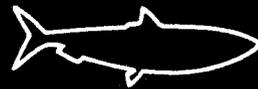




PROGRESS REPORT



STATE OF CALIFORNIA
DEPARTMENT OF FISH AND GAME
MARINE RESEARCH COMMITTEE

CALIFORNIA
COOPERATIVE
OCEANIC
FISHERIES
INVESTIGATIONS

Progress Report

1 July 1953 to 31 March 1955

Cooperating Agencies:
CALIFORNIA ACADEMY OF SCIENCES
CALIFORNIA DEPARTMENT OF FISH AND GAME
STANFORD UNIVERSITY, HOPKINS MARINE STATION
U. S. FISH AND WILDLIFE SERVICE, SOUTH PACIFIC FISHERY INVESTIGATIONS
UNIVERSITY OF CALIFORNIA, SCRIPPS INSTITUTION OF OCEANOGRAPHY

LETTER OF TRANSMITTAL

POST OFFICE BOX 807
LOS ALTOS, CALIFORNIA

HONORABLE GOODWIN J. KNIGHT
Governor of the State of California
Sacramento, California

DEAR SIR: We respectfully submit a report on the progress of the California Cooperative Oceanic Fisheries Investigations for the period 1 July 1953 through 31 March 1955.

The report is divided into three main sections. In the first we briefly review sardine research since the beginning of the program. In the second, we depart from the format of the first three reports of this series to present a formal scientific paper. This is *Population Dynamics of the Pacific Sardine*. The authors are Frances N. Clark, Director of the State Fisheries Laboratory, Marine Fisheries Branch, California Department of Fish and Game, and John C. Marr, Chief, South Pacific Fishery Investigations, U. S. Fish and Wildlife Service, and Director, Marine Life Research Program of the University of California's Scripps Institution of Oceanography.

The publication of this paper under the auspices of the Committee does not necessarily mean that the members of the Marine Research Committee subscribe to all of the conclusions reached in the paper; other conclusions are possible; as the paper itself discloses, the authors disagree on some aspects of the sardine problem. The paper does represent the best effort of two of the chief research workers in the field to construct a general theory that will explain many aspects of the sardine problem. The third major section of the report lists all publications that have arisen from the work under the California Cooperative Oceanic Fisheries Investigations.

Respectfully,

J. G. BURNETTE, Chairman
Marine Research Committee
D. T. SAXBY, Vice Chairman
RICHARD S. CROKER, Secretary
J. R. BIVEN
SETH GORDON
ROBERT C. MILLER
JOHN V. MORRIS
WM. J. SILVA
GILBERT C. VAN CAMP

ABSTRACT

In 1954, Nature conducted an oceanographic-fisheries experiment far beyond the scope of man.

Sardines spawned off southern California earlier and over wider distances than at any time since the start of the expanded sardine investigations in 1949.

Ocean temperatures off southern California were consistently warmer than in previous years.

The fishing season saw some sardines taken as far north as Avila.

In southern California, sixteen times the previous season's catch was taken.

The sardines came from off Mexico.

Whether they will return to California next year is beyond our present ability to forecast, but in this spring of 1955 they are spawning again in the southern California-northern Baja California center.

When the scientific data for 1954 are completely reviewed, we should be several strides nearer to being able to forecast where the sardines are, how many there are, and if they can be caught.

The important thing to remember is that the year 1954 was the one the scientists have been waiting for, a better year to contrast with the five bad ones previously studied.

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PART I: THE MARINE RESEARCH COMMITTEE, 1947-55

It seems unlikely that any marine fishery in California will face a situation more baffling than did the sardine industry in 1947-48. For several years the succulent little Pacific sardines had formed the basis of one of the nation's great fisheries. Approximately half a million tons were being taken annually; in some seasons the catch went well above that figure. Monterey's Cannery Row was known all over the world; less noted but equally thriving sardine ports were San Francisco and Los Angeles Harbor, with San Diego playing a minor role.

After dropping somewhat in the early 1940's, in 1947-48 the catch plummeted to a low of a little over 100,000 tons. Several scientific agencies had investigated the fish to the best of their means. But it was clear that there was not enough factual information on hand fully to explain the disaster or to predict the future of the fishery. Particularly needed was information on sardine behavior and distribution, to find out the influence of oceanic conditions on the sardine.

It was under these circumstances that the Marine Research Committee was formed by legislative action. The membership consisted of five men from the sardine industry, one public representative, and three ex-officio members—one from the Fish and Game Commission, two from the Department of Fish and Game.

A special tax was put on sardine landings and was later expanded to cover anchovies, jack mackerel, Pacific mackerel, herring, and squid. All but a fraction of these funds has been spent by the Marine Research Committee to foster research on oceanic fishes.

Bad as it was, the 1947-48 season was by no means the lowest ebb of sardine fishing in California. Much worse was to come. In the 1953-54 season only about 3,500 tons of sardines were landed in California, virtually all from southern California waters.

By that time, the scientists had worked for almost five years on intensified sardine investigations. They believed that they knew the answers to some aspects of the problem. But they had been working in an era when oceanic conditions seemed uniformly hostile to sardines. They had a great deal of detailed information on very bad years. What they sorely needed was comparable information on good years.

The scientists were working under the California Cooperative Oceanic Fisheries Investigations, as the expanded sardine studies have come to be known. The program was modeled upon investigations carried on continuously since 1919 by the California Department of Fish and Game and augmented after 1937 by the U. S. Fish and Wildlife Service. The plans for the joint oceanographic-fisheries research cruises were based on investigations undertaken between 1929 and 1932 and again between 1937 and 1940 by the Depart-

ment of Fish and Game and expanded in 1939 through 1941 by the cooperative efforts of Scripps Institution of Oceanography and the Fish and Wildlife Service. Scripps, Fish and Wildlife Service, California Fish and Game, and California Academy of Sciences planned the present broad program of investigations in 1947 and Hopkins Marine Station joined in the work in 1951. Their money has come from various sources.

To date more than four million dollars has gone into this program from state, federal, and industry sources. Of the total, the Marine Research Committee has directed the spending of \$772,960 in the fiscal years 1948-49 to 1954-55.

Of this sum, the Scripps Institution has received 29.6 per cent. Since 1949, as a rule, two university vessels have put to sea each month. These ships have sailed over 300,000 miles covering oceanic waters in a region that extends from the Oregon border to the tip of Baja California and 200 to 300 miles at sea. As a result, a large proportion (in 1954-55, an estimated 65 per cent) of the money Scripps has received through the University for marine life research has been spent on the collection of data at sea and its processing. Only the lesser share has been available for the important work of analysis of the data and conducting special studies. With the Marine Research Committee grants, the Institution has been able to undertake studies of the food of the sardines, of some oceanic plants, of the genetics of sardines. In addition, it has supplied editorial and illustrative services for the publications of the Marine Research Committee.

The South Pacific Fishery Investigations of the U. S. Fish and Wildlife Service has been given \$378,509, or 49.0 per cent, of the sum. The Fish and Wildlife Service has used the money to expand its studies of the eggs and larvae of sardines and to continue its joint studies with the Department of Fish and Game of the commercial catch, and to participate, with its vessel *Black Douglas*, in the routine oceanic surveys.

The California Department of Fish and Game has received 7.8 per cent of the total. This was used in part to purchase equipment, in part for salaries in connection with the Department's sardine studies. Through its regular budget the Department has conducted young fish and adult fish surveys, has kept records of the catch and age and sizes of sardines, mackerels and anchovies as well as all other commercial species, has participated in the very important scale reading program, and has collected material at sea for the use of the other agencies.

It has supplied one or more ships as needed, regu- larly the *Yellowfin*, occasionally the *N. B. Scofield*. At least one vessel has been at sea during approxi- mately ten months out of each year.

The California Academy of Sciences has received 7.5 per cent of the total. This agency has conducted studies of live sardines in the Steinhart Aquarium, investigating schooling behavior, feeding behavior, differences in behavior at different controlled tem- peratures, and behavior in an electrical field. (This last opens up at least the possibility of a new method of selective fishing, since sardines swim toward the positive electrode, and the largest fish are most easily affected.)

Stanford University's Hopkins Marine Station at Pacific Grove joined the program in the 1951-52 fiscal year. It has received 2.7 per cent of the total, using the money to conduct oceanographic studies in and near Monterey Bay, which will be of great value, particularly at such time as sardines return to that area.

The Committee has spent 3.4 per cent of the total on general operating expenses and the printing of its reports.

The Committee has been able to direct the expendi- ture of 97.5 per cent of the total returns from the special tax; 2.5 per cent was required to be paid into the Fish and Game Preservation Fund. This money, because of a quirk in the law which has just been changed, has not been available for any purpose whatever.

In reviewing the course of the investigations, it would be difficult to separate the results that have been obtained with "Marine Research Committee money" from those with "University money," "Fish and Game money," or "Federal money." But many results have been obtained; they appear in the form of reports and of papers in the scientific journals. By 1 January 1955, almost 150 such papers dealing with the sardine program had appeared. (These are listed later in this report.)

In April, 1947, the staffs of the California Depart- ment of Fish and Game, the U. S. Fish and Wildlife Service, and the Scripps Institution of Oceanography conferred and recommended a program of research that eventually was adopted as the expanded sardine program. It is interesting to compare this plan with the achievements of the program:

1947	1955
BIOLOGICAL RESEARCH	
I. Recruitment.	
a. Measurement of amount of spawning.	One major spawning area off southern California was known as early as 1930; a second off Baja California has been delineated. In 1954, approximately 325,000 billion sardine eggs were spawned in contrast to 440,000 in 1953, 145,000 in 1952, and 610,000 in 1951. Amounts of eggs of other species are also measured.
b. Measurement of the abundance of larvae.	This has been done annually.
c. Measurement of the relative abundance of year-class before it enters the fishery.	This has been done every year since 1950, for the several species, and has enabled comparisons with previous surveys made in 1938, 1939, and 1940.
d. Measurements of the sizes of year-classes in the commercial fishery.	This work, which has been done every year since 1932, and which has provided the basis of much of the research on the sardine, has continued.
e. Studies of the spawning stock on the spawning grounds.	These have been conducted whenever possible.
II. Availability of the stock to the fishermen.	
a. Analysis of the commercial catch.	This work, begun in 1919, is also of a continuing nature, and has been done.
b. Exploratory work on and off the fishing grounds during the fishing season.	This has been done.
c. Exploratory food studies.	This has been done insofar as it concerns sardines. There has been some work on other species.
III. Investigation of rapid methods of plankton collection and analysis.	
This work was done in the early years of the program. It provided tools and techniques that are becoming standard in the field.	
IV. Physiological studies of behavior, feeding, and nutrition.	
These studies are continuing.	
V. Dynamics of the sardine population and fisheries.	
This is being done. A paper that represents an attempt to construct a general theory of sardine populations comprises the major part of this report.	
PHYSICAL AND CHEMICAL OCEANOGRAPHY	
Approximately 6,000 "oceanographic stations" have been occupied. The informa- tion gained from these cruises should make the California waters the best under- stood in the world and will be basic to any future studies of the eastern Pacific and its resources.	

In addition to these tasks accomplished, valuable new information has been gained on species that are now little exploited or not at all, such as hake and sauries, which have been found to be present in large numbers.

The Committee has thus been instrumental in the progress of a program that has enormously expanded our knowledge of the California waters. A dramatic instance of the potentialities of such information occurred last fall:

The biggest news in sardine research in 1954 occurred outside the laboratory. Nature obligingly conducted an oceanographic-fisheries experiment far beyond the scope of man.

Between two and five billion sardines came north from Mexican waters to provide California with the best catches since 1951-52.

The fish started coming northward in the spring. Egg-and-larva surveys showed widespread spawning quite early in the year.

Water temperatures showed a marked increase in the early spring.

Together, these factors indicate that wide spawning off southern California may depend largely on the right temperature at the right time of year. And if the sardines come to southern California to spawn, they may remain there (or return) to be caught.

This theory has been advanced several times, but it has never been possible to nail it down before. For five long years (1949-53) ocean temperatures off the coast varied so little from year to year that oceanographers would have had to concede that if fish were responding to these slight differences they were more acute than our most sensitive measuring instruments.

Then early in 1954, ocean conditions changed.

The first evidence of the change came from charts of surface temperatures. These are plotted up after each cruise. They showed a consistent warming off southern California in the spring months.

Now it is known that warming extended throughout a layer of water at least 300 feet deep.

Second evidence of changing conditions came as plankton collections were sorted. Sardine eggs and larvae turned up from regions where none had been found in the past two years.

In July, fishermen reported schools of adult sardines around the Channel Islands and large schools were seen from the air near Hueneme. The opening of the southern California season, on 1 October, found the fish available in numbers not seen since

1951-52. More than 60,000 tons were caught. That was many times the previous season's catch.

These sardines were not members of a large, new year-class. Age composition studies showed that the 1952 and 1951 year-classes contributed about a third each. Of the remainder, the 1948 year-class produced one-third. These 1948 fish were surprisingly small. They were the "little, old" fish that usually appear in only insignificant numbers off southern California. They are fish that were spawned and spent their first years off Baja California.

The return of the sardines did not take the scientists by surprise. It had been pointed out in the last progress report that "the success or failure of the fishery in the immediate future will be largely determined by the number of sardines that may move from the Baja California waters into our fishing grounds."

The next question is, will the sardines return next season? And if so, in what quantities?

The first cruises of 1955 have shown the water is as warm as it was in 1954. By taking spot samples, it has been learned that in March and April there was extensive spawning off southern California. The fish surveys will tell where the sardines are. With this evidence, the scientists should be able by summer to predict whether enough sardines will be available to give the State a substantial fishery in the coming season. It is already known that the incoming year-class, that of 1953, is not a very good one. That is shown by the egg-and-larva counts and by the young-fish surveys. The 1952 year-class stands out as the best spawned in these five lean years, being one and one-half times the size of any of the others. But this and the other year-classes present in the fishery may appear in sufficient numbers to insure a profitable catch.

Research lags events. It is still not known exactly whether other aspects of the ocean changed as strikingly as did temperature in 1954, or if the food supply of the sardines changed. Scientists are working on these problems.

Without research, the revival of the industry in southern California would have been almost impossible to explain. Now it seems possible that the data will be on hand to explain several aspects of fluctuations in sardine populations and perhaps other fish populations. The information may eventually lead to accurate prediction of how many fish there are, where they are, and if they can be caught.

PART II: POPULATION DYNAMICS OF THE PACIFIC SARDINE

by

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POPULATION DYNAMICS OF THE PACIFIC SARDINE

SOME GENERAL CONSIDERATIONS

Man is interested in renewable resources, such as marine fish populations, from the standpoint of Man and not from the standpoint of the resource. This is so obvious as to constitute a truism, yet the implications are often overlooked. So far as a population of fish is concerned, the only thing which is of importance to that population is that it not be reduced (by whatever means) to a size below which it can no longer perpetuate itself. Any other facets of Man's interest in the resource, while they may be influenced or modified by the biology of the fish, have their basis in the economic and social aspects of Man's behavior. Thus it is considered worthwhile to try to hoard certain plants or animals or geographic areas because of the esthetic value while other plants, animals or geographic areas are exploited because of economic value. Maine herring are primarily harvested as juveniles rather than as adults because there is more economic demand for this product. The California sardine industry grew to such large magnitude because of the demand for meal and oil, rather than for canned fish. And so on.

This point is raised to demonstrate that what is done with a resource is essentially governed by the needs or desires of Man and, in a sense, has little or no connection with the resource *per se*. It is essential that this not be overlooked: ignoring this simple fact can almost hopelessly confuse related but quite distinct problems.

At the present stage of our knowledge, there is rather universal agreement that the only way Man can affect a population of marine fishes is by fishing (and, perhaps, by pollution in special situations). That is, we cannot economically fertilize large areas of the sea, nor can we treat epidemics in fish populations, nor hope to stock the ocean by means of hatchery-reared fish. There is further agreement that Man can affect fish populations by varying the amount of fishing and by varying the method of fishing. There is, however, disagreement about the nature and magnitude of such effects.

According to one theory, big spawning populations produce bigger year-classes than do small spawning populations. Therefore, one might suppose that reducing the total catch would make the spawning population bigger and therefore result in the production of bigger year-classes. Although this assumption has been made many times, it has not been demonstrated for any marine fish. The possibility that this theory does not conform to the facts will be discussed below. Unfortunately, this assumption is perhaps more often

made tacitly than explicitly. There must, of course, be a critical population size below which the population will not be able to perpetuate itself.

In species which tend to grow rapidly and are subject to a low rate of natural mortality, a group of fish of a given year-class will, for a period of time, gain more total weight through growth than it will lose by the natural death of some of its members. Conversely, a group of fish which grows slowly and is subject to a high rate of natural mortality will lose more total weight through deaths than it will gain through the growth of those fish surviving. In the case of a rapidly growing species, it is obviously profitable, in terms of total weight, to leave the fish in the sea until the growth-death ratio is most favorable. This has, in fact, been done in the case of some of the bottom-dwelling species simply by increasing the mesh size of the trawls and allowing the smaller fish to escape and continue growing before being caught. Of course, in order to make an intelligent decision about what particular mesh size to choose, information must be available about growth rates and death rates.

What Causes Fluctuations in the Size of a Fish Population?

Fluctuations in the size (numbers) of a population of adult fish arise from the difference between the number of fish which leave the population (die) during a given time period and the number of new fish which enter the population (fish of a new year-class) during that same time period. Obviously, when the number of deaths exceeds the number of recruits the population will decrease in size and, conversely, when recruitment exceeds deaths the population will increase in size. (As mentioned above, the size of a population in weight will vary according to the ratio of increase through growth and decrease through deaths.)

Deaths may arise from a variety of causes. These include capture by Man (a form of predation), predation by other animals, disease, parasitism, "red tide," starvation, senility, lethal genes, and so on. Deaths from the first-named cause are commonly termed fishing mortality. All other causes are lumped under natural mortality, partially as a matter of convenience and partially as a reflection of general ignorance about the specific cause of natural mortality in any given situation.

The death rates from fishing and from natural causes can clearly be variable and will be influenced by many factors, so that it is difficult to generalize about them. Two features are of interest, however. One of these concerns the fact that when fishing mortality is imposed on a population, natural mortality

is to some extent replaced by fishing mortality. That is, some of the fish which would have died naturally during a given time interval are caught instead. The other feature, and by far the most important one, is that as far as we can judge from all the observations that have been made, fishing and natural mortality exert their greatest influence on the size of the population existing at the time they occur. Opinions differ about their effect on the size of future additions to the population, *i.e.*, year-classes which will be produced subsequent to the time the mortalities occur.

There must, of course, be some "critical," minimum spawning stock size below which year-class size is a function of stock size, as we have already stated. This critical stock size has not yet been measured for any marine fishes. Above this minimum stock size all present evidence indicates that the magnitude of additions to the population (the size of individual year-classes) is not determined by the number of eggs spawned, but rather by variations in survival rate between the time the eggs are spawned and the time the resulting fish have grown large enough to enter the population. This means that the size of any particular year-class is determined, not by the number of adult fish (above the minimum) which produce it, but rather by variations in the environment which affect survival rate after the eggs are spawned.

As to the relative importance of death rates and entering year-class size in producing variations in population size, there can be no question but that variation in year-class size can produce much greater variations in population size. Obviously, the number of deaths can only amount to some fraction of the total population at any given time. On the other hand, the size of any given year-class can, and has been observed to, exceed the size of the population to which it is added (for example, in the Pacific sardine, the Pacific mackerel and the Atlantic haddock). One might expect that the importance of an individual year-class would tend to be reduced in a population made up of many year-classes and accentuated in a population made up of only a few year-classes. There are, however, notable exceptions to this generalization (for example, the famous 1904-class of Norwegian herring, which dominated the fishery for many seasons with as many as 17 other year-classes in the fishery at the same time).

What Causes Fluctuations in the Catch From a Fish Population?

Fluctuations in the catch from a fish population can be caused by fluctuations in the size of the population, fluctuations in the degree of availability of the population to the fishery and fluctuations in the amount of fishing effort. The causes of fluctuations in the size of a fish population have already been considered. We need only examine the remaining two sources of fluctuations in catch.

In a free economy, variations in the amount of fishing effort will ordinarily be governed by economic laws. Fishermen will tend to seek those species which will be most profitable and to avoid those which are unprofitable. (We are considering here the fact that, all other conditions being constant, a reduction in effort will result in a reduction of catch and an increase in effort will result in an increase in catch. The effect of fishing effort at a given time upon abundance at some subsequent or future time is considered elsewhere in this paper.)

The degree of availability of a population to a fishery has been observed to vary widely between successive time intervals. The phenomena which are involved in fluctuations in availability are not understood and, in fact, the existence of availability phenomena is not yet universally recognized. However, it is easy to suggest ways in which availability operates to affect the catch. In a hook-and-line fishery, fish which stop feeding during the spawning period are unavailable during that period. Fish which are taken over part of a migratory route are unavailable before the migration starts or if the route shifts. The geographic shift of the center of a population may make a population more or less available to a fishery, depending on whether the population shifts into or out of the area of the fishery. A change in the behavior or depth distribution of a schooling fish could easily lead to great fluctuations in the catch. The recitation of such examples could be continued at great length, but these should serve to illustrate that changes in availability are real and can cause large variations in the catch.

In assigning relative importance to abundance, fishing effort and availability with respect to catch fluctuations, no firm generalities can be made, owing to the different situations obtaining in the different fisheries for different species. We may, for the moment, consider fishing effort to be constant and weigh the relative importance of abundance and availability under such a condition. It is still impossible to generalize beyond the facts that both abundance and availability can cause tremendous fluctuations in catch, and that their relative importance will have to be determined for each specific situation. One might expect that abundance would tend to be more important in determining the catch in a fishery which is carried out over the entire range of a population, whereas availability would tend to be more important in a fishery which is carried out over only a fraction of the range of a population.

Data available from the different fisheries of the world indicate that fluctuations in either abundance or availability can produce fluctuations in the catch at least in the order of 25 to 1 and, in all probability, much greater (for example, in the Pacific sardine, the Irish pilchard and the Atlantic mackerel).

Background of Sardine Biology and of the Fishery

The Pacific sardine (*Sardinops caerulea*) is a relatively small, herringlike, pelagic fish which is most commonly found in groups or schools. Some of these schools may contain as many as ten million fish, although one million or less is a more common number. The depth to which such schools may descend is not known. Most of Man's experience has been, of course, with schools at or near the surface. Furthermore, sardine spawning takes place between the surface and a depth of 125 feet, with most of it concentrated at a depth of approximately 30 feet.

The distribution of the sardine has been known to include the area from the Gulf of California and off the west coast of Baja California, northward to southeastern Alaska and offshore as much as 350 miles. We do not know what determines the distribution of the sardines (although some possibilities will be considered subsequently), but we infer that the sardines tend to distribute themselves with respect to their variable ocean environment and not with respect to the fixed geographic or political reference points which Man is prone to use.

On the basis of tagging experiments and from evidence on the size and age composition of the catch in the different localities, it is known that sardines move about between the different localities within the general area of total distribution. Such movements have been believed to constitute a definite north (in spring and summer) and south (in fall) migration. The evidence for this will be reconsidered in subsequent sections of this paper.

Sardine spawning is largely concentrated in the spring months. Notable exceptions to this are the progressively later spawning period as spawning proceeds from south to north and the fall spawning in some bays on the west coast of Baja California. Two major spawning centers are known: one off southern California and one off central Baja California. It is also known that in some years spawning has occurred as far north as Oregon and Washington. Spawning also has been reported in the Gulf of California, but very little is known about the sardines in this area.

It is well known that the success of spawning in sardines, as in many other species, is highly variable. In some years many young fish survive and produce very large year-classes and in other years middling or very small year-classes result.

Sardine eggs take about three days to hatch. At hatching, the larvae are tiny, threadlike creatures about 0.1 inch in length. By the time they are one year old, they are about 5.6 inches in total length, 7.7 inches at age 2, 9.1 inches at age 3, 10.0 inches at age 4 and so on. Almost half of the total length is

achieved in the first year and by age 10 the total length is only 11.8 inches.

Some sardines are believed to live as long as 25 years. However, such old fish are exceedingly rare and the bulk of the population is ordinarily made up of fish one to four or five years old. Since the 1932-33 season, the average age of the fish in the catch has been 3.2 years. For individual seasons during this period, the average age has ranged from 2.0 to 4.8 years in the 1948-49 and 1933-34 seasons, respectively. Obviously, when a superabundant year-class enters the population the average age of the population will be low. In successive years, as this large year-class "moves through" the population (*i.e.*, becomes older), the average age will progressively increase. This tendency will be emphasized when a large year-class is followed by a series of exceptionally small year-classes.

Adult sardines are both filter and particulate feeders. That is, they swim through the water with their mouths open and use their gill rakers (a straining apparatus) to filter or strain from the water the small plants and animals and also at times pick out food items from the water (Radovich, 1952a). Studies have been made of stomach contents of sardines, but their food preferences, if any, are not known. The larvae do not yet have this filtering apparatus developed. Because of their small size, they are limited as to what they may eat. The eggs and young stages of copepods are believed to form a large part of their diet.

Very little is known about the behavior of the sardine, or the influence of the environment upon sardine behavior and distribution. We have only a few scattered bits of information, such as that the two major spawning centers are in areas of recently upwelled water which has certain unique chemical and physical characteristics. But we do not know why sardines spawn in these areas and not in other areas of upwelled water. There is a suggestion of differences in schooling behavior in different parts of their range; surface schooling at night off California and by day off the Pacific Northwest. But we do not know why this is so. Thus, the major questions about behavior remain unanswered.

Turning from the fish to the fishery, fishing areas have been located off Vancouver Island, British Columbia, off Grays Harbor, Washington, off Astoria and Coos Bay, Oregon, off San Francisco, Monterey, San Pedro and San Diego, California, and off Ensenada and Cedros Island, Baja California. The growth of the fishery is well known and has been documented by Schaefer, Sette and Marr (1951) and in various publications of the California Department of Fish and Game (see Clark, 1952). The landings, by area and for the whole coast, are shown in Figure 1 and Table 1.

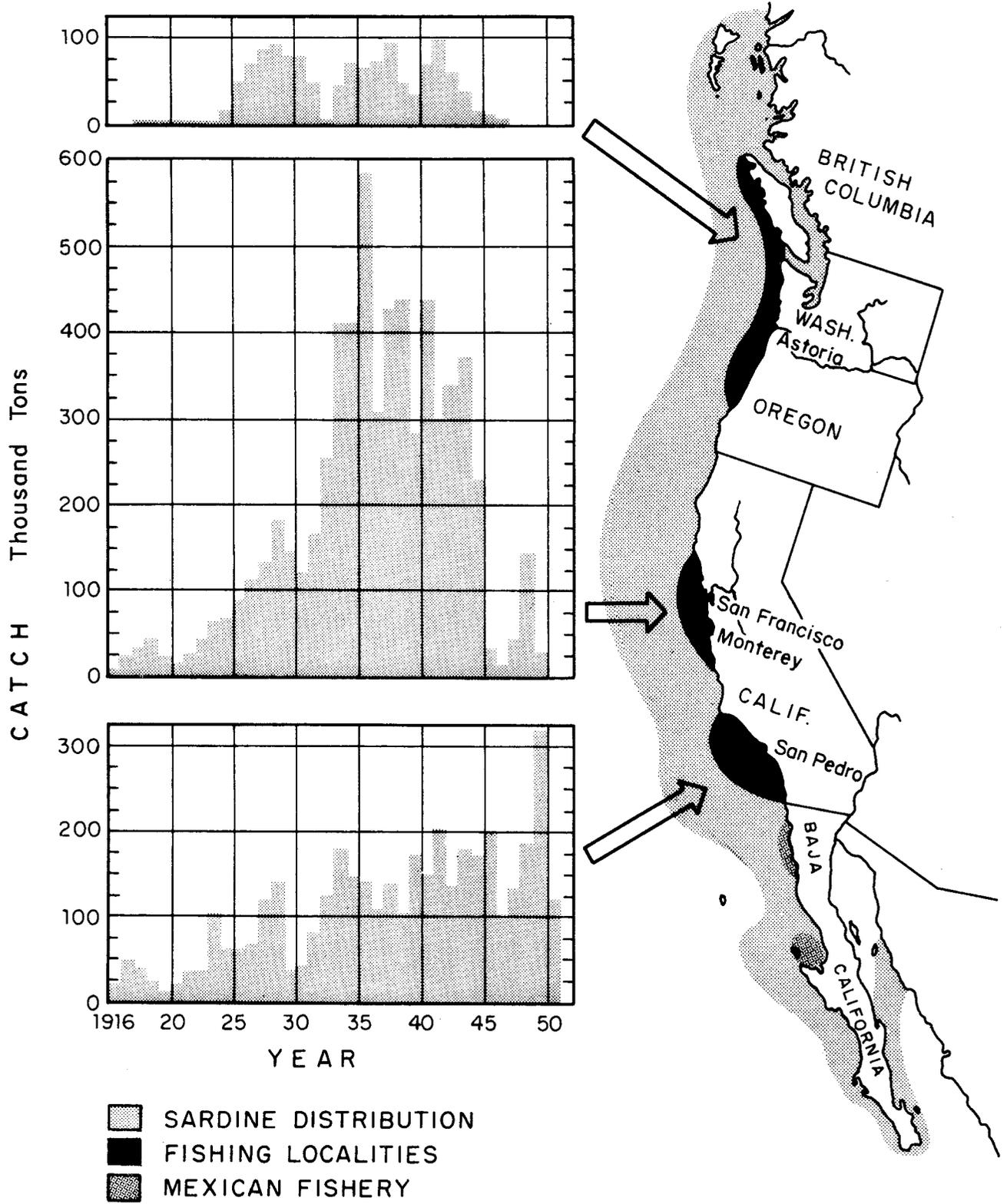


FIGURE 1. Panel A. Distribution, fishing areas and catch of the Pacific sardine, 1916-17 through 1953-54 seasons. Distribution shown by light areas, fishing areas shown by dark areas, catch for each area shown by histograms.

TABLE 1
TONS AND NUMBERS OF SARDINES IN THE CALIFORNIA CATCH. TONS IN THOUSANDS, NUMBERS IN MILLIONS

Seasons	Tons ¹	Numbers ²
1919-20	67	299
1920-21	38	293
1921-22	36	273
1922-23	65	452
1923-24	84	546
1924-25	173	1,149
1925-26	137	940
1926-27	152	913
1927-28	187	1,056
1928-29	254	1,593
1929-30	325	2,264
1930-31	185	1,243
1931-32	165	1,091
1932-33	251	1,518
1933-34	383	2,270
1934-35	596	3,784
1935-36	560	3,439
1936-37	726	4,285
1937-38	417	3,072
1938-39	575	5,417
1939-40	542	4,682
1940-41	461	4,084
1941-42	587	5,319
1942-43	505	3,936
1943-44	478	3,452
1944-45	555	3,781
1945-46	404	2,804
1946-47	234	1,818
1947-48	121	907
1948-49	184	1,459
1949-50	338	2,608
1950-51	353	2,497
1951-52	129	957
1952-53	6	24
1953-54	4	20

¹ From Clark, 1952.
² From Calderwood, 1953, through 1950-51 and from Felin, et al. 1952, 1953, 1954, for the remainder of the seasons.

WHAT CAUSES FLUCTUATIONS IN THE SIZE OF THE SARDINE POPULATION?

Estimates of Population Size

Before we can consider how and why a population fluctuates in size, we must first be able to measure or estimate population size. In the case of a marine fish, this is an exceedingly difficult task which has to

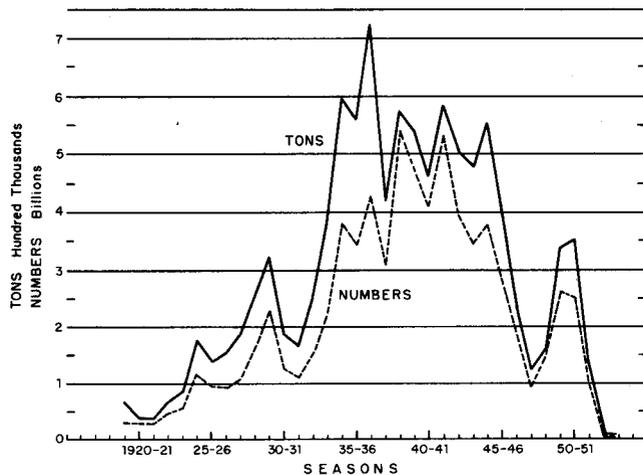


FIGURE 1. Panel B. California sardine catch.

be accomplished in some more or less indirect manner. Because these difficulties have attendant uncertainties, it is desirable to estimate population size by as many independent methods as possible, so that they may be compared one with the other.

In the accompanying Figure 2 and Table 2 are given all of the available estimates of sardine population size, from the 1932-33 through 1953-54 seasons. These include several more or less different kinds of estimates, based on (1) catch data, (2) catch and effort data, (3) catch, effort and age data, (4) tagging data, (5) accumulated age data,¹ (6) egg censuses and fecundity data, (7) scouting data and (8) scouting and catch data. These will be discussed in turn, with particular attention to the confidence or reliability which may be attributed to each and the direction in which they err (*i.e.*, whether or not they tend to be minimal or maximal). These estimates do not include fish less than one year old, very few year-old sardines and varying amounts of two-year-olds.

(1) CATCH DATA

The population estimates based on catch data are simply the number of fish, of all ages, landed in each season (column 1 in Table 2). The estimates prior to 1941 are derived from data given by Clark and Janssen (1945), Eckles (1954), and Hart (1943). Subsequent to 1941 the numbers of fish in the catch are given in a series of papers by Felin *et al.* (1948, 1949, 1950, 1951, 1952, 1953) and Mosher *et al.* (1949).

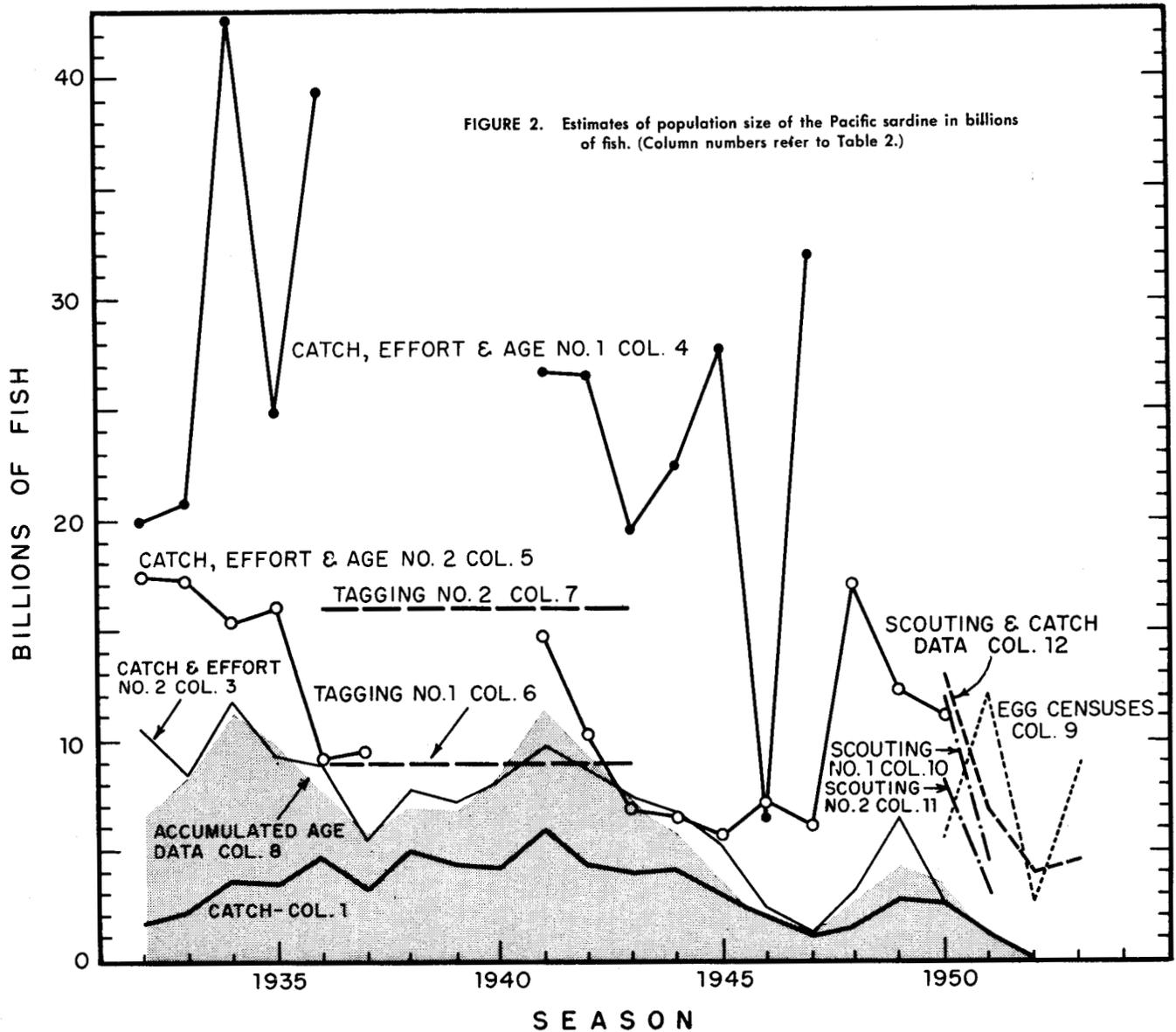
The error associated with this kind of estimate is negligible subsequent to 1941. The estimates prior to 1941 are not as precise as the later ones and the error may be somewhat larger.

The numbers of fish caught in a season are obviously minimal estimates of total population size. They fall below the true population size in the amount of the numbers of fish which survive to be caught in subsequent seasons, the numbers which are present on the fishing grounds but die naturally, and the numbers which are unavailable to the fishery and eventually die from natural causes. Furthermore, since fishing effort was low in the earlier seasons, natural mortality was probably greater in those seasons than in the later ones. In other words, the catch in the earlier seasons is a smaller fraction of the total population than it is in later seasons.

(2) CATCH AND EFFORT DATA

In order to adjust for the lesser amount of fishing effort in the earlier seasons, the total catch may be weighted by effort. This may be done by selecting a base year (1950-51 in this case), expressing the fishing effort in each of the other seasons as a fraction of that in the base year, and multiplying each season's catch by the appropriate ratio. Two series of effort data are available and are shown in Table 5 as

¹ What we call "accumulated age" has previously been termed the "virtual population" by Fry (1949).



absolute numbers and as fractions of the base year. The weighted catch data are shown in columns 2 and 3 of Table 2. These estimates more nearly approach the total population than do the unweighted catch data, but are still minimal. Both series indicate that the population in the 30's and early 40's was materially larger than in the more recent years.

(3) CATCH, EFFORT AND AGE DATA

The estimates based on these data arise from a method developed by Ricker (1940) and Silliman (1943) and elaborated by Widrig (1954). (The methods of computation are moderately complicated and are not essential to this discussion. Those interested in the details may find them in the works cited, especially the latter.) In order to obtain precise estimates from this method, it is necessary to have independent information about either the rate of natural mortality

or the degree of availability. Lacking these, it is possible to see how either must have varied under given conditions of the other.

Such estimates are shown in columns 4 and 5 of Table 2. They pertain to fish 2-rings and older.² The first series of estimates assumes that the fish have always been fully available. In order to explain the observed changes under this assumption, the annual rate of natural mortality would, in some seasons, have exceeded 80 per cent. Moreover, there is other evidence (which will be discussed later) which shows that availability was not constant over a period of seasons, that the fish were never fully available and that natural mortality probably was not that great, except possibly in the older fish.

² By "2-ring" is meant a fish with two annual marks on its scales and which is therefore in its third year of life.

TABLE 2
ESTIMATES OF POPULATION SIZE OF THE PACIFIC SARDINE, IN BILLIONS OF FISH

Season	1 Catch	2 Catch and effort No. 1	3 Catch and effort No. 2	4 Catch, effort and age No. 1	5 Catch, effort and age No. 2	6 Tagging No. 1	7 Tagging No. 2	8 Accumulated age data	9 Egg censuses	10 Scouting No. 1	11 Scouting No. 2	12 Scouting and catch data
1932-33	1.6	5.5	10.5	20.0	17.4	-- a	-- a	6.6	--	--	--	--
1933-34	2.2	5.6	8.4	20.8	17.2	-- v	-- v	8.3	--	--	--	--
1934-35	3.7	7.9	11.7	42.7	15.4	-- e	-- e	11.2	--	--	--	--
1935-36	3.5	6.1	9.2	24.8	16.0	-- r	-- r	9.8	--	--	--	--
1936-37	4.8	5.9	8.9	39.3	9.2	9.0 a	16.0 a	7.9	--	--	--	--
1937-38	3.2	3.6	5.5	--	9.5	9.0 g	16.0 g	5.7	--	--	--	--
1938-39	5.0	5.5	7.8	--	--	9.0 e	16.0 e	7.0	--	--	--	--
1939-40	4.3	5.0	7.2	--	--	9.0	16.0	6.8	--	--	--	--
1940-41	4.2	5.3	8.3	--	--	9.0 o	16.0 o	8.4	--	--	--	--
1941-42	6.0	7.0	9.8	26.7	14.8	9.0 v	16.0 v	11.5	--	--	--	--
1942-43	4.3	6.5	8.7	26.6	10.2	9.0 e	16.0 e	9.1	--	--	--	--
1943-44	4.0	5.4	7.3	19.6	6.9	9.0 r	16.0 r	7.0	--	--	--	--
1944-45	4.1	4.8	6.8	22.4	6.6	--	--	5.8	--	--	--	--
1945-46	3.0	3.5	5.1	27.7	5.7	-- p	-- p	3.6	--	--	--	--
1946-47	1.9	2.0	2.3	6.5	7.1	-- e	-- e	1.7	--	--	--	--
1947-48	1.0	1.1	1.2	32.0	6.1	-- r	-- r	1.4	--	--	--	--
1948-49	1.5	2.5	3.2	--	17.0	-- i	-- i	2.7	--	--	--	--
1949-50	2.8	4.5	6.4	24.5	12.3	-- o	-- o	4.3	--	--	--	--
1950-51	2.6	2.6	2.6	--	11.0	-- d	-- d	3.5	5.7	11.9	8.1	13.0
1951-52	1.0	--	--	--	--	--	--	1.0	12.2	4.6	3.1	6.8
1952-53	0.08	--	--	--	--	--	--	0.1	2.7	--	--	4.0
1953-54	--	--	--	--	--	--	--	8.8	--	--	--	4.5

1. Number of fish in the catch, all ages; a minimum estimate of population size
2. Effort from Clark and Daugherty (1952)
3. Effort from Widrig (1954)
4. Minimum estimate of population of fish 2-rings and older, under condition of full availability with natural mortality variable (Widrig, 1954)
5. Minimum estimate of population of fish 2-rings and older, under condition of varying availability with constant natural mortality of 33 per cent annually (Widrig, 1954)
6. Estimates of population of fish of commercial size given by Clark and Janssen (1945)
7. Estimates of population of fish of commercial size based on data by Clark and Janssen (1945); see also text footnote 3

8. Minimum estimate of population of fish 2-rings and older, based on numbers of fish actually caught
9. Estimate of total population of spawning fish, based on egg censuses and fecundity data
10. Estimate of total population of fish of commercial size, based on scouting and catch data
11. Estimate of total population of fish of commercial size, based on scouting data (weighted by area) and catch data
12. Estimate of total population of fish derived by considering catch to be $\frac{2}{3}$ of proportion of fish observed north of Ensenada by scouting

The second series assumes a constant annual rate of natural mortality of about 33 per cent. Under this condition, maximum availability varies from about 16 per cent to 100 per cent (since it is necessary to assume full availability in some base year).

It is highly probable, if not certain, that neither the rate of natural mortality nor availability is constant over a period of years. Until we have more information about these phenomena, it is impossible to state how reliable these estimates are, except to say that they are of the right order of magnitude. Because of the method by which the estimates are made, they are minimal.

(4) TAGGING DATA

The only large-scale tagging experiments on sardines were terminated at the entry of the United States into World War II. The results of this work have been summarized by Clark and Janssen (1945), who estimated that the average population of fish of commercial size (largely 2-rings and older), over the period 1936-37 to 1943-44, was about 9 billion fish (column 6, Table 2). In fact, they estimated the central California population to be about 9.0 billion fish and the southern California population to be about 9.3 billion fish and considered these to be two independent estimates of the same population. While

it has been demonstrated that sardines migrate between these two regions, nevertheless the fishing seasons in the two regions largely overlap in time and it is obvious that an individual fish cannot be caught in both areas. Therefore, the two estimates pertain in part to the same group of fish and in part to separate groups. In other words, the estimate to draw from these data is somewhere between 9.0 billion fish if one group and 18.0 billion fish if two separate groups. This is borne out by the fact that estimates based on accumulated age data (discussed later) show a minimum average population, 2-rings and older, of 8.0 billion fish during this same period.

Clark and Janssen (1945:30) estimate the "average fishing mortality independent of natural mortality" to be 35 per cent for the entire coast (but did not believe this to be a reliable estimate).³ Taking natural mortality into account, this is the equivalent

³One of us (Clark) does not believe that the tagging data should be used to estimate rates of fishing and natural mortality because of the effects of emigration and immigration throughout the areas fished. For the California fishery only, the above calculation yields an estimate of 43 per cent fishing mortality. Since the Pacific Northwest fishery was drawing from the same population and sardines were moving freely in both directions between the two fishing grounds, the mortality for the entire coast cannot be less than for California and the values are incompatible. The other (Marr) believes these data can be used to yield point estimates, the error of which is not known (see footnote 4). In fact, the difference noted by Clark is just what would be expected if emigration out of California were occurring and the difference could be used to yield a measure of such emigration.

of an exploitation rate of 28 per cent. On the basis of an average annual catch of 4.5 billion fish (Clark and Janssen, 1945:31), a total population estimate of about 16 billion fish results (column 7, Table 2).⁴ This population estimate is in agreement with one made by Clark in the present paper (see page 40).

It is impossible to ascertain the confidence to be assigned to estimates based on these tagging experiments, owing to the many possible sources of error. These include tagging mortality, tag shedding, and efficiency of tag recovery, for which corrections have been made, and variations in availability, including differential movements according to size, to name but four sources.

It is also impossible to ascertain whether such estimates are minimal or maximal, for the above-mentioned sources of error may affect the estimate in either direction, depending upon the nature of the error.

(5) ACCUMULATED AGE DATA

The population estimates arising from accumulated age data (column 8, Table 2) are, like the first estimate described, based on fish actually caught, but pertain to fish 2-rings and older. They differ from the first estimate in that fish present in a given season, but not actually caught until subsequent seasons, are included in the estimate for that given season. For example, the accumulated age population estimate for the 1942-43 season includes (a) all the fish caught in that season, (b) all of the fish of the 1940-class caught in subsequent seasons, (c) all the fish of the 1939-class caught in subsequent seasons, and so on, for each year-class (except the 1941 and 1942) present in the 1942-43 season. The data from which these estimates are developed are cited under the first estimate.

Subsequent to 1940, the error associated with this kind of estimate is negligible. Prior to 1941 there are two additional sources of error. First, for the period 1932-33 through 1937-38 ages were determined from otoliths. The otolith samples were not weighted to the catch at the time of sampling. Second, age data for the period 1938-39 through 1940-41 are incomplete and some interpolations have been necessary.

⁴It has been pointed out (Ricker, 1948:69-72) that the method used by Clark and Janssen to estimate the number of effective tags out at the beginning of the season of tagging, and consequently the rate of exploitation, is somewhat in error. However, it is possible to estimate the rate of exploitation in the first season after tagging under the condition that the annual natural mortality rate of the tagged fish is the same in the season of tagging as in the season after tagging. If natural mortality occurs concurrently with fishing mortality, then the rate of exploitation is 22.6 per cent for the California releases. If natural mortality occurs only between fishing seasons, then the rate of exploitation is 21.5 per cent. These rates lead to estimates of population size of about 19.9 billion and 20.9 billion fish, respectively. These estimates are based on recoveries for the whole coast, so emigration to the north of California is taken into account. Emigration to the south of California would tend to make the population estimates too high, but only slightly too high. Immigration to California from the south is taken into account.

The accumulated age population estimates are minimal. They fall below the true population size by the numbers of fish which are present on the fishing grounds but die naturally and by the numbers of fish which are unavailable to the fishery and eventually die naturally. The ratio of these estimates to the actual population size undoubtedly varies from year to year.

(6) EGG CENSUSES AND FECUNDITY DATA

Population estimates based on these data (column 9, Table 2) require that the total number of eggs spawned each year be determined and that the fecundity of the sardine be known. The size of the spawning population is then simply estimated by dividing the total number of eggs spawned in a given year by the number produced per female and multiplying by two, to take into account the males. These estimates refer, roughly, to one-half of the 2-ring fish and all older fish, since about one-half of the 2-ring fish spawn. It should be mentioned that these estimates are not necessarily strictly comparable to those based on catch data.

The methods of estimating the total number of eggs spawned per year have been described by Sette and Ahlstrom (1948) and by Ahlstrom (1954). Briefly, they involve taking regularly spaced samples throughout the spawning season and area, expressing these in terms of a standard volume of water and integrating over time and space to get the total for the year.

Fecundity estimates were given by Clark (1934) who found more than one maturing group of eggs in the ovaries of ripening females and concluded that sardines spawn, on the average, three batches of eggs per year. From her table of number of eggs spawned per batch, we have estimated that an average spawning comprises about 33,000 eggs and with three spawnings per season a total of approximately 100,000 eggs would be produced per female.

As in the case of estimates based on tagging, it is not now possible to state the confidence associated with the egg census-fecundity estimates. Errors may arise from either type of information. The greatest source of error in the egg census data accrues from necessary assumptions concerning the distribution of eggs between stations in space and time. Preliminary attempts to test these assumptions indicate that, at worst, the true number of eggs spawned in any given year may be as much as one-half or twice the estimate; the true number and the estimate may be much closer.

The greatest source of possible error in the fecundity estimates is the assumption that more than one batch of eggs is spawned per year. This needs further investigation and work toward its solution is being carried out. Obviously, if only two batches are spawned per year the population estimate would be

half again as large and if only one batch is spawned it would be tripled. If four batches are spawned per year, the population estimate would be reduced by one-fourth.

Although it is impossible to state whether these estimates are minimal or maximal, they are most likely minimal, since the majority of the sources of error tend in that direction.

(7) SCOUTING DATA

A sixth source of data with which to estimate population size is the schools of fish which are located and sampled from research vessels (Radovich, 1952b). The method includes an estimate of the rate of natural mortality, based on the decline in successive seasons of the younger year-classes which are not yet in the fishery. Two series of estimates arise, depending on how the data are combined (columns 10 and 11, Table 2).

In the first series (column 10), the pooled data (from all areas) for 1950 and the pooled data for 1951 are used to determine the total mortality rate for each year-class and for all year-classes combined. For the younger year-classes which are not yet in the fishery, the total mortality rate, about 40 per cent, is assumed to be the natural mortality rate. The total mortality rate for those year-classes in the fishery is about 56 per cent (from Radovich, 1952b, Tables 2 and 4). From those values, the fishing mortality rate can be estimated as 21 per cent. An estimate of the total population size follows from dividing the total commercial catch by the fishing mortality rate.

An alternative method leads to the second series (column 11). This method differs from the first only in the weighting of the data in each area by the linear distance of the coast in each area.

Scouting data on which to base population estimates subsequent to 1951 are not available.

The error associated with these estimates is unknown. Possible sources are the assumptions necessary to the method, including the assumptions that all or a constant proportion of the fish are distributed within the 100-fathom curve, that the north and south extent of the population is included in the surveys, that samples obtained from individual schools are representative of those schools, and that schools in the several areas contain approximately the same number of fish.

Neither can it be stated with certainty whether these estimates are minimal or maximal.

(8) SCOUTING AND CATCH DATA

Another way of utilizing the scouting data to estimate population size is to compare the percentage of fish found by the surveys to be north of Ensenada in the fall with the number of fish caught that season (Radovich, 1952b; Marine Research Committee, 1953). For example, in 1951, 28 per cent of the fish

were north of Ensenada. If half of these were caught, then 14 per cent of the population was 0.96 billion fish and the total population was 6.8 billion fish (column 12, Table 2). If the whole group were caught, which is highly improbable, the population estimate would be 3.4 billion fish. The latter estimate is minimal.

Again, the possible error of such estimates is unknown. The possible sources include those discussed under (7), plus assumptions concerning the percentage of the fish north of Ensenada that were caught.

Similarly, the remarks under (7) concerning whether the estimates are minimal or maximal apply here.

Summarizing the information on estimates of the size of the sardine population, such estimates are available from the 1932-33 season to the present. They have been made by several different methods, at least one of which, the egg census, is completely independent of the others. The possible sources of error in these estimates have been stated, the confidence or reliability which may be attached to each has been given, and whether they tend to be minimal or maximal has been indicated. Two estimates ("catch" and "accumulated age") have the least error associated with them. But they are both minimal estimates, as explained above. The error associated with the other five estimates has not yet been assessed.

The extremes of estimated population size over the period 1932-33 to 1953-54 have been in the order of 2 billion to 30 billion, with an average minimal population size over this period of perhaps about 6 billion fish. (This estimate of average population size is based on accumulated age data and is therefore minimal. The true value is unknown; it may be as much as twice as great.) The range in population size from 1950-51 to 1953-54 has been 2 billion to 12 billion with an average size of about 5.6 billion fish. (These latter estimates are based on egg census-fecundity data and are most likely minimal.)

There is no cyclic pattern in time of the fluctuations in population size. The accumulated age estimates show peaks of abundance in the middle 30's, in the early 40's and in the late 40's.

While, as indicated, there is some uncertainty about the exact absolute value to assign to these fluctuations in population size, there is no doubt that such fluctuations are real. We may now consider the origin of these fluctuations in the size of the sardine populations.

Additions to the Populations—Year-Class Size

Such fluctuations in population size (in numbers), as earlier described, arise from the difference between the additions to and the subtractions from the population during a given time period. Because of the characteristics of the sardine fishery, a convenient time period to consider is one year; the additions to

the population will consist of the members of a new year-class and the subtractions from the population will consist of those fish which are caught or otherwise die. (On a weight basis a population may also increase through the growth of its members. This is discussed in a subsequent section on "yield per recruit.")

Minimal estimates of the size of the 1930- through 1950-classes are available from the same data which provide the accumulated age estimates of total population size. These are given in Figure 3 and Table 3.

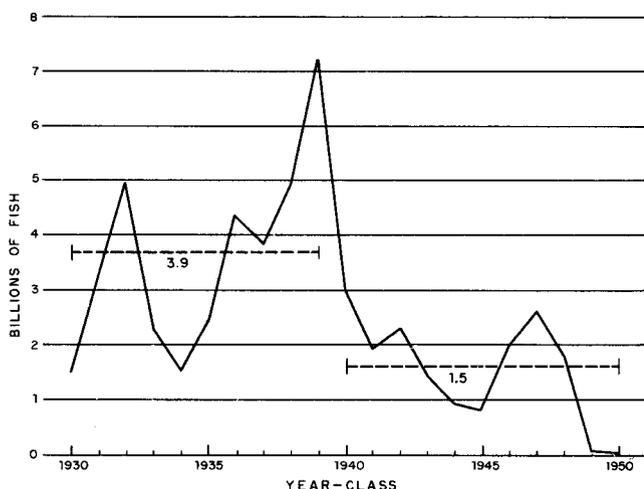


FIGURE 3. Estimates of year-class size of the Pacific sardine, classes 1930 through 1950. Estimates are derived in the same manner as the accumulated age population estimates, and include fish two rings and older.

TABLE 3

ESTIMATES OF YEAR-CLASS SIZE AND SPAWNING STOCK SIZE IN THE PACIFIC SARDINE, IN BILLIONS OF FISH

Season	1 Enter- ing year- class	2 Size of entering year- class	3 Catch	4 Popu- lation (accu- mulated age)	5 Popu- lation less entering year- class	6 Column (2) ÷ column (5)	7 Spaw- ning stock size
1932-33..	1930	1.5	1.6	6.6	5.1	0.29	5.9
1933-34..	1931	3.3	2.1	8.3	5.0	0.66	6.7
1934-35..	1932	4.9	3.7	11.2	6.3	0.78	8.7
1935-36..	1933	2.3	3.5	9.8	7.5	0.31	8.7
1936-37..	1934	1.5	4.7	7.9	6.4	0.23	7.2
1937-38..	1935	2.5	3.0	5.7	3.2	0.78	4.4
1938-39..	1936	4.3	4.1	7.0	2.7	1.59	4.8
1939-40..	1937	3.8	3.4	6.8	3.0	1.27	4.9
1940-41..	1938	4.9	3.8	8.4	3.5	1.40	6.0
1941-42..	1939	7.2	5.6	11.5	4.3	1.67	8.0
1942-43..	1940	3.0	4.1	9.1	6.1	0.49	7.6
1943-44..	1941	1.9	3.5	7.0	5.1	0.37	6.0
1944-45..	1942	2.3	3.6	5.8	3.5	0.66	4.6
1945-46..	1943	1.4	2.7	3.6	2.2	0.64	2.9
1946-47..	1944	0.9	1.2	1.7	0.8	1.12	1.3
1947-48..	1945	0.8	0.7	1.4	0.6	1.33	0.9
1948-49..	1946	2.0	1.0	2.7	0.7	2.86	1.7
1949-50..	1947	2.6	2.5	4.3	1.7	1.53	3.0
1950-51..	1948	1.8	2.6	3.5	1.7	1.06	2.6
1951-52..	1949	0.05	0.9	1.0	0.95	0.05	
1952-53..	1950	0.01	0.08	0.1	0.09	0.01	

1. At age 2-rings.
2. Accumulated age, at age 2-rings.
3. All fish age 2-rings and older.
4. Accumulated age, all fish 2-rings and older.
- 6 and 7. Accumulated age, one-half of 2-ring fish and all older.

The average minimal year-class size (at 2-rings) over this period is 2.5 billion fish. The range in year-class size has been 0.01 to 7.2 billion fish, a ratio of 1:720. If the smallest year-class (1950) is omitted, the ratio is 1:144. If the two smallest (1950 and 1949) are omitted, the ratio is 1:9. However, since these two smallest year-classes have so drastically affected the sardine population, they cannot be disregarded. They are in part responsible for the abrupt decline in the sardine fishery during the 1952-53 and 1953-54 seasons.

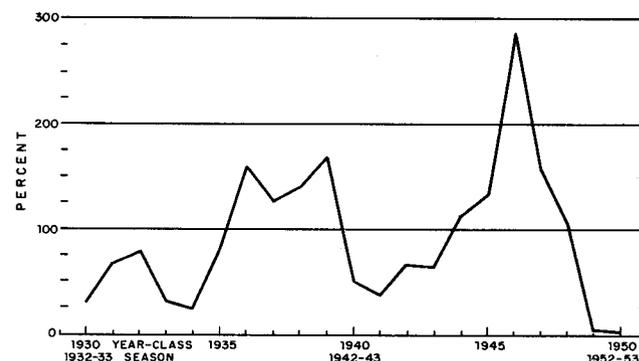
In addition to the estimates of absolute year-class size, it is pertinent to compare each year-class to the population to which it is added. Such comparison is given in column 6 of Table 3 and is shown in Figure 4. This is simply the size of each year-class expressed as a percentage of the population to which it is added. Over the entire period, year-class sizes have, on the average, amounted to 91 per cent of the stock sizes to which they were added. The range is from 1 per cent to 286 per cent.

As in the case of the estimates of stock size, there is also uncertainty about the absolute value to assign to the estimates of year-class size. But again there is no doubt that year-classes do vary in size and that these variations are considerable, not only between year-classes, but also with respect to the populations to which the year-classes are added.

What is the source of these variations in year-class size? Unfortunately we cannot yet identify precisely the source (or sources). We can, however, eliminate some potential sources as possibilities and indicate in general what the source must be.

As was mentioned earlier, it has been postulated (or assumed) by a number of fishery biologists that year-class size is in fact a function of spawning stock size. Although the exact form such a relationship would take is not known on theoretical grounds, some subjective examples have been given (see Herrington, 1948, and Ricker, 1954, for example). In general, this hypothesis is based on the following reasoning: When

FIGURE 4. Size of each entering year-class of sardines (age 2) compared to remainder of population.



spawning stock size is small, year-class size is small, because relatively few eggs are produced and the resulting larvae must endure considerable inter-specific competition. As stock size increases, greater numbers of eggs are produced, inter-specific competition is less important and larger year-classes result. As stock size continues to increase, intra-specific competition becomes limiting and year-class size again decreases.

It is important to note that under this hypothesis, if such a relationship is to obtain consistently from year to year, then all other conditions (*i.e.*, environmental variables which influence survival rate) must be constant. If such a relationship is to obtain on the average, then the deviations of individual years from this average may be attributed to variations in the environment (*i.e.*, all other conditions are not constant).

It is obvious that at some small spawning stock size, year-class size must be a function of stock size. Above this particular stock size, whatever it may be, there exist the possibilities that the hypothesized relation obtains because survival rate is relatively constant or that the hypothesized relation does not obtain because the variations in survival rate are so great as to obscure the relationship. In considering any particular species, there are, then, two important questions: (1) What is the spawning stock size below which year-class size is a function of stock size? (2) Above this spawning stock size, what is the magnitude of variations in survival rate relative to the magnitude of variations in spawning stock size?

Before examining the sardine data with respect to these questions, we may consider in general what might be expected under three possibilities: (1) year-class size a function of stock size only; (2) year-class size a function of environment only; and (3) year-class size a function of both stock size and environment. If year-class size is a function of stock size only, then variations in year-class size would not exceed variations in stock size. Furthermore, variations in stock size should produce predictable variations in the size of year-classes. On the other hand, if year-class size is a function of environment only, then variations in year-class size could exceed those in stock size. In fact, we might *a priori* expect them to, since we know that the environment is highly variable. Variations in stock size would not be expected to produce predictable variations in the size of year-classes. Finally, if both variations in stock size and in environment are operating, the resulting data become complicated and it is very difficult to measure the effect of either factor independently of the other.

We have been unable to reach an agreement on whether the size of the spawning stock determines the size of the year-classes. In the following few pages each of us will in turn outline his reasoning on this point.

Marr's interpretation is this:

"One might approach this problem by comparing average stock size and average year-class size in two different periods. For example, we may compare these averages for the periods 1932-1939 and 1940-1950. (This division is arbitrary: there is no theoretical reason for it.) The averages are:

	1932-1939	1940-1950
Stock size-----	6.4 billion	4.1 billion
Year-class size-----	3.9 billion	1.5 billion

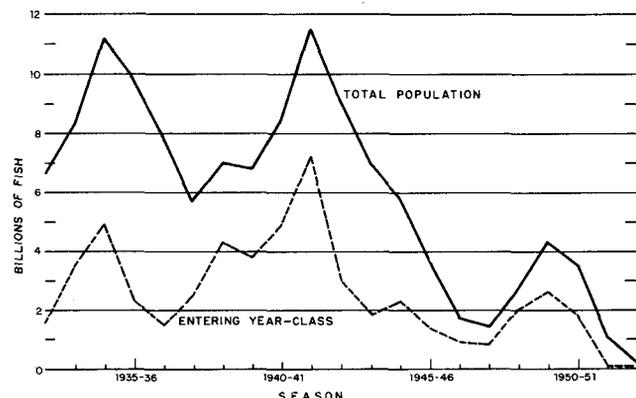
The difference between average stock size in the two periods is significant. The difference between average year-class size in the two periods is significant. Both average stock size and average year-class were smaller in the more recent than in the earlier period.

"However, even though the differences between the two periods are significant, the method of averaging over two time periods does not enable us to tell which is cause and which is effect. That is, we cannot tell whether year-class size decreased because stock size decreased or whether stock size decreased because year-class size decreased. If, for example, year-class size decreased in the later period because of environmental conditions, then stock size would decrease as a consequence.

"In order to be able to make a choice between the two alternatives, we must examine the data by individual years. If stock size decreased as the result of an independent decrease in year-class size, we would expect to find that stock size increased when large year-classes were added to the stock and that stock size decreased when small year-classes were added.

"We have already seen (Figure 4) that over the period 1932-33 through 1952-53 year-classes have, on the average, amounted to 91 per cent of the populations to which they were added. In Figure 5 are shown the total population (column 4, Table 3) and the size of the entering year-class (column 2, Table 3),

FIGURE 5. Pacific sardine: Size of entering year-class compared with total population, in numbers, 1932-33 through 1952-53.



1932-33 through 1952-53. Here the year-classes are associated with the populations which they entered, not with the populations which produced them. It is obvious that the increases and decreases in total population size are associated with increases and decreases, respectively, in the size of the entering year-classes.

“In general on the basis of logic, and specifically from the data of Figures 4 and 5, it is obvious that the size of the entering year-classes has a large influence on the size of the populations to which they are added.

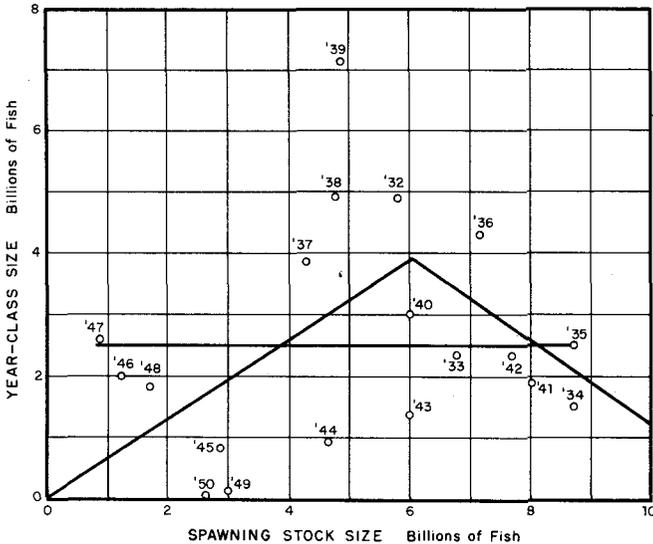


FIGURE 6. Pacific sardine: Year-class size plotted as a function of spawning stock size.

“Now, to consider the alternative, what influence does the size of the spawning stock have on the year-classes it produces? In Figure 6, year-class size (column 2, Table 3) is plotted as a function of spawning stock size (column 7, Table 3). Year-class size is compared with stock size in the season following spawning; i.e., the 1932-class with stock size estimated in the 1932-33 season, etc. As previously stated, all of these estimates are minimal. Furthermore, since the range of the sardine is now about one-third of its former range and since in some recent years its range has been almost entirely outside of the distribution of the U. S.-Canadian fishery, the more recent estimates of year-class size fall below the true size to a greater extent than do the earlier estimates.

“Inspection of Figure 6 suggests that, for the sardine, the small spawning stock size below which year-class size is a function of stock size, must be at or below the smallest stock size observed. Furthermore, above this stock size there is no apparent relationship between year-class size and spawning stock size (over the range of observed stock sizes).

“In order to test the latter statement, a curve was drawn (subjectively) such that it would give the smallest possible variance and conform in general to

the hypothesis. This is shown by the two lines (inverted-V) in Figure 6. The horizontal line passes through the common mean of all the points. The variance about the fitted line is 16 per cent less than the variance about the line through the common mean. However, this small difference is not significant; it is such that it could have arisen by chance alone. Similar results were obtained in testing other possible relationships.

“We may now reiterate, for the sardine, the answers to the two questions posed above: (1) Year-class size is a function of spawning stock size only at or below the smallest observed stock size. (2) Above this stock size, and over the observed range of stock sizes, variations in survival rate are so large that they obscure any theoretical relationship which may exist between stock size and year-class size.”

Clark’s interpretation is this:

“There are several approaches to the problem of determining the relation between spawning stock size and the size of the year-class produced by a given spawning stock. As shown by Marr, the stock sizes and the resulting year-class sizes of the 30’s exceeded those of the 40’s, the stock sizes by 1.6 times and the year-classes by 2.3 times. As demonstrated by Figure 5 a decrease in year-class size results in a decline in the total population when the year-class is two or three years old and has reached maturity. This relation is clear and easily demonstrated. The influence of stock size on year-class size is not so clearly evident.

“To clarify this point, the size of the spawning stock to the year-class it produces is compared in Figure 7. The data for this figure are taken from column 2, Table 3, for year-class size and column 7 for size of spawning stock. The spawning stock in a given season is compared with the year-class produced at the termination of that season, i.e., 1932-33 season with 1933 year-class. This comparison again demonstrates that both population and year-class sizes were at a higher level in the 30’s and the early part of the 40’s and that a decline in both occurred in the late 40’s and early 50’s.

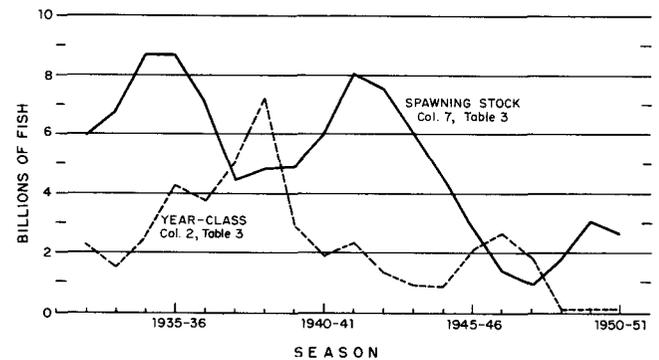


FIGURE 7. Pacific sardine: Size of spawning population compared with size of year-class produced by each season's spawners.

“In four seasons, 1937-38, 1938-39, 1946-47 and 1947-48, the resulting year-class exceeded in numbers the estimated numbers in the population which produced it. The 1939-class was 1.5 times the spawning stock and the 1947- and 1948-classes twice the stock size. Presumably this indicates unusually favorable environmental conditions when these year-classes were produced. The 1947- and 1948-classes, produced under favorable conditions but at low population levels, were, however, less than half the size of year-classes produced under a combination of favorable environment and high population levels. This suggests that low year-class level in the more recent seasons has a high probability of being associated with low population levels. Of further concern is the continued low level of recruitment from the year-classes following 1951. Evidence from the fish surveys (Radovich, 1952b, and following seasons) indicates that the 1952 through 1954 year-classes have added little more to the population than did the 1949, 1950 and 1951 year-classes.

“A further suggestion of the relation between spawning stock and year-class size is to be found in Figure 6. A spawning stock size of less than 4 billion fish produced no year-class exceeding 2.5 billion, whereas when stock sizes were larger than 4 billion, seven of the resulting year-classes equalled or exceeded 2.5 billion and only six fell below this amount. These data suggest that a stock size at some point between 4 and 8 billion might correspond to the theoretical value (Ricker, 1954) at which the resulting year-class is the least dependent on stock size, thus representing the optimum stock size for greatest recruitment. Below this range (4-8 billion) year-class size may be in part dependent on stock size because too few eggs are produced. Above this range year-class size may again be partly dependent on stock size.”

We may summarize the answers to the two questions posed above: (1) What is the spawning stock size below which year-class size is a function of stock size? We do not agree in our interpretation of the available data. (2) Above this spawning stock size, what is the magnitude of variation in survival rate relative to the magnitude of variation in spawning stock size? We can only state that either there is no relationship between year-class size and stock size, or, if there is such a relationship, the natural variation about it is so great that the relationship is obscured.

Let us seek the causes of variations in year-class size in the environment. Forty years ago Hjort (1914) suggested that the size of a year-class was fixed early in its history and, in fact, during the first few days or weeks of its existence. He reasoned that to survive newly hatched larvae must have adequate amounts and kinds of food available at the time of yolk sac

absorption and the presence or absence of food at this stage determined the size of the year-class.

No evidence bearing on Hjort's hypothesis was available until Sette (1943) presented an early survival curve for one year-class of Atlantic mackerel. During the first sixty days of life, which his data covered, there was no “critical period,” but rather a constant rate of decline or survival. The survival rate was so small, however, that a very small change, projected into the future, would make a tremendous change in the size of the year-class as adults.

We now have similar data for the sardine for three different year-classes:

<i>Year-class</i>	<i>Survival per 100,000 eggs to age 1 month</i>
1950 -----	775
1951 -----	750
1952 -----	1,675

None of these year-classes is very large; in fact, they are all very small. Nevertheless, the survival rate to age 1 month is about twice as large for the 1952-class as it is for the 1950- and 1951-classes. Young-fish surveys indicate that as 0-ring fish the 1952-class was still about twice as large as the two preceding year-classes.

We cannot state with any assurance what the specific causes of these variations in survival rates are. It is fairly safe, if general, to state that they are the result of the interaction of varying rates of death from predation and death from starvation. Both of these, however, represent complex biological and physico-chemical chains which we do not yet understand.

Summarizing the information on year-class sizes, the 1930- through 1950-classes have averaged 2.5 billion fish and have varied from 0.01 (1950) to 7.2 (1939) billion fish. These year-classes have averaged 91 per cent of the size of the populations to which they were added, but have ranged from 1 per cent to 286 per cent. Over the range of stock sizes observed, there is a difference of interpretation as to whether year-class size is a function of stock size (see preceding pages). Survival rate during the first few weeks of life and again at about six months is being measured each year, but the specific causes of variations in these rates have not yet been found.

Subtractions From the Population—Mortalities

As mentioned previously, losses from a population arise from deaths or mortalities. Some of these are attributable to fishing and the remainder to a host of natural causes. If a fishery is appropriately distributed with respect to the fish population, it is possible, by determining the age composition of the catch in successive seasons, to estimate the total mortality rate. It is not possible to partition total mortality into

fishing and natural mortality without additional information, which might be obtained by a tagging experiment, for example.

However, if fishing effort is not appropriately distributed with respect to the fish population, the estimate of total mortality rate will pertain to the *fished* population and not necessarily to the total population. Fish which move from the unfished to the fished population, or vice versa, will introduce anomalies into the estimates of total mortality rate. Fish moving into the fished population will cause the estimate of total mortality to be too low; those moving out will cause it to be too high.

The latter situation obtains in the case of the sardine (*i.e.*, fish moving in and out of the fished population). With this limitation in mind, we will consider the various available estimates of mortality rates; fishing and natural as well as total.

(1) TOTAL MORTALITY RATES

These rates may be estimated from (a) catch, effort and age data, (b) tagging data, (c) accumulated age data, (d) scouting data, and (e) length frequency distributions and growth data (Table 4 and Figure 8).

(a) **Catch, effort and age data:** The method and source of data have been referred to in an earlier section. The estimates are given in columns 1 and 2 of Table 4. They assume that availability is not constant and that natural mortality is constant at an annual rate of about 33 per cent. The first series of estimates (column 1) pertains to only the fished area, while the second (column 2) pertains more nearly to the total population.

Using the second series of estimates, we see that total mortality increased up to the 1936-37 season, was fairly constant up to the 1941-42 season, increased to 1944-45 and dropped after that. Total mortality has averaged about 57 per cent over the period 1935-37 through 1950-51.

The amount of error in these estimates is unknown, but may be as much as 15 per cent. Since the estimates assume full availability in season 1944-45 and since the fish are probably never fully available, the estimates tend to be maximal.

(b) **Tagging data:** Clark and Janssen (1945) and Janssen (1948) summarized returns from California taggings on all fishing grounds. From these summaries the ratio between all tags recovered in one sea-

TABLE 4
PACIFIC SARDINE: ESTIMATES OF MORTALITY RATES (IN PER CENT)

Season	Total mortality				Fishing mortality						Natural mortality		
	1 Catch, effort and age data No. 1	2 Catch, effort and age data No. 2	3 Tagging	4 Accumulated age	5 Catch, effort and age data No. 1	6 Catch, effort and age data No. 2	7 Tagging No. 1	8 Tagging No. 2	9 Scouting	10 Egg censuses	11 Tagging No. 1	12 Tagging No. 2	13 Scouting
1932-33.....	51	39	--	24	22	8	-- a	-- a	--	--	--	--	--
1933-34.....	55	42	--	25	28	12	-- v	-- v	--	--	--	--	--
1934-35.....	59	51	--	33	32	23	-- e	-- e	--	--	--	--	--
1935-36.....	63	50	--	36	37	21	-- r	-- r	--	--	--	--	--
1936-37.....	71	71	--	59	48	48	28-50 a	22-39 a	--	--	33	39	--
1937-38.....	72	55	65	53	50	27	28-50 g	22-39 g	--	--	33	39	--
1938-39.....	75	--	66	59	53	--	28-50 e	22-39 e	--	--	33	39	--
1939-40.....	73	--	75	50	51	--	28-50	22-39	--	--	33	39	--
1940-41.....	69	--	50	45	46	--	28-50 o	22-39 o	--	--	33	39	--
1941-42.....	74	59	48	49	52	32	28-50 v	22-39 v	--	--	33	39	--
1942-43.....	69	62	58	45	45	36	28-50 e	22-39 e	--	--	33	39	--
1943-44.....	71	67	87	50	48	44	28-50 r	22-39 r	--	--	33	39	--
1944-45.....	73	73	77	62	51	52	--	--	--	--	--	--	--
1945-46.....	73	69	70	75	50	46	-- p	-- p	--	--	--	--	--
1946-47.....	81	45	--	71	61	16	-- e	-- e	--	--	--	--	--
1947-48.....	81	41	--	50	61	10	-- r	-- r	--	--	--	--	--
1948-49.....	68	38	--	37	44	6	-- i	-- i	--	--	--	--	--
1949-50.....	66	49	--	58	41	20	-- o	-- o	--	--	--	--	--
1950-51.....	85	51	--	74	68	24	-- d	-- d	21	46	--	--	40
1951-52.....	--	--	--	90	--	--	--	--	--	7	--	--	--
1952-53.....	--	--	--	80	--	--	--	--	--	3	--	--	--
1953-54.....	--	--	--	--	--	--	--	--	--	--	--	--	--

1. Pertinent to the available population only, with natural mortality constant at about 33 per cent.
2. Pertinent to more nearly the total population, with natural mortality constant at about 33 per cent.
3. From tag recovery tables given by Clark and Janssen (1945).
4. Numbers of fish caught divided by "accumulated age" estimate of number of fish in the population.
5. See footnote 1.
6. See footnote 2.

- 7 a d 8. Higher values from tagging data given by Clark and Janssen (1945); lower values derived by Marr from the same data; see also text footnote 3.
9. Derived from data given by Radovich (1952).
10. Numbers of fish caught divided by "egg censuses" estimates of a number of fish in the population.
11. See footnote 3; see also text footnote 3.
12. See footnote 8; see also text footnote 3.
13. See footnote 9.

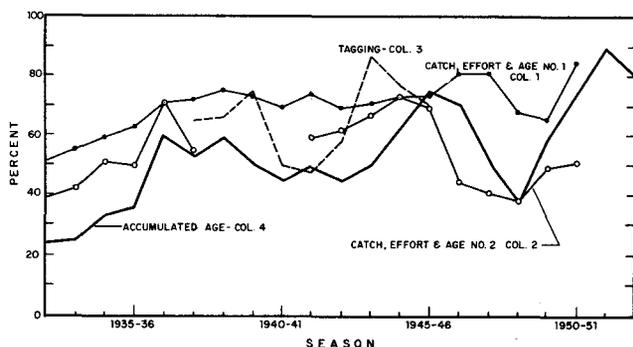


FIGURE 8. Panel A. Pacific sardine: Estimates of total mortality.

son and all tags recovered in the next season was calculated for the seasons 1937-38 through 1945-46. This series of ratios (column 3, Table 4) constitutes the second estimate of total mortalities. In the late 30's, mortalities varied from 65 to 75 per cent, in the early 40's dropped to about 50 per cent and then increased to 70 or 80 per cent. The values are in close approximation to the ratios in the second series of catch, effort and age data (column 2, Table 4) and the accumulated age calculations (column 4, Table 4).

The error associated with these estimates depends on, among other things, the dispersion of tagged fish over the fishing grounds and their availability to the fishermen. The confidence associated with them, and whether they tend to be minimal or maximal, is unknown.

(c) Accumulated age data: The number of fish caught during a season divided by the accumulated age estimate of the number of fish in the population at the beginning of that season will provide an estimate of total mortality rates. Such estimates are given in column 4, Table 4.

These estimates are unbiased point estimates; they are neither maximal nor minimal.

(d) Scouting data: Total mortality estimates arise from scouting data through comparisons of the reduction in numbers of a particular year-class sampled in two or more successive seasons. Radovich (1952b) has given estimates of total mortality rates between 1950 and 1951 for several year-classes:

Year-class	Mortality (per cent)
1950	45.1
1949	25.0
1948	39.5
1947	69.8
1946	75.8
1945	87.0
1944	100.0
1943	100.0

The error associated with these estimates is not known but it is probably greater for the 1946 and older year-classes than for the younger ones (owing to fewer numbers in the population).

Similarly, whether they are minimal or maximal is not known.

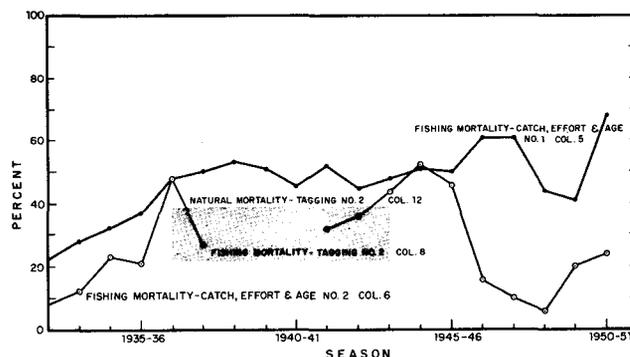


FIGURE 8. Panel B. Pacific sardine: Natural mortality and fishing mortality.

(e) Length and growth data: Silliman (1943) used length frequency distributions and a sardine growth curve to derive an estimate of 40 per cent total mortality during the period 1925-33.⁵

The reliability and possible bias of this estimate is not known.

(2) FISHING MORTALITY RATES

These rates may be estimated from (a) catch, effort and age data, (b) tagging data, (c) scouting data, (d) accumulated age data and (e) egg censuses and catch data.

(a) Catch, effort and age data: Estimates based on these data are given in columns 5 and 6, Table 4. The first series are estimates of fishing mortality rates with natural mortality assumed constant at 33 per cent and with availability varying. These rates pertain to the fished population.

The second series pertain to the total population; *i.e.*, availability has been taken into account. They are, however, maximal owing to the fact that it is necessary to assume full availability in some base year.

(b) Tagging data: In columns 7 and 8, Table 4 appear the estimates of average fishing mortality over the period 1936-37 through 1943-44 as given by Clark and Janssen (1945)—the higher values—and as recalculated by Marr from the same data—the lower values. Clark and Janssen, however, questioned the use of tag returns as Marr has applied them. Clark and Janssen made estimates of 39 to 50 per cent fishing mortality from tag returns. These values are in better accord with the estimates from "catch, effort and age data" of columns 5 and 6 than are Marr's tagging data calculations.

(c) Scouting data: As explained previously, estimates of mortality rates arise from observing the

⁵ Silliman (1943) also estimated total mortality during the period 1937-42 to be 80 per cent. This estimate was based on the age composition of the catch in the 1941-42 season. Unfortunately, during this season the youngest year-classes were the largest and the older classes the smallest. This led to too great an estimate. The accumulated age estimate for the same period, a maximal estimate, is only 51 per cent (range 45-59 per cent); the tagging estimate average is 61 per cent (range 48-75 per cent).

decline in numbers of fish in particular year-classes sampled in two or more successive seasons. Because younger year-classes are not yet in the fishery, the total mortality rates for these year-classes may be considered natural mortality rates. The total mortality of the older year-classes includes fishing mortality. With these data it is also possible to estimate fishing mortality (column 9, Table 4).

This estimate of fishing mortality is minimal since it assumes that total mortality for the younger year-classes results from natural causes only. The younger year-classes are subject to a limited fishery and the majority of the younger fish were found on the southern end of the range of the surveys. There is a high probability that some of these fish moved farther south and were out of the surveyed area in the second year. Too high an estimate of natural mortality results in too low an estimate of fishing mortality.

(d) Accumulated age data: The estimates arising from these data (column 4, Table 5), which were described under "Total Mortality," are also maximal estimates of fishing mortality. They are maximal because they do not take into account natural mortality.

(e) Egg censuses and catch data: Another estimate of fishing mortality (column 10, Table 4) may be obtained by dividing the number of fish caught by the total population size, as estimated from egg censuses and fecundity data (see Table 2).

(3) NATURAL MORTALITY RATES

At present we have only two sources of estimates of natural mortality rates: (a) tagging data and (b) scouting data.

(a) Tagging data: As in the estimates of total population size and of fishing mortality, Marr and Clark again differ in the use of tagging data to obtain estimates of natural mortality. The estimates (33 per cent and 39 per cent) given in columns 11 and 12 of Table 4 are derived from Marr's calculations. According to Clark and Janssen, the natural mortality based on tag returns would be estimated at 22 to 36 per cent.

(b) Scouting data: Natural mortality rates are estimated from these data by methods already described (column 13, Table 4).

In summary, while mortality rates are difficult to estimate, estimates based on accumulated age data show, for example, that total mortality increased from about 24 per cent in 1932-33 to 59 per cent in 1936-37, fluctuated around 50 per cent from 1936-37 to 1943-44 and around 65 per cent between 1944-45 and 1952-53. The high rates in recent years are in part, at least, artifacts caused by the unavailability of sardines on the California fishing grounds resulting in a greatly reduced catch. In the 1952-53 and 1953-54 seasons fishing mortality and, in all probability, total mortality were actually reduced.

WHAT CAUSES FLUCTUATIONS IN THE CATCH OF SARDINES?

In an earlier section we stated that fluctuations in the catch from a fish population can arise from three sources: fluctuations in fishing effort, fluctuations in the abundance of the population and fluctuations in the availability of the population. We may examine these three sources with respect to fluctuations in the catch of the sardine.

Fluctuations in Fishing Effort

The amount of fishing effort (or data from which this may be derived) has been given for British Columbia for the period 1925-1932 by Hart (1933), for Oregon and Washington for the period 1935-43 by Marr (1950), and for California for the period 1932-33 to 1950-51 by Silliman and Clark (1945), Clark and Daugherty (1950, 1952) and Widrig (1954). These data are shown in Table 5. We will confine our discussion to the effort expended in California, since these data cover the longest period and since the bulk of the catch was made off California. Further, we will confine our remarks here, about the effect on the catch of changes in effort, to those changes occurring in a particular season. The possibility of any long-term effects of effort on the size of

TABLE 5
PACIFIC SARDINE: ESTIMATES OF FISHING EFFORT

Season	California				Oregon-Wash- ington	British Co- lumbia
	1	2	3	4		
1925-26	--	--	--	--	--	1,041
1926-27	--	--	--	--	--	2,558
1927-28	--	--	--	--	--	4,166
1928-29	--	--	--	--	--	5,843
1929-30	--	--	--	--	--	5,054
1930-31	--	--	--	--	--	3,642
1931-32	--	--	--	--	--	2,748
1932-33	448	3,408	229	6,546	--	1,775
1933-34	600	2,545	392	3,824	--	--
1934-35	717	2,130	476	3,149	--	--
1935-36	876	1,743	570	2,630	43	--
1936-37	1,237	1,234	807	1,857	113	--
1937-38	1,366	1,118	867	1,729	135	--
1938-39	1,399	1,091	958	1,565	288	--
1939-40	1,314	1,162	894	1,677	278	--
1940-41	1,124	1,358	763	1,965	38	--
1941-42	1,304	1,171	921	1,628	187	--
1942-43	1,010	1,512	742	2,020	29	--
1943-44	1,122	1,361	824	1,819	34	--
1944-45	1,305	1,170	906	1,655	--	--
1945-46	1,315	1,161	881	1,701	--	--
1946-47	1,485	1,028	1,212	1,237	--	--
1947-48	1,358	1,124	1,215	1,234	--	--
1948-49	921	1,658	711	2,108	--	--
1949-50	947	1,612	652	2,299	--	--
1950-51	1,527	1,000	1,499	1,000	--	--

1. Boat-months from Clark and Daugherty (1952).
2. Ratio of values in column 1 to effort in 1950-51.
3. Boat-months from Widrig (1954).
4. Ratio of values in column 3 to effort in 1950-51.
5. Boat-weeks, from Marr (1950).
6. Boat-days, derived from Hart (1933).

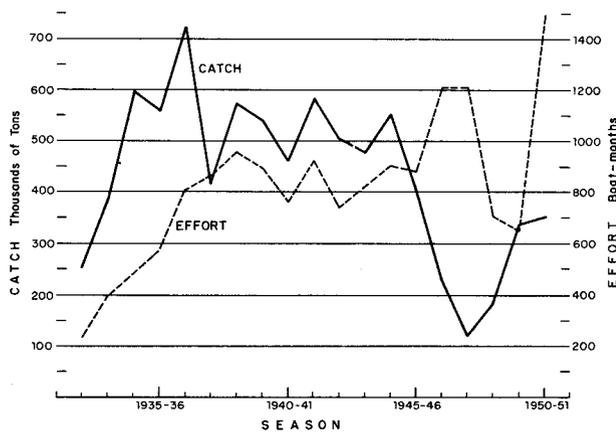


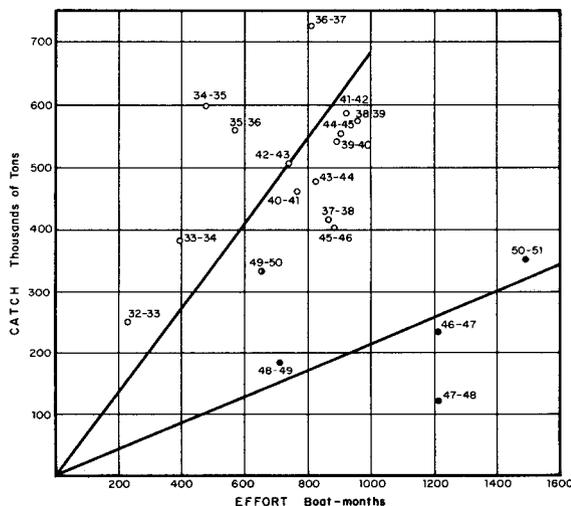
FIGURE 9. Pacific sardine: Fishing effort and catch in California, 1932-33 through 1950-51.

the population and thus on the catch is considered in other sections of this paper.

In Figure 9 are shown, for California, the total catch curve and the total effort curve, for the seasons 1932-33 through 1950-51. Prior to the 1946-47 season, and in general, when effort increased catch increased and vice versa. There are, of course, exceptions to this generalization; *i.e.*, in the 1937-38 season effort increased slightly whereas the catch dropped to about 57 per cent of that of the previous season.

Since changes in effort tend to be accompanied by corresponding changes in catch, one would expect that if catch were plotted as a function of effort, the points would tend to cluster about a line. If the effort units are not competing with each other, this should be a straight line. For a given population size, as effort units are increased in number they will eventually compete with each other and the straight line will curve to the right. The data are plotted in this manner (Figure 10) and, with variations, of course, the points

FIGURE 10. Pacific sardine: Relation of fishing effort and catch in California, 1932-33 through 1950-51.



prior to 1946-47 do fall about a straight line. The deviations from this trend line may be attributed to deviations in the size of the available population from the average size of the available population that obtained over the period.

However, in the 1946-47 and subsequent seasons, with the possible exception of the 1949-50 season, the average size of the available population shifted to a different and much lower level (see Table 2). Part of this shift was caused by a decrease in availability (evidence given in subsequent section) and part by the presence, in the available population, of a series of average or below average size year-classes (see Figure 3 and Table 3).

It is also of interest to compare estimates of total mortality rates with changes in fishing effort. Shown in Figure 11 are fishing effort (column 3, Table 5),

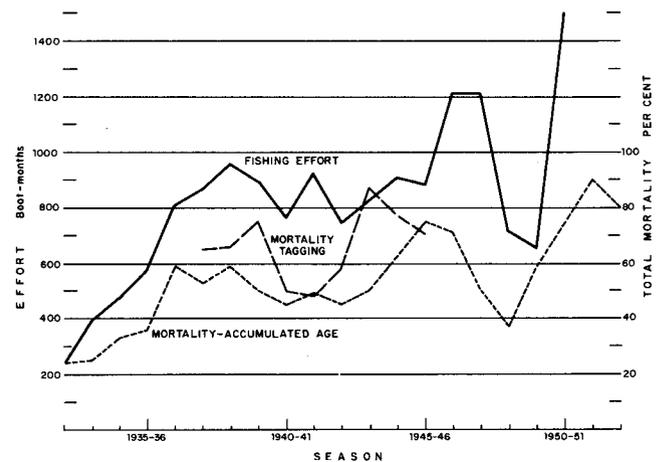


FIGURE 11. Pacific sardine: Comparison of fishing effort (col. 3, Table 5) with estimates of total mortality from tagging (col. 3, Table 4) and from accumulated age data (col. 4, Table 4).

estimates of total mortality rates from tagging data (column 3, Table 4) and from accumulated age data (column 4, Table 4). The amount of effort rose from slightly more than 200 boat-months in the 1932-33 season to slightly more than 800 boat-months in the 1936-37 season, and thereafter fluctuated around 850 boat-months through the 1945-46 season. In subsequent seasons the average level was perhaps somewhat higher, with much wider variations. The trend in total mortality rate estimated from accumulated age data closely follows the trend in intensity. An association between effort and total mortality estimated from tagging data, if there is one, is less evident.

Fluctuations in Abundance

Pertinent to the preceding discussion is a comparison of the number of fish entering the population each year (new year-classes) with the number of fish removed from the population by the catch. This is given

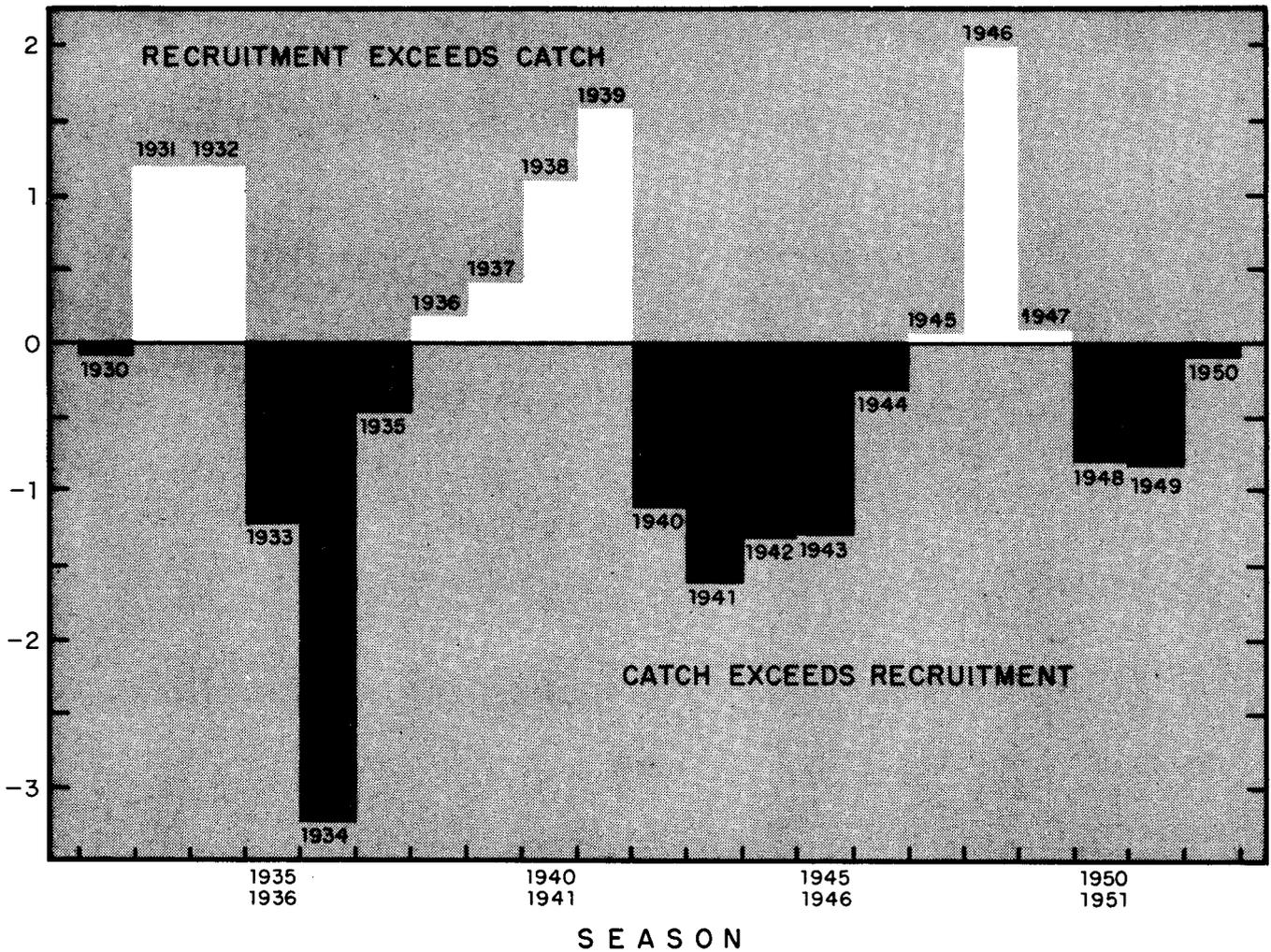


FIGURE 12. Pacific sardine: Comparison of size of entering year-class (at age 2) with catch (age 2 and older) in same season. Year-class size estimates are based on accumulated age data and are minimal.

in Figure 12 (see also Figure 4). Year-class size is the accumulated age estimate based on fish 2-rings and older (see column 2, Table 3, and Figure 3). As previously mentioned, these estimates are minimal in the amount of the numbers of fish which are present on the fishing grounds and die naturally and in the numbers of fish which are unavailable and eventually die naturally. The numbers of fish caught are based on the data summarized in column 1, Table 2, and differ from those data only in the omission of 0-ring and 1-ring fish.

In Figure 12 the horizontal line indicates the exact balance of recruitment and catch. It does not indicate a population of constant size. Points above the horizontal line indicate that recruitment exceeded catch, and, conversely, points below the line indicate that catch exceeded recruitment. The exceedingly interesting feature of this figure, is that over the period 1932-33 through 1952-53 the total estimated recruitment has amounted to about 91 per cent of the observed catch; catch has exceeded recruitment by 4.4 billion fish.

Since the recruitment estimates are minimal (they include only that portion of each year-class that was caught by fishermen), it is quite possible, if not probable, that the true recruitment has equalled or exceeded the catch.

This relation between catch and population changes is also reflected in a comparison of fishing effort with changes in total mortality (Figure 13). Fishing effort is expressed as the numbers of boat-months required to supply the tonnage taken each season in the California fishery (column 1, Table 5). In Figure 13 the boat-months are expressed in percentages of 1950-51 to make them directly comparable with the mortality measures (column 4, Table 4), which are also in percentages. The relationship between the trends in total mortality and fishing effort indicates the direct effect of Man on the supply of sardines that he fishes. Increased fishing effort produces corresponding increase in total mortality and decreased effort a decrease in total mortality. The comparison begins in 1932-33 when the industry was starting on its last rapid expansion and continues to the collapse in 1951-52. In

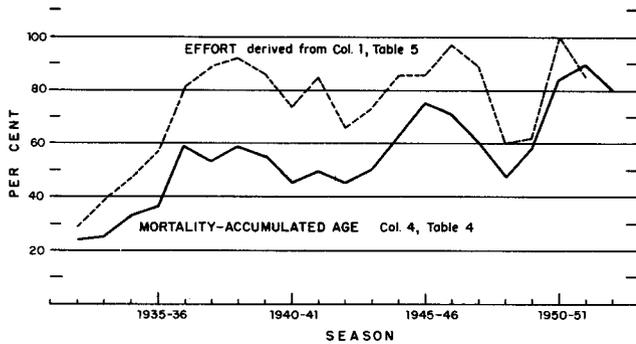


FIGURE 13. Comparison between fishing effort and total mortality rate in the sardine population.

the early 30's total mortality approximated 25 per cent and increased to about 60 per cent at the end of that decade. During this time effort reached its first maximum. In the first half of the 40's effort dropped somewhat and total mortality declined to about 50 per cent. Then renewed effort was expended and total mortalities again increased to about 70 per cent. At the close of the 40's effort and mortality declined and again increased in the early 50's.

The implications of this are important, for while recruitment and catch have been approximately equal, the catch and the population, in some recent years at least, have decreased in size. Such a decrease in catch may have four possible causes: (1) The population was reduced in size by fishing mortality, as a consequence of which subsequent year-classes were reduced in size. (2) Year-classes were reduced in size by natural variations in early survival rate independent of the size of the spawning stock. (3) Availability decreased. (4) Natural mortality rate increased. Any or all of these factors may be working independently or concurrently.

We disagree on (1) and (2) above (see pp. 23-25). Under (3) there is evidence, which will be discussed in a subsequent section, which shows that availability is variable and that it has decreased in recent years. Under (4) the few available data which permit estimates of natural mortality rates yield about the same estimate for an earlier and a recent period. A reduction in year-class size plus a decrease in availability are the main factors we believe to be responsible for the recent decline in the sardine catch.

Fluctuations in Availability

The factor of availability is well known to fishermen, although, to be sure, they do not use that term. Availability has been defined by Marr (1951:163-4) as "... the degree (a percentage) to which a population is accessible to the efforts of a fishery." In an earlier section, some examples of how availability operates has been given.

We may now categorize these. In the first place, there may be actions of the sardine which influence the degree of availability on a more or less local basis. These may be classified under the term behavior (or micro-behavior). Examples of behavior-connected availability include (1) schooling at the surface only at some particular time during a 24-hour period; (2) formation of small schools upon which it is unprofitable to set; (3) formation of less dense schools which are not readily seen; and so on.

A second category of actions which influence the degree of availability is less clearly defined, but has to do with the movements of sardines; i.e., the geographic distribution of sardines and how this changes with time as the result of non-random or random movements of the fish. Clearly, actions of this nature could have much more important and widespread effects on availability than would variations in micro-behavior.

The third and final category is of a somewhat different nature than the other two. It has to do with whether or not there exist subpopulations, or races, within the total sardine population. If there are such subpopulations, the importance of their distribution with respect to the distribution of the fishery is obvious; such subpopulations might be entirely within the range of the fishery, only partially or in variable amounts within the range of the fishery, or never within its range.

We will consider each of these three categories separately.

(1) BEHAVIOR

Unfortunately, almost nothing is known about sardine behavior or the causes of such behavior (excepting, of course, the considerable, but unpublished knowledge of the fishermen). We do know, of course, the general features associated with the fact that sardines are a pelagic, filter-feeding, schooling species, and these have been cited earlier.

Experiments conducted by Groody (Marine Research Committee, 1950) showed that the tendency to form close schools was increased at temperatures from 12° down to 6°C (53.6° to 42.8°F), whereas this tendency was reversed at temperatures from 12° up to 25°C (53.6° to 77.0°F). Marr (1950) showed that the highest catch per unit-of-effort in the Oregon and Washington fishery tended to be made in seasons of lowest average daily temperatures and the lowest catch per unit-of-effort tended to be made in the seasons of highest average daily temperatures. The experiments of Groody may explain these observations; i.e., a school of a given diameter may be denser and contain more fish at lower temperatures than it does at higher temperatures.

Other experiments by Groody (Marine Research Committee, 1950) show that feeding behavior may be induced by chemical stimulation.

Experiments by Groody *et al.* (1952) on behavior in an electrical field do not seem to be pertinent to the problems of behavior in nature.

(2) MOVEMENTS

Tagging experiments conducted between 1935 and 1942 by the California Department of Fish and Game, the Fish Commission of Oregon, the Washington Department of Fisheries, and the Fisheries Research Board of Canada give direct information about the movements of sardines. Altogether, approximately 140,000 fish were tagged and released in four general areas: Pacific Northwest, central California, southern California and Baja California. The experiments demonstrated the following:

(a) Fish tagged at any locality from southern California north to British Columbia were recaptured on all fishing grounds from southern California to British Columbia (Table 6). Fish tagged off central and northern Baja California were recovered in large numbers in the southern California catch, moderately in the central California catch and negligibly in the catch of the Pacific Northwest. No tags were recovered from the two lots tagged and released south of Sebastian Vizcaino Bay, Baja California (*i.e.*, in Magdalena Bay and south).

(b) Dispersal of tagged fish throughout the range of the species is difficult to examine in detail owing to lack of recovery facilities in Baja California. However, the available data (Table 7) show that fish tagged off southern California tended to move more to the north than did the fish tagged off central California tend to move south. On the other hand, tags put out off British Columbia became increasingly more available to the southern California fishery than to the British Columbia fishery. Fish tagged in southern California were equally distributed on all fishing grounds.

TABLE 6

SARDINE TAG RECOVERIES (AT 100 PER CENT EFFICIENCY) PER 1000 FISH TAGGED

Recovery Area	Release Area			
	Pacific Northwest	Central California	Southern California	Baja California
Pacific Northwest.....	2.1	6.2	7.2	0.1 ¹
Central California.....	2.4	59.5	53.7	12.2
Southern California.....	1.5	14.1	29.4	44.1
Baja California.....	No recovery facilities			
Totals.....	6.0	79.8	90.3	56.4 ²

¹ One tag recovered in Washington.

² No recovery facilities in region of release.

TABLE 7

SARDINE TAG RECOVERIES (AT 100 PER CENT EFFICIENCY) PER 1000 FISH TAGGED PER BILLION FISH CAUGHT

Recovery Area	Release Area				Total
	Pacific Northwest	Central California	Southern California	Baja California	
Pacific Northwest.....	0.7	2.0	2.1	--	4.8
Central California.....	0.1	2.6	2.1	0.9	5.7
Southern California.....	1.1	1.0	1.9	4.7	8.7
Baja California.....	No recovery facilities				

(c) Fish tagged off Baja California, from Sebastian Vizcaino Bay northward, gradually dispersed throughout the California fishing grounds, and there was one recovery off Washington. Over three-fourths of the recoveries were made in the southern California area, however. Owing to the greater distance from the California fishing grounds, the dispersal was slower in the first season after tagging (Table 8) than for fish tagged off California. The total number of returns per thousand (56.43 for Baja California, 90.26 for southern California and 79.80 for central California) indicates, however, that in the California fishery the ratio of Baja California fish to California was 56.43/90.26 and 56.43/79.80 and thus the recovery rate of Baja California tagged fish was 60 to 70 per cent of the California tagged fish. These percentages reflect the relative availability of the Baja California and California sardines to the U. S.-Canadian fishery. The tag returns of these fish for the successive seasons after tagging are compared with those of fish tagged off California in Table 8.

(d) The recovery of all tagged fish in southern California in relation to the number of fish taken in the commercial catch was 1.5 times as great as in the central California region (Table 7). As noted above, fish tagged off southern California were recovered in all areas in about the same proportion as the

TABLE 8

SARDINE TAG RECOVERIES PER 1000 FISH TAGGED AT 100 PER CENT RECOVERY EFFICIENCY

Season after tagging	Fish tagged off Baja California		Fish tagged off Southern California		Fish tagged off Central California	
	Number	Per cent	Number	Per cent	Number	Per cent
1st.....	21.70	38.5	57.22	73.4	50.35	63.1
2d.....	19.26	34.1	21.43	23.7	18.61	23.3
3d.....	11.05	19.6	6.82	7.6	6.93	8.7
4th.....	3.11	5.5	2.65	2.9	3.04	3.8
5th and over.....	1.31	2.3	2.14	2.4	0.87	1.1
Total.....	56.43	100.0	90.26	100.0	79.80	100.0

total catch and the greater concentration of tagged members in this area came from fish tagged off Baja California. It might be concluded from this that the density of tags was greater in fish tagged off Baja California than in fish tagged off central California, and therefore the population off Baja California was somewhat smaller than that off central California during the period of tagging experiments.

The results of these tagging experiments tend to yield an estimate of average movements over the duration of the tagging period. Clark (1952:373) summarized sardine movements as follows: "By the end of their first year they have evidenced a slight northward movement and in each succeeding year this northward migration becomes more pronounced. These northward movements occur during the summer months and a return southward takes place in the late fall and winter . . ." Deviations from this average condition could result in changes in availability. We believe that some of the observed changes in availability were a result of just such deviations in movements. For example, even when the population was much larger than it is now, sardines did not appear in British Columbia waters during certain seasons. This happened in 1933, for example, when the catch fell to less than a tenth of what it was in 1932 or 1934. Again in 1939, the year we point to as an example of northern spawning, sardines did not reach British Columbia, and the small British Columbia catch of that season was obtained off Washington.

Two outstanding examples of changes in availability can be cited for the California fishery. Between the 1945-46 and the 1946-47 seasons, there was a much greater than expected decline in all year-classes in the fishery. Between the 1948-49 and the 1949-50 seasons, on the other hand, the decline was much less than expected. In fact, some year-classes showed an increase. Since there must have been some natural mortality between these two seasons this increase in numbers on the fishing grounds can be explained only by increased availability in 1949-50. This anomaly of increased availability resulted from an influx of fish, perhaps from Baja California.

The portion of the population off Baja California that becomes available to the California fishery varies considerably. During the period 1939 to 1945, we estimate that the fish off Baja California became about 60 to 70 per cent as available to our fishery as were fish off southern California. The fish scouting surveys of 1950, 1951 and 1952, when compared with the spawning surveys of the same years, indicated that in 1950 there was . . . "a net northward movement of about 28 per cent of the adult population. In 1951 the net northward movement was about 25 per cent . . ." (Marine Research Committee, 1953:29). There was no detectable net northward

movement of fish in 1952, nor again in 1953, and partly as a result of this decrease in availability, the catches of the 1952-53 and 1953-54 seasons have amounted to only a few thousand tons. In the 1954-55 season sardines again appeared on the southern California fishing grounds in appreciable numbers. In the spring of 1954 widespread sardine spawning occurred off southern California for the first time in three years. Concurrently, water temperatures in this area were higher in the spring and summer of 1954 than for several previous years.

The extent of the variation in availability of the sardine population is extremely difficult to measure and has, in fact, not yet been measured satisfactorily. Widrig (1954) has estimated availability over a period of years. His estimates are maximal, since it is necessary, by his method, to assume full availability in some base year. Some of his estimates are:

<i>Season</i>	<i>Per cent availability</i>
1941-42 -----	58.0
1942-43 -----	79.7
1943-44 -----	87.8
1944-45 -----	100.0
1945-46 -----	96.3
1946-47 -----	28.1
1947-48 -----	21.8
1948-49 -----	21.8
1949-50 -----	78.7
1950-51 -----	53.0

These estimates exceed the true availability in the amount that availability was not 100 per cent in the 1944-45 season. The error associated with these estimates is not known.

(3) SUBPOPULATIONS

A definition of subpopulation that is acceptable to all is difficult to provide, even as systematists still strive for a universally acceptable definition of species or subspecies. A subpopulation, in the sense in which we use it, is a group of fish of less than specific rank (and probably of less than subspecific rank, although recognition of a subspecies tends to be more subjective than recognition of a species and varies more between individual workers) which is genetically self-sustaining. Under this definition it matters not whether fish of different subpopulations (if there are such) intermingle or do not intermingle during the rest of the year, so long as they segregate and there is, during the spawning season, interbreeding (or opportunity for such) only between the members of each group.

Since, in the case of the sardine, it is impractical or impossible to use the more direct approach of the geneticist in solving this problem, we must use indirect methods. If there are no subpopulations of sardines, we would expect to find that each individual is more or less like every other individual, provided that there are no environmentally produced differences. If there are subpopulations, we would expect to find that each individual is more like the other members of the

same group and less like individuals of the other sub-populations, again provided that there are no environmentally produced differences (or, if there are, that we can recognize them as such).

In essence, then, the problems are (1) to determine whether or not there are differences between groups, and, if there are such differences, (2) whether or not they are a reflection of inherited differences. We may examine each of these in turn.

(1) There is evidence (from tagging, especially; see previous section) that the sardine stocks from central Baja California to British Columbia intermix, at least outside the spawning season. On the other hand, there are a number of lines of evidence which might indicate that the mixture is only partial, and that the population is heterogeneous, rather than homogeneous. These include (a) the existence of more than one spawning center, and (b) differences in size, (c) in age composition, (d) in meristic characters, (e) in scale types and (f) in growth rates in different parts of the population range.

(a) **Spawning areas:** There is a major spawning area off central Baja California and a major spawning center off southern California. The number of eggs deposited in the latter was greatly reduced in 1952 and 1953. These two centers are connected by a narrower region along the coast in which spawning also occurs. Spawning occurs in the spring months in these centers, although somewhat later in the one off southern California than in the one off central Baja California. In some years (1939 especially) there has been spawning off northern California, Oregon and Washington in the summer months. Spawning in all of these regions takes place over about the same temperature range, 13.0°-16.5°C (55.4°-61.7°F).

Spawning occurs in the bays, such as Sebastian Vizcaino, along the west coast of Baja California in the fall months at temperatures of 18°-23°C (64.4°-73.4°F).

Spawning is also known to have occurred in the late winter throughout much of the Gulf of California, but little more is known about it.

TABLE 9

PACIFIC SARDINE: AVERAGE STANDARD LENGTH (IN MM) OF SARDINES IN THE COMMERCIAL CATCHES IN DIFFERENT AREAS (TEN YEAR-CLASSES IN AVERAGE FOR EACH AREA)

Area	Number of rings						
	1	2	3	4	5	6	7
British Columbia.....	179	201	223	236	242	246	249
Washington and Oregon ..	174	200	224	235	243	246	248
San Francisco.....	176	207	221	227	232	240	247
Monterey.....	172	203	218	225	232	240	243
San Pedro.....	183	200	208	214	220	226	---

(b) **Differences in size:** Sardines of the same ages, especially when 3-rings or older, are considerably larger, on the average, in the Pacific Northwest than in San Pedro, and intermediate in size, on the average, in central California. This is shown in Figure 14 and summarized in Table 9. These differences, presumably arising from differences in growth rates in the several areas, are possible only if the population is not randomly mixed. The effect of mixing would be to minimize differences; hence the fact that such differences persist in the several areas despite some emigration and immigration, is good evidence that the population is not randomly mixed at all times.

(c) **Differences in age:** It was pointed out in the discussion of sardine tagging that older fish tend to be caught in the northern portion of the range (Pacific Northwest). Data on age composition of the commercial catch, in the several fishing areas, support this observation. To illustrate, the average age compositions in three fishing areas, Pacific Northwest, Monterey, and San Pedro, are given for the period 1941-42 through 1945-46 in Table 10 and Figure 15. Whereas 39 per cent of the fish taken in the Pacific Northwest were 5-rings or older, only 10 per cent of the fish taken at Monterey and 4 per cent of the fish taken at San Pedro were this old.

(d) **Differences in meristic characters:** Aside from vertebral numbers, little attention has been paid (in the literature) to other meristic characters of sardines. Vertebral studies have been made by Hubbs (1925), Hart (1933) and Clark (1947). Clark found as much variation in the vertebral numbers of adult sardines within localities as she did between localities, except that the average vertebral number of one sample (31 fish) of adults from the Gulf of California was more than 0.50 vertebra lower than collections from any other locality. Average vertebral numbers of young fish from southern Baja California and the Gulf of California were less than the average numbers from more northern localities.

TABLE 10

PACIFIC SARDINE: AVERAGE AGE COMPOSITION IN DIFFERENT FISHING AREAS DURING THE 5-YEAR PERIOD 1941-42 THROUGH 1945-46

Age (rings)	Pacific Northwest		Monterey		San Pedro	
	Per cent of total	Cumulative per cent	Per cent of total	Cumulative per cent	Per cent of total	Cumulative per cent
1.....	1.31	1.31	10.82	10.82	13.15	13.15
2.....	15.96	17.27	36.03	46.85	39.01	52.16
3.....	19.01	36.28	27.15	74.00	31.53	83.69
4.....	24.69	60.97	15.82	89.82	12.40	96.09
5.....	20.62	81.59	7.13	96.95	3.14	99.23
6.....	11.50	93.09	2.36	99.31	0.64	99.87
7.....	4.46	97.55	0.56	99.87	0.08	99.95
8 and older.....	2.45	100.00	0.13	100.00	0.05	100.00

(e) **Differences in scale types:** Scales collected from sardines in the northern part of their range differ from those collected in the southern part (Felin, 1954). The northern type, characteristic especially of many fish of the 1939-class, had relatively small first year's growth and rapid subsequent growth. The year rings (annuli) are well defined. Southern type scales have much fainter year marks, a proportionately large first year's growth, and smaller but more uniform subsequent growth.

The northern type sardine probably originated from spawning off southern California (and to the north) and the southern type from spawning off central Baja California. The major part of the fish collected in southern California have southern type scales, while the majority of fish in the north have the northern type; evidence of only partial mixing of the population.

(f) **Differences in growth types:** Evidence for such differences has already been given in the sections (b) and (e) above. A more complete discussion is given by Felin (1954).

(2) There is, then, a considerable body of evidence indicating that the sardine population throughout its range differs with respect to several characteristics. We may next consider the question of whether or not such differences are in fact inherited.

(a) **Spawning areas:** We know from sardine spawning surveys that there are at present two main centers of sardine spawning, one off southern California, the other off central Baja California. These two centers are connected by a narrow region along the coast in which only a little spawning occurs. Do individual fish spawn in both centers, or is their spawning restricted to one or the other? Serological and chromatographic techniques are being explored as possible tools for distinguishing between races of sardines. The possibility of obtaining information on this point through a tagging program is being given serious consideration. The renewed spawning off southern California in 1954 is evidence that sardines from Baja California will move northward to spawn in the southern California area and therefore the fish from the two areas cannot be considered to belong to separate subpopulations.

A group of sardines that, on the other hand, might constitute a separate race occurs off southern Baja California and in the Gulf of California. Clark (1947) on the basis of lower vertebral numbers (51.2, as compared to the average of 51.7 for all sardines "north of southern Baja California") concluded that "sardines living off southern Baja California probably comprise a distinct group which does not mix with the northern fish; or if a mixture occurs, the proportion of southern fish to the total northern population is small."

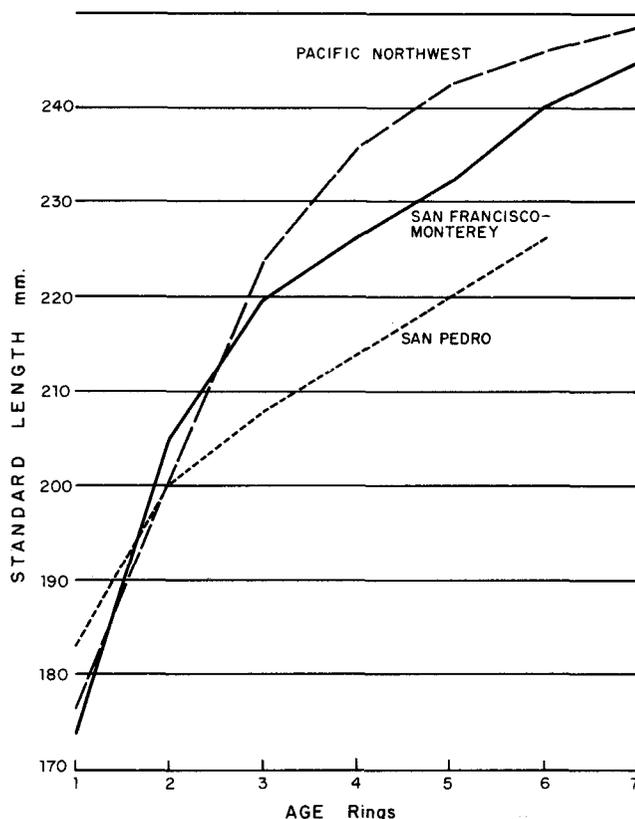


FIGURE 14. Pacific sardine: Observed growth curves (size on age) of sardines in several areas.

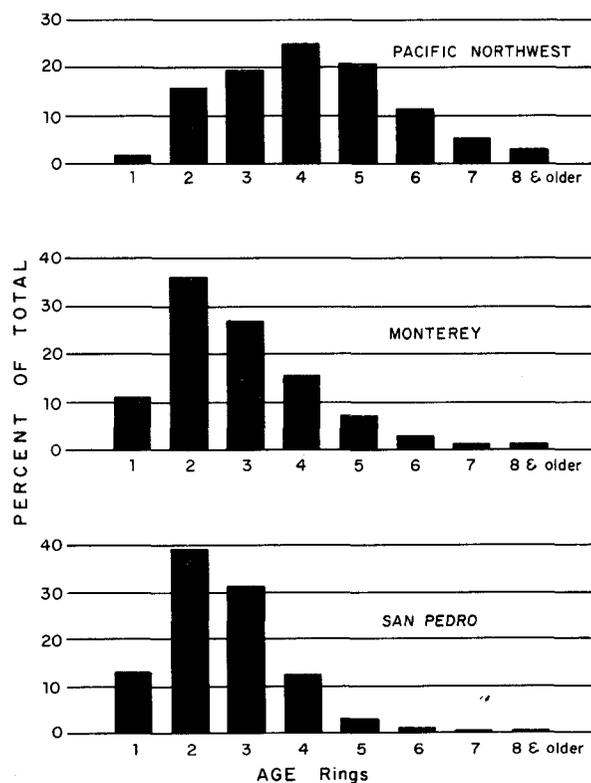


FIGURE 15. Pacific sardine: Average age composition in different fishing areas during the 5-year period 1941-42 through 1945-46.

During the recent spawning surveys off-season spawning has been found to occur in Sebastian Vizcaino Bay and other bays to the south, under very different environmental conditions than spawning at other seasons (at temperatures about 4°C (7.2°F) higher, etc.). Scales obtained from these fish are of a different type, and have a different growth pattern than other sardines. It has been called the "Bay" type. This group of sardines may be the same as the "southern" population of Clark. The group appears to be separated from the main body of sardines both in time of spawning and in the environmental conditions under which spawning takes place. They may thus constitute a "physiological" subpopulation. If so, differences in vertebral numbers may only be a secondary characteristic which is induced by the environment. (In this connection, see Taaning, 1952.) This, however, does not preclude the use of vertebral numbers as a tool for estimating the admixture of fish from different areas.

(b)-(e) **All other differences:** All of the other observed differences mentioned above could be either inherited or environmentally produced. Experiments are being carried out to determine the nature of growth differences. Preliminary work (serology and chromatography) has been done to determine if subpopulations characterized by biochemical differences exist. Definitive results have not yet been obtained.

WHAT INFLUENCE DOES MAN HAVE ON THE SARDINE POPULATION?

In the introductory sections of this paper, we pointed out that the only way in which Man can affect a population of marine fishes is by varying the amount of mortality imposed on the population by fishing. And further, there are only two basic biological problems which Man needs to solve if he wishes to know if and how the amount of fishing can be varied in order to produce desired and predictable results in the catch (which results are often referred to as the "maximum sustained yield").

One of the problems has to do with the gain in weight through growth of a given group of fish, as compared with the loss in weight through the death of some members of that group. This relationship is generally termed "yield per recruit" by fishery biologists. The choices here are whether to restrict fishing by size (age) of fish and, if it is to be restricted, to determine the optimum size at which to start catching the fish. (Variations in the yield per recruit will also occur with changes in the amount of fishing effort, for a given age at first capture.)

The other problem has to do with whether year-class size is a function of stock size or whether year-class size is independent of stock size. If year-class size is determined by stock size, then what stock size

produces the maximum year-class size? There is the further question of how to control fishing so as to best control stock size. The two possibilities include (1) regulating the amount of catch without regard to the amount of effort involved in making that catch and (2) regulating the amount of effort expended.

Yield Per Recruit

Quite independent of the relation of year-class size to spawning stock size, the catch (in weight) to be expected from a given year-class depends simply on four interacting conditions: (1) the fraction of the population taken, say, annually by the fishing effort; (2) the natural mortality rate; (3) the growth pattern; and (4) the age at first capture.

It is not difficult to compute the catches obtainable from any species whose growth pattern and natural mortality rate are known. Generally, the growth pattern of a species is fairly well known from past collections, or can be determined. Inferences as to what it will be in the future are usually fairly accurate. Growth patterns of sardines are well known.

The natural mortality rate of a species is rarely known or even estimable directly. However, we can examine the yield per recruit relation for various given natural mortality rates, and decide from the several possibilities what probability we wish to attach to each. Further, we can select natural mortality rates which are pertinent to the sardine.

Now the yield per recruit will vary with different fishing mortality levels as well as with different ages at which the fish are first captured. Both effects can be evaluated for given conditions of effort.

We believe that even if the yield per recruit relationship in the sardine is such that it would be profitable (in terms of increased catch) to restrict fishing by size of fish, it would be entirely impractical to do so, owing to the nature of the fishery; *i.e.*, the size of the fish in a school usually cannot be determined until after the net has been set and pursed; increasing mesh size would result in an increase in the occurrence of "Christmas trees," and so on. Nevertheless, it is of general interest to examine this relationship.

In the examples given in Figure 16, the rates of natural mortality and fishing mortality used are indicated in each panel. The growth pattern used in all panels is that observed at Monterey. Under the conditions stated, each panel shows the results that would obtain at three different ages at first capture; 1-ring, 2-ring and 3-ring. In each example we have started with an initial population of the same size. The top curves in Figure 16 show what would happen, in terms of weight, to this initial population under the different stated conditions. The lower curves show what the catch (weight units indicated by the numbers) would be under the stated conditions.

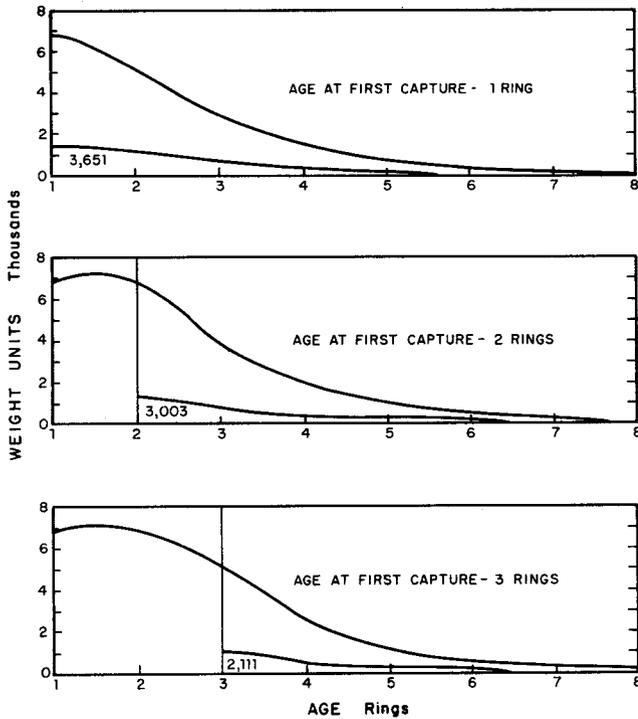


FIGURE 16. Panel A. Fishing mortality=26 per cent; natural mortality=39 per cent.

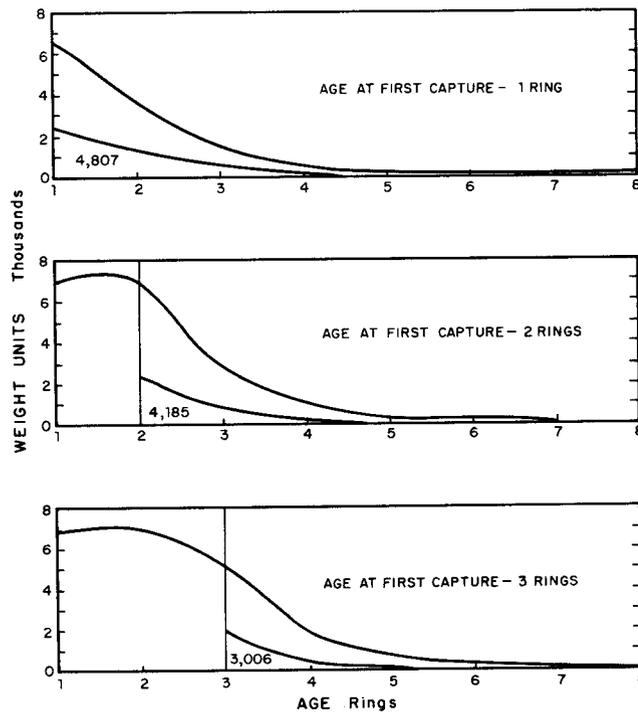


FIGURE 16. Panel B. Fishing mortality=45 per cent; natural mortality=39 per cent.

Examination of Figure 16 shows that unless the natural mortality rate is below about 20 per cent, the greatest catch in weight is obtained with the greatest rate of fishing mortality and an age at first capture of 1-ring (Panels A and B). If, however, the natural mortality rate is low, the greatest catch in weight will result from an older age at first capture; *i.e.*, 2-ring in the example given (Panel C).

Conditions most closely approximating those that have obtained in the sardine fishery are shown in the middle curve of Panel B. (It should be remembered that mortality rates are probably not constant over the years and that our estimates of them are only estimates.)

A more generalized and somewhat different group of yield per recruit curves is given in Figure 17. These curves show, for three different rates of natural mortality and for an age at first capture of 2-rings with the growth pattern observed at Monterey, how the yield per recruit changes with changes in fishing mortality and, consequently, with the amount of fishing effort. (The translation of fishing mortality into fishing effort will depend upon the areal distribution of effort with respect to both the density and areal distribution of the fish.)

These curves show that as fishing mortality (and fishing effort) increase, total catch increases. At some point, of course, the catch per unit-of-effort will decrease rapidly as additional fishing mortality (effort

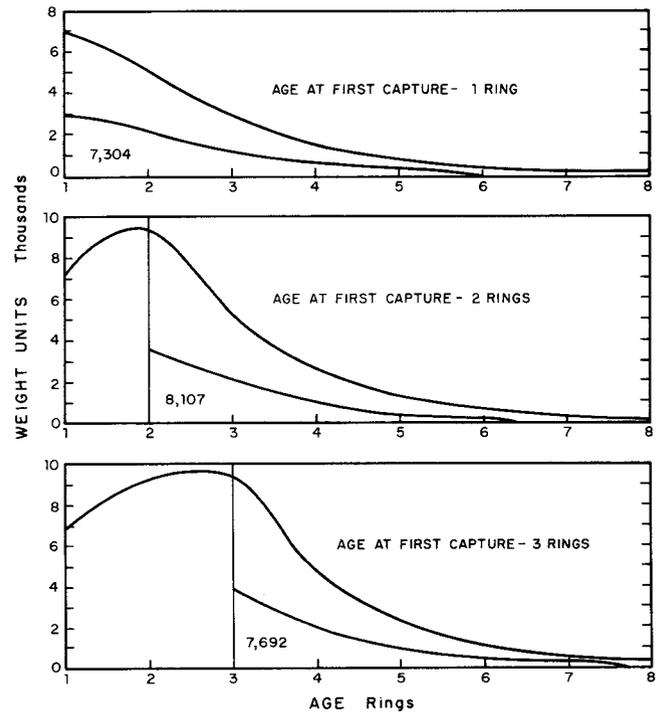


FIGURE 16. Panel C. Fishing mortality=45 per cent; natural mortality=18 per cent.

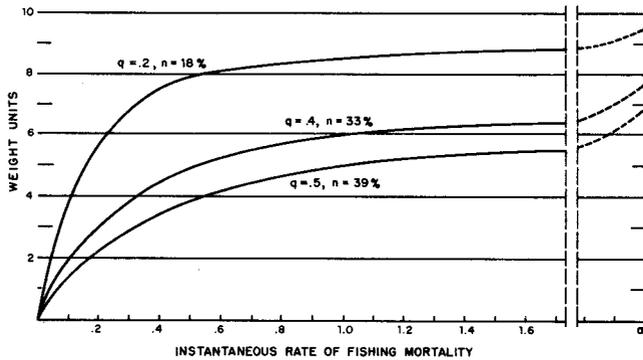


FIGURE 17. Pacific sardine: Yield per recruit (in weight units) over different instantaneous rates of fishing mortality for three different instantaneous rates of natural mortality; based on observed Monterey growth pattern and an age at first capture of 2 rings (q =instantaneous rate of natural mortality; n =annual rate of natural mortality).

units) is added, but the total catch will continue to increase.

In other words, under the conditions stated and from the standpoint of increase in weight alone, there is no gain in letting 2-ring and older fish remain in the sea to grow larger; on the contrary, they will lose more weight through natural deaths than they will gain through growth.

Year-Class Size vs. Stock Size

As explained earlier in this report, if year-class size is a function of stock size, it is theoretically possible to control the stock size so as to produce year-classes of maximum size. (Conversely, if year-class size is not a function of stock size, then controlling stock size will have no effect on year-class size.)

Thus, it is pertinent to inquire into what results would have been produced had an attempt been made to control stock size. As previously stated, this might be done by (1) controlling the total catch (*i.e.*, setting a bag limit) or (2) controlling the amount of effort (*i.e.*, limiting the number of boat-months). We will consider each of these possibilities in turn.

The authors have drawn different conclusions from the data. The lines of reasoning of each will be presented in turn. Marr concludes:

“Controlling boat catch: It has recently been stated by Croker (1954:7) ‘. . . that had [sardine] landings been limited to 300,000 tons a year in the early 1940’s, there would be no sardine crisis now.’ It is, of course, not now possible to state categorically what would have happened and what conditions would exist now, had a particular action been taken some 14 years ago. But it is possible to estimate what would have happened and what conditions would exist now, using as a basis for the estimate the available information about sardines which has been discussed in this report.

“Surely the most immediate and direct effect of limiting the total catch in the past would have been

to reduce the fraction of the population caught in those seasons when the limit was lower than the actual catch made. Thus the population size of fully recruited fish in subsequent seasons would have been larger than was actually the case. To suggest *how much* larger, one must have estimates of (a) the rate of natural mortality, (b) availability, (c) effort unit effectiveness on the available population, (d) growth pattern, and (e) year-class size. The various estimates which have been made and which are given earlier in this report describe the following conditions:

“(a) Estimates of natural mortality are about 39 per cent by number (which is equivalent to 25 per cent by weight).

“(b) The availability of the population is considered to be that which was observed, except that those fish which would not be caught because of the limit are considered to be *fully* available in subsequent seasons. (This may be overly generous.) This includes the fact that the catch under a limit, whatever that catch might be, would be distributed geographically in proportion to the observed catch.

“(c) Effort unit effectiveness is considered to be that which was observed, except that up to 50 per cent of the fish which would not be caught because of the limit could be taken in subsequent seasons. That is, no more than 50 per cent of the ‘carry-over’ fish could be caught in any one season. This is probably a generous condition, judging from the estimates of fishing mortality.

“(d) The growth pattern used was that observed at Monterey.

“(e) Year-class sizes are considered to be the same as those observed. Evidence presented above indicates that year-class size does not appear to be a function of stock size and therefore an increase in stock size (as a result of fish that would not have been caught because of the limit) would not result in an increase in year-class size. And also

“(f) Population size is considered to be that which existed (see Table 2 for estimates), except as increased by ‘carry-over’ fish.

“The actual total catch and the estimated effects of a total catch limit of 300,000 tons applied in 1941, based on the conditions stated above, are shown in Figure 18. From this figure it may be seen that the hypothetical limit was actually exceeded in the 1941-42 through 1945-46 and the 1949-50 and 1950-51 seasons. Of the six seasons in which the actual catch fell below the hypothetical limit, in only one (1946-47) would the limit have been attained. There would still have been a decline in the other five seasons, a decline virtually as precipitous as that which actually obtained in the 1951-52 through 1953-54 seasons. The increase in catch that would have resulted from this hypothetical limit amounts to about 240,000 tons. The decrease in catch that would have resulted from this

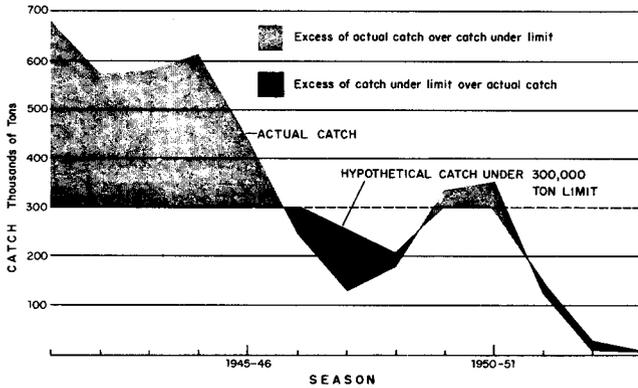


FIGURE 18. Pacific sardine: Total actual catch and hypothetical catch that would have been made under a limit of 300,000 tons set in 1941 (with a natural mortality rate of 39 per cent by numbers).

limit amounts to about 1,480,000 tons, or a net decrease in catch under the hypothetical limit of about 1,240,000 tons over the period 1941-42 through 1953-54.

“Variations in the rate of natural mortality will, of course, change the effects of limits on the total catch. The lower the rate of natural mortality, the longer will the fish not caught (because of the limit) remain in the population and be subject to being caught in subsequent seasons. For example, a group of fish 2-rings and older under a natural mortality rate of 10 per cent by numbers would lose an average of 2 per cent by weight per year, under a rate of 20 per cent by numbers would lose 10 per cent by weight, 30 per cent by numbers 18 per cent by weight, 40 per cent by numbers 26 per cent by weight, and so on.

“This is illustrated in Figure 19, which is identical with Figure 18, except that a natural mortality rate of 23 per cent by numbers (13 per cent by weight) has been used. Under this condition of lower natural mortality rate, a limit of 300,000 tons would have been attained in the 1946-47 through 1948-49 seasons, but a precipitous decline in the total catch would still have occurred in the 1951-52 through 1953-54 seasons. The net difference in total catch over the whole period would have amounted to a decrease of about 568,000 tons.

“On the basis of the evidence presented in the previous sections of this report, Figure 18 represents the best estimate now possible of what effect a total annual catch limit of 300,000 tons imposed in 1941 would have had.”

Clark concludes:

“The effect of holding the seasonal catch to a certain tonnage can be estimated in yet another way. In addition to the proposal to hold the California catch to 300,000 tons annually, consideration is given to the Pacific Northwest fishery with an allowance of

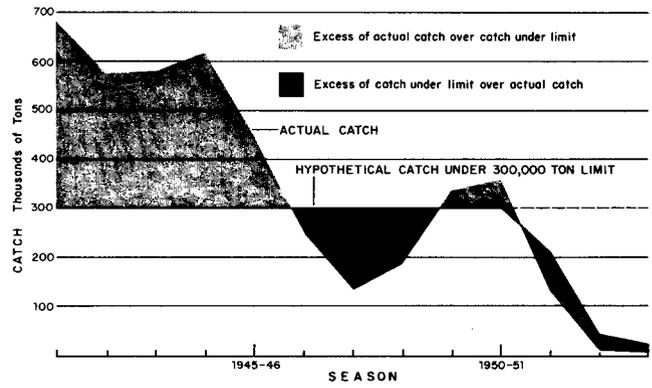


FIGURE 19. Pacific sardine: Total actual catch and hypothetical catch that would have been made under a limit of 300,000 tons set in 1941 (with a natural mortality rate of 23 per cent by numbers).

an annual tonnage of 50,000 tons. This would approximate a 50 per cent reduction from the maximum tonnage taken in the northwest and would correspond to a similar cut from about 600,000 tons to 300,000 tons for the California fishery.

“Since 1941-42 we have a measure of the age composition and total numbers of fish caught in the fisheries of both areas and we know the population must have been large enough to yield these fish to the fishermen’s nets. By a trial-and-error process we can determine how large the population must have been at the beginning of the 1941-42 season and how much must have been added to it by new year-classes in each succeeding season to maintain the catch that was actually taken in the following seasons. To simplify the calculations, we will assume that no sardines are caught until they are between two and three years of age and when they are “two-going-on-three” that they are as available to the fishery as are the older sardines. (Some one-year-olds are actually caught and some three-year-olds are not yet available, so this simplification should balance these two conditions.)

“To estimate the number of new recruits, beginning with the 1939-class we have calculated the number of each new year-class caught per boat-month when two and when three years old and expressed these numbers in percentage of the 1939-class. Because fish younger than the 1949 group were not yet old enough to be so measured, the 1950 to 1953 year-classes were expressed in percentage of the 1949 group as measured on the annual surveys of the *M. V. Yellowfin* (Table 11).

“In 1941-42 a little over 6 billion fish were caught in the fisheries of California and the Pacific Northwest and the 1939-class comprised 53 per cent of these (Felin and Phillips, 1948). By trial and error we can determine the size of the population at the beginning of 1941-42 large enough to yield the numbers taken in succeeding seasons. Of this population 53 per cent

TABLE 11

RELATIVE SIZE OF EACH YEAR-CLASS OF SARDINES BASED ON THE SUM OF THE NUMBERS TAKEN IN THE CALIFORNIA FISHERY PER BOAT-MONTH WHEN TWO AND WHEN THREE YEARS OLD

Year-class	Number per boat month ¹	Per cent of 1939	Per cent of 1949 ²
1939	3,974,700	100.0	--
1940	1,880,300	47.3	--
1941	1,104,600	27.8	--
1942	1,589,300	40.0	--
1943	938,400	23.6	--
1944	476,900	12.0	--
1945	409,300	10.3	--
1946	1,636,100	41.2	--
1947	2,144,000	53.9	--
1948	1,308,000	32.9	--
1949	55,000	1.4	100
1950	-----	-----	83
1951	-----	-----	84
1952	-----	-----	150
1953	-----	-----	80

¹ From Clark and Daugherty, 1952.
² Estimated from fish surveys.

would have belonged to the 1939-class, and with the percentages of Table 11 a measure of the number in each succeeding year-class can be derived. For this trial-and-error calculation we must also consider natural mortality. This has been variously estimated between 20 and 40 per cent if Man takes nothing. Two trials were made, therefore, one based on a 20 per cent natural mortality and one on 40 per cent. Fishing and natural mortality were combined into total mortality by the use of tables given by Ricker (1948).

“Starting with an assumed population of 20 billion fish in 1941-42 the calculations were carried out and it was found that the population need not have been as large as this to continue the fishery through the most critical period in 1946-47 and 1947-48. The number was then reduced by one billion steps until the point was reached where the fishery could not have con-

FIGURE 20. Size of population required to yield the number of fish taken with 20 per cent natural mortality and the 1939 year-class comprising 53 per cent of the total in 1941-42.

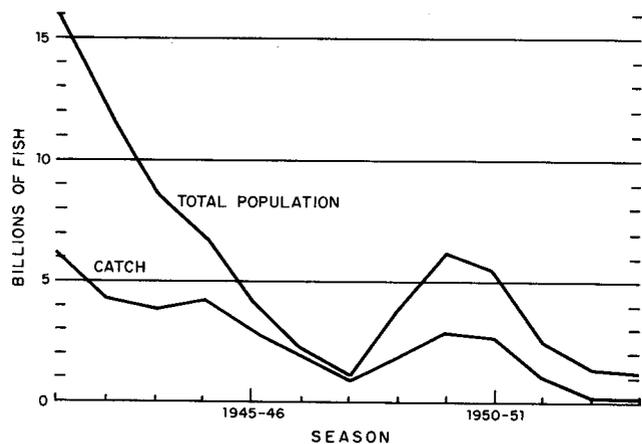


TABLE 12

CALCULATIONS OF SIZE OF THE SARDINE POPULATION NECESSARY TO YIELD THE NUMBERS TAKEN IN THE PACIFIC COAST CATCH FROM 1941-42 THROUGH 1953-54. THE 1939 YEAR-CLASS COMPRISED 53 PER CENT OF THE TOTAL POPULATION IN 1941-42; NUMBERS IN MILLIONS

Season	Number in population			Mortality percentage		
	Older fish	New year-class	Total	Catch	Fishing	Total
Natural Mortality 20 Per cent						
1941-42	7,520	8,480	16,000	6,041	38	49
1942-43	8,160	4,011	12,171	4,343	36	48
1943-44	6,329	2,357	8,686	3,966	46	56
1944-45	3,822	3,392	7,214	4,076	57	65
1945-46	2,525	2,001	4,526	2,963	65	71
1946-47	1,313	1,018	2,331	1,917	82	85
1947-48	350	873	1,223	965	79	83
1948-49	208	3,494	3,702	1,788	48	57
1949-50	1,592	4,571	6,163	2,754	45	55
1950-51	2,773	2,731	5,504	2,590	47	56
1951-52	2,422	119	2,541	957	38	49
1952-53	1,296	99	1,395	24	2	20
1953-54	1,116	100	1,216	20	2	20
Natural Mortality 40 Per cent						
1941-42	8,930	10,070	19,000	6,041	32	55
1942-43	8,550	4,763	13,313	4,343	33	55
1943-44	5,991	2,799	8,790	3,966	45	63
1944-45	3,252	4,028	7,280	4,076	56	70
1945-46	2,184	2,377	4,561	2,963	65	77
1946-47	1,049	1,208	2,257	1,917	85	90
1947-48	226	1,037	1,263	965	76	84
1948-49	202	4,149	4,351	1,788	41	61
1949-50	1,697	5,428	7,125	2,754	39	59
1950-51	2,921	3,313	6,234	2,590	42	61
1951-52	2,431	141	2,572	957	37	58
1952-53	1,080	117	1,197	24	2	34
1953-54	790	118	908	20	2	34

tinued through the critical time interval. The trials finally selected are shown in Table 12 and Figures 20 and 21. These indicate that at 20 per cent natural mortality the population in 1941-42 must have been as large as 16 billion fish and at 40 per cent, 19 billion. Since in 1946-47 and 1947-48 fishing mortality would have been 75 to 85 per cent at this low population level (a highly improbable figure), presumably the initial population was larger than the size assumed or new year-classes contributed more to the population than here estimated. In order to make the following test as severe as possible we have chosen this smallest possible estimate of population size.

“What would have happened to a population of this size if the catch had been held to 350,000 tons? Since lowering the take will leave more older fish in the population it is necessary to estimate not only the number of fish remaining in each succeeding year but also to convert these numbers to tons. From these two values the number of fish per ton can be calculated. This conversion of numbers to tons was made on the assumption that each new year-class would

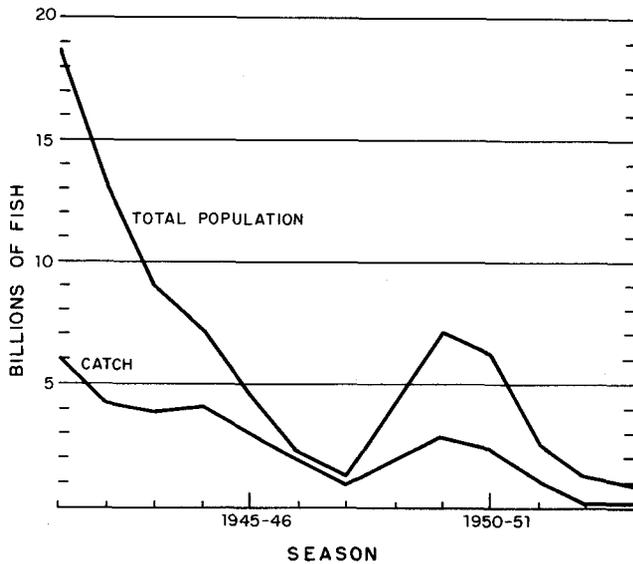


FIGURE 21. Size of the population required to yield the number of fish taken with 40 per cent natural mortality and the 1939 year-class comprising 53 per cent of the total in 1941-42.

average 195 mm standard or 9 inches total length and comprise 9,000 fish per ton. Older fish were assumed to average 220 mm or 10.2 inches and run 6,000 fish to the ton. (See Clark, 1952, for numbers of fish per ton.)

“The resulting calculations (Tables 13 and 14 and Figures 22 and 23) indicate that the fishery could have continued at 350,000 tons through 1951-52 if natural mortality were 20 per cent and through 1950-51 if natural mortality were 40 per cent. Since there was almost no recruitment to the fishing grounds after 1950 it is inevitable that the fishery would have failed eventually. In this calculation as

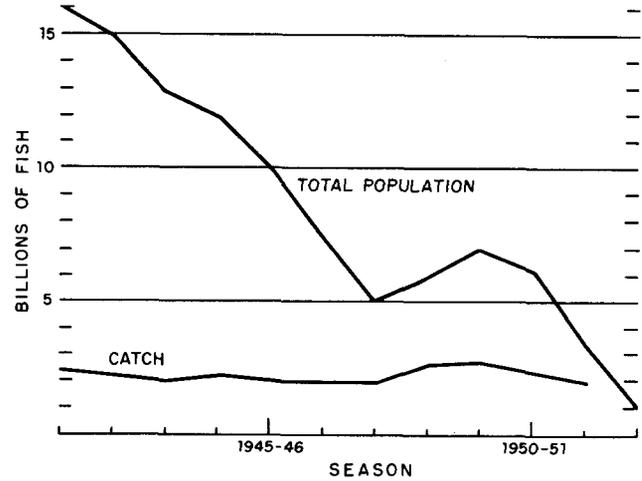


FIGURE 22. Effect of holding fishing at 350,000 tons annually with 20 per cent natural mortality, an initial population of 16 billion fish in 1941-42 and the 1939 year-class comprising 53 per cent of this total.

in the first trials, the percentage taken by the fishery at 40 per cent natural mortality is improbably high in 1947-48. As indicated above, the test is too severe; the population initially must have been larger or the recruitment greater in later seasons. Any correction for this would indicate that the fishery could have continued longer at the 350,000-ton level.

“In the above estimates no allowance was made for the possibility that recruitment might have been at a higher level under controlled fishing. With lessened fishing intensity the population and the fish in the population would have been larger, more eggs would have been produced, spawning might have been extended over a wider area and a better survival of young fish might have resulted.

TABLE 13
EFFECT OF HOLDING TOTAL CATCH TO 350,000 TONS ANNUALLY WHEN TOTAL POPULATION IN 1941-42 CONTAINED 16 BILLION FISH OF WHICH 53 PER CENT WERE FROM THE 1939 YEAR-CLASS AND NATURAL MORTALITY WAS 20 PER CENT. NUMBERS IN MILLIONS

Season	Size of population						Mortality Percentage		
	Numbers			Tons ¹			Catch		
	Older fish	New year-class	Total	Older fish	New year-class	Total	Numbers	Fishing	Total
1941-42	7,520	8,480	16,000	1,253,333	942,222	2,195,555	2,550	16	33
1942-43	11,040	4,011	15,051	1,840,000	445,667	2,285,667	2,305	15	30
1943-44	10,536	2,357	12,893	1,756,000	261,889	2,017,889	2,236	17	32
1944-45	8,767	3,392	12,159	1,461,167	376,889	1,838,056	2,315	19	34
1945-46	8,025	2,001	10,026	1,337,500	222,333	1,559,833	2,250	22	36
1946-47	6,417	1,018	7,435	1,069,500	113,111	1,182,611	2,200	30	43
1947-48	4,238	873	5,111	706,333	97,000	803,333	2,227	44	54
1948-49	2,351	3,494	5,845	391,833	388,222	780,055	2,623	45	55
1949-50	2,630	4,571	7,201	438,333	507,889	946,222	2,664	37	48
1950-51	3,745	2,731	6,476	624,167	303,444	927,611	2,443	38	49
1951-52	3,303	119	3,422	550,500	13,222	563,722	2,125	62	69
1952-53	1,061	99	1,160	176,833	11,000	187,833	2,162	--	--

¹ Number of tons of older fish estimated at 6,000 fish per ton and of new year-class at 9,000.

COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

TABLE 14

EFFECT OF HOLDING TOTAL CATCH TO 350,000 TONS ANNUALLY WHEN TOTAL POPULATION IN 1941-42 CONTAINED 19 BILLION FISH OF WHICH 53 PER CENT WERE FROM THE 1939 YEAR-CLASS AND NATURAL MORTALITY WAS 40 PER CENT. NUMBERS IN MILLIONS

Season	Size of population						Mortality Percentage		
	Numbers			Tons ¹			Catch		
	Older fish	New year-class	Total	Older fish	New year-class	Total	Numbers	Fishing	Total
1941-42	8,930	10,070	19,000	1,488,333	1,118,889	2,607,222	2,550	13	42
1942-43	11,020	4,763	15,783	1,836,667	529,222	2,365,889	2,335	15	43
1943-44	8,996	2,799	11,795	1,499,333	311,000	1,810,333	2,280	19	46
1944-45	6,369	4,028	10,397	1,061,500	447,556	1,509,056	2,412	23	48
1945-46	5,406	2,377	7,783	901,000	264,111	1,165,111	2,338	30	53
1946-47	3,658	1,208	4,866	609,667	134,222	743,889	2,289	47	64
1947-48	1,752	1,037	2,789	292,000	115,222	407,222	2,397	86	91
1948-49	251	4,149	4,400	41,833	461,000	502,833	3,062	70	80
1949-50	880	5,428	6,308	146,667	603,111	749,778	2,945	47	64
1950-51	2,271	3,313	5,584	378,500	368,111	746,611	2,618	47	64
1951-52	2,010	141	2,151	335,000	15,667	350,667	2,147	100	--

¹ Number of tons of older fish estimated at 6,000 fish per ton and of new year-class at 9,000.

"It has been shown above that the average size of a new year-class in the 30's was twice that of the 40's, and that the population in the 30's exceeded that of the 40's by 1.6 times. On the assumption that a population equal to that of the 30's might have increased the recruitment by 1.5 times, tests were made of the potential yield of a stabilized fishery by increasing the recruitment of the 1940 and subsequent year-classes 1.5 times. This still allows for the effect of environment on the survival of young sardines and merely tests the possible result of having more eggs deposited. At the higher recruitment level in the 40's and at a 40 per cent natural mortality the fishery at 350,000 tons per year could have continued through 1952-53; then the fishery would have declined owing to the almost complete lack of young fish after 1950-51. Since 1948 the number of sardines in each year-class has been less than anything since 1930 (the period over which we have estimates of year-class size). Either because of low population levels not enough spawn has been produced to take advantage of favorable environmental conditions or the environment has been too poor to produce good spawn survival regardless of the number of eggs deposited. Not only must enough eggs be produced but they must be deposited in the favored localities. The largest year-class known (1939) resulted from heavy spawning off central California and northward, which suggests that better recruitment results from spawning to the northward as far as the Pacific Northwest and until recently the eggs deposited on the grounds off southern California made a major contribution to each new year-class.

"After 1950 there was no spawning on the northern grounds and until 1954 fewer eggs were found on the southern California grounds. Between 1948-49 and 1954-55 almost no sardines were found off central

California and the Pacific Northwest and the number of fish declined rapidly off southern California. Therefore, these waters could not be seeded. In 1954 spawning again increased on the southern California grounds and the size of the resulting year-class should give another estimate of the relation of population size to recruitment size at a time when spawning occurs in a favorable area.

"Assuming that the distribution of the fish and the distribution of the catch would have remained constant as it was in 1941-42 until 1952-53, the effect of a managed fishery of 350,000 tons through the 12-year period would have yielded 4,200,000 tons. In this time interval 4,279,000 tons were taken. Thus under the second estimate of the effect of limiting the catch to a fixed seasonal tonnage, the fishermen and the processors would have experienced almost as great a catch and less disruption to the industry. Presumably the Pacific Northwest would have preferred management since no fish have been taken in this area since 1948-49. San Francisco and Monterey fisheries would have profited by management and the southern California industry would have been in a better condition had management prevailed.

"It is not now possible to state categorically what would have happened under some different set of conditions than those that actually obtained. We can only say for the two examples given *this* would have happened, *provided* that the necessary assumptions were fulfilled. The two estimates of the effects of catch limits are both based on assumptions the validity of which is not known, and it is not now possible to draw any firm conclusions about what might have happened to the sardine populations and to the fishery under a predetermined and constant annual tonnage. The best estimates available (Figures 22 and 23),

however, indicate that the fish population and the industry would be in a better condition had such controls been in effect.”

Concerning the second point, Marr has concluded:

“(2) Controlling the amount of effort: ‘It has recently been proposed by Schaefer (1954), that a maximum yield of sardines could be produced by controlling the amount of fishing effort. He examined some data on catch and fishing effort of sardines in the light of some postulated relationships between population size and population growth rate. Under his hypotheses, the sardine population would yield a maximum catch of 600,000 tons if fishing effort were held at 870 boat-months, as measured by Clark and Daugherty (1952). This he labeled as ‘equilibrium catch’—that is, a mean catch about which actual catches, given 870 boat-months of effort, would fluctuate (\pm about 250,000 tons) owing to variation in the effect of the environment. He assumed fishing effort to be the ‘driving force,’ as have many other writers. Presumably, fishing effort ‘drives’ stocks down by increasing the total mortality rate they suffer. This would surely reduce the annual average stock size from its natural state, but, so far as the data show, smaller stock sizes will not necessarily produce smaller year-classes. Schaefer’s curve of equilibrium stock is largely determined by the three seasons’ data, 1932-33 through 1934-35, when effort was lower than in recent years. We have noted that the 1931- and 1932-classes were well above average, and the stock sizes in the middle 1930’s were not in equilibrium. Judging from the extreme variation in year-class for a given stock size which we have observed in the available sardine data, the population has never been in equilibrium. Within the range of estimated stock sizes we have observed, the year-class sizes are quite independent of stock size. Since we find no maximum in our yield per recruit curves (by weight) at effort less than infinity, we would expect no greater yield to be obtained with any less fishing effort.

“Schaefer’s conclusion that catch can be predicted if the amount of effort is known, is presented graphically in his Figure 9 (1954:52). It is of more than passing interest to observe that the sardine catch may be predicted at least as well (if not with less variance) simply by stating that the catch in any given season will be the same as the catch in the preceding season. This is shown in our Figure 24, in which the solid line indicates the suggested relationship and the broken lines indicate 200,000 tons above or below the solid line. Only three points fall outside these limits. Thus the amount of environment-caused variation would make an effort limit ineffective or, at best, very inefficient as a means of changing the stock size. In fact, we would expect to find no pre-

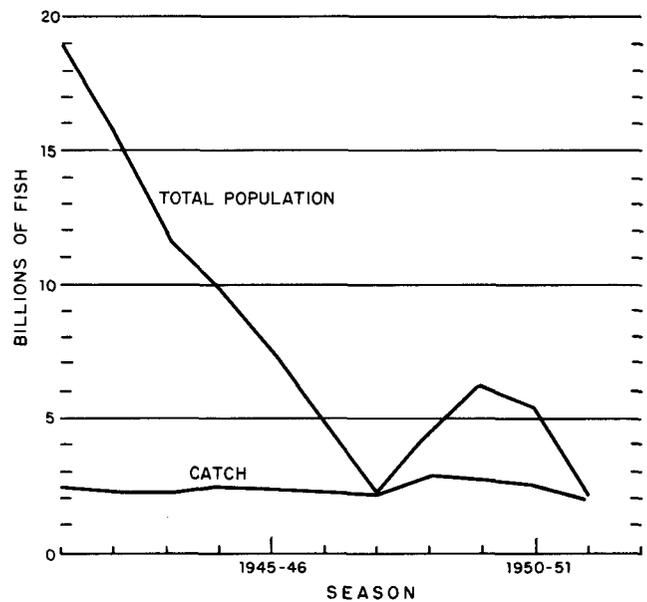


FIGURE 23. Effect of holding fishing at 350,000 tons annually with 40 per cent natural mortality, an initial population of 19 billion fish, and the 1939 year-class comprising 53 per cent of this total.

dictable effect of a change in fishing effort on the stock, as separable from the changes we should expect that are independent of fishing.”

WHAT IS THE OUTLOOK FOR THE FUTURE?

There are relatively few species for which the prediction of future catches has been attempted. There are few if any records of long periods of successful predictions for any species. There is no such record for the sardine, for the very good reason that the information necessary to successful predictions has not been, and is not yet, available.

Information Necessary for Prediction

If we wish to successfully predict the catch of a species we need information of the following five kinds:

(1) FISHING EFFORT

In order to predict the catch we obviously need to know how much fishing effort is to be expended in making that catch. It is probably fairly easy to estimate this quantity, drawing upon knowledge of the amount of effort expended in previous seasons, information on economic conditions and on competent opinion from industry members. It is also possible to make several catch estimates, each based on a different but possible amount of fishing effort.

(2) YEAR-CLASSES ALREADY IN FISHERY

We must have some information about the sizes of the year-classes which have previously entered the catch. We do not need to know the absolute sizes of

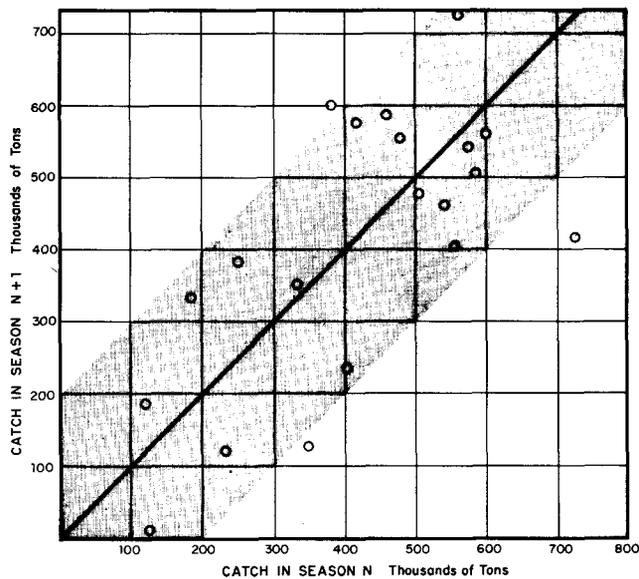


FIGURE 24. Pacific sardine: Relationship of the California catch in each season ($N+1$) with the catch in the previous season (N), 1932-33 through 1953-54 seasons.

these year-classes, but at least need to know the size of each year-class relative to the other year-classes. We also need to have this information over a period of years, so that we may know the rate of decline to be expected of the year-classes from each age to the next.

(3) ENTERING YEAR-CLASSES

The size of a year-class (or year-classes) entering the catch for the first time will influence the catch. The direction of the influence will depend on whether that year-class is small, average or large relative to previous entering year-classes and also on whether there are few or many year-classes in the catch in any one season.

(4) NATURAL MORTALITY

We have to know what the rate of natural mortality will be, at least relative to the previous seasons. A decrease in natural mortality might be expected to increase the size of the available population (over that expected with the previously observed rate of decline) and an increase in natural mortality, by the same token, to decrease its size.

(5) AVAILABILITY

As we have shown, changes in availability can have a tremendous influence on the catch. We need to know whether the fish will be available to the same extent, or to a greater or lesser extent, than they were in the previous season. While it is not essential that we know the absolute availability fraction, we at least have to know what it will be relative to the previous season.

Predictions of the Sardine Catch

In order to predict the sardine catch, we must consider each of the necessary kinds of information:

(1) FISHING EFFORT

The amount of fishing effort expended on sardines in some recent years has decreased, but not as much as might be expected. Since Pacific mackerel, jack mackerel and sardines may all be taken at the same time and place and with the same gear, any boat that is fishing is scouting for all three species. When sardines become available to the California fishery as they did in the 1954-55 season, fishing effort upon sardines would be resumed. It would not immediately approach previous levels, owing to the fact that there are now fewer processing plants to handle the catch and to the fact that at present the bulk of the catch is canned and a further limit is thus placed on shore-side facilities. For example, the effort expended in the 1954-55 season was limited by economic conditions.

(2) YEAR-CLASSES ALREADY IN FISHERY

The last large year-class which was in the fishery was the 1948-class and even this year-class was probably only about one-third available to the fishery. By now fish of the 1948 and older year-classes are 6 or more years of age and cannot be expected to contribute much to the fishery, owing to natural mortality. The 1949-class was very small, the 1950- and 1951-classes little, if any, larger. The 1952-class, at one month and at six months of age, was about twice the size of the two preceding ones.

(3) ENTERING YEAR-CLASSES

Preliminary estimates indicate that the 1953- and 1954-classes are about equal in size to the 1950- and 1951-classes.

(4) NATURAL MORTALITY

As previously indicated, natural mortality is difficult to measure, but one series of estimates arise from data collected on the scouting surveys.

(5) AVAILABILITY

We have no estimate of the degree to which the population will be available in subsequent seasons.

The events of 1954 show that sardines from the central Baja California area can also spawn off southern California. Fish from the two areas cannot, therefore, be considered to belong to two separate sub-populations. The occurrence of widespread spawning off southern California in the spring of 1954 and the presence of fish on the southern California fishing grounds in the fall of 1954 were associated with certain changes in oceanographic conditions. Among the latter was the occurrence of warmer water earlier in the year than was true for immediately previous years. This condition approached, in fact, that of earlier years (1941, for example).

The presence of fish on the southern California spawning grounds and on the fishing grounds in 1954 does not represent something new. Rather, it is a return to previous conditions which were interrupted

for several years. We do not yet know enough about the relationship between fish and environment to be able to do any long-range predicting, but we may be able to predict over the time from spring to fall.

In summary of the future outlook, we may state that a continued revival of the sardine industry will depend upon: (1) the production of larger year-classes at more frequent intervals than has recently been the case and (2) an increase in the degree to which the population is available to the fishery. We do not, as yet, understand the factors influencing both of these phenomena.

SUMMARY AND CONCLUSIONS

What Are the Questions?

The present crisis in the sardine industry has given rise to a number of questions, which, we believe, may be expressed as follows:

(1) What causes fluctuations in the size of the sardine population?

(2) What causes fluctuations in the catch of sardines?

(3) What influence does Man have on the sardine population?

(4) What is the outlook for the future?

What Are the Answers?

By gathering together as much published and unpublished data on sardines as we have been able to, by considering these data in one body, and by drawing upon principles discovered in other fishery studies as well as other fields, we have reached what we believe to be the most complete answers to these questions that it is now possible to give. They are not offered in the sense of being final answers, but they are useful as a summary of present knowledge, as an aid in clearing up misconceptions, and, perhaps especially, in emphasizing the nature and extent of the problems remaining.

(1) Fluctuations in the size of the sardine population arise from differences between additions to the population (entering year-classes) and subtractions from it (natural and fishing deaths). Estimates of the size of the sardine population over the period 1932-33 to 1953-54 are in the order of 4 to 40 billion fish in the 1930's, 2 to 25 billion in the 1940's and 1 to 15 billion in the first half of the 1950's, with an average minimal population of about 6 billion fish.

The additions to the population, or year-classes, from 1930 through 1950 have varied in minimal size from 0.01 in 1950 to 7.2 billion fish in 1939, with an average minimal size of 2.5 billion fish. The specific causes of such tremendous variation in year-class sizes are not known. Any theoretical relationship that might exist between spawning stock size and year-class size is obscured by environmental influences.

One interpretation (Marr) of the data is that year-class size is a function of stock size only at, or below, the smallest stock sizes observed. An alternative interpretation (Clark) is that stock sizes below 4 billion fish produce smaller year-classes than do stock sizes above 4 billion fish. Studies of survival rate during the first month of life indicate that survival in the 1952-class was about twice that in the 1950- or 1951-classes.

The subtractions from the population (deaths) are difficult to measure. The total mortality rate increased from about 24 per cent to 59 per cent between 1932-33 and 1936-37, was fairly constant around 50 per cent until about 1943-44, and fluctuated around 65 per cent to 1952-53. Fishing mortality estimates are between 20 and 30 per cent in the earlier period and between 50 and 60 per cent in the later period. Natural mortality estimates are between 20 and 40 per cent and do not appear to have changed greatly. Better estimates of mortality rates, especially natural mortality rates, are needed.

(2) Fluctuations in the catch of sardines may be caused by fluctuations in the amount of fishing effort, fluctuations in the abundance of the population, and fluctuations in the availability of the population.

Between 1932-33 and 1945-46 an increase in effort tended to result in a corresponding increase in catch and a decrease in effort tended to result in a corresponding decrease in catch. This relationship was immediate. After 1945-46 an increase in effort resulted in little or no increase in catch. Reasons for the decline in total catch are to be sought, therefore, in variations in abundance and availability.

We have already discussed under (1) above the causes of fluctuations in abundance. Estimates indicate that the population in the 1950's was one-half to two-thirds of the population in the 1930's.

Availability phenomena belong to one or another of three categories; local variations in behavior, the geographic distribution of the population with respect to the geographic distribution of the fishery, and the distribution of subpopulations (if such exist) with respect to the distribution of the fishery.

Local behavior variations may be represented by temperature-connected differences in the density of fish within schools, age-connected differences in schooling behavior and so on.

Evidence of variations in fish distribution with respect to the distribution of the fishery accrue from tagging experiments, the failure of fish to reach British Columbia in 1933 and 1939, a greater than expected number of fish entering the California catch in 1949-50 and a lesser than expected number in 1946-47, failure of a net northward movement between spring and fall across the U. S.-Mexican Boundary in 1952 and 1953 and the influx of sardines from

Baja California waters into southern California waters in the spring, summer and early fall of 1954.

Differences between subpopulations, as we use the term, must have a genetic basis. There is evidence of heterogeneity in the sardine population from the existence of perhaps four spawning centers and from differences in size, in age composition, in meristic characters, in scale types and in growth rates in different parts of the population range. We do not yet know if these differences are of genetic origin or if they are induced by the environment. The events of 1954 show that the southern California and central Baja California groups are not distinct.

(3) The two possible ways in which Man may influence the population are considered. Controlling the size (age) at first capture is impractical in the sardine fishery. But sardine yield-per-recruit curves are such that the present fishery tends to produce the maximum yield (weight) per recruit.

If year-class size is not a function of spawning stock size, then controlling stock size by controlling catch could not be expected to cause the production of bigger year-classes. Estimates (based on available data) of the effect of a 300,000-ton limit on total catch applied in 1941 show that the reduction in catch between the 1945-46 and 1949-50 seasons would have been less severe than the actual decline, but that the decline following the 1950-51 season would have been virtually as severe and as precipitous as that actually observed, and a net decrease in catch of about 1,240,000 tons would have resulted. If the natural mortality rate had been lower than that used in the previous estimate, the 1945-46—1949-50 decline would not have occurred, but the decline following the 1950-51 season would have occurred and a net decrease in catch of about 568,000 tons would have resulted.

If year-class size is a function of stock size, then controlling stock size by controlling total catch could be expected to cause the production of bigger year-classes. Estimates (different than those preceding) of the effect of a 350,000-ton limit on total catch (including the Pacific Northwest) applied in 1941 show that the fishery could have been maintained through 1952-53 before it suffered a marked decline owing to the very low recruitment level of the 1949

and subsequent year-classes. The total tonnage taken would have approximated that actually taken by the uncontrolled fishery.

Since we do not know the validity of the assumptions on which any of these tests are based, we cannot state categorically how a fishery controlled at a fixed tonnage might have affected the sardine population between 1941 and 1953 and how much Man would have been able to harvest from that population.

(4) The information requisite to successful and precise predictions of sardine catch is not now available. The major lacks (and this suggests future emphasis in sardine research) are information about availability changes and natural mortality changes. Estimates of the relative size of entering year-classes are available, but need to be refined.

Even so, it is apparent that there will be no sudden and large revival of the sardine industry until there are a series of larger year-classes than have recently been produced and until there is an increase in the degree to which the population is available to the fishery. We cannot predict when these events will occur, but there is no evidence to indicate that, sooner or later, they will not occur.

ACKNOWLEDGMENTS

Manifestly the preparation of a report such as this requires in one way or another the efforts of many individuals over a long period of time. Where appropriate, many of these have been cited in the text. Many others have supplied data, suggestions and comments. Without their help this report could not have been written. Special mention should be made of two of the staff of the U. S. Fish and Wildlife Service; E. H. Ahlstrom who gave particular help with the section on availability and T. M. Widrig for his assistance with the section on the influence of Man on the sardine population. R. S. Croker and John Radovich, on the staff of the California Department of Fish and Game, aided materially in the development of the sections on the relation between size of spawning population and size of year-class and on the influence of Man on the fishery.

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PART III: PUBLICATIONS

(NOTE: This list comprises all formal publications arising from the California Cooperative Oceanic Fisheries Investigations to 31 December 1954. Processed reports which are not available for general distribution have been omitted, but those which appear in regular series and are generally available are included. In several instances, scientists from two or more of the cooperating agencies have written papers jointly. To avoid duplication, these papers appear in this list under the senior author's agency.)

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