages of the same year classes under a hypotheses that fluctuations in these stock sizes must be correlated if the following conditions are satisfied: (1) these stocks are actually related in the course of ontogeny, (2) the older three stocks are not overexploited, (3) the accessibility and vulnerability of the stocks do not remarkably vary between year classes, and (4) the estimates of abundances are reliable. Actually high correlation coefficients, ranging between 0.90 and 0.98, were found for most of 8 to 10 year-classes between the four stocks except the immatures in the bays.

Taking the correlations between stock sizes as well as information on spawning, migration, age and duration of life span, it has been concluded that no fishing activity exerts any serious damage on the anchovy stocks in the major fishing grounds. The correlations between *sirasu* catch and either one of the older stages reveal that the fishing did not reduce the youngest stock severely. The fisheries in the bays exploited only a portion of the immature stock. The two-boat purse seiners aiming at the adults did not exploit 0-age fish so seriously as to affect the stock sizes of I- and II-age fish. The exploitation of II-age fish did not affect size of the major local group because the oldest anchovy may die within the year, and may not much contribute to the reproduction (Hayasi 1961, 1962b).

The level of stock sizes during 1950 through 1959 was assessed on the basis of the reproduction curve proposed by Ricker (1954). In constructing the curve for the Japanese anchovy, the abundance of eggs in any two successive years was used because this measure is free from such a bias as inherent to the catch statistics, and because the spawners are mainly I-age fish. The egg abundance spawned by two successive generations are not well correlated with each other, except those reproducing in 1950 through 1952, which produced less than 500×10^{12} eggs. Therefore, it can be stated that the classes spawning since 1953 were large enough to supply a large amount of landings (Hayasi 1961, 1962b).

On the basis of the correlations, formulae are given for predicting the catches of 0 and II age adults in several months or two years prior to the fishing seasons. Application of the formulae to the catch for past data showed that the predicted amount agreed with the actual catch for 8 or 9 years out of 10 (Hayasi and Kondo 1962). With the use of those formulae and catch statistics, the landings have been predicted as about 26,000 tons for 0-age adults during October through December of 1961, and about 50,000 tons for the II-age adults in the early half of that year. The actual landings of 0- and II-age adults in those periods were 23,000 tons and 47,000 tons, respectively (Hayasi 1962b). This procedure was not applied for the following seasons because of occurrence of the remarkable anomaly of the environmental conditions (Nakai *et al.* 1964). Thus, the prediction based on the correlations between catches at different stages are applicable only in the case when the migratory route of fish, type of fishery, and environmental conditions

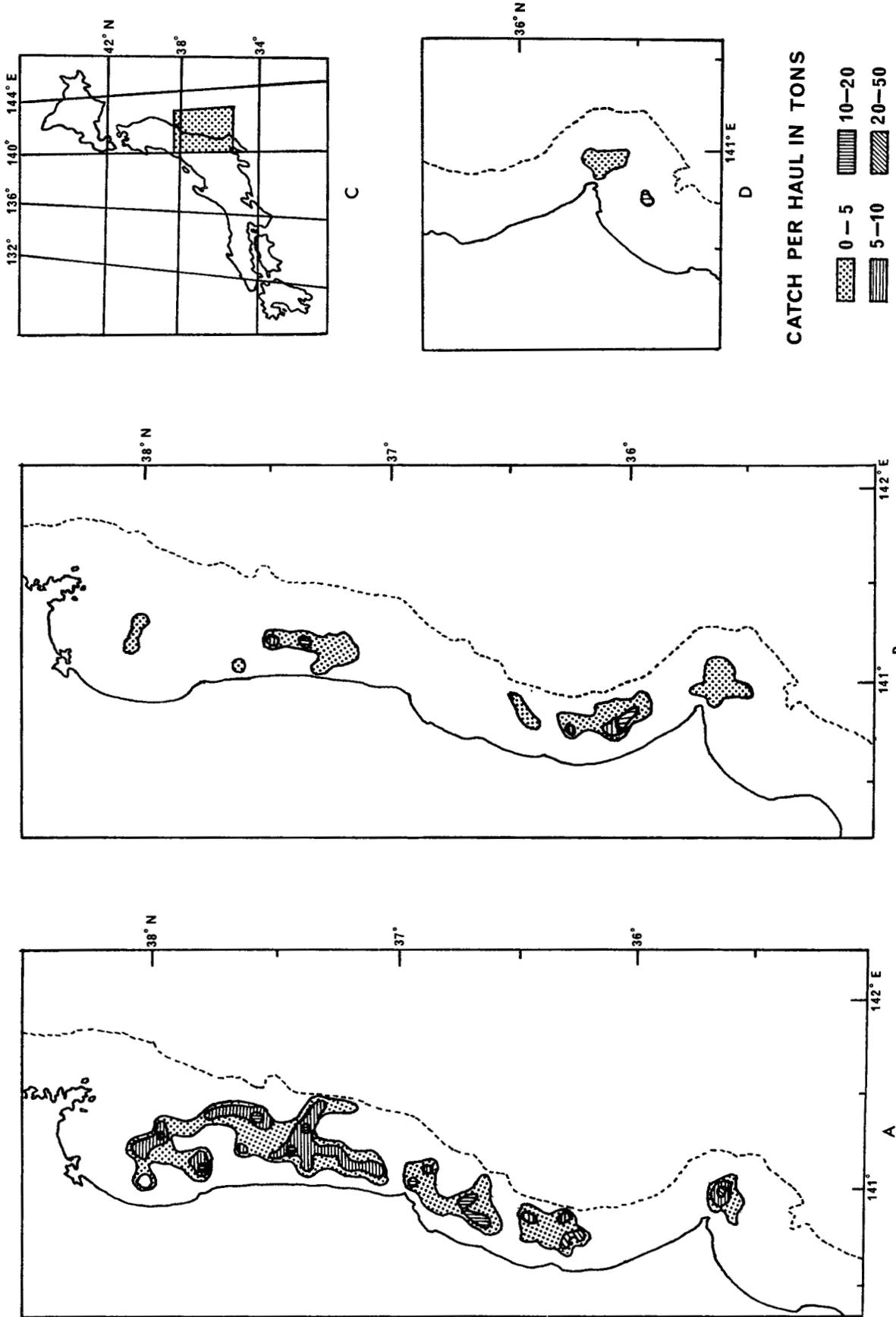


FIGURE 3. Difference of density distribution of the adult sardine at three yearly cycles of life in 1963-64 season. A. Early southward migratory cycle; B. later southward migratory cycle; C. general locality of the fishing grounds in question; and D. spawning cycle. The density is expressed by average catch per haul by purse seiners.

are nearly constant for a length of time. (Hayasi and Kondo 1962b, Hayasi 1962b).

Asami (1962) estimated the monthly mortality coefficients of the anchovy in the eastern waters along Kyusyu and Sikoku as 0.115 by fishing and 0.136 by natural causes. He also estimated the dispersion coefficients that extended between -1.090 and +2.910, being much larger than the mortality coefficients in the absolute value.

Abundance of food organisms, competitors, and predators are found to contribute obviously in determining the stock size of the anchovy (Yokota *et al.* 1961, Nakai *et al.* 1962). It was found that the analytical study was impractical for the anchovy stocks but the estimated rates of decrease and growth of the postlarvae and immatures in the western Pacific waters along Honsyu suggested the possibility to increase the amount of catch (Tanaka 1960).

In spite of a number of scientific works upon the anchovy, the present system of knowledges has not provided any objective way for development of techniques to predict the fish population as a living resource. In other words, the biological information is not unified as an *idea* since the fishery biology has treated the phenomena only superficially, even if many refined techniques have been adopted.

In order to consider biological mechanisms underlying fluctuation in the catch, it is necessary to start from the simple fact that the fish appear in a particular place in a particular season of the year. This fact must be due to the biological rules that the fish assemble in a particular way at a particular developmental stage or yearly cycle of life, or, in other words, that the fish behave independently from, as well as dependently to, the environmental conditions. The mode of assembly must be the most fundamental biological project of the investigations in order to understand where, when and how, and why, the fish appear.

Up to now, three ways were adopted for expressing the mode of assembly of fish: (1) map of distribution, (2) map of migratory route, and (3) map of catch. The maps of distribution and migratory route indicate the biological rules, but are deficient in that they show only an aspect of life. Therefore, these maps, despite their biological basis, are not applicable for indicating the most reasonable way of fishing. The map of catch does not indicate any biological rule, because the natural and social factors are not distinguished there. In this regard, we must re-evaluate and criticize the technique proposed by Vinogradov (1945), who started from the work by Greene (1913). Vinogradov (*loc. cit.*) presents maps indicating the density distribution of the king crab for each of the yearly cycle of life. Indeed his maps would present moments to approach the biological rules governing the assembly of the species, since the mode of assembly must differ depending upon the yearly cycle of life that comprises particular physiological requirements. Unfortunately, his method did not exhibit any further advance, however. The most fundamental reason for the deficit is that the yearly cycle of life was not con-

sidered as a series of categories comprising life of species, systematic fraction and developmental stage.

In order to understand way of life, therefore, it is necessary to express the mode of assembly through drawing maps of major aspects in the life for each of these categories. This series of maps, called fishing map, must give the moment to approach the mode of assembly of the fish. As an example of the fishing map, here is shown density distribution of the adult sardine in a fishing ground on the Pacific waters along Honsyu (Figure 3). The maps indicate differences in the mode of assembly based upon the yearly cycle of life, not only in geographical position but also in density (Hayasi 1965, Kubo and Hayasi 1964, Tokai Reg. Fish. Res. Lab., 1964). Thus works on the individual aspects must start from the fishing maps that may essentially express the mode of assembly on the basis of the substantial knowledge upon the life of species.

The annual change in the mode of assembly thus expressed will improve recognized *substance* of the life of species. Namely, the fishing maps drawn for any particular yearly cycle of life may deform from year to year. The yearly deformation in the mode of assembly have been caused by inadequate classification of the maturation phase, or yearly changes of the environmental conditions or of the fishery activities. Therefore, the classification of the yearly cycle is to be inspected at first. It should be noted that the inspection of the yearly cycle of life covers the inspection of the related categories which mutually define themselves. Discovery of any inadequate classification means advance of the investigations of the life of species. If no misclassification is discovered, the deformation will be attributed to the yearly change of environments, and then of the fishing activity. Repeating the procedure, it is possible to examine the three factors underlying the phenomena. Further consideration on the existence of fish indicates such series of conceptions as community, species population, systematic fraction, migratory group, shoal and individual. Actually the latter conceptions are more fundamental, while the biologist usually commences his study under the former conceptions such as community or species population. It is necessary to treat the conceptions from community to shoal in order to assess the species population itself, however. Similar systems of conceptions are required for the studies on environments and productive power of human beings. We may be able to consider real relationships between fishes, environments and productive power through examinations of the three systems but not by direct comparison of phenomena based on the individual aspects.

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PRESENT STATE OF THE INVESTIGATIONS ON THE ARGENTINE ANCHOVY *ENGRAULIS ANCHOITA* (HUBBS, MARINI)

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INTRODUCTION

The present economic structure and the population growth in Argentina render more manifest every day the necessity for paying increased attention to problems concerning sea fisheries in this country. The importance of the Argentine sea, with its abundant fishery resources, as a source for obtaining basic proteins has become increasingly evident, and therefore the need for studying the marine environment and its resources becomes a very necessary task.

As one would naturally assume, priority is given to those marine organisms whose economic importance is greatest. Among these species of economic interest is the anchovy (*anchoita*).

Research on the anchovy, up to 1960, the date on which the "Instituto de Biología Marina" of Mar del Plata was created, was in a preliminary stage, with some few papers on the subject that, although quite valuable, were rather scattered. From that date on these studies were intensified, and became a long term project. Despite the existence of several obstacles of various kinds, *e.g.* the lack of a sea research ship for field work and exploratory fishing, financial problems, etc., the research done on the anchovy to date constitutes a considerable progress towards a basic knowledge of this species.

The aim of the present work is to compile the available data on the Argentine anchovy which refers to fishery, general biology, and its economic importance to Argentina.

FISHERY

The fishery exploitation of the anchovy reflects the overall picture of fisheries in Argentina. It is typically of little intensity, has low efficiency per unit effort, is limited to a short seasonal period, and is associated with an underdeveloped canning industry, which is concentrated in a single port (Angelescu, 1963).

The anchovy together with the mackerel (*caballa*), both of which are of great economic importance, form the basis of the coastal fishery production.

Coastal fishery is understood herein to be that wherein natural resources in the proximities of the coast are exploited with low tonnage boats (3-30 tons), having operational range of 1 to 6 days, and without refrigeration facilities (Figure 1). The predominant type of vessel for coastal fishing is a small boat without any cabin, manned by a skipper and a crew from 4 to 10 sailors. In the fishing of the anchovy, pairs of boats generally work in association. In most cases the fishing is done within a radius of from

2 to 30 miles from the port. The boats leave at dawn and return to port from noon up to the early hours of the night.

The fishing craft used for the anchovy is a type of roundhaul net.

The figures given below illustrate and emphasize the importance of the anchovy in the Argentine fisheries. These figures refer to the last available data for the year 1963 given by the "Dirección General de Pesca y Conservación de la Fauna". (General Directory of Fisheries and Wild Life Conservation) of Argentina (1963).

TABLE 1
PRODUCTION OF COASTAL SEA FISHERY IN METRIC
TONS FOR 1963

Anchovy (<i>anchoita</i>) <i>Engraulis anchoita</i>	Mackerel (<i>caballa</i>) <i>Scomber japonicus</i>	Other Species	Total
12,520.4 23.6%	11,585 21.8%	28,933 54.6%	53,039.2 100%

Although the large schools of anchovy are scattered throughout vast extensions of the sea, the area of exploitation is quite small, and almost the totality of the fishing is done in the area bounded by the parallels 37° and 39° S. The principal port, both for the fishing and the industrialization of the anchovy, is Mar del Plata, in the Province of Buenos Aires (lat. 38° S). In 1963, out of the 12,520.4 tons of the total catch of anchovy, 11,795.6 tons came from the Mar del Plata area.

The fishing for anchovy is a seasonal activity depending upon the migrations performed by this species between the coastal region and the open sea. The catches of anchovy are obtained mainly in the months of September, October and November. The greatest peak appears in October. In 1963, 88.6% of the total catch for the anchovy was obtained during these 3 months. During the anchovy season, the majority of the coastal boats work on anchovy fishing.

A certain portion of the catch is destined for consumption as fresh fish, but the greatest part is industrialized. For this reason the fishing of the anchovy is mainly regulated by a *pro rata* system. The canning industry communicates its needs to the center which groups the skippers of coastal fishery boats, and they distribute the requested amount according to the number of boats serving the factories.

It is to be emphasized that the Argentine fishing industry concentrates mainly on the elaboration of products from the mackerel and the anchovy. There



FIGURE 1. Typical coastal boats, Port of Mar del Plata.

are many different processes for the anchovy, ranging from simple salting (similar to herring salting), to sterile canning with oil or sauces.

On the other hand, the scales of the anchovy which become detached very easily from the body and accumulate abundantly on the sides of the boats during fishing, have proved to be valuable material for the manufacture of cosmetics and ornamental objects. During one fishing season, about 15,000 Kg of scales can be gathered.

The possibilities for the exploitation of the anchovy are beyond the present absorption by the canning industry. It will be possible to expand the present exploitation by dedicating the anchovy to other industrial ends, such as production of oils, flour, etc. as well as encouraging and aiding its consumption as fresh fish. Also, by expanding the fishing areas, using better fishing equipment and taking appropriate economic measures, a much greater advantage could be obtained from this important natural resource.

GENERAL BIOLOGY

General Characteristics

The Argentine anchovy was named as a new species, *Engraulis anchoita*, in 1935 by Hubbs and Marini (Marini 1935). This latter author was of the opinion

that this species was already included in scientific literature, but under names which were taxonomically inappropriate.

The anatomy of *Engraulis anchoita* shows characteristics typical of the entire genus *Engraulis*, the members of which are particularly distinguished by the large opening of the mouth which is ventrally situated. The snout is projected anteriorly, forming a slight prominence.

The main meristic characteristics of this species, according to Marini (1935) and Fuster de Plaza and Boschi (1958) are as follows: vertebrae 45-45; gill rakers 23-39 and 32-48; anal rays 19-25; dorsal rays 16-19; lateral line scales 40-42.

This species has a wide geographical distribution, from San Sebastian Island, Brasil (lat. 24° S) in the north, to a location near San Jorge Gulf, Argentina, (lat. 42° S) in the south (Figure 2). The vertical distribution depends upon the location of the thermocline. The anchovy does not reach waters with temperatures inferior to 9°-10° C, that is, at depths of 20-50 m in the open sea (Angelescu, Fuster de Plaza, 1962).

The data available on this species refer mostly to the anchovy of the areas of the Province of Buenos Aires, which is the fishing region concerned.

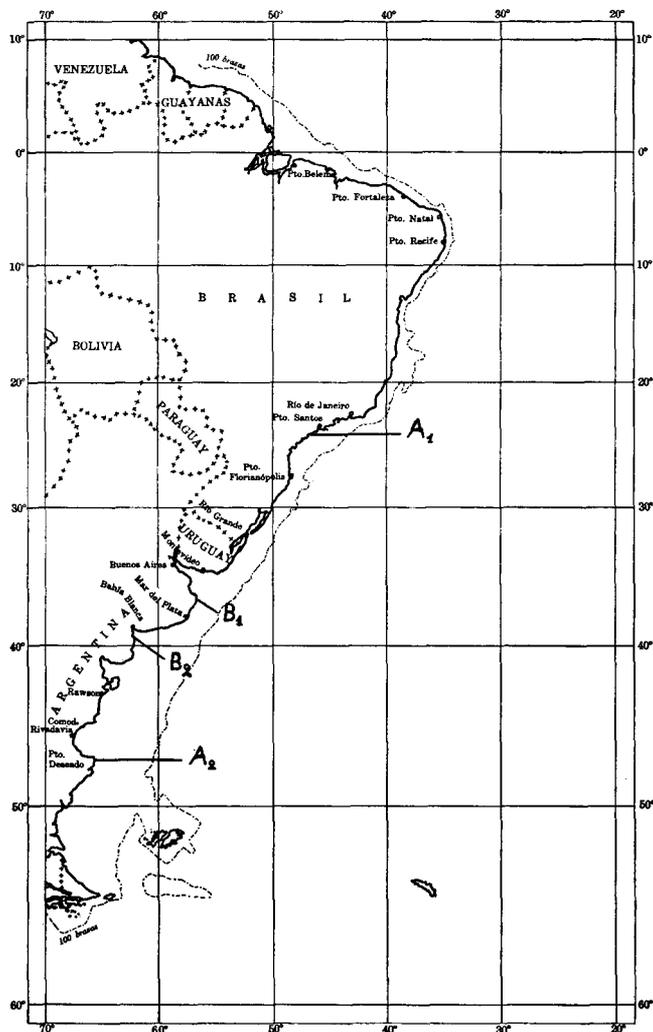


FIGURE 2. Distribution and fishing limits of the Argentine anchovy. A₁-A₂-Geographical distribution. B₁-B₂-Area of the approximate fishing totality.

Population Problems

In 1958, Fuster de Plaza and Boschi (1958) had assumed the existence of different anchovy populations with differentiable meristic characteristics. Further investigations by Fuster de Plaza (1964) led to confirmation of this assumption and established the existence of two different anchovy populations: one whose reproduction takes place in the Spring and another, whose reproduction takes place in the Autumn. This conclusion has been based on meristic differences (mean number of vertebrae), distribution of modal classes of the samples over a period of time, biological differences in such variables as growth rate and the attainment of the first sexual maturity in individuals of both populations, and also in observations of the state of maturity of the gonads throughout the year. This conclusion is partially supported by results obtained by the present author (1965). These results are based on data obtained from eggs, larvae and juveniles of the anchovy. They were gathered

by systematic sampling throughout the year, and were elaborated with quantitative methods. They show that the reproduction of the anchovy takes place in its most intensive rhythm during October, as temperatures of 11.5°-14° C, and reaches a slight peak in February, at a water temperature of 20° C. The present author has also shown by means of experiments that the optimum temperature for the embryonic development of the anchovies spawning in October is between 10°-17° C, and that a temperature of 20° seems to be off the optimum point. This observation may also lead to the same assumption of the existence of two different populations of the anchovy with different physiological characteristics.

This problem becomes somewhat complicated by the fact, discovered by the present author, that the Argentine anchovy reproduces throughout the entire year. The problems arising from the populations of *Engraulis anchoita*, such as is the case with other species are very complex and await further and more detailed research.

Fecundity

There are data published on the fecundity problem of the anchovy by Fuster de Plaza (1964), who determined the degree of fecundity of the Spring anchovy alone. There are no available data on the Autumn anchovy. This is due to difficulties in obtaining study material, since this population is not subject to commercial exploitation at present. The results obtained are based on counts of the number of oocytes of greater length in the ovaries of mature females. In the ovaries of the females which are in process of maturation, four different egg groups of differing degrees of maturity can be distinguished. When spawning is near, three of these groups can be more clearly observed. During the spawning the females lay the first oocytes from the group of greatest oocytes, and after a certain period of time lay oocytes from the second group. After this partial evacuation, the females leave the spawning area, retaining in their ovaries oocytes in different stages of development.

There exists, in this species, as in several other species of fish, a strong correlation between the number of oocytes in the ovary and the total length of the individual. For instance, the number of oocytes observed in the group of greatest size for females of different total lengths are, according to Fuster de Plaza:

Total length (mm)	115	140	160	175	190
Number of oocytes	4,400	9,368	15,084	21,954	24,920

Reproduction and Early Life History

The first sexual maturity of the anchovy is strongly related to the minimum length and, according to Fuster de Plaza (1964), anchovies of the Spring population reach their first maturity when they are 120-130 mm long, while those from the Autumn population reach theirs when their length is 115-120 mm. This author states that from July to August, adult individuals of the Spring population gradually

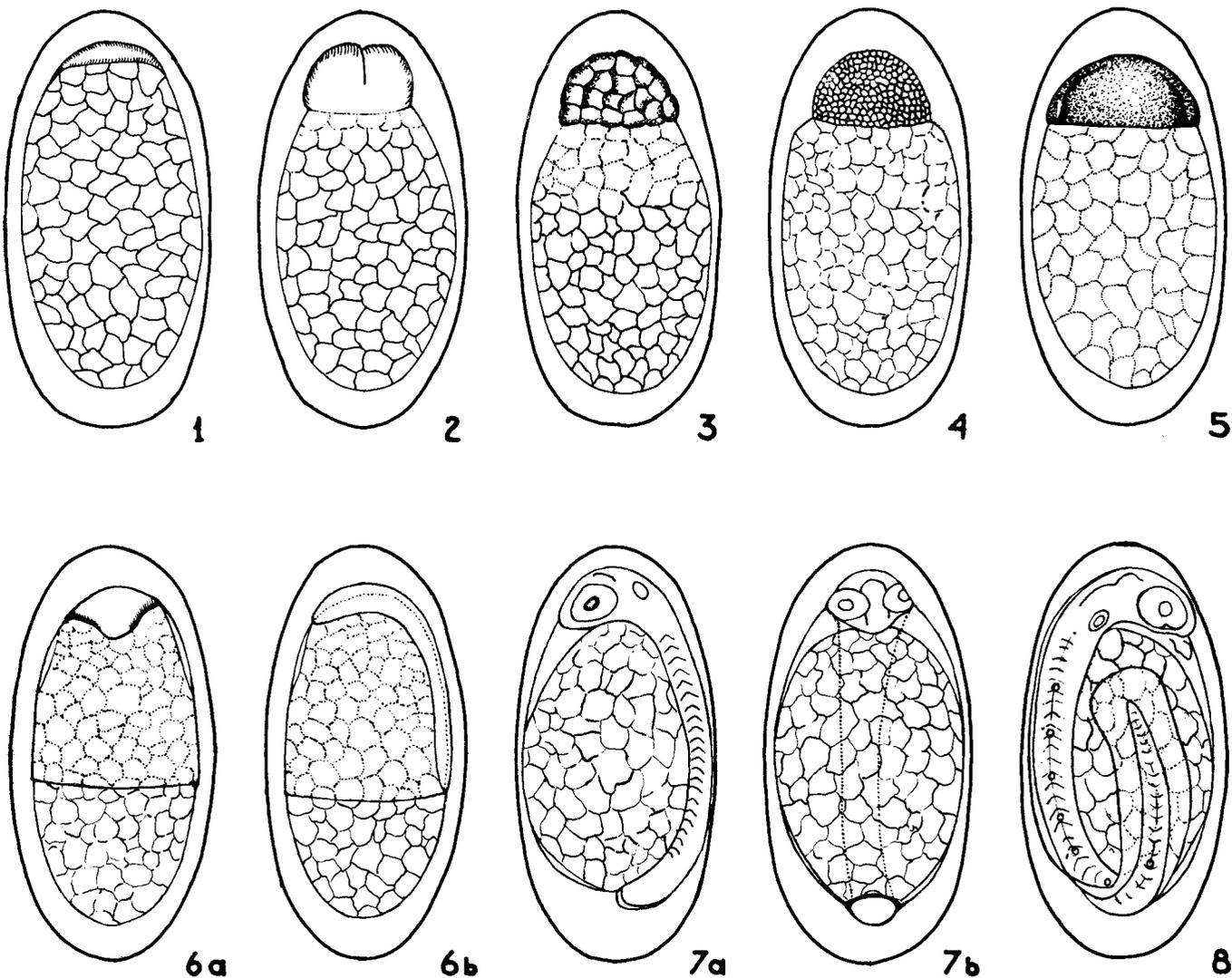


FIGURE 3. Embryonic development of the anchovy (*Engraulis anchoita*). 1. Formation of the first cell; 2. Two-blastomere stage; 3. Formation of the blastula; 4. Blastula; 5. Gastrulation; 6. Neurula, a) frontal and b) lateral view of same; 7. Commencement of the separation of the caudal region from the vitelline sac; 8. Embryo immediately prior to hatching (from Dz. de Ciechowski 1965).

approach the coast in the area near Mar del Plata, where they appear forming great schools from September onwards. The schools stay in the area until the beginning of Summer, when they start moving towards the open sea. A similar migration occurs with the adult individuals of the Autumn population that also migrate for reproduction in the period from February to March. After spawning, they return to the open sea.

The problem of the reproduction and embryonic and larval development of *Engraulis anchoita* has been studied in greater detail by the present author, who has incorporated the results in the papers presently in press. It has been possible to determine the exact period of reproduction of this species on the basis of appearance and disappearance of the eggs, larvae and juveniles of the anchovy in the sea. This has been accomplished by a systematic collection of the material and the use of quantitative methods.

The intensity of spawning was related to changes in sea temperature. The reproduction of the anchovy starts in September, very close to the coast, at a temperature of about 10° C, and reaches its peak in October at a temperature of about 11°–13 °C. From November onwards the anchovy continues its reproduction in a more or less intensive form, and apparently, more towards the open sea. In February, the spawning intensity reaches a slight peak. In March, the intensity of spawning seems to decline and apparently takes place more towards the open sea. Spawning continues in this manner until September. The existence of two periods (October and February) of greater intensity agrees with the results given by Fuster de Plaza (1964) on the basis of an examination of adult individuals.

There occurs in the anchovy a daily spawning rhythm, ranging from 8 pm until 12 pm. The determination of this daily rhythm by the present author

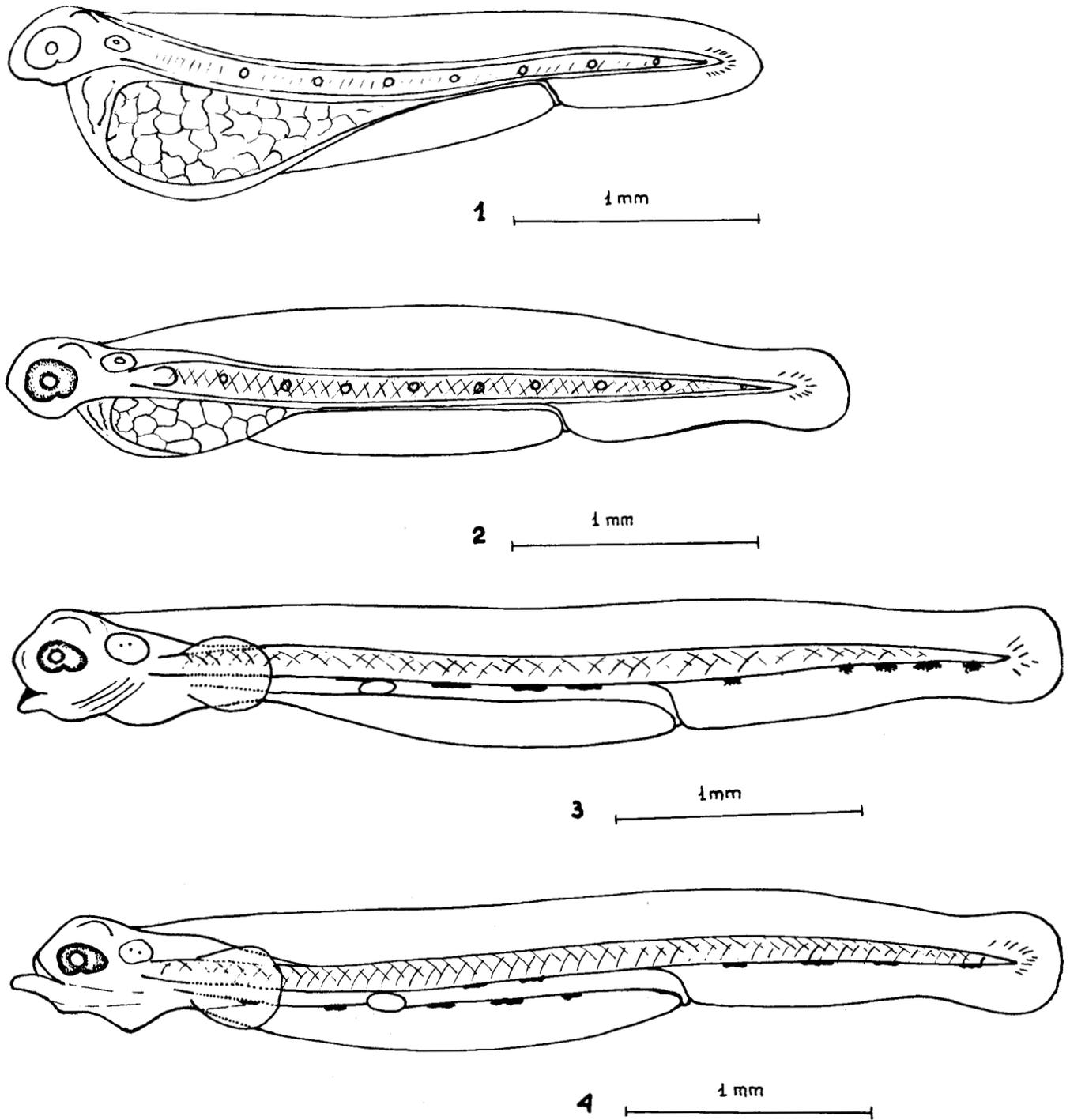


FIGURE 4. Larval development of the anchovy (*Engraulis anchoita*). 1. Recently hatched larva; 2. 2½-days larva; 3. 4-days larva; 4. 10-days larva (from Dz. de Ciechomski 1965).

enabled her to obtain mature female anchovies (which is impossible during other hours of the day), and to successfully achieve their artificial fecundation.

The embryonic development of the anchovy is quite rapid. The most detailed drawings and descriptions of the embryonic and larval development have been given in a paper by the present author, "Observaciones sobre la reproducción y desarrollo embrionario

y larval de la anchoita argentina (*Engraulis anchoita*)" (Figures 3, 4, 5).

The measurements of the eggs show rather pronounced variations: 1.15–1.55 mm for the major axis and 0.66–0.80 mm for the minor axis.

In the earlier stages of development, the eggs float vertically with their blastodiscs pointing downwards. As the enveloping of the yolk progresses, the

orientation of the eggs becomes increasingly horizontal. At the stage of Kupffer's vesicle, the egg floats horizontally, coming closer to the bottom during the last stages of development.

The hatching mechanism is always the same. Once this stage is reached, the membrane of the egg suffers a neat incision at a distance from the cephalic end equal to $\frac{1}{3}$ the total length of the egg. After rupture has taken place, the embryo frees itself from the egg membrane in about 3 minutes. It should be emphasized that the rupture occurs always at the same distance in respect to the total length of the egg.

The vitelline larva of the anchovy measures 2.70–3.40 mm at birth. The larva is rather undeveloped at birth and does not show pigmentation on any part of its body. The heart at work is quite visible, but no blood circulation can be observed in the vessels. These appear to be typical characteristics of planktonic larvae. The pigmentation begins to appear the third day after hatching. After 4 or 5 days, the vitellum has been reabsorbed and the mouth begins to be functional.

It is impossible at present to breed larvae of the anchovy in aquaria for a period of more than 8 to 10 days. After this time all the larvae die, probably because of the lack of appropriate food.

Ossification in the larvae of the anchovy commences relatively late, and the first ossified elements, *cleithrum* and *dentale*, appear when the larvae have a total length of 6 mm. When the larvae have reached a length of 33–34 mm, they have lost all of their larval

characteristics except the snout. At the length of 44–45 mm, they resemble completely the adult individuals, and therefore pass into the juvenile stage.

The influence of some environmental factors: temperature, salinity, light and mechanical factors, upon the embryonic development of the anchovy is known. This information has been obtained by the present author by means of experimental research, and has been given in a paper presently in press. The temperature has of course a certain influence upon the speed of development. As was stated above, the development is quite rapid. It lasts for 68–72 hours at a temperature of 14°–15 °C and for 50–53 hours at 19°–20° C. The optimum temperature for embryonic development appears to be in the range of 10°–17° C. These data refer to the October anchovy which reproduces at lower temperatures than the Autumn anchovy, whose temperature range might be different. A temperature of 4° C is lethal.

Experiments upon the influence of salinity have shown that the Argentine anchovy is not so tolerant in respect to salinity threshold as some of its relatives, such as *Engraulis encrasicolus*. The salinity boundaries within which *Engraulis anchoita* develops in more or less normal manner might be fixed between 25.8% and 50%. Outside of this range, the development is abnormal, with frequent production of monstrosities.

Light does not seem to have any sensible influence upon the embryonic development of *Engraulis anchoita*. The embryos of the anchovy are very sensitive

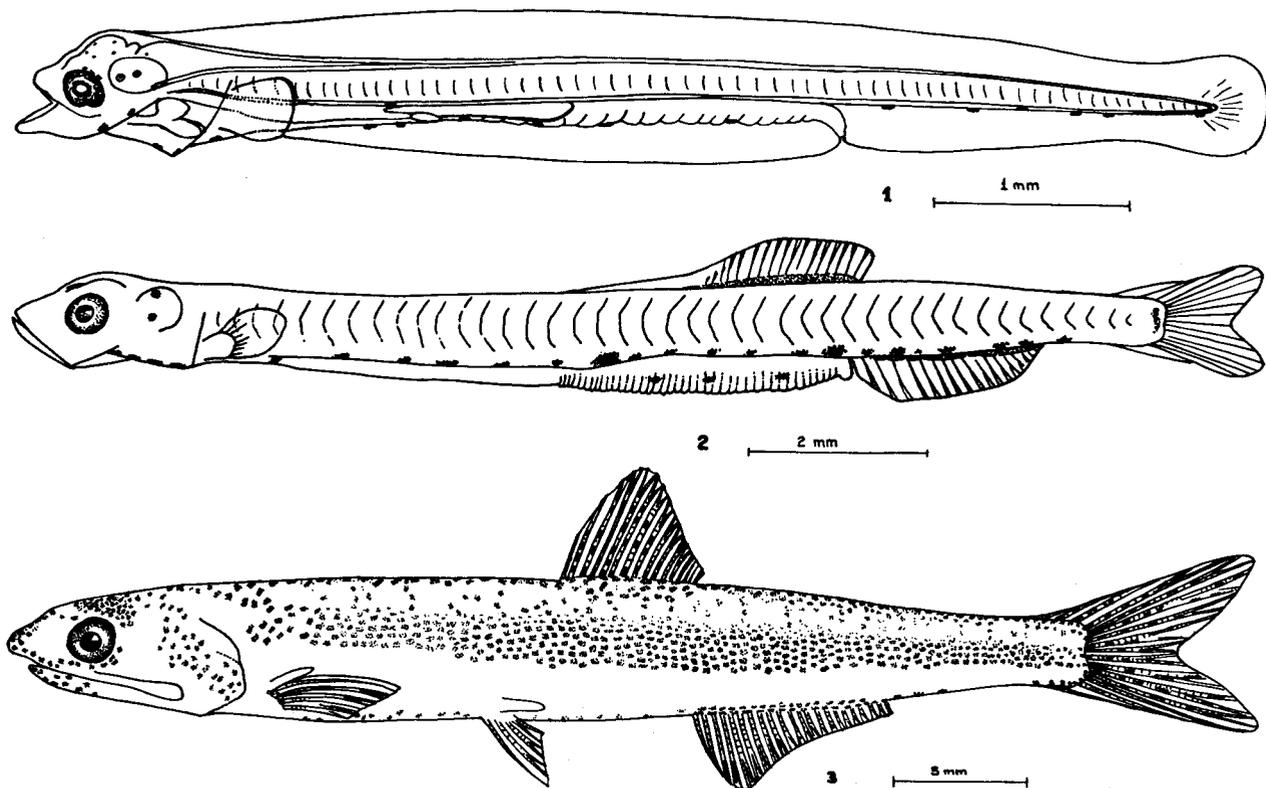


FIGURE 5. Termination of larval development of the anchovy (*Engraulis anchoita*). 1. 6 mm larva; 2. 13.5 mm larva; 3. Juvenile of 44 mm (from Dz. de Ciechowski 1965).

to the influence of mechanical factors. This sensitivity is at its peak in the earliest stages of development, including early gastrulation. In view of this fact the present author believes that high seas and storms might have some influence upon the fate of anchovy embryos which are, at the time, in this stage of development.

Growth, Age, Condition Factor, and Metabolism

The Argentine anchovy is a fish of short life that reaches its sexual maturity and becomes already a subject of commercial fishing at the age of one year. The problems concerning its growth, age, condition factor and metabolism were studied by Fuster de Plaza (1964). The results obtained by the same worker are based upon a statistical elaboration of data, applying the method of Petersen. According to Fuster de Plaza, the distribution of the samples in modal classes through time show the existence of two populations of anchovy; the spring and autumn populations, with their corresponding growth parameters. Both populations show an active growth until the end of the third year of life. From then on, growth decays sensibly. The calculated length at the fourth year of life is 185 mm for the spring anchovy, and 175 mm for the autumn anchovy. Growth is halted in both populations during the winter months. According to Fuster de Plaza, the total lengths of the anchovy during the first 4 years of life are as shown in Table 2 (Petersen Method).

TABLE 2
MODAL CLASSES IN MM

	1 ₁	1 ₂	1 ₃	1 ₄
Spring population -----	130	150	175	185
Autumn population -----	110	135	165	175

Little is known about the growth of the anchovy in its first stages of life. In a paper currently in press, the present author shows that the analysis of the monthly distribution of length frequencies of larvae and juveniles, taking into consideration the first moments of intensive spawning, seems to indicate that the juveniles of anchovy reach a length of 60 mm when they are in the third month of life.

According to Fuster de Plaza, the rate of weight increase in the adult anchovy is greater than the rate of length increase, and the development of the body takes place in a more or less harmonious manner along the three body axes. Also, the value of the Condition factor K shows a progressive increase with the growth of the individuals. For adult individuals in the open sea, during their period of intense nutrition, this factor is of 0.70 to 0.90, whereas for juveniles individuals in coastal waters, the same factor ranges from 0.50 to 0.73.

The degree of fatty accumulation in the viscerae of the anchovy is related to the stage of development of the sexual glands. The greater deposits of fat are found in anchovies which have gone through the reproductive process and are in a state of repose.

Fuster de Plaza has determined also the metabolic specific factor k , following criteria due to Bertalanffy,

who considered the metabolism of fishes to be proportional to body surface. The average value of this factor for the anchovy is 8.75. It also appears that there is no sensible decline of the metabolic rate with the increase of the length.

Feeding

The present author has undertaken studies of the food and feeding habits of larvae and juveniles of anchovy. The characteristics of the alimentation at different developmental stages have been related to the morphological changes taking place throughout the development of the individual. The first results (not yet published) show that the anchovy larvae which are 3–5 mm long (that is, after reabsorption of the vitellus) feed almost exclusively on the eggs and nauplii of Copepoda, and small eggs from other organisms. In larvae from 5 mm to 35 mm long, it has been impossible at the present to find remnants of food. This should be due to the structure of the digestive tract, which in this stage of development is like a straight tube, with a slight ketch of stomach in the greater larvae. From the length of 35 mm on, the percentage of individuals in whose intestines food is found, becomes higher.

The basic food for individuals from 35–80 mm long are Copepoda in all stages of development: eggs, nauplii and adult forms. Besides Copepoda, there are also to be found juveniles of Decapoda and other Crustacea, eggs from various marine organisms and more rarely, larvae from fishes and Mollusca. In the food of juveniles from 40 mm long are found Radiolaria, and Acantharia, but in scarce amounts. In the food of juveniles with a length of more than 50 mm there appear Diatomea and Dinoflagellata, always with other zooplanktonic forms.

Fuster de Plaza (1964) and Fuster de Plaza and Angelescu (1962) obtained somewhat different results with respect to the alimentation of the juveniles of anchovy. They found their food to be primarily composed of phytoplankton. In individuals from 50 mm to 100 mm long in the primarily phytoplanktonic food, they found a predominance of Diatomea. As the juveniles approach the adult stage, the alimentation becomes preferentially zooplanktonic.

According to said authors in the food of individuals from 150–190 mm long, there are Copepoda, especially from the family Calanidae, pelagic Amphipodae (*Parathemisto* spp.), Sergestidae (*Sergestes* spp.) and sometimes juveniles of anchovies and other fishes.

The anchovy is plainly a plankton feeding species and is located in a low trophic level, near the primary production link.

Migrations

Although many data are lacking for a precise determination of the population dynamics of the anchovy, it is possible with the available data to reach some conclusions on the migration of large schools of anchovies in the area of the Province of Buenos Aires.

As was shown in the preceding sections, the migrations of the anchovy are both trophic and reproductive in character. On this matter there are data published

by Fuster de Plaza (1964), and Angelescu and Fuster de Plaza (1962).

During the vital cycle of this species, the juveniles find their first trophic habitat in coastal waters, where they remain the entire year until they reach their first sexual maturity. After spawning they migrate toward open sea regions, where they find abundant food. The same thing happens to the older adults that reach coastal waters in order to reproduce. Therefore trophic migrations are complemented by reproductive migrations in an alternating cycle throughout the seasons of the year, between coastal and open sea waters.

In the period from November to May, the majority of the schools made up by adult anchovies concentrate in the middle region of the continental shelf and in the neighborhood of the continental slope. The summer trophic habitat of the adults coincides with the areas of greatest wealth in nutrients and plankton. From July to August, with the maturation of the sexual glands, the adults of the spring population begin to approach the coastal waters for spawning. In this way, large schools of anchovies appear in the coastal waters from September on. After spawning is accomplished they return to open sea regions.

The same migration pattern is shown after a certain period of time by the adults of the autumn population. As a result of these migrations, the anchovy reaches during the summer months its greatest extension in the horizontal plane of the Buenos Aires continental shelf.

Other Data

There are some preliminary data from studies of the blood of *Engraulis anchoita*. According to Conroy and Rodriguez (1964) and Conroy (personal communication) the quantity of erythrocytes in 1 cc of blood is 2,300,000 and their dimensions are 7.5 microns wide and 12.0 microns long. The average percentage of hemoglobin (Sahli) is 79. In gm/100 ml this value is 12.64. Another study by Conroy (personal communication) on bacteria shows that the viable bacterial count of the anchovy immediately upon arrival in port is between 158,000 and 250,000/g of flesh.

BIOECONOMICAL IMPORTANCE OF THE ANCHOVY

As was shown earlier, the anchovy is an important commercial product. Nevertheless, its greatest bioeconomic value evolves from the fact of its being a true "forage fish" for a great number of fishes, and, therefore, due to its low trophic level, a carrier of energy towards the upper trophic levels.

The subject of the importance of the anchovy in general bioeconomics has been widely treated by Angelescu and Fuster de Plaza (1962) and Fuster de Plaza (1964). These authors show that the anchovy, due to the great density of its schools and its wide distribution, is a key link in the intermediary stage of the bioproduction process, in connection with fishery exploitation in various areas of the sea.

Anchovy populations are subject to intense predation by mackerel (*Scomber japonicus*) and hake (*Merluccius merluccius hubbsii*), both of which are basic species of the Argentine fishery industry. As was pointed out by the aforementioned authors, the distribution of the anchovy in the area of the Province of Buenos Aires encompasses within its geographic boundaries the distribution area of the hake in the open sea. In the first region mentioned, the anchovy is the most important food, available in its juvenile stage, for the mackerel. In the second region it becomes, at the adult stage, the main source of food for the hake. In order to emphasize the importance of the anchovy in the bioeconomics of fisheries, the above mentioned authors made an approximate determination of the amount of anchovies taken by the mackerel and the hake during the warm weather season. According to these calculations, the fishing volume of the anchovy with an annual average of 10,000 tons, represents only a 3.3% of the amount consumed by the biomass of mackerel and hake caught commercially. The total catch of these two species during the Summer is approximately equivalent to a consumption of biomass of juveniles and adults of anchovy of up to 300,000 tons.

On the other hand, the anchovy is a major source of food for other fish eating marine organisms, especially predatory fishes of economic importance, marine mammals, and birds.

It appears from these facts that the anchovy, due to its intermediary position between primary production, zooplankton, and the consumers at higher trophic levels, is the species of maximum importance in the maintenance of the biomass of predatorial fishes.

A detailed study of these interspecific trophic relationships, by Angelescu and Fuster de Plaza is at present in an advanced stage of elaboration.

RESEARCH PROGRAM

Because of the great bioeconomic importance of *Engraulis anchoita*, it was considered opportune to establish an extensive plan of studies for this species in all the stages of its vital cycle.

The biological study of the anchovy, which is a part of the research program of the "Instituto de Biología Marina" of Mar del Plata, has been conceived as a ten-year project, and includes the analysis of meristic characters, fecundity, reproduction, alimentation, growth rate, sexual maturity and length distribution. A biostatistical sampling project of commercial landings of anchovy in the Mar del Plata area has been organized. This project is carried forth throughout the entire year, with the aim of establishing the structure and the dynamics of the populations.

Studies are aimed at a better understanding of the biology of the anchovy in its earliest life stages, that is, at problems related to the embryonic and larval development, alimentation and growth of larvae, and their behavior.

An intensive research programme is at present under way on the trophic relationship between the anchovy and other species of fishes, especially the mackerel and the hake, whose rates of ingestion, duration of digestion, total metabolism, etc., are being determined.

In the chemical aspect of the programme, studies are being made on the seasonal variation of the chemical composition, and on the bacterial spoilage of the anchovy under various conditions.

All these studies will be improved and intensified at the beginning of 1965 from a plan of technical assistance for fisheries drawn by the United Nations Special Fund and the Argentine Government.

On the other hand, experiments for another technique of anchovy fishing have recently been started, with different commercial aims. With this technique, a larger type of fishing vessel and another type of round trawl net are used in order to catch a greater number of fishes in a single haul. The product of these catches will be used in the manufacture of fish flour.

SUMMARY

In the present paper existing data of the investigations on the Argentine anchovy *Engraulis anchoita* are given. The following problems are considered:

- 1) Fishery
- 2) General biology
 - a) general characteristics
 - b) population problem
 - c) fecundity
 - d) reproduction and early life history
 - e) growth, age, condition factor, and metabolism
 - f) feeding
 - g) migrations
 - h) other data
- 3) Bioeconomical importance of the anchovy
- 4) Research program

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INFLUENCE OF SOME ENVIRONMENTAL FACTORS UPON THE EMBRYONIC DEVELOPMENT OF THE ARGENTINE ANCHOVY *ENGRAULIS ANCHOITA* (HUBBS, MARINI)¹

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An extensive literature exists on the problem of the influence exerted by several environmental factors upon the early stages of development in fishes. Other workers have dealt with this subject either from the point of view of obtaining a deeper knowledge of the biology of the species under research, or from the standpoint of solving some practical problems through their studies. Thus the majority of these publications refer to species of economical importance.

The object of the present work was to study the influence exerted upon the embryonic development of the Argentine anchovy *Engraulis anchoita* by the following environmental conditions: temperature, salinity, light, and mechanical factors. Special attention was given to the temperature, since this factor undergoes greater changes during the spawning period of the anchovy. The reproductive season of this species is quite long (Dz. de Ciechowski, 1965; Fuster de Plaza, 1964), lasting for approximately 9 to 10 months, and therefore the temperature varies considerably throughout this period. The investigation herein described was aimed at the determination of the developmental rate at different temperatures, and at an establishment of the optimal values and limits within which the embryonic development of the anchovy normally takes place.

In the case of salinity, an attempt was also made to establish the limiting values within which the normal embryonic development of the anchovy could take place. It was also the aim of this research to obtain salinity data in order to compare them with the values recorded for other related species of great salinity tolerance.

In the case of light, it seemed to be of interest to determine whether this factor exerts any influence upon the embryonic development of the anchovy.

Upon noting the great mechanical susceptibility of the eggs of *Engraulis anchoita*, it was considered of interest to study this phenomenon in detail. The investigation was thus directed towards a determination of the developmental stages of the embryo at which this susceptibility manifested itself with the greatest intensity. A study of this problem is of particular interest since high seas and storms may have some influence upon the fate of anchovy embryos which happen to be in development under those circumstances. Rollefson (1930), in his work on the cod, has shown that intense wave movement does have an

effect on the embryonic eggs of fishes. According to this worker, the years of very good catches were always preceded by years of light winds and fine weather during the reproduction season of this species.

MATERIALS AND METHODS

As basic material for the experiments, eggs obtained by artificial fecundation as well as eggs collected from plankton were used. Artificial fecundation was accomplished using the method usually employed to this end. The eggs obtained from plankton were selected so as to use those which were in early stages of development, (i.e., up to the beginning of the blastula stage).

For the experiments concerning the influence of temperature, the eggs obtained from artificial fecundation were placed in different aquaria, some being kept within a temperature ranging from 19° to 20° C., some within 14° to 15° and others at 4° C. The temperature of 19° to 20° C. was obtained by means of a thermostat; the 4° C. by placing the aquarium inside a refrigerator, whilst the 14°-15° C. corresponded to the room temperature at that time. For technical reasons, it was impossible to obtain temperatures ranging from 8° to 10° C.

In the experiments made concerning salinity, the following procedure was used: to obtain salinities lower than normal, distilled water was added to the filtered sea water; to obtain salinities higher than normal, a suitable amount of sodium chloride was added. Experiments were made with the following salinity values: 3.9 ‰; 8.4 ‰; 16.8 ‰; 25.2 ‰; 33.5 ‰; 50 ‰, and 60 ‰.

To study the influence of light, an aquarium containing eggs in development was kept in complete darkness, another one was kept under continual illumination, whilst a third was maintained with natural light as a control.

The study of the mechanical susceptibility of the embryos was made by submitting the embryos at different stages of development to the effects of different pressure, and of shocks resulting from their being dropped from different heights. To study the pressure factor, the eggs were placed between two slides, three at a time, arranged so as to form a triangle. Progressively larger weights were then placed upon the slides. After each manipulation the eggs were examined under the microscope in order to determine the resistance of the membrane and of the embryo. These

¹ This paper has been prepared through the sponsorship of the Council for Scientific and Technical Research of Argentina.

weights which produced the rupture of the membrane, or which produced signs of destruction in the embryos, were considered to be critical weights. This method is similar to the one used by Galkina (1957), in her work on the herring of the Okhotsk Sea. In order to submit the eggs to shocks, they were taken in approximately equal amounts by means of a pipette, and were dropped upon a nylon tulle tautly extended on the concave side of a petri dish. The eggs were dropped from heights of 25 and 50 cm. The embryos used were in the following stages of development: the beginning of blastula, early gastrulation, the stage at which the blastoporic ring exceeds the equator of the eggs, and embryos in the stage of tail growth. The eggs submitted to shock were placed in aquaria and the following day the mortality rate was determined. A similar method was employed by Rollefson (1932) for determining the susceptibility of cod embryos.

The eggs used for the light, salinity, pressure and shock experiments were kept at a temperature ranging between 14° and 15° C. The embryos used in all the experiments developed from eggs of anchovies which approached the shore for reproduction in October. This last observation is necessary, especially in regard to experiments on the influence of temperature, since it is known that embryos from anchovies spawning in summer (for instance) at much higher temperatures of the water, can show different physiological characteristics with respect to the temperature factor.

INFLUENCE OF TEMPERATURE

As is well known, the rate of the embryonic development of a given species is directly related to the temperature. The higher the temperature, the more rapid the developmental processes take place (Leiner, 1923; Vucetić, 1957, etc.). In this respect the anchovy follows the general rule. At the temperature of 14°–15° C., hatching occurs 69 to 72 hours after fertilization; at 19°–20° C., 50 to 53 hours after fertilization. The rate of development within the aforementioned temperatures is shown in Table 1.

Besides the differences in developmental rate, other phenomena related to temperature became apparent.

TABLE 1
THE EMBRYONIC DEVELOPMENT OF THE ANCHOVY AT DIFFERENT TEMPERATURES

Stage of development	Hours of development	
	14–15° C.	19–20° C.
First cell formation.....	0 h 35 m	0 h 35 m
Two—blastomere stage.....	1 h 10 m	1 h 00 m
Four—Blastomere stage.....	1 h 40 m	1 h 20 m
Early blastula.....	2 h 25 m	2 h 00 m
Blastula.....	5 h 00 m	4 h 20 m
Early gastrula.....	16 h 45 m	15 h 30 m
Closing of the blastopore.....	33 h 30 m	29 h 00 m
Blastopore closed. Stage of Kupffer vesicle.....	39 h 00 m	32 h 30 m
The embryo occupying $\frac{3}{4}$ of perimeter.....	56 h 30 m	44 h 30 m
The embryo occupying $\frac{1}{4}$ of perimeter.....	66 h 00 m	50 h 00 m
Hatching.....	69 – 72 h	51 – 53 h

Within 14° to 15° C., 90 to 95% of hatching is obtained with very few anomalous cases, whilst within 19° to 20° C., 80 to 90% of the eggs hatch, and anomalies appear with greater frequency. These anomalies consist mainly in axial deviations, especially in the region of the tail. Differences in the length of the larvae born at these different temperatures have not been observed. The influence of the temperature was manifested also in the heart beat. The heart beat of an embryo immediately prior to hatching, at temperatures within 14° to 15° C., was on the average 65 to 70 beats per minute, whilst at temperatures between 19°–20° C., it was about 100 beats per minute.

A temperature of 4° C. was lethal for the embryos of anchovy. Eggs placed at 4° C. in the early blastula stage showed a complete halt in their development. After 5 to 6 days, and always in the same stage, they died and became opaque. When eggs which had been kept for 1 to 2 days at 4° C. were transferred to aquaria at a normal temperature (14° C.), their death occurred more quickly. Thus the lower temperature seems to cause irreversible changes.

From the aforementioned results, there seem to be grounds for making certain assumptions with regard to the optimal temperatures for the embryonic development of the anchovies reproducing in spring.

As has been mentioned in a previous publication (Dz. de Ciechomski) the anchovy begins to spawn in a rather intensive way at 10° to 11° C. The greater spawning intensity is achieved within 11.5° to 13.8° C. Thus a temperature of 10° C. may be considered as the lower limit of the optimal temperature range for development. It has been noted that development at a temperature within 19°–20° C. does not take place in a completely normal manner, and thus there seems to be an upper temperature limit to the optimal range. The assumption which can be made from these data is that the anchovy which spawns in the spring has its optimal developmental range within 10° C. and 16°–17° C. These values might be somewhat different for individuals of the same species that reproduce in summer at higher water temperatures.

INFLUENCE OF SALINITY

A large number of species of the clupeid group show great tolerance in respect to the salinity factor. For the embryonic development of *Clupea harengus*, Ford (1928) gives salinity limits from 4.8‰ to 37.8‰. Holliday and Blaxter (1960) give the values 5.9‰ to 52.5‰ (for the same species). Demir (1963) observed that *Engraulis encrasicolus* in European waters can develop normally within salinities from 9‰ to 37.5‰. For the species of the family *Engraulidae* which live in waters close to the American Continent, no sufficient data are available at present on this problem.

In the case of the Argentine anchovy (*Engraulis anchoita*) it has been possible to establish that it does not possess as great a tolerance in respect to salinity thresholds for its embryonic development.

Anchovy eggs which are transferred at any stage to water of a lower than normal salinity sink and

continue their development whilst lying on the bottom of the aquarium. Upon transferring the eggs at the blastula stage to water with a salinity of 3.4‰, most of the embryos die within a short time. Many eggs increase in size and take the shape of a very wide barrel. This phenomenon is probably caused by perturbations in osmoregulation. Some of the embryos reach the Kupffer visiele stage, all of them showing anomalies in the axial part. The axis of the embryo takes the form of an "S" or a sinuous shape, as is shown in Figure 1. At this stage all of the eggs die. When the transfer has been made while the embryos are still in the stage at which the tail has already been separated from the vitellus, the embryos continue their development only for a short time. Then they come to show axial alterations as in the preceding case, and they die. The embryos transferred in the

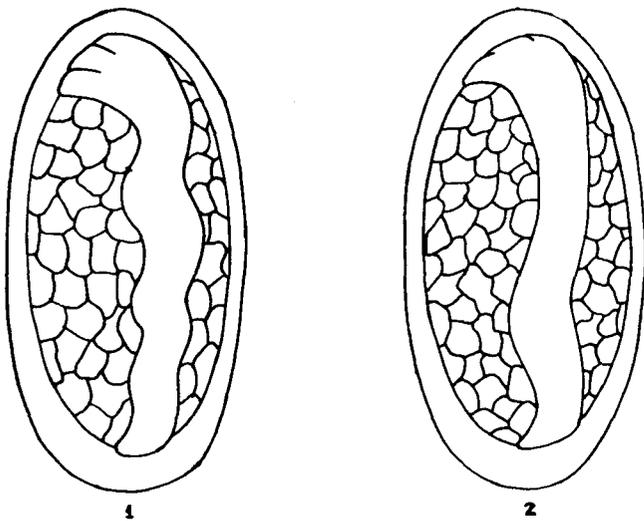


FIGURE 1. Embryos of the anchovy maintained at salinity 3.4‰ showing anomalies in the axial part.

blastula stage to water with a salinity of 8.4‰ continue their development up to the stage in which the embryo occupies about $\frac{2}{3}$ of the perimeter of the egg. From this moment on the eggs all die. An increase in the size of the eggs is not observed as at 3.4‰ salinity, but most of the embryos show the same axial alterations.

The embryonic development seems to lag a little as compared to the controls. In water with a salinity of 16.8‰, the embryos develop at a somewhat slower rate than the controls and most of them (60 to 70%) are able to hatch. Among the resulting larvae a few appear to be normal but die soon after hatching. Most of the larvae hatch in an earlier stage of development than the controls and many of them show abnormalities, especially in the region of the tail. These latter results offer grounds for assuming that low salinity has a greater effect on the development of the embryo than upon the action of the hatching enzymes. With water of 25.8‰ salinity, normal hatching of approximately 60% of the eggs is obtained. These larvae do not differ from the controls and

appear to be normal. From the remaining 40% a small portion does not reach the hatching stage and most of the larvae show small abnormalities. Eggs in any stage of development, when kept in high salinity water, remain buoyant close to the surface. The value 33.5‰ corresponds to the normal salinity at which the anchovy spawns in the sea.

Observing the embryonic development of the anchovy in salinities higher than normal, several results are obtained. In water with 50‰ salinity, development continues in a more or less normal fashion. The hatching rate is high (90–95%) and few abnormalities are observed. The developmental rate appears to be to a certain degree higher than that of the controls. In water of 60‰ salinity, about 70% of the embryos reach the hatching stage. Most of the embryos that hatch are abnormal, and in most cases, show anomalies in the region of the tail (Figure 2). Some monsters are born almost without a tail. These

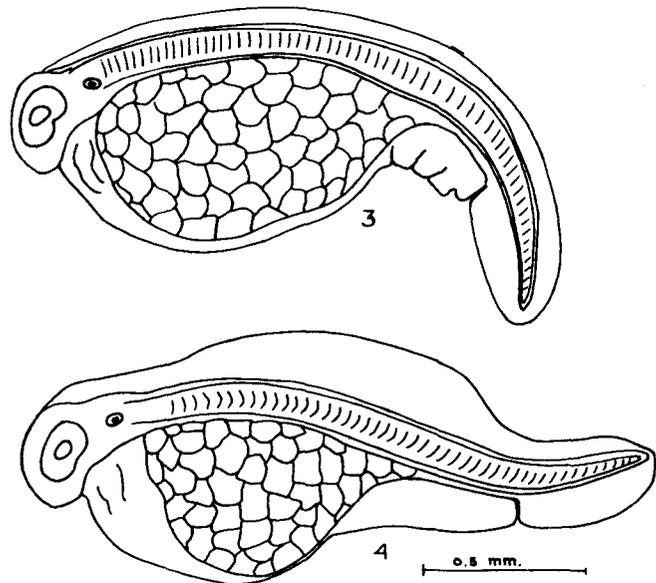


FIGURE 2. Monsters of the anchovy born in water of 60‰.

larvae reach a length of only 1.25–1.35 mm, whilst the length of the controls is about 3 mm. Malformation in the embryonic fin are observed in some larvae just after hatching, and an anomaly is also observed in the existence of a very large cavity in the anterior part of the vitellum. Similar abnormalities have been found by Nakai (1962) in the case of eggs of *Sardina melanostica* kept in salinities much higher than normal.

It can be assumed from these data that the Argentine anchovy does not show as high a tolerance in respect to salinity thresholds as do some related species, such as *Engraulis encrasicolus*. The limiting salinities, within which the embryonic development of *Engraulis anchoita* can take place more or less normally, would be fixed at 25.8‰ and 50‰. This phenomenon might be due to the fact that the Argentine anchovy lives in a habitat undergoing slight changes in salinity, and that, therefore, it has not

had to need to develop adaptative trends in respect to this factor. The present author (Dziekonska, 1958), as well as other workers, holds the view that individuals of one species from water of a certain salinity might reproduce in waters whose salinity is lethal for other individuals of the same species living in waters of lower salinity (Ivlev, 1940).

INFLUENCE OF LIGHT

Experiments have shown that the influence of light is not a factor of great importance in the embryonic development of *Engraulis anchoita*. Eggs which were kept in complete darkness developed and hatched in a normal way, and no differences were observed in respect to the controls.

In aquaria kept under continual illumination, hatching took place earlier and a greater number of anomalies was observed, although this latter fact is possibly the result of a temperature increase due to illumination rather than to the effect of light itself.

The relative indifference of the embryos in respect to light is probably due to the fact that the eggs of the anchovy are planktonic and thus they stay fairly close to the surface of the sea, and are exposed to the rays of the sun as well as to darkness. Also, their development is quite rapid and, therefore, both the presence and absence of light acts upon their development during a brief period of time. In the case of some species of salmonids, for instance, it has been shown that light generally has a negative influence. In the case of this species, its development requires a long time and takes place in natural conditions, in darkness, under sand or pebble beds (Eisler, 1957; Willer, 1928). The embryos of *Pleuronectes*, which develop under natural conditions similar to those of the anchovy, also appear to be indifferent to the effect of light. (Johansen, Krogh, 1914).

INFLUENCE OF MECHANICAL FACTORS

Anchovy eggs which are submitted to pressure react in different ways, according to the developmental stage which the embryos have reached. The results of the experiments are shown in Table 2. As may be observed, the embryo appears to be more susceptible to pressure during the early stages of its development.

TABLE 2

RESISTANCE OF THE ANCHOVY EMBRYOS AND EGG MEMBRANE SUBMITTED TO THE EFFECTS OF DIFFERENT PRESSURE DURING VARYING STAGES OF DEVELOPMENT (WEIGHT IN GMS)

Stage of development	Maximum w. membrane	Maximum w. embryo
Early blastula.....	160	slide
Early gastrula.....	--	slide
The blastop. ring exceeds the equator of the egg.....	110	slide
Closing of the blastopore.....	200	slide
Embryo—Kupffer's vesicle.....	170	3-5
Commencement of the separation of the caudal region of the vesicle sac.....	140	10
Embryo occupying 2/3 of perimeter.....	130	16
Embryo prior to hatching.....	75	40

Up to the closing of the blastopore, the weight of the slide alone is sufficient to destroy the embryo. After the vitellus is completely enveloped, the resistance of the embryo increases. Close to the hatching stage, the weight of the slide together with a weight of 40 gm is necessary for the destruction of the embryo. This phenomenon seems to have its explanation in the fact that the vitellus is protected by the envelopment of embryonic tissues, and therefore offers greater resistance. This slight susceptibility of the anchovy embryo before hatching does not agree with the observations of Schaperclaus (1940), upon the eggs of *Esox lucius*. This author found that the resistance of the embryos of this species in respect to the pressure factor decreases sharply just before hatching.

As is shown in Table 2, the resistance of the egg membrane becomes greatest at the stage corresponding to the closing of the blastopore, and decreases sharply immediately prior to hatching. This phenomenon may be attributed to the effect of the hatching enzymes, which at this stage act by lyzing the chorion.

The experiments concerning the effect of shock in eggs dropped from different heights leads to conclusions analogous to those suggested by the pressure experiments. The results are depicted in Figure 3. As

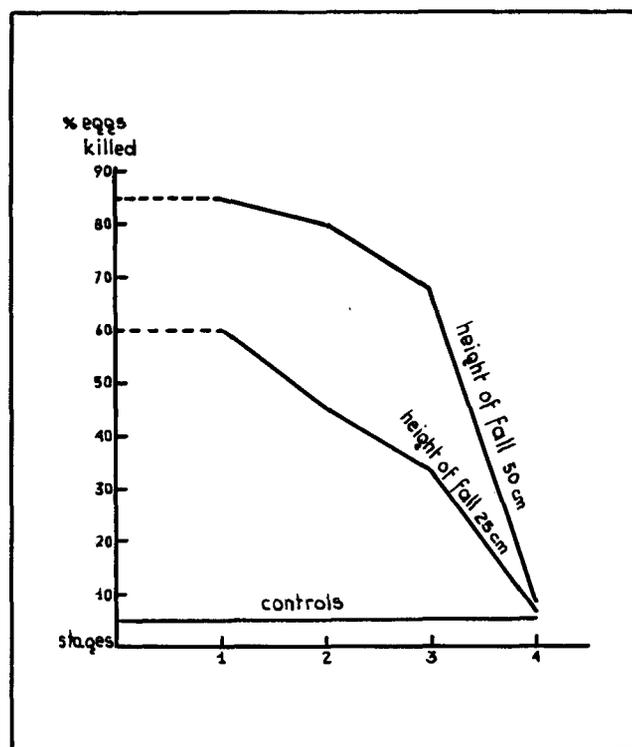


FIGURE 3. Percentage of anchovy eggs at differing stage of development killed after falls from different heights.

it was impossible to obtain suitable materials for performing experiments upon the early cleavage stages, no conclusions will be drawn on the susceptibility of the embryos during the early stages of development. The earliest stage at which the embryos were submitted to shock was the early blastula. In this stage,

eggs dropped from a height of 50 cm had a mortality rate of 85%, while those dropped from 25 cm had a mortality rate of 60%. As development continues, the susceptibility, though diminishing slightly at the beginning, remains at a high rate, and as the enveloping of the vitellus progresses, the susceptibility decreases. At an advanced embryonic stage, the resistance increases so much that little difference is observed between the mortality rate of the embryos submitted to the experiment and that of the controls. These results agree with the observations made by Rollefson (1932), who, in the case of the genus *Gadus*, also recorded an increase of the resistance throughout the development of the embryo. This observation does not agree, however, with the data given by Lindroth (1942) for the embryos of *Salmo salar*. In his experiments, he reached the conclusion that the resistance of the embryo in this species is not related to the enveloping of the vitellus, and that it can decrease in the last stages of development.

The data which have been obtained, showing the high susceptibility of anchovy embryos to mechanical factors, lead to the assumption that high seas and storms might have an influence upon the fate of developing embryos which are in the sea at that time. This assumption has grounds, too, in the observations made by other workers (Rollefson, 1930; Carruthers, Parrish, 1951), who have shown that high seas can kill the embryos of some species of the genera *Gadus* and *Pleuronectes* at a critical stage of their development. Thus, they were able to forecast on the basis of meteorological conditions, especially wind data, the volume of the catches of gadids two years prior to their entry into commercial fishing.

SUMMARY

The influence of temperature, salinity, light and mechanical factors upon the embryonic development of the Argentine anchovy *Engraulis anchoita* (Hubbs, Marini) has been established.

1) The embryonic development of the anchovy within the temperature range 14°–15° C. lasts from 68 to 72 hours, whilst within 19°–20° C., it lasts from 50 to 53 hours. A temperature of 4° C. was found to be lethal. The optimal temperature range for the anchovy hatching in the spring appears to be from 10° to 17° C.

2) Embryonic development takes place normally at salinities ranging from 25.8‰ to 50‰. Salinities above or below this range produce very pronounced abnormalities in the embryos.

3) Light does not appear to have any particular influence upon the embryonic development of the anchovy.

4) Anchovy embryos show great susceptibility to mechanical factors (pressure, shock). This susceptibility becomes more pronounced during the earlier stages of development, including early gastrulation. The assumption is made, on these grounds, that high seas and storms can destroy the developing embryos. The resistance of the egg membrane shows its greatest intensity in the stage corresponding to the closing of the blastopore and diminishes sharply immediately prior to the hatching of the egg.

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INVESTIGATIONS OF FOOD AND FEEDING HABITS OF LARVAE AND JUVENILES OF THE ARGENTINE ANCHOVY *ENGRAULIS ANCHOITA*¹

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INTRODUCTION

Up to the present time no papers on the feeding of the larvae of marine fishes have been produced in Argentina. The present contribution is the first study of this nature referring to this area of the Southwest Atlantic and it deals with problems related to the feeding habits of the larvae and juveniles of the Argentine anchovy.

The purpose of this paper is to study the food and feeding habits of the anchovy larvae from the time at which the larvae begin to be able to feed, to the time when the juveniles approach the adult stage. This study has been based upon a quantitative and qualitative determination of the food components, to obtain a better assessment of the contribution of the different groups of organisms to the diet of the larvae and juveniles of the anchovy. The characteristics of the feeding of the young forms of the anchovy at different stages of development were studied in relation to the morphological changes which take place throughout the growth of the individuals. The morphological characters most closely related to the feeding process in fishes are: the digestive tract, the gill rakers and the dimensions of the mouth. Therefore, in the present work, special emphasis has been given to a detailed study of these morphological elements. Also, an analysis of the changes in the feeding of the larvae and juveniles of the anchovy during different seasons of the year has been attempted.

Together with the anchovies, juvenile individuals of another species, *Austroatherina incisa*, were gathered. The individuals of this species share the habitat of, and are found mixed with those of the anchovy. The purpose of collecting other material was to study the intestinal content of the individuals of this other species with the aim of obtaining comparative material as a frame of reference for the anchovy, taking especially into account the competition for their food supply. The results of the analysis of the feeding habits of the juveniles of *A. incisa* will be found in another paper by this author (Ciechomski, in press).

MATERIALS AND METHODS

The larvae and juveniles of anchovy which were used as material for this study were collected from coastal waters off Mar del Plata. The juveniles were obtained from every month of the year. The larvae of sizes 3.0–4.9 mm and 5.0–22.0 mm were obtained only

during the summer. A total of 1,705 larvae and juveniles has been studied, ranging in size from 3.0 to 90.0 mm. From these, 503 individuals contained food, the remainder having their digestive tracts empty.

For the elaboration and presentation of the data, the months of September, October, and November have been considered spring, December, January, and February were considered as summer, March, April, and May autumn, and June, July, and August winter.

The material to be studied was fixed on the spot, right after its collection, with formaldehyde, in order to stop the digestive processes, since this was convenient in view of the study made of the intestinal content. Further treatment of the material was continued in the laboratory.

Each individual was measured and its digestive tract was separated under a magnifying glass. The examination of the intestinal content was performed under the magnifying glass and the microscope. All of the components were separated, counted and measured by means of a micrometric eyepiece. For assessing the weight of the individuals, a list of mean weights was made in which the larvae and juveniles of anchovy were classed in total length classes with 2 mm intervals.

Plankton samples were obtained together with the anchovies, and the predominant forms were noted. Although this appraisal was not made in a quantitative manner and was not expressed numerically, it was considered useful as an indication of the feeding selectivity of the fishes which were studied.

In the quantitative treatment of the data, one of the methods used was the determination of the frequency of occurrence. The calculation of the weight of the total food ingested and of the percentage composition of the various food components was based on the mean live weight of the planktonic organisms which make up the diet of the anchovies. Since at the present time no data are available on the weight of these planktonic organisms, which are the basic food supply of the larvae and juveniles and, in some cases, of adult planktofagous fishes, for the most of the planktonic components the volume was determined by the method of volume shift. In other cases, when dealing with very small organisms of irregular shape, such as some diatoms (*Coscinodiscus*, *Triceratium*, etc.) the volume determination was accomplished geometrically. Multiplying the volume by the corresponding group index (Hagmeier, 1961) the mean weights of the organisms were obtained. The following

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table shows the values calculated for the volume and weight of some of the planktonic components.

TABLE 1

WEIGHT OF SOME PLANKTONIC ORGANISMS MOST FREQUENTLY FOUND IN THE FOOD OF THE LARVAE AND JUVENILES OF MARINE FISHES

Organisms	Mean dimension (m)	Mean volume (mm ³)	Hagmeier coefficient	Mean weight (mg)
Diatomea				
<i>Coscinodiscus</i> spp.	124 x 32	0.000160	1.1	0.000175
<i>Triceratium</i> spp.	145 x 114 x 60	0.000496	1.1	0.000545
Peridinea				
<i>Erwiaella</i> sp.	48 x 36	0.0000325	1.05	0.000034
Copepoda				
Calanoida	1000	0.0120	1.04	0.0125
" "	1000-2000	0.1330	1.04	0.1373
" "	2000-3000	0.4580	1.04	0.4714
" "	3000-4000	1.4280	1.04	1.4851
" "	4000-5000	4.0000	1.04	4.1600
Harpacticoida				
(<i>Euterpina</i> acut.)	480 x 850	0.0095	1.04	0.0100
Cyclopoida	356 x 176+ 240 x 130	0.0050	1.04	0.0052
Cladocera				
<i>Evadne nord.</i>	420-780	0.0092	(1.04)	0.0095
Larvae of Lamelli-branch	200-344	0.0044	---	0.0044
Anchovy eggs	1370 x 720	0.3780	---	0.3780
Fish eggs	1000	0.5230	---	0.5230

Of course, these calculations are not free from error, especially in the case of the Copepoda, which have been classed by great groups and by size classes, instead of by separate species, which would have been more correct. In the present conditions, a more refined treatment was not feasible.

For the calculation of the ingestion coefficient the food weight was divided by the weight of the individual, and the result was multiplied by 1,000.

The measurements of the dimensions of the mouth were made by means of the micrometric eyepiece. The mouth was opened by means of very thin needles and the length and width of the mouth were measured under approximately the same angle. The first branchial arch of the left side was used always for observing the development of the gill-rakers.

INCIDENCE OF FEEDING

The incidence of feeding was remarkably low, especially in some of the size classes of larvae. In Table 2 the values for the incidence of feeding for larvae of different lengths are shown.

As is shown in Table 2, the incidence of feeding varies greatly with the size of the larvae and juveniles of the anchovy. It is relatively high for the larvae whose lengths fall within the 3.0-4.0 mm class. The larvae in this group have just reabsorbed their yolk and have begun to feed themselves. While the growth of the larvae continues the incidence of feeding de-

TABLE 2
INCIDENCE OF FEEDING IN LARVAE AND JUVENILES OF THE ANCHOVY

Length of Organism (mm)	Number of Organisms	Incidence of Feeding
3.0- 4.0	56	52.2
4.0- 5.0	42	18.2
5.0- 9.0	50	0
9.0-20.0	350	5.7
20.0-30.0	360	9.2
30.0-40.0	320	17.9
40.0-50.0	282	57.3
50.0-90.0	245	78.6
Total	1705 larvae 503—Number of organisms containing food	

creases sharply, reaching the value 0 for individuals in the 5.0-9.0 mm class length. In those larvae whose lengths exceed 9.0 mm the incidence of feeding begins to increase gradually, but at a low rate, until the time at which the larvae reach a length of 40 mm. Beyond the 40 mm length the number of larvae containing food increases clearly and in the juveniles of 50.0-90.0 mm this number reaches a more or less constant and rather high level. It should be emphasized that the fact that larvae which did not contain food were found in such a scarce number has been experienced during 3 years, regardless of the season of the year.

This low incidence of feeding found in larvae of a species of the family Engraulidae is not an isolated fact, but has been observed with different species of this family and of those of the Clupeidae. Berner (1959) while studying the feeding habits of the northern anchovy, *Engraulis mordax* found that among the 13,620 larvae which he examined only 211 had ingested any food. Lebour (1921), who studied the food habits of numerous young clupeids, found that the percentage of individuals containing food was very low. The incidence of feeding in the larvae of other groups of fishes appears to be higher (Lebour 1920, Wiborg 1948, etc). While studying the food of the larvae and juveniles of *A. incisa* which were collected together with those of the anchovy (Ciechomski, in press) the present author found that all of the individuals which were examined contained food in their intestinal tract.

The phenomenon of the low incidence of feeding in the families Engraulidae and Clupeidae has been a subject of detailed analysis by numerous authors. There exist, as a consequence, several theories which attempt to explain this fact. Some authors try to explain this phenomenon as a consequence of the selectivity of the nets, which would tend to collect those larvae which were weak and underfed (Berner 1959, Soleim 1942, and others). Other authors think of this phenomenon as a consequence of the characteristics of the digestion of these species, which, according to them, is very rapid. The old theory of Pütter, according to whom fishes are able to feed upon the organic matter which is dissolved in the water, has been sustained by Morris (1955). This author thinks this possible on the basis of the fact that the larvae

of some species of marine fishes, including those of *Engraulis mordax*, have an extensive layer of mucous cells over the surfaces of the back of the mouth. Morris believes that "... the mucosa might serve as a mechanism for collecting important quantities of dispersed organic matter. . .". Nothing concrete can be said at this time concerning these assumptions.

Other authors, such as Schumann (1965) take into account the diurnal feeding habits of these species. The diurnal habits of the feeding of fishes and especially of that of their larvae and juveniles have been pointed out by several authors: Schumann (1965) for *Sardinops caerulea*, Ercegovic (1962) for *Clupea pilchardus*, Duka (1961) for *Engraulis encrasicolus*, etc. No matter what differences may exist among the observations of these various authors, most of them agree that the larvae of these fishes feed exclusively during daylight. They note that during the day, there are times at which the ingestion of food is more intensive, but no ingestion of food has been observed to take place during the night.

In the case of the Argentine anchovy, some assumptions can be made in this connection, taking into account all of the points of view mentioned and the author's own observations. The hypothesis of the effects of net selectivity upon the larvae during their collection was rejected, since the larvae with the lowest incidence of feeding were gathered in great numbers by means of a large net of purse-seine type with which the loss of the larvae was highly improbable. Furthermore, the larvae collected were in very good condition and did not appear to have starved. Plankton samples collected simultaneously showed the presence of numerous organisms which could be used as food by the larvae.

Nothing can be said here on the diurnal feeding habits of the anchovy because it was impossible to obtain samples during the night or during twilight hours. All of the material was collected during daylight and generally at about noon. Therefore, if it is assumed that the anchovy behaves in this respect like other species of marine fishes which feed exclusively during daylight, the fact of finding larvae with their intestinal tract devoid of food can not be accounted for by the diurnal feeding habits.

No studies have been made, up to the present time, which could cast light on the problem of the digestion of food by the larvae of *E. anchoita*. As a consequence of this, the present analysis is based mainly on comparisons with other related species, for which a better understanding of these processes has already been attained. Duka (1961) has reported that the speed of digestion in larvae of 6-7 mm in length of *E. encrasicolus* of the Black Sea, at a temperature of 23° C., is from 2-2.5 hours. But, on the other hand, according to Schumann (1965) the speed of digestion for nauplii of *Artemia salina* by larvae of *E. mordax* of the Pacific, off California, is much greater. This author has observed that "... an average of 25 seconds is required by larvae of 15 mm in length or larger to pass an *Artemia* nauplius from the mouth to approximately one-half of the length of the digestive tract. Progress of a food particle (*Artemia*) through

the remainder of the gut is much slower, with an average of 2 minutes required for food to reach the end of the gut and form a food plug." It appears then, that a very short time interval is required for an ingested particle to disappear from the intestinal tract of the larvae of *E. mordax*.

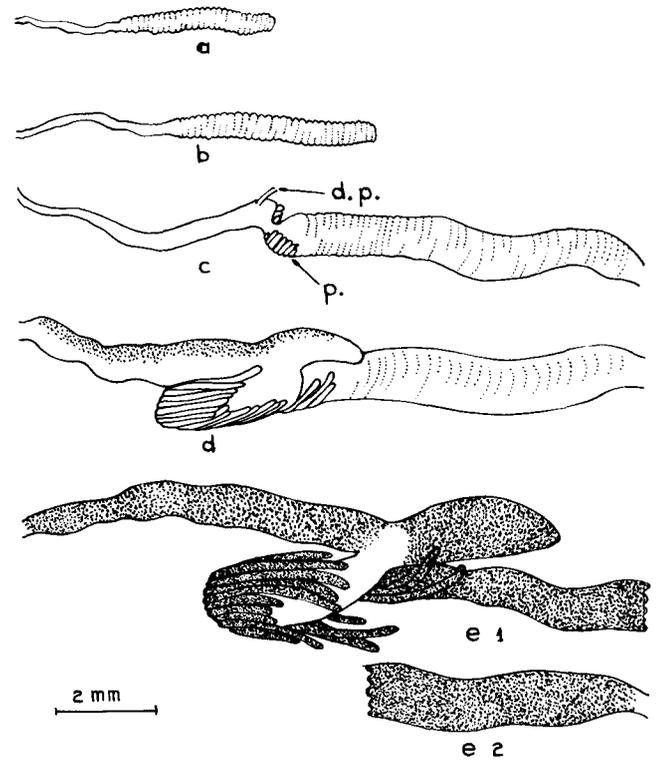


FIGURE 1. Development of the digestive tract of the anchovy larvae. p—pyloric appendices, d—ductus pneumaticus. The drawings correspond to the following lengths of fish: a—9.2 mm, b—15.0 mm, c—33.0 mm, d—38.0 mm, e₁ and e₂—50.0 mm.

Figure 1 shows the development process of the digestive tract of *E. anchoita*.

As is shown in the drawing, the digestive tract of the larvae, until they reach a length of at least 33 mm, is a short and completely straight tube, differentiated only in the anterior and posterior parts. In the larvae of 33 mm length a sketch of the stomach and rudiments of the pyloric appendices appears. At a length of 38 mm the stomach and pyloric appendices show themselves in a rather developed state and the pigment of the anterior part of the intestine begins to appear. In the juveniles of 50 mm, the part corresponding to the stomach is well developed and the whole digestive tract resembles that of an adult individual. This type of digestive tract structure, in the shape of a straight tube, is typical of the engraulids and clupeids. The very straightness and shortness of the digestive tract may favor a rapid digestion and excretion. It can also be assumed that at the moment the anchovy larvae are caught, an artificial acceleration of the excretion processes or the vomiting of the intestinal content could take place. By observing the drawings (Figure 1) it can be seen that the intestinal

structure shaped like a straight tube is maintained in those larvae whose incidence of feeding is lowest. The differentiation of the digestive tract coincides with the increase in the incidence of feeding. Mention should be made of the fact that the intestine of the larvae and juveniles of *A. incisa* gathered together with those of the anchovy, and having a 100% incidence of feeding (Ciechomski, in press), is not straight, but presents several folds.

It is more difficult to find an explanation for the relatively high incidence of feeding in the young larvae which are just beginning to feed. A similar phenomenon has been reported by Berner (1959) for *E. mordax*. This author found that the greatest percentage of feeding larvae was among the smaller ones. Further discussion of these facts should be withheld pending more detailed information regarding the physiology of the digestion, and behavior of the anchovy larvae.

COMPOSITION OF DIET AND SIZE OF FOOD ORGANISMS

The results obtained for different years were very similar, and therefore the material from both annual cycles has been treated collectively. The data are shown in Tables 1 and 2.

In Table 3 the results for the smaller larvae, 3.0-4.9 mm, and for those of 12.5-22.5 mm are given. Table 4 shows similar data for larvae and juveniles whose lengths range from 22.0 to 90.0 mm. The group comprising larvae whose length ranged between 9.0 and 20.0 mm was not included in the tables in view of the scarce number of individuals available. Within the intestines of the larvae falling in this group, the only food found was Copepoda with the following percentage of weight rate for the components: eggs

**TABLE 3
PERCENT INCIDENCE AND PERCENT WEIGHT RATES OF DIFFERENT FOOD ORGANISMS IN ANCHOVY LARVAE, IN SUMMER**

	Larvae: 3.0-4.9 mm		Larvae: 12.5-22.0 mm	
	Percent incidence rate	Percent weight rate	Percent incidence rate	Percent weight rate
Miscellaneous eggs.....	8.69	7.20	5.58	5.58
Eggs of Copepoda.....	69.56	45.05	5.58	5.58
Nauplii of Copepoda.....	60.86	47.75	-----	-----
Copepodita.....	-----	-----	11.76	10.37
Calanoida.....	-----	-----	64.70	49.63
Harpacticoida.....	-----	-----	11.76	8.24
Cyclopoida.....	-----	-----	23.52	2.96
Cladocera.....	-----	-----	23.52	17.64

**TABLE 4
PERCENT INCIDENCE AND PERCENT WEIGHT RATES OF DIFFERENT FOOD ORGANISMS IN LARVAE AND JUVENILES OF THE ANCHOVY, IN DIFFERENT SEASONS OF THE YEAR**

Organism	Spring		Summer				Autumn				Winter	
	Juveniles 45.5-86.0 mm		Larvae 22.0-42.0 mm		Juveniles 42.0-90.0 mm		Larvae 28.0-42.0 mm		Juveniles 42.0-86.0 mm		Juveniles 41.0-86.0 mm	
	Percent incidence rate	Percent weight rate	Percent incidence rate	Percent weight rate	Percent incidence rate	Percent weight rate	Percent incidence rate	Percent weight rate	Percent incidence rate	Percent weight rate	Percent incidence rate	Percent weight rate
Eggs of Copepoda.....	--	--	6.89	1.72	--	--	--	--	--	--	--	--
Nauplii of Copepoda.....	8.69	0.26	8.62	--	4.76	2.29	5.26	--	8.33	0.19	--	--
Copepodita.....	--	--	13.79	0.95	4.76	7.14	10.52	--	4.16	1.40	--	--
Calanoida.....	100.00	55.25	48.27	39.14	61.90	30.36	89.47	79.21	95.83	41.11	65.95	40.56
Harpacticoida.....	86.95	29.56	13.79	9.13	11.90	12.20	73.68	14.20	66.60	32.08	29.78	11.30
Cyclopoida.....	34.78	2.05	5.17	2.50	2.38	3.45	21.05	0.50	16.66	1.20	12.76	1.20
Cladocera.....	21.73	0.06	51.60	30.99	30.95	4.45	26.31	2.13	60.41	2.48	29.78	15.96
Larvae of Decapoda.....	13.04	0.63	3.44	0.85	2.38	2.00	--	--	8.75	2.87	2.12	0.61
Larvae of Cirripedia.....	4.34	--	--	--	--	--	--	--	25.00	4.56	2.12	--
Amphipoda.....	--	--	--	--	--	--	--	--	--	--	2.18	2.12
Euphausiidae.....	--	--	--	11.90	--	6.98	--	--	6.25	0.63	--	--
Undetermined Crustacea.....	--	--	3.44	1.41	11.90	7.36	--	--	--	--	4.25	4.05
Larvae of Polychaeta.....	4.34	--	--	--	--	--	--	--	4.16	0.82	--	--
Larvae of Lamellibranch.....	26.08	0.30	1.72	1.72	--	--	--	--	43.75	1.34	14.89	0.42
Apendicularia.....	--	--	--	--	--	--	--	--	--	--	6.38	0.27
Miscellaneous Eggs.....	13.04	--	5.17	6.67	57.14	7.89	--	--	10.41	--	21.27	2.12
Fish Eggs.....	17.39	1.19	1.72	0.02	7.14	1.32	--	--	8.33	1.62	--	--
Fish Larvae.....	--	--	1.72	1.72	11.90	6.63	--	--	--	--	--	--
Anchovy Larvae.....	--	--	1.72	1.68	7.14	7.14	--	--	--	--	--	--
<i>Peridinium</i> sp.....	--	--	--	--	--	--	--	--	16.66	--	19.14	--
<i>Ezuiella</i> sp.....	34.78	1.67	5.17	--	4.76	--	5.26	3.96	47.91	0.17	--	--
<i>Ceratium</i> sp.....	--	--	1.72	--	--	--	--	--	--	--	--	--
Miscellaneous Diatomea.....	52.17	0.02	1.72	--	2.38	--	--	--	31.25	--	31.91	0.06
<i>Coscinodiscus</i> spp.....	69.56	1.15	--	--	--	--	--	--	70.83	6.36	55.31	4.97
<i>Triceratium</i> spp.....	43.47	3.96	--	--	--	--	--	--	4.16	0.04	21.27	10.04
<i>Biddulphia sinensis</i>	4.34	--	--	--	--	--	--	--	--	--	2.12	--
Foraminifera.....	4.34	--	--	--	--	--	--	--	--	--	4.25	--
Radiolaria.....	--	--	17.24	--	33.30	--	--	--	--	--	--	--
Detritus and Sand.....	17.39	1.66	--	--	--	--	--	--	12.50	1.05	27.65	5.92
Undetermined.....	13.04	2.24	1.72	1.00	4.76	0.79	--	--	3.08	2.08	19.14	2.40

of Copepoda, 5.0%; Calanoida, 79.2%; Cyclopoida, 15.8%. Information on the food of larvae within the 5.0–9.0 mm length class is lacking, since, as is noted in Table 1, no individuals of this class containing food in their intestinal tracts were found.

As is shown clearly in the tables, the larvae and juveniles of the Argentine anchovy are zooplankton-fagous from their earliest stages, and the contribution of the phytoplankton to their diet is quite small. Furthermore, Fuster de Plaza and Boschi (1958), and Angelescu and Cousseau (1966), have found that the diet of the adult anchovy is made up almost exclusively of zooplankton.

The diet of the larvae which are just beginning to feed actively is made up almost exclusively by eggs and nauplii of Copepoda. The basic food supply for the 9.0–22.0 mm length class is also comprised of the Copepoda at various stages of their development. The highest frequency of occurrence and the highest percentage of weight correspond to the Calanoida. Together with the copepods the Cladocera appear abundantly. These results refer only to the summer season, since it was not possible to collect larvae of anchovy of this small size during other seasons of the year.

For the larvae and juveniles in the 22.0–90.0 mm length class, it was possible to give an account, as shown in Table 4, of the food composition throughout the year. As can readily be seen, the main components of the diet for this group are also various groups of Copepoda, especially the Calanoida. Among these groups the Cyclopoida are the least important, in this respect. Among the Calanoida, the most frequently encountered species were *Paracalanus parvus* and *Centropages spp.* and among the Cyclopoida, *Oithona minuta* and *Corycaeus spp.* Among the Harpacticoida, only one species was found: *Euterpina acutifrons*.

After the Copepoda, the Cladocera, which are especially abundant in both summer and winter, follow in importance as food for the larvae and juveniles of the anchovy. They are represented by two species: *Podon polyphemoides* and *Evadne nordmanni*.

Larvae of Decapoda and Lamellibranchiata are found in some individuals during all seasons of the year, but in quantities of slight significance in respect to the total food supply. The same observation applies also to the eggs of various marine organisms, although their share in the total weight is somewhat greater than that of the aforementioned larvae. Most of the eggs of fishes found in the food content were anchovy eggs in spring, during October, and eggs of *Prionotus sp.* during February and March.

Under the heading "undetermined", remains of fish muscles, which originated in all probability from the bait used by fishermen, were included.

The contribution of phytoplankton to the diet of the anchovy deserves a more detailed analysis. As is shown in Table 4 the phytoplankton most frequently found in the food supply were the diatoms *Coscinodiscus spp.* and *Triceratium sp.* and the dinoflagellates *Exuviaella spp.* Although these organisms are found in many individuals and are occasionally very abun-

dant, their significance in the total weight is low. The most important place among the phytoplankters is certainly occupied by *Coscinodiscus spp.* and *Triceratium sp.* During the summer a lesser contribution of the phytoplankton organisms is observed in the anchovy diet.

Biddulphia sinensis, which appeared with the other diatoms, was treated separately, since the presence of this diatom, with long and acute appendices, in the food supply of the anchovy was considered to be of interest. The rather limited contribution of the phytoplankton to the diet of the anchovy as shown by the data of the present paper does not coincide with the results obtained by Fuster de Plaza and Boschi (1958), who found a predominance of phytoplankters in the diet of the juveniles of this species.

An interesting fact that should be noted is the absence of phytoplanktonic organisms from the diet of the larvae of smaller sizes. This is partially coincident with the findings of some authors, who have shown that the larvae or juveniles of some species of fishes feed upon relatively large organisms at first, and then change to smaller items as they grow. This is the case for *Cetengraulis mysticetus* (Bayliff 1963), *Sardinops caerulea* (Hand and Berner 1959), *Brevoortia tyrannus* (June 1957) *Sardina pilchardus* (Andreu 1960), etc. It seemed logical to expect to find phytoplankters more abundantly in the diet of the smaller larvae, and this was assumed so before completing this study, since these organisms are the smallest components of the diet. The larvae of the smallest size in whose digestive tract some individuals of *Exuviaella* were found measured 26.0 mm. This was an exceptional case, since the phytoplankters were found in greater abundance and most frequently in larvae of 38.0–40.0 mm in length and longer.

Figure 2 shows the relationship between the width of the mouth and the range of prey width. The width of the prey has been considered rather than the length, in the assumption that the possibility of ingestion for a given organism depends more upon its width than upon its length. The correlation found between the width of the mouth and the length of the larvae is lineal.

After the time at which the larva reaches a length of 40 mm the width of the mouth increases at a greater rate, and the mouth begins to resemble that of an adult anchovy. The dimensions of the largest organisms ingested by larvae with lengths of 3.0–5.0 mm range between 100 and 150 μ . In the larvae of 12.0–40.0 mm, although the dimensions of the mouth have increased considerably, the size of the largest prey stays at a more or less constant level, between 200 and 500 μ . Preys of much greater size are rarely found. The organisms of the smallest size begin to appear in the intestinal content from the time at which the larvae reach a length of 38 mm.

The phenomenon of the retention of organisms of small sizes is related, as is well known, to the filtering action of the gill-rakers.

In Figures 3 and 4 the development of the gill-rakers in the larvae whose length ranges from 13.5 to 90.0 mm is shown. The first sketches of the future

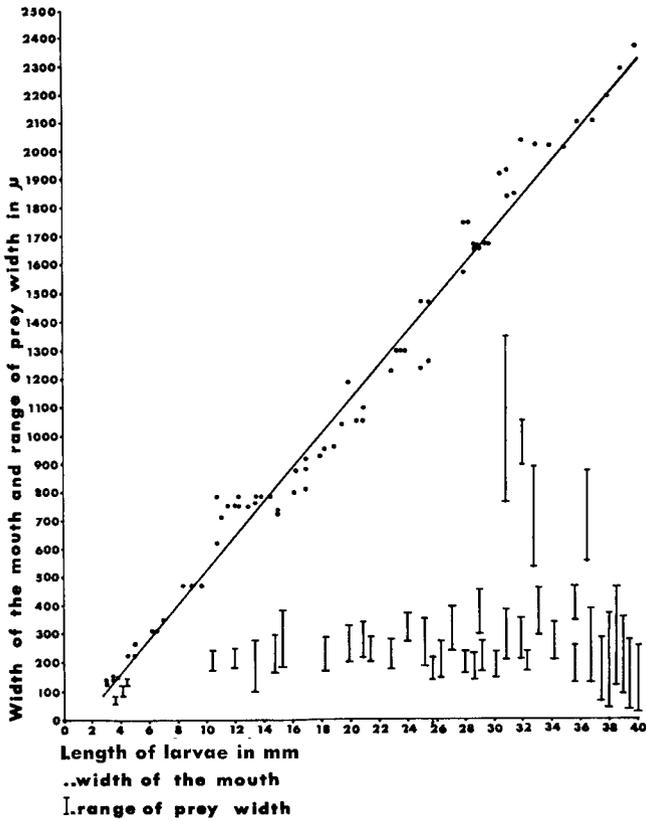


FIGURE 2. Relationship between the width of the mouth and range of prey width in the anchovy larvae of different lengths.

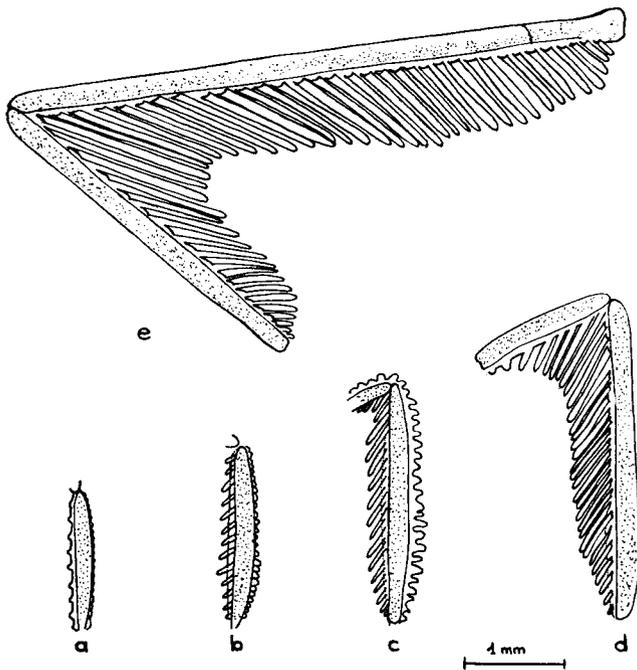


FIGURE 3. Branchial arches of anchovy larvae, showing the appearance and development of the gill-rakers. The drawings correspond to the following lengths of fish: a—13.5 mm, b—18.2 mm, c—24.0 mm, d—31.0 mm, e—42.0 mm.

gill-rakers appear as small protuberances on the first branchial arch, when the larva reaches a length of 13.5 mm. In the larva whose length reaches 24 mm, the gill-rakers, of which there are about 20, reach a length of 315 μ . Over the gill-rakers, some slightly noticeable protuberances appear. These protuberances will transform themselves into the future denticles. In the larvae having a length of 31 mm the gill-rakers (about 32) reach a length of 720 μ and the number of protuberances corresponding to future denticles increases. As the larvae grow the gill-rakers also increase rapidly in length, and they reach a length of 1,800 μ in the larvae having a length of 42 mm. At this stage the protuberances have become denticles. The juvenile having a length of 50 mm has approximately 50 gill-rakers, which are slightly den-

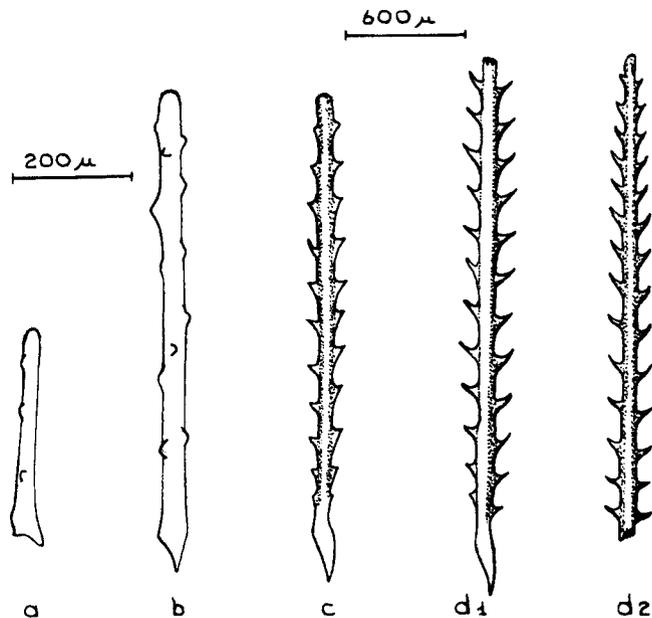


FIGURE 4. Development of the gill-rakers in the larvae and juveniles of the anchovy, showing the development of the denticles. The drawings correspond to the following lengths of fish: a—24.0 mm, b—31.0 mm, c—50.0 mm, d₁ and d₂—90.0 mm.

tled and have a length of about 2,250 μ (Figures 4c and 5a). The juvenile with a length of 90 mm has some 90 denticled gill-rakers measuring 4,800 μ in length (Figures 4d and 5a).

As is seen through this brief analysis of the development of the gill-rakers, the filtering apparatus of the anchovy begins to be functional by the time the larvae have reached a length of 38 mm. Just at this stage of development the small phytoplanktonic organisms begin to appear in the diet, probably by having been retained in the filtering net of the larvae. It can be further assumed that the absence of phytoplankters in the diet of the adult individuals of anchovies of larger sizes is also related to changes which take place in the filtering apparatus, which could become a coarser filtering net because of the increase in the distance between the gill-rakers, which is produced by the growth of the branchial arch.

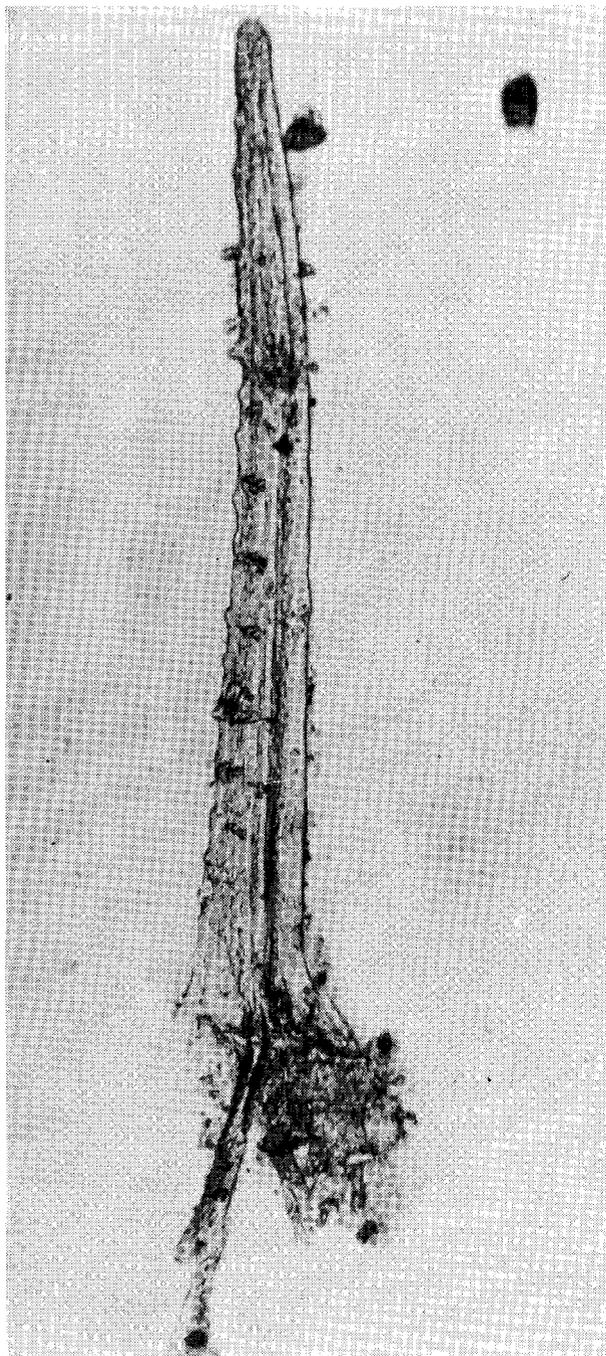


FIGURE 5a. Gill-raker of the anchovy *Engraulis anchoita*, 50 mm long.

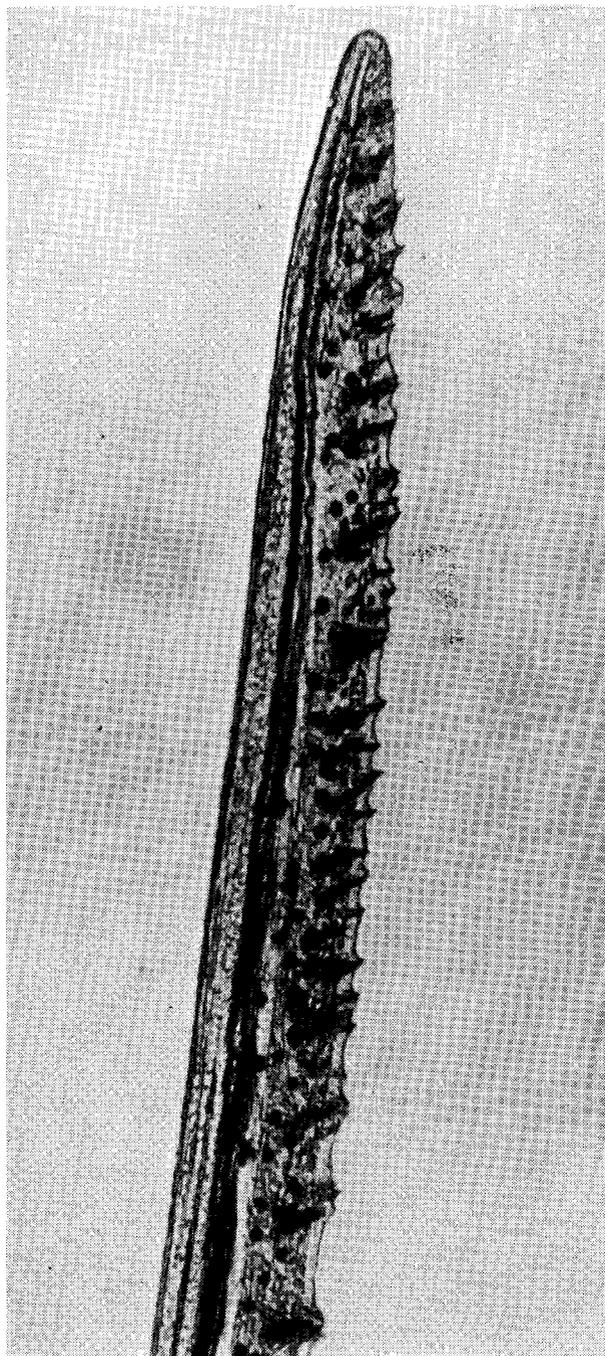


FIGURE 5b. Gill-raker of the anchovy *Engraulis anchoita*, 90 mm long.

In order to effect a better interpretation of the relationship between the structure of the filtering apparatus and the diet of the anchovy, it seemed to be of interest to compare the structure of the gill-rakers of the Argentine anchovy with those of the Peruvian "anchoveta" *Engraulis ringens*, whose diet is based on the phytoplankton. This comparative study was made possible through the kind assistance of R. Jordán, of Peru, who sent, at the request of this author, larvae and juveniles of the Peruvian "ancho-

veta". The results obtained from the examination of this material are quite interesting. As can be observed in Figures 5a and 6a the structure of the gill-rakers of the juveniles of 50 mm in length is quite similar in both species. On the gill-rakers of the juvenile of *E. ringens* the denticles appear to be just a little longer than those of *E. anchoita*. The study of the intestinal content of 10 juveniles of this length of *E. ringens* showed that it is somewhat similar to that of *E. anchoita* at this stage of development, and that

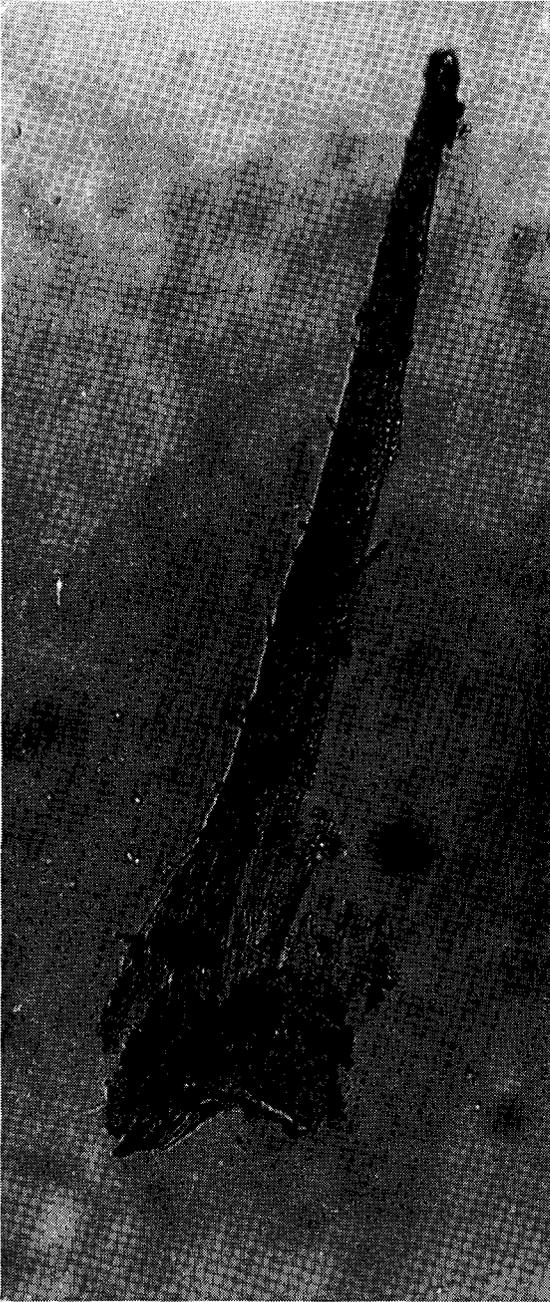


FIGURE 6a. Gill-raker of the anchoveta *Engraulis ringens*, 50 mm long.

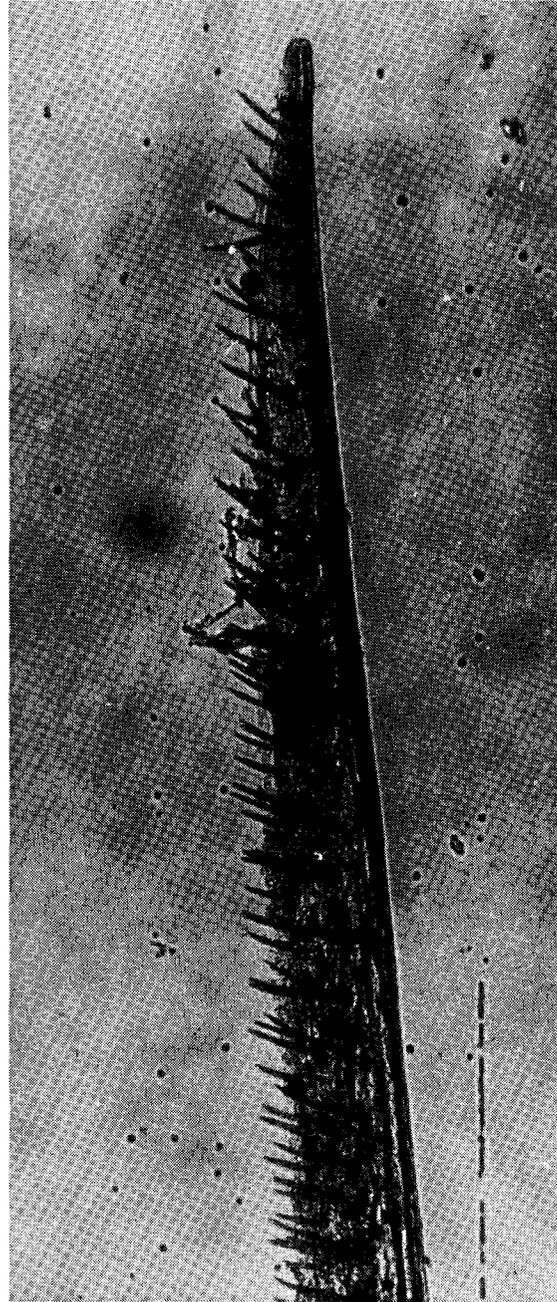


FIGURE 6b. Gill-raker of the anchoveta *Engraulis ringens*, 90 mm long.

it is made up mainly by Copepoda. On the contrary, the aspect of the gill-rakers of the juveniles having a length of 90 mm shows great differences between the two species (Figures 5b and 6b). The gill-rakers of the juveniles of *E. ringens* are longer and with more numerous and longer denticles. At this stage of their development the individuals of this species have a diet based completely on phytoplankton.

Another finding which deserves to be interpreted is the presence of an amount of detritus and very fine sand grains in the intestinal content of some of the juveniles of the 41.0–90.0 mm length class. The

intestinal content of these individuals contained also a great quantity of *Triceratium*, a diatom which is abundant in water layers which are close to the bottom. In the spring the skeletons of benthic Foraminifera were found in the food of three individuals.

The highest value, both for the frequency of occurrence and for the percentage weight rate, of detritus in the intestinal content of the juveniles of the anchovy was found during the winter. During the summer, on the contrary, no individual has been found containing benthic elements in its intestine. The aforementioned findings show that the juveniles

of the anchovy which live in waters which are not deep have some tendency to look for their food near the bottom. These iliofagous tendencies are more marked during the winter.

SELECTION OF FOOD

In connection with the problem of the selection of food by the Argentine anchovy, only some general considerations can be made. The lack of exact quantitative data on the composition of the plankton collected with the fishes studied precludes a more detailed analysis of this subject. Nevertheless, the available data allow some general conclusions on this problem.

The species of copepods from the group of the Calanoida and *Euterpina acutifrons*, which are frequently and abundantly found in the diet of the larvae and juveniles of the anchovy are also the most abundant species in the plankton. The great quantity of Cladocera in the intestinal content, especially during some winter and summer months, coincides with the abundance of this microcrustacean in the plankton. Again, the presence of fish eggs in the food supply, especially during the spring and summer, coincides with the appearance of these eggs in the plankton. In some cases, remains of fish muscles were found in the food, which in all probability was part of the bait used by the fishermen to attract the fishes, as was mentioned earlier.

All of the information obtained suggests that the larvae and juveniles of the anchovy do not select much of their food, and that they feed upon the food which is present in greater abundance. As a consequence, their diet may be quite dependent upon the patterns of plankton dispersal. Another very important factor is the accessibility of the food as determined by the size of the prey and the dimensions of the mouth of the fish. Only more detailed quantitative data on the composition of the plankton and experimental studies on the feeding habits of the larvae of the anchovy can clarify this interesting problem.

OTHER CONSIDERATIONS

Another interesting fact in the study of the larvae and juveniles of the anchovy is that the quantity of food found in their intestinal tracts was generally small. In many cases the ingestion coefficient was lower than 0.01. It was believed, as a consequence, that any analysis based on the calculation of these coefficients as, for instance, in the case of the juveniles of *A. incisa* which were studied simultaneously (Ciechomski, in press), could lead to erroneous conclusions.

In respect to the problem of feeding competition between the larvae and juveniles of the anchovy with those of *A. incisa*, it can be assumed that, in spite of the great similitude between their diets, there is no real chance that these species should compete for their food. This is based on the abundance of the planktonic organisms and on the fact that all of the individuals studied were apparently in good condition.

SUMMARY

The subject of the present paper has been the food and feeding habits of the larvae and juveniles of 3.0–90.0 mm of length of *E. anchoita* from coastal waters off Mar del Plata, Argentina. The following results have been obtained.

The incidence of feeding found varies with the size of the larvae and juveniles. The lowest values are found in larvae of 5.0–30 mm in length. The assumption is made that this phenomenon can be likely related to the structure of the digestive tract of the larvae at this stage of development.

The Argentine anchovy is almost exclusively zooplanktonic from its earlier life stages. The main component of the diet of both larvae and juveniles is Copepoda in all of their developmental stages. Among them the Calanoida are the most abundant group.

Phytoplanktonic organisms were found in greatest abundance in the diet of juveniles of 38.0 mm of length and larger. This phenomenon is related to the changes which take place in the filtering net of the larvae along with the development of the gill-rakers.

The comparisons between larvae and juveniles of the Argentine anchovy *E. anchoita* and those of the Peruvian "anchoveta" *E. ringens* has been made.

The juveniles of the anchovy show some iliofagous tendencies, especially during winter.

The assumption is made that the larvae and juveniles of the anchovy do not choose their prey much and that they ingest the food that they find in greater abundance.

It is assumed that there is no chance of feeding competition between the larvae and juveniles of the anchovy and those of *A. incisa*.

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A BRIEF DESCRIPTION OF PERUVIAN FISHERIES

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INTRODUCTION

As is true of nations with access to the sea, fishing in Peru has deep roots in history. Yet, despite its antiquity, the industry showed little sign of progress until the last 3 decades of the present century beyond the simple utilization of species in fresh state and in the salted and sun-dried forms.

The turn of the 1930's ushered in the beginning of fishery industrialization. The first attempts were at fish canning, which remained on an extremely small scale until the early 1940's. Then, with the construction of the Frigorífico Nacional, experiments began in fish freezing. However, failure to find acceptance for the product derived, both at home and abroad, led to the discontinuation of this operation, only to be resumed by other interests after the Second World War.

The outbreak of the war in 1939 opened up new product and market outlets. The canning industry especially underwent great expansion when the United States entered the war, since a sudden, great demand was created for fish in hermetically sealed containers. Salted fish was also greatly sought, and Peru began its exports of this commodity with the creation of UNRRA. Another product also exported during this period was fish liver and oil (from *tiburón*, *bonito* and *atún*).

The end of hostilities in 1945 brought with it the end of Peru's export boom of war-sought fishery products. Foreign sales of salted fish and fish liver and oil ceased completely. Even canned fish (*bonito*) exports were threatened, as the United States imposed restrictions to protect its domestic production. Despite this, however, the Peruvian canning industry managed to retain a sufficient share of markets to allow it to continue in operation without an alarming cut-back in production. Subsequently, the investment of U.S. capital in canning operations led to further expansion of this industry (1947 onwards). At the same time, a few freezing plants were installed to produce for the U.S. market. Such, briefly, is the story until the "anchoveta rush".

The relatively recent blossoming forth of the anchoveta fishery for fish meal reduction overshadows all past fishery performance and, indeed, exemplifies a growth pattern hardly equalled in the history of industrial development. During less than a decade (1955-1963), the industry emerged from a position of obscurity to occupy first place among the world's fish meal producers. Concurrently, it became the country's leading exporter and principal earner of foreign exchange, excelling the performance of such basic Peruvian export industries as cotton, copper, and sugar.

The impact of the "anchoveta wonder" on the Peruvian economy was little short of explosive both in time and scope. In the short lapse of time previously

mentioned (less than 10 years), there emerged a fleet of over 1,700 modern purse seiners, a processing industry consisting of upwards of 150 meal and oil reduction plants, and a number of auxiliary and ancillary establishments for boat building and repairing, machinery manufacturing and the production of other fishing requisites. As a consequence, the economy registered a sudden upsurge in employment; and, by the end of 1962, upwards of 100,000 people were engaged directly or indirectly in the anchoveta fishery, more than 20 times the number employed in similar activities 10 years previous.

From the beginning of fisheries industrialization, as late as the 1930's, development was conditioned upon production for export, with but minor reliance on the domestic market. This growth pattern has been even more prevalent during the birth and expansion of the anchoveta industry. In effect, industrialization has led to the separation of the fishing industry into two distinct sectors, one catering to foreign demand, the other reliant on domestic needs; and unfortunately, advances in technology and general efficiency took place in the former almost in complete isolation of the latter. In consequence, the consumable fish industry catering to the national market scarcely felt the wave of industrialization.

This industry, upon which the domestic fish market is dependent for supplies, is typically a conglomeration of small boat enterprises decentralized throughout the country's coastal zones. There are close to 8,500 fishermen fishing in craft ranging from "caballitos" to motor boats of 22' to 30' in length. Except for the widespread substitution of nylon for cotton nets, and the gradual acceptance of outboard and marine engines, there is little evidence of modernization in the industry. Productivity per man is low and many species are greatly underexploited.

FISHING GROUNDS

Fishing operations are carried on throughout most of the Peruvian coast, which extends for 1,400 miles, with a calculated area within the 100 fathom curve of about 26,800 square miles, although the commercial fishery is concentrated in the central and northern zones. This concentration seems to stem from the influence of purely physical factors, namely, the characteristics of the coast and the width of the continental shelf.

The topography of the coast, as well as the location of the fishing base relative to population and business centers, has a known vital influence on fishery development—industry normally locates where natural conditions are least adverse. Where the coast is rugged and exposed, with little or no shelter for boats and poor landing and shipping facilities, where easy access to market is wanting, etc., the obstacles to fishery development are difficult if not economically undesir-

able to overcome. To a large extent, this is the situation which prevails along a large segment of Peru's south coast, particularly from Pisco to Camaná; and many of the resident fishermen of the area have little more than risen above the economic status of fishing for their own nutritive sustenance. By contrast, the central and northern sections of the coast are better endowed to meet the requisites of fishermen in the pursuit of their trade; and here is where the best fishing harbours have been developed (although still deficient in facilities), and where the largest number of processing plants and concentrations of fishermen are to be found.

The influence of the characteristics of the coast on fishery exploitation is of course linked with the availability of the resource and the nearness of fishing grounds. Traditionally, Peru's fishery is inshore. Except for a limited number of vessels that occasionally pursue tuna in its offshore or deep sea habitat, fishing is confined to the continental shelf. And since this shelf varies greatly in width from north to south, it is not surprising that the greatest fishery concentration occurred in the shelf's widest zones, namely, the central and northern areas. (In the extreme north, around Punta Folsa, the shelf is 5 nautical miles wide while in the south, around Punta Pescadores and Punta Islay, its width is but 2 to 3 miles. Between these extreme points, the shelf varies greatly in width, reaching a maximum of 70 miles in and around Sechura Bay.)

While fishermen are largely concentrated in the central and northern sections of the coast, with fishery exploitation also centered in these areas, there is considerable movement of fishermen and boats to the Southern Region at certain seasons of the year. Fishing, therefore, is not regional—it takes place in varying degrees of intensity along the entire shore.

LANDINGS AND PROSPECTS

According to the Fisheries Direction of the Ministry of Agriculture, total registered landings of fish and shellfish in 1963 amounted to 6,794,408 metric tons. In order of importance the principal species which featured in this catch were:

Anchoveta	<i>Engraulis ringens</i> (Jenyns) -----	6,634,835.8
Bonito	<i>Sarda chilensis</i> (Cuvier and Valenciennes) -----	90,652.9
Barrilete	<i>Katsuwonus pelamis</i> (Linnaeus) ---	16,911.3
Atún	<i>Neothunnus macropterus</i> (Schlegel) -----	11,230.8
Caballa	<i>Pneumatophorus peruanus</i> (Jordan and Hubbs) -----	7,911.4
Machete	<i>Ethmidium chilcae</i> (Hildebrand) ---	7,863.0
Lorna	<i>Sciaena deliciosa</i> (Tschudi) -----	7,184.3
Cojinoba	<i>Neptomenus crassus</i> (Starks) -----	6,126.4
Tollo	<i>Mustelus mento</i> (Cope) -----	4,333.7
	<i>M. maculatus</i> (Kner and Steindachner)	
	<i>M. dorsalis</i> (Gill)	
Cabrilla	<i>Paralabrax callaensis</i> (Stark) ----	3,850.3
Corvina	<i>Sciaena gilberti</i> (Abbott) -----	3,508.2
		6,794,408.1

Other species, more than 50 in number, accounted for less than 27,000 tons.

The preponderance of the anchovy in the above statistics is obvious without scrutiny. It represents more than 97% of total landings (for conversion into fish meal and oil), leaving less than 3% for human food use. Indications are that this pattern will not change appreciably in the immediate future—the anchoveta fishing fleet is expanding, the country's fish meal production capacity is being increased, either through new plant construction or extension, and little is in sight by way of development in other sectors of the fishing industry.

The rapid pace at which the anchoveta fishery developed from 1955 on did not permit growth according to those criteria considered most consistent with rational exploitation. The main emphasis was on quick investment, production and sale, which was feasible and quite understandably pursued in the natural and institutional environment which prevailed—an obviously immense resource, nearly ideal fishing conditions (closeness to grounds and good weather), free entry into the industry, and a favourable and growing market. In the circumstances, expansion in the first phase of development proceeded without much concern over the effects of the fishing pressure on the anchoveta stock.

Gradually, preoccupation developed over the limits of expansion, and a marine research institute was established in 1960 with the principal aim of studying the anchoveta resource and the complex of biological, oceanographic, technological and economic factors affecting conditions of catch and utilization. These studies are continuing, with primary emphasis on biology and oceanography, because of industry demands for better knowledge of the resource. This alone, of course, will not suffice for a complete rationalization of operations. More attention must be given to the technological and economic aspects of the fishery.

Apart from the anchoveta fishery, the best prospects for expansion or development appear to be in the exploitation of mullet and certain pelagic species, such as bonito, herring, mackerel and sardine. Some bottom fish may also be exploited more extensively as the Government directs more attention to meeting some of the country's protein requirements. The need with respect to the expansion of these relatively minor fisheries centers principally in the delimitation of resource distribution and in improving the technology and economics of operation.

STATISTICAL TRENDS IN THE ANCHOVY FISHERY

The fishing events presented graphically in the appended diagrams are largely self-explanatory. Only short comments are therefore given here.

Development of the Industry

Basic information on the development of the anchovy fishery in Peru is given in Tables 1 and 2. Here are recorded the number of fishermen, number

TABLE 1

Year	Fishermen (N°)	Anchovy Boats (N°)	Fishmeal Plants (N°)
1955	1,800	175	16
1956	2,400	220	27
1957	2,800	272	39
1958	3,400	321	53
1959	5,200	426	63
1960	8,600	731	89
1961	12,000	846	105
1962	17,000	1,070	120
1963	23,000	1,756	150

TABLE 2

Year	Total Anchovy Landings (Metric Tons)	Fishmeal Production (Metric Tons)	Fishmeal Exports ('000, Soles)
1955	58,707.0	20,069.1	37,805.7
1956	118,726.0	30,968.8	67,211.0
1957	325,623.8	64,479.5	135,035.2
1958	737,019.5	126,909.4	271,052.4
1959	1,942,385.5	332,352.3	861,592.8
1960	3,310,156.7	553,256.5	1,056,443.2
1961	5,010,930.0	863,766.0	1,328,567.2
1962	6,691,520.7	1,120,796.0	2,678,265.4
1963	6,634,835.8	1,159,233.0	2,809,572.1

of fishing boats, number of fishmeal plants, total anchovy landings, fishmeal production and the value of fishmeal exports for the period 1955-1963. (This is also supplemented with Figure 1, which shows monthly anchovy landings during recent years).

Geographical Distribution of Landings

As shown by the map and graphs in Figure 2, industrial fishing centers are not evenly distributed in Peru. This distribution is in the first place dependent upon harbour facilities, communications and access to fresh water. Weather conditions are also quite important and are more stable in the northern area, where the fishing industry is largely concentrated. However, it is by no means certain that the location of the industry corresponds to the actual distribution of the anchovy stock. Better geographical distribution may be the next step in the development of the anchovy industry, and it appears that modern fishing methods (Sonar) can make this possible.

Seasonal and Yearly Trends in Fishing Success

The seasonal and yearly trends are described in two ways. In Figure 3, the percentage distribution of landings by months is shown, (based on the annual total). With slight variations fishing events have occurred in a very regular manner, with low catches during winter. In Figure 4, a more detailed analysis

1000
TONS

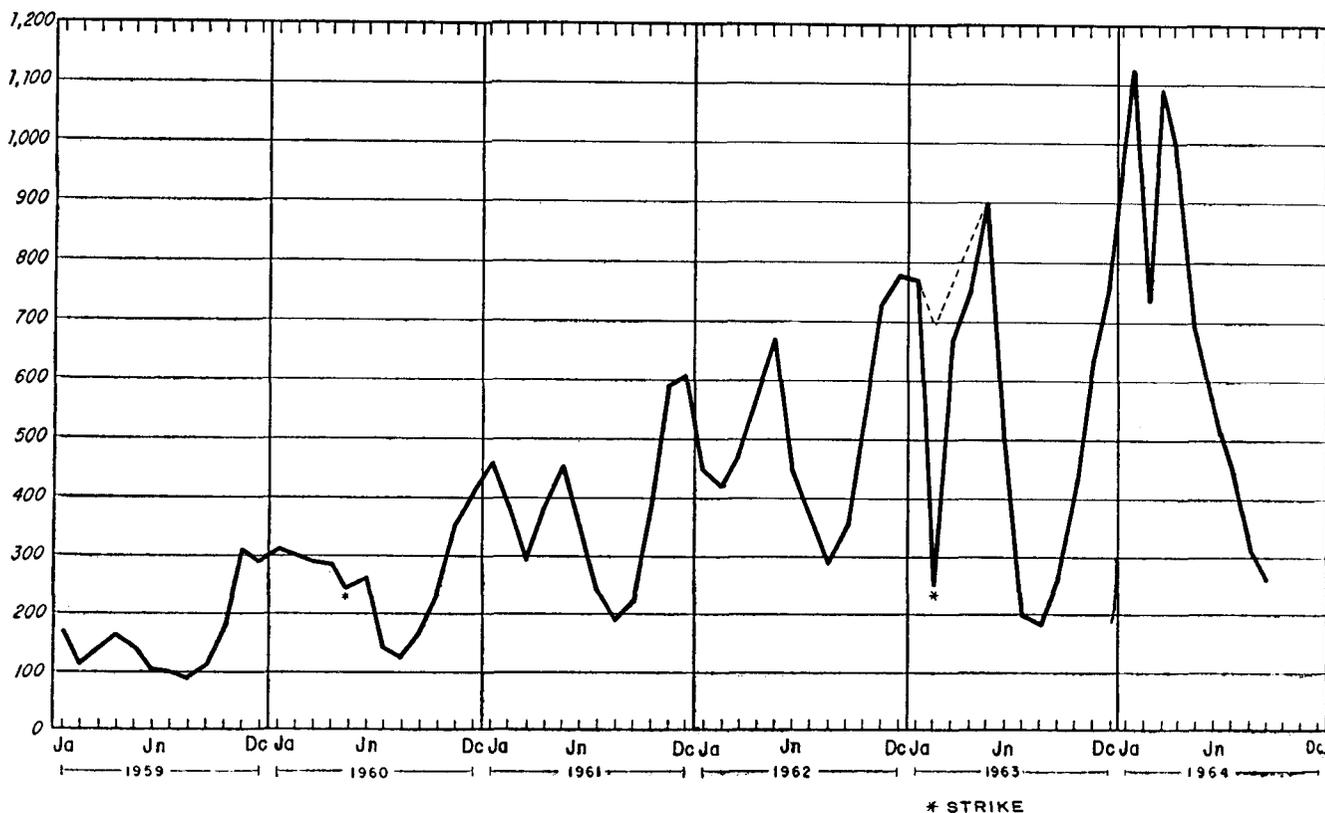


FIGURE 1. Monthly landings of the Peruvian anchovy during 1959 to 1964.

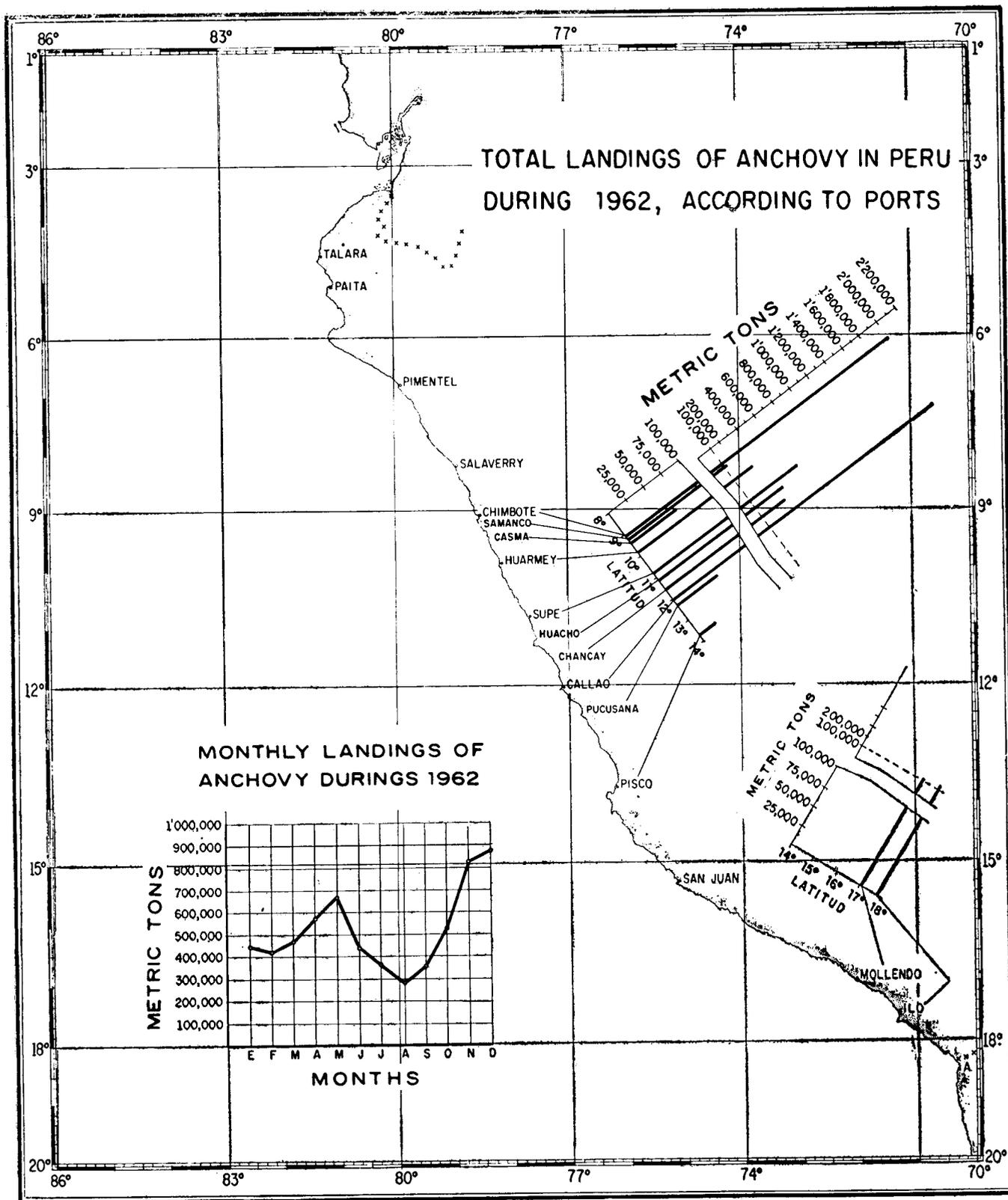


FIGURE 2. Geographical distribution of anchovy landings during 1962. Inserted are landings by ports and by months.

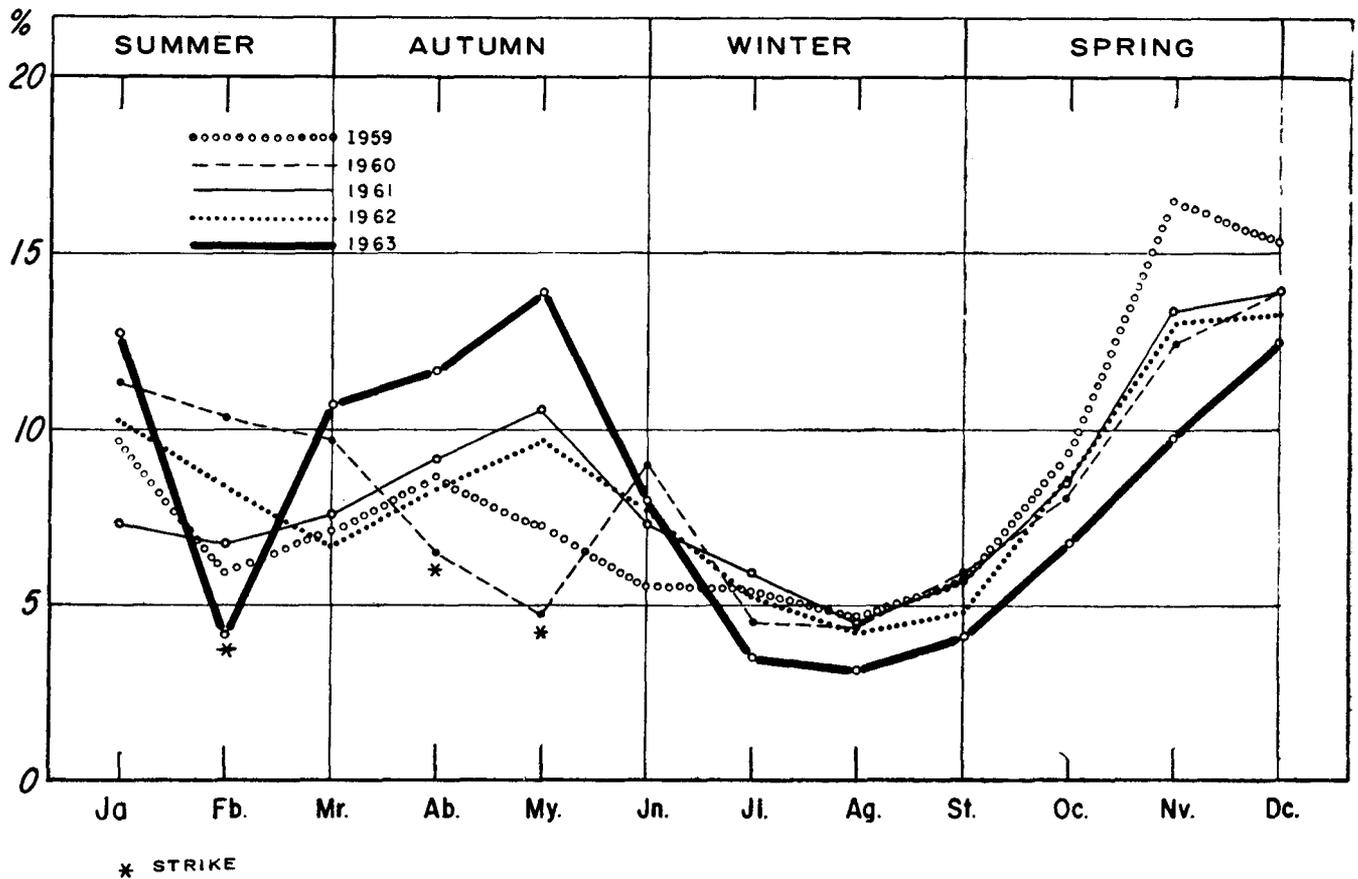


FIGURE 3. Monthly percentages of landings for the years 1959 to 1963.

of fishing success is given by using catch per unit of effort data. The graph shows monthly deviations from the overall mean per gross registered ton for the period 1959-1962.

The events in different fishing areas show a strikingly similar pattern. The drastic changes taking place during the last year are clearly evident, but this is treated in another paper and lies outside the scope of the present treatment.

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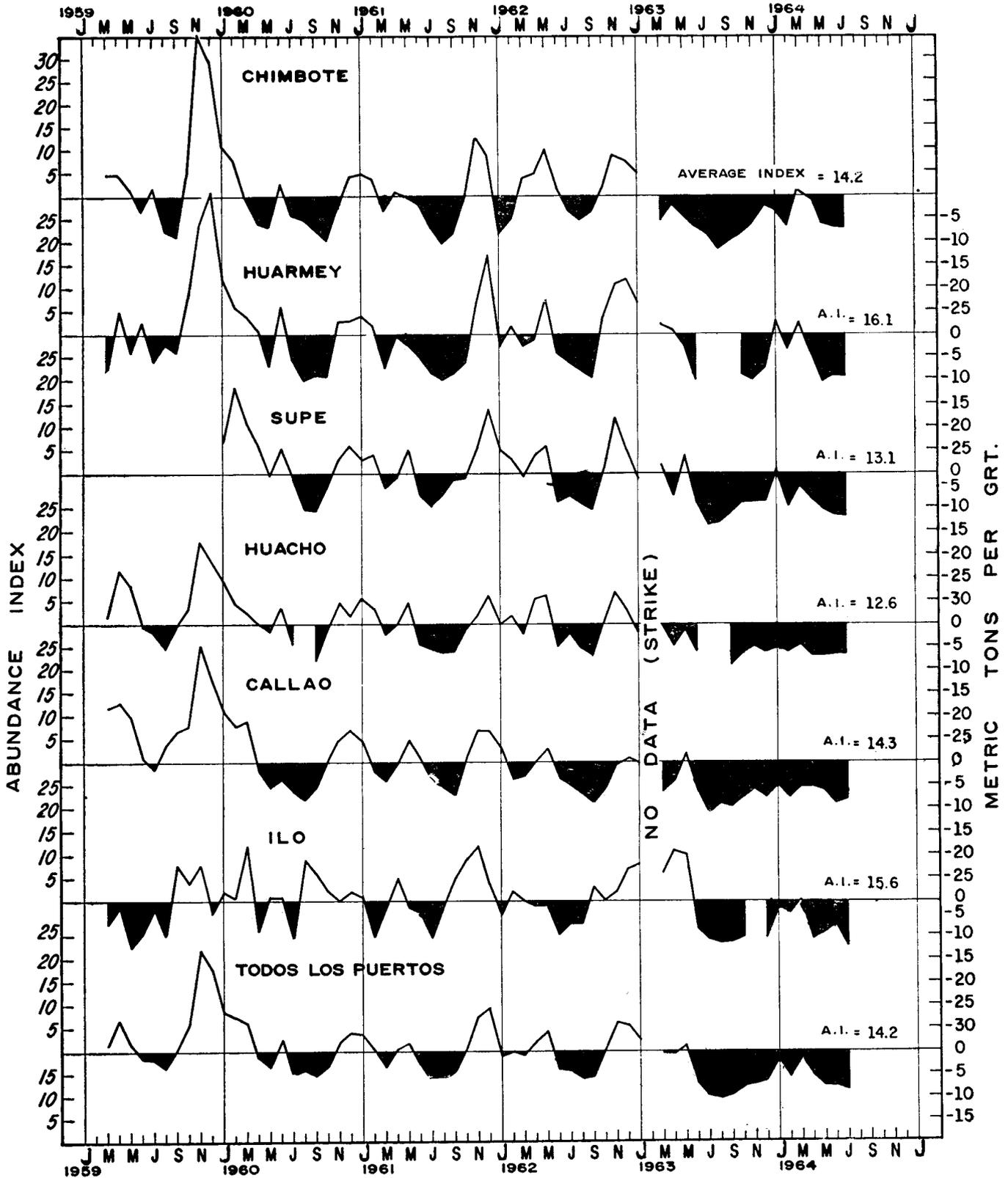


FIGURE 4. Monthly deviations of catch in tons, per GRT vessel calculated from the mean of 1959 to 1962, for different ports.

PRELIMINARY RESULTS OF STUDIES ON THE PRESENT STATUS OF THE PERUVIAN STOCK OF ANCHOVY (*ENGRAULIS RINGENS JENYNS*)

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INTRODUCTION

This report presents the results of an analysis made in September 1964 of all data then available on the Peruvian anchovy. It was presented to the Peruvian Marine Institute and written in a form intended for circulation to non-experts in stock assessment. It is a follow-up of work reported on by Saetersdal and Valdivia (1964) and by Saetersdal et al (1965).

The Result of the Fishery

As can be seen from the figures giving the total catch (Table 3) an increase of catch from 1962 to

THE FISHING EFFORT AND THE CATCH

The Fleet and Its Capacity

Table 1 shows the number of vessels that has operated during the whole years 1959-1963 and during the first part of 1964. Table 2 shows the distribution by holding capacity and the estimated total capacity of the fleet. The number of vessels increased by 60% from 1962 to 1963 and the capacity increased by nearly 80%. The data of the fleet from January to June 1964 indicate a continued, but lower increase.

**TABLE 1
NUMBER OF VESSELS IN OPERATION, 1959-1963 AND JANUARY-JUNE 1964 BY MATERIAL OF CONSTRUCTION**

Material of Construction	1959	1960	1961	1962	1963	Jan-Jun 1964 ¹
Wood.....	343	578	650	763	1,009	930
Steel.....	11	75	100	188	377	434
Wood and Steel.....	--	--	--	--	4	1
Without Data.....	1	1	3	145	366	456
Totals.....	355	654	753	1,096	1,756	1,821

¹ Provisional data.

**TABLE 2
DISTRIBUTION OF VESSELS BY HOLDING CAPACITY AND ESTIMATION OF TOTAL CAPACITY OF THE FLEET IN OPERATION 1959-1963 AND JANUARY-JUNE 1964**

Capacity in tons	1959	1960	1961	1962	1963	Jan-Jun 1964 ¹
10/19.....	--	1	1	--	--	--
20/29.....	22	16	10	3	3	2
30/39.....	45	47	36	23	14	8
40/49.....	62	68	55	54	50	13
50/59.....	49	50	45	41	40	26
60/69.....	78	122	130	118	115	89
70/79.....	41	82	86	86	94	73
80/89.....	34	116	147	146	155	147
90/99.....	15	99	141	182	211	339
100/109.....	3	25	45	128	274	186
110/119.....	1	5	21	52	155	168
120/129.....	--	8	12	68	154	154
130/139.....	1	1	2	12	35	43
140/149.....	--	2	3	13	40	49
150/159.....	--	3	2	5	9	10
160/169.....	--	2	6	9	12	16
170/179.....	--	--	--	1	4	7
180/189.....	1	3	2	1	5	12
190/199.....	1	1	1	--	1	2
200/209.....	--	--	--	--	1	1
230/239.....	--	1	2	1	1	1
250/259.....	--	--	--	--	1	--
260/269.....	--	--	--	--	9	8
Without data.....	2	2	6	153	373	467
Total.....	355	654	753	1,096	1,756	1,821
Total Capacity.....	21,015	47,620	58,945	99,000	176,000	--

¹ Provisional data.

² Include estimations for vessels without information of capacity.

**TABLE 3
CATCH BY PORTS AND YEARS 1959-1963 AND CATCH IN JANUARY-JUNE 1964**

Ports	1959	1960	1961	1962	1963	Jan.-June 1964 ¹
Chimbote.....	549,904	736,301	1,259,302	1,999,795	1,767,095	1,484,437
Samanco.....	85,532	90,086	135,480	129,114	95,298	83,961
Casma.....	53,612	59,336	49,473	64,669	44,246	117,602
Huarmey.....	246,294	264,280	261,019	308,175	247,976	205,617
Supe.....	2,405	128,189	373,622	655,131	753,452	594,367
Vegueta.....	--	--	--	--	--	46,971
Huacho.....	78,511	164,036	264,414	421,609	517,054	292,655
Chancay.....	59,558	44,642	99,708	369,555	545,339	334,689
Callao.....	754,047	1,310,746	1,925,074	1,965,989	1,771,648	1,018,961
Pucusana.....	18,970	32,201	47,516	55,559	56,688	31,510
Tambo de Mora.....	--	--	--	--	143,518	300,110
Pisco.....	--	--	--	23,943	59,276	80,487
Atico.....	--	--	--	--	32,371	46,697
Mollendo.....	8,623	27,926	44,820	125,836	121,885	73,250
Ilo.....	51,242	85,859	119,281	148,352	263,418	346,968
Other ports.....	--	--	--	6,897	--	--
Totals.....	1,908,698	2,943,602	4,579,709	6,274,624	6,419,261	5,058,284

¹ Provisional data.

TABLE 4A

AVERAGE ANNUAL CATCH FOR VESSELS GROUPED BY 5 FEET OF LENGTH 1959-1963. ALL THE COUNTRY, CHIMBOTE AND CALLAO
All the Country

Length (ft.)	1959		1960		1961		1962		1963 ¹	
	Catch	Vessels	Catch	Vessels	Catch	Vessels	Catch	Vessels	Catch	Vessels
25-29.....	1,750	1	2,250	1						
30-34.....	2,607	7	1,650	5	1,875	4	2,750	1		
35-39.....	2,598	23	2,050	10	2,000	4	1,500	2		
40-44.....	3,210	25	2,861	18	2,750	12	2,861	9		
45-49.....	4,146	53	3,375	36	3,604	24	3,120	27		
50-54.....	6,854	48	5,592	79	5,417	72	5,282	62	3,509	21
55-59.....	7,109	39	6,905	68	6,590	81	6,784	89	4,762	34
60-64.....	9,750	19	7,421	114	8,500	214	8,965	242	5,897	171
65-69.....	--	--	10,750	1	9,000	26	10,716	104	7,442	233
70-74.....	--	--	--	--	--	--	11,350	15	8,393	24
75-79.....	--	--	8,822	7	8,750	10	11,550	15	6,910	19
80-84.....	--	--	6,250	2	10,500	2	19,250	1	4,792	1
90-94.....	--	--	--	--	--	--	--	--	10,098	3
Total vessels.....	--	215	--	341	--	449	--	567	--	506

¹ Incomplete data.

TABLE 4B
CHIMBOTE

Length (ft.)	1959		1960		1961		1962		1963 ¹	
	Catch	Vessels	Catch	Vessels	Catch	Vessels	Catch	Vessels	Catch	Vessels
35-39.....	--	--	2,750	2						
40-44.....	2,806	9	1,750	2						
45-49.....	4,083	9	3,583	3	2,750	1	2,750	1		
50-54.....	6,219	16	5,071	14	5,204	11	5,679	14	3,188	5
55-59.....	7,762	17	6,795	22	7,250	26	7,361	27	5,092	14
60-64.....	9,650	10	7,211	38	8,796	76	10,040	81	5,910	65
65-69.....	--	--	--	--	10,188	8	13,056	31	7,884	68
70-74.....	--	--	--	--	--	--	11,850	10	8,692	12
75-79.....	--	--	7,750	2	16,750	1	15,250	2	7,429	5
80-84.....	--	--	--	--	10,500	2	19,250	1	4,792	1
90-94.....	--	--	--	--	--	--	--	--	10,098	3
Total vessels.....	--	61	--	83	--	125	--	167	--	173

¹ Incomplete data.

TABLE 4C
CALLAO

Length (ft.)	1959		1960		1961		1962		1963 ¹	
	Catch	Vessels	Catch	Vessels	Catch	Vessels	Catch	Vessels	Catch	Vessels
35-39.....	2,306	9	--	--	--	--	1,750	1		
40-44.....	4,062	8	3,167	6	3,625	4	5,250	1		
45-49.....	4,900	20	3,750	17	4,150	10	3,361	9		
50-54.....	8,397	17	5,683	30	5,417	30	4,875	20	3,759	5
55-59.....	7,417	9	7,424	23	6,538	26	6,202	31	4,512	7
60-64.....	11,750	3	7,650	45	8,282	78	7,881	84	5,414	36
65-69.....	--	--	10,750	1	9,295	11	9,266	31	7,057	54
70-74.....	--	--	--	--	--	--	16,750	1	8,149	7
75-79.....	--	--	9,167	6	8,464	7	12,321	7	7,205	7
80-84.....	--	--	--	--	9,750	1	--	--	--	--
Total vessels.....	--	66	--	128	--	167	--	185	--	116

¹ Incomplete data.

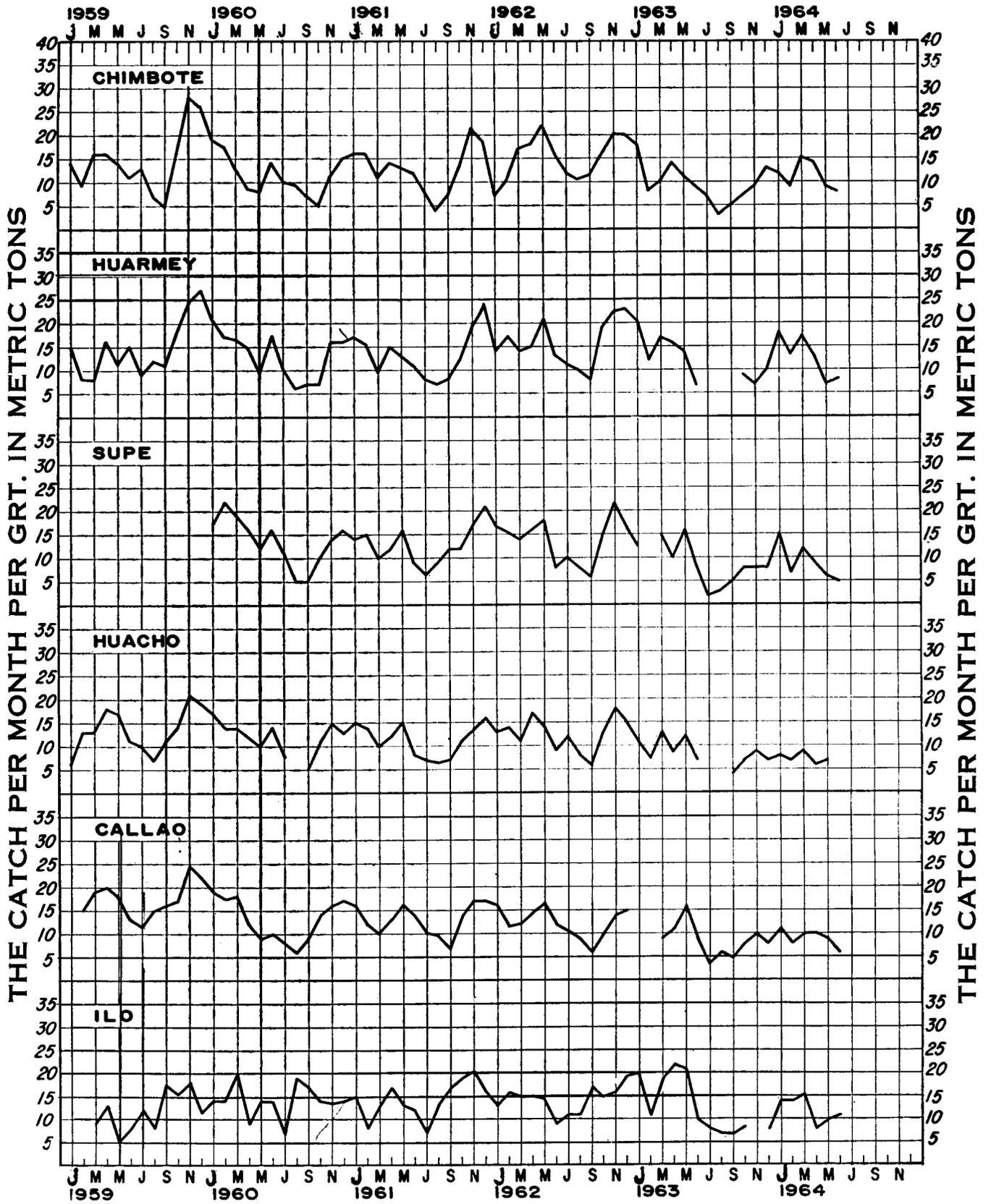


FIGURE 1. The catch per month per gross register tonnage.

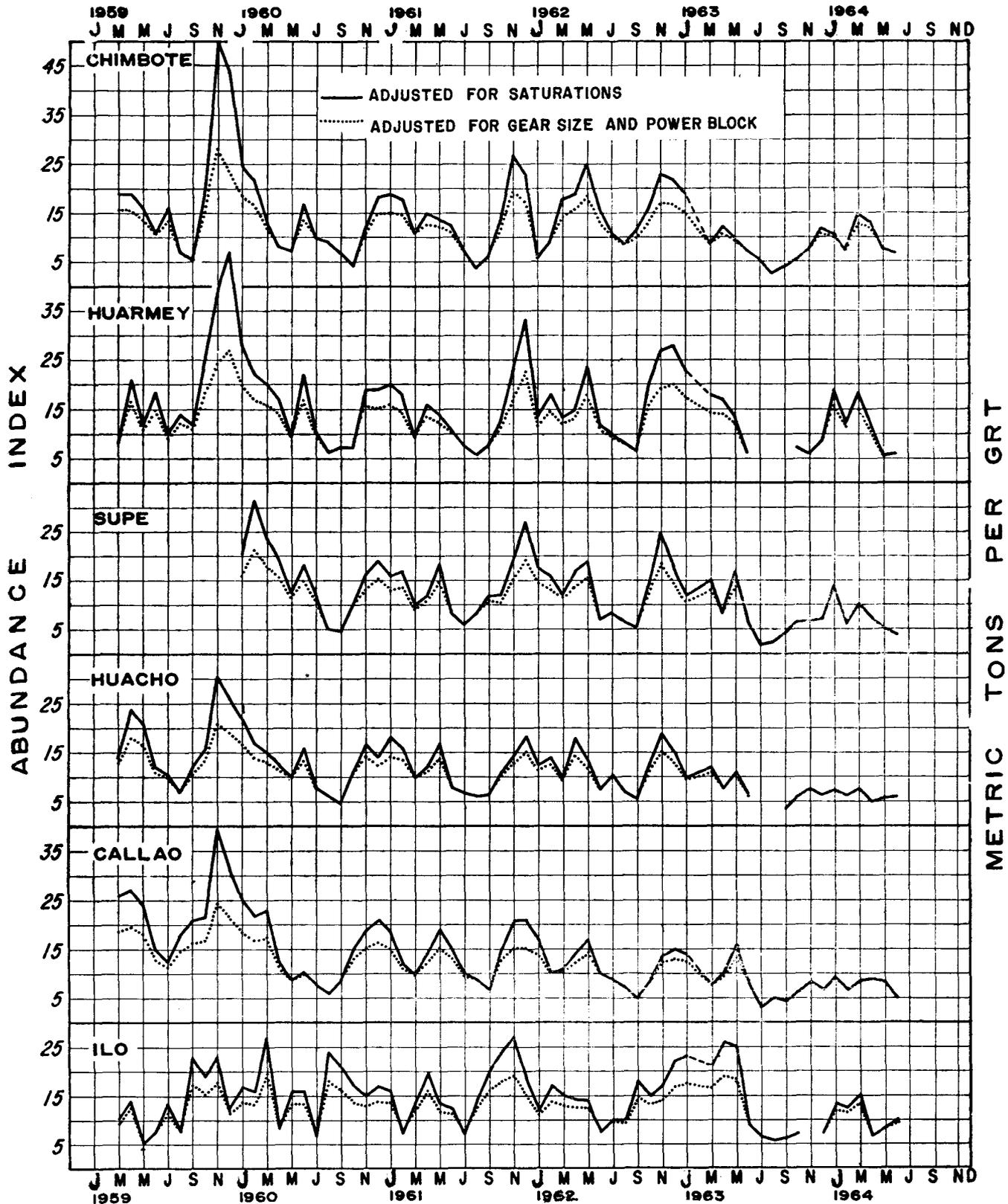


FIGURE 2. Abundance index corrected for change of fishing power A, and for effect of saturation B.

1963 corresponding to that of the effort did not take place. The total landings of 1963 was only about 2% over that of 1962.

The low fishing results of 1963 are also evident from that data of the mean catch by vessel-length-groups over the whole year (Table 4). The 1963 averages are down 30 to 40 percent as compared to 1962, and they are the lowest figures since 1959.

We may thus conclude that relatively speaking 1963 was a poor year for the anchovy fishery. Only because of the great increase of fishing effort did the total quantity landed slightly surpass that of the previous year.

ESTIMATES OF THE FLUCTUATIONS IN THE ABUNDANCE OF THE ANCHOVY POPULATION

The Catch Per Unit of Effort

In our previous report, we showed that a convenient time-unit of effort is the work of the vessels during 1 month and that the standardization of the vessels can most easily be accomplished by using the gross

registered ton as a unit of measure. We thus use catch per month per GRT as our basic measure of abundance. Figure 1 demonstrates this *uncorrected abundance index*.

The Abundance Index

Because it is thought that improved equipment and increases of size of gears has affected the fishing power of the vessels since 1959, some corrections need to be made in this measure of catch per unit of effort. The corrections made are described in our previous report, and for the period July 1963-June 1964, the same correction has been applied as for the first part of 1963. This corrected index is shown in Figure 2. It is also believed that when the fish is very abundant saturation of vessels will depress the c.p.u.e. A vessel cannot catch more than its capacity, even

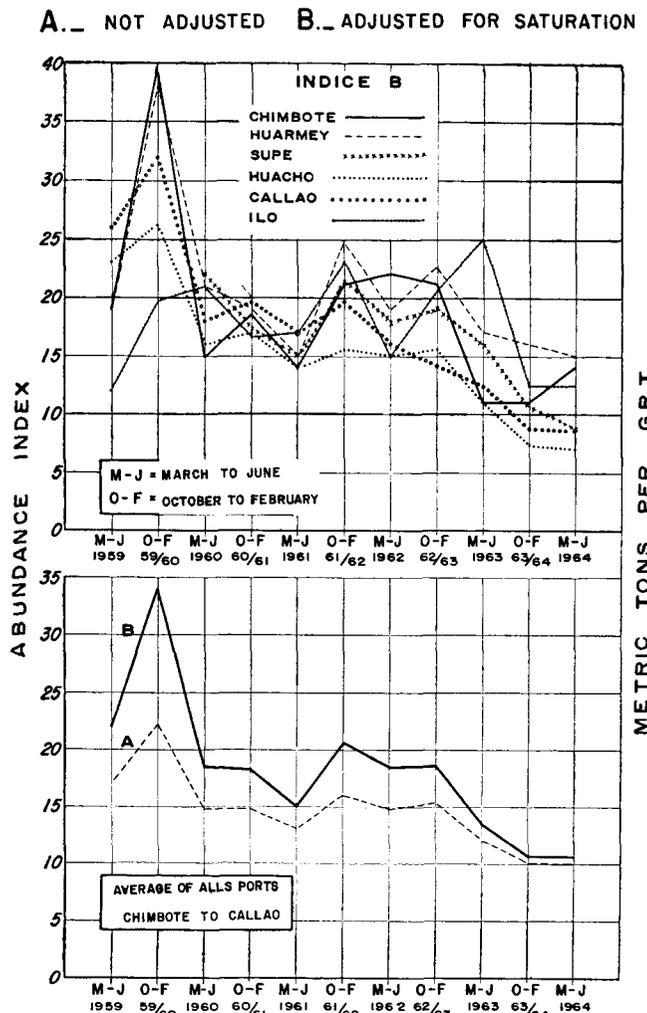


FIGURE 3. Summary of abundance by fishing season.

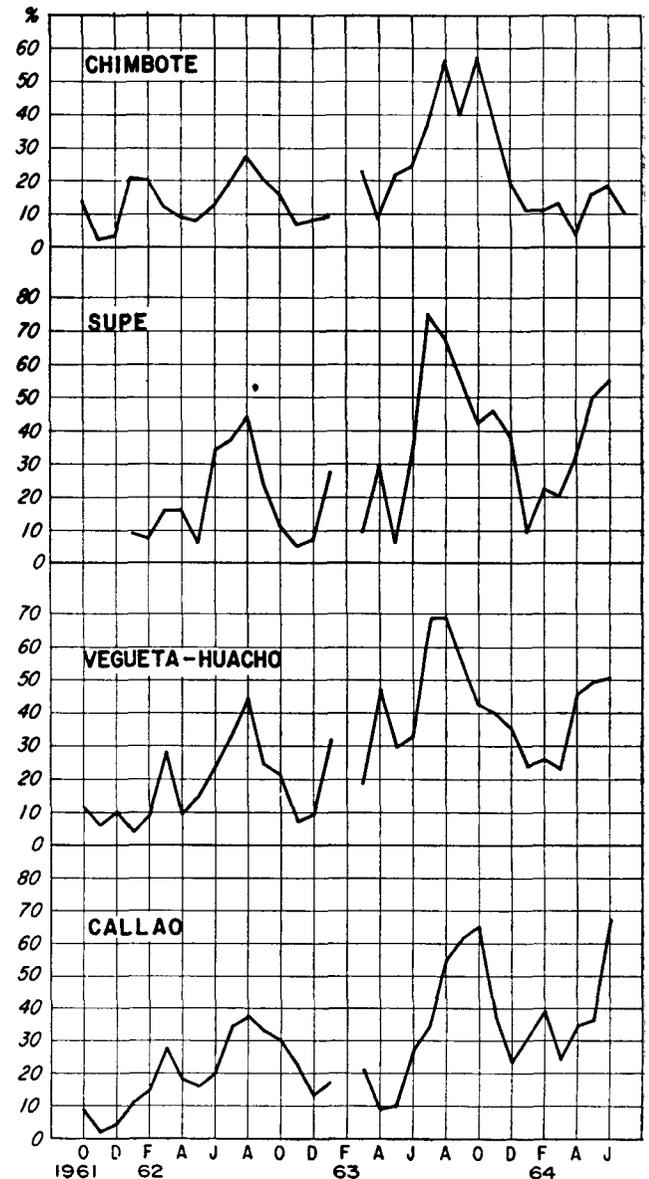


FIGURE 4. Percent trips without catch.

if the sea was full of fish. When incorporating an assessment also of this saturation effect, the index B. Figure 2 is the result. It is seen from these figures that the abundance during 1963 was low in all ports. Figure 3 shows summary by fishing seasons from which the decline during 1963 and 1964 is evident. The decline is most drastic in the central ports

Callao, Huacho, Supe, but it is also clearly present in the mean value of all ports between Callao and Chimbote. The most prominent feature of these curves is the absence in 1963/64 of the usual peak abundance of the October to February fishing season. The abundance indices of the last part of 1963 and the first part of 1964 are the lowest on record since 1959.

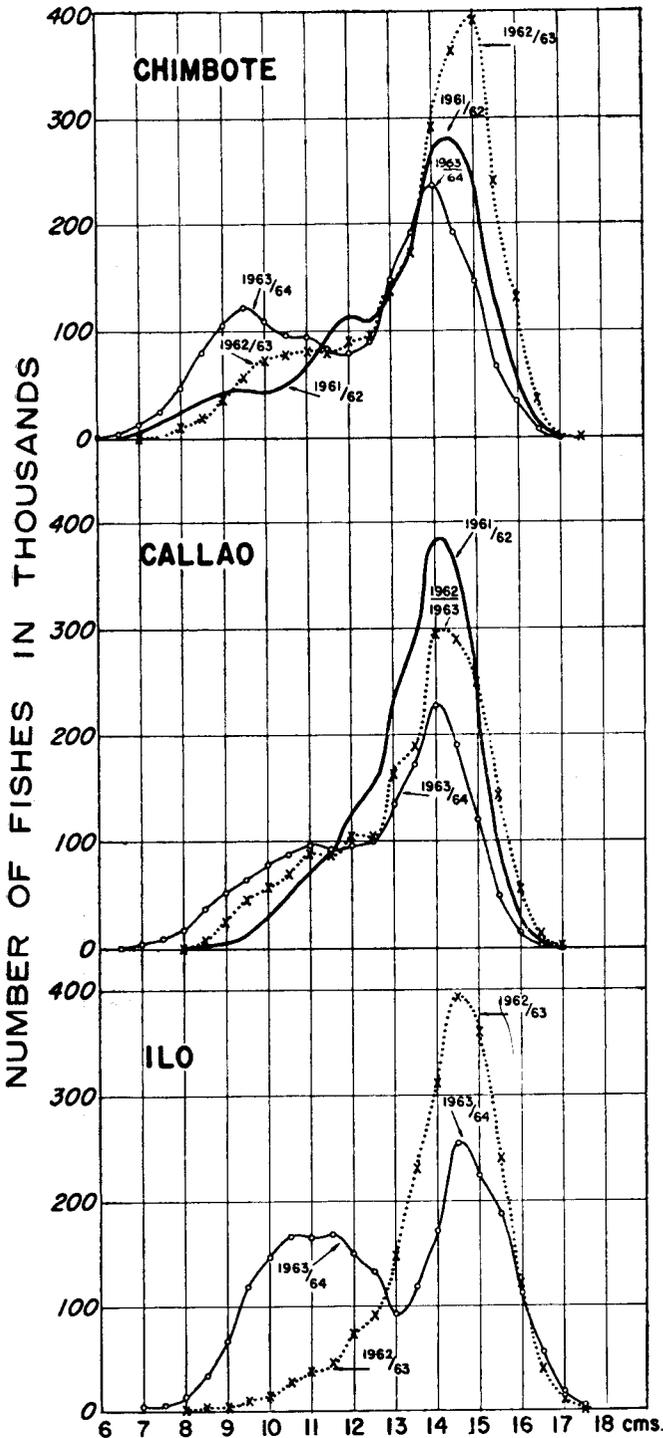


FIGURE 5. Annual length-abundance curves. Chimbote, Callao and Ilo. March to February.

Trips Without Catch

The records of poor fishing and the estimates of low abundance during this time are confirmed by data collected on number of unsuccessful trips of vessels. Figure 4 shows how trips without catch have increased since June 1963. The ports of Supe, Huacho and Callao show also very high figures during 1964 while Chimbote seems to be back on a normal value this year.

THE SIZE OF THE ANCHOVY

Figure 5 shows the annual size-abundance curves March through February for the three years since 1961. The striking feature of these curves is the low abundance of the big adult fish (14 cm and more) during the last year. The monthly length-curves which are available, but not shown in this report, show that this decline of abundance of adult fish started already in the last part of 1962. It became prominent during 1963. Figure 6 shows the estimated abundance of fish of sizes of 14-15 cm. or more (adult anchovy, consisting of usually several spawning groups) by month from March 1961 onwards.

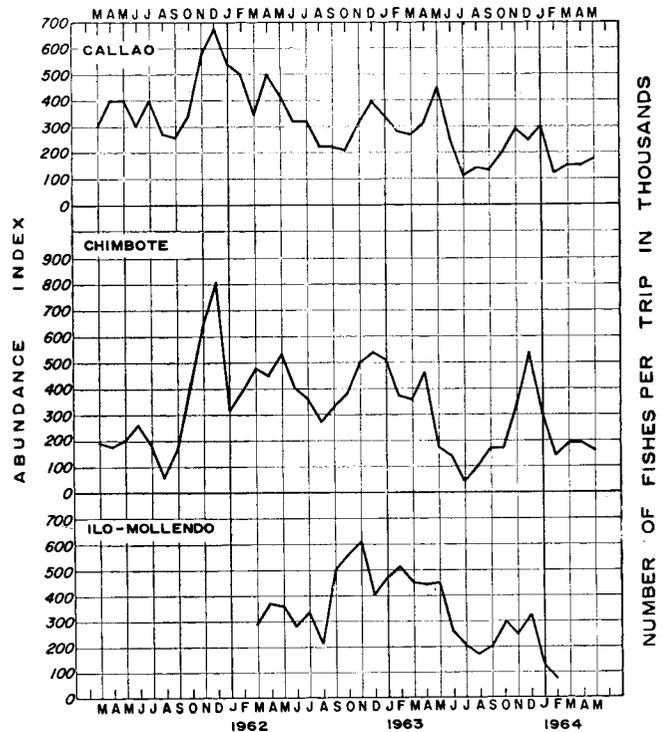


FIGURE 6. Modal abundance of adult group 14-15 cm. from length-abundance curves.

The low values since June 1963 is striking in all three ports Chimbote, Callao, and Ilo. It seems then that the reason for the poor fishing of 1963 was the low abundance or low availability of the big adult fish during this period.

CAUSES OF REDUCED ABUNDANCE OF BIG ADULT FISH

Natural Fluctuations of Recruitment

There is one phenomenon that is known to have caused great fluctuations of stock size in a number of marine fish populations, i.e., natural variations in recruitment brought about by varying success of survival of eggs and larvae from the different broods. The results of our length-measurements indicate that such types of fluctuations do occur also in the Peruvian anchovy stock. Although direct age-determina-

tions are not available, it is possible from the size compositions to determine the age of the young fish and the size abundance curves offer a possibility to assess the abundance of the year-classes. In Figure 7, we have plotted the abundance of the recruit-groups 1961 through 1964 as measured in two different ways, by their modal abundance and by the estimated total number caught per unit of effort. Figure 7 also shows the abundance of the adult fish as the mean value of the months November through May each year. The recruitment apparently dropped off from 1961 to 1962 and a further reduction took place in 1963. In 1964, however, a very strong group was recruited to the fishery. As Figure 7 demonstrates, the reduction that occurred in the abundance of the adult fish is parallel to that of the recruits up till the season November 1963 to May 1964. We expect that there will be a time lag of about one year between the stage at which we measure the abundance of the recruit-group (usually March to June) and the time when the group has reached the adult stage and thus may influence the abundance of this group of 14-15 cm fish. Figure 8 shows a comparison of recruitment and abundance of adult fish when applying such a time-lag. A straight line from zero could be fitted reasonably well to these points, and confiding in these results we could conclude that fluctuations in the recruitment give cause to similar fluctuations in the abundance of the total stock which again brings about considerable variations in the success of the fishing. Before drawing this conclusion, however, we should await the results of the fishery during the period November 1964 through May 1965. The high recruitment of 1964 should bring about a considerable increase of the abundance of adult fish during this season. If this happens we think that the above conclusion can safely be drawn. It would then be a matter of great practical importance to be able to

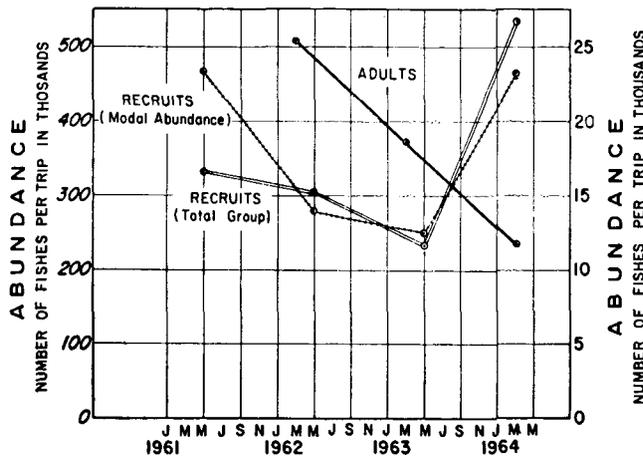


FIGURE 7. Abundance of recruit groups and the groups of adult fish. Chimbote and Callao together.

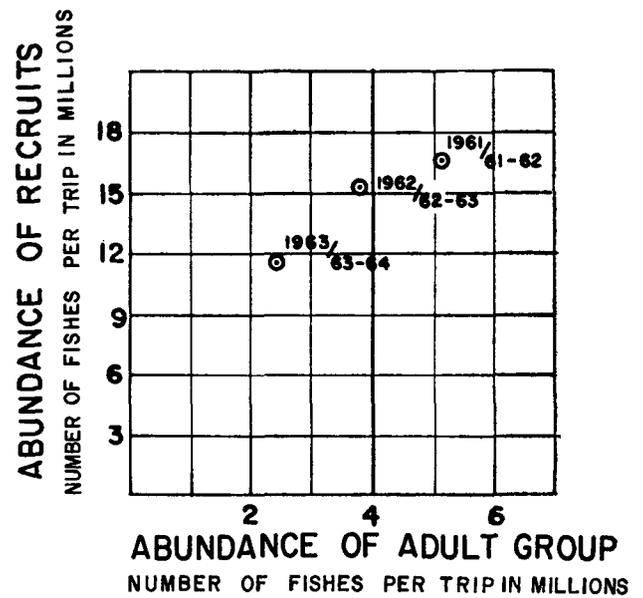
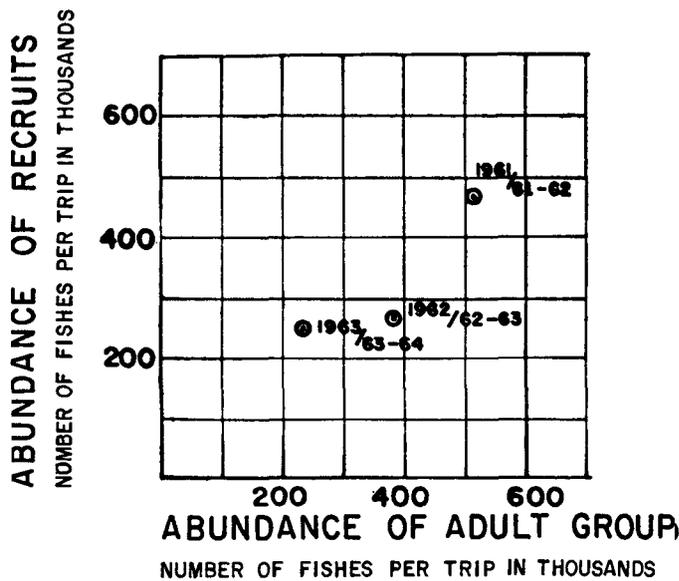


FIGURE 8. Relation between abundance of recruit groups and groups of adult fish. The abundance of the recruit group is measured in two different ways.

measure recruitment-strength as accurately as possible so as to get a better basis for forecasting yield fluctuations.

Effects of the Fishery on the Stock

There is little doubt that a fishery of about 6 million tons per year must have some effects on the anchovy population. The total mortality rate must have increased. By how much we do not know, but from a rough assessment of predation of birds and fish it is not unreasonable to think that the mortality has at least been doubled. We should expect that it would be possible to demonstrate the effects of this increase of mortality on the size composition of the fish. Such demonstrations are, however, complicated by the fluctuations in recruitment. A longer series of data is necessary to compensate for the natural fluctuations in the size composition, and thus provide a normal average basis for a comparison.

The comparisons of recruitment and adult fish abundance shown in Figure 8 have one feature which may indicate an increase of total mortality. The expectation of a straight-line relationship passing zero is only valid if the total mortality has been unaltered during the period of observation. If mortality increases one would expect the abundance of the adult group to fall off more than that of the recruits. A tendency of this nature can be seen in the data plotted in Figure 8.

We expect to be able to make more definite statements concerning the effects of the fishery on the stock after the season November 1964 to May 1965. If the abundance of the population of adult fish and thus the success of fishing do not rise to the expected

“normal” level during this season as a result of the high recruitment in 1964, then it must be concluded that the fishing mortality influences the stock to a marked degree.

In practice the effects of increased mortality and the resulting lower average size and age of the fish in the stock would be a corresponding decrease of the mean size of the fish caught in the fishery. The total stock abundance would also on the average be lower with a decrease of the catch per unit of effort. The yield would be more variable from year to year because it would to a greater extent depend upon the fluctuating abundance of the recruit fishes. This of course would make the operation of the industry more difficult with higher costs of raw material and less continuity of operations. It is, however, not thought that any lasting or permanent harm will be made to the stock by this form of over-exploitation. The recruitment in big oceanic fish stocks does not seem to be directly related to the size of the spawning stock: big-year-classes can result from the spawning of poor-ones. The direct economic effects on the industry will be those arising from expensive and in periods scarce raw material. These effects can, however, be serious enough as we have seen from the state of the industry during 1963-64.

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AN ATTEMPT TO ESTIMATE ANNUAL SPAWNING INTENSITY OF THE ANCHOVY (*ENGRAULIS RINGENS* JENYNS) BY MEANS OF REGIONAL EGG AND LARVAL SURVEYS DURING 1961-1964

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INTRODUCTION

From the beginning of our investigations in August 1961, until June 1964, we have covered three anchovy spawning cycles. During this period we have collected quantitative samples with the Hensen net at 1,422 localities in northern Peruvian waters. A description of eggs and larvae of the Peruvian anchovy was published in 1963 (Einarsson and Rojas de Mendiola), and a preliminary description of the frequency and distribution of eggs and larvae was presented at the "Primer Seminario Latinoamericano sobre el Océano Pacífico Oriental" (Einarsson, Rojas de Mendiola, and Santander, in press). The present paper carries this analysis a step further and describes the yearly areal variations in spawning intensity, as well as the variations within the whole northern region from Callao to Punta Aguja, the main fishing area now under exploitation.

For the purpose of this analysis we use only samples taken during the spawning season from August of one year to March of the next. The total number of stations occupied during the three spawning cycles was 847. Of these, 185 were occupied during 1961-62, 317 during 1962-63, and 345 during 1963-64.

The number of eggs and larvae are calculated as number per square meter of surface in a column 50 meters deep. As in our previous study the average values are given in two ways; firstly, as average values per station, which reflect the spawning intensity within the area as a whole, and secondly, as average values per positive station which reflect the spawning intensity within the boundaries of the spawning area. The material is in many ways faulty, due to uneven timing of cruises and also because all areas have not been investigated on every cruise. In spite of this we find this analysis worthwhile, and the results seem to tally with other kinds of evidence, derived from an entirely different approach.

ANNUAL AREAL VARIATIONS IN SPAWNING INTENSITY

We have divided the Peruvian coastal waters latitudinally into 2° areas from north to south as seen in Figure 1. In this evaluation only areas B-E come under consideration, since anchovy spawning does not occur in area A and our material is insufficient as regards the more southern areas. The material is graphically presented in Figure 2.

The areas fall clearly into two groups, B and C constituting one, D and E the other (Figure 3). In the first group the spawning intensity has been on a high level during the three spawning cycles, the period 1962-63 yielding the highest values, especially in the average per positive station. This means that the spawning was intensive but confined to restricted zones. Only area B shows this maximum also in the average values per station, during the said period, while area C shows declining values from the first to the third spawning cycle.

Areas D and E show a rather marked decline in the values during the two latter spawning cycles, especially in the numbers per station, and we must conclude that during the latter two cycles the spawning was both of lesser intensity and geographically less extensive.

While the values were fairly similar in all areas during the first spawning cycle, the last two cycles show values which sharply decrease from north to south.

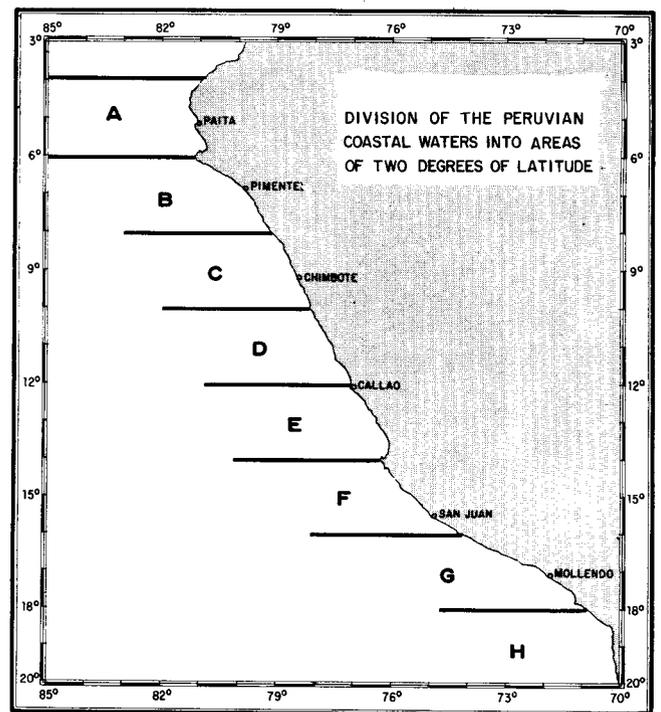


FIGURE 1.

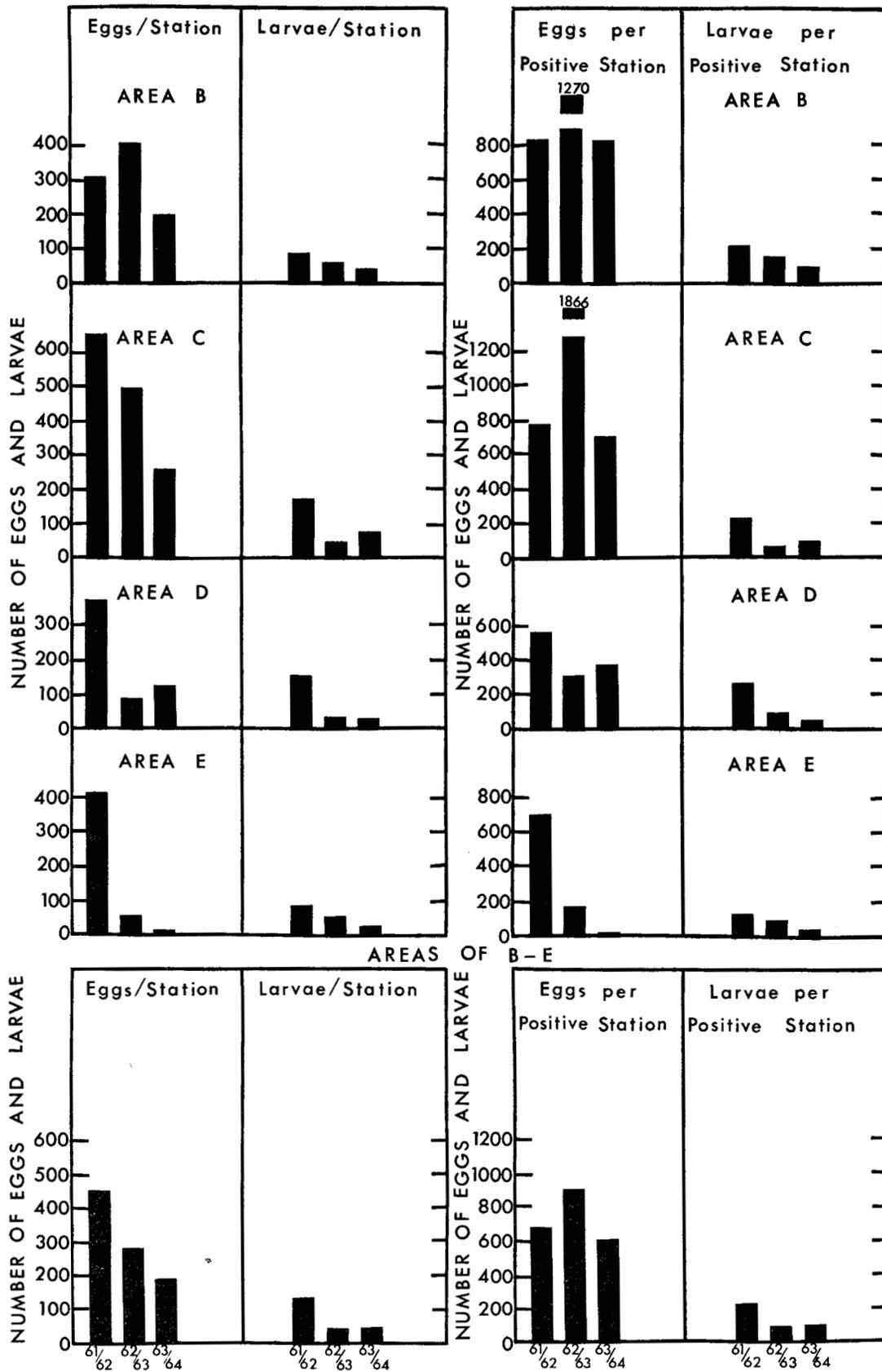


FIGURE 2.

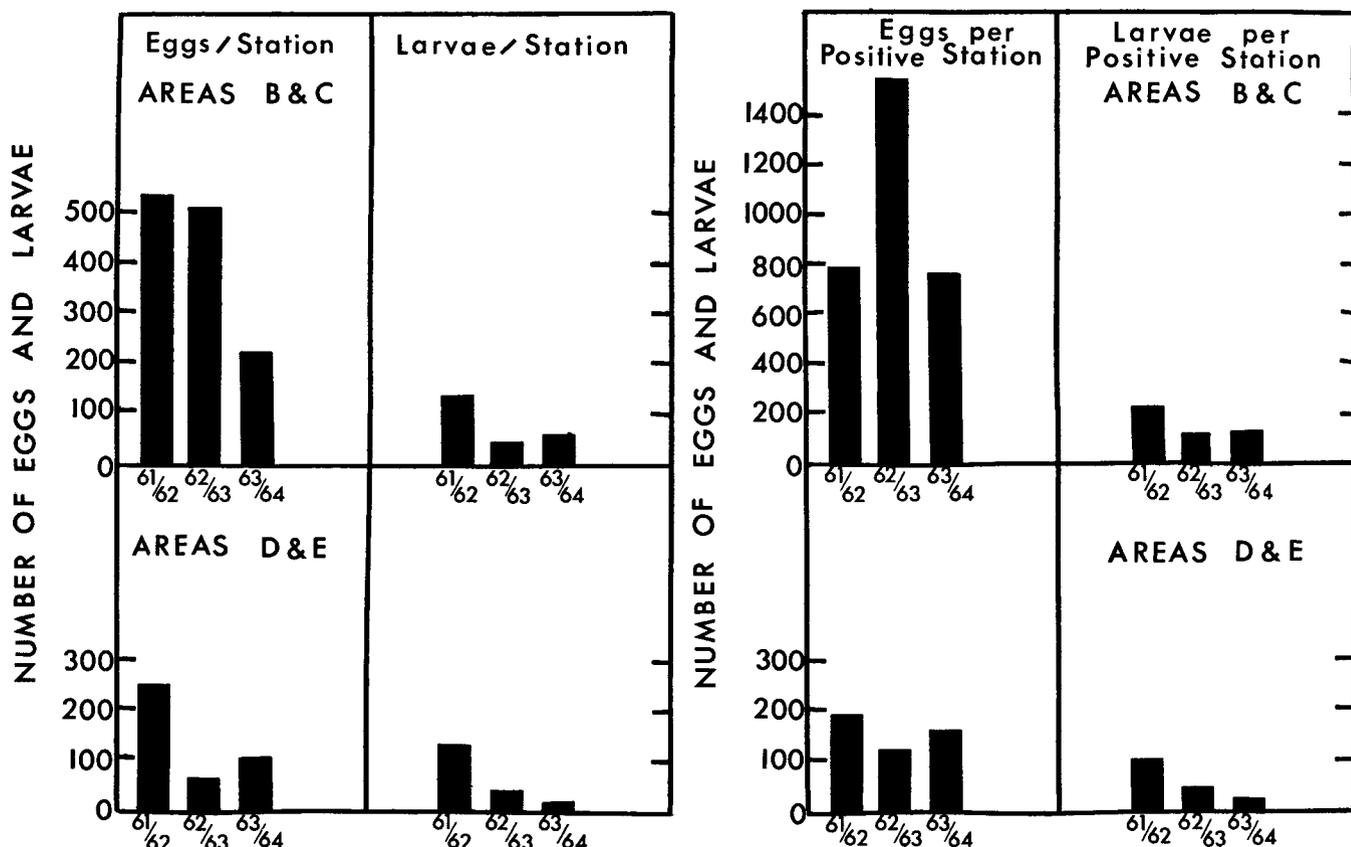


FIGURE 3.

TABLE 1
AVERAGE NUMBERS OF EGGS PER STATION AND PER POSITIVE STATION IN AREAS B-E, DURING THREE SPAWNING CYCLES (1961-1964)

Spawning Cycle		Total Number of Eggs	Average per Positive Station	Number of Positive Stations	Number of Stations	Average per Stations	Percent of Positive Stations
1961-62							
August	1961	37,407	634	59	93	402	63
October	1961	4,692	1,173	4	4	1,173	100
December	1961	345	57	6	10	34	60
January	1962	6,546	2,182	3	13	504	23
February	1962	34,695	708	49	65	534	75
		83,685	691	121	185	452	65
1962-63							
October	1962	3,045	132	23	66	46	35
November	1962	56,745	1,113	51	136	417	37
January	1963	549	137	4	19	29	21
February	1963	26,001	1,444	18	96	271	19
		86,340	899	96	317	272	30
1963-64							
August	1963	23,793	580	41	112	212	37
October	1963	16,431	747	22	91	181	24
November	1963	16,767	798	21	55	305	38
February	1964	8,340	363	23	87	96	26
		65,331	610	107	345	189	31

TABLE 2
AVERAGE NUMBERS OF LARVAE PER STATION AND PER POSITIVE STATION IN AREAS B-E, DURING THREE SPAWNING CYCLES (1961-1964)

Spawning Cycle		Total Number of Larvae	Average per Positive Station	Number of Positive Stations	Number of Stations	Average per Stations	Percent of Positive Stations
1961-62							
August	1961	13,101	234	56	93	141	60
October	1961	1,338	669	2	4	334	50
December	1961	327	54	6	10	33	60
January	1962	1,674	239	7	13	129	54
February	1962	8,583	232	37	65	132	57
		25,023	232	108	185	135	58
1962-63							
October	1962	417	13	32	66	6	48
November	1962	3,150	57	55	136	23	40
January	1963	129	21	6	19	7	32
February	1963	10,089	202	50	96	105	52
		13,785	96	143	317	43	45
1963-64							
August	1963	6,285	108	58	112	56	52
October	1963	5,154	99	52	91	57	57
November	1963	2,727	160	17	55	50	31
February	1964	1,464	49	30	87	17	34
		15,630	99	157	345	45	46

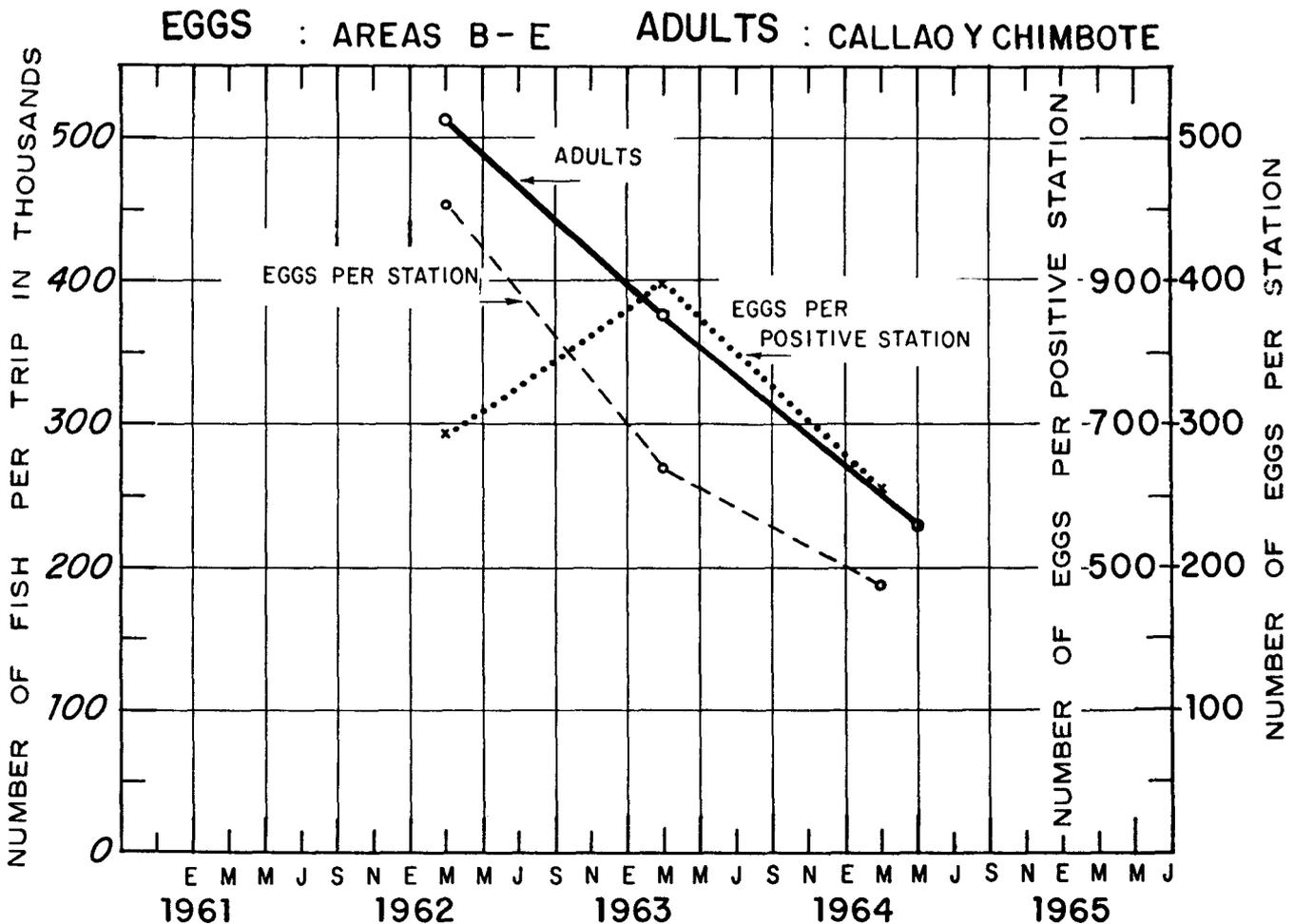


FIGURE 4.

ANNUAL REGIONAL VARIATIONS IN SPAWNING INTENSITY

The material has been summed up for the whole region in Tables 1 and 2, and graphically presented in the lower part of Figure 2.

The evidence shows that the spawning intensity in the region as a whole, measured by number of eggs per station, has been declining during the three spawning cycles and during 1963-64 was less than half of that observed during 1961-62. The average numbers per positive station indicate that there was a concentrated spawning effort during the 1962-63 cycle. We have demonstrated that this happened only in areas B and C.

A COMPARISON BETWEEN SPAWNING INTENSITY AND ABUNDANCE OF ADULTS

In their recent contribution on the present status of the Peruvian stock of anchovy, Saetersdal, Valdivia, Tsukayama and Alegre (this volume) draw attention to the reduced abundance of big adult fish from 1962 to 1964. In their Figure 7 they show the abundance of the adult fish as the mean value of the

months of November through May each year, the abundance being measured in numbers of adult fish per trip. In Figure 4 we have compared these data with the spawning intensity during the corresponding period, as measured by the average number of eggs per station for the whole northern region. The abundance of adults refers to data from Chimbote and Callao combined, and should thus be comparable. There is a striking similarity in the rate of decline.

A COMPARISON BETWEEN SPAWNING INTENSITY AND RECRUITMENT

The relation between spawning intensity and recruitment is much more complex than the relation discussed in the preceding paragraph. So far we know nothing about egg mortalities and their causes, larval mortalities, larval drift and the subsequent fate of the young individual until it enters the fishery at a size of about 8 cm. This phase in the life history of the anchovy is still shrouded in mystery and the need to fill this gap in our knowledge, is imperative.

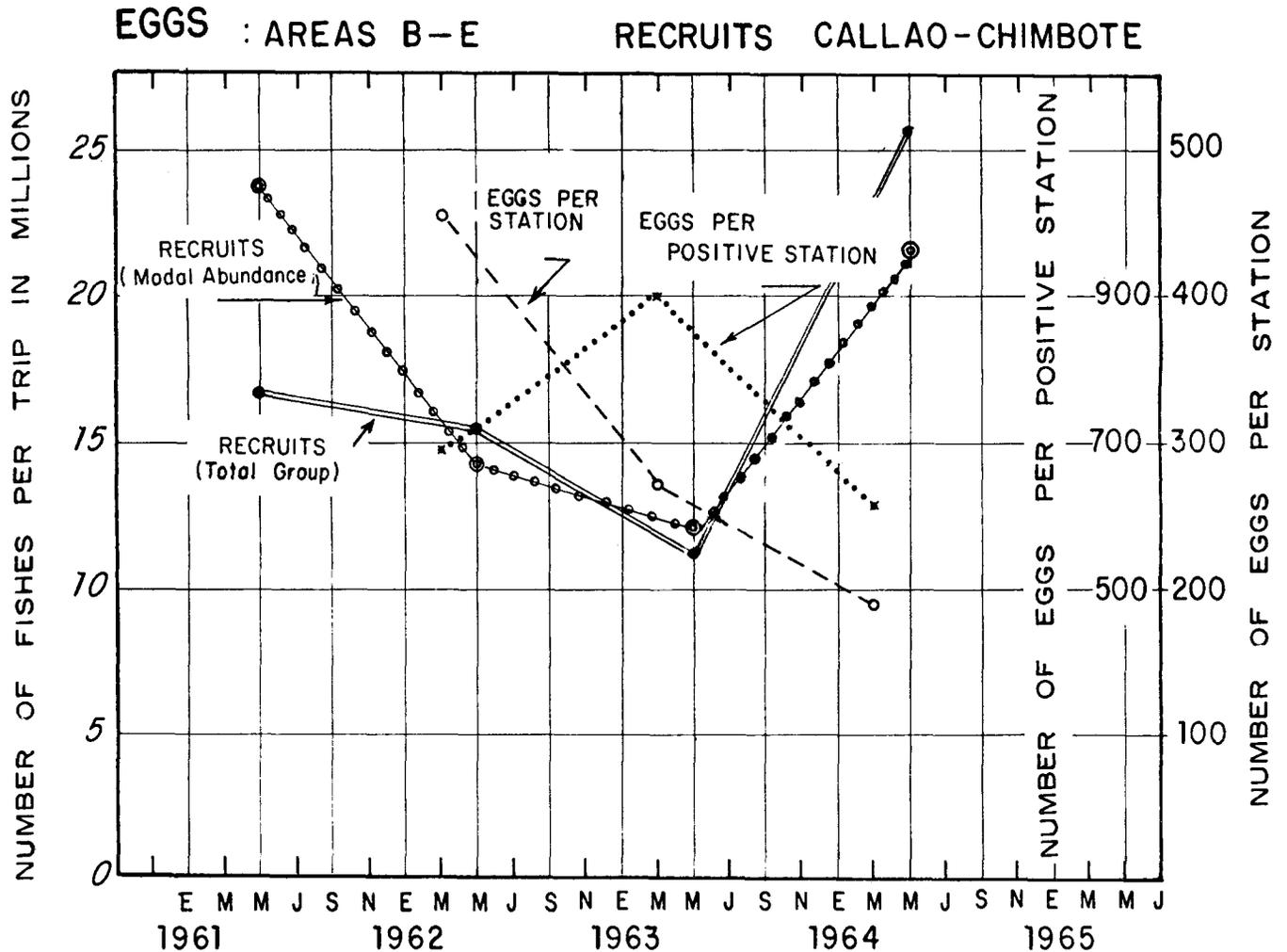


FIGURE 5.

In their paper, Saetersdal, Valdivia, Tsukayama and Alegre (this volume) have measured the abundance of the recruitment groups 1961 through 1964 in two different ways: first the modal abundance, expressed as average values for the highest modal abundance during the recruitment period, and second the estimated total number caught per unit of effort, as measured by number of recruits per trip. They found the decline in the abundance of adult fish parallel to that occurring in the abundance of re-

cruits up till the season November 1963 to May 1964. However, in 1964, they found a very strong recruit group appearing in the fishery.

In Figure 5 we have compared the recruit abundance with the spawning intensity, as measured by egg numbers per station and per positive station for the region as a whole. The new strong recruit group did not at any rate originate through a widespread spawning, as shown by the low number of eggs per station. But it is quite possible that a strong

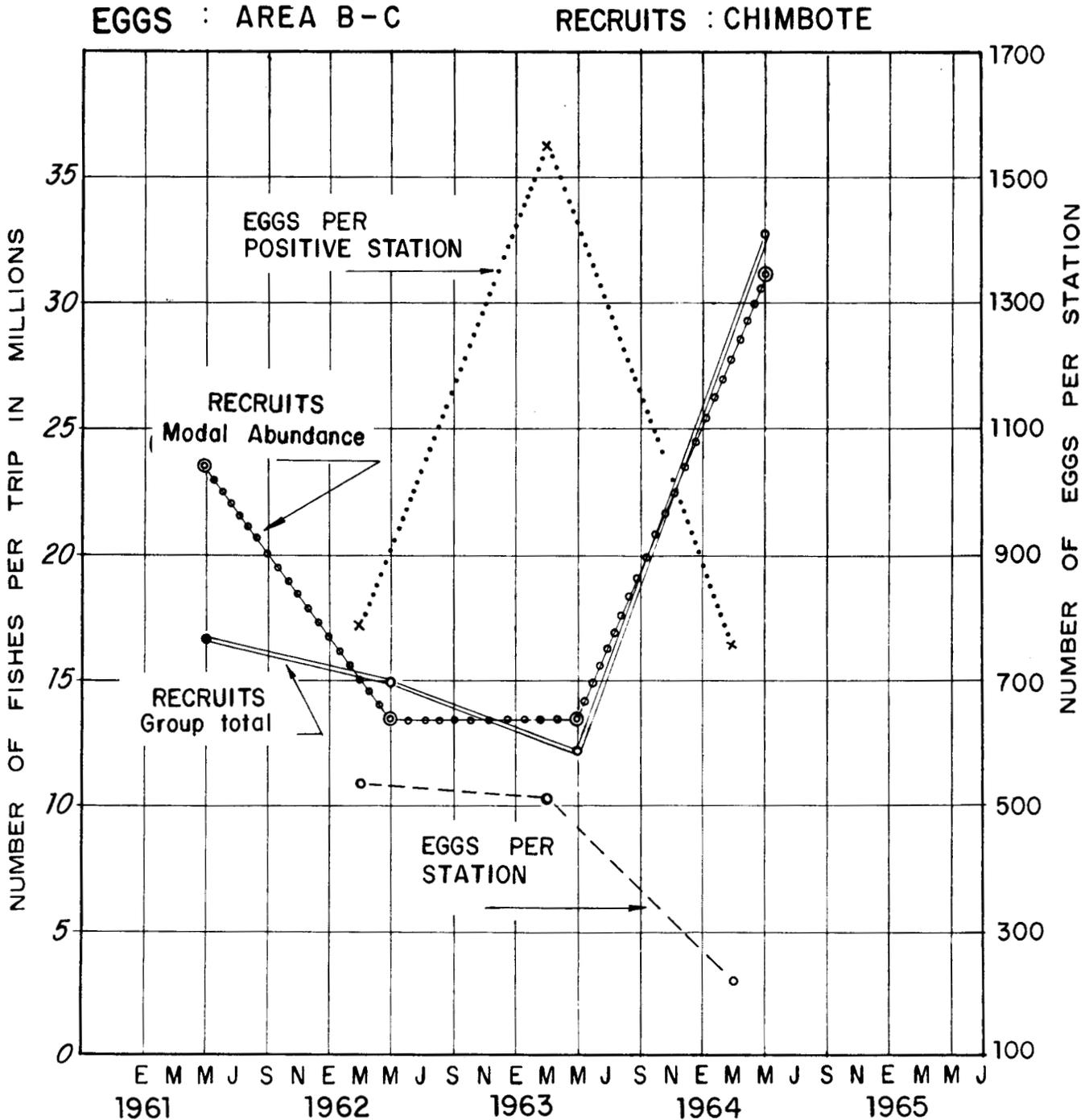


FIGURE 6.

recruit group originates through intensive and concentrated spawning and subsequent favorable conditions for survival. Ahlstrom (1959, p. 203) thought first that a widespread spawning of the California sardine favored greater survival and bigger recruitment, but a closer analysis of later data led him to doubt this conclusion.

It was stated that a strong recruit group could originate from an intense but geographically restricted spawning. This, however, did not occur as a result of the intensive spawning observed in areas B and C during 1962-63. The resulting group was poor according to the abundance estimates shown in Figure 6. On the other hand the low egg numbers in 1963-64 gave rise to an estimated rich recruit group. Evidently more effort is needed to tie up biological facts and oceanographic evidence.

The best conformity between egg numbers and recruitment strength was found in areas D and E as shown in Figure 7. Here the trend follows the same pattern both as regards eggs and recruits.

FREQUENCY OF LARVAE

It must be borne in mind that the Hensen net is very selective as to larval sizes caught. Only the

youngest stages (less than 10 mm in length) are effectively retained by the net. We still lack experimental evidence as to incubation time and the rate of larval growth, but presumably the incubation time is shorter than the growth time of larval stages effectively retained. Until this time factor has been studied the numbers of eggs and larvae are not directly comparable, but if larval growth represents a longer time the numbers of larvae are maximal numbers in comparison, and we can conclude that

TABLE 3
PERCENTAGES OF ANCHOVY LARVAE VERSUS EGGS IN THE HENSEN NET HAULS 1961-1964

	Percent of larvae per positive Station	Percent of larvae per Station
Winter.....	28	32
Spring.....	10	13
Summer.....	22	29
Autumn.....	37	33
Average percent.....	20	25

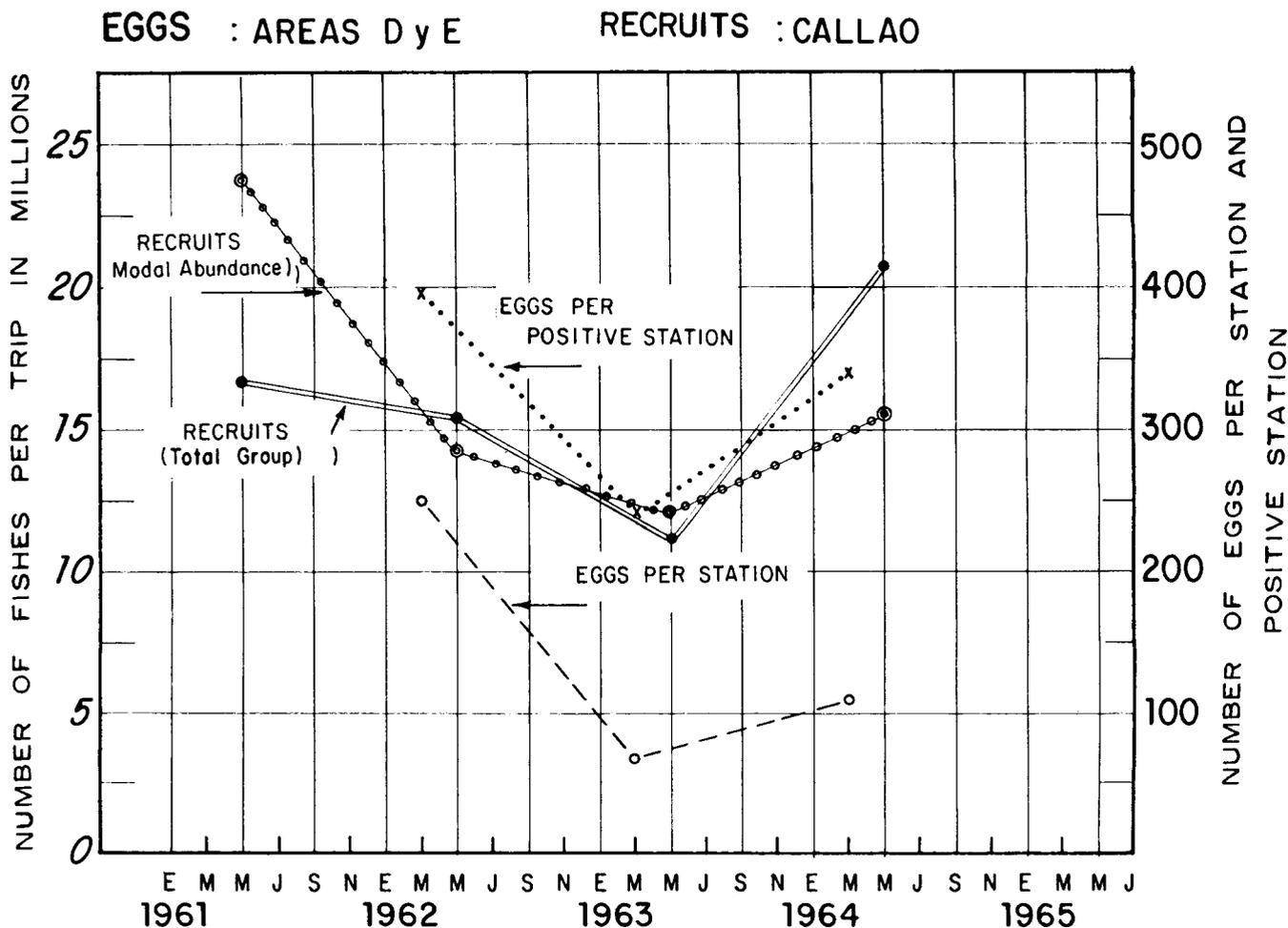


FIGURE 7.

mortality during the initial growth phase is not lower than that indicated by direct comparison between egg and larval number.

Adding up the whole material we find the percentage values of larvae versus eggs as shown in Table 3, the material being divided according to seasons.

The higher percentages of larvae per station reflects the effect of dispersal. The larval frequencies are much lower during the spring months. In fact the difference is so great that it must reflect higher egg mortalities during these months.

In Figure 8 we have shown graphically the larval percentages according to spawning cycles for the

different areas. It will be seen that areas B and C follow the same trend with the lowest values during the 1962-63 cycle. It was shown above that a concentrated spawning effort occurred in these areas during this spawning cycle and it seems that this resulted in increased egg mortalities. It will be noted that the recruitment estimates and the percentage frequencies of larvae in these two areas follow the same pattern.

During the two latter spawning cycles area E shows a quite different trend with very high larval percentages and this is also true for area D during the 1962-63 cycle. We ascribe these phenomena to a low spawning intensity within the area, coupled

LARVAL PERCENTAGES ACCORDING TO AREA

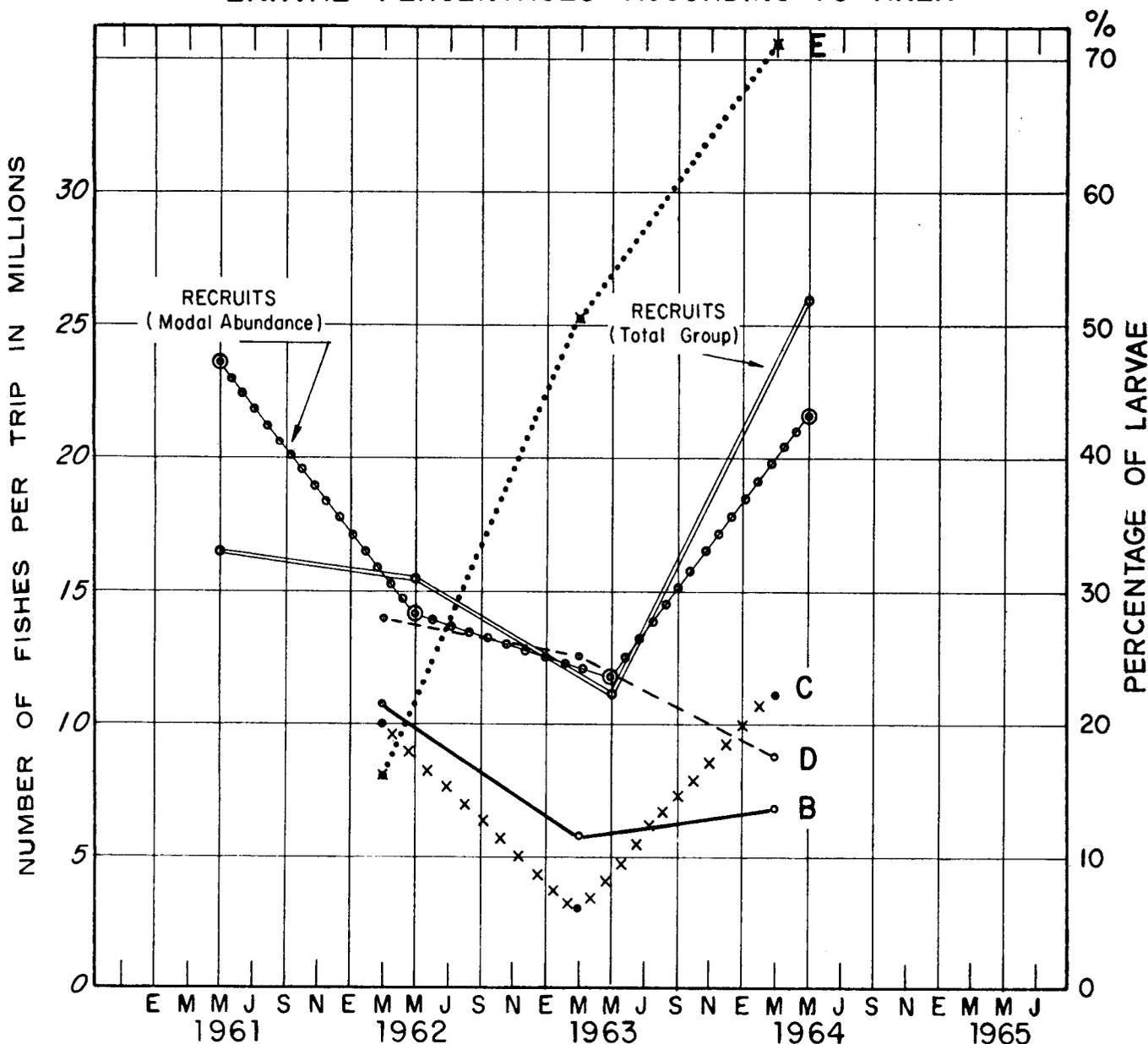


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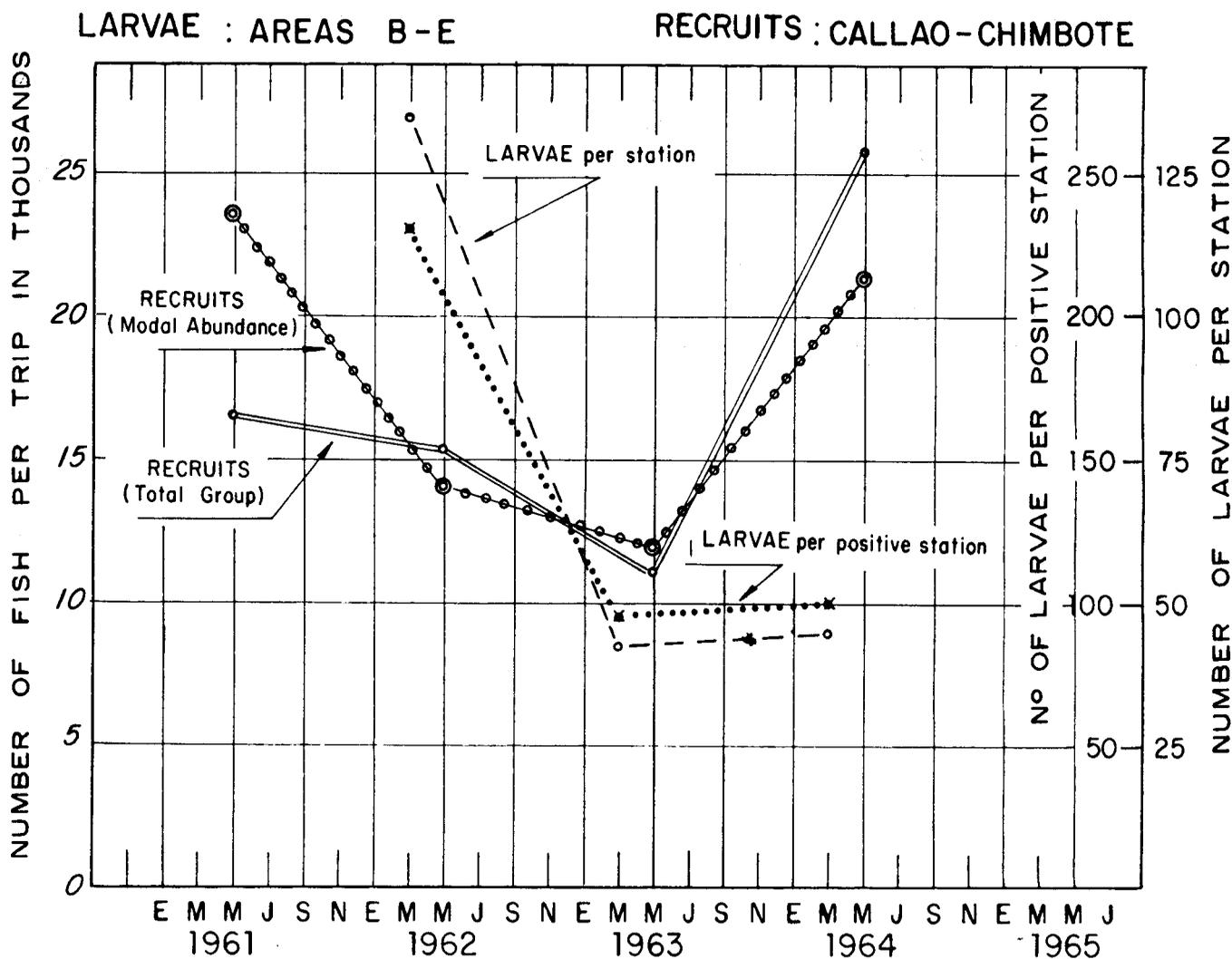


FIGURE 9.

with larval drift into the area from a spawning center lying to the south, the coastal current displacing the larval stock northwards from the spawning center. This could be verified as regards area D during 1962-63, but observational data are not sufficient from area F to establish this conclusion.

A COMPARISON BETWEEN LARVAL ABUNDANCE AND RECRUITMENT

We can presume that a closer relationship exists between larval abundance and recruitment strength than between spawning intensity and recruitment strength. However, our conclusions are limited by the fact that we have only been able to examine the abundance of the earliest stages in the growth of

In Figure 9 the number of larvae and recruit abundance are compared for the region as a whole. The highest numbers of larvae were found during the 1961-62 spawning cycle, but the resulting recruit

group was not outstanding. The big recruit group appearing in 1964 seems not to have been derived from a rich larval stock in the region as a whole.

The evidence suggests that during the three spawning cycles larval abundance was highest during 1961-62, there was a big decline during 1962-63 and then a substantial increase during 1963-64, but not up to the 1961-62 level. Roughly this sequence reflects what has happened in recruitment, but the series of observation is too short to afford firm conclusions.

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THE PREDATION OF GUANO BIRDS ON THE PERUVIAN ANCHOVY (*ENGRAULIS RINGENS* JENYNS)

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INTRODUCTION

The Peruvian anchovy is regularly preyed upon by a variety of animals belonging to different orders of the animal kingdom. Among those that thrive on its abundance are invertebrates, such as medusae and squids, and a multitude of carnivorous fishes, birds and mammals. Two great industries owe their existence to the stock of anchovy: the guano industry, based on the collection of the bird droppings, which have served as a fertilizer of the soil from ancient times and the fishmeal industry, man's exploitation of the anchovy resource, a recent innovation.

Although the majority of the birds that inhabit the Peruvian islands and coasts prey upon the anchovy to some extent, the list of the principal predators is not extensive. The main species are the following:

- Family: Spheniscidae
Spheniscus humboldti Meyer—"Peruvian penguin"
- Family: Procellariidae
Puffinus griseus (Gmelin)—"Sooty shearwater"
- Family: Pelecanidae
Pelecanus occidentalis thagus Molina—"Peruvian pelican"
- Family: Sulidae
Sula variegata (Tschudi)—"Gannet"
Sula nebouxi Milne-Edwards "Blue-footed booby"
- Family: Phalacrocoracidae
Phalacrocorax bougainvillii Lesson—"Cormorant"
Phalacrocorax gaimardi (Lesson)—"Red-footed shag"
Phalacrocorax brasilianus (Humboldt)—"Bigua cormorant"
- Family: Laridae
Larus pipixcan Wagler (migratoria)—"Franklin's gull"
- Family: Sternidae
Larosterna inca (Lesson)—"Inca tern"

Three of these species, the "guanay" (cormorant), the "piquero" (gannet), and the "alcatraz" (pelican), are the main consumers, because of their great numbers. These are the species that transform the anchovy into the valuable fertilizer, which is de-

posited in more than 40 islands and headlands along the Peruvian coast.

Because of their overwhelming importance, the present discussion on the predation of birds on the stock of anchovy is limited to these three species.

SPECIES COMPOSITION AND GEOGRAPHICAL DISTRIBUTION OF THE MAIN POPULATION CENTERS

In the order of importance the main guano producers are cormorants, gannets, and pelicans. The epicenter of their distribution lies between lat. 6° S. and lat. 12° S. The birds occupy this zone during spring and summer, when they form their densest concentrations; subsequently, during autumn and winter, the birds are more dispersed and their area of distribution is greatly enlarged, extending from lat. 1° N. to lat. 38° S. The quantities and locations of the main bird colonies along the Peruvian coast are shown in Figure 1.

The number of adult birds, based on graphical censuses made in December, 1962 and February, 1963, was estimated as being about 18 millions (Jordán and Fuentes, 1964), with the following frequencies of species:

	<i>Millions Percent</i>	
Cormorant	14.89	82.4
Gannet	2.76	15.3
Pelican	0.42	2.3

During the last 20 years this relative frequency does not seem to have changed substantially.

FOOD AND FEEDING

The anchovy constitutes 96% of the food of the cormorant (Jordán 1959) and at least 80% of the food of the gannet and the pelican. During periods of low availability of the anchovy, due to changes in the oceanic climate of the Peru current or other causes, the birds suffer from malnutrition which eventually leads to cachexia and death. This is the reason why the birds are completely dependent on the availability of the anchovy.

The feeding habits of the three species differ, both as regards fishing methods and time of food collecting.

The cormorant dives and swims underwater in the pursuit of its prey to depths that exceed 12 m. The search begins at 6 AM during the reproductive pe-

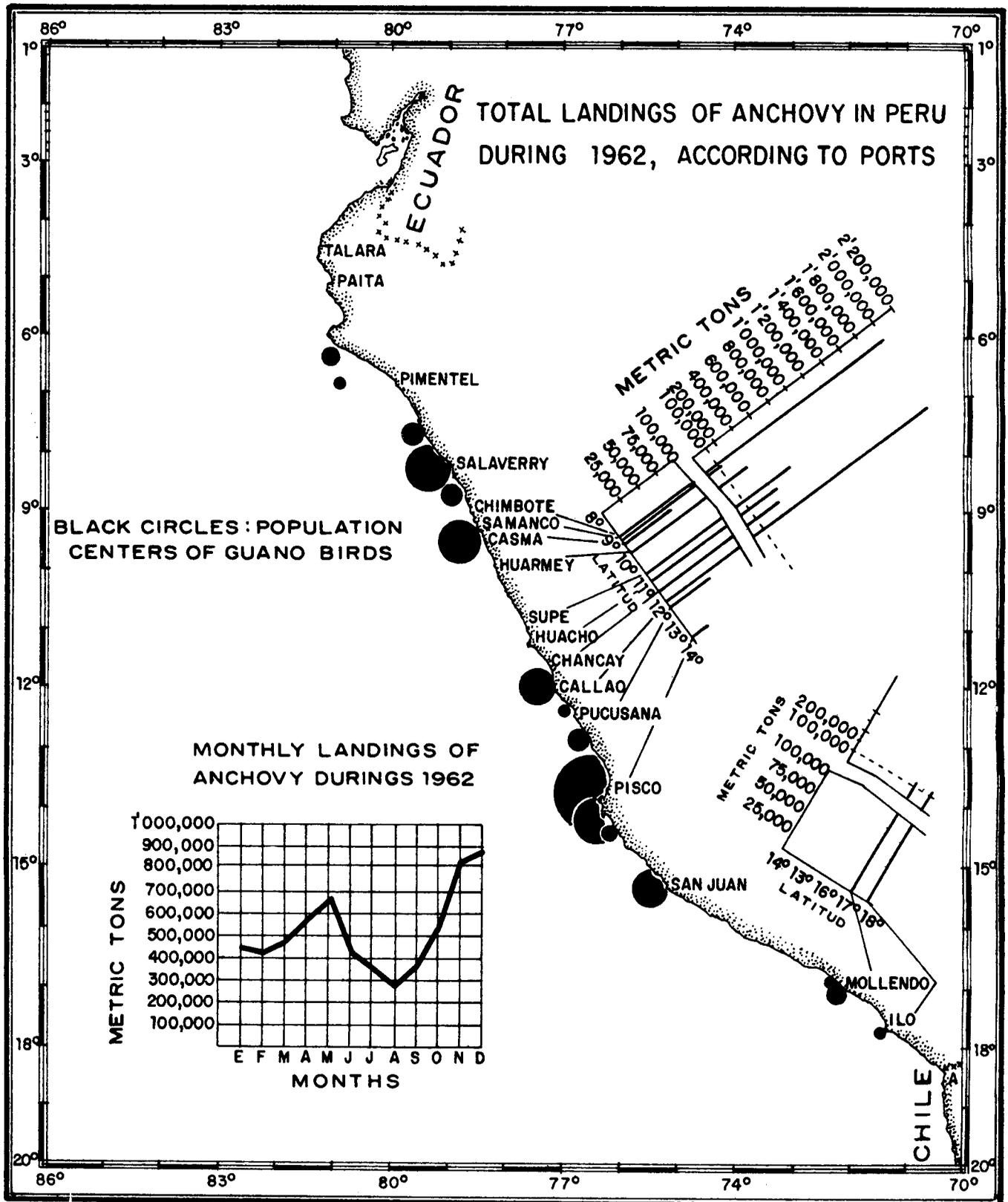


FIGURE 1. Geographical distribution of population centers of guano birds and anchovy landings during 1962.

riod and after 8 AM during the rest of the year. The fishing activity lasts until sunset.

The gannet dives from a certain air altitude to reach the depth required, probably not exceeding 15 m of depth. The feeding hours begin at dawn and continue during daylight.

The pelican dives from the air in a manner similar to that of the gannet, but rarely submerges the whole body. The sea depth reached is therefore limited to the length of its neck. This species feeds at different hours of the day and also during the night.

It has been stated that the operative range of these birds, with special reference to the cormorant, is between 30 and 40 nautical miles and they clearly prefer to seek their food near the coast rather than offshore. However, the gannets and the pelicans may be encountered more than 50 miles offshore.

Frequently the three species are found fishing in the same areas, competing with each other. On the other hand there also exists a kind of cooperation in detecting the fish schools. The flocks of cormorant are seen flying towards fishing areas first detected by gannets and pelicans, or vice versa.

A study of the sizes of anchovies devoured by the birds, based on examinations of the stomach contents of the cormorant, showed that they capture all size groups between 2 and 14.5 cm SL or 3 and 16 cm TL (Figure 2). This size composition demonstrated

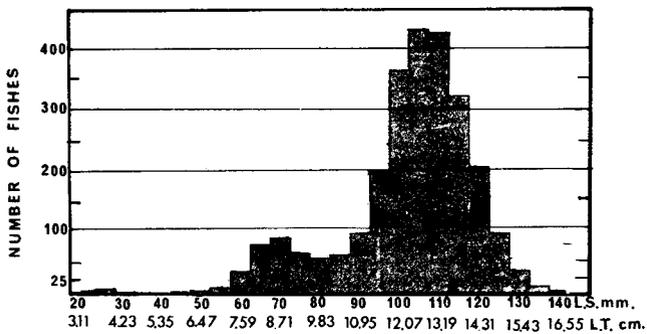


FIGURE 2. Size distribution of anchovies in the stomach contents of the guanay. Material collected during 1954-1957.

that the birds can prey upon somewhat smaller fish than those generally caught in the purse seines of the fishermen. This shows that the birds are not selective as to size of the anchovy and are able to capture small sizes, down to 2 cm in length, if they are within their reach.

FOOD CONSUMPTION AND GUANO PRODUCTION

It is estimated that a cormorant, weighing 2 kilograms, consumes an average of 430 grams of food per day (Jordán 1959) and the minimal daily requirement seems to be 200 grams (Barreda 1959).

Different methods have been used to calculate the rate of transformation of food to guano. Gamarra (1941) concluded, from experiments on birds in captivity, that 1 ton of guano was produced from 31 tons of fish. However, more extensive observations

demonstrated that 1 ton of guano is produced by a smaller fish intake. Vogt (1942) found the rate of transformation from food to guano to be 7.3:1 and Hutchinson (1950), using biochemical analysis, suggests that the cormorant could produce 1 ton of guano from between 9.8 and 15.3 tons of anchovy. Avila (1954) found that the conversion factor is between 6.7 and 7.8 and recent experiments carried out by us indicate that an average of 8 tons of anchovy are needed to produce 1 ton of guano. It can be mentioned that the fishmeal factories use about 6 tons of anchovy to produce 1 ton of fishmeal.

According to available information each bird produces between 40 and 70 grams of guano per day.

During the last 54 years the average annual harvest of guano was 130,000 metric tons, with marked annual fluctuations, related mainly to high mortalities of guano birds during certain years when sources of food ran low. The great increase in guano harvesting between 1946 and 1956 is connected with better management of the bird colonies, primarily due to improvement of the nesting sites and protection of various headlands, where important centers of nesting were successfully established.

NUMBERS OF BIRDS AND THE ANCHOVY CATCH BY THE BIRDS

The guano birds and the fishermen are two of the main groups of predators on the anchovy stock. Therefore, it is of interest to establish the magnitude of the bird predation and define the pressure exerted on the anchovy population in different areas.

It was estimated that each bird (cormorant) consumes an average of 430 grams of anchovy per day. Annual bird censuses have yielded data from which we can estimate the quantity of anchovy consumed by the three species of guano birds each year (Table 1).

TABLE 1
ESTIMATED NUMBER OF BIRDS AND QUANTITIES OF ANCHOVY EATEN BY THE BIRDS PER DAY
(in metric tons)

Year	Estimated number of birds (census data)	Anchovy consumed per day in tons
1961-----	12 x 10 ⁶	5,000
1962-----	18 x 10 ⁶	8,000
1963-----	16 x 10 ⁶	7,000

An estimate, based on these values, leads us to the conclusion that annually the guano birds consumed between 1.8 and 2.8 million tons of anchovy during the period 1961-1963.

The geographical and quantitative distribution of the birds in the summer of 1962 is shown in Figure 1. This distribution has remained unchanged during the last years.

If we group the bird numbers according to the areas of two latitudinal degrees (data from the 1962 and 1963 censuses), it will be seen that the distri-

bution was rather uniform along the coast between lat. 8° S. and lat. 14° S. (Table 2). At both ends of the distributional range lower numbers are encoun-

TABLE 2
NUMBER OF GUANO BIRDS, IN THOUSANDS, IN THE COASTAL AREAS OF PERU, ACCORDING TO AREAS OF TWO LATITUDINAL DEGREES

Year	South Latitude					
	6° to 8°	8° to 10°	10° to 12°	12° to 14°	14° to 16°	16° to 18°
1962	1,141	2,027	3,700	5,539	4,309	296
1963	1,603	3,840	4,719	2,813	4,749	350

tered, because ecological factors exert their influence. We can conclude that, at least during spring and summer, the pressure on the anchovy stocks was rather uniform in the whole range between lat. 8° S. and lat. 14° S.

The situation is rather similar as regards the fishing zones exploited by the fishermen as will be seen from Figure 1 and Table 3.

TABLE 3
LANDINGS OF ANCHOVY (IN THOUSANDS OF TONS) DURING 1962-63 ACCORDING TO AREAS OF TWO LATITUDINAL DEGREES

Year	South Latitude					
	6° to 8°	8° to 10°	10° to 12°	12° to 14°	14° to 16°	16° to 18°
1962	--	2,501.8	1,446.3	2,045.5	--	274.2
1963	--	2,155.9	1,816.3	2,031.4	--	419.5

Two main centers of landing stand out: Chimbote (lat. 9° S.) and Callao (lat. 12° S.), which together account for about 50% of the total catch landed in Peru. Intermediate centers are developing rapidly as is also the area between lat. 12° S. and lat. 14° S. (Tambo de Mora and Pisco). Thus it will be seen that fishermen and birds exploit and exert heavy pressure on the anchovy stock in the whole area between lat. 8° S. and lat. 14° S.

There are some very densely populated bird centers, such as La Vieja Island (lat. 14° 17' S.) and the headland Punta Culebras (lat. 9° 57' S.), each of which is temporarily inhabited by about 3 million adult birds, which means that they have to fish about 1,200 tons of anchovy per day for their sustenance.

It was found possible to estimate roughly the great changes that have occurred in the population size during the last 54 years, using the annual harvesting of guano as a basis. Decreases during certain years coincide with changes in the oceanic climate of the Peruvian current. It has been shown (Jordán and Fuentes 1964) that during these abnormal years, the availability of the anchovy for the birds was greatly diminished, which resulted in the break-up of colonies and heavy mortalities.

The marked changes that have occurred in the population size of the guano birds during the period 1955 to 1963, are shown in Figure 3. The increased

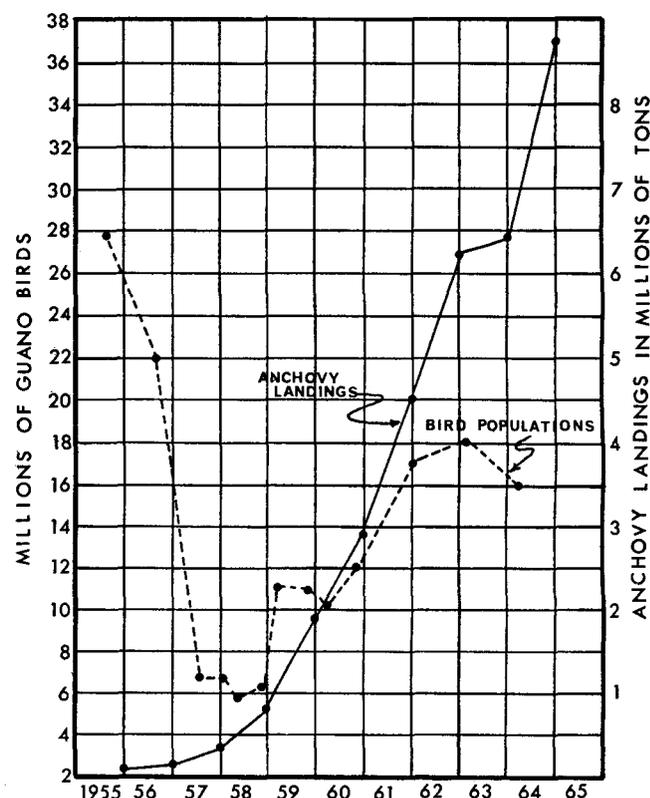


FIGURE 3. The population size of the guano birds and anchovy landings during 1955 to 1964.

anchovy catches by the fishing fleet during the same period are also shown.

The population estimate for 1955 (28 million birds) represents the highest peak ever reached during the last 54 years. During this year the birds may have taken some 4 million tons of anchovy out of the sea, while fishing was still at a low level.

After the great fall in bird numbers that occurred during 1957 and 1958, a steady increase was noted until the beginning of 1963, occurring simultaneously with an enormous increase in the yields of the fishery, which reached about 6 million tons in 1962. During this year the birds extracted some 3 million tons of anchovy out of the sea. A new wave of bird mortalities occurred in the autumn and winter of 1963 (June to September), which reduced the population size considerably at the end. The fishery caught 8.8 million tons of anchovy, apparently without having caused food shortages for the birds.

The future of the guano industry and the fishing industry is entirely dependent on the anchovy resource. From our study of the fluctuations in the population size of the guano birds it can be inferred that the anchovy stock is vulnerable when subjected to marked changes in the oceanic climate. A too heavy predation under such circumstances may have far reaching consequences for the delicate balance

existing in the autonomous regime of the fauna of Peru current.

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SUMMARY OF BIOLOGICAL INFORMATION ON THE NORTHERN ANCHOVY *ENGRAULIS MORDAX GIRARD*

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INTRODUCTION

The northern anchovy has long been recognized as one of the most abundant fishes in the northeastern Pacific Ocean and a sizable latent resource (Croker, 1942; Chapman, 1942). In recent years the anchovy population has increased dramatically. Egg and larva surveys by the U.S. Bureau of Commercial Fisheries show that the population trebled between 1951 and 1958 and has increased even further since (Ahlstrom, 1965). Despite its great abundance the anchovy has never been the object of a large-scale fishery.

DISTRIBUTION

Adult northern anchovies occur from the Queen Charlotte Islands, British Columbia to Cape San Lucas, Baja California. They are most common from about San Francisco to Magdalena Bay, chiefly in coastal waters. Eggs and larvae have been taken as far as about 300 miles offshore.

Hubbs (1925) described a separate subspecies (*E. m. nanus*) which inhabits San Francisco Bay and tolerates much-reduced salinities. In both mean and modal number of vertebrae the bay subspecies has two fewer than the ocean subspecies. It is a much smaller fish, the largest found by Hubbs measured 99 mm TL. Its head averages longer, the body deeper and more compressed. The early development is also apparently more accelerated and transformation from postlarval to juvenile stages occurs at a much smaller size.

Similar brackish-water forms also are known for the European anchovy (*E. encrasicolus*) and Australian anchovy (*E. australis*) (Blackburn, 1950).

Subpopulations

McHugh (1951) delineated three northern anchovy subpopulations on the basis of differences in numbers of dorsal, anal, and pectoral fin rays; vertebrae; and gill rakers. The three subpopulations occur from British Columbia to central California, off southern California and northern Baja California, and off central and southern Baja California.

Miller (1956), on the basis of age and size compositions of central and southern California commercial and live bait catches, aerial surveys, and sea surveys, gave possible evidence of "local" stocks of fish. Work currently is underway by the U.S. Bureau of Commercial Fisheries using serological techniques to delineate possible genetically distinct stocks of northern anchovies.

Habitat

Anchovies are pelagic schooling fishes, generally found in coastal waters. During recent years, their offshore occurrence has expanded markedly as the population has increased. Like their congeners, northern anchovies exhibit some seasonal movements. During fall and winter they apparently move offshore and return inshore in spring. Fall surveys by the Department's R/V ALASKA indicate that anchovies occur well below the surface during the day and move to the upper layers of the ocean at night. The European anchovy (*E. encrasicolus*) makes similar diurnal movements at this time of year. Off the coast near Santa Barbara during November, 1964, anchovies were noted on the depth recorder in a thin band along the bottom during the day, but at night they rose toward the surface to form a band 20 to 50 feet thick. Our sampling also indicates that large fish are less available in inshore waters during winter.

During periods of warmer-than-average water temperatures, adult anchovies become less available in the inshore waters. Fish-of-the-year apparently tolerate somewhat higher water temperatures than adults. Our sampling program has shown that 0-age-group fish predominate in inshore live bait catches during periods of warm water. During the 1957-59 "warm-water years" our research vessel surveys showed that large anchovies no longer frequented inshore areas but were more numerous offshore. While live bait fishermen were experiencing difficulty in catching large fish, vessels conducting seismic oil exploration occasionally were killing large anchovies well offshore from usual areas of abundance.

On Department sea surveys for the years 1955 through October, 1964, samples of anchovies were caught in water temperatures ranging from 8.5° to 25.0°C. between northern California and Magdalena Bay, Baja California (Table 1). Of 617 samples caught where surface temperatures were recorded, 75.9 percent of the catches occurred in waters having surface temperatures between 14.5° and 20.0°C. Off California and northern Baja California (north of lat. 31°N.) 340 samples were taken in temperatures ranging from 8.5° to 21.5°C. Of these, 72.5 percent occurred between 14.5° and 18.5°C. Off central and southern Baja California 277 anchovy samples were taken in water temperatures ranging from 13.0° to 25.0°C., 65.0 percent between 17.0° and 21.5°C.

TABLE 1
 NUMBER OF STATIONS WHERE ANCHOVY SAMPLES WERE CAUGHT
 BY DEPARTMENT OF FISH AND GAME RESEARCH VESSELS,
 1955-1964 BY SEA SURFACE TEMPERATURE

Temperature °C.	North of Lat. 31°N.	South of Lat. 31°N.	Total
8.5	1	--	1
9.0	1	--	1
9.5	2	--	2
10.0	1	--	1
10.5	2	--	2
11.0	2	--	2
11.5	4	--	4
12.0	5	--	5
12.5	5	--	5
13.0	12	1	13
13.5	6	2	8
14.0	11	4	15
14.5	38	7	45
15.0	23	10	33
15.5	31	10	41
16.0	35	7	42
16.5	28	10	38
17.0	32	27	59
17.5	22	29	51
18.0	20	20	40
18.5	17	21	38
19.0	13	17	30
19.5	13	13	26
20.0	10	15	25
20.5	4	15	19
21.0	1	9	10
21.5	1	14	15
22.0	--	8	8
22.5	--	8	8
23.0	--	15	15
23.5	--	8	8
24.0	--	5	5
24.5	--	1	1
25.0	--	1	1
Total	340	277	617

Anchovy larvae have been taken in water temperatures ranging from 10.0° to 19.7°C.; approximately 95 percent were taken between 14.0° and 17.4°C. (Ahlstrom, 1959). Ahlstrom also found that, on the average, the larvae occurred mostly between 24 and 48 m although they also were abundant in the upper 23 m.

Anchovy eggs were sampled in 1953 and 1954 in temperatures ranging from 9.9° to 23.3°C. (Ahlstrom, 1956). He used water temperatures at 10 meters as representative of the upper mixed layer where anchovy eggs occurred. Most eggs were taken in temperatures between 13.0° and 17.5°C.; however, 10 percent of the spawning sampled in these years occurred at temperatures below 13.0°C.

REPRODUCTION

Maturity (age and size)

A few northern anchovies first reach sexual maturity at about 90 to 100 mm SL at the end of their first year of life. About 50 percent are mature at 130 mm SL when they are between 2 and 3 years old. All are

mature when 150 mm long or 4 years old (Clark and Phillips, 1952).

Fecundity

Although little has been published on the fecundity of the northern anchovy, each large female spawns an estimated 20 to 30 thousand eggs annually and spawns two or three times each year. There is always a reservoir of maturing eggs in the ovary of an adult female in spawning condition.

Spawning

Anchovy spawning, although recorded from British Columbia to below Magdalena Bay, Baja California, is heaviest between Point Conception, California and Point San Juanico, Baja California. Most spawning has occurred within 60 miles of the coast, although it has been recorded to about 300 miles offshore. In waters north of Point Conception spawning intensity has been variable. During some years such as 1950 and 1954, heavy spawning has occurred in the area while in others such as 1953 and 1955 there has been very little (Ahlstrom, 1956). Ahlstrom also noted that in the area south of Point Conception there are two major spawning areas, one off southern California and northern Baja California, and the other off central and southern Baja California. The southern sector, between 1951 and 1955, consistently had the most eggs and larvae. From 54 to 85 percent of the larvae were taken there.

Spawning has been noted in every month of the year particularly in the southern part of the anchovy's geographical distribution. The peak spawning period is during late winter and spring. Bolin (1936) noted that most spawning takes place in Monterey Bay from December to June; however, he also noted that eggs have been taken in the southern portion of Monterey Bay during each month of the year.

The eggs and larvae of anchovies are pelagic and float passively in the upper layers of the ocean. According to Bolin (1936) anchovies spawn regularly at 10 PM. Spawning takes place in the upper mixed layer in temperatures ranging from 9.9° to 23.3°C. with most eggs occurring in temperatures between 13.0° and 17.5°C. (Ahlstrom, 1956). The threshold temperature for anchovy spawning is about 11.5° or 12.0°C. Fertilization of the eggs takes place in the water immediately after spawning and is so successful that an unfertilized egg is rare (Ahlstrom, 1956). The eggs are ovoid, as is typical of all engraulids, and float with the major axis perpendicular to the surface of the water. As the embryo grows the egg rolls over on its side so the major axis becomes horizontal and the embryo hangs underneath (Bolin, 1936).

Development

The egg and early larval stages were first described by Bolin (1936). The ovoid eggs are 1.23 to 1.55 mm along the major axis and 0.65 to 0.82 mm along the minor axis. They are clear and translucent and require from 2 to 4 days to hatch depending on the temperature of the water. Bolin noted that in the

Monterey Bay area hatching takes place about 62 hours after spawning.

Newly-hatched larvae are 2.5 to 3 mm long. The yolk sac is rather large and elongated, tapering to a point posteriorly. The yolk sac is absorbed entirely within 36 hours. The larvae are elongated, transparent and threadlike. In the early stages the mouth is terminal and they do not begin to look like the adult form until they are about 1 inch long.

AGE AND GROWTH

Clark and Phillips (1952) first determined the age and rate of growth for the northern anchovy. Miller (1955) studied the validity of scales for determining the ages of anchovies and concluded that scales mounted dry between two glass slides were satisfactory. He also concluded that annual rings were formed on the scales during the early winter and spring months and all fish showed new annuli by the middle of April. Growth rates decreased during late summer and fall (August–November).

Clark and Phillips (1952) presented a growth curve for anchovies taken in southern and central California and determined average sizes through age VII (Table 2, Figure 1).

TABLE 2
AVERAGE LENGTH AT EACH AGE OF THE ANCHOVY IN THE CALIFORNIA FISHERY (CLARK AND PHILLIPS, 1952)

Age	Standard length (mm)	Total length (mm)	Total length (inches)
1	92	108	4.3
2	120	142	5.6
3	139	163	6.4
4	152	178	7.0
5	161	188	7.4
6	167	195	7.7
7	171	200	7.9

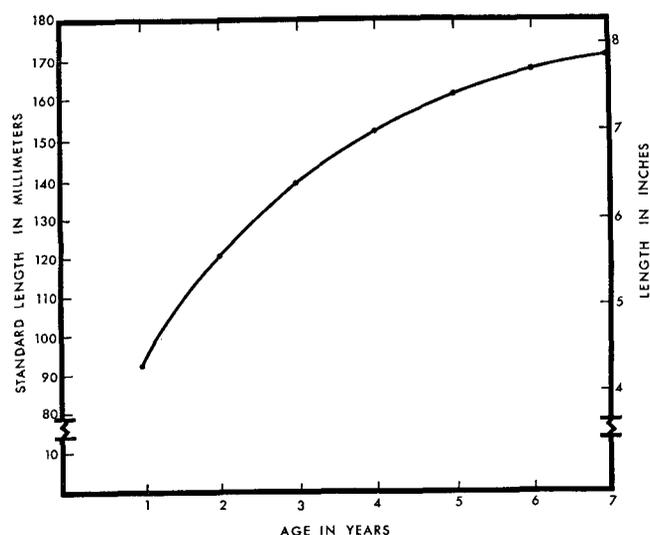


FIGURE 1. Growth curve for the northern anchovy in California.

In general the anchovy is short-lived; individuals over 7 inches long and 4 years of age are rare, although anchovies 9 inches long and 7 years old have been taken.

FOOD

Although statements that adult northern anchovies feed on zooplankton have been common, no definitive study of their food habits has been published as yet. Such studies of anchovy food are only now in their early stages. Some work has been done on the food of larvae. Berner (1959) found that larvae collected in 1954 ate chiefly crustaceans, mostly copepods in various developmental stages.

Anchovies are apparently indiscriminate filter feeders and are chiefly daytime feeders. They have been observed to be predatory on small fish at times, even their own kind. We have observed this several times. We have also noted 1½-inch fish in the stomachs of 5½-inch anchovies.

COMPETITORS

The chief competitor of the northern anchovy is almost certainly the Pacific sardine (*Sardinops caeruleus*). Competition begins in the larval stages and probably continues through life. Sardines and anchovies eat about the same foods and both occur in greatest abundance between Point Conception, California and Magdalena Bay, Baja California.

PREDATORS

The list of anchovy predators would certainly include almost every predatory species in our waters. Although the list of anchovy predators in our waters includes a great many species of fishes, birds, and mammals, we know very little of the actual quantities of anchovies consumed or what percentage of the predator diet is made up of anchovies in relation to other forage species. Available quantitative studies show that anchovies constituted 12.8 percent by volume of the diet of California yellowtail (*Seriola dorsalis*) (Craig, 1960) and 29.1 percent by volume of the diet of king salmon (*Oncorhynchus tshawytscha*) off San Francisco (Merkel, 1957). Qualitative studies have shown anchovies to be an important constituent in the diets of all of the large predatory game fish off California. It is interesting to note that the Pacific bonito (*Sarda chiliensis*) population has blossomed concurrent with the tremendous growth of the anchovy population. Between 1951 and 1963 the bonito catch by party boats increased from 6,300 fish in 1953 to a high of 1,200,000 fish in 1960. Since then, the bonito catch has dropped from 850,000 in 1961 to 775,000 in 1963. Suffice to say, the anchovy is probably the number one forage species in the inshore waters of California and Baja California at the present time. Despite this apparent forage demand the anchovy population has still continued to grow in size at a phenomenal rate (Ahlstrom, 1965).

FISHERY

The California anchovy fishery is in reality two distinct fisheries, the commercial fishery and that for live bait. Both are quite modest compared to anchovy fisheries in other parts of the world. In fact, the amount of anchovies consumed by the guano birds of Peru (an estimated 3¼ million tons annually) approximates a large portion of the entire population size of our species (see Jordán, this volume).

Commercial Fishery

The commercial fishery in California is carried on exclusively with roundhaul nets, and except for the

period from 1952 through 1957 when the failure of California's sardine fishery forced the purse-seine fleet to turn to other species, most catches have been made by small boats employing lampara nets.

Commercial Catch

Under commercial catch are included fish used in canning for both human consumption and pet foods; fresh, frozen, and salted fish sold at fresh fish markets; dead bait used by both sportsmen and commercial fishermen; fish used for feeding at fish hatcheries and mink farms; and offal used for reduction into meal and oil.

The Department of Fish and Game has tabulated the amounts of fish and fishery products landed in California since 1916 (Table 3). From 1916 to 1938 between 30 and 973 tons were landed annually, mostly for dead or salted bait. In general, less than 200 tons were landed annually during this period. Slightly increased tonnages were landed between 1918 and 1921 for reduction into meal and oil in central California. Legislation requiring a special permit from the Fish and Game Commission to reduce whole fish stopped this activity in 1922.

In 1939 increased catches of anchovies were made for grinding into "chum" for use in the southern California "scoop" fishery for Pacific mackerel (*Scomber diego*). With the decline of sardines and Pacific mackerel in the years immediately following World War II varying amounts of anchovies were packed to supply foreign and domestic markets for canned wetfish. The period of greatest activity in the anchovy fishery was between 1952 and 1957 when from 20,273 to the all time high of 42,917 tons were landed. Most of this was canned either "sardine style" for export or for pet food. Since 1957 the commercial catch has varied between 1,400 and 5,800 tons chiefly due to a lack of demand by canners.

Live Bait Fishery

This unique fishery is carried on expressly to supply fishermen with live fish for use as bait or chum. Fishing for live bait was introduced locally in 1910 by Japanese albacore fishermen who used blanket nets; lampara or bait nets, as used now, were introduced into the live-bait fishery in 1912.

The mainstay of the live-bait fishery is the northern anchovy which comprises up to 98 percent of the total live-bait catch. Other species included in the catch are Pacific sardines, white croaker (*Genyonemus lineatus*), queenfish (*Seriphus politus*), Pacific mackerel, jack mackerel (*Trachurus symmetricus*), and Pacific herring (*Clupea pallasii*).

Bait nets are usually 120 to 140 fathoms long by 20 to 30 fathoms deep and are generally constructed of synthetic fibers such as nylon. Mesh sizes vary from 6 to 8 inches in the wings to ½ inch in the bag.

The live-bait fishery is carried on at most coastal ports between San Francisco and San Diego. Los Angeles-Long Beach Harbor is the most important fishing area, supplying over 80 percent of the live bait used in southern California in recent years. Although live bait taken in coastal areas is located

TABLE 3
CALIFORNIA ANCHOVY LANDINGS BY PORT, 1916-1964
(IN TONS)

Year	Eureka	San Francisco	Monterey	Santa Barbara	Los Angeles	San Diego	Total
1916	--	119.8	125.7	--	20.1	--	265.6
1917	--	50.1	187.8	--	26.4	--	264.3
1918	--	134.2	270.2	--	24.7	4.9	434.0
1919	--	153.0	352.5	--	288.4	10.8	804.7
1920	--	110.6	156.9	--	2.3	15.1	284.9
1921	--	87.6	741.4	--	5.2	139.1	973.3
1922	--	75.4	68.2	--	182.4	0.2	326.2
1923	--	92.0	42.5	--	19.0	--	153.5
1924	--	5.3	148.5	1.7	17.9	--	173.4
1925	--	13.0	0.7	--	32.8	--	46.5
1926	--	1.7	24.3	--	4.1	--	30.1
1927	--	139.1	28.3	--	16.1	0.6	184.1
1928	--	62.8	87.7	--	27.9	0.3	178.7
1929	--	119.8	41.0	--	30.4	--	191.2
1930	--	130.9	21.7	--	5.2	1.9	159.7
1931	--	82.3	52.4	--	18.9	0.1	153.7
1932	--	73.8	60.0	--	15.8	--	149.6
1933	--	92.5	45.4	--	20.7	--	158.6
1934	--	33.5	63.7	--	31.5	--	128.7
1935	--	37.2	38.2	--	14.0	--	89.4
1936	1.0	66.5	15.1	--	14.9	--	97.5
1937	--	51.0	22.1	--	40.0	--	113.1
1938	--	125.9	17.0	--	224.6	--	367.5
1939	--	107.4	6.0	--	960.5	--	1,073.9
1940	--	6.9	18.7	--	3,125.9	7.3	3,158.8
1941	--	0.3	16.6	16.6	2,019.1	--	2,052.6
1942	--	2.7	74.5	--	769.7	0.2	847.1
1943	--	39.4	99.2	--	646.8	--	785.4
1944	--	55.0	424.0	--	1,465.1	1.4	1,945.5
1945	0.2	146.0	63.9	--	598.3	--	808.4
1946	--	131.9	124.0	2.5	702.2	0.2	960.8
1947	2.2	195.1	7,747.9	99.7	1,423.5	1.8	9,470.2
1948	6.8	190.1	3,627.8	102.1	1,486.2	4.9	5,417.9
1949	--	108.2	741.4	240.8	566.6	4.1	1,661.1
1950	0.4	169.3	1,273.3	145.9	850.1	0.3	2,439.3
1951	--	142.0	2,525.0	100.8	703.2	6.4	3,477.4
1952	--	2,915.5	19,867.8	3,516.8	1,578.7	12.6	27,891.4
1953	--	1,536.3	6,847.5	17,367.6	17,164.9	1.4	42,917.7
1954	0.7	130.9	122.6	8,403.7	12,546.0	1.2	21,205.1
1955	--	103.3	3,441.8	1,630.8	17,166.7	3.2	22,345.8
1956	--	194.0	4,829.2	278.7	23,158.4	--	28,460.3
1957	0.5	5.1	742.9	77.5	19,440.5	7.2	20,273.7
1958	--	1.4	271.2	313.5	5,212.9	2.3	5,801.3
1959	--	15.0	186.4	404.9	2,979.7	0.9	3,586.9
1960	--	0.3	645.3	12.8	1,870.9	--	2,529.3
1961	--	114.8	1,893.7	27.1	1,820.2	--	3,855.8
1962	--	5.7	594.0	14.9	767.2	0.2	1,382.0
1963	--	13.9	1,680.1	5.7	585.5	--	2,285.2
1964	--	15.1	1,416.6	0.5	1,053.6	1.7	2,487.5

most commonly either visually or with fathometers, the most successful method is to attract the bait schools at night with lights. This latter method, developed in the Los Angeles-Long Beach Harbor area, employs a small skiff with a gasoline-powered generator which supplies 500- to 1000-watt lights. The light both attracts and holds bait schools so that they can be netted.

After being caught, the bait is either sold directly from the bag of the net or transferred to one of the various holding facilities for sale later.

Live Bait Catch

In 1935, California initiated a program of personal interviews with live-bait fishermen to obtain information about the extent of the fishery. Since 1939, the Department has collected fishing logs. The present version of the logs is combined with personal interviews and sampling to determine the amount of fish sold as live bait, the species composition of the catch localities of catch, and fishing effort. Catches are recorded by the fishermen in "scoops" which are converted into pounds by Department personnel.

Live-bait catches have fluctuated between 4,000 and 7,000 tons annually since 1950 (Table 4). In recent years, sales have been estimated at about 1.5 million dollars per year.

POPULATION

Age Composition

The Department routinely sampled the commercial anchovy catch from 1952 through 1957 and has sampled the live bait catch since 1955. Age compositions have been determined cooperatively with the U.S. Bureau of Commercial Fisheries. The commercial anchovy season extends from April 1 through March 31.

In central California, particularly, the age composition of the catch has been somewhat variable. From 1952-53 through 1953-54, ages II, III, and IV predominated the landings. Beginning in 1954-55, following increased anchovy fishing, the 1954 year-class began to dominate the landings. In 1954-55, 80.4 percent was fish-of-the-year; in 1955-56, 79.0 percent was 1954 year-class fish as 1-year-olds and in 1956-57, this time as 2-year-olds, the 1954 year-class contributed 73.8 percent of the catch. Fish up to 6 years old were sampled. The central California fishery seems to depend upon sporadic good year classes from a localized population. This agrees with the report of Ahlstrom (1956) that good spawning success is intermittent in the area north of Point Conception.

The commercial catch off southern California between 1952 and 1957 was comprised chiefly of 1- and

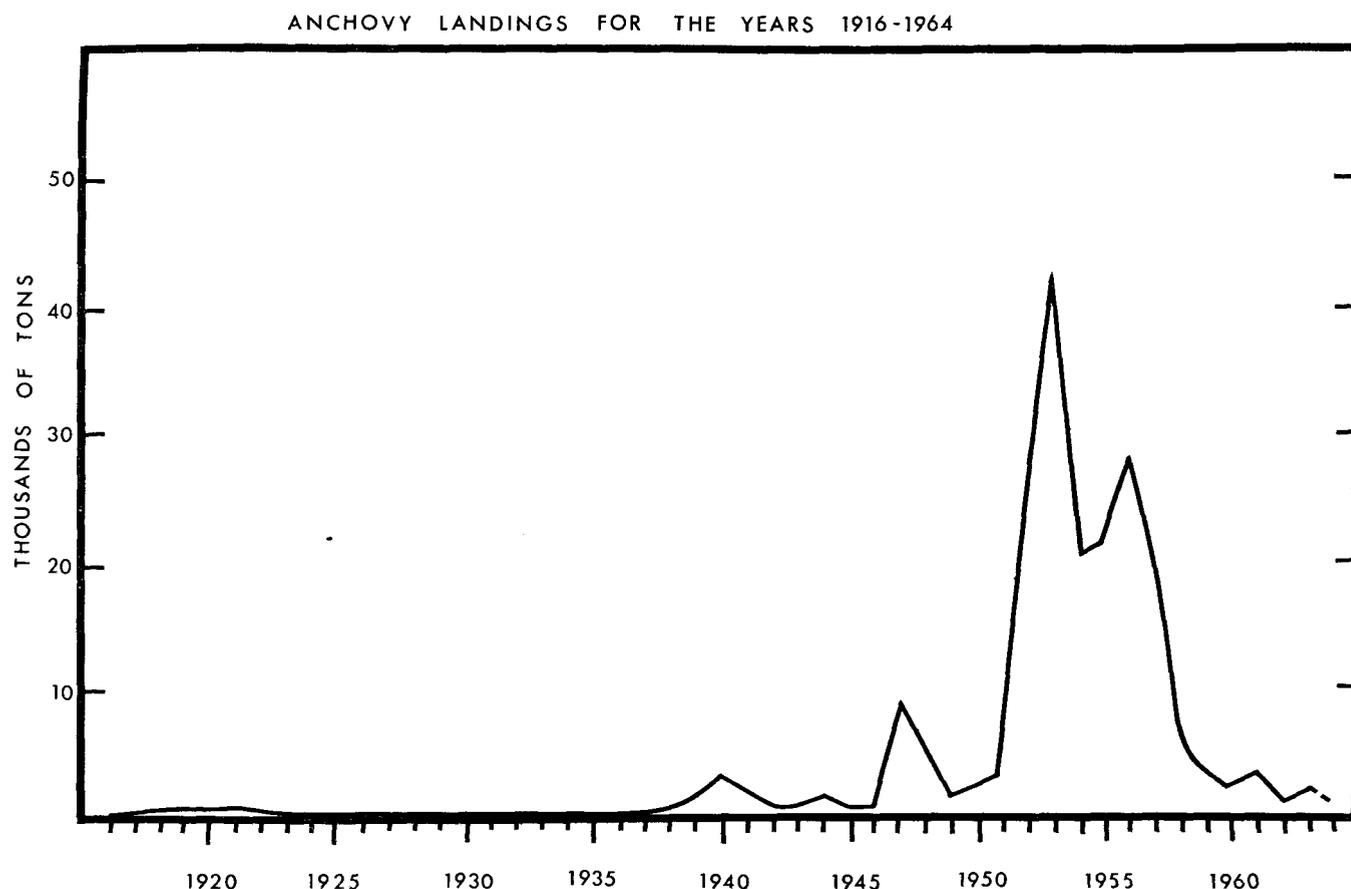


FIGURE 2. California Commercial Anchovy Landings, 1916-1964 (in tons).

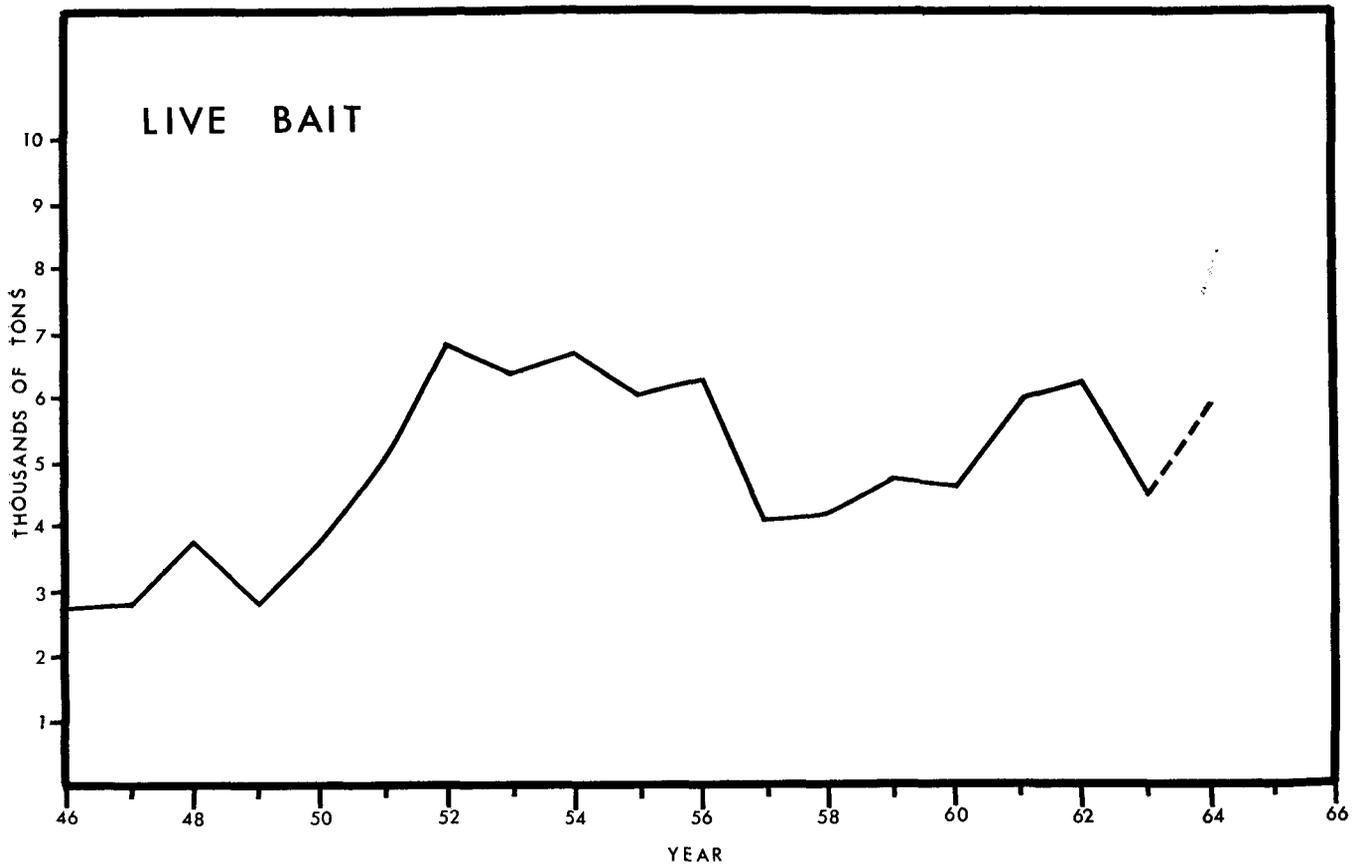


FIGURE 3. Live-bait catch of anchovies in California, 1939-1964 (in tons).

TABLE 4
LIVE-BAIT CATCH OF ANCHOVIES IN SOUTHERN CALIFORNIA,
1939-1964 (CATCH FROM 1942-45 NOT RECORDED)

Year	Catch (tons)
1939	1,503.2
1940	2,006.0
1941	1,587.7
1942	257.5
1943	--
1944	--
1945	--
1946	2,748.1
1947	2,854.0
1948	3,725.5
1949	2,802.4
1950	3,823.8
1951	5,141.9
1952	6,810.4
1953	6,391.5
1954	6,686.0
1955	6,125.4
1956	6,331.8
1957	4,110.1
1958	4,235.9
1959	4,737.5
1960	4,657.5
1961	5,912.5
1962	6,166.5
1963	4,442.0
1964	5,191.0

2-year-old fish with varying amounts of fish-of-the-year. The 1954 year-class also dominated this catch; however, not so completely as in central California. The oldest fish sampled in the southern California commercial fishery was 5 years old (Table 5).

The live bait catch between 1955 and 1962 was consistently dependent upon 1- and 2-year-old fish each year. One-year-olds contributed 38.9 to 56.3 percent of the catch and 2-year-olds, 30.6 to 51.5

TABLE 5
AGE COMPOSITION OF THE COMMERCIAL NORTHERN ANCHOVY
CATCH FOR THE SEASONS 1952-53 THROUGH 1956-57

	Percentage composition by age						
	0	1	2	3	4	5	6
Central California							
1952-53	1.9	6.9	31.6	33.3	19.7	6.2	0.4
1953-54	7.7	9.8	35.8	28.5	14.5	2.9	0.8
1954-55	80.4	5.5	4.8	4.0	5.0	0.3	--
1955-56	10.1	79.0	8.1	2.3	0.3	0.2	--
1956-57	6.0	9.5	73.8	8.5	2.1	0.1	--
Southern California							
1952-53	38.3	19.9	30.6	18.0	13.1	0.1	--
1953-54	17.2	32.0	34.8	13.4	2.3	0.3	--
1954-55	10.7	52.9	29.5	5.6	1.2	0.1	--
1955-56	4.3	49.5	36.2	10.0	--	--	--
1956-57	1.4	18.8	61.8	16.1	1.7	0.2	--

percent. Very few fish over 3 years old are taken in the live-bait fishery (Table 6).

TABLE 6
AGE COMPOSITION OF THE NORTHERN ANCHOVY LIVE-BAIT CATCH FOR THE YEARS 1955-1962

Season/Year	Percentage composition by age					
	0	1	2	3	4	5
1955.....	8.8	43.0	41.8	6.4	--	--
1956.....	2.1	39.9	51.5	5.9	0.6	--
1957.....	3.2	35.5	37.1	19.7	4.3	0.3
1958.....	4.8	56.3	33.6	4.5	0.8	--
1959.....	2.5	53.9	40.5	2.8	0.3	--
1960.....	4.4	38.4	47.8	9.4	--	--
1961.....	6.5	38.9	37.9	14.9	1.8	0.1
1962.....	9.6	46.2	30.6	10.4	3.6	0.2

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CO-OCCURRENCES OF SARDINE AND ANCHOVY LARVAE IN THE CALIFORNIA CURRENT REGION OFF CALIFORNIA AND BAJA CALIFORNIA

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This is a report on the co-occurrences of sardine and anchovy eggs and larvae in the collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) during 1951-60. More important, it is also a study of the interaction between two species of fish—both filter-feeders on planktonic organisms—occupying the same trophic level. This study leads further into the problem of whether there is a limit to the biomass of sardines plus anchovies that can be accommodated in the environment and whether one species increases in abundance only at the expense of the other.

During the period of the CalCOFI surveys, which began in 1949, the population of the Pacific sardine (*Sardinops caerulea*) as determined from the distribution and abundance of eggs and larvae, decreased markedly, especially since 1954. In contrast, the population of the northern anchovy (*Engraulis mordax*), as determined from the distribution and abundance of larvae, increased spectacularly. This relation brings up the question of whether the anchovy is moving into the ecological niche previously occupied by the sardine.

CalCOFI survey cruises have been made off California and Baja California for more than 15 years. Coverage was fairly intensive in 1949-60, when cruises were made at approximately monthly intervals. In 1961-64, cruises were spaced at quarterly intervals. Temporal coverage, consequently, was much better during the decade 1951-60, the years dealt with particularly in this report.

One of the difficulties in working up the observations on sardine and anchovy eggs and larvae is the massiveness of the data. Even the data for the 10-year period, 1951-60, are based on more than 16,000 separate collections. Anchovy larvae occurred in 6,755 collections, or 42.1 percent of the total, and sardine larvae in 2,133, or 14.3 percent. These data can be examined in many different ways. For example, the sardine and anchovy larvae from all collections are measured by 1-millimeter intervals, for abundance and survival studies. Was survival of larvae better in samples where anchovy and sardine larvae co-occurred, or in samples where the larvae of one species occurred alone? What was the relation of co-occurrences to the temporal and areal distributions of the larvae of the two species or to their relative abundances per haul? What was the influence of changing environmental conditions on the frequency with which sardines and anchovies co-occurred?

The CalCOFI survey cruises initially were planned to delimit and assay the distribution and abundance of the planktonic eggs and larvae of the Pacific sardine to determine indirectly the distribution and abundance of the adult population at time of spawning and to obtain information on the factors affecting

the survival of year classes. Sardine spawning was found to have an extensive and variable areal distribution and to take place during much of the year, especially off Baja California. Consequently, we tried to cover systematically a rather large area of the ocean off California and Baja California.

The CalCOFI station pattern is illustrated in Figure 1. Inasmuch as I plan to discuss the distribution and abundance of eggs and larvae in different parts of the CalCOFI region, I have subdivided it into 7 areas—three off California and four off Baja California. The station lines included in each area are as follows:

Area	Station Line
Northern California	40- 57
Central California	60- 77
Southern California	80- 93
Northern Baja California	97-107
Upper central Baja California	110-120
Lower central Baja California	123-137
Southern Baja California	140-157

Not all areas were covered on each cruise. Four were consistently worked—those lying between station lines 80-137. The majority of cruises also included the central California area. Usually only 1 or 2 cruises per year were made off northern California and southern Baja California. With rare exceptions, only a single plankton haul was taken at each station occupied during a cruise.

In the course of obtaining information about sardine eggs and larvae, we also obtained information about many other fishes with planktonic young. Even at the beginning of the surveys, sardine larvae were outnumbered by larvae of northern anchovy (*Engraulis mordax*), hake (*Merluccius productus*), rockfish (*Sebastes* spp.), and usually jack mackerel (*Trachurus symmetricus*).

The occurrence of numerous species of larvae led to a decision to identify and enumerate all the kinds in the collections. This decision posed problems in identification, but these were solved with perseverance. It became evident that surveys of eggs and larvae constituted one of the indispensable methods of resource evaluation. Most pelagic fishes have planktonic stages that can be sampled more simply and quantitatively than the adults.

Larvae of the Pacific sardine and northern anchovy occur mainly off southern California and off most of Baja California. The sardine also occurs throughout the Gulf of California. The northern anchovy, a somewhat more temperate species, does not occur in the Gulf, and its larvae seldom occur south of Magdalena Bay. It ranges farther north, however, than the sardine. In recent years there has been little spawning off central California (north of Pt. Conception) by either anchovies or sardines, although

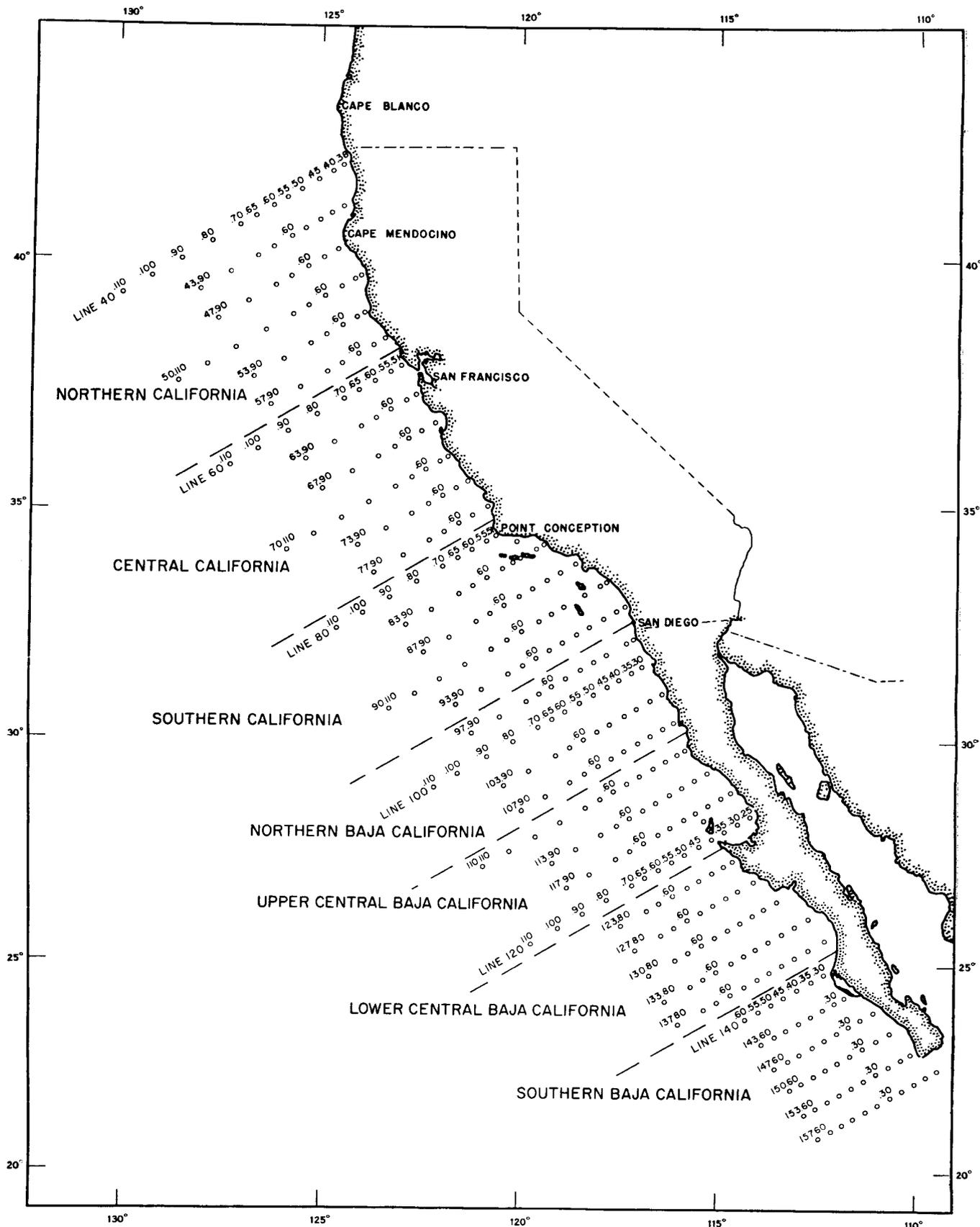


FIGURE 1. Basic CalCOFI station grid off California and Baja California (station lines 40-157); divisions into areas are indicated.

anchovy spawning was common during 1958 and 1959. Some anchovies spawn as far north as British Columbia.

A most important consideration of the data of 1951-60 is that we could define no such thing as an "average" distribution or abundance of either species. Each year differed from every other year. The distributions of both species changed from year to year; the changes reflected their response to the varying oceanic environment. The changes in abundance of the two species, however, were more systematic, as is noted later.

Examples of changing distributions are pointed out here. One of the most marked changes in the distribution of sardine eggs and larvae occurred in the 1953 and 1954 season. In 1953, nearly all sardine spawning was off central Baja California; only about 1 percent was to the north. In 1954, spawning spread distinctly northward, and was widespread off both northern Baja California and southern California. The spawning in these "northern" areas increased to more than 38 percent of the season's total.

Variations in the spawning may be temporal as well as areal. A marked temporal change in sardine spawning occurred off southern California in 1958. During the preceding years which were characterized by below-average temperatures in winter and early spring off southern California, most spawning was in May and June. In 1958, after temperatures had been above average in the eastern North Pacific since mid-1957, the peak of sardine spawning was in January 1958, and spawning extended over a 7-month period, from January to July.

Changes in the distribution of anchovy eggs and larvae were less spectacular, but nonetheless real. In 1956, one of the colder years in the California Current region during the 1950's, anchovy larvae were much more numerous off southern Baja California (lines 140 and south) than in previous years. In most years less than 1 percent of the anchovy eggs and larvae collected were from this area, but in 1956 the area contributed nearly 20 percent of the season's total. This change, in effect, indicated a southward extension of anchovy spawning of some 40 to 80 miles. In contrast, anchovy spawning spread northward in 1958 and 1959. During the 7 years before 1958, less than 1 percent of anchovy larvae were from CalCOFI stations off central California (north of Pt. Conception); the larvae were collected at only 58 of 803 stations occupied. The number of occurrences of anchovy larvae off central California rose to 101 in 1958 and 133 in 1959. In 1959 anchovy larvae occurred at more than half of the stations occupied off central California and constituted more than 10 percent of the total larvae from all areas. With the return of normal temperatures in 1960, the number of occurrences of anchovy larvae off central California dropped to 48.

Two markedly contrasting years, 1954 and 1962, illustrate changes in the areal distributions of the two species that also reflect changes in abundance. The areal distribution and relative abundance of sardine and anchovy larvae in 1954 are shown in

Figure 2. During this year, sardine larvae were even more widely distributed than anchovy larvae. Note particularly that even in the offshore waters of southern California, sardine larvae were more abundant and more widely distributed than anchovy larvae. This distribution of sardine larvae (and eggs) was the most extensive ever encountered during CalCOFI surveys.

The distributions of anchovy and sardine larvae during 1962 are shown in Figure 3. Anchovies were widely distributed; they were collected at nearly one-half of the stations (454 of the 919 occupied). Sardine larvae occurred at 58 stations, or in only slightly more than 6 percent of the stations occupied during the year. Most occurrences of sardine larvae (38 of the 58) were in the summer and fall cruises, mostly from off central Baja California. Anchovy larvae outnumbered sardine larvae in 1962 collections by more than 90 to 1.

The two species have somewhat different seasonal distributions. This difference is illustrated in Figure 4, which shows for each species the percentage of the yearly total that was taken in each month during 1952-59. The peaks of abundance of the two species and the yearly patterns of abundance show little correspondence. Anchovy larvae tended to be markedly less abundant during the last half of each year, whereas sardine larvae usually had a second peak of abundance in August-September. This late-season abundance was confined to Sebastian Viscaïno Bay and adjacent waters off central Baja California, and represents the spawning of the southern sub-population.

Anchovy larvae outnumbered sardine larvae in the California Current region even at the time of high abundance of the sardine, as was the situation during spawning surveys off southern California in 1940 and 1941. The ratio of larval anchovies to sardines was 1.18: 1 in 1940 and 1.66: 1 in 1941. These values are ratios of numbers of larvae, not the biomass of the two respective populations. An adult anchovy weighs only about one-fifth as much as an adult sardine and has a shorter life span. John MacGregor (personal communication) has estimated that an anchovy produces about twice as many eggs per unit of weight as does a sardine. If survival is even roughly similar during the egg and larval stages of sardines and anchovies, then larvae can be converted to adult biomass by equating one sardine larva to two anchovy larvae.

Stations are not equally spaced in the CalCOFI survey pattern, but tended to be more closely spaced nearshore than offshore on all cruises and to be spaced closer throughout the survey area during the peak periods of spawning. It is necessary therefore to adjust for such unequal spacing when deriving estimates of abundance. This adjustment is accomplished by integrating collection data over area. Such a treatment of data on abundance yields what we term a "census estimate." The estimates are derived for individual cruises, and each yearly estimate is simply the summation of monthly cruise estimates. Tables

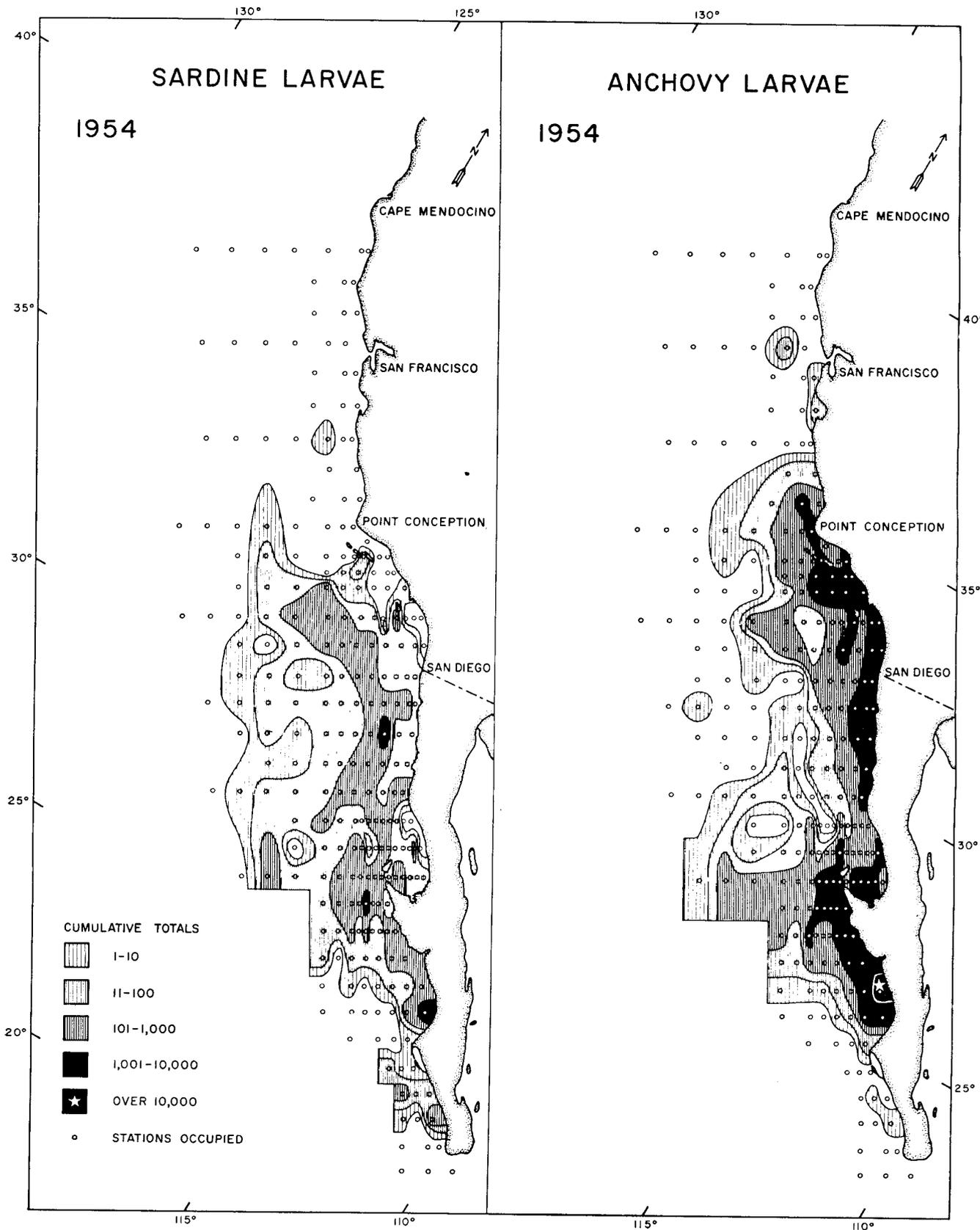


FIGURE 2. Distribution and relative abundance of sardine and anchovy larvae in the CalCOFI survey area in 1954.

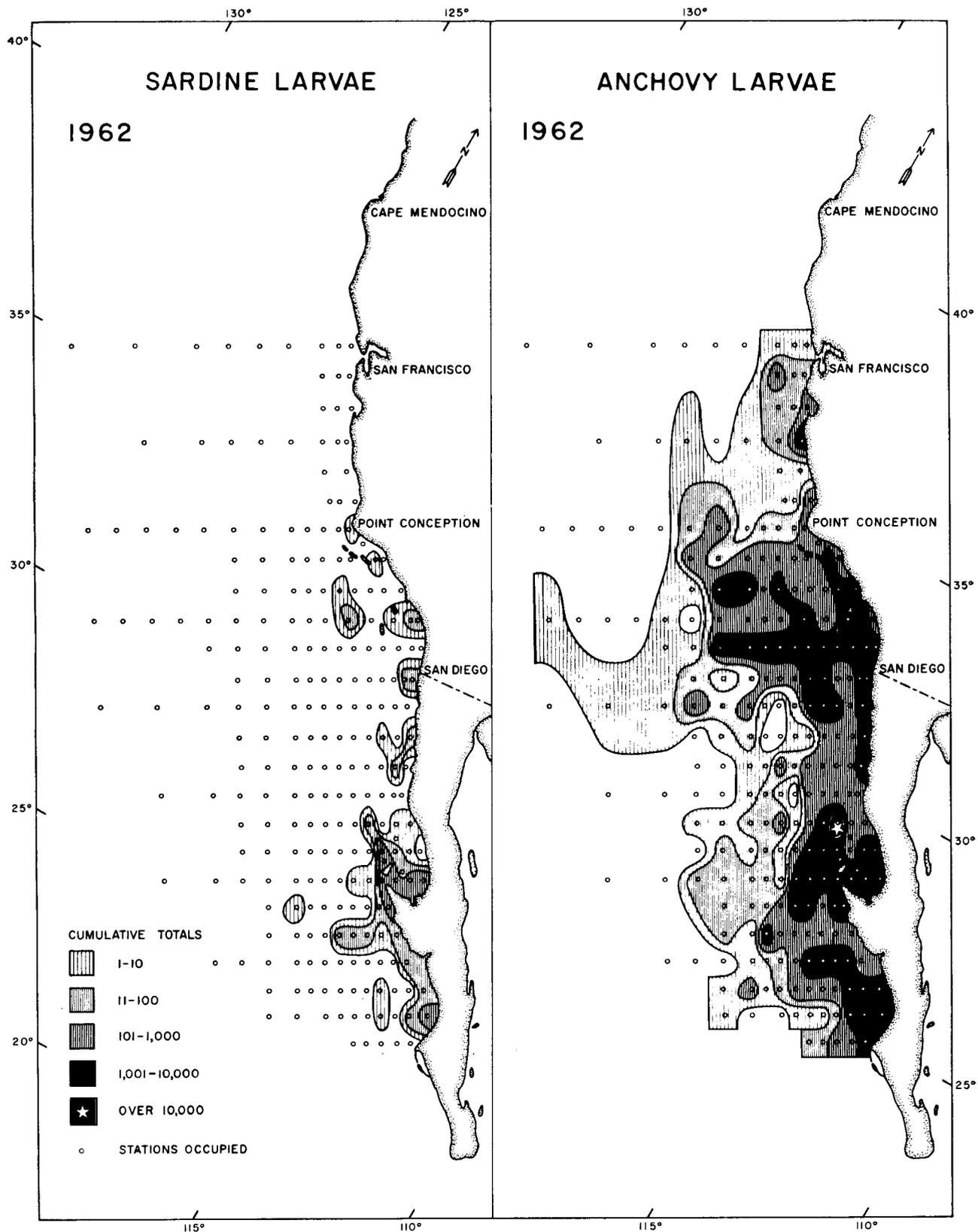


FIGURE 3. Distribution and relative abundance of sardine and anchovy larvae in the CalCOFI survey area in 1962.

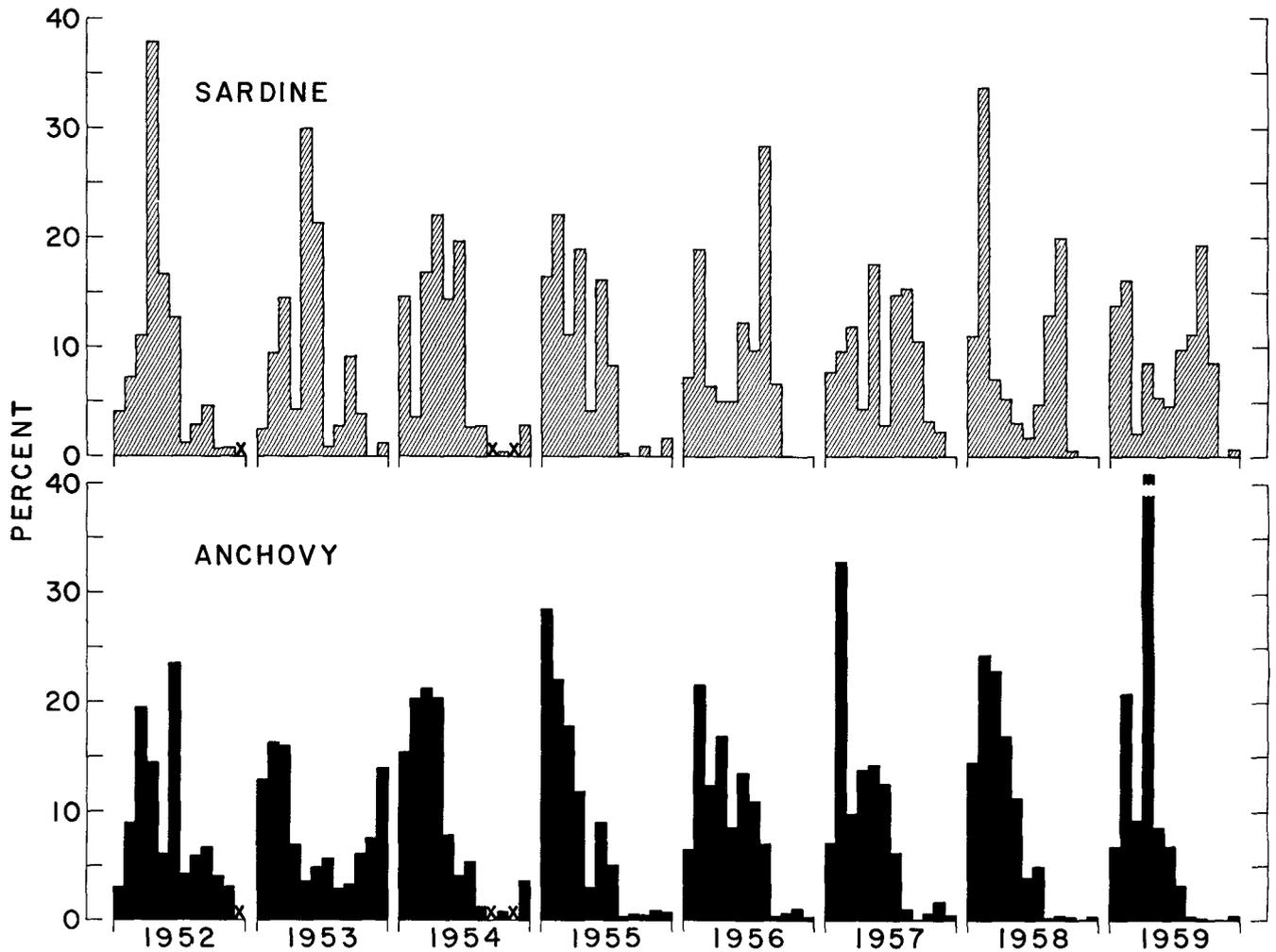


FIGURE 4. Percentages of the yearly total of sardine larvae (upper panel) and anchovy larvae (lower panel) taken in each monthly cruise, 1952-59. Spaces for each year on the abscissa depict a total of 12 months. X indicates no cruise was made.

TABLE 1
CENSUS ESTIMATES OF ABUNDANCE OF SARDINE LARVAE, BY YEAR AND AREA, 1951-59
(Estimates in Billions)

Area and station lines	Year								
	1951	1952	1953	1954	1955	1956	1957	1958	1959
Estimated number of larvae									
Northern California (40-57)-----	0	0	0	0	0	0	0	0	0
Central California (60-77)-----	3	0	0	2	0	0	47	7	7
Southern California (80-93)-----	146	189	2	1,691	528	433	569	491	427
Northern Baja California (97-107)-----	391	95	29	1,379	997	379	176	137	89
Upper central Baja California (110-120)-----	1,857	1,792	2,539	1,410	1,970	1,848	1,070	1,486	306
Lower central Baja California (123-137)-----	3,317	3,234	1,363	2,136	368	846	402	531	286
Southern Baja California (140-157)-----	60	156	87	679	478	389	168	179	44
Total -----	5,774	5,466	4,020	7,297	4,341	3,895	2,432	2,831	1,159
Percentage of yearly totals taken in each area									
Northern California (40-57)-----	0	0	0	0	0	0	0	0	0
Central California (60-77)-----	0.05	0	0	0.03	0	0	1.93	0.25	0.60
Southern California (80-93)-----	2.53	3.45	0.05	23.17	12.16	11.12	23.40	17.34	36.84
Northern Baja California (97-107)-----	6.77	1.74	0.72	18.90	22.97	9.73	7.24	4.84	7.68
Upper central Baja California (110-120)-----	32.16	32.78	63.16	19.32	45.38	47.44	44.00	52.49	26.40
Lower central Baja California (123-137)-----	57.45	59.17	33.91	29.27	8.48	21.72	16.53	18.76	24.68
Southern Baja California (140-157)-----	1.04	2.85	2.16	9.31	11.01	9.99	6.91	6.32	3.80
Total -----	100.00	99.99	100.00	100.00	100.00	100.00	100.01	100.00	100.00

TABLE 2
CENSUS ESTIMATES OF ABUNDANCE OF ANCHOVY LARVAE, BY YEAR AND AREA, 1951-59
 (Estimates in Billions)

Area and station lines	Year								
	1951	1952	1953	1954	1955	1956	1957	1958	1959
Estimated number of larvae									
Northern California (40-57)-----	12	9	--	0	--	0	--	30	0
Central California (60-77)-----	371	140	2	962	20	205	71	3,196	5,750
Southern California (80-93)-----	2,112	1,769	5,203	10,295	7,450	4,673	21,010	21,853	25,529
Northern Baja California (97-107)-----	825	1,279	2,460	4,536	8,425	1,944	3,261	7,415	3,633
Upper central Baja California (110-120)-----	4,015	6,972	10,755	7,122	17,914	15,395	7,628	12,733	13,167
Lower central Baja California (123-137)-----	7,671	6,867	5,260	15,491	3,828	8,858	8,437	11,439	6,055
Southern Baja California (140-157)-----	95	35	--	9	21	7,433	34	262	34
Total -----	15,101	17,071	23,680	38,415	37,658	38,508	40,441	56,928	54,168
Percentage of yearly totals taken in each area									
Northern California (40-57)-----	0.08	0.05	--	0	--	0	--	0.05	0
Central California (60-77)-----	2.46	0.82	>.01	2.50	0.05	0.53	0.18	5.62	10.61
Southern California (80-93)-----	13.98	10.36	21.97	26.80	19.78	12.14	51.95	38.39	47.13
Northern Baja California (97-107)-----	5.46	7.49	10.39	11.81	22.37	5.05	8.06	13.02	6.71
Upper central Baja California (110-120)-----	26.59	40.84	45.42	18.54	47.57	39.98	18.86	22.37	24.31
Lower central Baja California (123-137)-----	50.80	40.23	22.21	40.33	10.17	23.00	20.86	20.09	11.18
Southern Baja California (140-157)-----	0.63	0.20	--	0.02	0.06	19.30	0.09	0.46	0.06
Total -----	100.00	99.99	100.00						

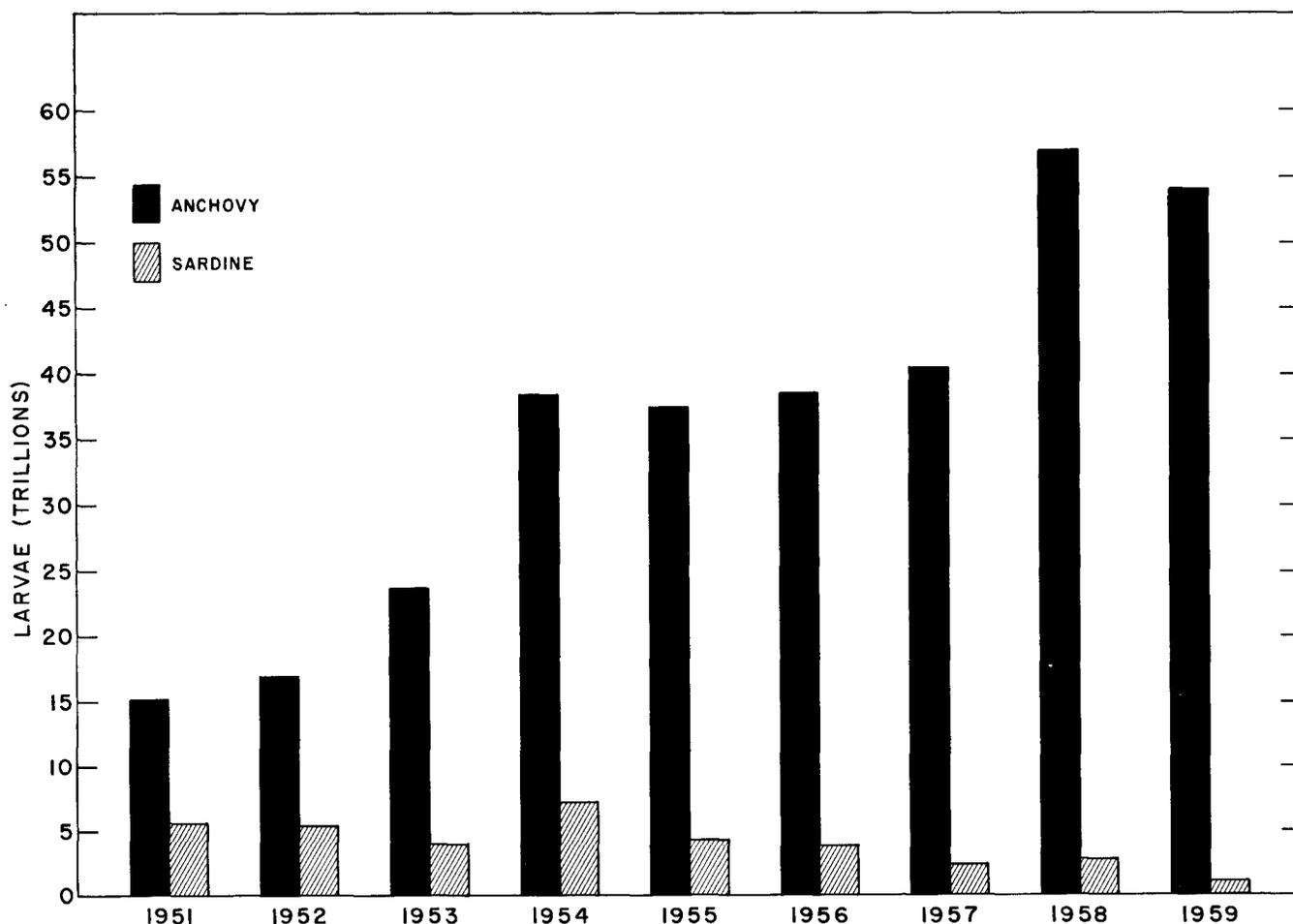


FIGURE 5. Annual census estimates for the total CalCOFI survey area of sardine and anchovy larvae, 1951-59.

1 and 2 show census estimates for sardine and anchovy larvae, respectively, for 1951-59, summarized by year and area. Census estimates for 1960 are not included, simply because they have not been worked up as yet. The estimates of sardine larvae ranged from a high of about 7.3 trillion in 1954 to a low of about 1.2 trillion in 1959. Anchovy larvae increased from 15.1 trillion to more than 38 trillion between 1951 and 1954, remained at this level through 1957,

and then increased further to about 55 trillion in 1958 and 1959 (Figure 5). Anchovy abundance appears to have almost quadrupled during the 1950's, while sardine abundance progressively decreased after 1954. Whereas anchovy larvae outnumbered sardine larvae by less than 3:1 in 1951, the ratio had increased to more than 45: 1 by 1959. Abundance of anchovy larvae increased further from 1960 to 1965. Although this change is not shown or expressed in

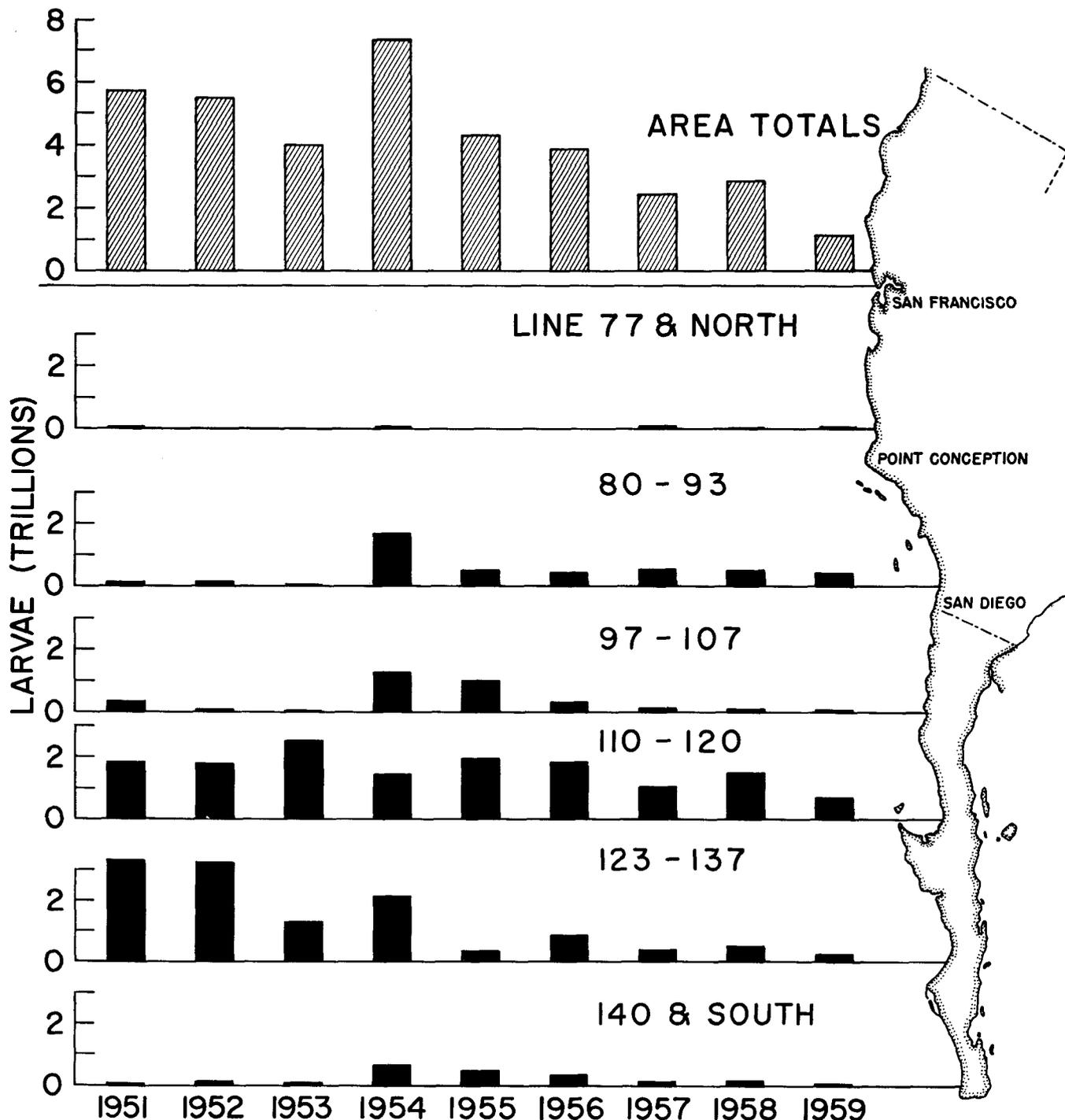


FIGURE 6. Sardine larvae: Annual census estimates by area, 1951-59.

terms of census estimates (only four cruises were made per year after 1960, rather than 10 to 12), other methods of evaluating the increase indicate that abundance more than doubled between 1958 and 1965.

The census estimates permit a better evaluation of abundance of sardine and anchovy larvae in the 7 areas of the CalCOFI region during 1951-59.

As already noted, sardine eggs and larvae were obtained more consistently off central Baja California (lines 110-137) than off northern Baja California and southern California (Figure 6). Sardine larvae were

proportionately more abundant, however, off lower central Baja California (station lines 123-137) during 1951-54 than later. Off northern Baja California (lines 97-107) and southern California (lines 80-93) abundance was low in 1951-53 but proportionately higher during 1954-59.

Throughout the decade only negligible numbers of sardine larvae were taken off central California (lines 60-77) and none off northern California. The numbers taken off southern Baja California (lines 140-157) undoubtedly would have been higher if this area had

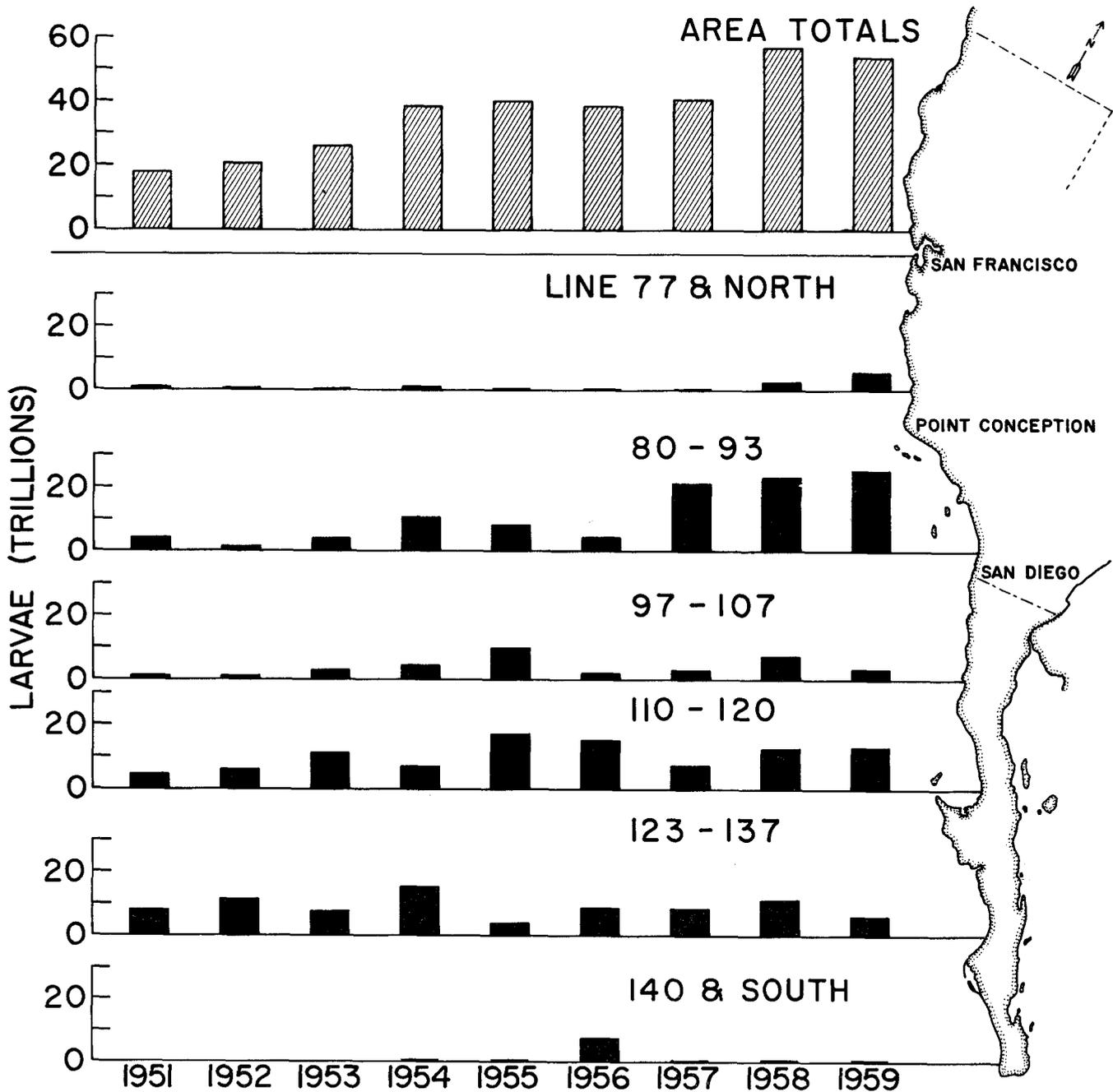


FIGURE 7. Anchovy larvae: Annual census estimates by area, 1951-59.

TABLE 3

SARDINE LARVAE¹: SUMMARY OF TOTAL OCCURRENCES, CO-OCCURRENCES WITH ANCHOVY LARVAE, AND OCCURRENCES IN HAULS WITHOUT ANCHOVY LARVAE IN THE CALCOFI SURVEY PATTERN, BY AREA AND YEAR, 1951-63
(Station lines given below each area²)

Year	Total occurrences of sardine larvae							Co-occurrences of sardine and anchovy larvae							Occurrences of sardine larvae alone								
	Cent. Calif. 60-77	So. Calif. 80-93	No. Baja Calif. 97-107	Upper cent. Baja Calif. 110-120	Lower cent. Baja Calif. 123-137	So. Baja Calif. 140-157	Total	Cent. Calif. 60-77	So. Calif. 80-93	No. Baja Calif. 97-107	Upper cent. Baja Calif. 110-120	Lower cent. Baja Calif. 123-137	So. Baja Calif. 140-157	Total	Cent. Calif. 60-77	So. Calif. 80-93	No. Baja Calif. 97-107	Upper cent. Baja Calif. 110-120	Lower cent. Baja Calif. 123-137	So. Baja Calif. 140-157	Total		
Monthly cruises																							
1951.....	1	23	26	55	55	9	169	0	10	12	47	46	3	118	1	13	14	8	9	6	51		
1952.....	0	25	21	101	109	6	262	0	12	9	65	79	2	167	0	13	12	36	30	4	95		
1953.....	0	3	8	110	91	7	219	0	3	2	72	74	0	151	0	0	6	38	17	7	68		
1954.....	1	42	92	132	96	11	374	0	22	42	86	79	4	233	1	20	50	46	17	7	141		
1955.....	0	26	72	94	47	17	256	0	12	34	79	32	3	160	0	14	38	15	15	14	96		
1956.....	0	22	39	61	38	11	171	0	3	15	55	32	4	109	0	19	24	6	6	7	62		
1957.....	6	21	22	83	31	12	175	2	9	16	60	20	3	110	4	12	6	23	11	9	65		
1958.....	2	71	26	53	30	13	195	2	67	23	44	26	6	168	0	4	3	9	4	7	27		
1959.....	5	68	16	53	25	5	172	5	66	15	43	20	3	152	0	2	1	10	5	2	20		
1960.....	0	40	26	46	18	10	140	0	39	21	39	14	8	121	0	1	5	7	4	2	19		
Total.....	15	341	348	788	540	101	2,133	9	243	189	590	422	36	1,489	6	98	159	198	118	65	644		
Quarterly cruises																							
1961.....	0	16	6	16	13	1	52	0	12	6	16	10	1	45	0	4	0	0	3	0	7		
1962.....	0	9	6	22	21	0	58	0	8	6	20	18	0	52	0	1	0	2	3	0	6		
1963.....	3	19	25	28	20	1	96	3	16	23	24	19	1	86	0	3	2	4	1	0	10		

¹ No sardine larvae were obtained off northern California (station lines 40-57).

² Includes additional closely spaced stations on inshore ends of station lines.

TABLE 4

ANCHOVY LARVAE: SUMMARY OF TOTAL OCCURRENCES, CO-OCCURRENCES WITH SARDINE LARVAE, AND OCCURRENCES IN HAULS WITHOUT SARDINE LARVAE IN THE CALCOFI SURVEY PATTERN, BY AREA AND YEAR, 1951-63
(Station lines given below each area)

Year	Total occurrences of anchovy larvae							Co-occurrences of sardine and anchovy larvae							Occurrences of anchovy larvae alone									
	No. Calif. 40-57	Cent. Calif. 60-77	So. Calif. 80-93	No. Baja Calif. 97-107	Upper cent. Baja Calif. 110-120	Lower cent. Baja Calif. 123-137	So. Baja Calif. 140-157	Total	No. Calif. 40-57	Cent. Calif. 60-77	So. Calif. 80-93	No. Baja Calif. 97-107	Upper cent. Baja Calif. 110-120	Lower cent. Baja Calif. 123-137	So. Baja Calif. 140-157	Total	No. Calif. 40-57	Cent. Calif. 60-77	So. Calif. 80-93	No. Baja Calif. 97-107	Upper cent. Baja Calif. 110-120	Lower cent. Baja Calif. 123-137	So. Baja Calif. 140-157	Total
Monthly cruises																								
1951.....	6	43	89	59	107	95	11	410	0	0	10	12	47	46	3	118	6	43	79	47	60	49	8	292
1952.....	1	11	110	92	169	134	2	519	0	0	12	9	65	79	2	167	1	11	98	83	104	55	0	352
1953.....	--	2	228	91	199	165	0	685	--	0	3	2	72	74	0	151	--	2	225	89	127	91	0	534
1954.....	0	15	259	124	187	169	4	758	0	0	22	42	86	79	4	233	0	15	237	82	101	90	0	525
1955.....	0	7	218	120	178	94	7	624	0	0	12	34	79	32	3	160	0	7	206	86	99	62	4	464
1956.....	0	5	168	82	151	107	23	536	0	0	3	15	55	32	4	109	0	5	165	67	96	75	19	427
1957.....	--	17	187	94	172	98	12	580	--	2	9	16	60	20	3	110	--	15	178	78	112	78	9	470
1958.....	5	96	272	145	164	85	11	778	0	2	67	23	44	26	6	168	5	94	205	122	120	59	5	610
1959.....	0	133	311	116	197	120	11	888	0	5	66	15	43	20	3	152	0	128	245	101	154	100	8	736
1960.....	0	48	280	193	256	173	27	977	0	0	39	21	39	14	8	121	0	48	241	172	217	159	19	856
Total.....	12	377	2,122	1,116	1,780	1,240	108	6,755	0	9	243	189	590	422	36	1,489	12	368	1,879	927	1,190	818	72	5,266
Quarterly cruises																								
1961.....	--	30	115	84	102	69	1	401	--	0	12	6	16	10	1	45	--	30	103	78	86	59	0	356
1962.....	--	26	129	91	105	92	11	454	--	0	8	6	20	18	0	52	--	26	121	85	85	74	11	402
1963.....	--	40	171	97	133	97	4	542	--	3	16	23	24	19	1	86	--	37	155	74	109	78	3	456

been sampled as consistently as the others off Baja California.

The distribution of anchovy larvae was somewhat different than that of sardines (Figure 7). Anchovy larvae were important in the area off central California (lines 60-77) only during 1958 and 1959, and in the southernmost area (lines 140-157) only during 1956; they were taken in only a few hauls off northern California (lines 40-57). In the remaining areas, they were more consistently represented throughout the 10-year period than sardine larvae. Anchovy larvae, like sardine larvae, were more abundant off California during the warm years, 1957-59. In these years, the center of anchovy abundance shifted from central Baja California to southern California.

I wish now to deal more specifically with occurrences and co-occurrences of larvae and eggs of the

two species. Information concerning occurrences and co-occurrences of the two species in the seven areas are summarized in Tables 3 and 4. For completeness, I have included information on occurrences and co-occurrences of both species for 1961-63, as well as for 1951-60. The total number of stations occupied on CalCOFI cruises during each year, 1951-63, are summarized by area in Table 5. These summations are not limited to regular CalCOFI stations, but include extra occupancies and special cruises (Table 6). However, the analysis that follows is based on the data for 1951-60.

Throughout the CalCOFI survey period, anchovy larvae always have occurred in more collections than sardine larvae (Figure 8). In the 1950's as a whole, anchovy larvae occurred in 3.1 times as many hauls as sardine larvae. The disparity was lowest in 1952

TABLE 5
SUMMARY OF STATIONS OCCUPIED ON CalCOFI SURVEY CRUISES, BY YEAR AND AREA, 1951-63
(Station lines given below each area)

Year	Northern California 40-57	Central California 60-77	Southern California 80-93	Northern Baja Calif. 97-107	Upper central Baja Calif. 110-120	Lower central Baja Calif. 123-137	Southern Baja Calif. 140-157	Total
Monthly cruises								
1951.....	45	243	337	258	263	201	89	1,436
1952.....	29	164	350	287	352	277	14	1,473
1953.....	0	119	478	249	319	267	13	1,445
1954.....	13	109	418	274	352	271	36	1,473
1955.....	7	95	403	302	353	212	79	1,451
1956.....	54	112	395	280	308	182	76	1,407
1957.....	0	101	364	287	360	267	114	1,493
1958.....	41	230	459	352	391	274	105	1,852
1959.....	22	232	572	419	473	345	119	2,182
1960.....	62	165	439	341	420	286	113	1,826
Total.....	273	1,570	4,215	3,049	3,591	2,582	758	16,038
Quarterly cruises								
1961.....	0	128	237	183	209	191	5	953
1962.....	0	85	243	185	210	182	15	920
1963.....	0	81	266	206	218	226	12	1,009

TABLE 6
STATIONS OCCUPIED ON REGULAR CalCOFI CRUISES AND SPECIAL CRUISES, INCLUDING EXTRA OCCUPANCIES, 1951-64

Year	Regular occupancies	Late March cruise	Extra occupancies of regular stations	Special tows	Additional inshore stations	Multiple occupancies (not included)	Total
Monthly cruises							
1951.....	1,436	0	0	0	0	0	1,436
1952.....	1,376	63	34	0	0	0	1,473
1953.....	1,346	63	36	0	0	0	1,445
1954.....	1,473	0	0	0	0	0	1,473
1955.....	1,425	0	26	0	0	(166)	1,451
1956.....	1,399	0	8	0	0	0	1,407
1957.....	1,493	0	0	0	0	0	1,493
1958.....	1,851	0	1	0	0	(34)	1,852
1959.....	2,180	0	2	0	0	0	2,182
1960.....	1,810	0	1	15	0	(24)	1,826
Total.....	15,789	126	108	15	0	(224)	16,038
Quarterly cruises							
1961.....	944	0	9	0	0	0	953
1962.....	919	0	1	0	0	0	920
1963.....	881	0	3	0	125	0	1,009
1964.....	877	0	7	0	319	0	1,203

¹ Includes 54 stations occupied on Norpac.

and 1954, when they were collected only twice as often as sardine larvae, but increased yearly in 1955-60; in the 1960 collections, anchovy larvae occurred seven times as often as sardine larvae. A corresponding increase appeared in the co-occurrences of anchovy larvae in the collections containing sardine larvae, from 62 percent in 1954 to about 87 percent in 1960.

Obviously, as one species becomes more abundant and more widespread than another, it will occur alone more frequently, and thus be free from possible competition. When anchovy larvae are collected in seven times as many hauls as sardine larvae, as in 1960, the possible co-occurrences with sardine larvae would be only 14 percent. In fact, sardine larvae co-occurred with anchovy larvae in one haul out of eight (12.4 percent), while anchovy larvae co-occurred with sar-

dine larvae in six hauls out of seven (86.5 percent).

For the decade as a whole, anchovy larvae co-occurred in 1,489 (69.8 percent) of the 2,133 hauls that contained sardine larvae, whereas sardine larvae occurred in only 1,489 (22.0 percent) of the 6,755 hauls that contained anchovy larvae. Thus, anchovy larvae were present in two of every three hauls that contained sardine larvae, whereas sardine larvae occurred in little more than one of five hauls containing anchovy larvae. If interspecies competition is a factor in the survival of larvae, and co-occurrence is a measure of competition, then the anchovy should have had a decided advantage over the sardine.

Another factor must be considered: sardine larvae are less likely to occur with anchovy larvae in some areas of the CalCOFI grid than in others (Tables 7 and 8). Anchovy larvae have had decidedly less com-

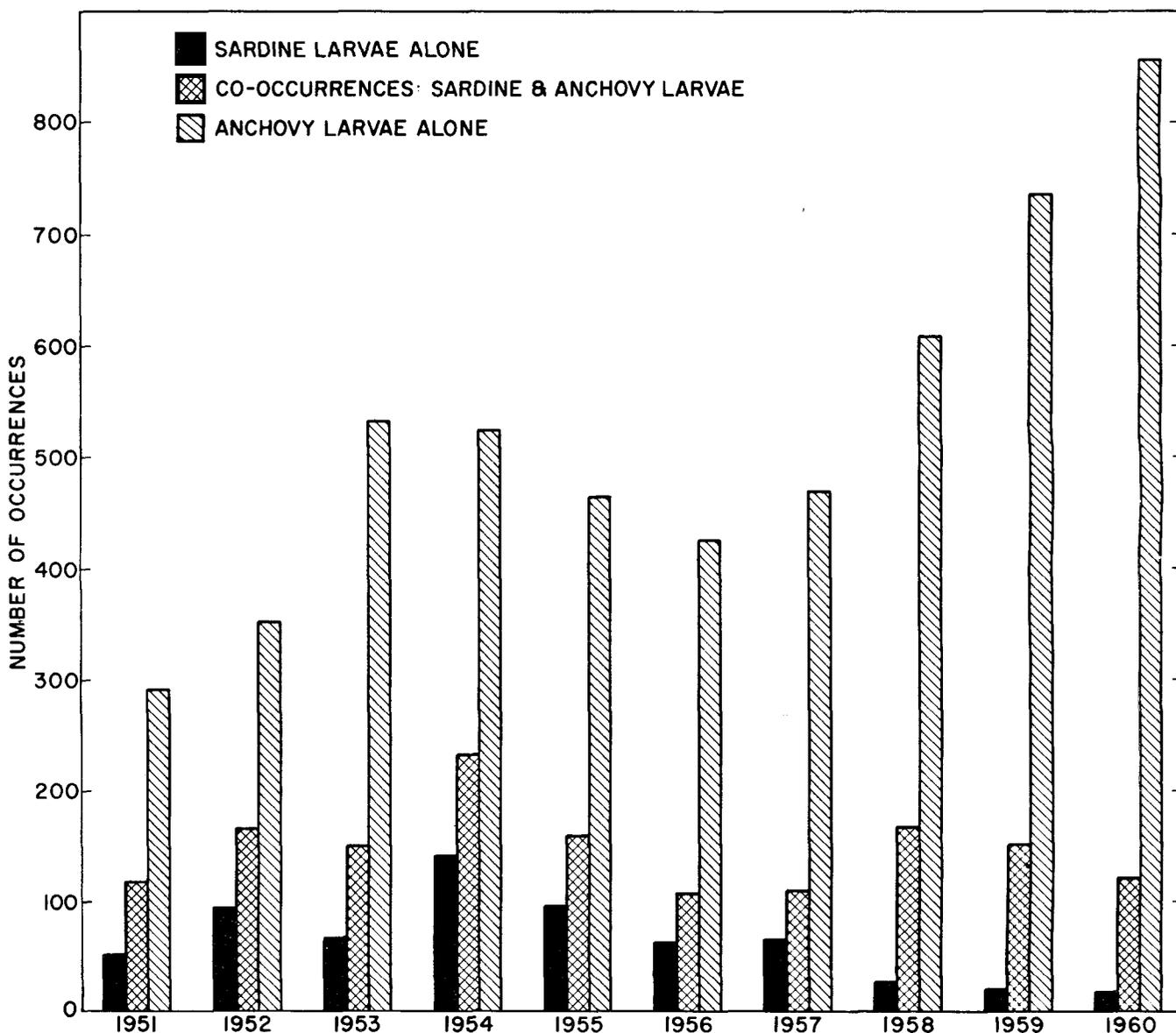


FIGURE 8. Graphic presentation, by year, of the number of CalCOFI plankton collections containing 1) sardine larvae alone, 2) both sardine and anchovy larvae, and 3) anchovy larvae alone, 1951-60

TABLE 7

SUMMARY OF TOTAL STATION OCCUPANCIES, OCCURRENCES OF SARDINE LARVAE, AND CO-OCCURRENCES WITH ANCHOVY LARVAE, BY AREA, 1951-60

Area and station lines	1951-60 total occupancies	Occurrences of sardine larvae	Percentage of positive hauls	Co-occurrences with anchovy larvae	Percentage of co-occurrences
Northern California (40-57).....	273	0	0	0	0
Central California (60-77).....	1,570	15	1.0	9	60.0
Southern California (80-93).....	4,215	341	8.1	243	71.3
Northern Baja California (97-107).....	3,049	348	11.4	189	54.3
Upper central Baja California (110-120).....	3,591	788	21.9	590	74.9
Lower central Baja California (123-137).....	2,582	540	20.9	422	78.1
Southern Baja California (140-157).....	758	101	13.3	36	35.6
Totals.....	16,038	2,133	13.3	1,489	69.8

TABLE 8

SUMMARY OF TOTAL STATION OCCUPANCIES, OCCURRENCES OF ANCHOVY LARVAE, AND CO-OCCURRENCES WITH SARDINE LARVAE, BY AREA, 1951-60

Area and station lines	1951-60 total occupancies	Occurrences of anchovy larvae	Percentage of positive hauls	Co-occurrences with sardine larvae	Percentage of co-occurrences
Northern California (40-57).....	273	12	4.4	0	0
Central California (60-77).....	1,570	377	24.0	9	2.4
Southern California (80-93).....	4,215	2,122	50.3	243	11.5
Northern Baja California (97-107).....	3,049	1,116	36.6	189	16.9
Upper central Baja California (110-120).....	3,591	1,780	49.6	590	33.1
Lower central Baja California (123-137).....	2,582	1,240	48.0	422	34.0
Southern Baja California (140-157).....	758	108	14.2	36	33.3
Totals.....	16,038	6,755	42.1	1,489	22.0

petition in the northern part of the CalCOFI survey area. Off central California (station lines 60-77) sardine larvae occurred in less than 1 percent of the collections, while anchovy larvae occurred in 24 percent. In this area the percentage of co-occurrence of sardine with anchovy larvae was only 2.4 percent. Off southern California, anchovy larvae occurred in more than 50 percent of all collections made during the 1950's, and sardine larvae in only 8.1 percent. Hence, even though the co-occurrence of anchovy larvae with sardine larvae was 71.3 percent, sardine larvae occurred in only 11.5 percent of the collections that contained anchovy larvae. Off southern California the anchovy must have had a decided advantage.

The region in which the two species might have competed most intensely was off central Baja California. In this region sardine larvae occurred in one of every three hauls containing anchovy larvae; anchovy larvae occurred in three of every four hauls containing sardine larvae.

The occurrences of eggs in our plankton hauls were less frequent than occurrences of larvae. Probably a major reason for this lower frequency is that eggs of both the Pacific sardine and the northern anchovy hatch in only 2 to 4 days, depending on water temperature; consequently the eggs in any given haul represent a relatively short time span. A sample of larvae, on the other hand, can contain specimens accumulated during a span of perhaps 30 days or more. Sardine eggs, on the average, occurred in only about

70 percent as many collections as sardine larvae. Anchovy eggs, which are not fully retained by the standard CalCOFI net, occurred in little more than a third as many hauls as anchovy larvae. Hence, the frequency of occurrence and, as it happens, co-occurrence of eggs is less than for larvae. In only 1958 and 1959 did sardine eggs co-occur in more hauls with anchovy eggs than they occurred alone. For the decade as a whole, anchovies spawned in the same waters with sardines only about 30 percent of

TABLE 9

COMPARISON OF AVERAGE NUMBER OF LARVAE PER HAUL OF "CO-OCCURRENCES," WITH SAMPLES CONTAINING SARDINE OR ANCHOVY LARVAE ALONE

	Sardine larvae			Anchovy larvae		
	All hauls	Alone	Co-occurring	Co-occurring	Alone	All hauls
1951.....	65.5	21.4	84.5	124.5	50.9	72.1
1952.....	93.8	82.5	99.9	192.2	88.2	121.8
1953.....	68.8	63.3	71.2	186.4	142.4	152.1
1954.....	72.0	47.9	86.5	304.0	172.3	212.7
1955.....	55.6	47.5	60.4	302.2	201.6	227.5
1956.....	90.7	57.2	109.9	329.0	232.0	251.8
1957.....	56.2	67.9	49.3	315.7	238.1	252.8
1958.....	58.9	27.0	64.0	610.4	169.5	264.0
1959.....	31.2	34.4	30.7	473.4	183.7	233.7
1960.....	60.6	17.8	67.3	494.9	271.5	299.1
Average.....	65.3	46.7	72.4	333.3	175.0	208.7

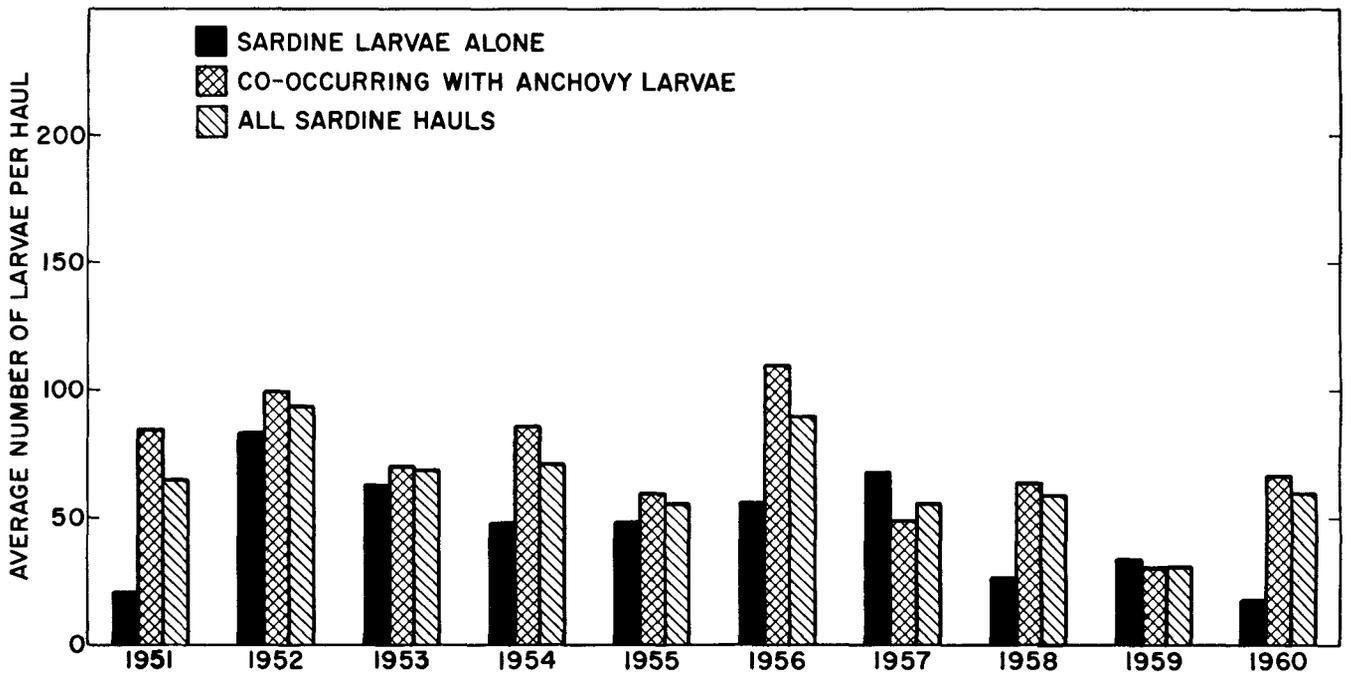


FIGURE 9. Comparison of the annual average number of sardine larvae obtained per haul, 1) in hauls containing sardine larvae alone, 2) in hauls in which sardine larvae co-occurred with anchovy larvae, and 3) in all hauls containing sardine larvae, 1951-60.

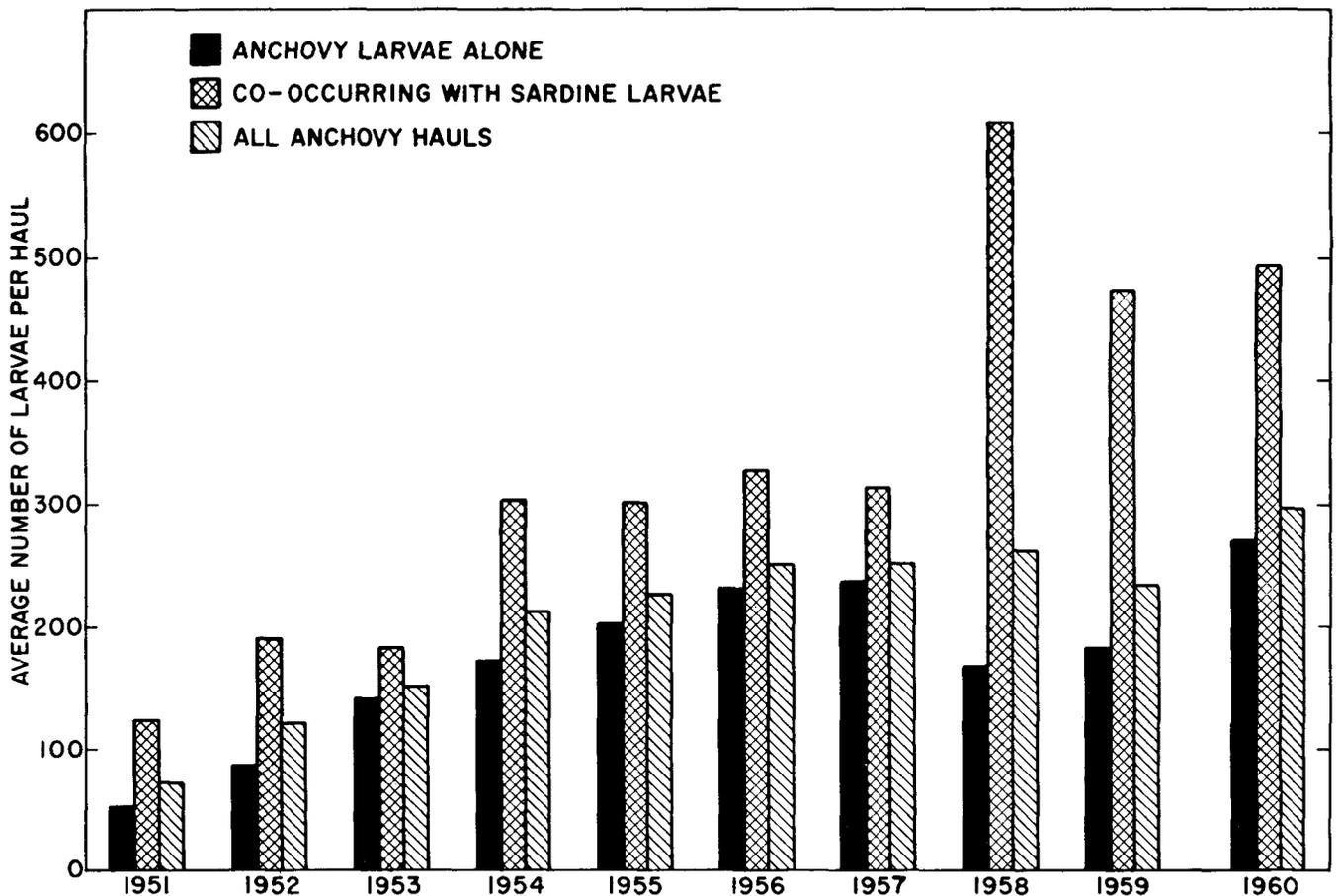


FIGURE 10. Comparison of the annual average number of anchovy larvae obtained per haul, 1) in hauls containing anchovy larvae alone, 2) in hauls in which anchovy larvae co-occurred with sardine larvae, and 3) in all hauls containing anchovy larvae, 1951-60.

the time. In contrast, the larvae of anchovies co-occurred with sardine larvae about 70 percent of the time.

The numbers of larvae in "co-occurring hauls" compared with hauls containing only one or the other species alone are summarized in Table 9 and illustrated in Figures 9 and 10. More larvae were obtained per sample in hauls where the two species co-occurred

than in hauls where they occurred alone. The consistently larger numbers of anchovies taken in hauls containing sardine larvae over numbers in hauls containing anchovies alone, usually by about 2 to 1, was especially striking. Numbers of sardine larvae in samples that contained anchovy larvae usually were also considerably larger than in hauls where they occurred alone—only two exceptions in the 10-year series.

TABLE 10

SARDINE LARVAE—ALL OCCURRENCES: AVERAGE NUMBER PER POSITIVE HAUL ($\times 10^2$), SUMMARIZED BY SIZE AND YEAR, 1951-60

Size class (mm)	Year										Un-weighted average
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	
3.0	1,608	2,632	1,782	2,193	1,390	3,049	1,287	1,566	1,137	1,667	1,831.1
4.75	1,388	2,580	2,489	1,992	1,799	2,316	1,086	1,419	831	1,256	1,715.6
5.75	777	968	735	822	951	837	975	875	417	798	815.5
6.75	508	698	451	408	356	508	397	606	164	563	465.9
7.75	513	580	380	337	243	490	444	626	103	376	409.2
8.75	379	414	242	262	138	479	364	301	116	388	308.3
9.75	302	322	125	238	154	400	304	177	96	328	244.6
10.75	227	260	134	253	93	260	249	87	86	199	184.8
11.75	214	196	123	179	98	155	160	75	44	190	143.4
12.75	163	166	136	152	91	145	92	49	45	102	114.1
13.75	144	122	90	134	74	90	59	27	40	43	82.3
14.75	101	95	64	110	70	85	75	20	14	33	66.7
15.75	54	47	45	54	41	98	48	28	11	10	43.6
17.25	77.5	44.0	54.0	36.0	41.6	77.1	44.5	20.3	12.4	3.6	41.1
19.25	17.4	28.4	11.4	15.5	13.7	46.2	20.6	7.8	3.5	--	16.4
21.25	25.4	13.6	4.7	3.0	3.8	32.5	6.0	1.9	1.6	1.8	9.4
23.25	18.2	9.8	2.4	5.0	--	6.7	1.9	--	--	--	4.4
25.25 and larger	--	--	--	3.8	1.1	--	2.4	--	--	2.0	0.9
Disintegrated	32	199	6	--	2	--	4	1	--	100	34.4
Total	6,548.5	9,374.8	6,874.5	7,197.3	5,560.2	9,074.5	5,619.4	5,887.0	3,121.5	6,060.4	6,531.8

TABLE 11

SARDINE LARVAE—CO-OCCURRING WITH ANCHOVY LARVAE: AVERAGE NUMBER PER POSITIVE HAUL ($\times 10^2$), SUMMARIZED BY SIZE AND YEAR, 1951-60

Size class (mm)	Year										Un-weighted average
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	
3.0	1,953	2,648	1,718	2,747	1,492	4,068	969	1,784	1,078	1,763	2,022.0
4.75	1,833	2,557	2,602	2,252	2,135	2,321	811	1,567	816	1,422	1,831.6
5.75	1,005	776	680	869	1,028	917	1,130	934	442	901	868.2
6.75	655	809	535	446	309	682	367	629	167	641	524.0
7.75	678	740	480	379	185	655	293	675	109	422	461.6
8.75	512	529	268	300	128	638	339	313	123	445	359.5
9.75	397	421	136	294	167	537	296	178	98	375	289.9
10.75	304	364	107	362	101	325	227	90	90	230	220.0
11.75	285	267	146	262	112	209	134	77	45	214	175.1
12.75	220	233	143	223	104	197	45	53	39	112	136.9
13.75	187	166	104	190	84	84	65	29	40	46	99.5
14.75	129	107	68	156	76	106	108	22	12	38	82.2
15.75	71	62	46	81	48	132	68	27	9	11	55.5
17.25	102.5	44.0	57.3	54.0	44.8	69.9	47.6	15.8	10.5	4.1	45.0
19.25	16.5	19.8	11.6	21.3	16.2	24.2	9.7	7.1	2.1	--	12.8
21.25	35.0	14.0	6.8	2.2	4.2	15.2	9.5	2.2	--	2.1	9.1
23.25	22.4	4.0	3.4	8.0	--	5.6	3.0	--	--	--	4.6
25.25 and larger	--	--	--	6.2	1.7	--	3.8	--	--	2.3	1.4
Disintegrated	46	232	8	0	4	0	2	2	0	106	40.0
Total	8,451.4	9,992.8	7,120.1	8,652.7	6,039.9	10,985.9	4,927.6	6,405.1	3,080.6	6,734.5	7,239.1

The problem then is to account for the higher number of each species in hauls in which they co-occurred—to determine whether they were obtained in centers of heavier spawning for both species or whether survival was better in areas of co-occurrence. If the latter were true, it would be difficult to justify any hypothesis that postulates that competition between the two species would adversely affect their survival.

The average numbers of larvae per positive haul are summarized by size and year in Tables 10 to 15. For each species these data are summarized in three ways: (1) for all occurrences, (2) for hauls in which the larvae of one species co-occurred with those of the other, and (3) for hauls in which the larvae of a species occurred alone.

A semi-log plot (Figures 11 and 12) gives a simple method of illustrating changes in abundance with

TABLE 12
SARDINE LARVAE—OCCURRING ALONE (NO ANCHOVY LARVAE): AVERAGE NUMBER PER POSITIVE HAUL ($\times 10^2$), SUMMARIZED BY SIZE AND YEAR, 1951-60

Size class (mm)	Year										Un-weighted average
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	
3.0	810	2,604	1,922	1,276	1,217	1,257	1,826	222	1,580	1,059	1,377.3
4.75	357	2,619	2,237	1,562	1,236	2,306	1,552	505	952	201	1,352.7
5.75	249	1,307	859	746	820	696	712	510	228	142	626.9
6.75	166	503	266	346	436	201	448	465	140	66	303.7
7.75	129	298	158	267	340	198	699	326	62	83	256.0
8.75	72	212	183	199	154	198	407	226	57	25	173.3
9.75	83	149	101	144	132	158	318	171	82	29	136.7
10.75	48	78	192	73	78	146	286	68	57	--	102.6
11.75	51	71	72	42	74	61	204	68	38	36	71.7
12.75	31	48	120	33	69	54	173	27	91	44	69.0
13.75	47	44	61	42	58	99	50	13	42	28	48.4
14.75	34	74	56	34	59	47	18	9	26	--	35.7
15.75	13	21	43	10	29	38	14	34	28	--	23.0
17.25	19.6	43.9	46.6	6.2	36.4	89.8	39.2	48.1	27.0	--	35.7
19.25	19.6	43.6	10.7	6.0	9.5	84.8	38.9	12.2	14.0	--	23.9
21.25	3.3	13.0	--	4.5	3.3	62.9	--	--	14.0	--	10.1
23.25	8.2	20.2	--	--	--	8.7	--	--	--	--	3.7
25.25 and larger	--	--	--	--	--	--	--	--	--	--	0.0
Disintegrated	0	143	0	0	0	15	6	0	0	63	22.7
Total	2,140.7	8,291.7	6,327.3	4,790.7	4,751.2	5,720.2	6,791.1	2,704.3	3,438.0	1,776.0	4,673.1

TABLE 13
ANCHOVY LARVAE—ALL OCCURRENCES: AVERAGE NUMBER PER POSITIVE HAUL ($\times 10^2$), SUMMARIZED BY SIZE AND YEAR, 1951-60

Size class (mm)	Year										Un-weighted average
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	
2.5	871	2,266	2,356	4,396	3,198	2,611	3,447	4,181	4,791	7,266	3,538.3
3.75	871	1,768	2,974	3,221	4,724	3,964	4,076	5,476	5,104	5,536	3,771.4
4.75	1,081	1,380	2,611	2,625	2,789	2,885	3,432	3,493	2,688	4,240	2,722.4
5.75	1,164	1,540	1,852	2,564	3,009	2,732	3,156	3,317	2,412	3,624	2,537.0
6.75	1,107	1,471	1,592	2,637	2,554	3,120	2,956	2,837	2,173	2,908	2,335.5
7.75	723	1,267	1,182	1,925	2,052	2,818	2,515	2,243	1,809	2,006	1,854.0
8.75	453	846	891	1,418	1,573	2,306	2,055	1,680	1,349	1,340	1,391.1
9.75	303	561	676	913	1,112	1,857	1,451	1,135	1,031	928	996.7
10.75	187	370	424	581	712	1,273	888	764	702	578	647.9
11.75	144	241	268	376	388	751	558	494	407	391	401.8
12.75	76	135	129	239	237	402	312	311	277	243	236.1
13.75	43	74	88	132	136	194	162	177	181	154	134.1
14.75	28	64	51	84	85	100	101	109	120	115	85.7
15.75	19	43	30	49	49	51	54	65	92	63	51.5
17.25	13.7	62.9	35.2	40.2	66.8	57.8	67.5	67.0	91.3	81.3	58.4
19.25	4.3	28.4	12.5	23.5	23.4	40.5	16.8	29.1	37.8	36.8	25.3
21.25	2.6	20.9	7.8	4.4	7.0	2.8	11.3	8.9	9.9	9.5	8.5
23.25 and larger	12.3	13.7	11.6	4.2	8.6	7.4	6.8	3.1	3.0	11.4	8.2
Disintegrated	106	23	21	36	27	4	13	10	88	378	70.6
Total	7,208.9	12,174.9	15,212.1	21,268.3	22,750.8	25,176.5	25,278.4	26,400.1	23,366.0	29,909.0	20,874.5

increase in size. Two curves are plotted for each species, one illustrating abundance of co-occurring larvae, the other of the species taken alone.

The two curves for anchovy larvae tend to converge with increase in size. This convergence would be expected if survival were better in hauls in which the larvae of a species occurred alone, free from competition. It is well to remember that the upper curve

represents the average of 1,489 hauls and the lower the average of 5,266 hauls—large amounts of data.

Data on changes in relative abundance with increase in size are less consistent for sardines. The upper curve, sardine larvae in co-occurrences with anchovy larvae, necessarily is based on the same number of hauls as is its counterpart graph for anchovies (1,489), but the lower curve is based on considerably

TABLE 14

ANCHOVY LARVAE—CO-OCCURRING WITH SARDINE LARVAE: AVERAGE NUMBER PER POSITIVE HAUL ($\times 10^2$), SUMMARIZED BY SIZE AND YEAR, 1951-60

Size class (mm)	Year										Un-weighted average
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	
2.5	1,524	2,836	2,648	6,773	2,997	2,471	1,326	6,832	11,385	11,189	4,998.1
3.75	1,525	2,600	4,578	4,310	5,877	5,057	3,336	14,634	12,854	8,780	6,355.1
4.75	2,432	2,211	2,509	3,791	3,618	4,818	3,599	9,116	4,655	7,478	4,422.7
5.75	2,282	2,597	2,218	3,415	3,687	4,789	4,741	8,550	4,051	6,920	4,325.0
6.75	1,700	2,608	1,992	3,954	3,723	3,996	4,015	7,138	3,461	5,437	3,802.4
7.75	1,202	2,375	1,445	2,708	3,225	3,364	3,579	5,020	3,011	3,708	2,963.7
8.75	726	1,495	1,016	2,063	2,398	2,702	3,700	3,559	2,607	2,232	2,249.8
9.75	423	934	746	1,406	1,900	1,975	2,879	2,292	2,008	1,313	1,587.6
10.75	236	624	546	859	1,022	1,460	1,819	1,485	1,294	728	1,007.3
11.75	182	354	360	468	644	1,117	1,246	974	690	570	660.5
12.75	60	169	184	261	413	561	619	668	463	325	372.3
13.75	46	69	149	132	226	266	269	381	221	219	197.8
14.75	31	94	99	91	162	163	162	192	156	119	126.9
15.75	9	55	48	44	94	56	94	100	109	45	65.4
17.25	16.2	76.3	51.5	57.6	137.0	84.8	149.9	50.2	69.1	49.8	74.2
19.25	1.4	41.1	12.2	29.2	45.7	25.0	13.0	28.1	34.5	16.1	24.6
21.25	1.8	27.5	4.4	4.9	14.9	--	7.7	11.0	9.5	13.6	9.5
23.25 and larger	--	25.4	17.1	--	13.0	--	7.5	5.8	4.0	--	7.3
Disintegrated	53	27	18	30	28	0	6	5	275	343	78.5
Total	12,450.4	19,218.3	18,641.2	30,396.7	30,224.6	32,904.8	31,568.1	61,041.1	47,357.1	49,485.5	33,328.8

TABLE 15

ANCHOVY LARVAE—OCCURRING ALONE (NO SARDINE LARVAE): AVERAGE NUMBER PER POSITIVE HAUL ($\times 10^2$), SUMMARIZED BY SIZE AND YEAR, 1951-60

Size class (mm)	Year										Un-weighted average
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	
2.5	607	1,994	2,273	3,343	3,269	2,646	3,945	3,459	3,417	6,711	3,166.4
3.75	607	1,371	2,521	2,739	4,324	3,685	4,250	2,975	3,490	5,077	3,103.9
4.75	536	984	2,640	2,109	2,502	2,392	3,394	1,958	2,277	3,794	2,258.6
5.75	713	1,037	1,748	2,187	2,774	2,206	2,786	1,888	2,071	3,158	2,056.8
6.75	867	930	1,479	2,054	2,148	2,896	2,709	1,663	1,904	2,551	1,920.1
7.75	529	740	1,107	1,579	1,645	2,678	2,267	1,485	1,559	1,766	1,535.5
8.75	342	536	855	1,133	1,286	2,205	1,670	1,168	1,088	1,214	1,149.7
9.75	254	384	657	694	838	1,827	1,117	820	828	873	829.2
10.75	167	250	390	458	604	1,225	670	568	579	557	546.8
11.75	129	187	243	335	299	658	397	363	348	366	332.5
12.75	82	119	114	229	175	362	241	214	239	231	200.6
13.75	42	76	70	132	105	175	137	121	173	145	117.6
14.75	27	50	37	82	58	84	87	87	112	115	73.9
15.75	23	38	26	51	33	50	44	56	89	65	47.5
17.25	12.7	56.5	30.6	32.4	42.4	50.8	48.3	71.6	96.0	85.8	52.7
19.25	5.5	22.4	12.6	21.0	15.7	44.5	17.6	29.4	38.5	39.8	24.7
21.25	2.9	17.7	8.7	4.2	4.2	3.5	12.1	8.3	9.9	8.9	8.0
23.25 and larger	17.3	8.1	10.0	6.1	7.0	9.3	6.6	2.4	2.8	13.1	8.3
Disintegrated	127	22	22	38	27	5	14	12	49	382	69.8
Total	5,090.4	8,822.7	14,243.9	17,226.7	20,156.3	23,202.1	23,812.6	16,948.7	18,370.2	27,152.6	17,502.6

fewer hauls (644). Some of the irregularities in this curve, compared with the other three, may be due to fewer data.

At first glance at the two curves for sardine larvae, one gets the impression that survival may have been somewhat better in the co-occurring hauls. On closer inspection however, it is seen that larvae larger than 6.75 mm followed no consistent trend, except as noted below. The greatest difference in relative abundance was between the smaller larvae (3.0–5.75 mm long) and all larger larvae. This difference could be interpreted as poorer initial survival of sardine larvae in situations where they occur alone. An equally logical explanation for the difference, however, is based on the increasing frequency of co-occurrences of sardine and anchovy larvae with increase in size. It was noted earlier that the frequency of co-occurrence of sardine and anchovy eggs was markedly lower than for larvae. A natural corollary is that newly hatched larvae of the two species would co-occur less frequently than the larger larvae. The effect on abundance curves would be to increase the numbers of larger larvae in hauls in which the species co-occurred than in hauls in which they occurred alone. Furthermore, the two curves for sardine larvae do converge if all larger-sized larvae (17.25–25.25 mm) are taken into account. As many larger larvae were taken in

hauls in which sardines occurred alone as in hauls in which both species occurred—0.73 larvae per haul on the average.

Thus, the basic question has been answered; better survival was not indicated by the hauls in which both species were caught even though average numbers of larvae per haul were larger.

Although the analysis has been confined largely to the 1950's, the report can be brought up to date. Tables 3 and 4 include the number of occurrences and co-occurrences of sardine and anchovy larvae during the first 3 years of quarterly cruises, 1961–63. Anchovy larvae occurred in 43 percent of the hauls in 1961, 49 percent in 1962, and 54 percent in 1963. Sardine larvae occurred in 5 percent of the hauls in 1961, 6 percent in 1962, and 9.5 percent in 1963. (Data for 1963 are not closely comparable to those for other years because a number of closely spaced in-shore stations were added.) Anchovy larvae occurred in nearly 90 percent of the hauls containing sardine larvae. In contrast, sardine larvae occurred in only 13 percent of the hauls containing anchovy larvae. Co-occurrences of anchovy larvae with sardine larvae were even higher than in the late 1950's, and even a higher percentage of the collections of anchovy larvae contained no sardine larvae. Anchovy larvae now seem to be completely dominant.

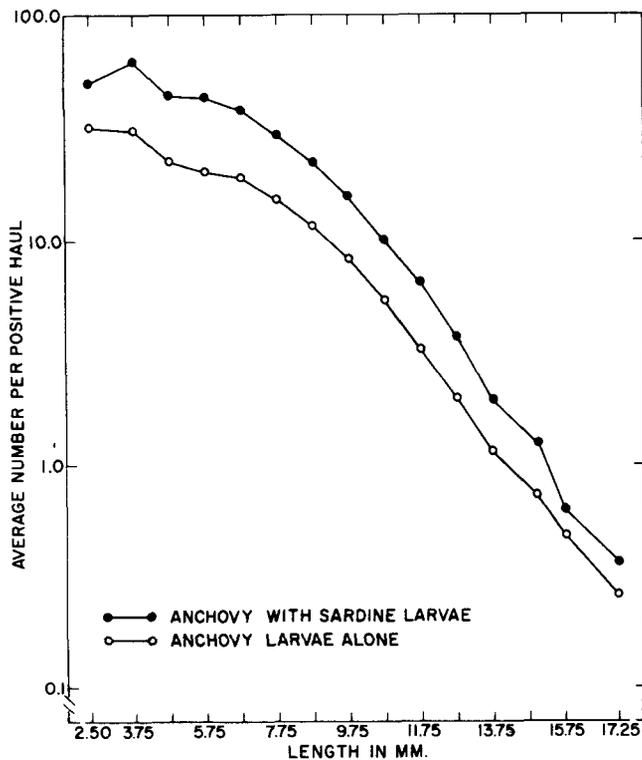


FIGURE 11. Comparisons of average number of anchovy larvae per positive haul as related to length (mm) for 1) hauls containing both anchovy and sardine larvae, and 2) hauls with anchovy larvae alone. Data for 1951–60 combined.

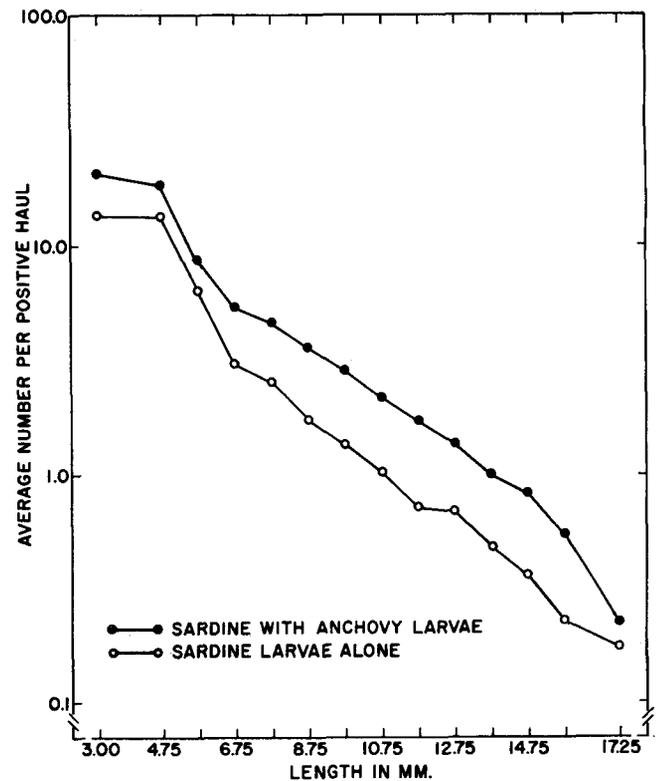


FIGURE 12. Comparisons of average number of sardine larvae per positive haul as related to length (mm) for 1) hauls containing both sardine and anchovy larvae and 2) hauls with sardine larvae alone. Data for 1951–60 combined.

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THE ACCUMULATION OF FISH DEBRIS IN CERTAIN CALIFORNIA COASTAL SEDIMENTS

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The fact that the remains of fish, such as scales and bones, are found in coastal marine sediments should, perhaps, not come as a surprise. Well preserved fish remains have been found in California marine sedimentary formations from Upper Cretaceous through Pliocene times. Furthermore, scales and bones of various species were reported in the surface sediments of the Catalina Channel by David (1947).

This paper presents some of the results of an initial attempt to study the distribution of fish remains at depth in the sediment. The discussion is limited to certain aspects of the distribution of fish scales. The main purpose of the paper is to point out the existence of material which could allow the introduction of a relatively long-time perspective into the character of the fisheries and oceanographic conditions off California.

The sediments used in the study were collected from the Santa Barbara Basin, off Santa Barbara, California. The basin has an oval configuration with the long axis parallel to shore. The sill depth is 475 meters and the area encompassed below sill depth is 600 km². The oxygen concentration at sill depth is about 0.4 ml/l. The oxygen concentration in the near-bottom water falls to 0.0 ml/l in the middle of

the basin at 580 meters, (Emery, 1960). The floor of this basin is an exception to usual basin floors. Here bottom-living animals and their sediment mixing effects have been consistently excluded by the virtual absence of oxygen in the bottom water. This anoxic water forms from the consumption of dissolved oxygen in the bacterial decomposition of organic matter, and the restriction of vertical circulation in the bottom waters. Thus sediments falling to the floor of the basin accumulate undisturbed and in serial order. There is evidence of occasional disturbance, but it is estimated that this amounts to a few percent of the total length. There are, however, slump or turbidite layers which constitute about ten percent of the core length. These are easily recognized by a marked color contrast at various levels in the cores.

Undisturbed sediments such as these provide an excellent framework for the study of ocean history. The absence of mechanical disruption allows the preservation of delicate organic remains such as the fish scales seen in Figure 1. The absence of mechanical disruption also preserves lithologic patterns. Major lithologic patterns, if they exist, allow physical correlation between adjacent cores. In addition if annual variations exist in the supply of certain components of

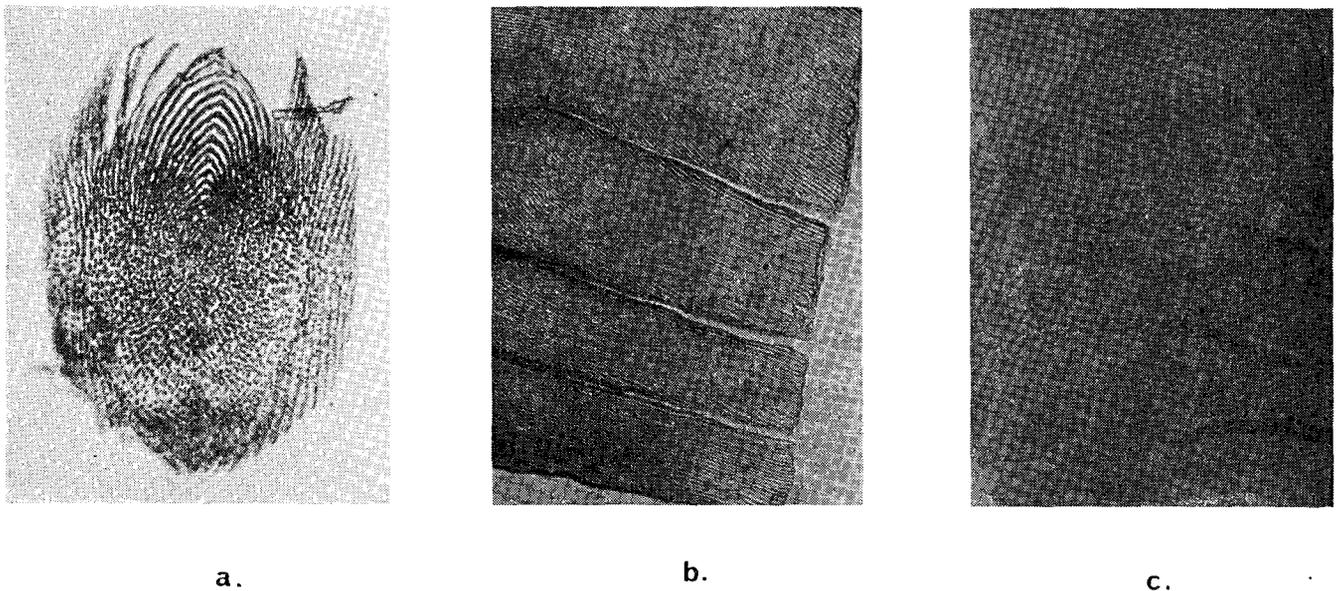


FIGURE 1. Representative fish scales found in the Santa Barbara Basin sediments.
a. Pacific hake, 72 centimeters below surface.
b. Pacific sardine, 89 centimeters below surface.
c. Northern anchovy, 79 centimeters below surface.

the sediment, for example a high contribution of land-derived detritus during a pronounced rainy season, then a yearly lithologic pattern may be preserved.

The existence of anaerobic conditions within the sediments must also contribute towards the preservation of organic remains. Anaerobic bacteria are unable to effect the breakdown of organic matter as completely as aerobic bacteria, and complex organic molecules are relatively immune from bacterial attack. Furthermore, anaerobic sediments appear to have a relatively high pH of about 8.0 thus insuring the preservation of inorganic carbonates and apatites, the latter being an important constituent of fish bones and scales, the former of fish otoliths.

The core samples used for this study were four cores obtained in the east central part of the basin, 34° 14' N; 119° 58' W, at a depth of 570 meters. The cores average 90 cm in length and have a combined area of 90 cm². The report of Emery and Bray (1962) provides the basis for estimating the age at the bottom of these cores at about 1000 years. The time equivalent of 1 cm, the subsampling distance, is then roughly ten years. For the purposes of this paper it will be assumed that a constant rate of sedimentation has prevailed. Preliminary examinations of laminae (yearly lithologic patterns) present in these sediments indicate this is a reasonable assumption.

The general procedure used in recovering fish scales and other coarse debris from sediment was the follow-

ing. The core was exposed and the main lithologic features noted. The core was then cut into one centimeter thick slices parallel to the stratification. The individual slices were placed in a 10 percent hydrogen peroxide solution for about one half hour in order to disaggregate the sediment. The resulting slurry was wet-screened through 0.5 and 0.06 millimeter mesh screens. Material such as scales, bones, and otoliths, was retained almost exclusively on the coarser screen. The scales were manually picked under a low-power binocular microscope and were permanently mounted on glass slides. Identification was made by comparison with a reference collection of scales assembled from the Scripps Institution of Oceanography Fish Collection.

The raw data from these cores is a centimeter by centimeter tabulation of numbers of scales. Three species have been identified and counted: the Pacific hake, *Merluccius productus*, the Pacific sardine, *Sardinops caerulea*, and the northern anchovy, *Engraulis mordax*. In these cores the three species account for 80 percent of the total scales.

By means of the correlation of lithologic patterns within the cores the data from the four cores have been projected into a single composite core. This procedure should emphasize scale abundance patterns over distances greater than the arbitrary sub-sampling distance of 1 cm. On the other hand, correlation errors should tend to mask abundance variations occurring at or near this distance. That is to say only abundance variations that are consistent for equivalent time pe-

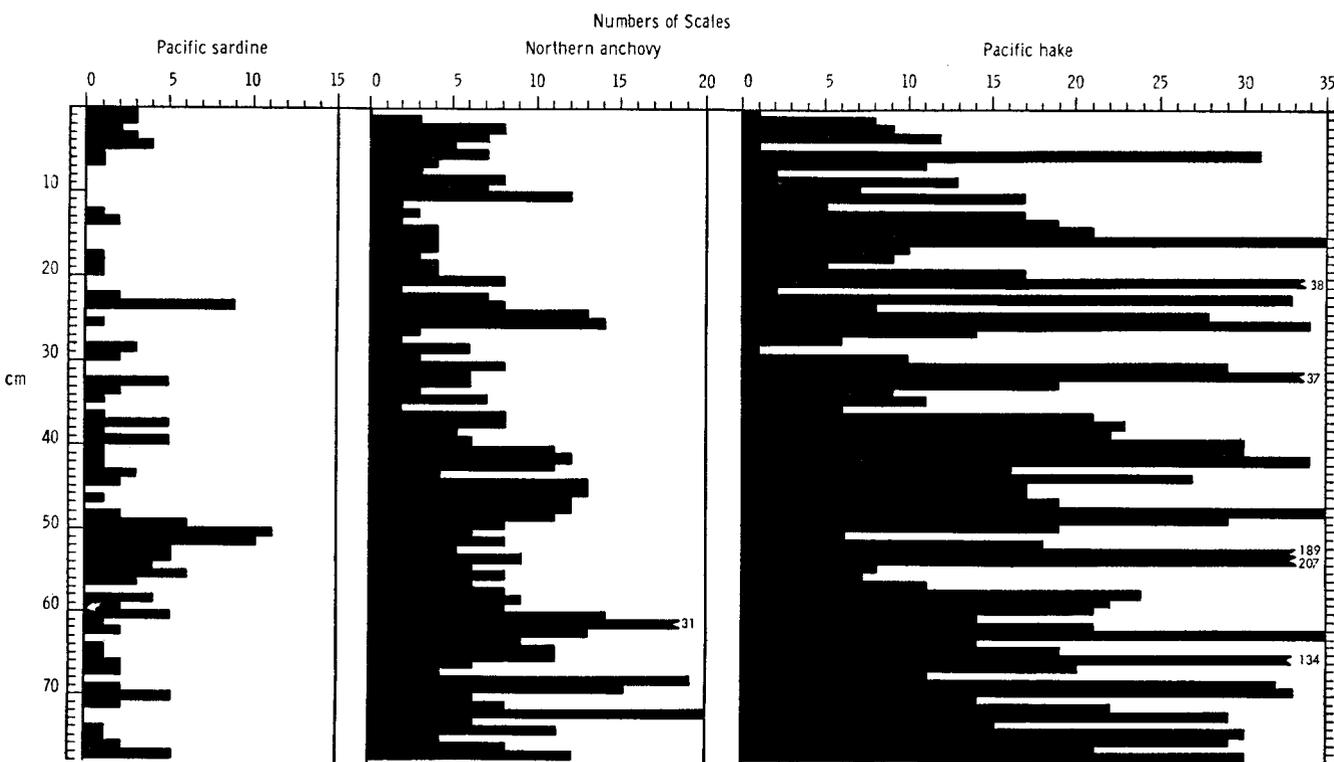


FIGURE 2. A plot of numbers of scales versus the core depth in centimeters. The occurrence of unusually high scale counts at a few centimeter levels in the case of the Pacific hake represents a high scale concentration in one of the four cores. In such cases the mean of the three other cores is taken to be more representative of the scale concentration at that level.

riods of over 50 to 100 years should be emphasized. The data have undergone a further modification in that only the finely stratified sediments have been retained for analysis. The intervening turbidite layers are assumed to have been quickly deposited and the top and bottom of such layers are considered isochronous.

The data for each of the three species are presented in Figure 2 as: a histogram plot of numbers of scales versus the centimeter depth in the core and in Figure 3 as a plot of cumulative numbers of scales versus the centimeter depth in the core. The numbers of scales are accumulated starting at the surface. If few scales are encountered in a region of the core, the slope of the cumulative curve will tend to the vertical, and if many scales are encountered the slope

of the cumulative curve will tend to the horizontal. In addition to the cumulative curves a representation of the frequency distribution for the three species is given in Figure 3. The presence of a number of scales in a centimeter section greater than or equal to the median number of scales per centimeter section is designated by a crossed square. An open square indicates a number of scales less than or equal to the median number. The median values of individual species are consistently included with the high or low value groupings to provide as even a split of the data as possible. In the case of the Pacific sardine and northern anchovy the median values are included with the low values group. In the case of the Pacific hake

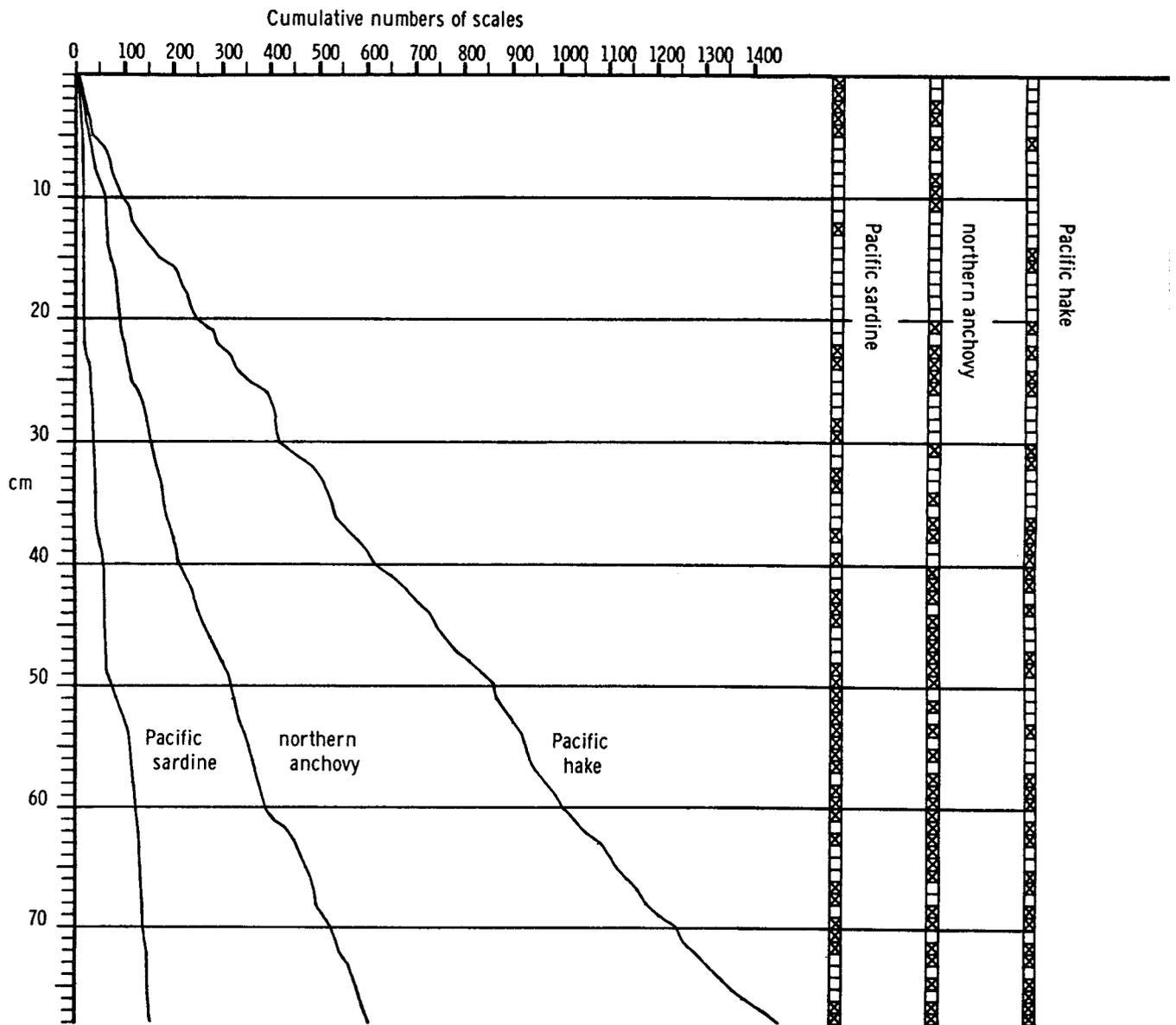


FIGURE 3. A plot of the cumulative numbers of scales of the Pacific hake, the northern anchovy, and the Pacific sardine versus the core depth in centimeters. A plot of the frequency relative to the median versus the core depth in centimeters. An open square indicates the number of scales for that centimeter is below or equal to the median number of scales per centimeter. A crossed square indicates a number of scales higher than the median number. Note—core length is foreshortened about 10 percent due to removal of turbidite layers.

the median values are included with the high values group.

The greatest number of scales that have accumulated in these sediments are those of the Pacific hake. A median number of 19 scales was found per centimeter; the total number encountered was 1430. The scales of the northern anchovy are next in abundance. The median number per centimeter was 7 and the total number was 605. The least abundant scales in these sediments are those of the Pacific sardine. This species has a median value of 1 scale per centimeter and a total number of 160.

An interesting aspect of the scale data is the sequential pattern accumulation. Inspection of Figure 2 shows that there are regions within the composite core where the abundance level of scale accumulation is consistently above or below the median value. This imparts a step aspect to the cumulative curves. In the case of the Pacific sardine steps in the cumulative curve indicating a marked increase in the level of abundance are present at 0-5 cm, 22-23 cm, 37-40 cm, and 49-50 cm. The latter step is by far the most pronounced. A number of steps are present in the cumulative curve of the northern anchovy notably at 7-10 cm, 2-28 cm, and 60-64 cm. The cumulative curve of the hake also shows a number of steps. It is instructive to note that the steps in the cumulative curve for each species do not necessarily occur at the same depths in the core. This suggests the steps in the abundance levels are probably not a reflection of changes in the rate of sedimentation.

The frequency curve representation in Figure 2 provides a convenient basis for an objective analysis of the sequential pattern of scale accumulation. Miller and Kahn (1964) suggest the runs test of Wallis and Roberts (1956) may be applied to test for non-random tendencies in geologic time series such as this. In a random pattern the probability that a data point will be above the median value is one half; the probability of a data point being below the median value is similarly one half. This leads to the expectation that the number of consecutive data points (runs) above and below the median will be $n/2 + 1$ where n is the total number of data points. The departure from randomness of a series can be tested by the standard

normal deviate of Wallis and Roberts. Applying this procedure to the scale data one finds the number of runs in the case of the Pacific hake is 32, in the case of the northern anchovy 36, and for the Pacific sardine 27. The expected number of runs is 40. The associated probabilities, that is, the probabilities of random series having an equal or greater number of runs are: the Pacific hake 0.26, the northern anchovy 0.22, and the Pacific sardine 0.005.

This analysis of the scale data implies that the scale abundances of the Pacific sardine are aggregated at certain levels of the core. Such a pattern of aggregation suggests changes in the abundance of the source of these scales. That is, over the last 1000 years the scales of the Pacific sardine found in these sediments seem to reflect periodic changes in the abundance of the Pacific sardine. Although similar abundance changes at specific levels in the core can be noted in the case of the northern anchovy and the Pacific hake, the runs analysis suggests that in the case of these two species there is not a marked tendency towards aggregation in time.

In summary, it may be inferred that relative to the Pacific sardine there has existed for the past 1000 years a more constant supply of northern anchovy and Pacific hake scales to these sediments.

This paper represents one of the results conducted under the Marine Life Research Program, the Scripps Institution of Oceanography's part of the California Cooperative Oceanic Fisheries Investigations, which are sponsored by the Marine Research Committee of the State of California. Acknowledgment is also made to Professor John D. Isaacs for the stimulation of this study.

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PART III
SCIENTIFIC CONTRIBUTIONS

THE PELAGIC PHASE OF *PLEURONCODES PLANIPES* STIMPSON (CRUSTACEA, GALATHEIDAE) IN THE CALIFORNIA CURRENT

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INTRODUCTION

The planktonic habit may be prolonged into or recur in the adults of two species of Galatheidæ. Harrison Matthews (1932) uses the terms "lobster-krill" or "whale feed" in reference to these: *Munida gregaria* (Fabricius) of southern South America and of New Zealand, and *Pleuroncodes planipes* Stimpson the red or pelagic crab of California and Mexico. Both occur at times as conspicuous concentrations of apparently adult crabs on which baleen whales are known to browse (Harrison Matthews, 1932); in addition, the studies of McHugh (1952) and Alverson (1963) on the tuna *Thunnus alalunga*, *Katsuwonus pelamis* and *Thunnus albacares* have shown that *Pleuroncodes* is a significant food item during their summer migration into the California Current; for *Thunnus* the pelagic crab may form up to 85% by volume of all stomach contents from certain areas during this period.

In addition to the normal methods of nutrition of galatheids (Nicol, 1932) both species of pelagic crabs are able to graze on phytoplankton by filtration; recorded by Matthews (1932), Beklemishev (1960) and Boyd (1963), this ability has been confirmed by studies at this laboratory which will be reported elsewhere.

The filtration mechanism is based on the highly setose second maxilliped which in post-larval *Munida* is very highly developed and distinguishes the *Grimothea* stage, in *Pleuroncodes* no such post-larval stage occurs and pelagic and benthic individuals are apparently indistinguishable from one another.

By its ability to graze, at least at times, on the phytoplankton, thus forming a rather direct link between primary production and commercially important predatory fish, *Pleuroncodes* merits study and it is the purpose of this paper to present a synthesis of the presently available data concerning its distribution in the California Current system. It is hoped that this may contribute to an understanding of the late summer "local banks" fishery for tuna in which the pelagic crab forms the dominant item of forage.

This study is based upon data from the regular pattern of stations of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) which are now available for a period of a decade and a half. Designed primarily to investigate the biology of the clupeid stocks of the California Current, these investigations included at every station a standard haul to

140 meters with a 1-meter zooplankton net; details of the sampling procedure and of the location of stations are described elsewhere (e.g. Ahlstrom, 1948; CalCOFI, 1963).

The data consist of records of the numbers of pelagic crabs removed in the laboratory from each zooplankton sample before voluming, and these numbers were extracted for the present study from the original data sheets. The actual specimens had neither been measured nor were subsequently retained except during 8 months of 1960 when the whole catch of pelagic crabs was measured by Boyd (1963) who recorded a range in standard carapace length of from 7 to 20 mm; it has been assumed here that the CalCOFI data to be discussed refer only to subadult and adult crabs within this size range.

A zooplankton net is not an ideal collecting instrument for pelagic crabs since a degree of avoidance certainly occurs, and for this reason the data have been used, as far as possible, non-numerically; because the number of individuals per haul is generally rather small and because the hauls are standardized, the data have not been transformed to numbers per standard volume.

There is no evidence to suggest that crabs in the pelagic phase migrate diurnally so that a population would descend during part of the day below the 140-meter level normally sampled, and although the data of Boyd (1963) and from recent work of this laboratory off Baja California suggest that diurnal migration may occur, it probably consists primarily of a withdrawal from only the upper tens of meters of water during daylight hours.

The present study was restricted, for practical considerations, to the years 1955-1962 inclusive, thus covering the end of the long and stable cool period which extended from the late 1940's to 1957 (Reid, 1960) and the years 1958-1959, when altered circulation in the California Current brought warmer conditions and an influx of southern organisms; also covered is the period of return to the more usual conditions which have subsequently persisted until the present.

GENERAL DISTRIBUTION IN THE INSHORE AREA

The CalCOFI stations fall into two groups: those inshore of station 70 on each line, which were worked at monthly intervals and extend (Figure 1) about 150 miles seawards between Point Conception and Cabo San Lucas; and those further offshore which

¹ Contribution from Scripps Institution of Oceanography.

were worked much less frequently and extend a further 150 miles seawards. These are referred to as the inshore and offshore areas, respectively.

In a consideration of the overall distribution of pelagic crabs within the inshore area, account must be taken of the change in distribution of many species in this area in 1958-1959 compared with the previous decade; these changes and the physical phenomena associated with them were discussed at the Rancho Santa Fe symposium (Sette and Isaacs, 1960) and subsequently Radovich (1961), Glynn (1961), and Boyd (1963) presented observational data which indicated that *Pleuroncodes planipes* was one of the species involved.

For the present purposes, therefore, two 3-year periods were considered separately and the percentage frequency occurrence of *Pleuroncodes* at each

station was calculated for each period. These data are presented in Figure 1 for the periods 1955-1957 and 1958-1960 inclusive, and despite the considerable differences in the latitudinal distribution between the two periods certain common features appear. In particular, there appears to be a correspondence between the distribution of crabs and the general distribution of upwelled water derived from coastal upwellings.

Coastal upwelling is known to occur, mainly in the first half of the year, at a number of points along the coasts of southern and Baja California (Reid et al., 1958), and examination of the charts of surface isotherms from CalCOFI cruises shows that it occurs most strongly at Cabo Colnett, Punta San Eugenio and Cabo San Lazaro (e.g., CalCOFI, 1963), and within the bights which lie to the south of these capes. It has been shown (Sverdrup et al., 1942) that

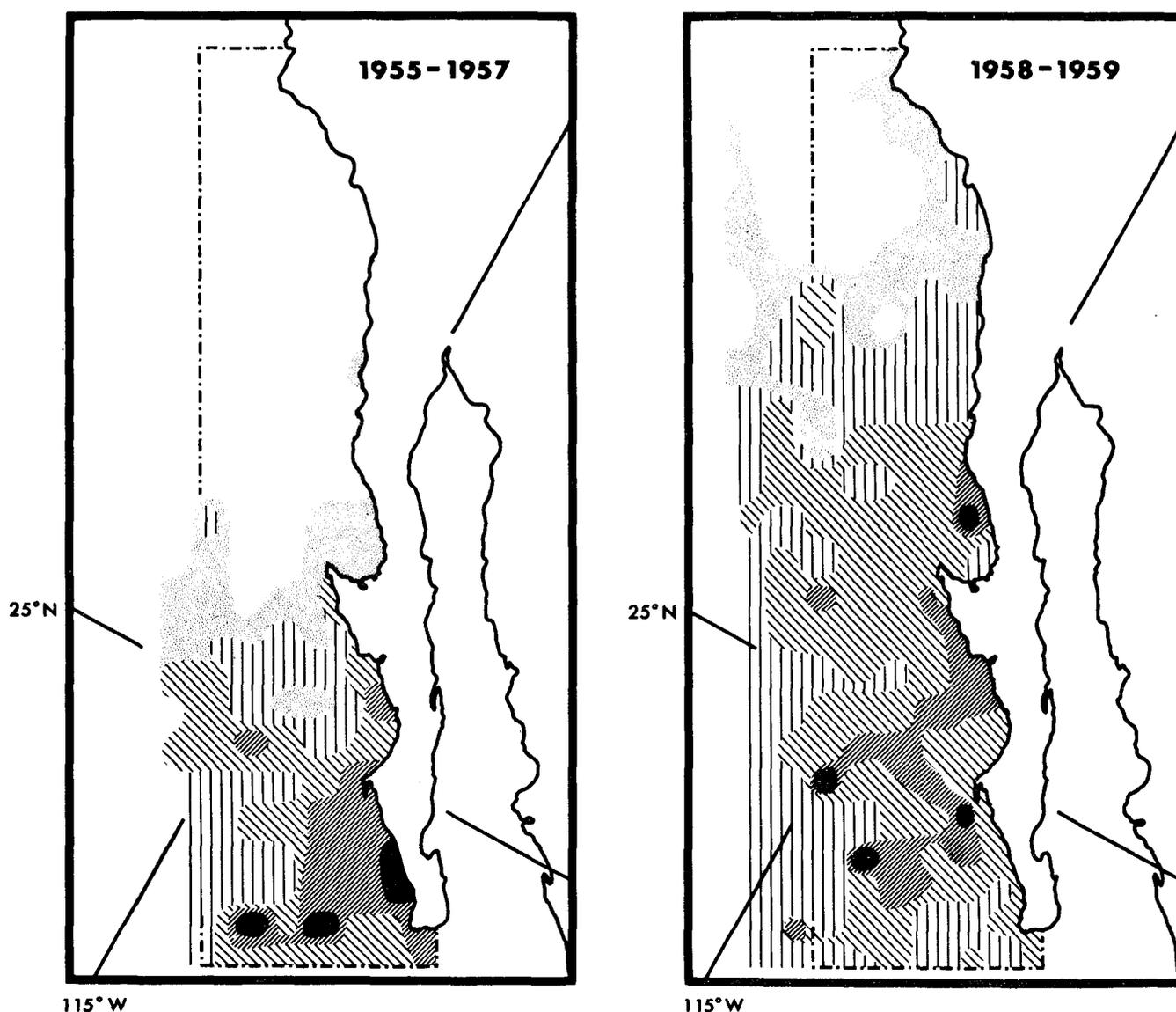


FIGURE 1. The percentage frequency of occurrence of adult *Pleuroncodes* at each of the CalCOFI inshore stations, data combined for the periods stated; the intensity of the shading is proportional to the percentage frequencies of occurrence, at the following intervals: 1-10%, 11-25%, 51-75%, 76-100% occurrence.

the water upwelled at the coast in the California Current drifts southward away from the coast as discrete tongues of cold surface water, and such tongues have been observed from Baja California coastal upwellings during the 1964 Scripps tuna oceanography studies (Scripps Institution of Oceanography, 1965). These studies have shown that biota, particularly phytoplankton, are more abundant in the upwelled water than elsewhere off this coast; examination of the charts of areal zooplankton abundance from the CalCOFI cruises (e.g., Thrailkill, 1956) confirm this statement.

Figure 1 shows that the highest frequencies of occurrence of *Pleuroncodes* during both periods studied appear to conform to the same pattern; that is, the highest frequencies are coincident with those areas expected to be most often occupied by recently upwelled water; during the 1964 cruises referred to above, the distribution of pelagic crabs could be

related quite closely to tongues of upwelled water (Blackburn, pers. comm.), thus confirming the general pattern revealed in Figure 1.

Pelagic *Pleuroncodes* are very patchily distributed and are occasionally encountered in very dense and extensive concentrations at or near the surface; it has been assumed that all CalCOFI hauls containing more than 50 crabs indicate the existence of such a concentration, since such numbers were taken in only 36 of the total of about 1500 zooplankton hauls studied; obvious concentrations tended to be avoided during sampling, so these data are minimal. The distribution of these 36 stations are shown in Figure 2 from which can be seen that these are situated mainly within the influence of upwelled water originating near the major capes of Baja California; thus, in this situation not only are pelagic crabs more frequently encountered as isolated individuals than elsewhere, but also as dense surface shoals.

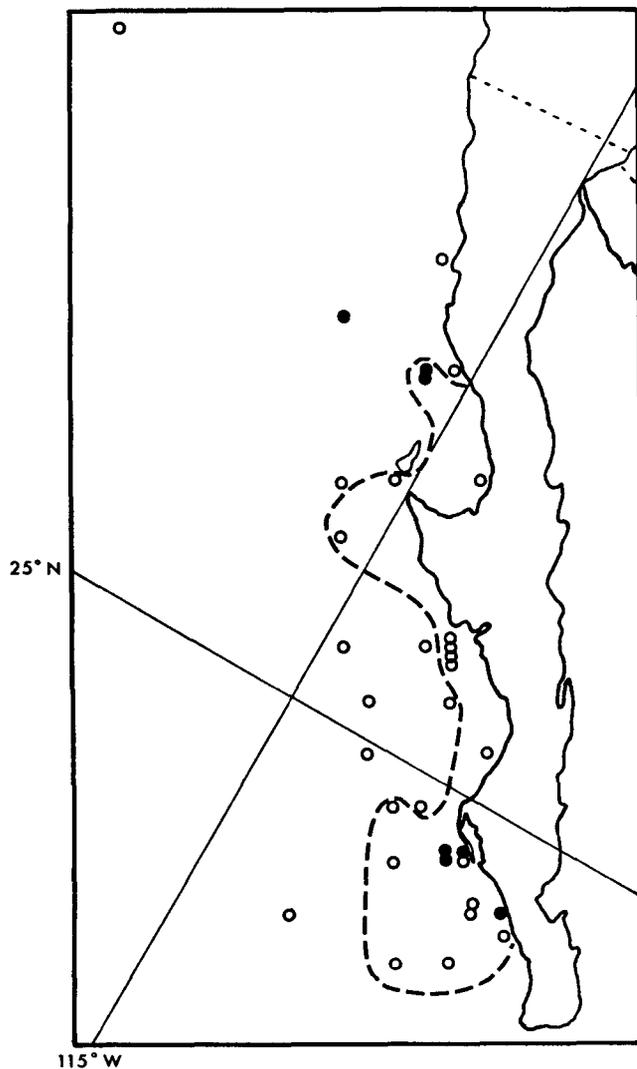


FIGURE 2. Distribution of all occurrences of more than 50 *Pleuroncodes* per haul; the line encloses all stations in the first half of the year showing that these tend to be closer inshore. Closed symbols, stations at which more than 100 crabs taken per haul.

DISTRIBUTION IN OFFSHORE AND OCEANIC AREAS

Within the CalCOFI offshore area less than 500 stations were worked during the 8-year period and at only 52 of these were pelagic crabs taken in the zooplankton tows; the temporal distribution is shown in Table 1 and the distribution spatially in Figure 3. Occurrences were restricted, in the main, to an area off Punta San Eugenio and to the years 1958-1960.

The between-years variation is very much clearer in these data than is the within-year variation which, if

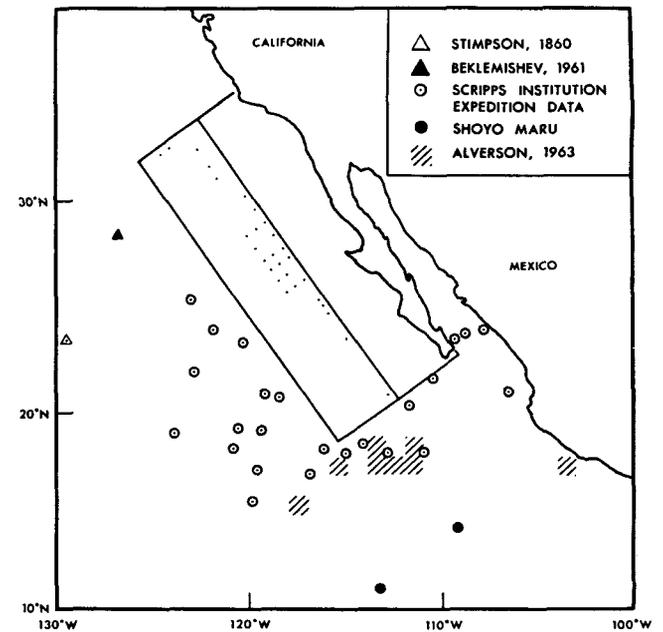


FIGURE 3. Distribution of *Pleuroncodes* in the offshore and oceanic area; the stations within the CalCOFI offshore area (indicated by a rectangle) at which the species occurred within the years 1955-1960 are shown by dots. The SIO expedition data includes the following cruises: Tethys, MidPac, Tuna Spawning, TO-58-1, TO-60-2 and La Pared.

it can be demonstrated, consists of a tendency for records to occur during the first 6 months of the year; this is difficult to determine with certainty because of the relatively low sampling intensity after July in each year. More than 50% of the occurrences were, in fact, restricted to the period January-June of 1959, a period during which particularly active northward movement of pelagic individuals was taking place within the inshore area.

Beyond the CalCOFI station pattern there are records of the occurrence of pelagic crabs from expedition results, although here the station density is even lower than in the CalCOFI offshore area; the known records from such sources are set out in Figure 3, which shows that these extend to about 1,000 miles offshore to the south-west of Baja California. There are several records from as far south as the Islas Tres Marias, but to the south of these islands only a single record exists, from the stomach contents of a single yellowfin tuna (Alverson, 1963). Records within the Gulf of California, where a population is known to exist (e.g., Boyd, 1963), are not shown in Figure 3.

It can be deduced from the data of Alverson (1963) that the relative frequency of occurrence of *Pleuroncodes* in the oceanic area is much less than closer to the coast; he recorded frequencies of occurrence of 88.2% in the inshore area compared to only 32.3% around the Revilla Gigedo Islands and even smaller frequencies south of the Gulf and off the Mexican west coast. Blackburn (MS) indicates lower volumes of *Pleuroncodes* per micronekton net haul in the oceanic area as compared with closer to Baja California.

Much further to the west, in the region of the Hawaiian Islands, there have been many investigations of the distribution of zooplankton and micronekton (e.g., King & Iverson, 1962) but apparently there are no records of the occurrence in the Central Pacific Ocean of pelagic *Pleuroncodes*; the question of the status and fate of the stocks in the oceanic areas of the Eastern Pacific will be discussed later.

VARIATION WITHIN YEARS, INSHORE AREA

The data are not entirely adequate for an analysis of seasonal variation of the distribution because the sampling frequency in the second half of the year was considerably lower than during the first half, particularly in the southern part of the inshore area. For example, no stations were worked in November south of Cabo Colnett from 1955-1960, and none during December from 1956-1960.

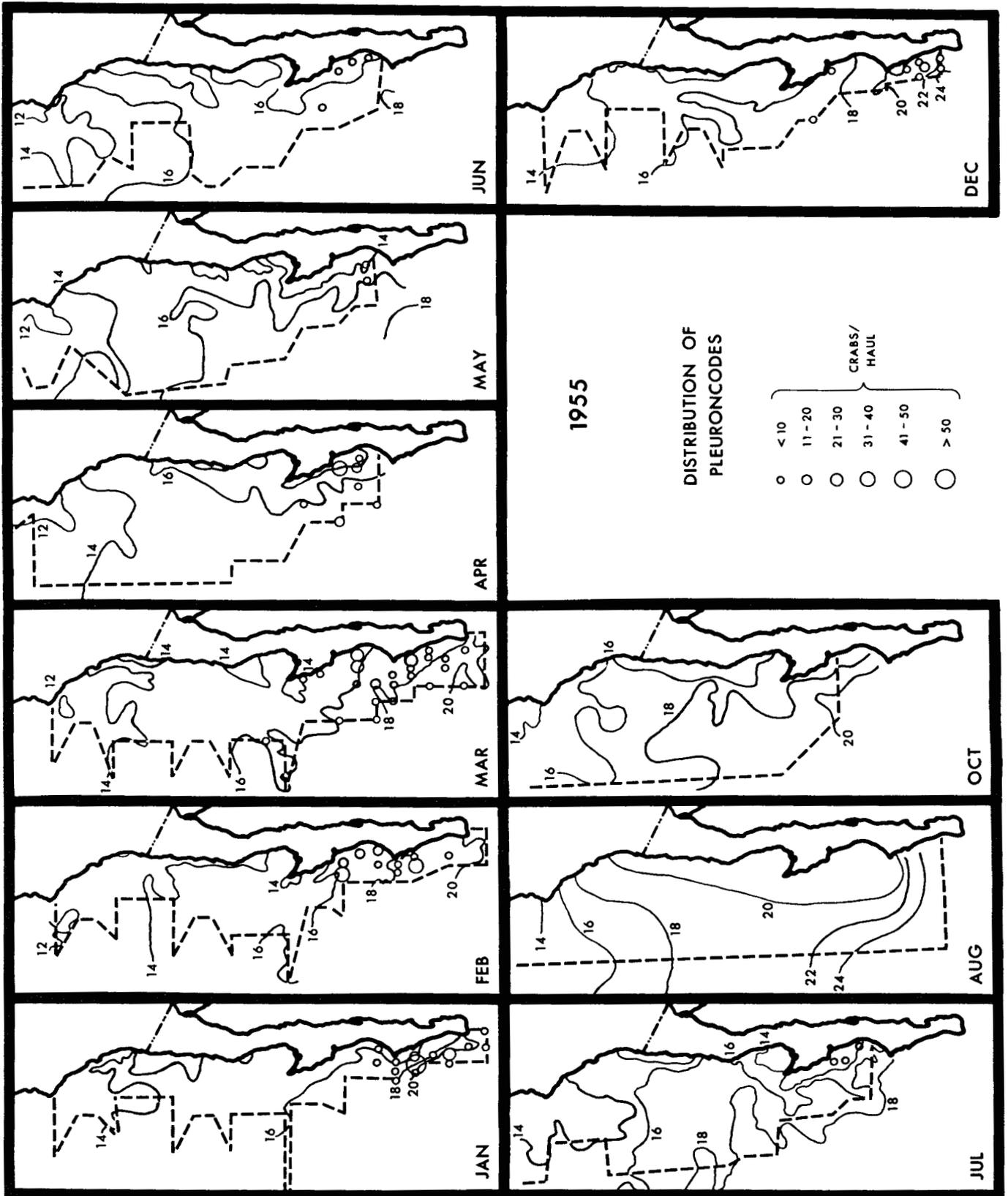
Within these limitations, the data indicate that pelagic crabs may be encountered in any month in the inshore area and that their occurrence follows no very clear seasonal cycle; this can be seen in the data from the years 1955 and 1958 (chosen because of relatively complete sampling coverage) presented in Figures 4a and 4b. It is possible (Figure 5) that, as in the offshore area, lower frequencies of occurrence may be found in the period August to December in some years, but the evidence is inconclusive.

That a seasonal cycle of occurrence should be difficult to demonstrate is perhaps not surprising in view of the marked eurythermy of *Pleuroncodes*. Table 2, which summarizes all records of the benthic phase of the species for which there are also environmental data, shows that temperatures down to 9.0° C. are tolerated, while Table 3 indicates that temperatures up to 28.0° C. are tolerated in the pelagic phase. The demonstration in Figure 4, therefore, that the distribution of pelagic crabs was apparently unaffected by the passage of the 16-24 °C. isotherms through the area in which the crabs occurred is not surprising, and suggests that some factor other than temperature must be the direct determinant of distribution patterns and cycles.

The role apparently played by upwelled water in determining the distribution of the pelagic phase suggests that the occurrence of the upwelling phenomenon itself may be correlated with the occurrence of pelagic crabs, and this hypothesis was tested in an area to the south of Punta San Eugenio. The occurrence of coastal upwelling can be determined most simply by the presence of surface isotherms running parallel to the coast, indicating an offshore tempera-

TABLE 1
 OCCURRENCES OF PELAGIC CRABS IN CalCOFI OFFSHORE AREA (STATIONS WEST OF .80 ON LINES SOUTH OF 110); FOR EACH YEAR
 COLUMN A = NUMBER OF POSITIVE OCCURRENCES, B = NUMBER OF STATIONS WORKED

	1955		1956		1957		1958		1959		1960		1961		1962		1955-1960 % occurrence
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
January	--	3	--	1	--	--	--	3	7	16	4	13	--	13	1	16	26.7
February	--	4	--	--	--	3	--	4	1	4	2	6	--	--	--	--	14.3
March	--	4	--	3	--	1	--	4	3	6	1	6	--	--	--	--	16.7
April	--	1	--	5	--	12	--	17	6	16	2	12	1	18	4	20	12.9
May	--	6	--	6	--	6	2	12	3	12	--	4	--	--	--	--	10.9
June	--	6	--	6	--	12	--	--	6	4	1	4	--	--	--	--	21.9
July	--	6	--	5	2	11	1	6	3	12	--	9	--	20	--	14	7.2
August	--	--	--	--	--	--	--	--	--	12	--	--	--	--	--	--	(+)
September	--	--	--	--	--	--	--	--	--	4	--	--	--	--	--	--	(+)
October	--	4	--	--	--	10	3	11	--	8	--	--	--	20	--	18	4.2
November	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
December	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	(+)
% occurrence	0.0		0.0		3.6		10.5		31.7		18.5		1.4		7.3		



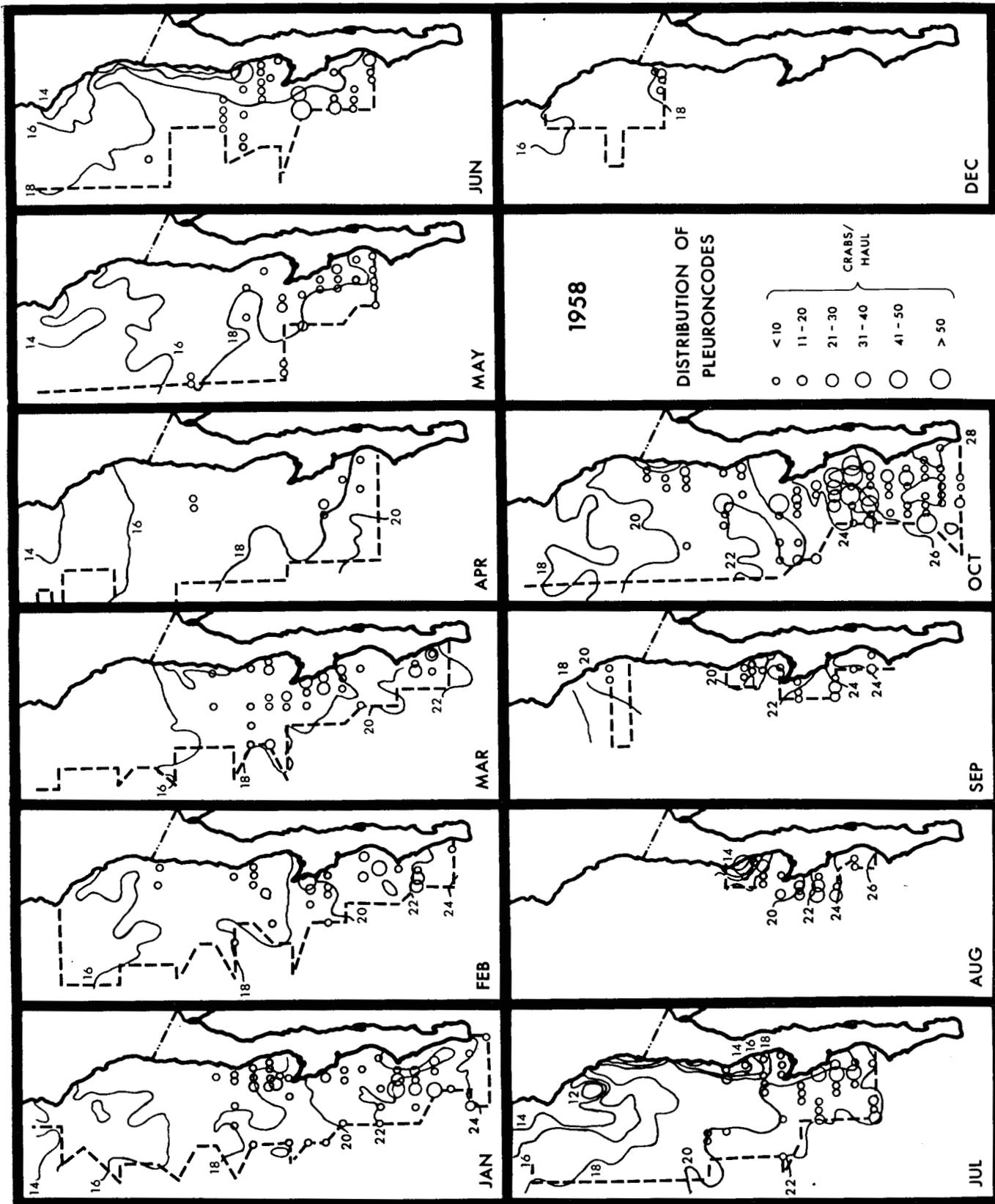


FIGURE 4. The distribution of *Pleuroncodes planipes* and certain surface isotherms monthly during the years 1955 and 1958. The region enclosed by the dotted line is that sampled during each cruise.

ture gradient; the temperature differences between two stations (127.34 and 127.40) off Punta San Eugenio was determined and from it was derived a monthly index of the intensity of upwelling at this cape.

These indices were then compared with the occurrence of red crabs in the upwelled water by reference to the numbers of occurrences and relative abundances per month at a small grid of seven stations to the southeast of the cape in the direction presumed to be taken normally by recently upwelled water. This investigation showed the regularity of the seasonal upwelling cycle from April until about July or August and also that the annual variation of frequency and abundance of crabs to have been far

greater than any seasonal variation. The regression between upwelling and frequency and abundance of pelagic crabs indicates a zero correlation.

VARIATION IN THE DISTRIBUTION BETWEEN YEARS

Observational data which showed that *Pleuroncodes* was included in those species which extended their range to the north during the period 1958–1959 has been presented by Berner (1960), Radovich (1961), Glynn (1961), and Boyd (1963); these data are summarized below:

December 1957—*Pleuroncodes* present off La Jolla.
April 1958—Present off Monterey.

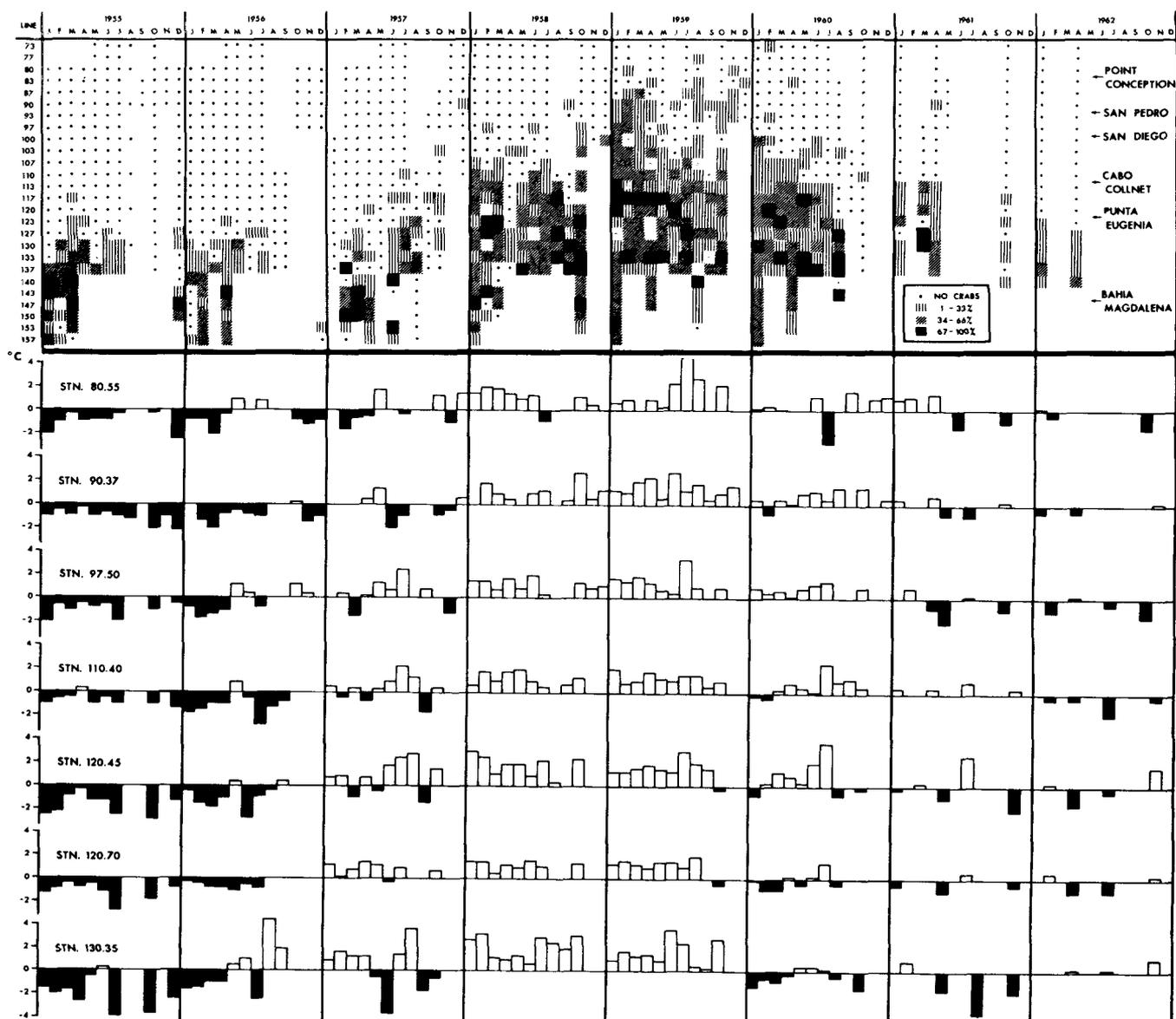


FIGURE 5. Monthly percentage frequency of occurrence of *Pleuroncodes* by station lines during the period 1955–1960 to show the northern range extension of the species during the warm years. The lower section of the figure indicates the temperature regime in terms of variation from the 6-year mean of stations selected as representative of conditions in the California Current between Cape San Lucas and Point Conception.

in the temperature regime, there are reasons to doubt a causative relationship even though this was implied by Radovich (1961); the area off Baja California to which the species was previously restricted was occupied throughout the period of northern range extension by apparently non-migratory crabs, and it is in any case doubtful if temperatures higher than those shown by Table 3 to be tolerated by pelagic crabs would have been encountered in the normal southern range of the species. Further, there is other evidence to show that organisms with little or no mobility were also involved at this time in the general northern movement of southern forms (Berner and Reid, 1961; Radovich, 1961).

Some mechanism beyond simply an ameliorating temperature regime is therefore required to explain these migrations, and this is to be found in the changes in the advective transport of surface waters which occurred in the California Current at this time (e.g., Sette and Isaacs, 1961). Although the 200 m flow is to the northward along Baja California and southern California throughout the year (Reid et al., 1958), the transport of adult pelagic crabs is presumably mainly in the mixed layer which flows predominately towards the south; there are four features of the California Current system (Reid et al., 1958, 1961) which *prima facie* seem to be relevant to the distribution of pelagic crabs: the Davidson Current, a northward coastal flow in winter which is effective only to the north of Point Conception; the great eddy south of Point Conception which leads to onshore flow throughout most of the year near Ensenada at around 32°N. and consequently to flow north and south from this point along the coast, reaching south to the region of Bahia Sebastian Vizcaino; the countercurrent which develops in winter along the coast of Baja California from Cabo San Lucas north to Punta San Eugenio where it meets the southerly flow from Ensenada; finally, the overall southward drift of the main current offshore of the above features.

In particular, the normally year-round coastal flow to the south between Ensenada and Punta San Eugenio as a consequence of the Point Conception gyre is probably of great significance in preventing the northward transport of southern species by the coastal countercurrents.

Examination of the charts of geostrophic flow for this area in the mimeographed CalCOFI data reports indicates that throughout 1955 and 1956 the situation was as described above; however, in the second half of 1957 a different pattern appeared; in July, for the first time, the whole coast from Bahia Sebastian Vizcaino north to San Diego was occupied by very disturbed flow containing a series of eddies which appear to have been capable of some transport towards the north, a situation already invoked by Johnson (1960) to explain the northward movement of phyllosoma larvae at this time; again, in October and December 1957 and in January 1958 the eddy extended unusually far south and close to the coast so that northward coastal flow effectively bridged the gap in northward flow from Punta San Eugenio. These data indicate that the correspondence between the start of range

extension of pelagic crabs and the appearance of conditions of flow which could transport them northwards from Punta San Eugenio is very good; the flow to the north in the permanent eddy and in the winter countercurrent north of Point Conception are sufficient explanation of transport further to the north once the latitude of San Diego is reached.

During early 1958 there is little evidence of coastal flow to the north except that connected with the permanent eddy, but in October, in the month in which it has been suggested above that northward movement of crabs began again, possibilities of such transport recurred; the permanent gyre extended very far to the south, at least to 29° 30' N. and was very close inshore at its southern end so that it produced coastal northern transport again from Bahia Sebastian Vizcaino; such transport was then continuous from this latitude to beyond Point Conception, where Davidson Current conditions were in effect. This situation coincided with the first reports of mass strandings at San Pedro.

Once again, in 1959 the same pattern was repeated: from June to September the permanent eddy extended further south than usual and the northward turn of the onshore flow occurred close to the coast, thus placing the beginning of northward flow farther south than usual; additionally, as in July 1957, the appearance of active eddies as far down as Bahia Sebastian Vizcaino gave further possibilities of northern transport. These eddies were contemporaneous with an active countercurrent south of Punta San Eugenio in August, and with Davidson Current conditions in the north from July until January 1960, in which month the final strandings of *Pleuroncodes* occurred in Monterey.

During April 1960, for the first time since the start of this series of observations in 1955, the eddy was so reduced as to be absent from the charts of geostrophic flow which thus showed an uninterrupted southward drift along the whole coast, including the bight to the south of Point Conception, from the latitude of Monterey south to Baja California del Sur; this pattern was repeated in July of the same year and suggests a mechanism which could flush the area north of Bahia Sebastian Vizcaino once more clear of *Pleuroncodes*—a flushing which certainly occurred during this period.

During the rest of 1961 and throughout 1962 the conditions returned to normal and it has been shown already that in these years *Pleuroncodes* was scarcely recorded north of the gap in the coastal countercurrent.

The two oceanic records in April 1958 referred to above may be explained, perhaps, by the same mechanisms as that suggested by Berner and Reid (1961) for occurrence of *Doliolum denticulatum* in the same area at the same time—by the southwesterly flow of a tongue of inshore water from an upwelling on the California coast to the north of Point Conception; it is likely that examination of the zooplankton from these stations would show the presence of a number of southern organisms.

While the oceanographic data are not complete and their correlation with the distribution of *Pleuroncodes* not devoid of subjectivity the correspondence certainly suggests that the circulation as indicated by charts of geostrophic flow is sufficient explanation of the major between-years variation in the distribution of *Pleuroncodes* during this period.

ECOLOGY OF THE PELAGIC PHASE

In the foregoing discussions *Pleuroncodes* has been considered as if it were a normal planktonic species, but it is also a very abundant member of the benthic community at 75–300 m along the continental edge of the west of Baja California, within the Gulf of California and on the west coast of Mexico south to the Islas Tres Marias (Boyd, 1963; Parker, 1963; Perkins, pers. comm.); the known distribution of the benthic phase is shown in Figure 6. If individuals have the capacity to alternate from benthic to pelagic phase and vice versa, a mechanism exists which could explain the irregularity of occurrence of the pelagic

phase in the plankton record through the individuals settling on, or leaving, the deposits.

The evidence to support this hypothesis is rather slight, however, and comprises mainly the demonstration by Boyd (1963) that the benthic stock in the area south of Punta San Eugenio examined by him overlapped in length frequency distribution with the pelagic stocks; only at the deepest station at which red crabs were taken by him was the modal length of the stock larger than had been recorded for individuals in the pelagic phase, so that by this criterion only at the deepest station was the population composed of individuals which must have finally settled into the benthic environment. Additionally, the hypothesis of alternation between the two phases is supported by the lack of morphological differentiation between pelagic and benthic individuals: benthic crabs retain the natatory setae fringing the appendages, and pelagic crabs retain the generalized form of the second maxilliped necessary for benthic existence, and only achieved in *Munida gregaria* after the pelagic *Grimothea* stage settles finally into the benthos.

While this is not, of course, direct evidence that alternation between the two phases occurs, it implies that such alternation is not impossible on morphological grounds, and that the pelagic phase is in some way comparable with the *Grimothea* of *Munida* thus being a post-larval extension or recurrence of the planktonic habit of the larvae, which in *Munida gregaria* is variable in duration, and hence in size attained, within rather wide limits (Harrison Matthews, 1932). It is postulated that in *Pleuroncodes planipes* the pelagic phase is comparable with the *Grimothea* stage, and that the lack of morphological specialization enables an individual, when the environment permits, to alternate between pelagic and benthic phases.

It is critical to a discussion of the ecology of the pelagic phase that its duration in the life of an individual should be established. Boyd (1963) inferred from his data on size distribution of benthic and pelagic stocks that the former contains individuals older than 2 years, while the pelagic individuals measured by him were only from 6 to 18 months old. From these data he inferred that it is only at carapace length of 25–28 mm, or about 2 years old, that the pelagic phase is finally abandoned.

A pelagic existence lasting 2 years renders it unlikely that an individual would be maintained throughout this period within the inshore area without being flushed seawards on the southwesterly flow of the California Current, and this could perhaps only be avoided if a considerable part of the period was spent temporarily in the benthic community. The distribution of pelagic crabs in the offshore and oceanic area (Figure 3) indicates that some flushing of individuals from coastal areas does occur.

Although relatively few individuals from the offshore and oceanic areas are available for study these suggest that such populations are mainly of small

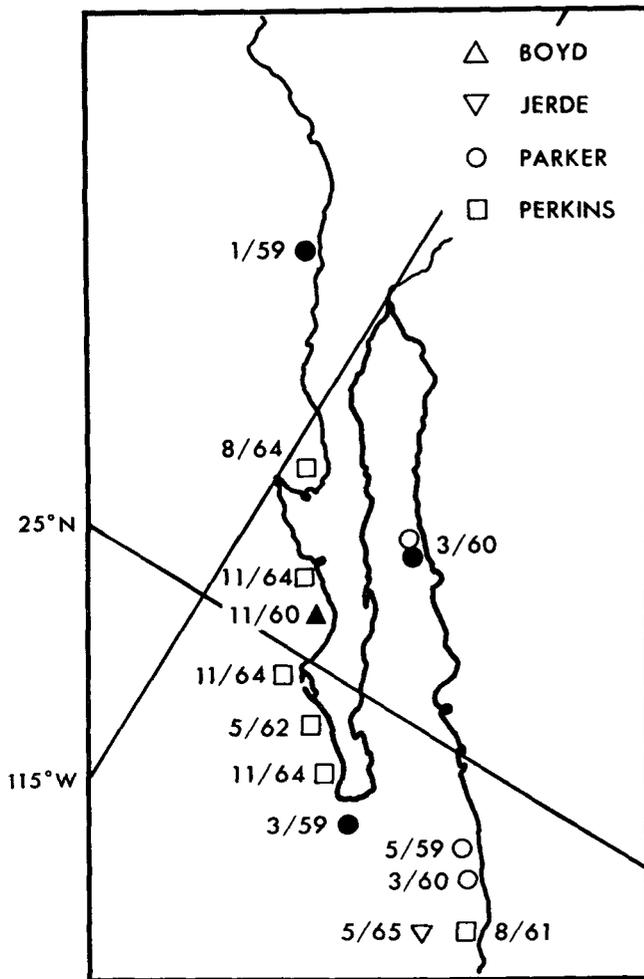


FIGURE 6. Distribution of the benthic records of *Pleuroncodes*; closed circles indicate the use of gear, such as a grab, in which there can have been no possibility of the crabs entering the gear in midwater.

individuals less than 1 year old. Thus, samples taken in July 1957 by the IATTC/STOR Tuna Spawning Survey around the Revilla Gigedo Islands showed a unimodal population having a modal length of 6 mm, while at Clarion Island the same population was present, but mixed with a second population, comprising less than 10% of the total, having a modal length between 10–12 mm. At Morgan Bank and at the Alijos Rocks the larger of these two size-groups was dominant and included more than 90% of the individuals.

Similarly, during the April 1965 La Pared expedition of SIO, the population of pelagic crabs found in the region of the Revilla Gigedo Islands and further to the southwest were unimodal at 12–13 mm and contained no individuals larger than 17 mm. Small numbers of pelagic crabs taken from tuna stomachs

at Clipperton Island by the *Shoyo Maru* were similar to these in size, as were those illustrated by Beklemishev (1960) as being typical of the population he investigated in the oceanic area north of the Revilla Gigedo Islands. Finally, Blackburn (pers. comm.) found that the inshore stocks off Baja California during August 1964 comprised individuals larger than these, except in the single case of a population at the extreme southwest of the station pattern, outside Morgan Bank, which was isolated from those further inshore and consisted only of small individuals similar in size to those listed above.

The inference apparently to be drawn from these data is that beyond the inshore area the flushed-out individuals appear to be derived not from the sub-adult and adult stocks of the inshore area which Boyd (1963) showed to have modal lengths up to 20 mm, but rather from the larval forms generated by this inshore stock.

There is only a single survey of the distribution of larvae and postlarvae (Cruise TO-64-1 of June, 1964) and this shows clearly the flushing-out of these forms (Figure 7) which are distributed in a linear manner from an origin to the south of Punta San Eugenio so that progressively older individuals were found progressively farther to the south along the main line of flow of the California Current; the numbers of individuals per standard volume did not diminish along the series and there was no indication that the megalops taken in the far south-west were random stragglers, so that the data was consistent with the major part of the population of larval forms being drifted offshore in the direction of the Revilla Gigedo Islands.

Johnson (1960) shows how a planktonic population of crustacean larvae can maintain itself in the California Current for periods of the order of 6 months and then settle effectively enough to maintain an adult population along the coast; it can be surmised that over a similar period (which is probably adequate to attain capability of first settlement to the benthos) a proportion of the larvae of *Pleuroncodes planipes* would similarly be maintained in the eddy system of the California Current without being swept out to sea. These might then commence alternation between the benthic and pelagic phase over the continental edge within their first 2 years of life.

It can be seen from Figure 3 that all the records of occurrence in the oceanic area are within the extension of the California Current, and none are within the Equatorial Counter Current to the south; this distribution carries the implication that there is no likely transport in the mixed layer which could return these individuals to the coast; however, a clear possibility exists of a simple descent to only about 200 meters to achieve return transport on the north-westerly flowing undercurrent.

This possibility is demonstrated, for example, by Reid (1965) who shows that the Pacific Intermediate Water moves north-eastwards towards the coast over much of the area occupied by offshore and oceanic pelagic crabs; the temperature tolerances of *Pleuroncodes* (Table 3) and the depth of benthic records in-

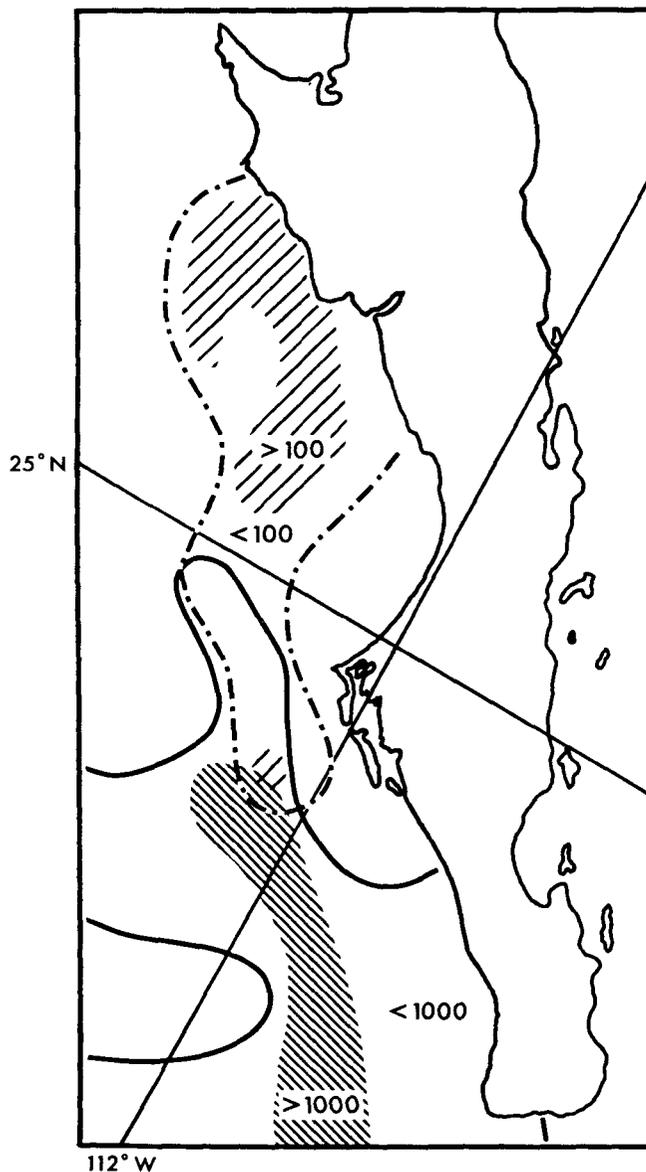


FIGURE 7. The distribution of larval (light shading) and postlarval (dark shading) *Pleuroncodes* during June, 1964.

dicates that prolonged residence at depths from 100 to 300 m, which would be required for such transport, are well within the capacity of the species.

Although most of the data on the distribution of pelagic crabs within the oceanic area come from normal oblique zooplankton hauls, integrated for depth, or from surface observations (e.g., Beklemishev, 1960), the only data which contain a depth element indicate that the highest densities of crabs were at depths suggestive of such return transport. During the La Pared cruise referred to above no crabs were observed at the surface west of about 113° longitude, but between 115 and 120° at the latitude of Clarion Island many crabs were taken in subsurface opening-closing net tows (Jerde, Berger, pers. comm.); their vertical distribution showed that they were distributed in the depth range 50–300 m even at night and that some of the largest concentrations (of more than 200 crabs per haul) occurred between 100–150 m, while down to 150–300 m concentrations of up to 60 crabs per haul occurred.

It is therefore postulated that a larva hatched in the inshore area off Baja California may either remain within the coastal eddies for the duration of its larval period and be recruited directly to the stock of pelagic sub-adults within the inshore area, or it may be flushed into the offshore areas while still a megalopa and be recruited to the offshore stocks of pelagic sub-adults. In the latter case while there appears to be a mechanism for purposeful return to the inshore areas, and although the data on the size structure of the population suggests that reproduction does not occur in the oceanic areas, these postulates cannot be directly proved.

Mass mortalities of pelagic *Pleuroncodes* by coastal strandings are well known (e.g., Stimpson, 1860; Matthews, 1932; Glynn, 1961; Boyd, 1963) as are massing of crabs in surface windrows at sea (Shimada in Boyd, 1963) and such observations suggest that at times pelagic *Pleuroncodes* may find themselves in inimical oceanographic situations; Boyd (1963) assumed that oceanic individuals in the California Current extension were in this state and were therefore expatriates contributing nothing further to the maintenance of the species.

This view and that expressed in the previous postulate are perhaps not entirely conflicting, for it is very likely that mortality during the offshore excursion is extremely high, and it may be presumed that the farther to the south-west a population of sub-adults is carried the greater will be the attrition by pelagic fish and other causes of mortality. (It is also very likely that even if the postulate of return migration on the undercurrent is shown to be correct, it will be found that there is a point of no return beyond which the crabs will be, as Boyd suggested for all oceanic individuals, expatriates of no further significance to the species as a whole.

It is now appropriate to consider the relative roles of the pelagic and benthic phase in the biology of the species in the inshore area; even here the proportion of the pelagic stock which at any time has the possibility of changing to the benthic phase is probably

rather small, due to the narrow continental shelf to the west of Baja California, since most of the individuals are over depths greater than those at which the benthic phase has been found. Thus, it follows that individual residence times in the pelagic phase must be of the order of weeks or months, rather than days, if indeed such pelagic individuals have previously settled temporarily into the benthos.

During the northern movement of 1958–1960 already discussed the plankton record indicates that for limited periods pelagic crabs disappeared from the CalCOFI samples (as, for instance, during June and July 1959) and this, together with the record of Parker (1963) of benthic crabs off Ensenada during this year and the observations of Sund and Quast (Boyd, 1963) of the occurrence of *Pleuroncodes* in the stomach contents of many species of demersal fish off San Diego, including some with very slight swimming powers (e.g., *Pimelometopon pulchrum* and *Scorpaena guttata*) and which may be presumed to have taken the crabs on, or very close to, the bottom; this again suggests that the disappearance from the plankton record may well be due to settlement into the benthic community.

The sequence of events during the recession from the northern extension of the range again suggests a residence time in the pelagic phase of some weeks or months, and also that the benthic individuals reentered the pelagic phase and were swept to the south again during this period.

SUMMARY

1. This survey of the ecology of the pelagic phase of *Pleuroncodes planipes* in the California Current indicates that this phase is comparable with the *Grimothea* stage of *Munida gregaria* in that it is an extension or recurrence of the larval habit, but differs from the *Grimothea* state in that no morphological differentiation is involved between the pelagic and benthic phases.

2. It is demonstrated that the distribution of the pelagic phase is restricted to water of the range 9–28° C., and that the bulk of the pelagic population occurs within 100 miles of the coast of Baja California, and that about 75% of the occurrences were in situations with 10 meter temperatures in the range 16–21° C.; the areas in which highest overall frequencies of occurrence and in which the very dense shoals occurred are those in which the influence of water derived from coastal upwelling and hence bearing high standing crops of biota is most likely to be felt.

3. Lower frequencies of occurrences are demonstrated in oceanic areas to the south-west of Baja California, and it is shown that these populations have their origin as larval forms generated over the continental shelf of Baja California and subsequently flushed out of this area on the offshore trend of the California Current. It is shown how a proportion of these could be returned to the coastal areas on the undercurrent formed by the Pacific Intermediate

Water below the California Current and its extension to the south-west.

4. Seasonal variation of occurrence of pelagic individuals in the coastal areas is rather slight, consisting only of a tendency for higher frequencies of occurrence in the first half of the year; however, the annual variation is very striking and a very extensive movement towards the north can be demonstrated during the years 1958-1960, culminating in occurrences to the north of Point Conception. This movement can be explained by reference to the changed patterns of transport in the oceanographic regime during this period, the patterns of geostrophic flow corresponding very well to what is required to explain the observed movements of crabs.

5. The relation between the benthic and pelagic phases appears to be complex, and it is suggested that during the first two years of life an individual may either be retained within the coastal eddies and alternate between benthic and pelagic environments, or it may be flushed out to the south-west with the possibility of returning subsequently to the coastal areas on the undercurrent within the first year or so of life; individuals older than this have not been found far offshore and are supposed either to have succumbed or to have returned to the coastal area. After the end of the second year of life the benthic habit appears to be finally adopted and no individuals older than this have been taken in the pelagic phase.

ACKNOWLEDGMENTS

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SUMMARY OF THERMAL CONDITIONS AND PHYTOPLANKTON VOLUMES MEASURED IN MONTEREY BAY, CALIFORNIA 1961-1966

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For thirteen years under the California Cooperative Oceanic Fisheries Investigations Program the Hopkins Marine Station of Stanford University has monitored the marine climate and phytoplankton of Monterey Bay. Approximately weekly cruises to six regular stations on the bay are made on the R/V TAGE. The information gathered is compiled and distributed to interested organizations and individuals in the form of mimeographed quarterly and annual data reports. A previous paper (Bolin and Abbott, 1963) describes the stations occupied and the procedures followed in sampling and analysis, and presents a summary of results obtained through December 1960. The present report summarizes some of the findings in the period January 1961 through December 1966, and brings up-to-date the curves shown in Figures 2A-B and 5A of the earlier paper.

Thermal conditions are shown in Figures 1A and 1B of the present report. In Figure 1A, the middle of the three curves depicts the monthly average of all surface temperatures taken on all cruises during each

month. The upper curve (average monthly maximum) shows monthly averages of the warmest surface temperature recorded on each cruise during the month. The lower curve (average monthly minimum surface temperature) is similarly derived.

The main hydrographic seasons on the bay are clearly indicated by the curves in Figures 1A and 1B. Divergence between average monthly maximum and average monthly minimum surface temperatures (upper and lower curves in Figure 1A, solid line in Figure 1B) occurs when upwelling of colder water over the Monterey Submarine Canyon lowers the temperatures in the center of the bay without bringing about correspondingly large drops in surface temperatures at the northern and southern limits of the bay. Upwelling is also accompanied by a marked increase in the thermal gradient in the upper 50 meters (Figure 1B, broken line). The thermal gradient may persist for a time in the late summer and early fall after upwelling has declined (compare solid and broken lines, Figure 1B, for August through October

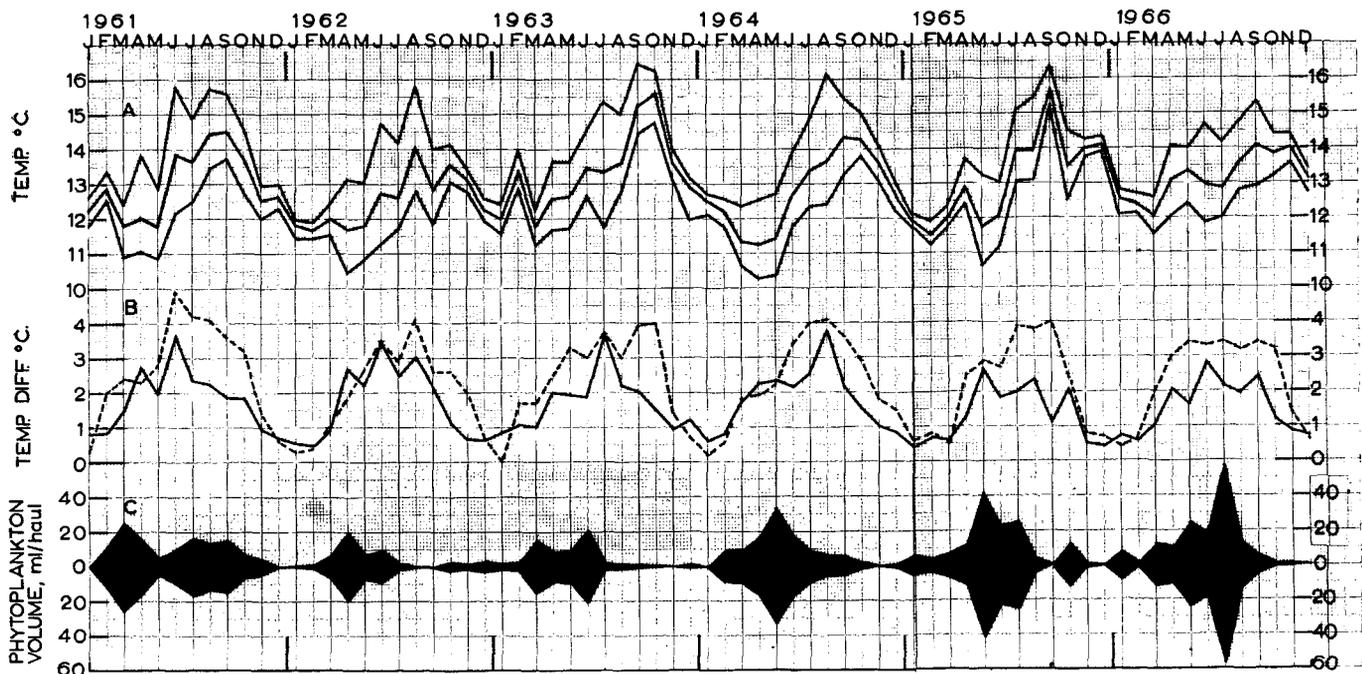


FIGURE 1. Monthly averages of temperature conditions and the volume of the phytoplankton standing crop in Monterey Bay, California, 1961 through 1966. A. Surface temperature ($^{\circ}\text{C}$), showing monthly means, average monthly maxima, and average monthly minima. B. Solid line—temperature difference ($^{\circ}\text{C}$) between average monthly maximum and average monthly minimum surface temperatures; broken line—temperature difference ($^{\circ}\text{C}$) between monthly means of temperatures at the surface and those at 50 meters depth. C. Monthly averages of the volume of the phytoplankton standing crop (ml/haul).

especially for the years 1961 and 1963); as upwelling ceases fog also decreases, and with sunnier weather and little turbulence a thermocline often develops which tends to preserve a temperature gradient. Also during these months, flushes of warmer oceanic water from offshore may flow in on the surface of the bay. The Davidson Current period of the winter months is clearly indicated in Figures 1A and 1B by the marked decline in surface temperatures, the close similarity of average monthly maximum and minimum surface temperatures, and the nearly uniform temperature conditions prevailing in the upper 50 meters as a result of mixing.

In Figure 1C the phytoplankton volumes represent monthly averages of wet settled volumes of phytoplankton per haul, 15 meters to the surface, taken in a $\frac{1}{4}$ meter net of 173 meshes/inch. Larger diatoms and dinoflagellates are retained, but not nanoplankton. Major increases in standing crop occur in spring and summer. For the 13-year period 1954–1966, maximum crops appeared most frequently in June, but in different years peaks fell in all months from March through July. *Chaetoceros* is usually the predominant genus in the bay in spring and early summer.

The most notable irregularity in the general seasonal temperature pattern shown in Figure 1A is the unusual warm peak which occurred in February 1963. This unseasonal warming, one phenomenon among many in a winter of unusual weather, appears in the records of shore temperatures taken along much of the temperate Pacific coast (Scripps Institution of Oceanography, 1964). February temperatures at most shore temperature stations in California, Oregon, and Washington exceeded temperatures recorded for that month in any year through 1966 since the warm years 1957–1959. In Monterey Bay this warm pulse was accompanied by conspicuous red tides and luminescence; the phytoplankton was dominated by *Peridinium*, with lesser numbers of *Ceratium* and *Gonyaulax* (Hopkins Marine Station, 1963). Red tides extended at least as far north as Point Montara and in

southern California were prevalent from near San Diego to Santa Barbara (California Marine Resources Operations, 1963). No unusual mortality of fishes or other marine organisms was noted, in Monterey Bay or elsewhere in California, but phytoplankton volumes obtained in Monterey Bay rose sharply in March.

A less conspicuous warm pulse during the Davidson Current period occurred in February 1961 (Figure 1A), and was reflected in shore temperatures taken at many points along the coast (Scripps Institution of Oceanography, 1962). In contrast to the situation in 1963, dinoflagellates formed less than 2% of the phytoplankton bloom accompanying and following the warm conditions. Instead, the phytoplankton consisted of a mixed population of diatoms characteristic of coastal waters; *Chaetoceros* and *Skeletonema* predominated, accompanied by lesser numbers of *Asterionella*, *Thalassiosira*, *Nitzschia*, and other forms. The character of the phytoplankton in the March bloom of 1963 suggests the growth of organisms brought in from oceanic waters offshore, while the March bloom of 1961 represents growth of resident populations characteristic of Californian coastal waters.

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SEASONAL VARIATION OF TEMPERATURE AND SALINITY AT 10 METERS IN THE CALIFORNIA CURRENT

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INTRODUCTION

The seasonal variation of temperature and salinity at 10 meters in the California Current is examined from the CalCOFI¹ data record, 1950-62. The CalCOFI station pattern off California-Baja California (Figure 1) has been occupied repeatedly since 1950. Surveys have been conducted on almost a monthly schedule although only a portion of the station pattern was covered each time. Only four surveys were conducted in 1961 and 1962. The sampling frequency of salinity for 1950-62 is shown in Figure 2. At some of the stations temperature was measured a few more times than salinity. Harmonic curves, comprised of the annual and semiannual components, were fitted to each station record by regression analysis using the method of least squares. The harmonic curves provide the description of seasonal variation. Along with the regression analysis are descriptive statistics.

The California Current System

The California Current is the eastern limb of the anticyclonic gyre that dominates the North Pacific Ocean. It is a broad sluggish current characterized by cool, low-salinity water. Warm high-salinity water is found to the west (central North Pacific) and south (vicinity of the Gulf of California). Upwelling along the coastal boundary of the current introduces cool, usually high-salinity water to the surface layer. Upwelling is the process whereby the wind component paralleling the coast (northwesterly) drives the surface water offshore; these waters are replaced by deeper waters.

The North Pacific gyre is largely wind-driven. Seasonal variation of the winds is indicated by seasonal variation of the strength and location of atmospheric pressure cells. The currents respond to variations in wind. This system was qualitatively described for the California Current region by Reid, Roden, and Wyllie (1958). A strong northerly wind component in spring through fall strengthens the Current. In winter the northerly component weakens or reverses and a countercurrent develops along portions of the coast. The seasonal variation of the winds has a most noticeable effect on coastal upwelling. Upwelling is strongest when the north and northwest winds are strongest. This situation occurs off Baja California in April and May, off southern and central California in May and June, off northern California in June and July, and off Oregon in August (Reid, Roden, and Wyllie, 1958).

The largest and most complex changes in circulation occur in the coastal region. A countercurrent is present in late fall, winter, and early spring from central California to British Columbia (cf. Sverdrup, Johnson, and Fleming, 1942; Schwartzlose, 1963). A nearly

permanent eddy is found among the Channel Islands off southern California. The eddy is weak or nil in March, April, and May (Schwartzlose, 1963; Reid, 1965). The countercurrent is usually continuous around Point Conception in November, December, and January. There is no countercurrent along northern Baja California, but major eddies do occur off southern Baja California.

An atlas of sea surface dynamic topography (referenced to 500 decibars) of the CalCOFI data is under preparation at the Scripps Institution of Oceanography (S10). The contours and gradients define the direction and speed of the geostrophic currents.

The variations of circulation and upwelling have a pronounced effect on the seasonal variation of temperature and salinity. The seasonal variation of these characteristics was discussed at length by Reid, Roden, and Wyllie (1958). They gave representative curves of the variations for diverse areas constructed from monthly means of CalCOFI data, 1949-55, and other sources.

The following paragraphs are quoted from a review of the earlier work by Reid (1960, p. 81). In place of seasonal variation curves to which his paragraphs refer, the reader may examine similar figures of this paper (Figures 8, 10, 13 and 14).

"... Far offshore the variation, which is principally the result of variation in radiation and exchange with the atmosphere, has a simple pattern with the greatest range in the highest latitude. Near the coast in the region of strong upwelling north of 34°N. the seasonal range is reduced and the cool period lengthened by upwelling. Between 28°N. and 34°N. the upwelling occurs earlier in the year, more nearly at the period of the offshore seasonal minimum, and increases the seasonal range. South of 28° N. it is the fall and winter countercurrent which accounts for the high range and delays the low until late spring.

"The seasonal variation in surface salinity . . . indicates that the direct effect of evaporation and precipitation is small, and, indeed, there is little coherence in the variation of the northern offshore stations. Inshore it is again the processes of upwelling in the north and the countercurrent in the south which dominate the seasonal variation. The effect of the spring and summer upwelling of deeper water to the surface in the north causes a wide range with the maximum value of salinity in summer. In the south the winter countercurrent brings highly saline water northward along the coast giving a maximum in winter. The two effects tend to cancel each other in the middle region between 28°N. and 34°N. latitude."

Recently, the seasonal variation of temperature and salinity at diverse levels in the Point Conception (Point Arguello) region has been examined in detail (Reid, 1965).

¹ California Cooperative Oceanic Fisheries Investigations.

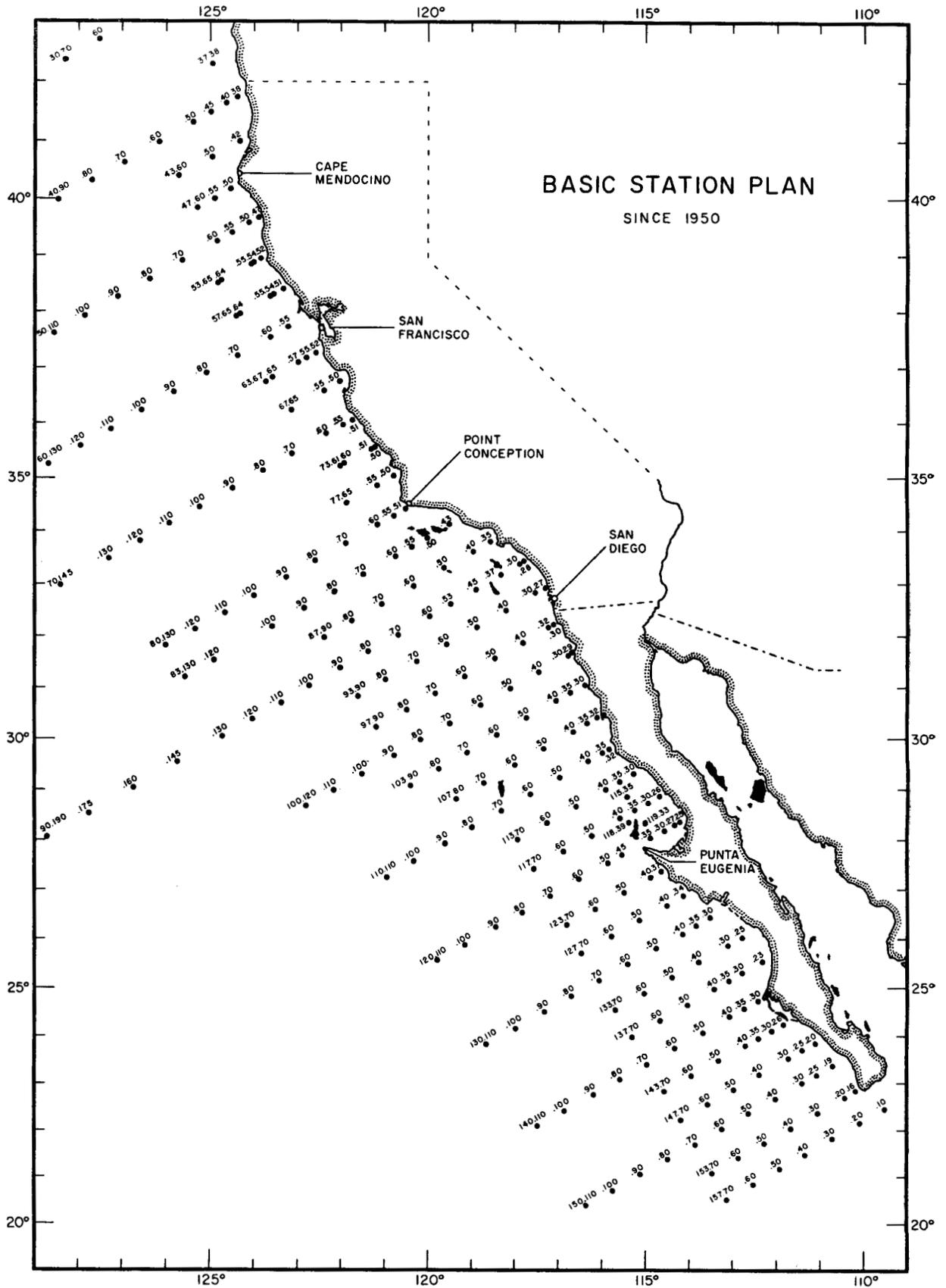


FIGURE 1. CalCOFI station plan since 1950.

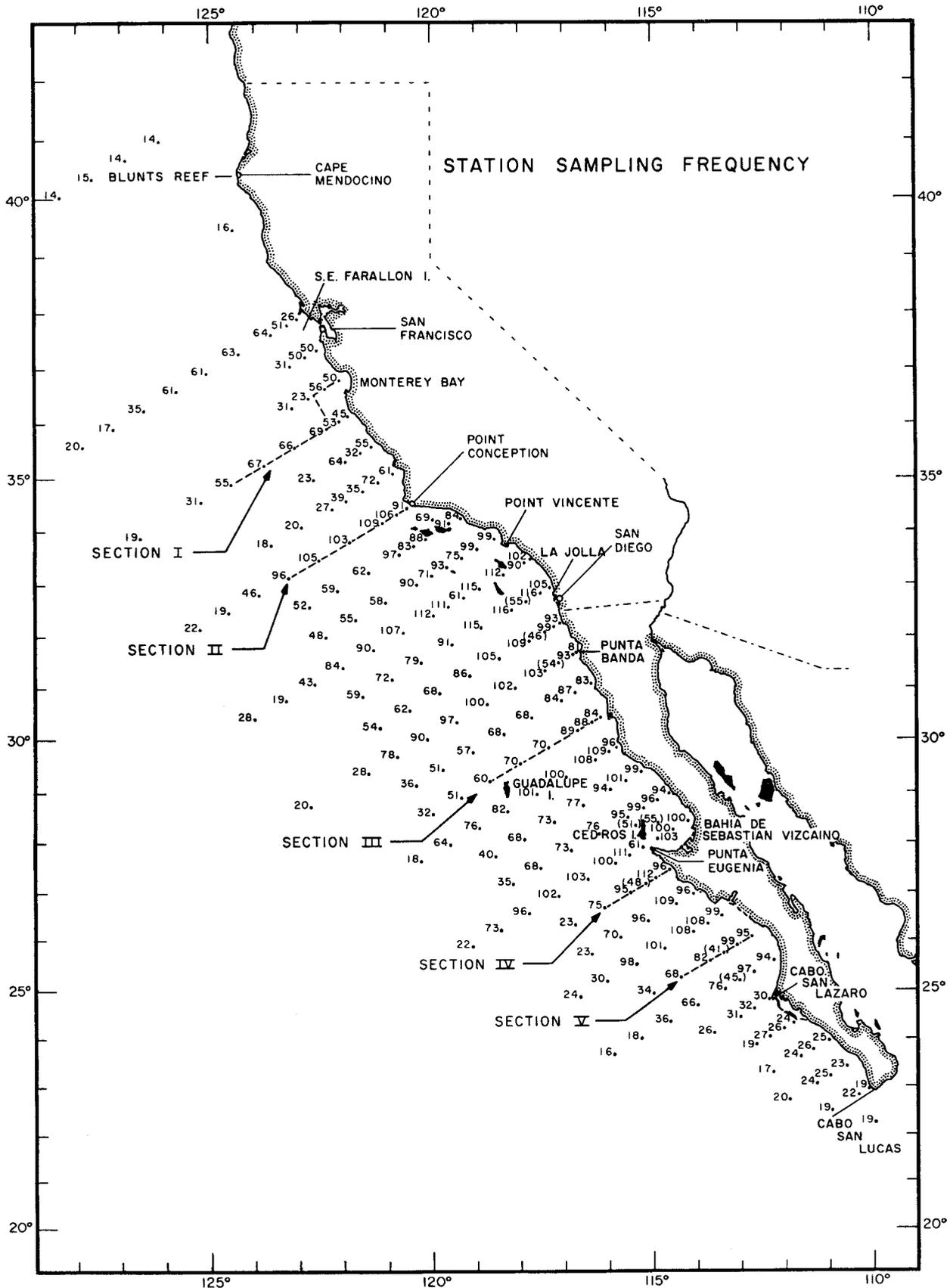


FIGURE 2. Station positions of data records used in the regression analysis and their sampling frequency, 1950—62. Sections refer to Figure 14.

The papers cited have described the major features of the variations in temperature and salinity in the California Current region. The present study employs a totally different method of analysis which substantiates the previous findings. Detail is provided in some areas and for some months that has not previously been available. Almost all of the statistical treatment is new.

California Cooperative Oceanic Fisheries Investigations Atlas No. 1 (1963) contains distributions charts of 10-meter temperature and salinity for each CalCOFI cruise, 1949-59. The atlas also presents charts drawn from 10-year monthly means of temperature and salinity. Near the end of this paper a brief comparison is made between the mean distribution charts of the atlas and those derived from the present analysis.

THE DATA

The CalCOFI data through 1959 are published in the series, Oceanic Observations of the Pacific. Data for more recent cruises are available in the data report series (unpublished) of the University of California Scripps Institution of Oceanography.

Records for 222 stations were selected for analysis from the CalCOFI 10-meter data for 1950-62 according to criteria of occupancy and location (Figure 2). Thirty percent of the stations were occupied 14 to 50 times, and the remainder 51 to 119 times. The stations with the lesser frequency of sampling are found at the seaward extreme of the station pattern, off Cabo San Lazaro and south, and scattered among the stations north of Point Conception. These station records were used to extrapolate charting of the distributions beyond the better sampled areas. The observations are not evenly distributed throughout the year but occur more frequently in April-July, and less frequently in September, November, and December. Figure 13 shows time plots of data records with all years folded into one 12-month period. (An explanation of Figure 13 is given under STATION REGRESSION CURVES.) Only one observation per month was used; when duplicate observations were made, usually the one nearest mid-month was used.

In addition to the CalCOFI data, portions of records from five shore stations (surface only) were analyzed:

	<i>Temperature</i>	<i>Salinity</i>
Blunts Reef -----	1955-62	1957-62
S.E. Farallon Island -----	1955-62	1957-62
La Jolla -----	1950-62	1956-62 ²
Guadalupe Island -----	1956-60	—
Cedros Island -----	1957-62	—

Observations were made daily. The records were collected by the U.S. Coast and Geodetic Survey and Scripps Institution of Oceanography (unpublished). For this analysis, monthly averages (daily observations averaged for each month of each year) were entered as initial data. Thus, there is one value per month comparable in number to the CalCOFI sampling

² Validity of salinity observations for 1944-55 were questioned by Roden (1961); hence, these observations were not included in this analysis.

program, but with some high frequency variation filtered out.

CHOICE OF THE 10-METER LEVEL

Hydrographic casts were made during about 80 percent of the station occupations; the remaining 20 percent were "net-haul" stations, where work consisted of biological sampling and a 10-meter temperature and salinity measurement. The 10-meter level was chosen to represent the upper mixed layer in lieu of a surface sample to avoid such transient conditions as might be caused by rain or river runoff and by diurnal heating and cooling. In some places a shallow summer thermocline may develop. When this thermocline is shoaler than 10 meters it is readily subject to wind stirring; hence, its existence is usually brief. These arguments do not obtain in the vicinity of Cabo San Lucas³ where oceanic fronts and other complex features persist (Griffiths, 1965).

ANALYSIS

An expression of the mean seasonal variation of a characteristic may be obtained from a digital record by Fourier polynomials, a method of harmonic analysis. Because the time intervals between data measurements are irregular, standard textbook formulas derived for processes sampled at equally-spaced intervals are unsuitable and hence an approach from basic concepts is necessary. A detailed description of each data record by harmonic analysis is not necessary; the only harmonics needed are those which contribute significantly to the description of the seasonal variation. This consideration leads to a different but totally equivalent approach which has an added advantage. The mean seasonal variation may be obtained by least squares regression of the data (considering each station record as a time series) to annually periodic sinusoids. Van Vliet and Anderson⁴ analysed sea surface temperature records for seasonal variation by fitting annual and semiannual harmonics to the observed data by regression analysis. Their analyses were performed on long records of daily temperature observations at four shore stations and two weathership stations. Least squares regression analyses for curve fitting is identical to the more common application of estimating linear relationships. The added advantage of this method is seen in the statistical approach; it is a natural adjunct of regression analysis to compute measures of dispersion, correlation coefficients, and significance parameters. Though less natural, such computations can be made with truncated Fourier polynomials.

Natural events driven by insolation tend to vary with an annual cycle that may be roughly described by a sinusoid. However, because the effect of insolation is often indirect, the rough approximation provided by the annual sinusoid can usually be refined by

³ Geographical locations are identified in Figure 2.

⁴ Statistical analyses of sea surface temperature time series (unpublished manuscript). U.S. Navy Electronics Laboratory, San Diego, Calif.

including the semiannual harmonic.⁵ The frequent 3- and 4-month gaps in the data records and the brevity of the records preclude any significant results from the third harmonic.

The general form of the regression curve is:

$$y = A_1 \cos\theta + B_1 \sin\theta + A_2 \cos 2\theta + B_2 \sin 2\theta + C$$

where θ is the angular equivalent of the day of year in radians. In least squares regression the sum of the squares of the data anomalies from the regression curve,

$$\sum_i [y_i - (A_1 \cos\theta_i + B_1 \sin\theta_i + A_2 \cos 2\theta_i + B_2 \sin 2\theta_i + C)]^2,$$

is minimized with respect to each of the five coefficients

where,

$$y_i = \text{data values indexed to } \theta_i$$

$$\theta_i = \frac{2\pi[(\text{month} - 1) 30 + \text{day}]}{360}$$

The resulting set of equations is solved simultaneously for the coefficients. The same coefficient formulas can be derived from the Fourier polynomial approach. When equal intervals are assumed (integral division of year) the formulas simplify to the standard textbook formulas for Fourier polynomial coefficients.

From the station regression curves were derived the long term mean (13-year), extreme values, and range. Statistics describing the data and the fit of the regression curve were computed by standard formulas. These statistics include standard deviation, standard error of estimate, coefficient of correlation, and the F -ratio test (null hypothesis: the mean provides as adequate a fit to the data as the regression curve). The coefficient of correlation refers to the correlation of the characteristic with time of year.

DISTRIBUTION OF THE 13-YEAR MEANS

The long term (13-year) mean of temperature (Figure 3) shows the influence of currents and upwelling. The mean temperature ranges from 12° C. near San Francisco to 24° C. near Cabo San Lucas. More than half the range (less than 18° C. to 24° C.) falls between Punta Eugenia and Cabo San Lucas, one-third of the total distance. The isotherms tend to parallel the coast along northern and central California with the colder water inshore, whereas the isotherms are nearly perpendicular to the shore along the southern part of Baja California. The colder inshore water along northern and central California is a mixture of cold waters from the North Pacific Current and cold waters upwelled along the coast. A second important upwelling region, indicated by a 16° C. isotherm, is near the coast immediately north of the United States-Mexican border and extending southward along northern Baja California. West of this upwelling region is a warm tongue-like feature extending into the island area off southern California.

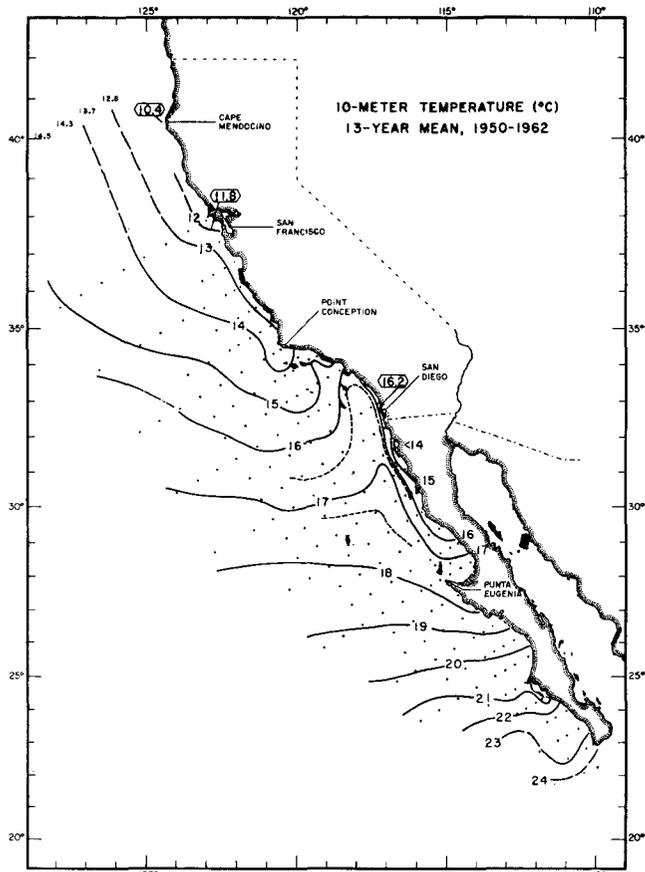


FIGURE 3. Ten-meter temperature (°C); 13-year mean, 1950-62. Interval: 1° C. In this and other figures thin, short-dashed lines show half intervals and thick, long dashes show continuation of standard-interval isopleths into regions of infrequent sampling. Boxed values refer to shore stations.

The long term mean salinity (Figure 4) ranges from less than 33.0‰ near Cape Mendocino to greater than 34.6‰ near Cape San Lucas. More than half this range is along southern Baja California. The largest gradients are in the southernmost portion of the CALCOFI area and in the upwelling region north of Point Conception. A low-salinity tongue, characteristic of the California Current, lies approximately 240 miles from and parallel to the northern California coast. The displacement of the low-salinity tongue farther offshore from the low-temperature tongue is evidently the consequence of the mixing of upwelled water, characteristically cold with high salinity, and California Current water, characteristically cold with low salinity. Along southern California and northern Baja California is a body of water with a nearly uniform mean salinity, 33.55‰ ± 0.05‰ and a small standard deviation, approximately ± 0.15‰. This area shows a complex distribution of mean temperature.

Reid, Schwartzlose, and Brown (1963) described a shoreward movement of water near latitude 31° N. to 32° N. Features in the 33.4‰ and 33.5‰ isohalines probably relate to this flow, as perhaps does the

⁵ Van Vliet and Anderson performed an autocorrelation analysis on the long records (7-40 years) of daily temperature observations and showed the semiannual harmonic contains a significant portion of the energy of seasonal variation in four of their six stations.

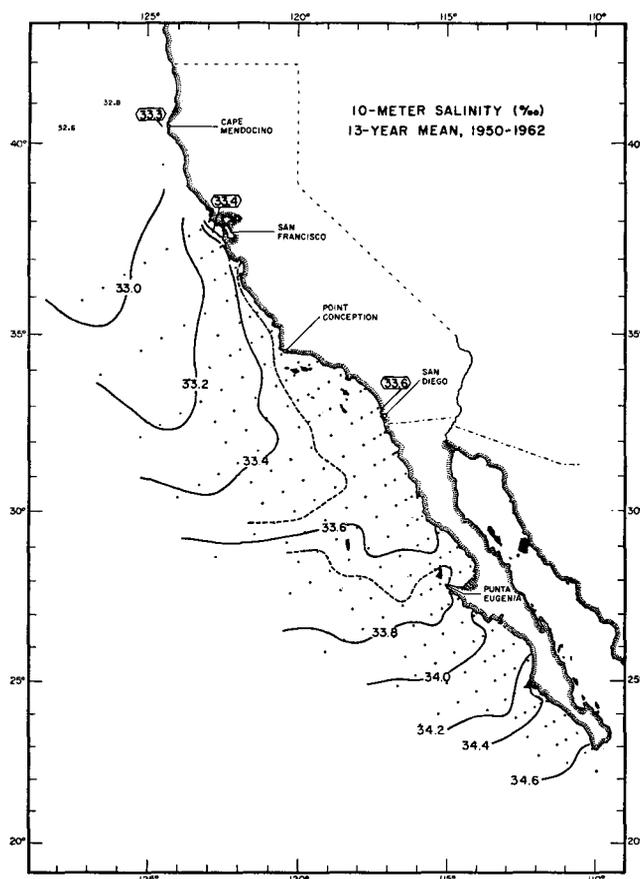


FIGURE 4. Ten-meter salinity (‰); 13-year mean, 1950-62. Interval: 0.2‰.

slightly larger salinity gradient northwest of Guadalupe Island. The limited coverage of the CalCOFI pattern does not show the southward and southwestward continuation of the low-salinity tongue as shown by mean-salinity charts of the North Pacific Ocean (see, for example, Schott, 1935; Morskoi Atlas, 1950; or Norpac Atlas, 1960).

The results of analyses at shore stations are shown as boxed numbers on these and other distribution charts. The mean temperatures at the Guadalupe Island and Cedros Island Stations are 0.5°C . greater than at the adjacent stations. In both cases the records covered only half of the 13-year period. When neighboring CalCOFI stations were analyzed with equally truncated records no differences could be found in the means. Thus, temperature regression values for the two island stations are misleading and are not given.

STANDARD DEVIATION ABOUT THE MEAN

The distributions of standard deviation about the 13-year means appear in Figures 5 and 6. This measure of dispersion combines the seasonal and nonseasonal influences.

The chart of standard deviations for temperature shows a band of small dispersion, less than 1.75°C ., extending across the CalCOFI region in a meridional

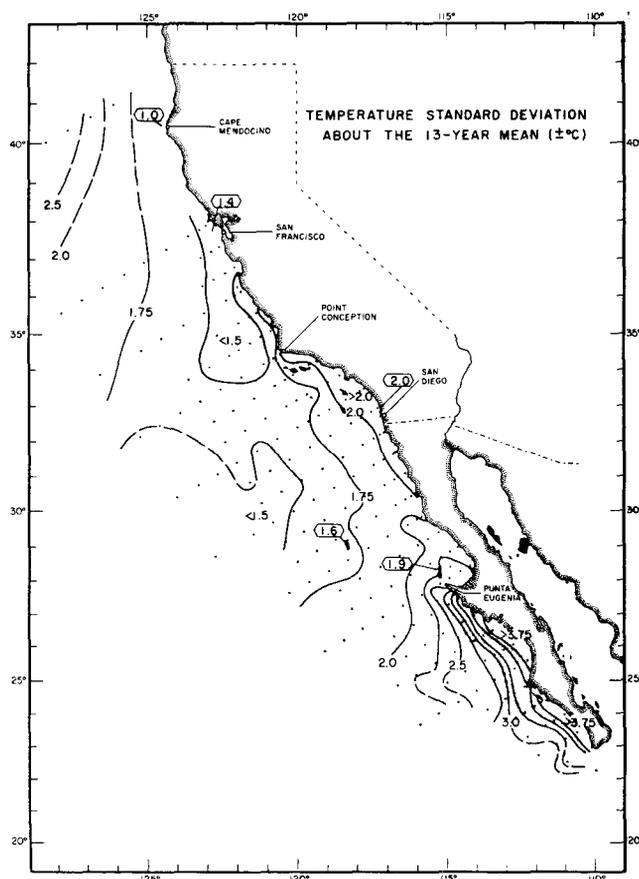


FIGURE 5. Standard deviation of temperature about the 13-year mean ($\pm^{\circ}\text{C}$). Interval: 0.25°C .

orientation. One area of minimum ($< 1.5^{\circ}\text{C}$.) is in the coastal upwelling region along central California. Another such area of minimum at the seaward extent of the coverage may be continuous with the zone of small temperature range in the sub-tropics (Thorade, 1909; Schott, 1935; Reid, 1962). Off northern California the standard deviation increases. A relative maximum ($> 2.0^{\circ}\text{C}$.) occurs along the southern California-Baja California coast. There is a coastal high south of Punta Eugenia having values greater than 3.75°C .

The chart of standard deviations for salinity shows a coastal maximum ($> 0.3\text{‰}$) in the vicinity of San Francisco Bay, and a decrease seaward and southward (to $< 0.15\text{‰}$). The seaward minimum in standard deviation connects with the coastal minimum of the mid-CalCOFI region within the 0.175‰ contour. The body of water with nearly uniform salinity of 33.55‰ off southern California has a very small standard deviation. A maximum occurs near Guadalupe Island which is in a location immediately south of a large salinity gradient to be seen in the distribution of mean salinity. The area of greatest standard deviation (0.35‰) is centered 70 miles offshore from southern Baja California.

The distribution of standard deviations for salinity has a general relation with the gradient of mean

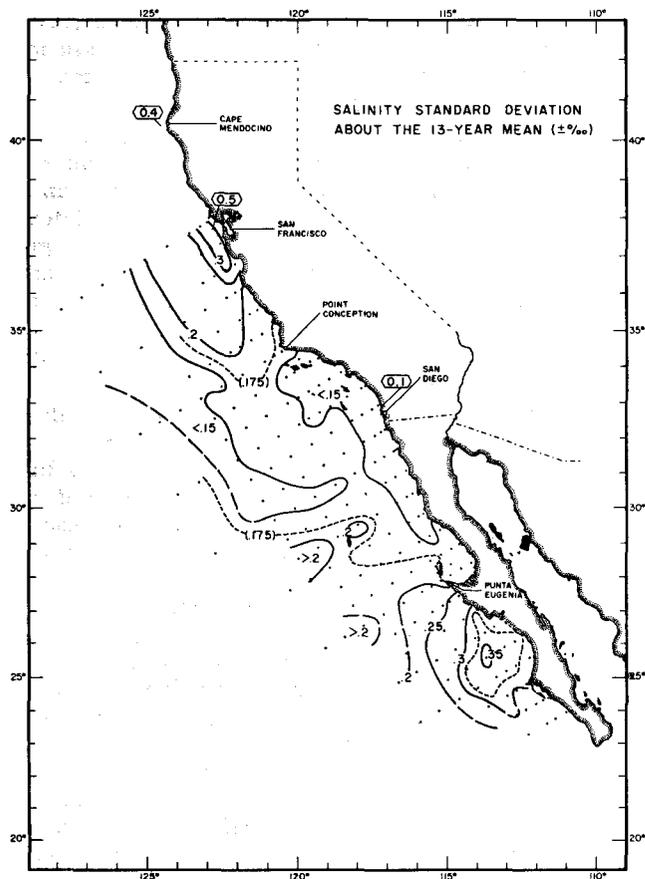


FIGURE 6. Standard deviation of salinity about the 13-year mean ($\pm\%$). Interval: 0.05‰.

distribution. Areas of large gradient coincide with areas of large dispersion, and areas of small gradient with areas of small dispersion. This circumstance probably results from a large ratio of nonseasonal (random) to seasonal variation in the salinity record. The increase in standard deviation near the western edge of the CalCOFI region is not well established but it corresponds to relatively large salinity gradients seen in charts for the North Pacific Ocean.

COEFFICIENT OF CORRELATION AND MEAN RANGE: TEMPERATURE

The coefficients of correlation for temperature and salinity are measures of the degree of relation between the characteristics and time of year.⁶

The correlation of temperature with time of year (Figure 7) has a coefficient greater than 0.80 over the greater portion of the CalCOFI region. The coefficient is greater than 0.85 along the western extent and in the southern half including the coastal region along southern Baja California. Coefficients are smaller in the upwelling regions—in a broad band along central California and in a narrow band from Point Vicente to Bahia de Sebastian Vizcaino. Small

⁶ $R = \frac{\text{variance explained by regression curve}}{\text{total variance}}$ ^{1/2}
where R is the coefficient of correlation.

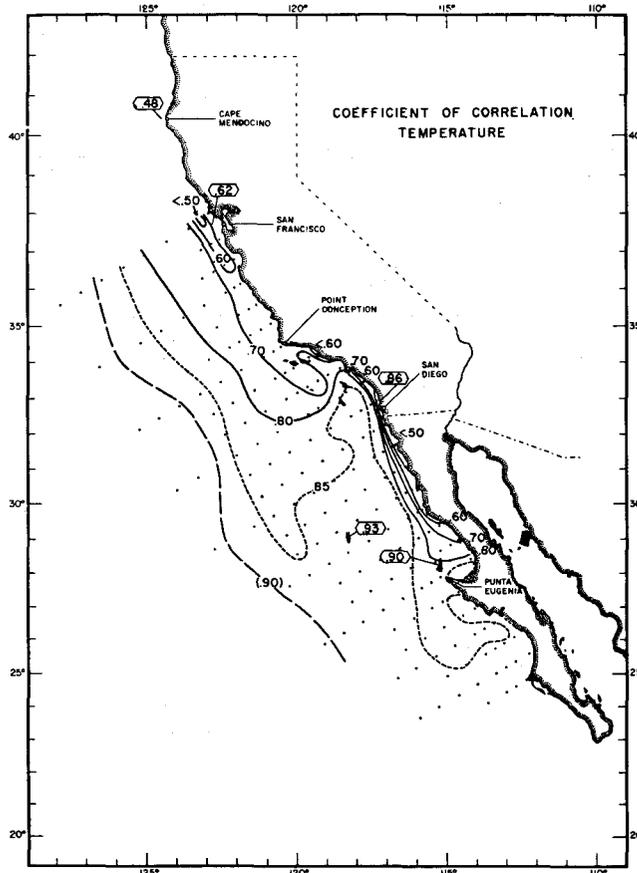


FIGURE 7. Coefficient of correlation for temperature. Interval: 0.1.

coefficients are caused either by large total variance, consequent on the sporadic nature of upwelling, or by small explained variance that results when effects of upwelling are out of phase with the solar heating-cooling cycle dominant elsewhere. A mixture of these effects is probable.

The *F*-ratio test⁷ was applied to the regression of the annual harmonic only.⁸ Where the null hypothesis is rejected at the 2.5 percent significance level the seasonal variation may be considered significant. The seasonal variation of temperature is everywhere significant.

An additional test, attributed to Stumph by Conrad and Pollak (1950), was applied to 12 representative stations. The probability *p* that an amplitude *A* might have been obtained by harmonic analysis of a particular set of random numbers is given by:

$$p = \exp \frac{-A^2}{n \sum_{i=1}^n a_i^2}$$

⁷ $F = \frac{\text{explained variance}}{\text{unexplained variance}}$ weighted by degrees of freedom. The degrees of freedom are determined by the number of variables in the regression equation and the sampling frequency.

⁸ Van Vliet and Anderson found by the *F*-ratio test that the semiannual harmonic significantly increases the explained variance in five of their six stations. Application of this test to the semiannual harmonics of the CalCOFI records is marginal in value because the number of data in each record is small.

where a_i is the amplitude computed from the i th cycle of the period concerned and n is the number of intervals of this period in the series. At all stations tested the probability computed with the annual harmonic of temperature is inconsequential (Table 1).

The distribution of temperature range, maximum of regression curve less minimum (Figure 8), closely reflects the distribution of standard deviation. The major exception is in the region of low correlation

TABLE 1
PROBABILITY THAT AN AMPLITUDE (ANNUAL HARMONIC) AS GREAT AS THAT CALCULATED MIGHT HAVE BEEN OBTAINED BY HARMONIC ANALYSIS OF PARTICULAR SET OF RANDOM NUMBERS

Station	Temperature	Salinity
60.60-----	0.01	0.17
60.80-----	0.01	0.84
73.60-----	2×10^{-3}	0.39
80.51-----	1×10^{-3}	3×10^{-1}
80.55-----	2×10^{-4}	0.02
80.70-----	3×10^{-5}	7×10^{-4}
80.90-----	1×10^{-4}	0.22
90.37-----	7×10^{-4}	4×10^{-4}
90.70-----	3×10^{-5}	0.03
107.32-----	2×10^{-5}	5×10^{-3}
107.35-----	8×10^{-5}	0.88
107.50-----	4×10^{-5}	2×10^{-4}

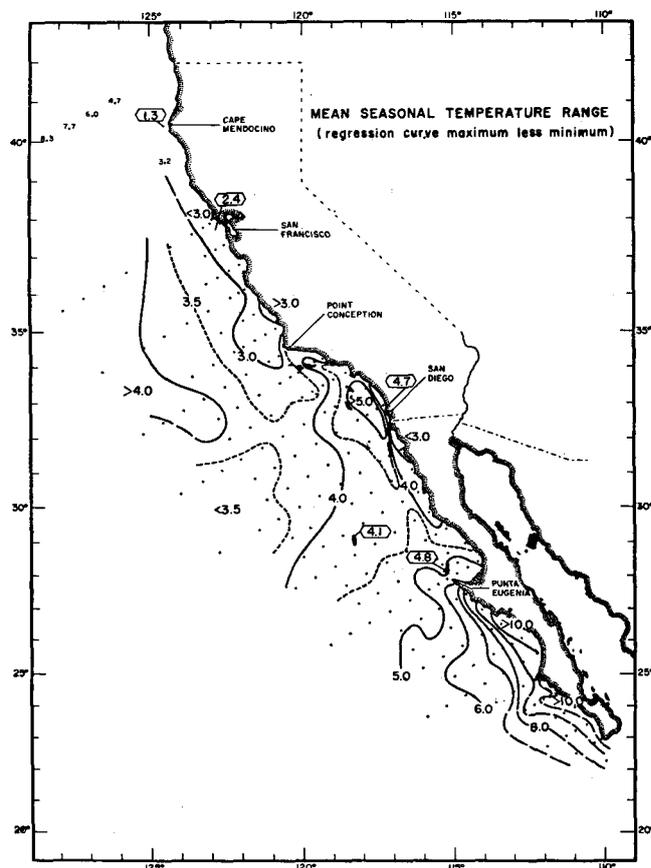


FIGURE 8. Mean seasonal temperature range which is defined as the regression curve maximum less the minimum. Interval: 1° C.

along the coast of southern California-northern Baja California. Here the standard deviation increases to the coast, whereas the seasonal range reaches a maximum 20 to 40 miles offshore.

Temperature range is less than 3.0 °C. in the northern California upwelling region. The band of small range is defined by the 3.5° C. isotherms, and has flanking areas greater than 4.0° C. The isolated area with range greater than 5.0° C. off San Diego coincides with the warm tongue seen in the mean distribution. Temperature range exceeds 5.0 °C. in Bahia de Sebastian Vizcaino and south of Punta Eugenia, increasing to greater than 10.0 °C. along the coast of southern Baja California.

The chart of temperature range is grossly similar to range charts of the North Pacific Ocean (e.g. Reid, 1962). Considerable detail has been added by the present analysis. Robinson (1957) prepared a chart of surface-temperature range for the northeastern Pacific Ocean from a comprehensive study of bathythermograph records (and of some serial hydrographic data). Her chart (her Figure 44) overlaps the present coverage north of 35° N. latitude and shows the band of small range displaced offshore at the latitude of San Francisco. Her values are generally greater by 1.5° C. to 2.0 °C. Closer examination has revealed that most of the differences between the range charts are caused by differences in the determination of the seasonal temperature maxima. During the period of heat gain in the region where the coverage of the charts overlap the temperature of the surface layer may occasionally exceed that at 10 meters by more than 1° C. This difference may result from warming of newly upwelled water or warming of water with shallow density stratification caused by river and bay effluent.

Wyrski (1964) prepared a chart of surface-temperature range for the eastern Pacific Ocean, 30° N. to 40° S. His chart is similar except in a narrow band along southern Baja California. In this region he did not find the range to exceed 7° C. The present analysis finds lower temperatures at the temperature minimum.

COEFFICIENT OF CORRELATION AND MEAN RANGE: SALINITY

The correlation coefficient for salinity (Figure 9) ranges from nominally zero to slightly greater than 0.70. There is a series of lobes having coefficients greater than 0.40. Only off southern Baja California are there any values greater than 0.60. The generally low values indicate that the nonseasonal variations dominate much of the salinity record.

The shaded areas show where the null hypothesis of the F -ratio is rejected at the 2.5-percent significance level. These areas of significant seasonal variation usually coincide with the areas having correlation coefficients greater than 0.40. The exception to this observation occurs north of 34° N. latitude where the sampling was less frequent. The probability com-

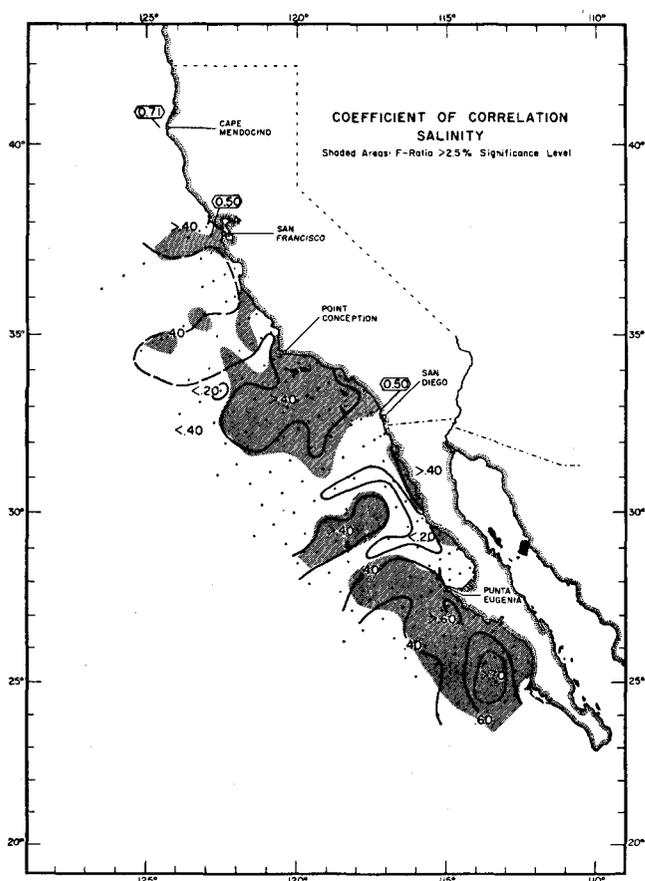


FIGURE 9. Coefficient of correlation for salinity. Interval: 0.2. Within the shaded areas the F -ratio is greater than the 2.5 percent significance level.

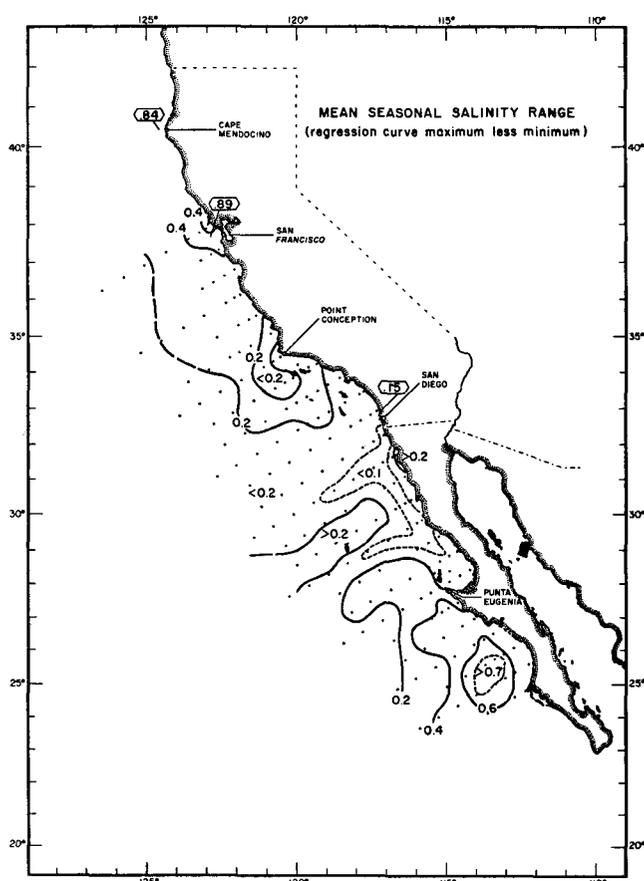


FIGURE 10. Mean seasonal salinity range which is defined as the regression curve maximum less the minimum. Interval: 0.2‰.

puted by Stumph's test for the salinity harmonics show large differences (Table 1). The same conclusions are drawn from this test as from the coefficient of correlation and F -ratio; the seasonal variation of salinity is real but small in comparison to nonseasonal fluctuations. Some areas need more frequent sampling to demonstrate a significant seasonal trend.

The distribution of the range of mean salinity (maximum of regression curve less minimum, Figure 10), reflects that of correlation coefficient and standard deviation, especially the former. Three major regions have a range greater than 0.2‰; two of them have ranges greater than 0.4‰. The maximum range contour, 0.7‰, is centered 100 miles offshore from southern Baja California. This maximum contains most of the stations which have a range equivalent to two standard deviations or more. The other region of range greater than 0.4‰ is found near San Francisco Bay. The shore station at S.E. Farallon Island which includes data for only 5 years, 1957-62, has a range of 0.9‰. This station exhibits an abrupt minimum in March coinciding with the peak discharges of the Sacramento and San Joaquin Rivers. The nearby CalCOFI stations were infrequently sampled in this month and thus may have produced an

abbreviated range. On the other hand, the range at the shore station was increased because samples were taken at the sea surface.

The range along northern Baja California is small; only one upwelling station (100.29) has a range greater than 0.2‰. Twenty miles offshore is a band of especially small salinity range. This band also displays an extremely small coefficient of correlation.

SHORE STATIONS

Some of the results of the analyses of data from shore stations are similar to those for local hydrographic stations. Results for Blunt's Reef station appear to be consistent with an extrapolation of more southerly results. The temperature analysis at S.E. Farallon Island is identical to that of neighboring CalCOFI stations. The salinity analysis for the same station (only 5 years of record) gave greater deviation, range, and correlation. The other shore stations have slightly smaller deviations and greater correlation coefficients than neighboring CalCOFI stations. These results may be caused by the filtering process of using monthly averages as shore station input data. The ranges did not differ among these stations.

REGRESSION CURVE EXTREMES

The extremes of the station regression curves and their months of occurrence are shown in contoured charts (Figures 11 and 12). The seasonal temperature minimum occurs in March over most of the oceans in the northern hemisphere temperate zone. The seasonal maximum occurs in September. The timing of the variation is altered near the coast in the CalCOFI area. In regions of upwelling and regions influenced by upwelled waters the minimum occurs late, usually in April and May. Off southern Baja California the late temperature minimum extends beyond the offshore influence of the coastal upwelling. In this latter region the anomaly in phasing of the temperature variation appears to result from seasonal variation in advection. A region off southern California has an early temperature minimum. The scale and location of this region offer evidence that the phase lead is caused by the pattern of the local currents. The seasonal temperature maximum occurs earliest (August) in a limited area off southern California. The coastal upwelling region of central California experiences its maximum temperature as late as the end of November. The maximum is slightly late at a few prominent upwelling stations along the Baja California coast.

Because the seasonal variation of salinity is considerably less regular than that of the temperature (at some stations the variation is not significant) the distribution of extreme dates is not as definitive as those for temperature. A general pattern is evident, however. Where the seasonal variation is significant seaward of the upwelling regions the salinity minimum is in spring and the maximum in fall. This timing agrees with the seasonal variation of advection and its probable effect on the distribution of mean salinity. In the upwelling regions along central California the maximum salinity is in summer, shortly after the minimum temperature is attained. The minimum salinity usually occurs in winter. The salinity extreme in the upwelling region along northern Baja California occurs earlier than for the region farther north. The salinity maximum along southern Baja California occurs in fall along with the countercurrent.

STATION REGRESSION CURVES

The complete data records and station regression curves for five representative stations are plotted in Figure 13. The dashed lines are drawn at plus and minus one standard error of estimate of the characteristic from the regression curve.

Station 70.52 is in the upwelling region, 6 miles from the shore and immediately south of Monterey Bay.⁹ At this station the correlation coefficients are

⁹The data plotted for station 70.52 were actually obtained at three stations, 70.51, 70.52, and 70.53 with an interval of 4 miles between 70.52 and the others. With one exception no two stations were occupied during the same cruise. The short distance between the stations was considered to be of minor consequence as compared to the month-to-month changes of temperature and salinity in the locale of the stations. Therefore, the data were combined as if observed at one station. Data were similarly combined at several other coastal CalCOFI stations.

low and standard errors of estimate are large. Data are scarce for the winter months. The dispersion of the salinity values is particularly large at the beginning of the upwelling season, April and May. The upwelling season along northern and central California is characterized by the low temperatures in spring and summer with accompanying high salinities. Sometimes the temperature and salinity anomalies show an inverse relation. In particular, the highest and lowest salinities for April have as their corresponding temperature observations the lowest and highest April temperatures, respectively.

Station 70.70 is 80 miles farther offshore. The temperature variation has a greater correlation coefficient, and a lesser standard error of estimate than at the nearshore station. The salinity record shows a poorer correlation and greater standard error of estimate. The offshore salinity variation is very different; its minimum is in spring. The very large positive temperature anomaly and negative salinity anomaly were observed in June 1958. The observations of this anomalous water show that its extent was limited (CalCOFI Atlas No. 1).

These two stations show the large standard error of estimate relative to the moderate ranges in seasonal variation that typifies the surface water in the CalCOFI area north of the latitude of Point Conception. The regression analysis of salinity is of marginal significance. The *F*-ratio test indicates that the regression curves of these example stations provide a better estimate of the salinity than the mean, although the regression curves of some neighboring stations are not significant. Stumph's test (calculated for neighboring stations but not for these particular stations) indicates that the salinity variation within each year may differ considerably from the mean regression curve.

Nonsignificant results from a regression analysis may be a direct result of a low sampling frequency. The stations off central California have moderate to poor sampling frequency and an uneven distribution of data within each year.

The regression curve and record of temperature for station 93.50 and similarly of salinity for station 87.50 also appear in Figure 13. Both stations are off southern California. The standard errors of estimate of the regression curves are small. The range of the salinity curve is moderate, having the same value as the spread of one standard error of estimate above and below the curve. Thus the correlation is moderate. The salinity curve is similar to that for the upwelling station, 70.52. Station 87.50 is just north of San Nicolas Island and over the submarine ridge of which San Nicolas is a part. The depth at this station is 73 meters. The corresponding temperature curve is similar to that of station 93.50 but has a lesser range and poorer correlation, 3.2° C and 0.67, respectively.

The late temperature minimum shown in the curve for 93.50 also appears in a few neighboring stations, all of which are downstream of the cold upwelled water added to the California Current at Point Conception and north. The corresponding salinity curve

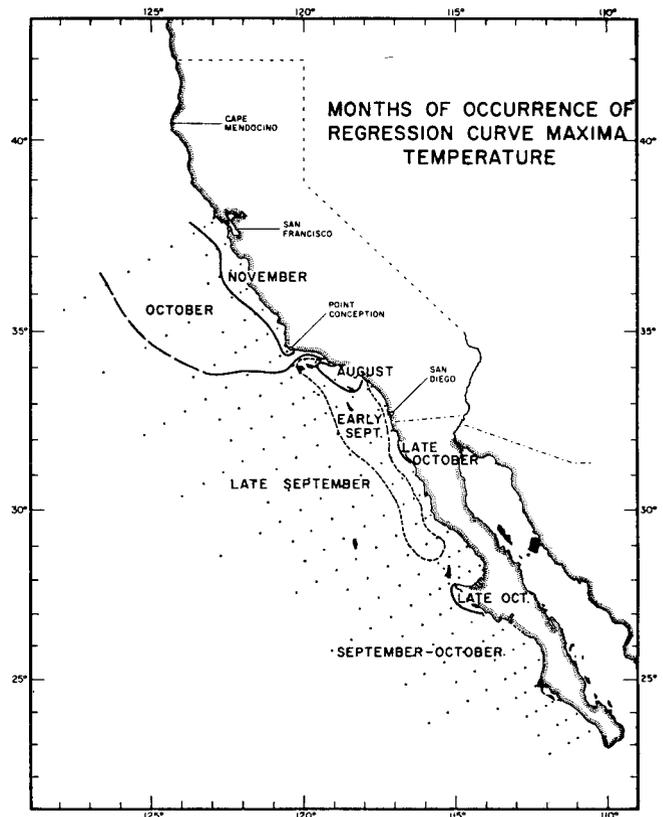
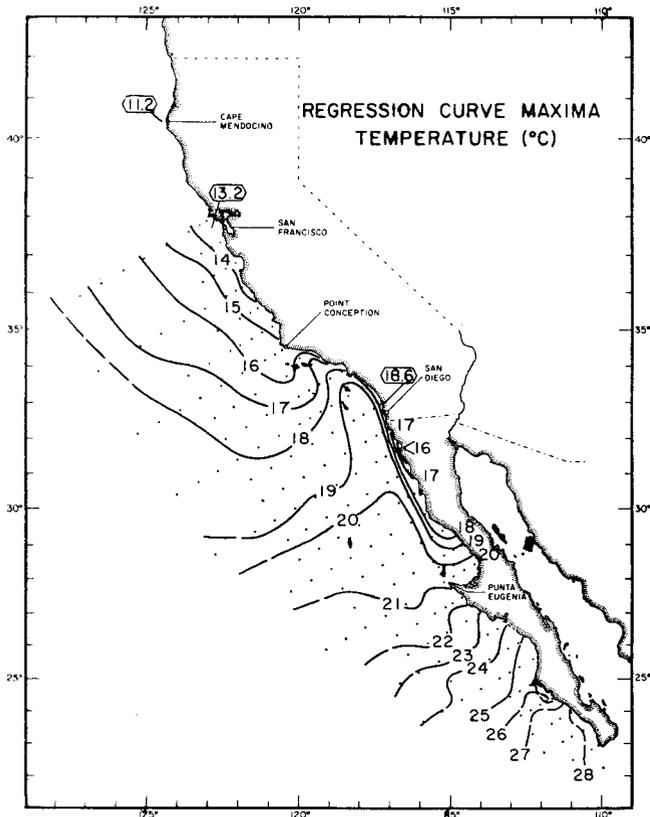
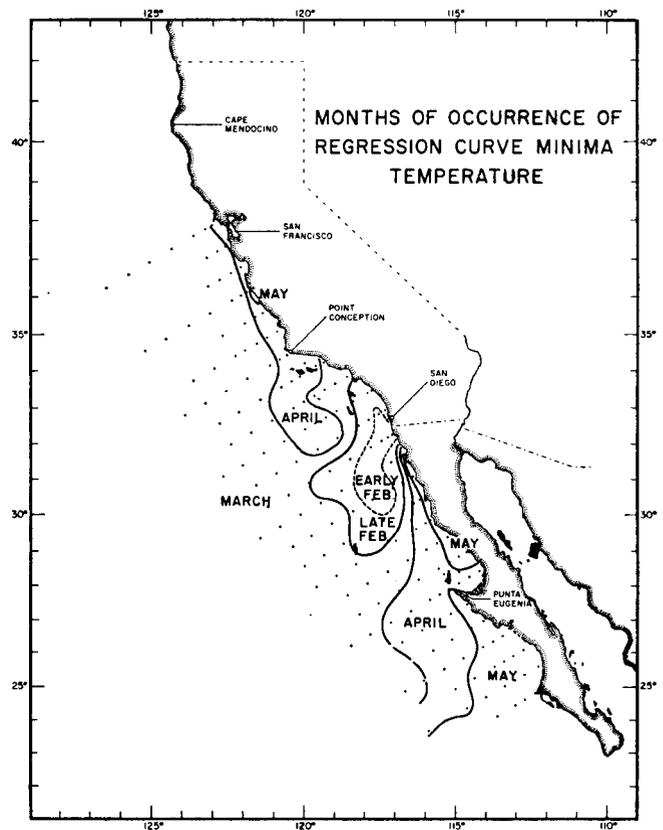
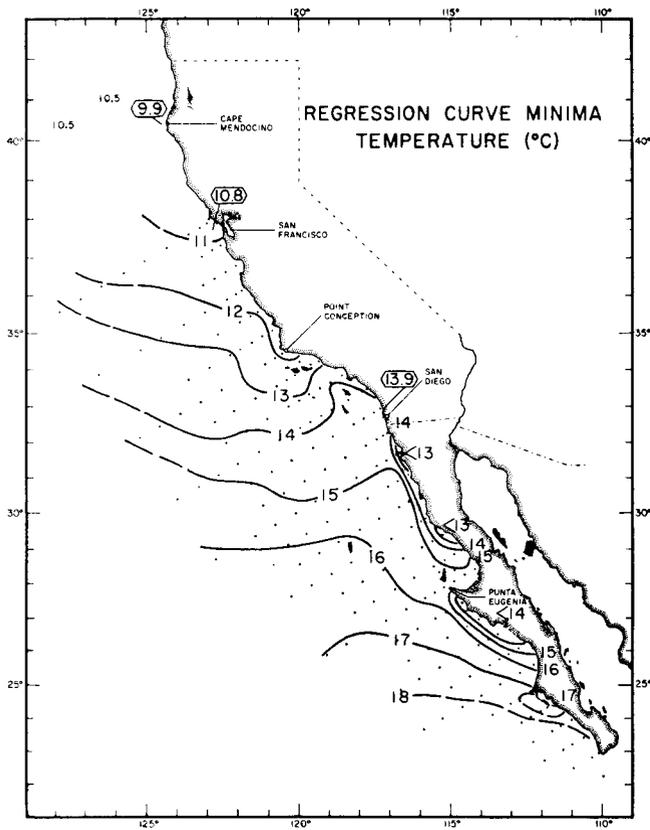


FIGURE 11. Extremes of temperature regression curves and corresponding months of occurrence.

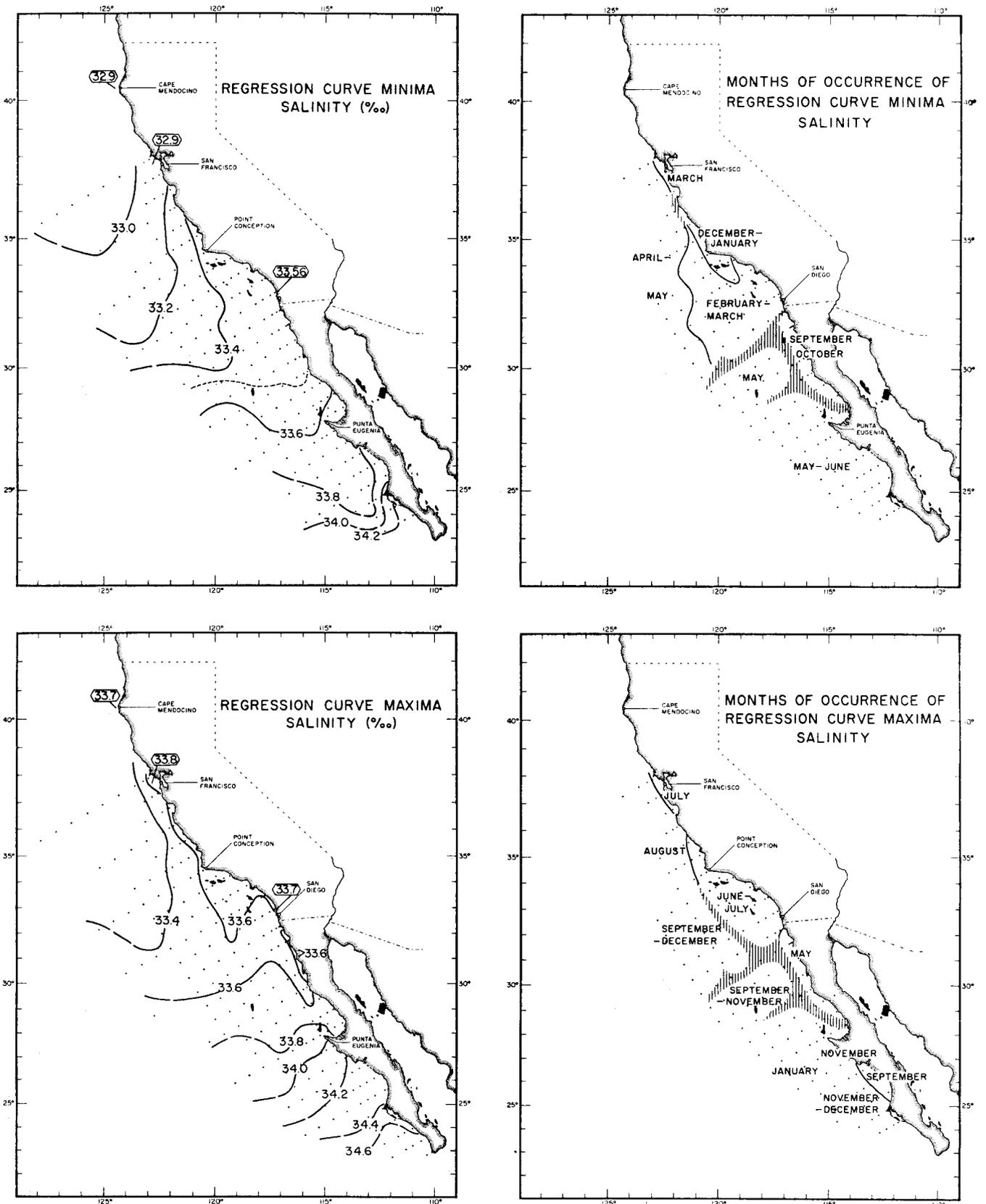


FIGURE 12. Extremes of salinity regression curves and corresponding months of occurrence.

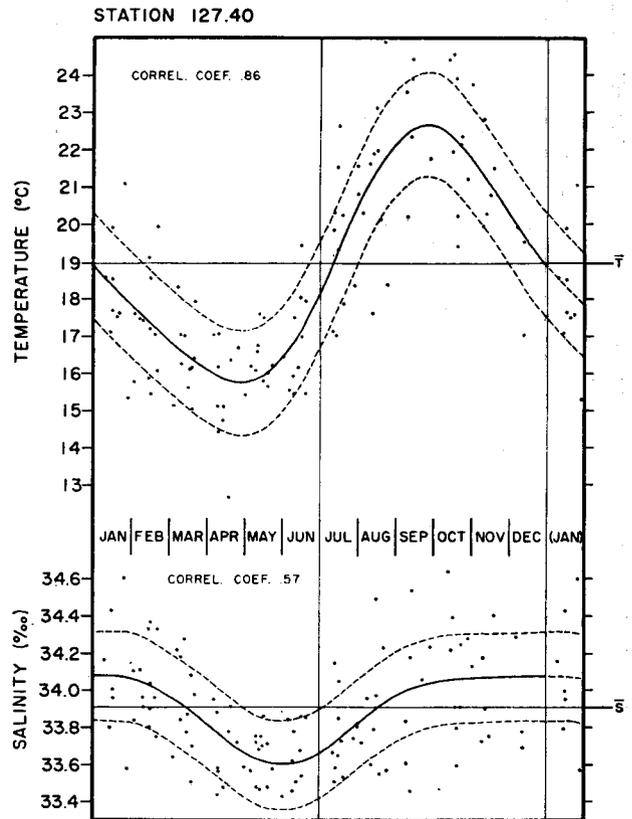
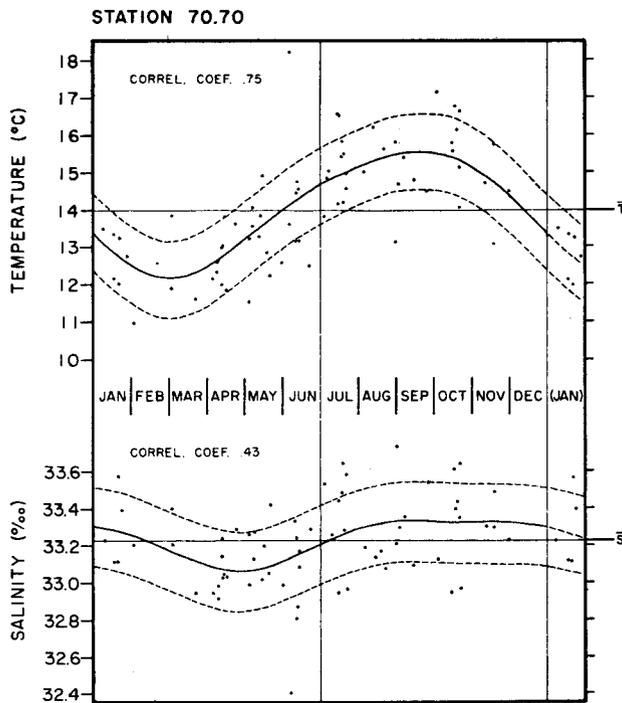
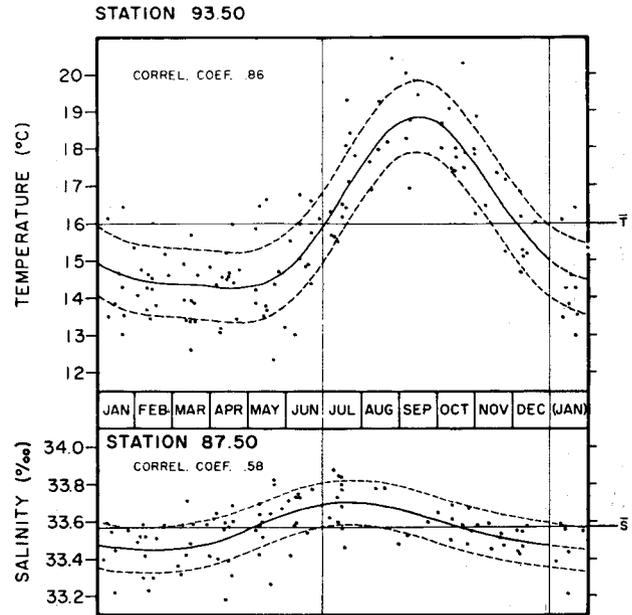
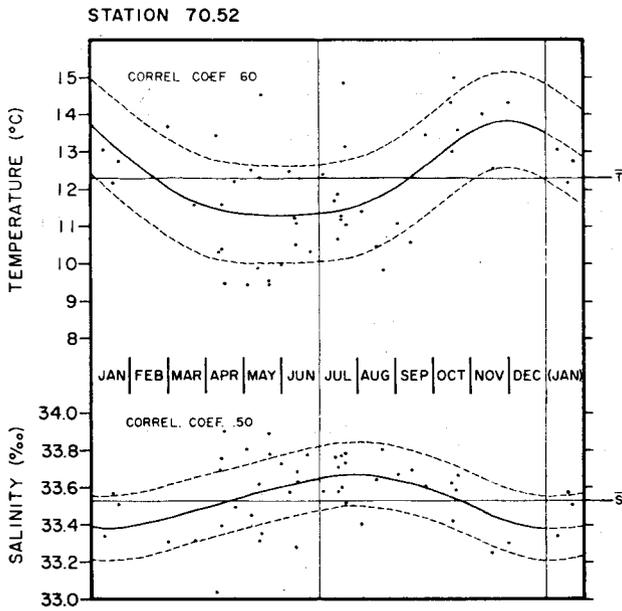


FIGURE 13. Station regression curves and observations. Station locations can be found with the aid of Figure 1. Horizontal lines are 13-year means. Dashed lines are drawn at plus and minus 1 standard error of estimate.

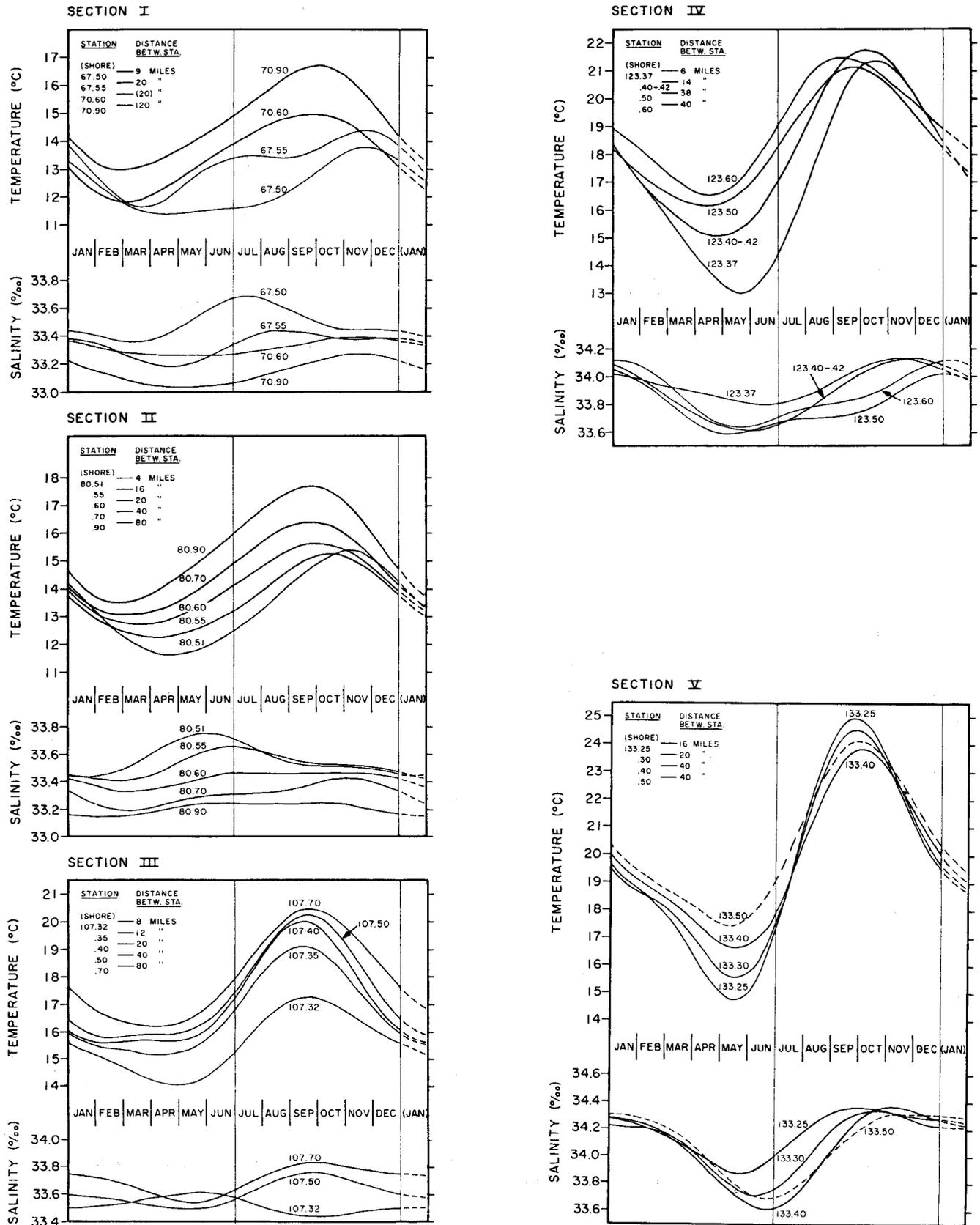


FIGURE 14. Station curves of seasonal variation of temperature and salinity grouped from lines perpendicular to the coast and labeled as sections. Sections locations are shown on Figure 2.

for 93.50 has a very small range and poor correlation, 0.17‰ and 0.33.

The temperature curve for station 127.40, off southern Baja California, has a 50-percent greater range than that for station 93.50, and a 50-percent greater standard error of estimate. These effects cancel to produce the identical correlation coefficient. The range of the salinity curve and its standard error of estimate are each greater by a factor of two than those for station 87.50; thus it also has the same correlation coefficient. At station 127.40 the seasonal temperature minimum is in late April and the seasonal salinity minimum in May. This aspect indicates an influence by some seasonal variation in circulation.

Station regression curves fall into regional patterns. Meaningful pattern variations occur perpendicular to the coast. Figure 14 gives station regression curves superimposed upon one another for easy visual comparison. For each graph, four or five stations were chosen that constituted a line section across the current and perpendicular to the coast. The locations of the line sections are shown as dashed lines in Figure 2. The jog in section I which includes stations from lines 67 and 70 was made to show typical station curves from stations that are well sampled. The distance between neighboring stations is given to provide the correct perspective of offshore temperature and salinity gradients. A time scale that is common to the temperature and salinity curves allows visual comparison of the variation of these characteristics.

As its temperature and salinity curves show, station 67.50 of section I is in an upwelling region. Station 67.55, 20 miles farther offshore, is similar to the offshore regime during the initial part of the upwelling season, but by midsummer the temperature curve responds to the effects of upwelling. The form of the corresponding salinity curve is also intermediate between those for the offshore and upwelling regimes.

Station 80.51, section II, near Point Conception does not maintain its low temperature as long as upwelling stations farther north. The slightly higher temperature at 80.51 than offshore in December and January may be caused by the winter countercurrent sometimes found along the coast.

The offshore temperature gradient along section III increases after the minimum temperature is reached and is largest at the time of the maximum temperature. Thus, the temperature gradient, but not the value of temperature, may indicate continued upwelling through September. Initial upwelling (station 107.32) brings high-salinity water to the surface. The salinity minimum follows the maximum by 4 or 5 months and coincides with the large temperature gradient. The salinity distribution charts for 10 meters (following text) for August through December reveal isolated low-salinity water in the upwelling region along the northern Baja California coast. This low-salinity water which replaces the isolated high-salinity water of May and June has its source in the salinity-minimum layer of the thermocline. The salinity mini-

um was described by Reid, Roden, and Wyllie (1958) and was the subject of a paper by Reid, Worrall, and Coughran (1964). These authors ascribed the minimum to freer horizontal mixing of the surface waters than of the thermocline water; the higher salinities of the west mix laterally into the surface water of the California Current more readily than into the thermocline layer. A study of data of CalCOFI hydrographic stations reveals that the salinity minimum which approximately corresponds to the 300 cl/ton thermocline anomaly¹⁰ surface extends to the coast in the latter half of the year. The higher salinity water upwelled in spring comes from a denser source. Thus, as the temperature gradients indicate, the upwelling may persist from spring through fall. Upwelling brings high-salinity water to the surface layers in spring and low-salinity water in fall. Though the offshore temperature gradient is maintained in this period the temperature goes from its seasonal minimum to its maximum.

Offshore, along section III, the salinity changes have phasing opposite to that of the nearshore regime in response to advection changes. In the intermediate region the opposing effects cancel and here no variation of salinity is found. This region has especially low correlation coefficient and range (Figures 9 and 10).

In surface distribution charts, station 123.37, section IV, appears to be the dominant upwelling station along a section of coast where the scope of upwelling is limited. The largest offshore temperature gradient occurs in late June, 2 months after the minimum temperature. Along station line 133, section V, the offshore gradient is largest at the time of the temperature minimum and an onshore gradient occurs at the maximum. Along both station lines the salinity minimum nearly coincides with the temperature minimum as in the offshore regions farther north. At this time an onshore salinity gradient is evident, perhaps produced by upwelling. Beginning in September, the four salinity curves of station line 123 fall into two groups, probably the result of a cyclonic eddy centered between stations 123.42 and 123.50 and the countercurrent.

DISTRIBUTIONS OF MONTHLY MEAN TEMPERATURE

Charts of mean temperature for each month were constructed from the curves of seasonal variation by digitizing the regression curves at midmonths (charts follow text). Smoothing of the contours was performed in the manner that gave greater emphasis to values at those stations which had relatively more frequent sampling (Figure 2). The stations offshore and south of Cabo San Lazaro were sampled infrequently during some seasons. In such situations, where the regression curve can only provide a tenuous

¹⁰ Montgomery and Wooster (1954). Approximately equivalent to the 24.97 σ_t surface.

interpolation, the values were excluded from the charts. Where the contours as drawn violate the given value, that value is shown in parentheses.

The seasonal variation of temperature off northern California can be characterized by noting the various positions of the 12° isotherm in the monthly charts. The broadest extent of water with temperatures less than 12 degrees occurs in March. Subsequent monthly charts show the development of a band of such cool water along the coast south to Point Conception. The 12-degree isotherm begins its retreat to the north in June and is not found in the last 3 months of the year. The maximum offshore temperature gradient from this cold upwelled water is in August.

The March temperature chart shows the tongue of warm water in the island area off southern California. This feature, which develops in prominence in subsequent months, occurs in the region of early (February) temperature minimum (Figure 11). It is produced from local differences in advection in conjunction with coastal upwelling (Reid, Roden, and Wyllie, 1958). The offshore waters are readily replenished with cold waters from the north whereas nearer shore the slower moving waters respond to the local heating. The coastal upwelling of deep cool waters causes the warmed nearshore waters to assume the tongue-like pattern. This feature appears in 10 of the monthly charts; the exceptions are January and February. Its greatest development comes in late spring and summer when the southern California eddy is reestablished.

The July and August charts both show an isolated warm region off San Diego. The separation of this region from the main body of water with the same temperature is significant and can be explained by the current flow. A northeasterly flow feeds water into the southern California eddy. Part of the northeasterly flow branches off to turn southeast along the coast of Baja California. The branching coincides with the center of the isolated warm region. At such a division the flow is sluggish. Along the northern Baja California coast the flow is relatively swifter and mixes with the upwelled water. This difference in rate of advection in conjunction with a net heat gain and the inclusion of upwelled waters produces the separation of warm waters. The isolated high-temperature region occurs in other months, though weakly, and would be revealed with a finer scale of contour interval.

In summer there is a 6° temperature difference between the warm waters off southern California, in the vicinity of Santa Catalina Island and the waters off Point Conception, approximately 120 miles distant. In winter the difference is less than 1°.

Upwelling along northern Baja California, as revealed by the temperature field, may occur throughout the year. Upwelling of cold waters is clearly characteristic of April through October; however, coastal temperatures remain less than offshore values throughout the winter. The temperature distribution

for individual CalCOFI cruises (CalCOFI Atlas No. 1) support this conclusion as to mean conditions. Small pockets of cold water are found along this coast in many winters. Because there is usually no seasonal countercurrent along northern Baja California, as is found elsewhere, the mass distribution associated with geostrophic balance (for a southerly flow) provides the tendency for lower inshore temperatures at 10-meters throughout the year. Along this section of coast the lowest temperatures occur in April, May, and June, and the largest offshore gradient occurs in July, August, and September. The temperature values at one station (100.29) near Punta Banda require an additional isotherm in seven of the monthly charts.

The upwelling south of Punta Eugenia is centered about station 123.37. The minimum temperatures again are in April through June, but the largest temperature gradient is in June and July. Upwelling ceases before September and does not resume until April. During the upwelling season the isotherms are nearly parallel to the coastline. By September the isotherms have swept northward and are nearly perpendicular to the coastline. During this change considerable warming takes place. In addition to *in situ* heating, an influx of more southerly warmer waters is suggested by the configuration of the isotherms. This influx also appears in the mean salinity distributions discussed later.

The data from the few cruises that extended to the southern tip of Baja California in the upwelling season indicate that a pattern similar to that seen off Punta Eugenia may exist off Cabo San Lazaro. The coolest water is found at station 143.26.

Whereas the distribution of mean temperature in the upwelling regions appears as smooth isotherms, the distributions for individual cruises—especially those with very close station spacing—show that the cold water appears as pockets and tongues. It is probable that higher frequency sampling of a denser pattern of stations would reveal a complex but significant distribution of mean temperature having recurrent upwelling pockets associated with coastal configuration, shelf topography, and local variations in wind stress. That the mean characteristics of a few nearshore stations define large and significant gradients supports this idea.

DISTRIBUTIONS OF MONTHLY MEAN SALINITY

Low-salinity water enters the CalCOFI region from the northwest. On the basis of the limited sampling available water of salinity less than 33.0‰ appears to be in or near the CalCOFI region throughout the year. There is little apparent seasonal variation of salinity in the low-salinity water, < 33.4‰, with the exceptions of the southeastward projecting tongue of water defined by the 33.4‰ isohaline, and the coastal upwelling regions. The tongue of low-salinity water extends farther to the southwest in spring than

in fall and, hence, its position correlates with the strength of the California Current. The coastal regime is complex and some difficulty results from the station spacing and sampling frequency. The station regression curves for stations near San Francisco Bay show marginal significance. The low-salinity effluent from the bay is greatest in the spring coincident with upwelling of high-salinity water north and south of the bay. A pattern of isohalines, broken at San Francisco Bay, is shown in charts for April through August. The pattern is simpler for the remainder of the year although the data for January, February, and March are not clear.

South of Monterey Bay water with salinity $> 33.4\%$ is always present in the mean. This salinity is greater than that found farther from the coast. The coastal high salinity is maintained by upwelling in the spring and summer and by the high salinity of the counter-current (either directly by the advection or by vertical mixing with submerged countercurrent waters) in autumn and winter.

Upwelling regions have high-salinity water in spring and summer. Beginning in March and carrying through until July an isolated high-salinity region develops along the coast north and south of Point Conception and among the Channel Islands. In August through October the isolated high-salinity region is found only among the islands having successively smaller extent. The large temperature gradient (6° C. in 120 miles in June) occurs within this body of water. In part, the high salinities are formed by upwelling in the vicinity of Point Conception and the distribution is further influenced by the circuitous flow of the large eddy. The mass distribution associated with geostrophic balance requires that denser water, in this instance the higher salinity water, be found at shoaler depths to the left of the direction of flow (in the northern hemisphere). The spring increases in current flow amplifies this effect. The reestablishment of the large eddy in June centers the denser water in the island region and causes the mixed layer to be thin. In the Channel Island region, at depth, there is a greater percentage of water of southern origin than offshore (Sverdrup and Fleming, 1941). This water has a higher salinity at a given density than water of northern origin. All of these facts favor high salinities in the island region.

The seasonal variation of salinity off southern Baja California is markedly affected by advection. Starting in spring and developing into early summer the isohalines bend sharply towards the southeast. The lower salinities form a tongue-like distribution. The higher salinities along the coast must in part be maintained by upwelling. The northwestward projection of high salinity water near Punta Eugenia in September indicates an influx of more southerly water and corresponds to a cyclonic eddy sometimes found there in this season.

NEW CHARTS COMPARED TO PREVIOUS CHARTS

The mean (monthly) temperature and salinity charts of CalCOFI Atlas No. 1 were constructed from station averages with a base period of 1950–59. Station averages based on fewer than five observations (for each month) were not used. Consequently, the distributions for some months have large gaps. The distributions of properties in the Atlas No. 1 charts and these newer charts are closely similar. The larger differences are in the salinity charts and in the areas of limited sampling. No attempt is made to provide representative differences because in some areas small differences may mean a large displacement of an isopleth whereas in other areas the opposite is true. The change in base period has an uneven effect depending upon sampling frequency and its change. The addition of the 33.5% isohaline (half of the standard interval) in the newer charts adds important definition.

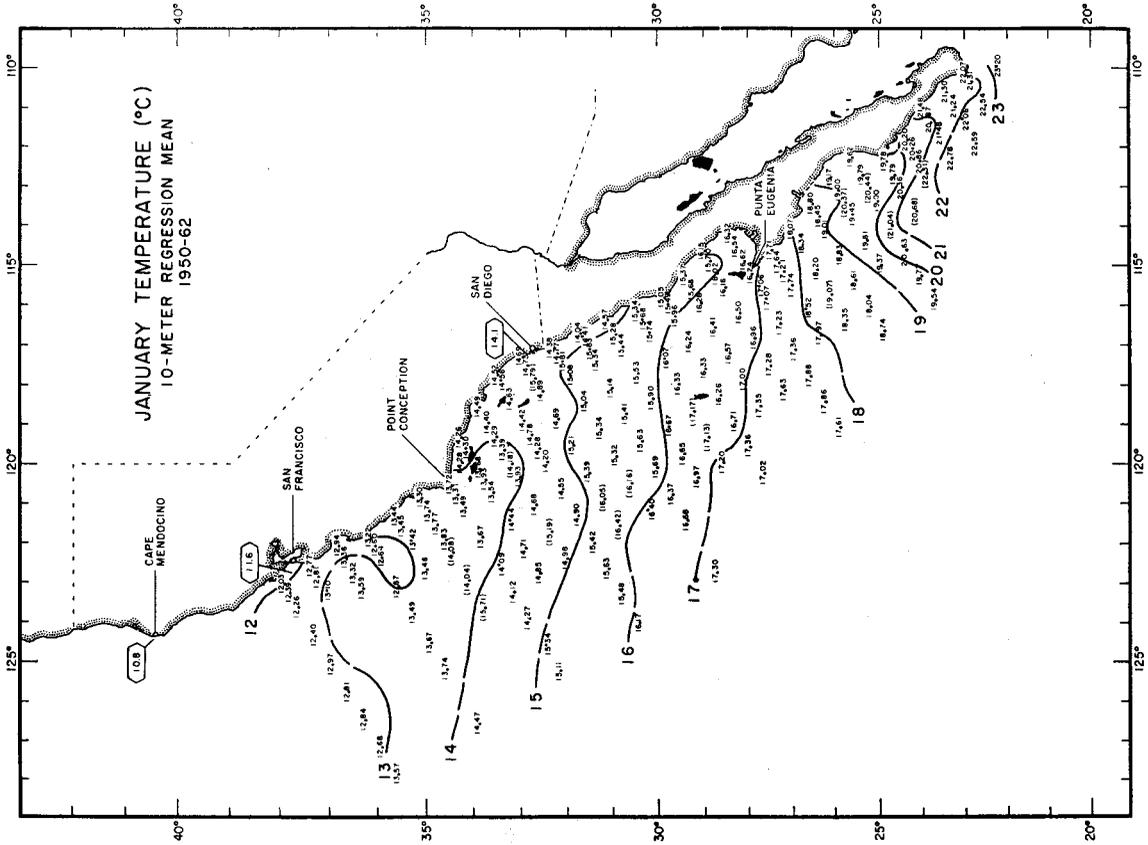
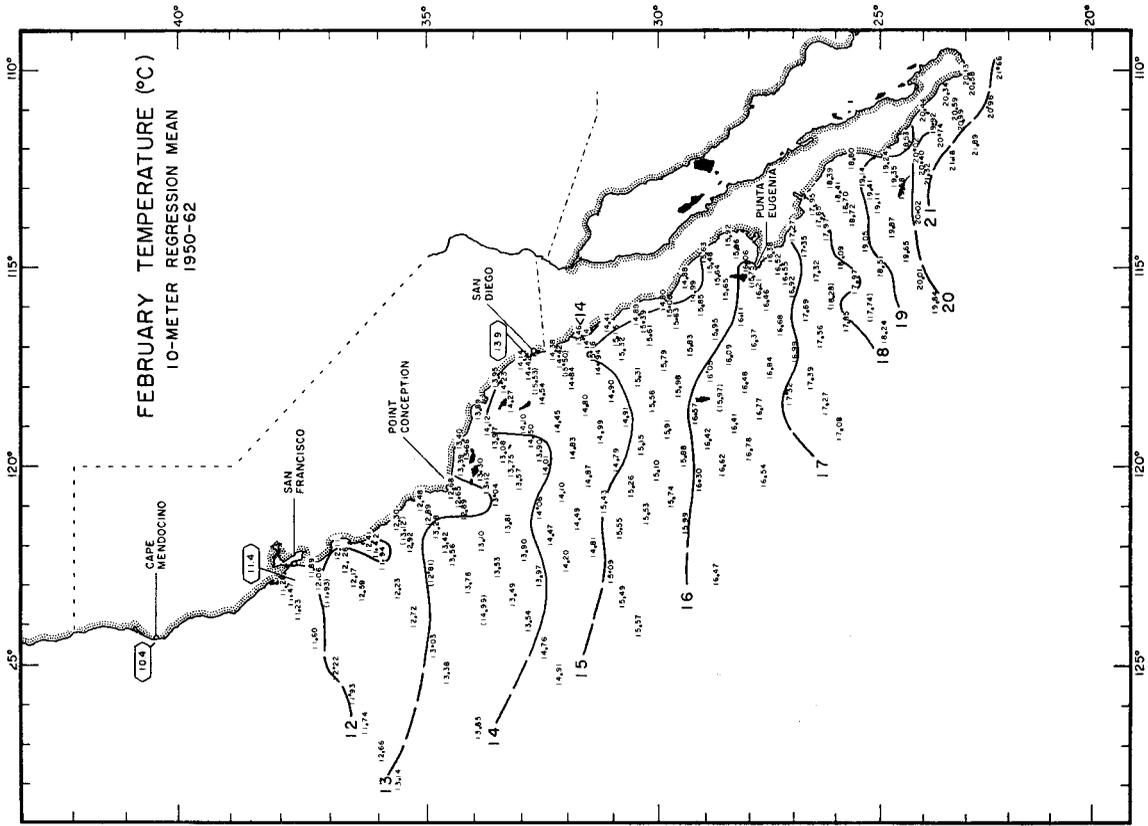
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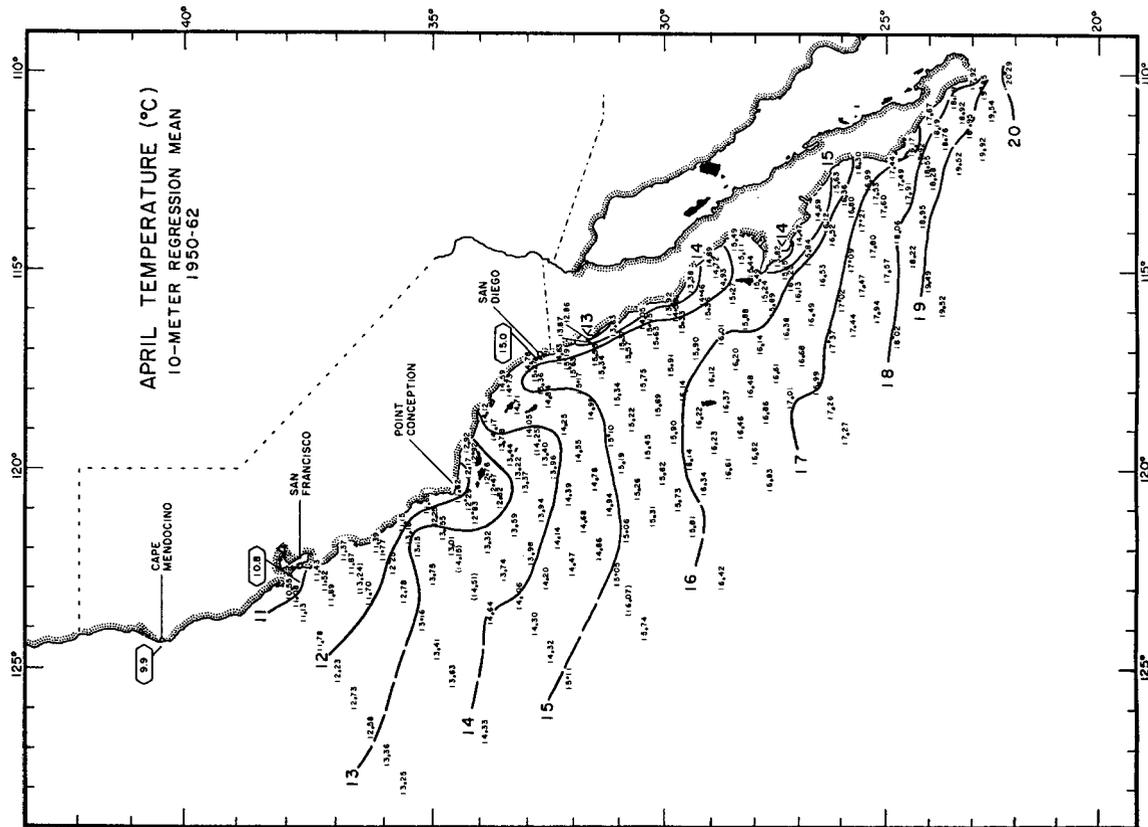
I thank Joseph L. Reid, Jr., and Gunnar I. Roden for guidance and many helpful suggestions. Marvin Cline did the computer programming.

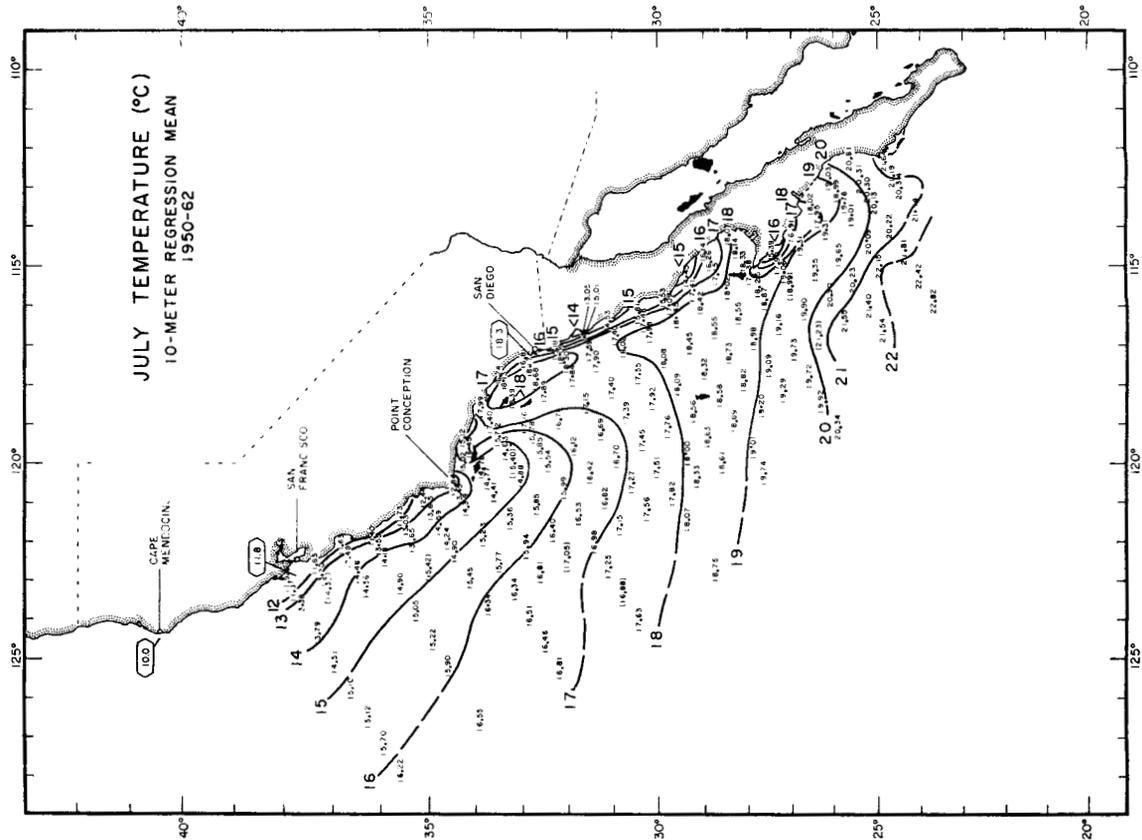
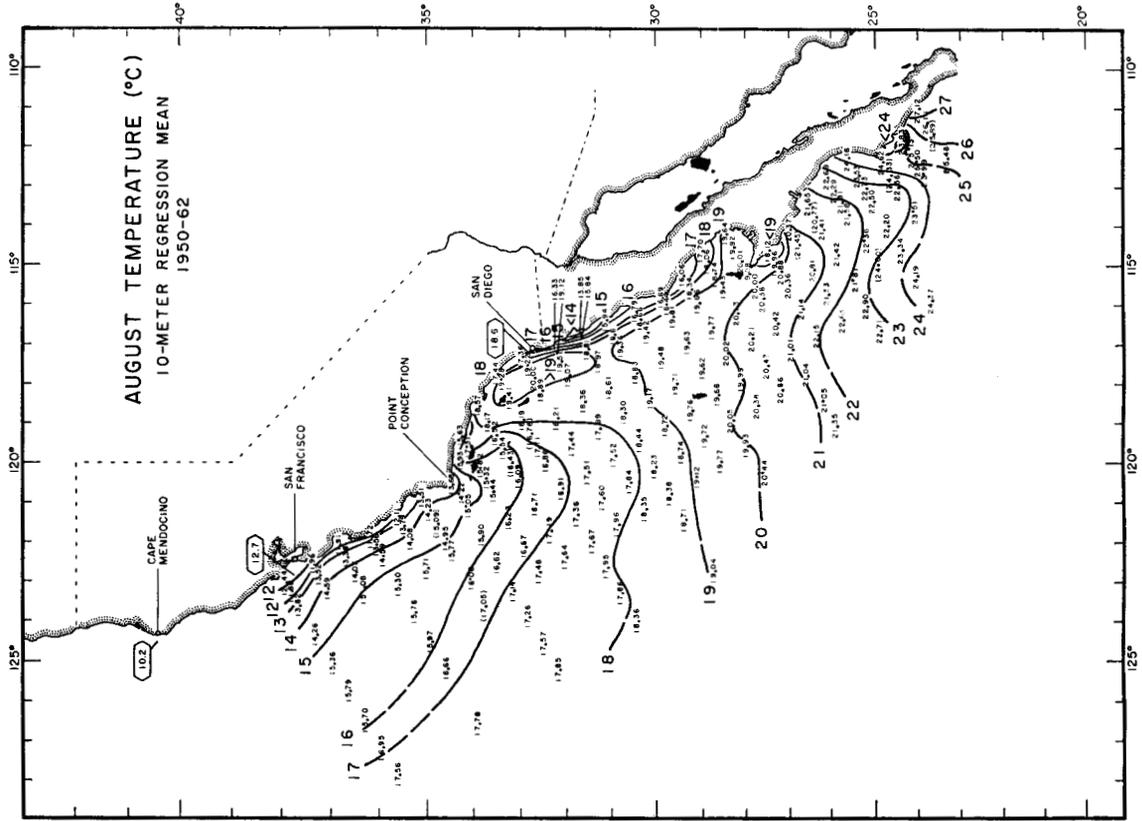
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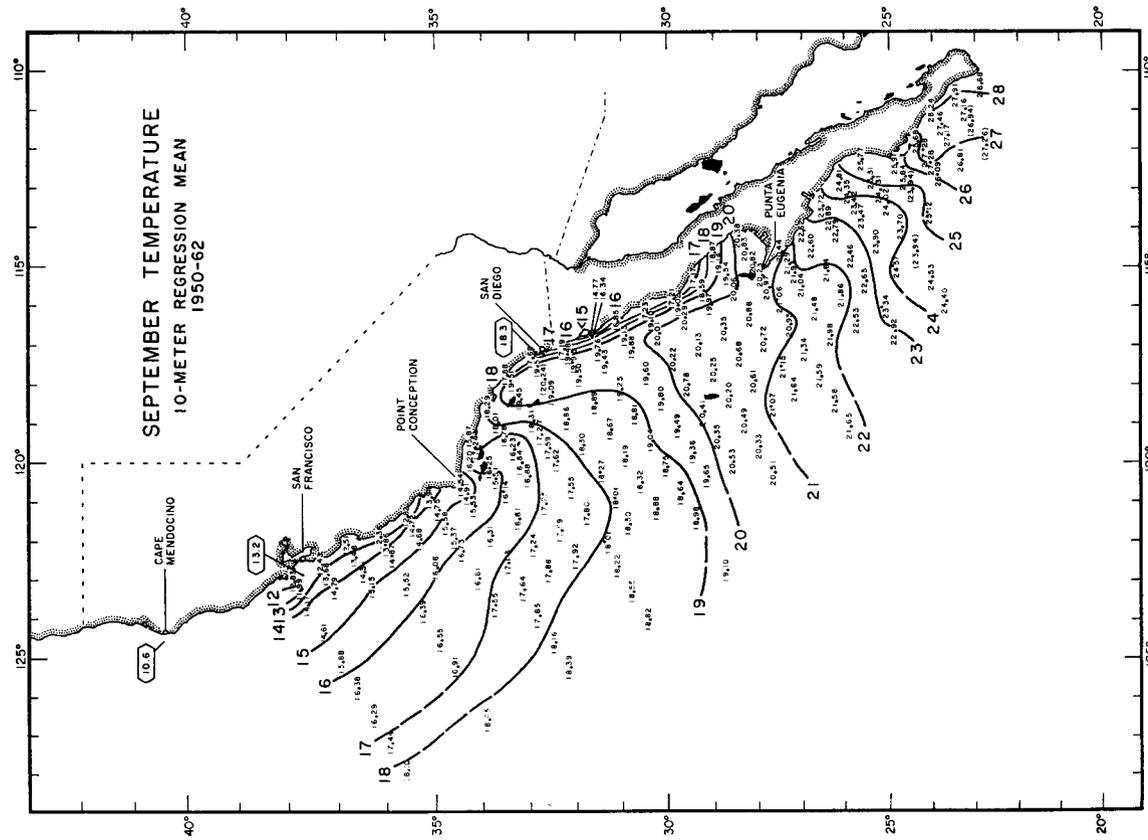
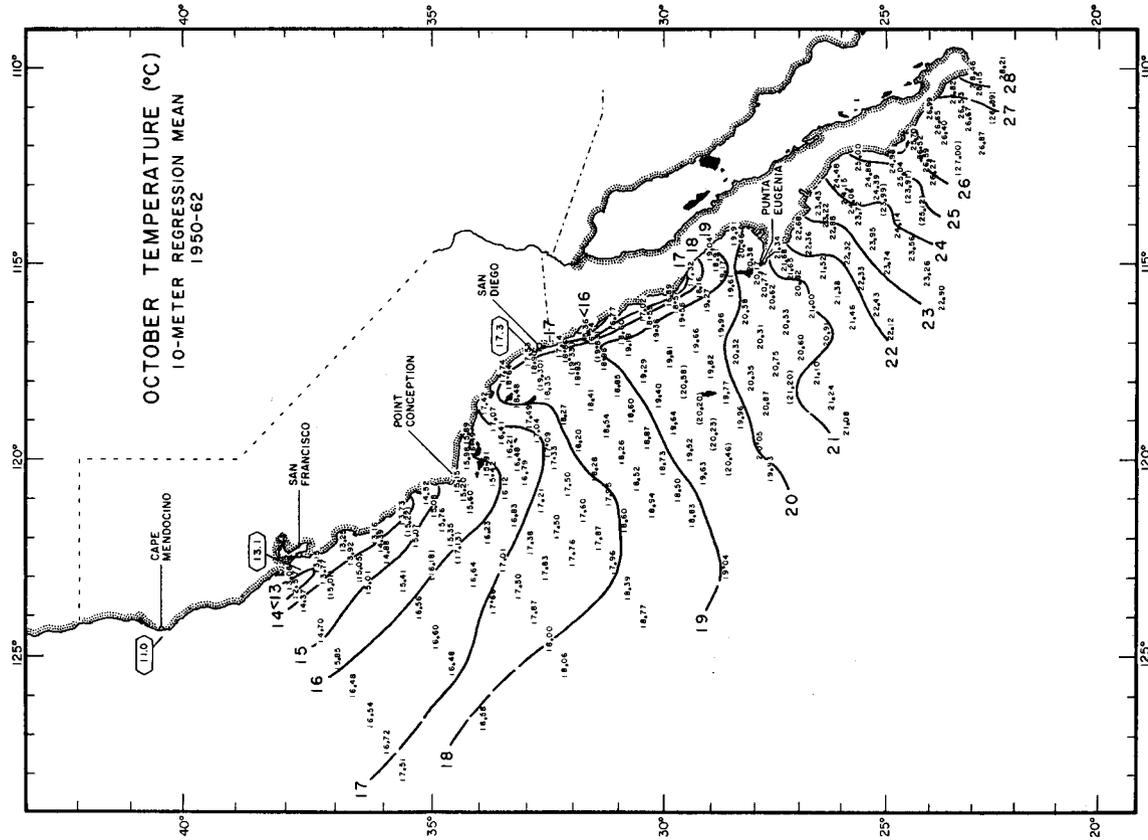
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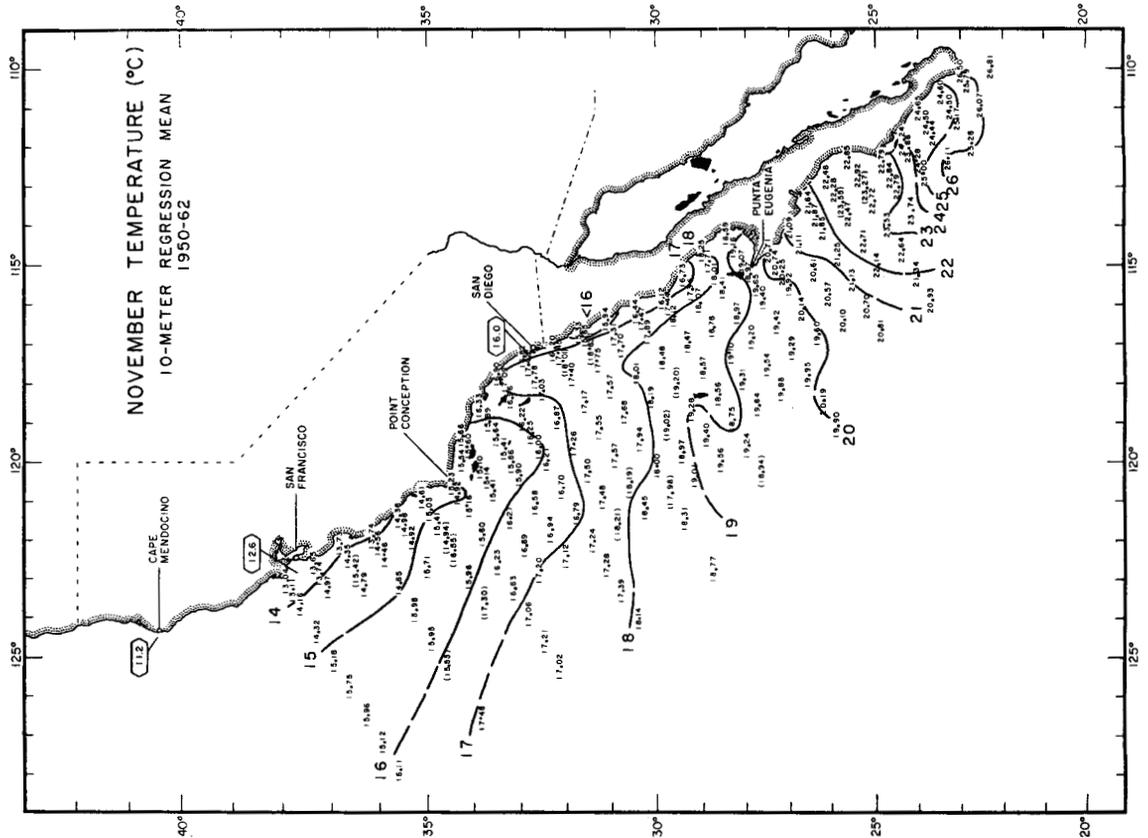
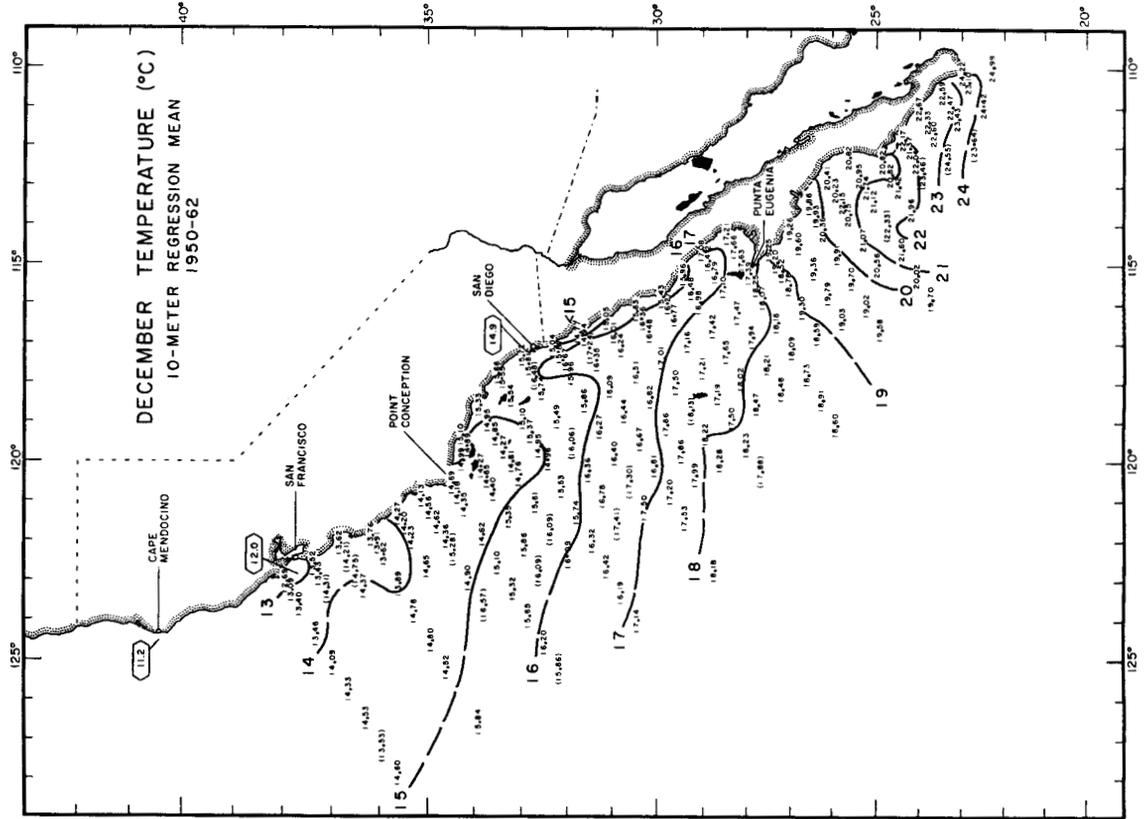
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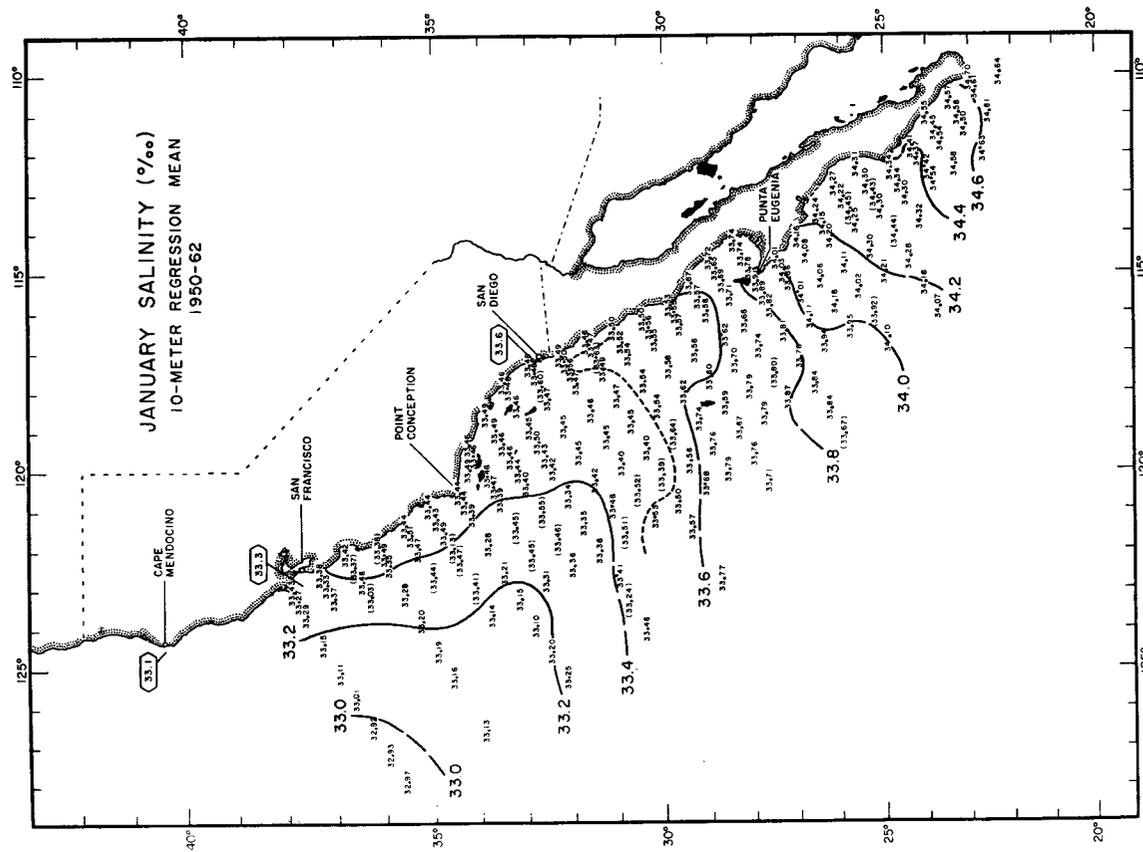
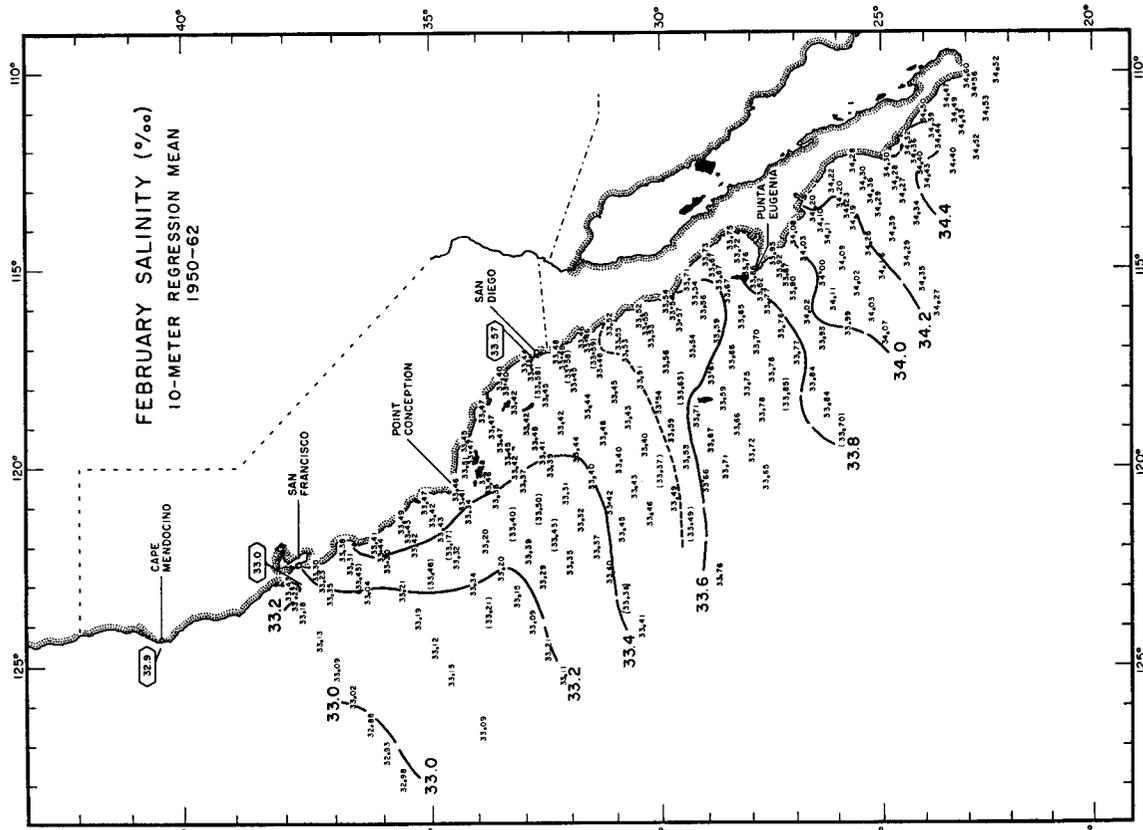


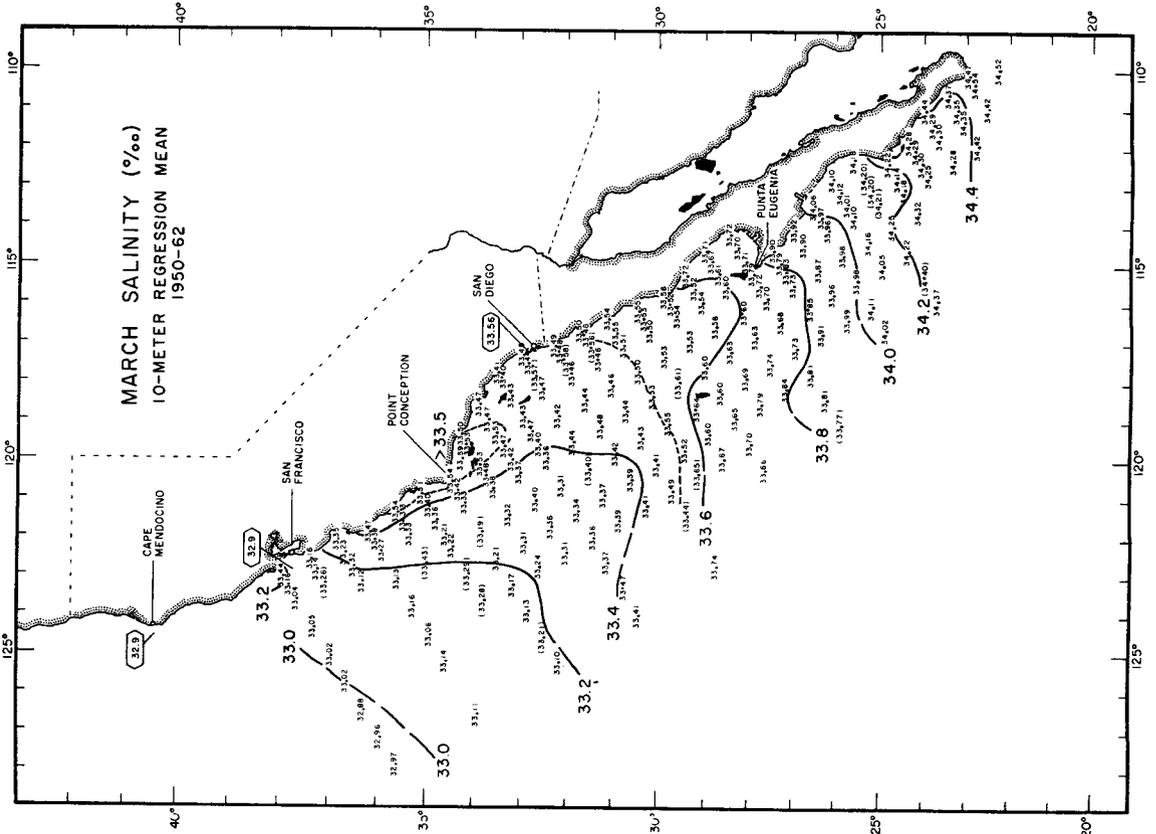
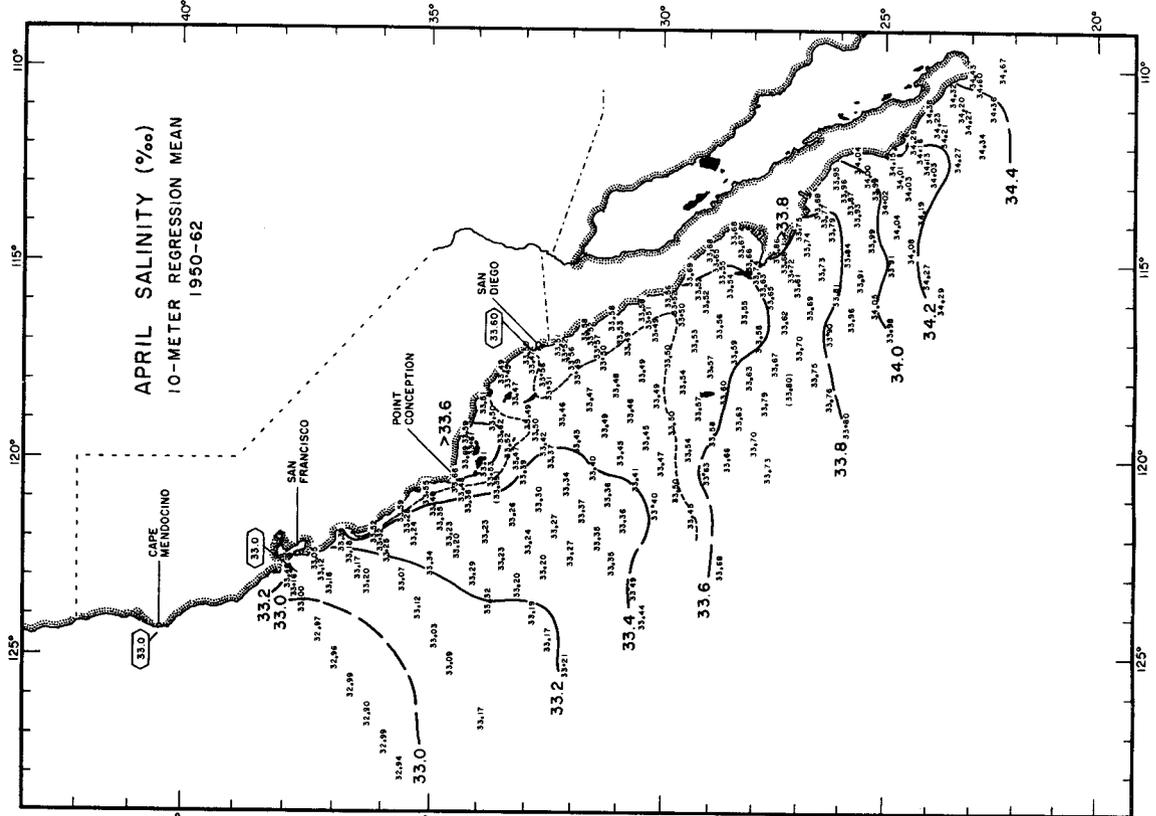


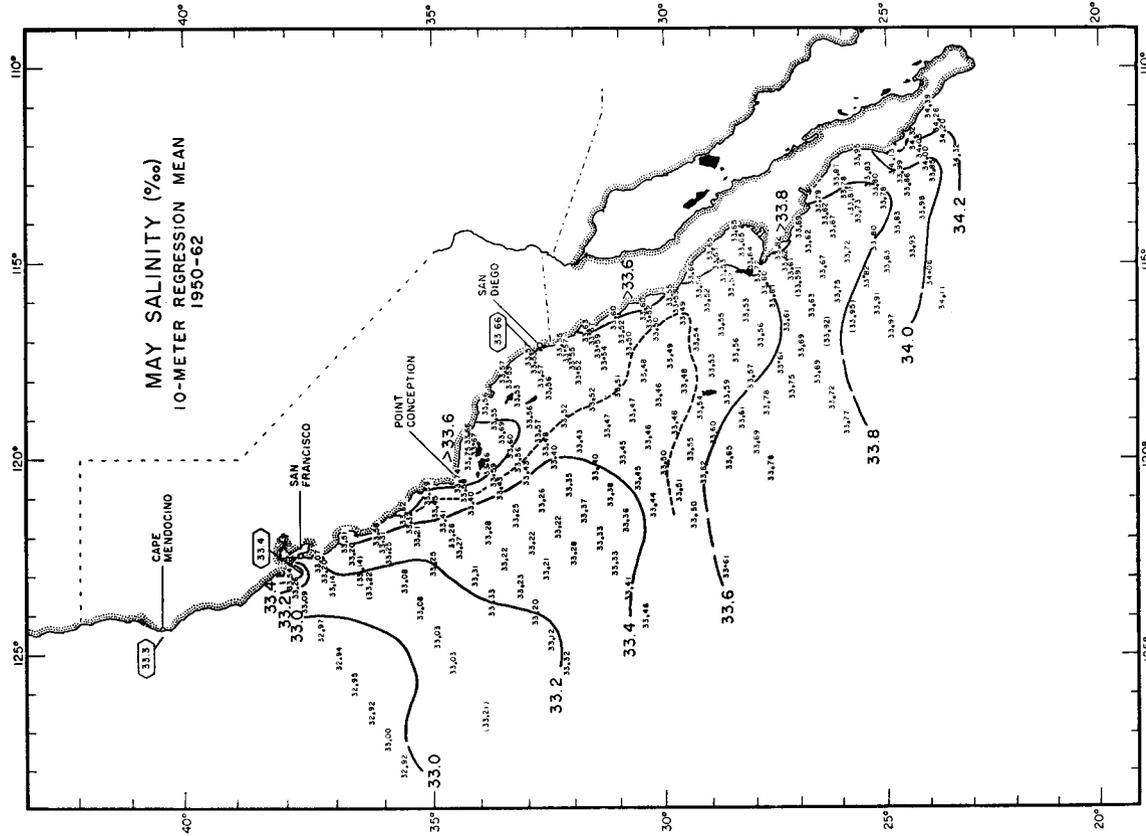
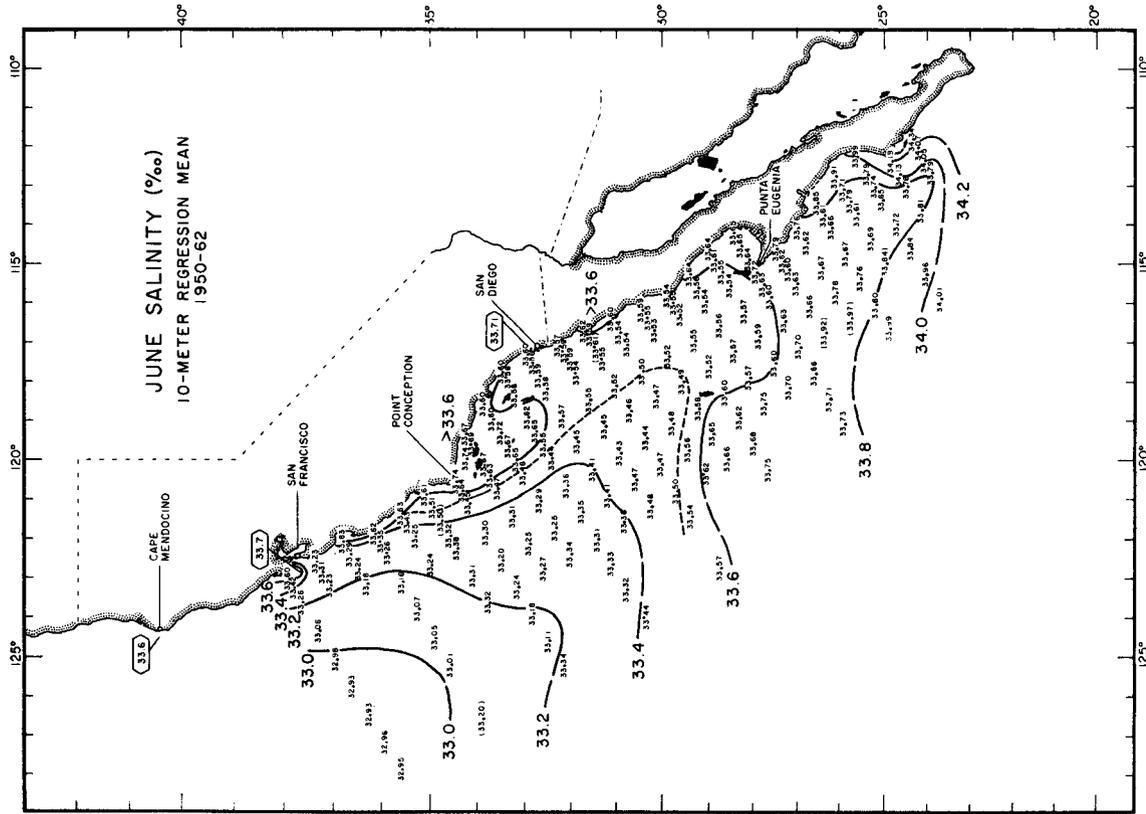


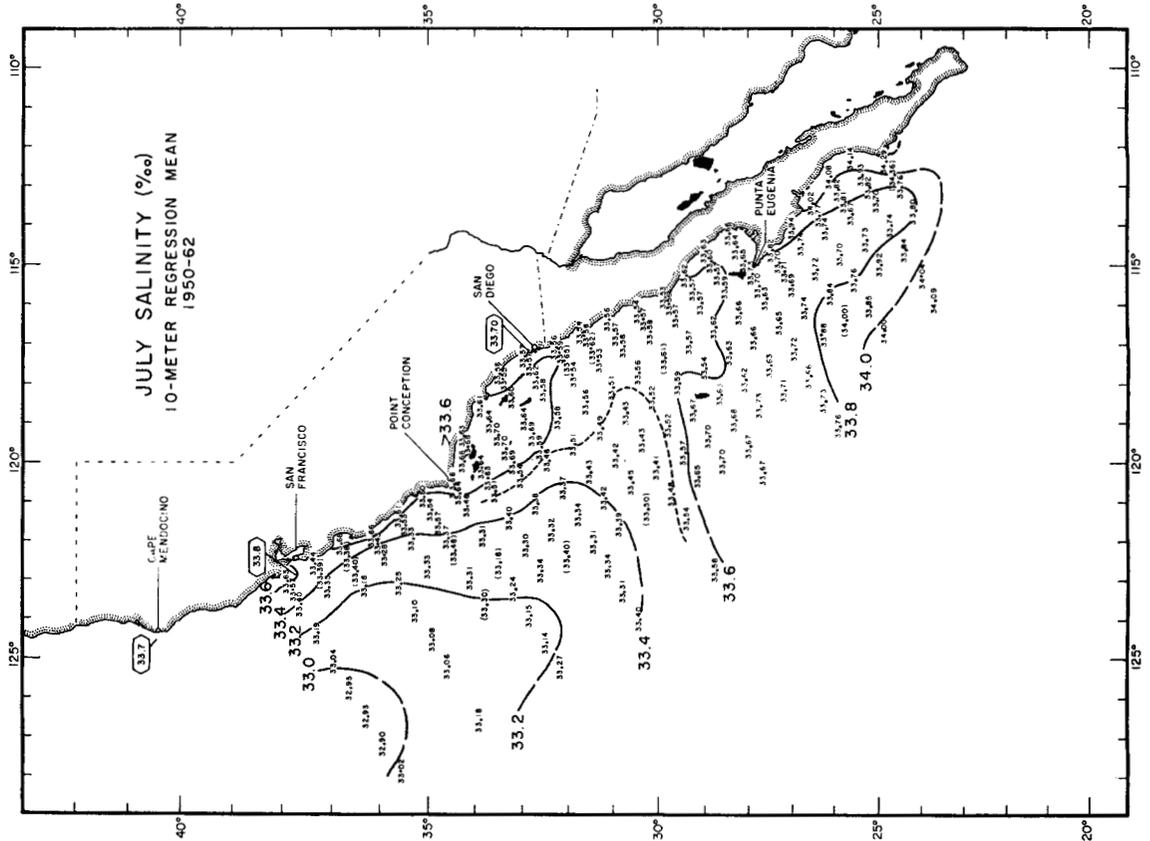
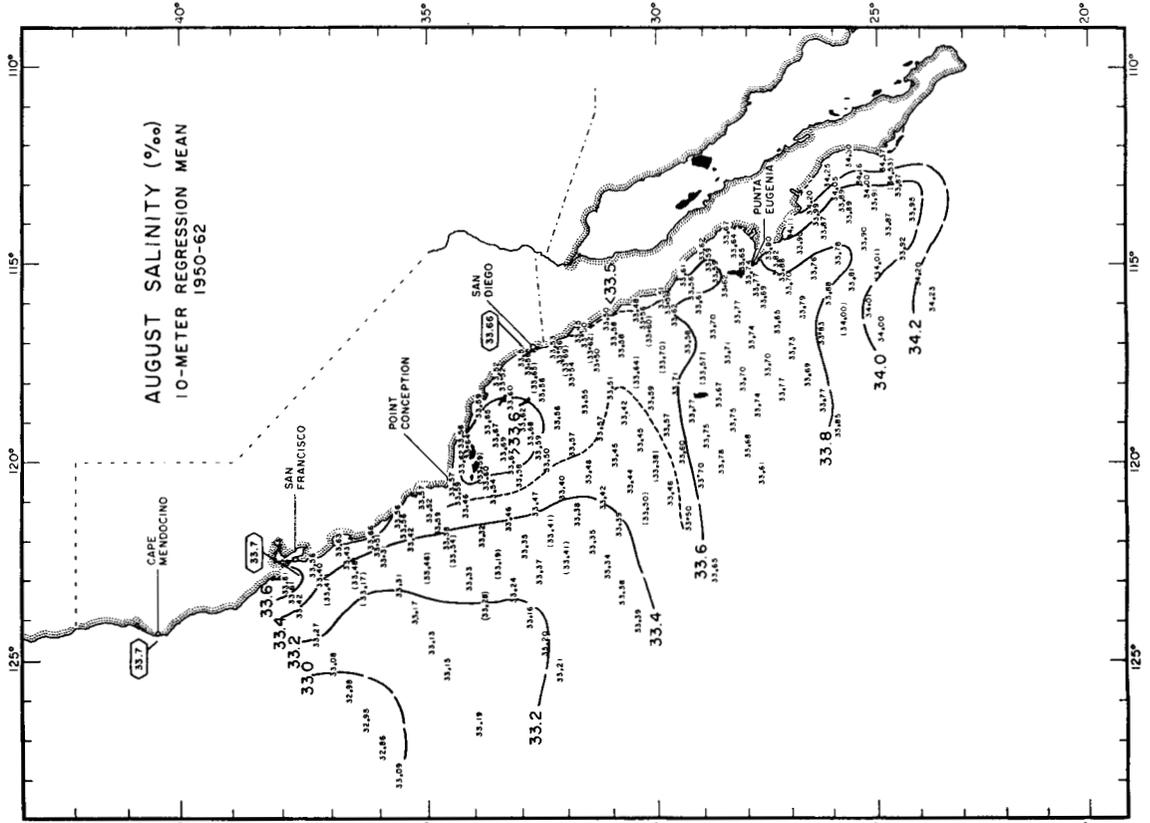


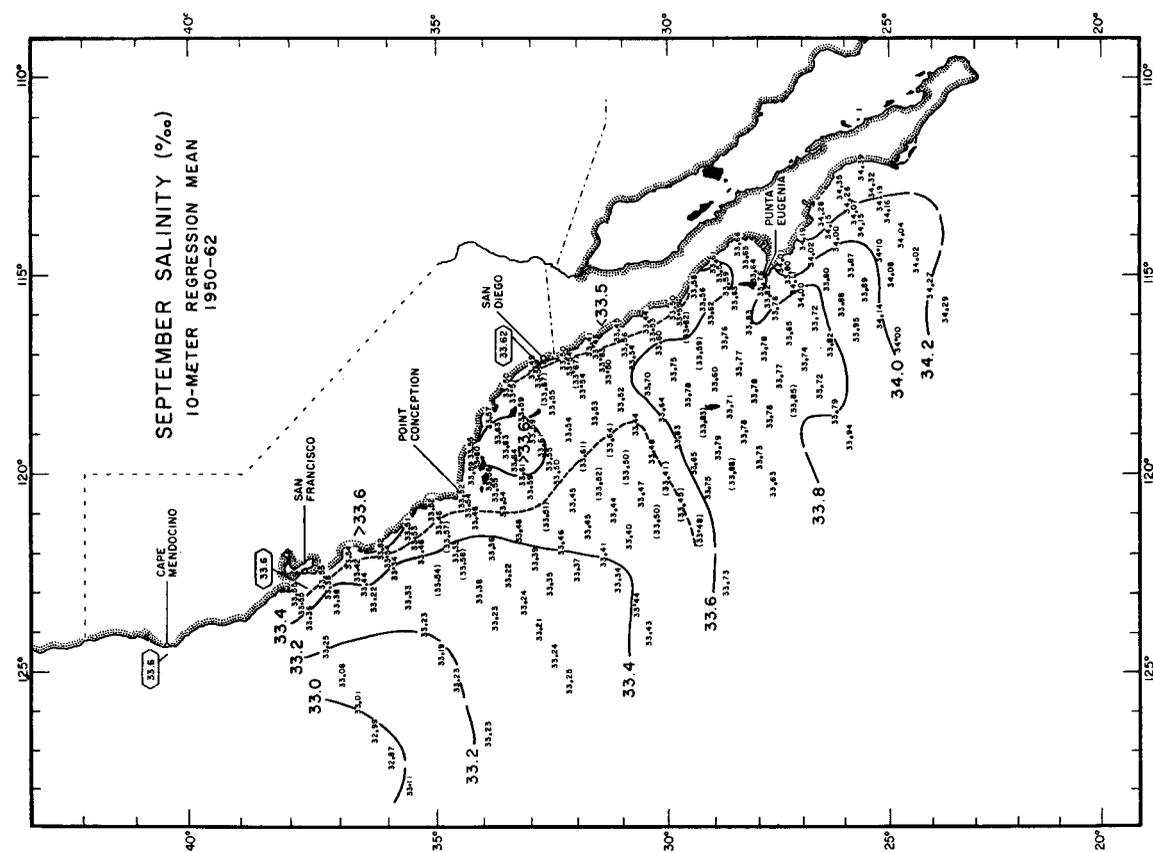
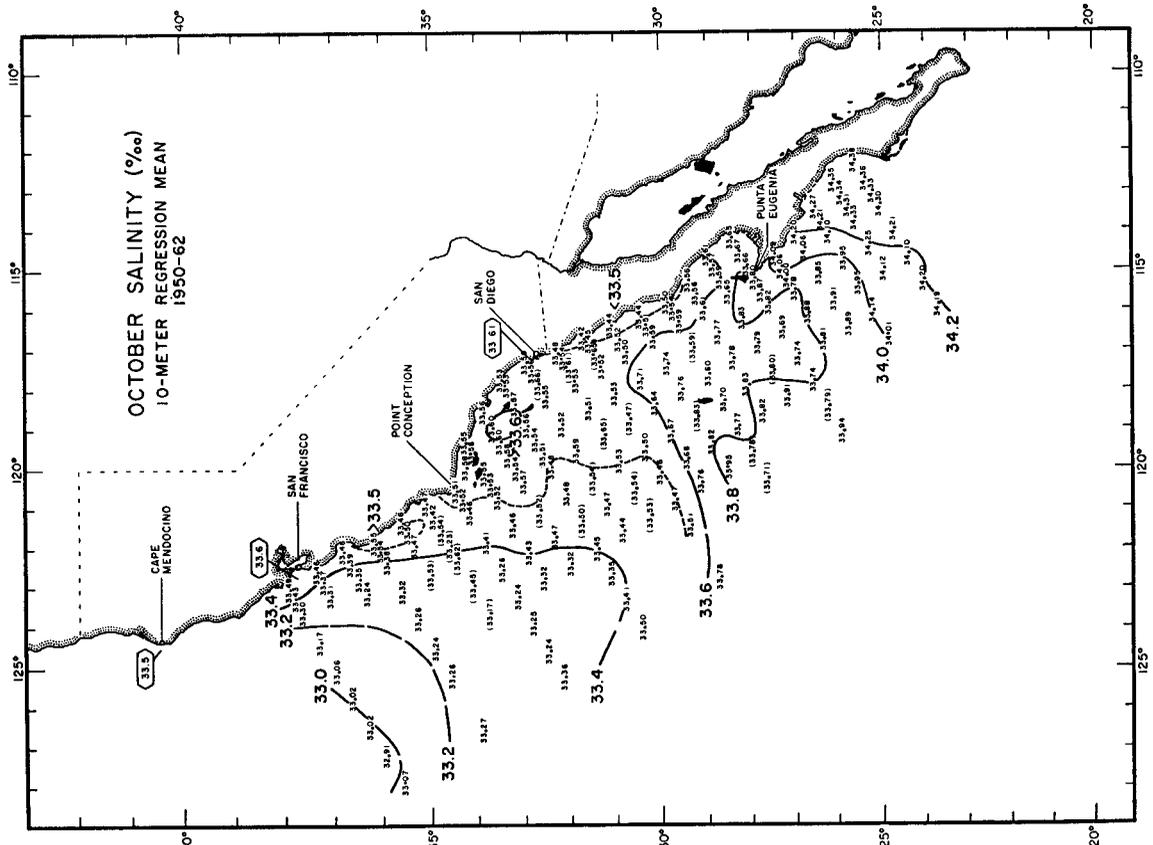


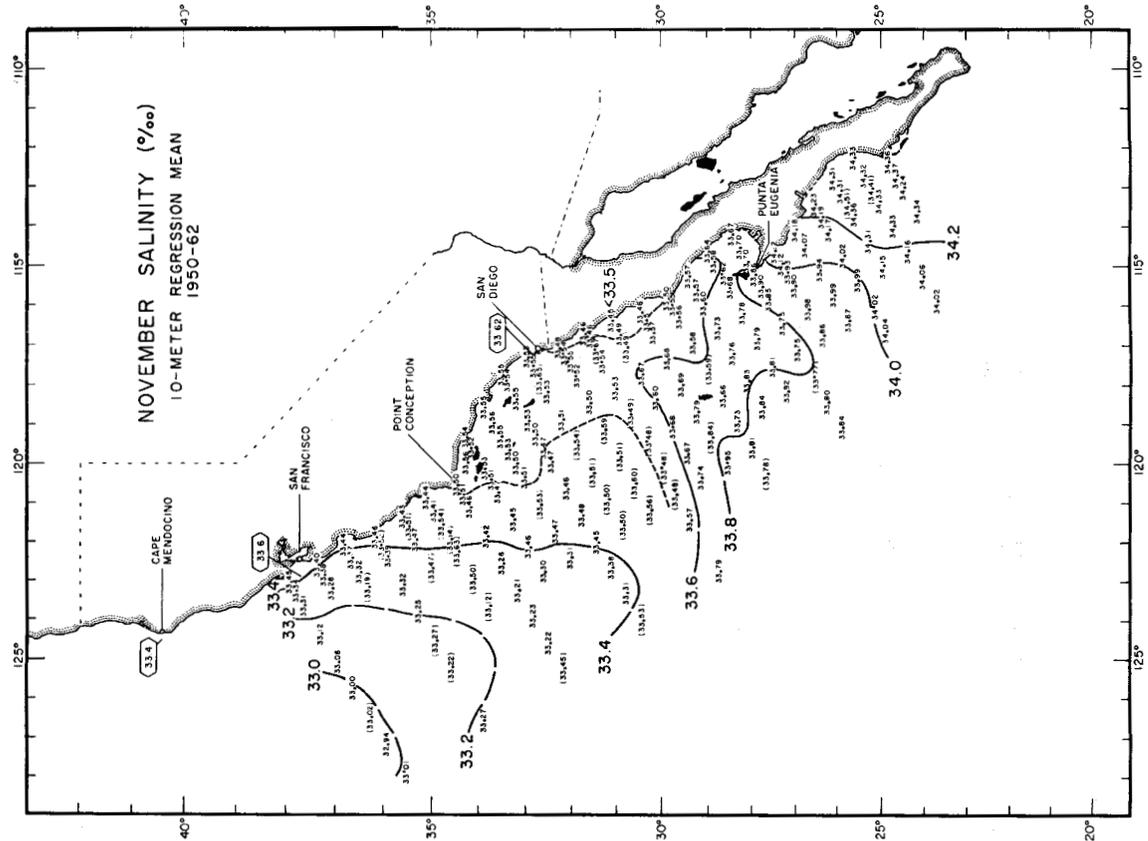
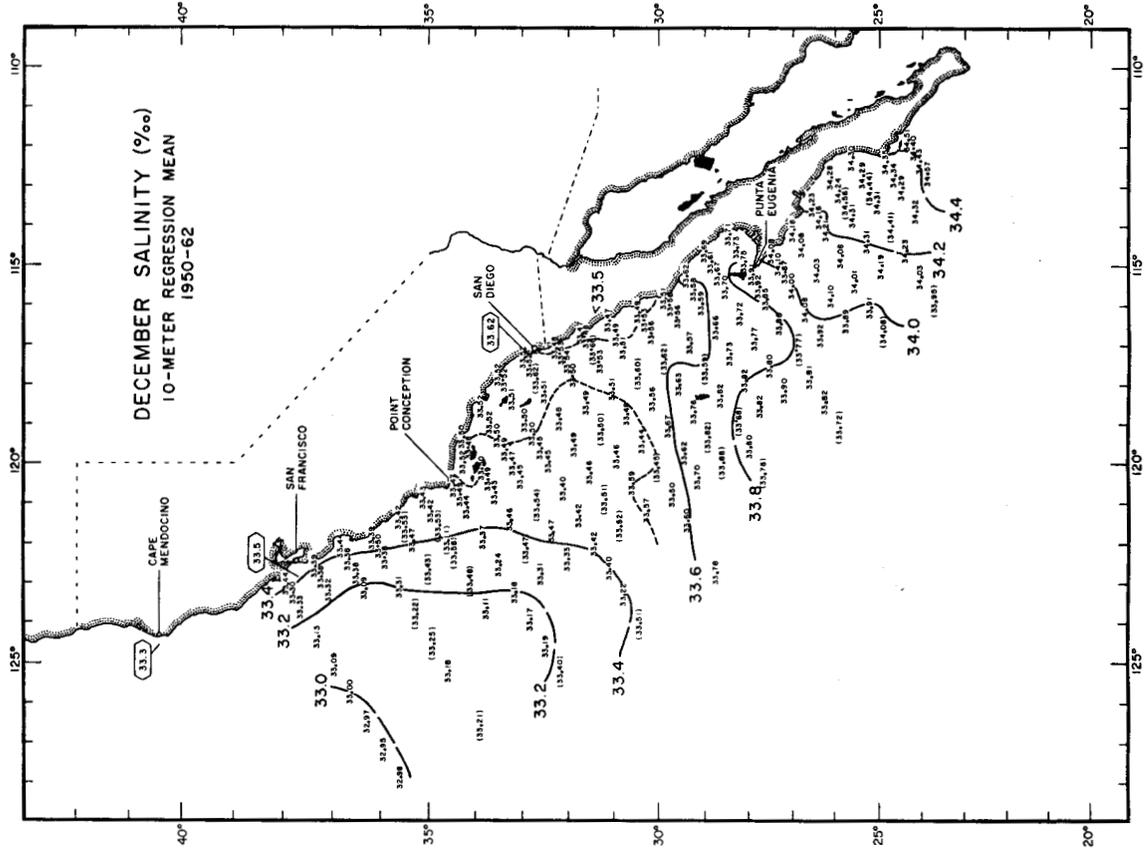




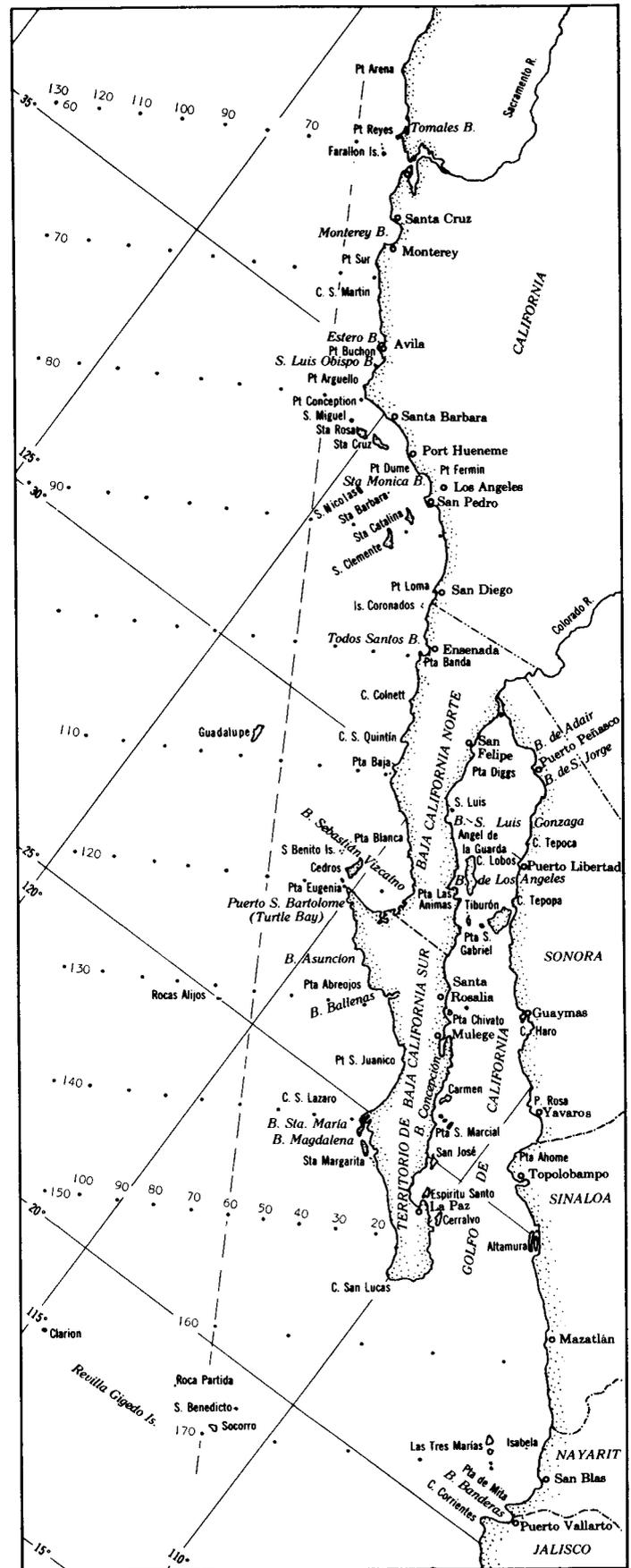
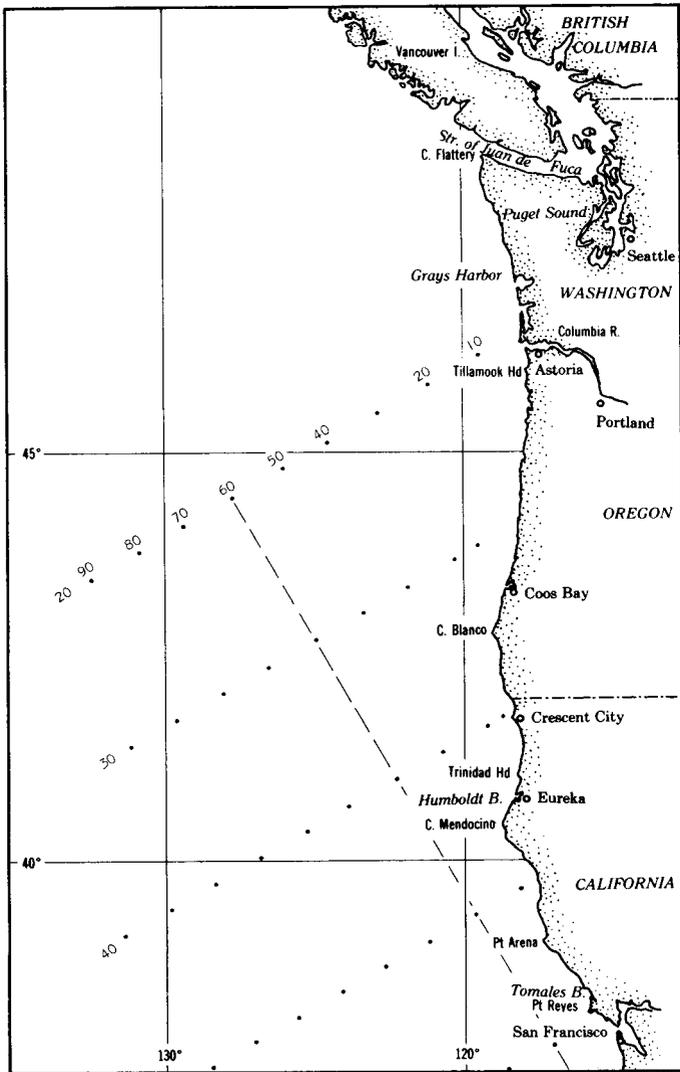








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These maps are designed to show essential details of the area most intensively studied by the California Cooperative Oceanic Fisheries Investigations. This is approximately the same area as is shown in red on the front cover. Geographical place names are those most commonly used in the various publications emerging from the research. The cardinal station lines extending southwestward from the coast are shown. They are 120 miles apart. Additional lines are utilized as needed and can be as closely spaced as 12 miles apart and still have individual numbers. The stations along the lines are numbered with respect to the station 60 line, the numbers increasing to the west and decreasing to the east. Most of them are 40 miles apart, and are numbered in groups of 10. This permits adding stations as close as 4 miles apart as needed. An example of the usual identification is 120.65. This station is on line 120, 20 nautical miles southwest of station 60.

The projection of the front cover is Lambert's Azimuthal Equal Area Projection. The detail maps are a Mercator projection. Art work by George Mattson, U. S. Bureau of Commercial Fisheries.

CONTENTS

	Page
I. Review of Activities	
1. Review of Activities July 1, 1963–June 30, 1966	5
2. Review of the Pelagic Wet Fisheries for the 1963–64, 1964–65, 1965–66 Seasons	21
3. Publications	22
II. Symposium on Anchovies, Genus <i>Engraulis</i>	
<i>John L. Baxter</i> , Editor	27
1. Oceanic Environments of the Genus <i>Engraulis</i> around the World	
<i>Joseph L. Reid, Jr.</i>	29
2. Synopsis of Biological Information on the Australian Anchovy <i>Engraulis australis</i> (White)	
<i>Maurice Blackburn</i>	34
3. A Note on the Biology and Fishery of the Japanese Anchovy <i>Engraulis japonica</i> (Houttuyn)	
<i>Sigeiti Hayasi</i>	44
4. Present State of the Investigations on the Argentine Anchovy <i>Engraulis anchoita</i> (Hubbs, Marini)	
<i>Janina Dz. de Cicchowski</i>	58
5. Influence of Some Environmental Factors upon the Embryonic Development of the Argentine Anchovy <i>Engraulis anchoita</i> (Hubbs, Marini)	
<i>Janina Dz. de Cicchowski</i>	67
6. Investigations of Food and Feeding Habits of Larvae and Juveniles of the Argentine Anchovy <i>Engraulis anchoita</i>	
<i>Janina Dz. de Cicchowski</i>	72
7. A Brief Description of Peruvian Fisheries	
<i>W. F. Doucet and H. Einarsson</i>	82
8. Preliminary Results of Studies on the Present Status of the Peruvian Stock of Anchovy (<i>Engraulis ringens</i> Jenyns)	
<i>G. Sactersdal, J. Valdivia, I. Tsukayama, and B. Alegre</i>	88
9. An Attempt to Estimate Annual Spawning Intensity of the Anchovy (<i>Engraulis ringens</i> Jenyns) by Means of Regional Egg and Larval Surveys during 1961–1964	
<i>H. Einarsson and B. Rojas de Mendiola</i>	96
10. The Predation of Guano Birds on the Peruvian Anchovy (<i>Engraulis ringens</i> Jenyns)	
<i>Rómulo Jordán</i>	105
11. Summary of Biological Information on the Northern Anchovy <i>Engraulis mordax</i> Girard	
<i>John L. Baxter</i>	110
12. Co-occurrences of Sardine and Anchovy Larvae in the California Current Region off California and Baja California	
<i>Elbert H. Ahlstrom</i>	117
13. The Accumulation of Fish Debris in Certain California Coastal Sediments	
<i>Andrew Soutar</i>	136
III. Scientific Contributions	
1. The Pelagic Phase of <i>Pleuroncodes planipes</i> Stimpson (Crustacea, Galatheidae) in the California Current	
<i>Alan R. Longhurst</i>	142
2. Summary of Thermal Conditions and Phytoplankton Volumes Measured in Monterey Bay, California 1961–1966	
<i>Donald P. Abbott and Richard Albee</i>	155
3. Seasonal Variation of Temperature and Salinity at 10 Meters in the California Current	
<i>Ronald J. Lynn</i>	157