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SECTION I.

INTRODUCTION

Dr C.E. Lucas

It was Dr Lionel A. Walford who, while Chairman of the Research and Statistics Committee, first suggested that ICNAF should hold a Symposium concerning the effects of the environment on the fisheries in its area, but it was not until March 1961 that a working party met at the Marine Laboratory in Aberdeen, with the specific task of advising the Commission on environmental matters.

In particular, the Commission requested advice on

(a) the effects of the environment on the survival of the eggs and larvae, growth, long-term abundance and distribution of cod in particular, but also of redfish and haddock;

(b) how studies of such matters might be directed so as not only to provide evidence of associations and correlations but also to lead to prediction;

(c) what fundamental studies requisite for such investigations and not already proceeding should be initiated;

(d) how plans could best be laid for holding an Environmental Symposium.

In order to prepare for their task, summaries of information already available to scientists working under the Commission were drawn up, and these at once revealed that, while there was an abundance of salinity and temperature data for the area, there was a relative scarcity of biological data and a greater scarcity of other physical and chemical data. Since that time, as the Symposium has shown, there has been some improvement, although this is still largely true, as is shown by the fact that, out of seventeen contributions concerning the effects of physical factors, fourteen were directed to evidence from temperatures.

It was in the light of such information that the Working Party recommended, and the Commission subsequently adopted, a general programme of environmental studies (ICNAF Redbook 1961: pp. 69-86), to include experimental and physiological investigations, and prepared a programme for a Symposium divided into eight sections, each concerning a specific aspect of fisheries environmental problems (p. 5). Of the former, it is possible to say now that several aspects of the environmental programme are in progress, in particular the first multi-ship survey of a considerable area of ICNAF waters has been completed under the leadership of Mr A.J. Lee, and reports on it are being prepared.

Only one significant change was made in the original programme for the Symposium, arising from the recently developed offshore fishery for herring in the southern part of the ICNAF area, as a result of which it was decided to provide an additional section, concerning the environmental aspects of the life of the herring in the North West Atlantic. A very important point, however, was the recognition that, while the Commission is responsible for a strictly prescribed area, neither the fish nor their environment are so restricted. Stocks of both cod and redfish, for example, extend almost continuously from the southern part of the area to the north, through Icelandic waters and across to the Barents Sea and Spitsbergen; other species also have wide distributions and the Commission resolved to request the assistance of scientists of the ICES area, in subscribing to a Symposium which in fact would be focussed on the principal groundfish of the North Atlantic area. Work done in the North Sea and other marginal seas was to be excluded, as also pelagic fish in general, but, although the objectives of the Symposium were to be limited in this way, it was also recognised that environmental aspects of research on other marine species might be very relevant, so that four special lecturers were invited to provide (a) an up to date account of the hydrography of the North Atlantic area and (b) reviews of environmental studies in relation to the Pacific tuna and sardine fisheries and the Atlantic herring fisheries. Moreover, although the special lectures were to be delivered in full during the Symposium, arrangements were made for all the other contributions to be written and circulated in advance, so that only brief accounts of them need be provided at the meeting, and the bulk of the time available could be given to discussion.

Reference should be made here to the arrangement to hold the Symposium in the FAO Building in Rome, for which ICNAF and the organisers are greatly indebted to the courtesy and hospitality of the Director General, Dr Sen, and his staff in Fisheries Division. This kind gesture not only solved an urgent problem, but provided a sense of occasion for the whole meeting. A sad feature was the inability at the last minute of the USSR representatives to attend the Symposium. The valuable contribution they would have made to the discussions was greatly missed. One consequence was that the organizers were greatly indebted to Mr B.B. Parrish for taking over Dr Ju Ju Marty's responsibilities at very short notice and for reporting on the proceedings of his Section G.

Most of the special lectures and contributions, in somewhat reduced form, are available for all to see in this volume, together with the reports of the Section Conveners. References are given to the few contributions which are being published elsewhere. It remains here to give some general impressions of what was undoubtedly a most interesting and valuable symposium, and to express my personal appreciation of the efforts not only of the special lecturers and contributors but of the Secretariat of ICNAF and all those who helped in various ways to prepare for and to organise the Symposium itself. Examples of the interest it attracted are the facts that some ninety contributions were received and that some seventy scientists attended from twelve countries, several from outside the North Atlantic area. An idea of the progress made in the last few years may be obtained by comparing this with a somewhat similar Symposium organized by ICES in 1951, which attracted only one "physiological" paper, whereas in 1964 it was possible to devote a whole session to experimental and physiological studies (although there was a general feeling that such work needed to be intensified considerably). It may also be fair to suggest that some of the lessons of that 1951 Symposium have still to be fully digested!

What then came out of the Symposium, apart from the special lectures and numerous contributions of which this volume is a permanent record - of facts and suggested correlations, hypotheses and ideas, and new growing points? Among other things, it attracted from the archives masses of data which might otherwise have taken long to see the light of day! It led to valuable discussions of present problems and future needs. If one has to select one most prominent problem, it concerns those correlations and associations suggested as illustrating relationships between different aspects of life in the sea, both in this Symposium and elsewhere. From one point of view, one of the chief objectives of the "environmentalists" has been to provide evidence for associations between two or more variables. In environmental studies, one is never concerned simply with any single factor, but always with its possible relationships to the fish and the fisheries themselves, and the usual approach is through the use of correlation analysis. But the elementary assumption that such a simple relationship exists in an inherently complex ecological system is all too often fraught with danger. It is a disturbing thought that we must immediately be dissatisfied with a "very good" correlation in such circumstances, if only because it is so unlikely that life in the sea is as simple as that, particularly when, as so often, the correlates may be separated by several ecological levels, as between the groundfish and the plankton, for example. Here and elsewhere there is the great danger of fallacious, or over-simplified, associations - and in several sections the dangers of this approach were apparent, particularly when trying to provide causal interpretations which might be used for prediction.

This is not to say that correlations should not be looked for and studied, but they require the greatest care in sampling and analytical techniques, and they require either the passage of time for their testing or the application of specific experiments to investigate the basis of the correlations. And even when the raw data are themselves sufficiently reliable, as, for example, series of temperature data with associated data concerning the abundance of organisms, say fish, there is always the snare that in fact the organism may not be responding in any direct manner to temperature, but that the association may in fact be with some other factor, itself associated with temperature. Also, simple temperature associations may themselves be modified by, say, food associations, or change markedly with season. Oceanographic parameters prescribe the containment of fish populations but nearly always we require much more basic knowledge of the ecology and dynamics of both the fish populations and the organisms with which they are associated. To just what factors are the organisms reacting? So often we know too little and there is the greatest need for more detail and more precise experiment and physiological study.

For all that, and particularly where reliable data can be obtained, we do need long series of records, such as temperature records, for associating with fishery data, either directly or through other variables in the ecological pyramid. Although no formal resolutions were passed in this Symposium (these were left for the Environmental Sub-Committee to consider)[1], it was widely recognised that one ultimate aim must still be to draw on past data so as to be able to predict future events, and that the effects of long-term climatic trends could be most important. Thus it was

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[1] See "Redbook" 1964, Part I: pp. 46-49.

particularly valuable to have comparisons of hydrographical events in the eastern Atlantic with those in the west, sometimes similar and sometimes otherwise. Such changes in environmental characteristics are far from simple, however, and they are best studied from long series of systematic data (such as some we have now which should be continued and indeed extended, perhaps particularly through the use of instrumented oceanographic buoys). But we urgently need to understand more of the motivation of these changes, the processes underlying them and perhaps particularly of their links with meteorological events, air-sea interface relationships, which themselves are of direct interest to fishermen, as some papers ably showed.

Turning now to experimental and physiological studies, despite the progress made during the last ten years, it was some of those who had helped to make this progress who were most conscious of the need for much more detailed knowledge than we have at present of fish physiology and behaviour, and particularly of the sensory channels and the hormone systems that regulate behaviour. How do fish and their larvae react to currents, for example, and how to changing light intensity? Data collection alone is inadequate for the understanding which is essential. Just as a knowledge of the processes determining vital changes in the oceans is essential, so we have to acquire more understanding of the organisms' reactions to such physical changes, and their rates of change, and of course to each other. While much of this work can and must be done in the laboratory, or on shore in relatively large tanks, much can only be usefully undertaken at sea, sometimes by the study of conditions and life within quite small areas: or within small populations where detailed observations can be made of the fish and the several aspects of their environment at the same time, such as has been suggested by the Herring Committee of ICES for the elucidation of key herring problems.

In fishery research one is, of course, concerned sooner or later with all levels of the ecological pyramid, and in the life of the fish itself there is always the question as to which stages in its life history are the most susceptible to environmental changes and on which to concentrate most productively. Apart from the obvious relevance of the adult stage, most attention so far has been devoted to egg and larval studies but, not for the first time, the question was raised in these meetings whether (a) the resources so far given have been adequate to provide significant results, and (b) in some instances at least, year-class strength and recruitment might not be determined more by mortalities at a rather later stage than those usually examined. In making these points, those concerned were seldom trying to suggest that the relationships existing between larval densities and fish stocks were irrelevant, but rather to ensure that henceforth investigations at this level should be intensive enough to support the conclusions that might be drawn from them, and also to ensure that too facile assumptions were not made that adult numbers depend, or do not depend, substantially on success during critical egg and larval phases. Many more, and more intensive, egg and larval surveys will undoubtedly be needed, but it is becoming evident that much more attention must be paid to the adolescent stages in the life of the fish which follow the first year of its life, and that mortalities should be followed through these as well as in the earliest stages.

Thus, in another context, the meeting was faced again with the need for intensive as well as extensive studies, and reference was naturally made to the ICNAF Environmental Survey, on which some communications were based, and Mr Lee briefly reported, during the final discussion. In many respects, despite unusual natural difficulties, it had been surprisingly successful - and had certainly shown how by international co-operation a large area can be covered several times in fair detail. Yet 1963 scarcely seemed to have been a "typical" year! Good egg production was followed by very sparse distribution of larvae, both of cod and redfish. Although the three surveys were made, the key to the critical point of larval failure may be missing. There was at once keen appreciation of the great efforts made and widely expressed views that at least one more set of surveys must be made (a) to examine conditions in another and possibly more "typical" year and (b) to do this, through international co-operation, in even greater detail.[2] For some purposes, of course, greater detail in certain parts only of the work may suffice.

It is scarcely necessary to add that once again the question was raised as to the information needed by the biologist from the hydrographer to solve his problem, and experience is showing more and more that the essential thing is for hydrographers and biologists - and members of other disciplines - to work together on these problems. This was stressed in the ICES Symposium on "Fisheries Hydrography" in 1951 by Professor Sverdrup, who said that hydrography "must take its place as an integral and indispensable part of the combined effort"! Paraphrasing Professor Sverdrup, the Chairman then said "It is the task of the biologist to demonstrate the reactions of the fish towards different types of environment. In the light of this knowledge the hydrographer should study the

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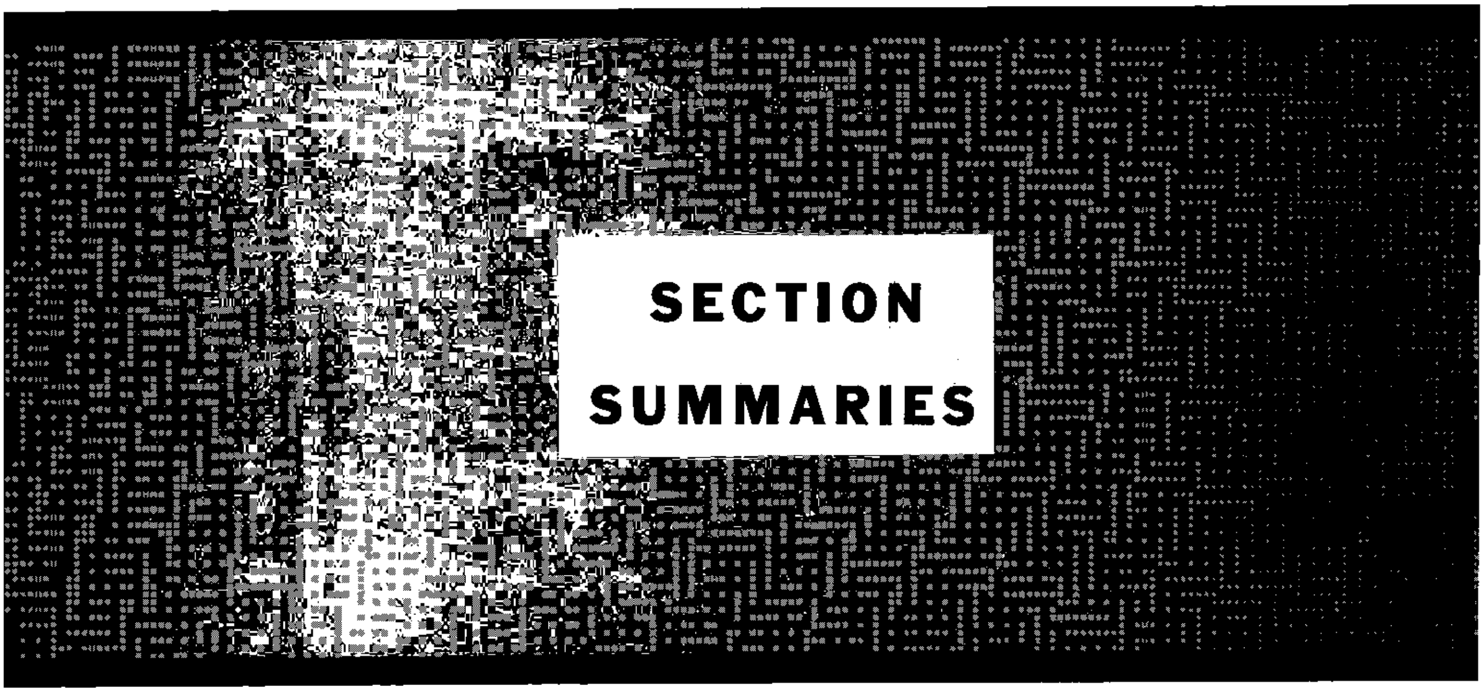
[2] See "Redbook" 1964, Part I: p. 49 and pp. 57-58.

processes by which the environment is changed, as well as its momentary condition, so as to be in a position to forecast hydrographic situations of fisheries significance". In particular he made a plea "for the hydrographer and the biologist to meet daily and to learn to write and speak so that each understands the other, as well as to disseminate their information speedily." This seems to apply as much today as it did then!

It also became clear that no longer can the "hydrographers" be content merely with measuring temperatures and salinities. In conjunction with their biological colleagues, they should also be measuring water movements, both large and small scale, and the nature and intensity of light at different times and places, and investigating their effects, along with more chemical aspects of the environment.

It might seem almost equally unnecessary to add that biologists and hydrographers, and others, must plan carefully so as to have a reasonable chance of securing the information that is seen to be needed. Yet not only are resources often inadequate enough for this, but often workers are almost too easily satisfied with what is available without the extra effort which alone can promise results. The sea is vast, and the fish roam widely in it. If our work is to be successful, then we have to plan for an ingenious and economical mixture of extensive investigations for certain purposes and intensive - indeed, intimate - investigations to provide the understanding of the processes, biological as well as physical, which govern events over the wider areas: and often the second of these must be tackled first! Indeed, as one of my colleagues expressed it, perhaps the greatest value of the Symposium was that it provided a valuable "confrontation" on several aspects of fisheries research. These and many other matters arising should give food for thought to environmental workers and fishery research generally for some time to come.

SECTION SUMMARIES



SECTION SUMMARIES

SECTION A
Effect of Physical Environmental Conditions on the Distribution of Adult Fish (*i.e.* Immediate and Seasonal Effects)

CONVENER: A.J. Lee RAPPORTEUR: J. Corlett

Contributions submitted to this Section were as follows (parentheses indicate original contribution number):

A-7 (A-1) "About Possible Fishing/Temperature of Water Relationship" by O. Cendrero

A-16 (A-2) "Interpretation of Fish Distribution in Respect to Currents in the Light of Available Laboratory and Field Observations" by T. Laevastu

A-10 (A-3) "Influence of Cold Water on Fish and Prawn Stocks" by Sv. Aa. Horsted and Erik Smidt

A-4 (A-4) "Cod and Low Temperature in St. Mary's Bay, Newfoundland" by W. Templeman and A.M. Fleming

A-5 (A-5) "Mass Mortalities of Marine Fishes in the Newfoundland Area Presumably Due to Low Temperature" by W. Templeman

A-8 (A-6) "Distribution of Haddock on the Grand Bank in Relation to Season, Depth and Temperature" by W. Templeman and V.M. Hodder

A-2 (A-7) "Seasonal Distribution of Cod (*Gadus morhua* L.) Along the Canadian Atlantic Coast in Relation to Water Temperature" by Yves Jean

A-3 (A-8) "Distribution of Haddock off the Eastern Canadian Mainland in Relation to Bottom Temperatures" by F.D. McCracken

A-11 (A-9) "Influence of the Temperature Regime Upon the Behaviour of Redfish off the West Greenland in Springs 1959-1961" by L.M. Pechenic and I.I. Svetlov

A-6 (A-10) "Research Vessel Catches of Cod in the Hamilton Inlet Bank Area in Relation to Depth and Temperature" by W. Templeman and A.W. May

A-15 (A-11) "Data on the Distribution of Tuna Fish Concentrations During the Feeding Period in Some Areas of the Atlantic Ocean" by V.L. Zharov

A-14 (A-12) "The Influence of Hydrographic and other Factors on the Distribution of Cod on the Spitsbergen Shelf" by R.J.H. Beverton and A.J. Lee

A-9 (A-13) "Distribution of Haddock on St. Pierre Bank (ICNAF Division 3Ps) by Season, Depth and Temperature" by W. Templeman and A.W. May

A-13 (A-14) "The Water Temperature as a Factor Guiding Fishes During their Migrations" by K.G. Konstantinov

A-18 (A-15) "Effects of Light upon Behaviour and Distribution of Demersal Fishes of the North Atlantic" by P.M.J. Woodhead

A-1 (A-16) "Relation of Temperature to Fish Abundance and Distribution in the Southern New England Area" by R.L. Edwards

SECTION B
Effect of the Environment on Pelagic and Early Demersal Stages of Groundfish

CONVENER: R.S. Glover   RAPPORTEUR: J.M. Colebrook

Contributions submitted to this Section were as follows:

B-1 "The Relationship Between the Distribution of *Sebastes* Larvae, Zooplankton and Temperature in the Irminger Sea" by J. Magnusson and I. Hallgrimsson

B-2 "The Analysis of Variation in the Plankton, the Environment and the Fisheries" by J.M. Colebrook

B-3 "A Preliminary Study of *Sebastes* Larvae in Relation to the Planktonic Environment of the Irminger Sea" by V. Bainbridge

B-4 "Redfish Larvae in the North Atlantic" by G.T.D. Henderson

B-5 "The Distribution and Behaviour of Pelagic and Early Demersal Stages of Haddock in Relation to Sampling Techniques" by John B. Colton, Jr.

B-6 "Factors Controlling Dispersal of the Pelagic Stages of Fish and their Influence on Survival" by A. Saville

B-7 "Comparative Characteristic of Some Biological Indices of the Bottom Stages of 0-Group Cod Belonging to the 1956, 1958, 1959, 1960 and 1961 Year-Classes" by I. Ja. Ponomarenko

B-8 "Drift Migrations and their Significance to the Biology of Food Fishes of the North Atlantic" by Ju. Ju. Marty

B-9 "Survival of the Youngest Stages of Fish and its Relation to Year-Class Strength" by J.A. Gulland

B-10 " Winds, Currents, Plankton and the Year-Class Strength of Cod in the Western Barents Sea" by J. Corlett

B-11 "On the Life-Cycle Pattern of Labrador Cod" by A.I. Postolaky

B-12 "Changes in the Recruitment to the Stock With Reference to the Environment and Mathematical Modelling with Notes to Changes" by T.F. Dementjeva

B-13 "On Primary Food Supply - the Base of Productivity in the Northwest Atlantic" by M.V. Fedosov and I.A. Ermachenko

B-14 "The Effect of Temperature and Current on the Distribution and Survival of Cod Larvae at West Greenland" by F. Hermann, P.M. Hansen and Sv. Aa. Horsted

B-15 "Notes on the Condition of Formation of the Arcto-Norwegian Tribe of Cod of the 1959-1961 Year-Classes During the First Year of Life" by A.S. Baranenkova

B-16 "The Relation Between the Feeding of Cod Larvae and Pelagic Fry and the Distribution and Abundance of their Principal Food Organisms" by T.K. Syssoyeva and A.A. Degtereva

B-17 "Dependency of Redfish Breeding and Larval Redfish Distribution on Water Temperature" by A. Kotthaus

B-18 "Some Results of Soviet Research Work on Ichthyoplankton in the Northwest Atlantic" by V.P. Serebryakov

Fluctuations in the fisheries are the result partly of migration, disease, predation and changes in the availability of the stock to capture but the greatest source of uncertainty about the yield is the variability of year-class strengths. This point was emphasized throughout the papers and during the discussion and it was clear that variations in the strength of a year-class must have their origins at some time before the fish enter the commercial fishery.

Such variations could result from changes in the numbers or mortality of eggs, through predation, developmental, metabolic or density dependent effects. Most of the authors and participants, however, thought it more likely that fluctuations in the strength of a year-class may arise during the planktonic or later phases of the development of the fish as the result of mortality or emigration. Gulland, in contribution B-9, draws hypothetical curves showing the sequence of phases of mortality: at first massive (and probably unrelated to year-class strength), then density dependent, followed by the critical phase when the year-class strength is determined.

There is adequate evidence of the dependence of larval fish on various aspects of their external environment. For example, the distribution and abundance of redfish larvae seem to be related to water temperature and the supply of their planktonic food (contributions B-1, B-3, B-4, and B-17). Russian work on the herring and anchovy shows that the abundance of larvae is dependent on the abundance of their food (B-12). Haddock larvae are found in the thermocline off the New England coast (B-5). The numbers of cod larvae off West Greenland are positively correlated with temperature (B-14). Some of the participants in the symposium discussed the effect of water currents on the drift and survival of larvae. For example, fluctuations in the abundance of haddock larvae at Faroe are related to the strength and direction of wind, presumably through its effect on water movements (B-6). In the same contribution, Saville provides a detailed analysis of wind, water movement and larval drift in the herring stocks of the Clyde. Predation of 0-group cod by older fish of the same species may be dependent on the growth rate and nutritional condition of the young fish (B-7).

There is less evidence of the dependence of year-class strength on the numbers of larvae although Gulland (B-9) quotes work which suggests that the abundance of plaice larvae in their later planktonic stages may be related to year-class strength and he gives indirect evidence of similar relationships in Lofoten cod, North Sea haddock and sock-eye salmon. Saville (B-6) shows that the abundance of haddock near the end of their planktonic phase near the Faroes was related to the numbers of one year old haddock which are a satisfactory index of subsequent recruitment to the fishery.

The analysis of such relationships must depend on adequate estimates of the distribution and abundance of the young stages. This information is difficult to obtain and has seldom been available in the detail and accuracy required. For this reason, fishery biologists have been compelled to study correlations between the parameters for which estimates are available; for example wind, temperature or planktonic food on the one hand, and the year-class strengths on the other. Saville (B-6) concludes that there is no relation between wind during the larval phase and subsequent year-classes of haddock in the North Sea or herring in the Clyde. Gulland (B-9), in a number of references to his own and other work, finds no relationship (or rather dubious ones) between wind, temperature or plankton and subsequent year-classes of Arcto-Norwegian cod. However, Corlett (B-10) using a different estimate of year-class strength, shows correlations between wind, dry weight of plankton and year-class strength of cod in the Barents Sea. Hermann, Hansen and Horsted (B-14) claim that drift of larvae is a major feature of the early life of West Greenland cod, but are unable to detect any relation between wind and brood strength. But they do find statistically significant correlations between temperature during the larval phase and the subsequent catch of 6-10 yr old fish.

It is not surprising that the results should be confusing and contradictory. In a hypothetical case, let us exclude food supply, predation, competition and metabolism, and assume that the size of a year-class is related to the numbers of larvae at some unknown stage of their life history and that these, in turn, are dependent on some unknown function of water movement which, in its turn, is partly a product of the bottom topography and the earth's rotation and partly under the influence of winds. In this very simple model, fishery biologists would often be able to test only the beginning and end of the chain (wind and year-class). Even without the added difficulty of detecting the relevant wind parameter and of deciding how to estimate the strength of a year-class, it would be surprising if a simple linear correlation co-efficient would be sufficiently sensitive to test the hypothesis. In the contributions and discussions the danger of fortuitous correlations was emphasized and, since each year yields only one pair of observations, research of this kind is likely to extend over a long period of years.

Some of the contributions drew attention to the importance of treating each population as a separate unit since growth, mortality and migration may differ in different patches of larvae. It was recognized that the numbers and distribution of larvae are dependent on a complex interaction of many factors. None of the physical and biological parameters of nature operates in isolation and it is a dangerous over-simplification to try to study them in isolation. The possibility of using multivariate methods to analyse the natural system as a whole is illustrated in contribution B-2, dealing with sources of variation in the plankton.

Repeatedly, in the discussion, it was emphasized that we lack the basic ecological and physiological knowledge which is essential for an adequate understanding of events in the fish stocks. Few of the papers mentioned other organisms in the community, except as food for fish. As Dr Ahlstrom's special lecture shows (p. 53-74), competition may be very important in determining the abundance of a commercial stock. It is notable that only one of the contributions (B-7) deals with 0-group fish. Fairly detailed statistics are available for the adults in fished stocks and there are modest collections of the planktonic stages but there is a most serious dearth of data about all the stages of the fish life cycle between the early larval stage and the entry of adults into the fishery.

One of the most successful developments in recent years has been the method of studying the population dynamics of adult fish in which mortality and growth rates are ascribed to different causes and built up into quantitative models of events in a population. A similar method has been used in studying plankton production by constructing a model of the major terms (such as photosynthesis, respiration and grazing) and inserting into the model as many as possible of the factors impinging on each of these (such as light, temperature, turbulence and nutrients).

It seems highly desirable that an attempt should be made to bring together these two levels of model-making, based on an adequate understanding of the whole system of interacting variables of which fish form a part. Steele (C-4) has made a tentative start in this direction with a model of the energy chain from photosynthesis to commercial fisheries.

Objectives of this kind will only be achieved if much greater facilities are available than in the past both for collections at sea and experiments in the laboratory. Frequent and detailed surveys will be needed to detect the critical events which determine larval mortality and year-class strength. But if such surveys are to be successful, it will be necessary to develop improved methods for sampling the larvae and young stages (B-5).

We are still left in doubt about the precise critical phase; indeed Baranenkova (B-15) concludes that every year-class has its own period of maximum mortality. It would seem that a much greater effort must be directed towards an ecological study of the young stages. Knowledge of these pre-recruit stocks is essential in attempts to predict and control fisheries. The technical and intellectual problems are very testing and progress will be dependent on the integration of the skills of marine scientists of many kinds, and on co-operation between laboratories and nations.

SECTION C

Effect of the Biological Environment (including parasites) on the Distribution of Adult Fish

CONVENER: W. Templeman RAPPORTEUR: A.W. May

Contributions submitted to this Section were as follows:

C-1 "Remarks on Effect of Food Animals on Cod Behaviour" by Sv. Aa. Horsted and Erik Smidt

C-2 "Food as a Factor or Indicator of Vertical Migrations of Cod in the Western Gulf of St. Lawrence" by Pierre Brunel

C-3 "Some Instances of Cod and Haddock Behaviour and Concentrations in the Newfoundland and Labrador Areas in Relation to Food" by W. Templeman

C-4 "Some Problems in the Study of Marine Resources" by J.H. Steele

C-5 "The Impact of the Environmental Factors on Survival of the Far Eastern Young Salmon During the Acclimatization of the Latter in the Northeast Part of the USSR" by E.L. Bakshtansky

C-6 "The Copepod Ectoparasite *Sphyrion lumpi* (Kroyer) in relation to Redfish (*Sebastes marinus* L.) in the Gulf of Maine" by G.F. Kelly and A.M. Barker

C-7 "Density-dependent Food Relationships with reference to New England Groundfish" by R.L. Wigley

Most of the papers of this section dealt with concentrations and behaviour of cod, haddock, and other groundfish due to food. It was apparent from these contributions (C-1, C-2, C-3, C-7) and from other contributions (A-6, A-10, A-11, A-12, E-2) that food can be a concentrating factor for commercial fish, allowing them to gather in large numbers within some part of a favourable temperature and depth range. These concentrations may be in different parts of the preferred temperature and depth range depending on the temperature and depth ranges of the food animals. It is evident that food can modify the temperature and depth preferences of fish and that such preferences can often be best explained in relation to food. The relationship of food to concentrations of commercial fishes should therefore be studied whenever catch and related temperature and depth data are being collected by research vessels.

In discussion Blaxter, with reference to cod becoming glutted with capelin and sinking to the bottom (C-3), wondered whether there was any connection between this behaviour and a report in the Underwater Naturalist of "sleeping" cod. Corlett raised the question of how long it takes cod to digest food. He noted that Brunel (C-2) quoted from Karpevitch and Bokoff that the time for digestion may vary from 5 to 6 days in the case of a fish meal and from 3 to 3 1/2 days for a *Gammarus* meal. Corlett's impression, from Barents sea cruises, was that digestion in cod was more rapid than this. Meyer, from personal observation, said that cod taken at mid-day in one of his cruises contained fresh capelin and those taken in the evening contained digested capelin. Templeman remarked that because of the fullness of cod stomachs in the Newfoundland area during the trap season digestion would take longer than this. Kohler said that cod kept in tanks digested a herring meal in 1 day but the cod were not glutted. Hempel said that plaice took 12-24 hr and saithe up to 3 days to clear the stomach, the time depending on stomach fullness and water temperature. Magnusson remarked that feeding of redfish in several areas occurred at well defined periods, thus the stomach would probably be cleared between these periods. Horsted noted that there were 2 daily periods of cod activity in Greenland in late summer and autumn. Food (plankton and capelin) taken in the morning period was all gone by evening. Edwards said that for 8 fish species investigated at Woods Hole there were clear-cut feeding periods, either once or twice a day. Indications from these, and from some observations at sea, were that the stomachs were cleared within 6 hr.

One paper (C-4) examined the energy dynamics of the related trophic levels from phytoplankton to commercial fish and concluded that a great deal of the information necessary to apply primary production and related plankton and benthos data to estimation of potential yield of commercial fish is lacking.

There was considerable discussion on the point raised by Beverton as to whether availability of food to adult fish is influenced by their own abundance. In comparing pre- and post-war plaice stocks in the North Sea (Steele) there was an increase in yield, but also an increase in growth rate after the war which is opposite to what is to be expected. It is necessary to distinguish between food as a controlling factor and food fluctuating independently of the fish (Beverton). The plaice food supply had evidently changed but this was not related to density of plaice. Plaice larvae and *Ammodytes* larvae compete for food and it is possible that *Ammodytes* may be "controlling" the plaice. The availability of food in relation to growth is likely to differ in different sizes of fish of the same species which use different sizes and kinds of food (Templeman). If large fish are greatly reduced in numbers the large food is not utilized. These kinds of food such as capelin, herring and launce may become more numerous and eat great numbers of the fry of the former predators such as the cod. If the smaller commercial fish are more numerous they are now competitors for food of a small size range and here density dependent effects may be more likely to occur. Flatfish in the Kattegat ate only 2% of the available bottom food and the large changes in stock size of Norwegian herring did not affect the growth rate (Hempel). These results indicate that other factors, rather than food supply are responsible for limitation of stock abundance.

Another contribution (C-6) described the distribution and abundance of *Sphyrion lumpi* in relation to redfish in the Gulf of Maine. In discussion it was noted that a well documented example of the effect of parasites on the distribution of adult fish is the great destruction and reduction in stock size of spring-spawning herring in the Gulf of St. Lawrence by at least 2 great epidemics caused by the fungus *Ichthyosporidium hoferi*. Lucas and Parrish mentioned that Kabata's work on haddock parasitized by *Lernaeocera* showed that condition factors, liver fat and red blood cell levels were lower in parasitized than in non-parasitized fish of the same length and age. Sundnes noted that the presence of *Lernaeocera* on Arcto-Norwegian cod has so far not been found to have any adverse effect on the parasitized individuals.

Yearly differences in success of survival of maturity of young Pacific pink and chum salmon, introduced into the Barents and White seas, were attributed (C-5), mainly to differences in predation by herring. These young salmon were also eaten by cod, saithe, sea trout and other fishes.

SECTION D

Effect of the Environment of the Growth, Survival and Age and Size at First Maturity

CONVENER: Paul Hansen RAPPORTEUR: A.C. Kohler

Contributions submitted to this Section were as follows:

D-1 "The Possible Effects of Temperature on the Fecundity of Grand Bank Haddock" by V.M. Hodder

D-2 "Relation of Periods of Successful Year-Classes of Haddock on the Grand Bank to Periods of Success of Year-Classes for Cod, Haddock and Herring in Areas to the North and East" by W. Templeman

D-3 " Changes in Growth, Feeding, and Density of Gulf of St. Lawrence Cod" by A.C. Kohler

D-4 "Temperature and Growth of Cod in Icelandic Waters" by J. Jonsson

D-5 "Some Problems of Zooplankton Production and the Problems of Fisheries" by W. Mankowski

D-6 "Cod Growth and Temperature in the Newfoundland Area" by A.W. May, A.T. Pinhorn, R. Wells and A.M. Fleming

D-7 "Possible Influence of Water Temperature on the Growth of West Greenland Cod" by F. Hermann and P.M. Hansen

D-8 "Relationship Between the Growth Rate and Density of Population of Haddock in the Barents Sea" by M.A. Sonina

D-9 "Changes in the Growth Rate of the Barents Sea Cod as Affected by the Environmental Factors" by T.F. Dementjeva and E.M. Mankevich

Of the eight contributions presented and discussed at the meeting, six dealt with growth (D-3, D-4, D-6, D-7, D-8 and D-9), one with the effect of the production of zooplankton on fatness of sprat and length of herring in the Baltic (D-5), and one with the relation of the occurrence of year-classes, in the stock of haddock on the Grand Bank, with year-classes of cod, haddock and herring in all regions in the North Atlantic (D-2).

The contributions concerning growth covered Newfoundland and the Gulf of St. Lawrence area, West Greenland, Iceland and the Barents Sea. In the contributions and in the discussion it was pointed out that many interrelated factors have influence on the growth, but that temperature is a primary one.

In one contribution (D-6) it was shown that in the Newfoundland-Labrador area water temperatures and growth of cod were very closely related. Laboratory experiments with cod from the Gulf of St. Lawrence area have shown a relation of growth to food consumption, and food consumption again was related to temperature (D-3).

Increases in growth rate could be related to special mortality of food organisms, as shown by Kohler, who described a case of epizootic in the herring stock in the area of St. Lawrence (D-3); this had the result that moribund herring became an easy prey for the cod.

It was shown in several contributions that abundance of food and higher temperatures produce good growth in different kinds of fish. In the Icelandic area it was shown that growth and water temperatures were positively correlated, so that in the warmer parts, the area west of Iceland, the growth was greater than in the colder areas north of Iceland, and in the still colder area east of Iceland where the growth was very slow (D-4).

Among other factors which have an influence on the growth of fish is the density of population. Some contributions suggested that it is the density of the combined stock of haddock in the Barents Sea (all age-groups), and not single rich year-classes, that cause changes in the growth (D-8). When a stock has been diminished, *e.g.* by strong fishing, the growth of the individuals increases.

It was shown in contribution D-5 that the production of zooplankton in the Baltic is strongly correlated with the growth of sprats and herring, and especially that the fat content increases strongly in years with good amounts of zooplankton.

In the discussion Corlett pointed out that fish having a fish diet rather than crustacean usually grew better: possibly because less energy is expended in gathering food and fish protein is more efficient than crustacean. Horsted also noted that, regarding differences in growth between species, slow-growing redfish eat mainly crustaceans while cod, which grow faster and larger, are fish eaters.

Contribution D-9 referred to Nikolsky's view that for each species there is an optimum temperature which is the most suitable for metabolism and provides the fastest growth; when the temperatures are above and below this optimum the growth decreases. In the discussion Beverton touched on this problem and referred to a contribution by Ursin incorporating temperature data in the Von Bertalanffy growth equation. Kohler added that recent laboratory experiments with cod growth at St. Andrews (N.B.) gave similar results.

Edwards noted the effects of water temperature on the growth of haddock in the Gulf of Maine which show an inverse relation to those being demonstrated for cod. This could be related either to distribution or to fact that haddock in this area may be living near the upper temperature limit mentioned by Beverton.

Temperature is selected for consideration as an environmental factor because it is very easy to measure, but it was pointed out that it was difficult to decide which temperature should be chosen as the relevant one. The ideal temperature would of course be the temperature of the water in which the fish live, but in most cases this will be impossible to measure. In the contributions surface temperatures have been used mainly.

In the discussion Blaxter questioned the use of the Van't Hoff relationship to compare lengths of fish at different temperatures (D-4), and also commented on the apparent anomalies regarding findings of improved growth of cod and $L\infty$ of the Bertalanffy equation at higher temperatures.

Colebrook commented on the possibility that techniques used for correlating temperature and growth might be invalid, but noted that, when a relationship appears in three widely separated areas, there is fairly strong evidence for its existence.

In referring to contribution D-6 Lee warned against assuming a simple relation between latitude and water temperature at fishing depths in the Northwest Atlantic. Isotherms often tend to run in a north-south rather than east-west direction, especially off Labrador.

SECTION E
Herring and the Environment in the ICNAF Area

CONVENER: B.E. Skud RAPPORTEUR: B.B. Parrish

Contributions submitted to this Section were as follows:

E-1 "Effect of Light on Movements of Herring in the Bay of Fundy" by S.N. Tibbo

E-2 "Distribution of Plankton and Summer Feeding of Herring in the Norwegian Sea and on Georges Bank" by E.A. Pavshtics

E-3 "Water Temperatures and the Herring Fishery of Magdalen Islands, Quebec" by L.M. Lauzier and S.N. Tibbo

E-4 "The Influence of Water Masses of the New England and Nova Scotia Shelf on the Formation of Commercial Concentrations of Herring" by V.A. Bryantsev

E-5 "Effects of Environment on Several Diseases of Herring from the Western North Atlantic" by Carl J. Sindermann

E-6 "Seasonal and Areal Distribution of Gulf of Maine Coastal Zooplankton, 1963" by Kenneth Sherman

E-7 "Ecology of Herring Larvae in the Coastal Waters of Maine" by Joseph J. Graham and Harold C. Boyar

E-8 "Distribution of Wintering Herring in the Southern Part of the Norwegian Sea According to Temperature Conditions" by L.R. Shmarina

The convener opened the section by outlining the planned schedule, which, following introductory remarks, was the presentation of contributed papers, a special discussion on Bay of Chaleur herring, and the general discussion.

The introductory remarks were directed toward a geographic orientation of herring distribution and fisheries in the Western North Atlantic. The major divisions within the known range from Greenland to Cape Hatteras were Newfoundland, Gulf of St. Lawrence, Nova Scotia, Gulf of Maine, Georges Bank, and the Middle Atlantic Bight. The major spawning areas and seasons were also discussed: spring spawning in Newfoundland, Gulf of St. Lawrence and Nova Scotia, and fall spawning in the Gulf of Maine and Nova Scotia.

The convener reviewed the types of fisheries practised in the ICNAF area and described the various gear utilized and the utilization of the landings. Total catch by country in the last two years was compared:

	1961	1962
Canada	80,000 metric tons	100,000 metric tons
USSR	70,000 " "	150,000 " "
USA	30,000 " "	85,000 " "
Total	180,000 " "	335,000 " "

The convener reviewed the past research efforts in the Western North Atlantic and outlined the results of the 1963 ICNAF meetings which concerned herring, and discussed the long-term needs of research on this species. The objectives of this section of the Symposium were then listed as follows:

1. To call attention to and discuss studies of the environment of herring in the ICNAF area.

2. Appraise recent environmental research on herring with the intent that areas of limited knowledge could be emphasized and that suggestions for programs to improve these deficiencies would be offered.

3. To stress specific problems of concern in the herring fisheries and to cite the relationship of the environment to these problems.

4. To compare the state of knowledge of herring biology in the ICNAF area with other herring fisheries of the world.

Following the presentation of Contributions E-1 to E-8, the convener called attention to those contributions in other sections of the Symposium which referred to herring. These were, according to subject:

HERRING AND THE PHYSICAL ENVIRONMENT

A-2 by T. Laevastu. "Interpretation of fish distribution in respect to currents in the light of available laboratory and field observations."
B-6 by A. Saville. "Factors controlling dispersal of the pelagic stages of fish and their influence on survival."
B-8 by Ju. Ju. Marty. "Drift migrations and their significance to the biology of food fishes of the North Atlantic."
B-9 by J. Gulland. "Survival of the youngest stages of fish, and its relation to year-class strength."
D-5 by W. Mankowski. "Some problems of zooplankton production and the problems of fisheries."
F-7 by T. Iles. "Factors determining or limiting the physiological reaction of herring to environmental changes."
H-3 by L. Lauzier. "Long-term temperature variations in the Scotian Shelf area."
H-8 by D. Bumpus and J. Chase. "Changes in the hydrography observed along the east coast of the United States."
H-9 by J. Tait and J. Martin. "Inferential biological effects of long-term hydrographical trends deduced from investigations in the Faroe-Shetland Channel."
I-1 by L. Lauzier. "Foreshadowing of surface temperatures at St. Andrews, N.B."
I-7 by J. Eggvin. "The possibility of forecasting oceanographic conditions in North-West European waters and their significance for fisheries."

PHYSIOLOGY AND BIOLOGY

F-1 by K. Kalle. "Oxygen dependence of vertical migration in shoaling fish."
F-2 by J. Blaxter. "Effect of change of light intensity on fish."
F-3 by F. Holliday. "The significance of environment/endocrine studies to the investigation and exploitation of fish stocks."
F-5 by G. Hempel. "Egg size and fecundity in relation to the environment."
F-8 by G. Sundnes. "Energy metabolism and migration of fish."
G-3 by H. Mohr. "Changes in the behaviour of fish due to environment and motivation and their influence on fishing."

INCIDENTAL REFERENCES TO HERRING

A-12 by R. Beverton and A. Lee. "The influence of hydrographic and other factors on the distribution of cod on the Spitsbergen Shelf."
C-5 by E. Bakshtansky. "The impact of the environmental factors on survival of the far eastern young salmon during the acclimatization of the latter in the north-east part of the USSR."
D-2 by W. Templeman. "Relation of periods of successful year-classes of haddock on the Grand Bank to periods of success of year-classes for cod, haddock and herring in areas to the north and east."
D-3 by A. Kohler. "Changes in growth, feeding, and density of Gulf of St. Lawrence cod."

The discussion period was then opened with a continuation of a topic first broached in Dr Hempel's section (F). The discussion concerned spring and fall spawning stocks in the Bay of Chaleur and was initiated by Dr Harden-Jones. Messrs. Skud, Parrish and Blaxter also participated and the validity of scale ratio and otolith nucleus as a method of indicating when a fish was spawned was discussed.

The general discussion of section contributions was then opened. (a) Blaxter drew attention to the differences in temperature preferences of herring in the Northwest and Northeast Atlantic as shown in contributions E-8 and E-3. In E-8, it is stated that spring spawning in the Norwegian Sea does not take place below about 3°C, but in E-3, spring spawning is quoted as taking place in the vicinity of Magdalen Islands at lower temperatures; good herring catches are even recorded there at -0.7°C. A somewhat parallel situation is observed with the cod, which appears to occur in colder water in the Northwest than in the Northeast Atlantic. Blaxter also asked whether there are any recorded instances of herring being found dead in cold water in the Northwest Atlantic. Templeman reported that some years ago, in May, herring had been observed floating, dead in Fortune Bay, but it could not, of course, be claimed that their death was necessarily due to the cold water. Herring are commonly found, in winter, in very cold water in bays, such as the Bay of Islands, off Newfoundland. These bays are completely covered with ice in winter, and the herring must spend a considerable part of this time in temperatures below 0°C.

Lauzier announced that the temperature of 2.1°C in the Magdalen Islands area should not be taken as a preferred temperature. In the middle of the season, the temperature is higher, at 5-6°C.

Holliday announced that herring larvae can live at super-cooled temperatures. (b) Parrish asked if large herring concentrations are ever found in the open sea to the south of Newfoundland (Grand Bank area) or in the area between Labrador and W. Greenland (Labrador Sea and Davis Strait).

Templeman replied that some trawl catches of up to several hundred herring have been taken on the southern Grand Bank. A few herring have also been caught by trawlers on St. Pierre Bank. However, no large catches have been reported from these Banks, and herring have not been recorded in cod stomachs in this area. Further, there are no records of herring from the Hamilton Inlet Banks area, either in catches or fish stomachs. Herring are found in the inshore, Labrador area and formerly a good fishery for large, fat herring took place off southern Labrador, mainly from late summer to autumn.

Hansen announced that herring also occur off W. Greenland, from the Southwest coast northwards to the Arctic Circle. The herring are usually very large fish, up to 45 cm in length. Some tagging experiments have been carried out on these herring, but the recaptures have been taken near to the tagging locality. Herring larvae have been caught in Southern Greenland waters, and fishermen report that there are herring in the open sea waters of the Davis Straits.

Lucas drew attention to the usefulness of predatory fish as samplers of prey species such as herring. Fish stomach analyses should be carried out in these areas.

Convener. There is no evidence of herring in Hudson Bay, but concentrations of *C. pallasii* occur around the north of Alaska.

Glover said that there were no records of herring larvae in the Hardy Plankton Recorder material from Ireland to Newfoundland.

(c) Bumpus questioned whether Labrador water was present in the Gulf of Maine to the extent indicated by Bryantsev in Contribution E-4. Insufficient Labrador water rounds Avalon Peninsula or the Tail of the Grand Bank for this to be possible. The water in the Gulf of Maine is a complex mixture of slope and coastal water, with minor contributions from the Scotian Shelf, with considerable Laurentian characteristics. The location of the herring concentrations concurs with the divergence of the cyclonic Gulf of Maine gyre and the anti-cyclonic Georges Bank eddy, and the retreat to the westward as the season progresses coincides with the breakdown and diffusion of these circulations.

Lauzier agreed with Bumpus' comments and pointed out that the Gulf of Maine water masses should be defined as a mixture of 5 water types and not 3, as Bryantsev has done. He further announced that while the relationship between herring catches and wind seems to be good during late winter and early spring, he would not expect it to be so in other seasons when thermal stratification is greater than in the winter.

(d) Dr Uda commented on the large long-term fluctuations in the Japanese herring and sardine fisheries in the Pacific. These appear to correspond with fluctuations and trends in warming and cooling of the waters in the area. In the cold regions, water transport is lower than in the warmer ones. The records indicate that with warming in the northern Pacific, the herring fishing grounds shift further to the north.

(e) Convener. Is there any evidence that herring change their spawning grounds? There is no evidence that the extensive spawning on Georges Bank was in existence 50 yr ago, whereas there was evidence of inshore spawning which is now very limited.

Templeman announced that in the Newfoundland area, spring herring spawn in late May-early June in shallow water (the milt patches can be easily seen) while autumn spawners spawn in considerably deeper water. It is possible that there is more continuity between spring and autumn spawning than we have observed. For example, Capelin on the east coast of Newfoundland begin spawning in very shallow water (on the beach); spawning then continues throughout July and August, extending gradually into deeper water as the inshore water warms up, until in August they may spawn down to 20-25 fathoms or deeper.

(f) Blaxter asked if, as a result of the southerly drift of larvae from Georges Bank, a substantial part of the larvae population is lost to the area? Edwards thought that they would not be lost in the Gulf Stream, but would be held in the Southwest drift, and so perhaps not lost to the Georges Bank stock.

Convener announced that Colton's observations on the drift of haddock spawning products from the Bank were very pertinent to this question; he also announced that investigations on the larvae of Pacific herring had concluded that larvae are probably lost to the population whenever they move outside the coastal zone.

The section was then closed and was briefly summarized later by the convener. He concluded that some of his objectives were optimistic, but that several areas of limited knowledge were emphasized and existed in European waters as well as in the ICNAF area. Of particular concern in the western North Atlantic was the problem of stock identification, including the separation of spring and autumn spawners. The importance of temperature, water movement and plankton distribution in relation to herring abundance was emphasized. These are in general agreement with the research interest of the ICNAF herring scientists and are areas which are actively being studied.

The convener also cited the excellent presentation of Mr Parrish as a guest speaker. His talk compared the herring fisheries of the western and eastern North Atlantic in terms of production and ecological boundaries which govern the distribution of herring stocks.

SECTION F
Physiological Reactions to Changes in the Environment

CONVENER: G. Hempel RAPPORTEUR: J.H.S. Blaxter

Contributions submitted to this Section were as follows:

F-1 "Oxygen Dependence of Vertical Migration in Shoaling Fish" by K. Kalle

F-2 "Effect of Change of Light Intensity on Fish" by J.H.S. Blaxter

F-3 "The Significance of Environment/Endocrine Studies to the Investigation and Exploitation of Fish Stocks" by F.G.T. Holliday

F-4 "Effect of Abiotic Factors in Young Stages of Marine Fish" by K. Lillelund

F-5 "Egg Size and Fecundity in Relation to the Environment" by G. Hempel

F-6a "Seasonal Changes in the Physiology of the Cod in Relation to its Environment - I. Seasonal Changes in the Physiological Reactions of the Barents Sea Cod, *Gadus morhua* L., Particularly Affecting Migration and Maturation" by A.D. Woodhead and P.M.J. Woodhead

F-6b "Seasonal Changes in the Physiology of the Cod in relation to its Environment - II. Physiological Reactions of Cod, *Gadus morhua* L., to Low Temperatures" by P.M.J. Woodhead and A.D. Woodhead

F-7 "Factors Determining or Limiting the Physiological Reaction of Herring to Environmental Changes" by T.D. Iles

F-8 "Energy Metabolism and Migration of Fish" by Gunnar Sundnes

F-9 "Supercooling and Osmoregulation in Teleosts of the Subarctic and Arctic Region" by J. Leivestad

The papers were divided into five main topics:

1. The internal environment (endocrine systems) - Holliday (F-3),Woodhead and Woodhead (F-6A).
2. Reproduction - Hempel (F-5), Hodder (D-1), Iles (F-7), with additional reference to Steele (C-4), Bakshtansky (C-5), Mankowski (D-5) and Martin and Kohler (H-7).
3. Importance of light - Blaxter (F-2), Woodhead (A-15), with additional reference to Colton (B-5), Mohr (G-3) and Tibbo (E-1). A film by Shaw was also shown.
4. Tolerance to the environment - Lillelund (F-4), Kalle (F-1), Leivestad (F-9), Woodhead and Woodhead (F-6B), with additional reference to Cendrero (A-1), Horsted and Smidt (A-3), Templeman and Fleming (A-4), Jean (A-7), Templeman and May (A-10), Beverton and Lee (A-12), Postolaky (B-11), Serebryakov (B-18).
5. The "artificial" environment - Sundnes.

The purpose of this last section was to provide some background information on immediate and delayed responses of fish to changes in the physical properties of the sea. The classical approach to this problem is the experiment in the aquarium where all factors but one are kept constant (or are assumed to be constant). The limitations of this method have been stressed. Fish live in the aquarium in an unnatural environment which offers only a selected range of stimuli, and where it is almost impossible to control some variables (*e.g.* atmospheric pressure). The variable supposedly under consideration is often changed over a wider range than that found in natural conditions.

Other variables (*e.g.* the effect of weather on fish movement) have not been studied in isolation at all. In spite of those limitations the potential value of the aquarium approach cannot be gainsaid. Nevertheless, a general improvement in experimental techniques is desirable in order to detect the interaction and influence of groups of environmental variables. For example, the reaction to light might change with different conditions of temperature or food supply. An increase of work done in fish pounds in sheltered areas of the sea is also desirable in an attempt to link aquarium results with investigations at sea.

Observations in the sea can provide valuable information on the importance of environmental factors if they are especially designed for an analysis of this kind, but a simultaneous measurement of the biological and hydrographical features of the habitat is essential. An analysis of data on commercial catches combined with information from meteorological records rarely reveals knowledge of the isolated effect of a single factor.

In general the physiological capabilities of fish, especially in the young stages, are wider than might be assumed from their distribution in the sea. Distribution may be partly imposed on young fish by the location of spawning grounds and the inability of the young stages to change their position substantially by active movements. However, the optimum for fish, or their preference for a certain range of conditions, are certainly narrower than the range of tolerance. One must differentiate between what a fish is capable of withstanding and what it "chooses" to do. Further, what may seem to be tolerance in a limited experiment may well prove to be deleterious over a longer term, or adverse conditions which fish can live in might later cause premature death or inability to reproduce. The dependence of a physiological process on an environmental factor is rarely a straight-line relationship. Curves with a maximum in the region of preference may be more common than detected so far. Tolerance, preference and the reaction of fish to an environmental factor may change seasonally or with different phases in the life history. The seasonal change in the temperature preference of Arcto-Norwegian cod and their survival near freezing point, and the drop in reactiveness of spawning herring, all described in this section, are good examples of this.

The question of preference is a central problem when considering the spatial distribution of fish and the establishment of physical and chemical boundaries in the otherwise continuous sea. These boundaries cannot always be defined by a single limiting factor, but rather as an accumulation of several conditions, which may be outside the preference of fish but within their range of tolerance. Under such stress the fish might become more sensitive to a single adverse influence. The changes in activity of fish at boundaries of this sort are of the highest importance as, indeed, are changes of activity of fish as a result of temperature, food supply, light or internally-controlled rhythms unconnected with boundaries.

The discussion on the effect of the environment on reproduction showed that we are very poorly informed on what controls spawning time, fecundity and egg size. Some knowledge of these aspects is essential in the furtherance of population dynamics and studies in early survival rates and recruitment. The need for combined studies in the laboratory and at sea has also been stressed. Besides direct influences on the reproduction of fish of a given size and age, indirect influences of the environment, such as food supply and temperature affecting growth rate and possibly maturation, have to be considered.

Most of our fisheries are carried out in the photic zone of the sea where light may have an important influence on the distribution and migration of fish, as well as being essential for feeding, shoaling and spawning in some species and affecting the hormonal cycles. The interrelationship between migratory behaviour and maturation as controlled by the endocrine glands has been discussed in this section in connection with new information on maturing herring and Arctic cod. Apart from light intensity, the effect of transparency on visibility underwater is of far-reaching importance. Comparative measurements of light intensity and visibility made at the same time as biological observations are highly desirable. The help of physical oceanographers would be appreciated in providing overall synoptic charts of light measurements on the sea bed. From these charts biologists could assess whether certain behaviour patterns, particularly visually-controlled net avoidance would, or would not, take place on the various fishing grounds at stated times.

Fish are not only influenced by the environment; they themselves affect their own environment and that of other fish. This is especially evident in a shoal. Reports on possible oxygen lack within a shoal and the reaction of fish to moving patterns of the background show this. The immediate effects of competition and predation on the activity states and growth rates of fish have not been discussed adequately, but the possible loss in terms of fish weight due to a highly active or over-stimulated existence has been mentioned. The value of further investigations in this field is evident.

The convener's thanks are due to his rapporteur, Mr J.H.S. Blaxter, who prepared the notes for this summary.

SECTION G
The Effect of the Environment on the Process of Fishing

CONVENER: B.B. Parrish RAPPORTEUR: J.G. Harvey

Contributions submitted to this Section were as follows:

G-1 "A First Look at Some Wave and Wind Data from Trawlers" by J.A. Ewing and N. Hogben

G-2 "Relationship Between Drift-Ice, Atmospheric Circulation and Fishing Possibilities off South-East Greenland During the First Halves of the Years 1959-1963" by A. Meyer

G-3 "Changes in the Behaviour of Fish Due to Environment and Motivation and Their Influence on Fish" by H. Mohr

G-4 "Bottom Contour and Nature of Grounds and their Significance for Trawl Fishery" by I.K. Avilov

Although only four contributions were presented to this section of the symposium, their subject matter provided abundant evidence and examples of the importance of various physical and biological factors in their effects on the process of fishing. The factors covered included climate and sea-state relationships, sea-bed topography and structure and biological features of the exploited stocks. The discussions on each are summarised below.

A. Climatic Factors (Contributions G-2 and G-1)

1. Meyer's data in contribution G-2 prompted a lively discussion on the importance of investigations of the relation between the occurrence and distribution of ice and meteorological conditions, especially atmospheric pressure and wind, and of the urgent need for the extension of sea-state forecasting in the northern fishing areas.

In reply to a comment from Lee that 1963 had been a bad ice-year in the area covered by the Norwestlant survey, Meyer said that reports from German trawler captains showed it to be an average year; this indicated that ice conditions in the Greenland area can change very rapidly. Laevastu referred to earlier statements of the importance of meteorological data in relation to ice-drift in the Greenland area, and pointed out that this area is the birthplace of sudden atmospheric depressions, which could be predicted somewhat in advance, using heat exchange computations. Harvey also referred to Bjerknes' comparisons between the changes in atmospheric circulation and Smed's surface temperature anomalies for this area.

Uda described the icing-up of trawlers in the North Pacific and asked if this was a frequent occurrence in the East Greenland area. Meyer said that this was not so, but mentioned the loss of two trawlers off Labrador, from icing, in February 1960. Similar losses of trawlers off West Greenland were mentioned by Hansen. Kotthaus also referred to the loss of a trawler in the Angmagssalik district through "black-frost" icing. Lee described the occurrence of this rare phenomenon on the *Ernest Holt* at Bear Island in 1953.

Meyer associated the increase in surface temperature anomaly in the East Greenland area since the war with the movement of haddock into these waters in recent years, catches of up to 30 baskets per hour has been caught. Hansen stated that no similar increase in haddock had been observed in the West Greenland area..

2. Ewing announced that in addition to the investigation described in his contribution G-1, other work was being carried out in conjunction with the British Meteorological Office, involving the analysis of data collected over the last 10 yr from observers on British merchant ships, covering the main shipping routes over the world.

There was considerable discussion of the interpretation and validity of the relationship between wind speed and mean wave height in Fig. 3 of Ewing and Hogben's paper. It was agreed that a number of factors could affect it, *e.g.* wind direction and the length of time it had been blowing, season, proximity to land-masses, etc. Ewing said that the wind speed and wave height data were skipper's estimates based on the appearance of the sea surface, but he announced that a comparison is being made between estimated wave heights and measured values taken by ship-borne wave-recorders.

Lee pointed out that, in Fig. 4, the accuracy of the estimates of wave-length appeared to improve as the wave-length increased above 200 ft. Ewing agreed that this was probably because at these lengths, the observers could use the lengths of the vessels as a yardstick. Uda suggested that currents would have an effect on wave height,but Ewing said that in the areas from which these data had been obtained, the currents were almost certainly too small to have any significant effect.

Laevastu concluded the discussion by drawing attention to the usefulness of comparative studies of this type of wind and wave data collected from trawlers in different areas, especially in providing information on sea-state condition for use in hydrographic forecasting and in fishing vessel design.

B. Sea-bed Topography (Contribution G-4)

Following his presentation of Avilov's contribution, Edwards described work done by Emery on bottom sediments, bottom topography and the associated benthic fauna in the sea areas off the Atlantic coasts of North America from the Gulf of Maine to Florida.

In reply to a question from the Chairman regarding the available information in other countries on bottom topography and structure of the fishing areas in the North-West Atlantic, Templeman stated that the grounds off Labrador were very badly charted. Cameron described the activities of the Canadian hydrographic service in this area, but emphasised that at present these are concerned principally with depth contouring, rather than determining the detailed nature of the sea-bed structure. Magnusson drew attention to the need for improved bottom charts for the East Greenland waters and of the Reykjanes Ridge. This was supported by Kotthaus who stated that the German charts of East Greenland were in error, most features appearing about 10 miles too far to the east. Meyer drew attention to the difficulty of charting in this area, which was out of range of the recognised navigation systems.

In conclusion, the Chairman pointed to the obvious advantages of international collaboration in the preparation of detailed fishermen's charts in large sea-areas like the North-West Atlantic, and suggested that a much larger scale version of Fig. 3 of Avilov's paper would provide valuable information for countries fishing in this region.

C. Biological Factors (Contribution G-3)

3. The importance of the effects of behavioural and distributional features on the accessibility and vulnerability of exploited fish stocks, as outlined in Mohr's paper was emphasised by the Chairman, who instanced the marked effects of diurnal variations in vertical distribution and the differences in behaviour of fish to fishing gear under visual and non-visual conditions as notable examples. Meyer explained that pelagic trawling for cod in Greenland waters was now being investigated in Germany and some good catches had been obtained. However, owing to unpredictable irregularities in vertical distribution, there was a need for trawl which could be fished either on the bottom or in mid-water, according to the observed distribution of fish.

D. Conclusions

In summing up, the Chairman highlighted the following items of major importance, arising from the discussions:

(a) the importance of more extensive information and forecast services, giving sea-state conditions, and especially of the ice-limits for the northern fishing areas;

(b) the need for international collaboration in the preparation of accurate, large-scale fishermen's sea-bed charts for the North-West Atlantic and East-Greenland fishing areas;

(c) the need for further intensive studies of distributional and behavioural factors influencing fish capture, and for close collaborations between biologists and gear design and improvement projects.

SECTION H
Effects of Long-Term Trends

CONVENER: L.M. Lauzier RAPPORTEUR: T. Laevastu

Contributions submitted to this Section were as follows:

H-1 "Recent Changes in the Benthos of the West Spitsbergen Fishing Grounds" by R.W. Blacker

H-2 "Anomalies of Sea Temperature at Station 27 off Cape Spear and of Air Temperature at Torbay-St. John's" by W. Templeman

H-3 "Long-Term Temperature Variations in the Scotian Shelf Area" by L.M. Lauzier

H-4 "Effect of Long-Term Temperature Trends on Occurrence of Cod at West Greenland" by P.M. Hansen and F. Hermann

H-5 "Variation of the Temperature of the Surface Waters in Areas of the Northern North Atlantic" by J. Smed

H-6 "On Long-Term Variability of Oceanographic Conditions and Stocks of Cod Observed in the Areas of West Greenland, Labrador and Newfoundland" by A.A. Elizarov

H-7 "Variation in the Recruitment of Cod (*Gadus morhua* L.) in Southern ICNAF Waters as Related to Environmental Changes" by W.R. Martin and A.C. Kohler

H-8 "Changes in the Hydrography Observed Along the East Coast of the United States" by D.F. Bumpus and Joseph Chase

H-9 "Inferential Biological Effects of Long-Term Hydrographical Trends Deduced from Investigations in the Faroe-Shetland Channel" by J.B. Tait and J.H.A. Martin

This is the second time that long-term hydrographic changes and their effects have been discussed by ICNAF scientists. The first time was during the 1953 Annual Meeting. During both symposia, the main factor considered for bringing long-term changes in evidence was water temperature. Changes in water temperature have a direct effect on the biological processes, on the physiological functions and on the distribution of animals. However, changes in temperature may be the result of changes in the circulation or of advection. Temperature changes may indicate a change in the composition of water masses including its biological and chemical (nutrient) contents - a change in productivity. Temperature changes may be, in many cases, "coincidental" with biological changes within the same body of water, both being the effects of a common cause.

The papers and discussions at this session were concerned with the evidence for, and causes and effects of long-term trends. Related subjects were discussed but two aspects were emphasized: first, the possible causative mechanism of long-term trends and the variations of these trends from western to eastern sectors of the North Atlantic; second, the difficulties in measuring the changes in the fisheries that may be attributed to long-term trends. The possible effects of long-term trends on distribution of fishery resources were summarized by Dr A.V. Tåning in a contribution presented to the first symposium in 1953. These effects pertained mostly to the northern areas. At the time Dr Tåning considered these effects, most scientists had in mind the recent warming or amelioration of climate. There are now instances of reversal of trends in some areas. Will the possible effects of recent cooling trends be the reverse of those considered by Dr Tåning? It is difficult to give an answer at present; we probably will find that the physical factors have only a secondary effect. Can we wait for another 10 yr or so for an answer?

May I make for this section on the effects of long-term trends the following recommendation:

considering that changes have taken place in the distribution of fish and in the yield of fisheries in the North Atlantic and that these changes may be attributed to long-term trends or changes in the environment, it is recommended that the observations of environmental factors at coastal stations and offshore points, including weather ships, be continued and encouraged with a dual objective in mind: first, to monitor the climatic conditions; second, to find ways and means for prediction of long-term trends which might infer readjustment of some of the fisheries.

I would like to thank all the contributors for their contributions and Dr T. Laevastu for his assistance, as rapporteur, and his help in the preparation of this report.

SECTION I
Forecasting Environmental Conditions

CONVENER: D.F. Bumpus RAPPORTEUR: R.L. Edwards

Contributions submitted to this Section were as follows:

I-1 "Foreshadowing of Surface Temperatures at St. Andrews, N.B." by L.M. Lauzier

I-2 "Factors Affecting Water Temperature in the Seas North of Norway" by J.G. Harvey

I-3 "Is Oceanographic Forecasting (Hydrosis) Feasible for Fisheries?" by T. Laevastu

I-4 "Daily Heat Exchange in the North Pacific; its Effects on the Ocean and its Relations to Weather" by T. Laevastu

I-5 "Notes on the Problem of Predicting Near Surface Temperature Gradients in the Open Ocean" by C. O'D. Iselin

I-6 "Forecasting Environmental Conditions in the Faroe-Shetland Channel Region" by J.B. Tait

I-7 "The Possibility of Oceanographical Forecasts in North-western European Waters and Their Significance for Fisheries" by J. Eggvin

I-8 "Oceanographic Predictions" by J.J. Schule

The contributions presented in this section ranged in subject matter from a general discussion of the feasibility and problems of forecasting (I-7, I-6, I-8, I-3) to demonstrations of attempts to relate changes to various factors such as meteorological conditions (I-5, I-4, I-1, I-2).

Several contributions contained both suggestions and evidence that many changes occur weeks and even months in advance of local phenomena, so that some forecasting can already be done even today. In this regard, Eggvin (I-7) notes the significant negative air temperature anomalies of 1963, the relative lack of clouds and other related changes that lead Norwegian scientists to anticipate that the deep water of the Norwegian Channel would stay cold for many months longer than usual with significant effects on the fisheries. This condition persisted during the late months of 1963 and even into January 1964. Tait (I-6) makes comparable observations concerning variations in salinity in particular, which cycles over longer periods of time. He states that "the variation is gradual, which lends to this particular phenomenon the aspect of climatic change in the sea, and the fact that it is gradual anticipates the possibility of forecasting it, provided observations in the region are sufficiently regular and systematic".

Schule (I-8) presented a thorough review of the problem and scope of operations involved in oceanographic prediction. He discussed four approaches to the problem, namely: 1) a system that concerned itself primarily with factors characterized by continuity or persistence beyond normal day to day changes; 2) the point prediction method, based on, for example a bathythermograph record, modified for a period of time by other predictable or observable factors such as wind, air temperature and cloudiness; 3) the dynamic approach, based on extensive model studies that could ultimately allow for minimum, although admittedly critical imput, to predict change over a wide area. High speed computer capability is mandatory, plus a considerably better general understanding of the hydrographic regions than presently exists for most areas; 4) the statistical approach, or *post hoc* approach based on what are today relevant and seemingly causal factors.

With regard to the fourth approach discussed by Schule, two contributions are of direct interest, namely I-1, Lauzier and I-2, Harvey. Lauzier examined surface temperature records for

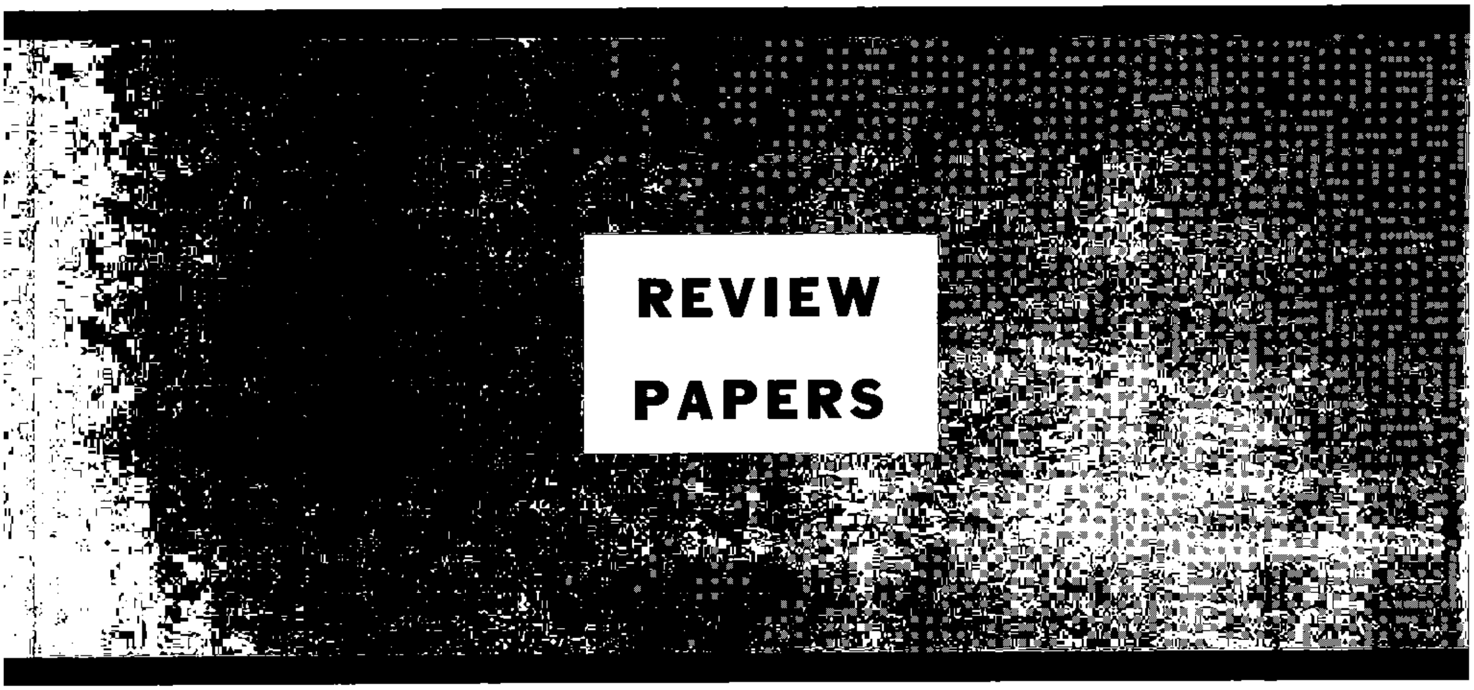
St. Andrews and other North American localities in detail to determine the degree of predictability that might be achieved without recourse to other data. He showed, for example, that one can predict annual means with a fair level of significance given previous means and the minimum temperature for the year under consideration. Harvey concerned himself more with factors having an apparent or relevant causal connection, such as wind velocity, cloudiness and air temperatures. Highly significant correlations were obtained even though horizontal advection appeared to be the dominant influence in change.

Professor Laevastu pointed out that many events are predictable on the basis of meteorological conditions.

In the discussion that followed, two aspects of prediction were touched upon - the pragmatic aspect of keeping the fishermen informed and that bearing on academic or research problems. In both the presentations and discussions it was apparent that considerable promise lies in the understanding of the relation between atmospheric and oceanographic phenomena.

In addition to regular systematic temperature and salinity measurements throughout the water column in strategic places, an improved field of current measurements and a monitoring of the changes in the location of oceanographic fronts would contribute toward predictive capabilities. Support in the way of communicative, analysis and forecast procedures need to be considered to make efficient use of the data collection. The Canadian and U.S. Navies already have a data collecting net, analysis sections, and radio facsimile broadcasts of certain aspects of the ocean environment. Cooperation between the fisheries oceanographic programs and the naval predictive services would enhance the interests of both groups.

REVIEW PAPERS



REVIEW PAPERS

NEW HYDROGRAPHICAL ASPECTS OF THE NORTHWEST ATLANTIC

By

Günter Dietrich[1]

INTRODUCTION

The ICNAF Committee, preparing the meeting in Rome, January 1964, asked me to give a general review of the hydrographic features of the Northwest Atlantic. I was eager to accept this request, but I must confess that I am in a poor position. On the one hand, I can refer to two excellent and comprehensive recent reviews by research workers who have had much more contact with this region than I have had. These are the reviews by Dunbar (1951) on eastern Arctic waters and by Hachey *et al.* (1954) on the waters of the ICNAF Convention Area. On the other hand, during 1963, the Northwest Atlantic was the subject of a great systematic international co-operation in the so-called NORWESTLANT Program, when a fleet of research ships made three surveys of the area. The results are still being prepared by our colleagues who participated in these cruises. This means that all basic knowledge to 1953 is at hand in the two publications mentioned and that all the new observations of the joint cruises in 1963 are not yet available. Thus my reason for saying I am in a poor position.

Because I do not want to bore you with known facts, I will refer to the ten years between 1953 and 1962. In 1958, in the middle of this period, the International Geophysical Year (IGY) sponsored a special oceanographic program called The Polar Front Survey in the North Atlantic. This program is outstanding in various ways:

1. It covered the whole North Atlantic from the line Newfoundland - Azores - Gibraltar in the south to the ice edge off Greenland and the Polar Sea in the north.
2. It covered the area twice, first in the winter and second in the summer of 1958, thus giving an insight into the annual variations in the water.
3. A total of 25 research ships of 11 nations participated in the work in a quasi-synoptic way in order to avoid non-stationary conditions as far as possible.

The map of oceanographic stations (Fig. 1) shows the area investigated in the summer of 1958. The same cruise lines were followed six months earlier in the winter of 1958. In all, about 2,500 hydrographic stations were made. Some results, based on the physical, chemical and biological observations of the single ships have already been published in about 100 papers. (Partly as special volumes in Deutsche Hydrographische Zeitschrift, edited by Bohnecke and Buckmann, 1959 and Rapports et Procès-Verbaux of the ICES, Vol. 149, 1961.) All hydrographical material is being worked up by an ICES working group of Mr A. Lee, Dr J. Eggvin, Mr M.V. Fedosov and myself. In the following I shall refer mainly to the first results of this investigation.

BOTTOM TOPOGRAPHY

The Northwest Atlantic Ocean is like a great bight of the Atlantic Ocean proper, with a relatively simple arrangement of the main forms of the ocean bottom. This is best shown in a new physiographic map by Ulrich (1963) (Fig. 2) which is an extension of a map published by Heezen *et al.* (1959) for the northern North Atlantic Ocean. The terminology is the same as used by Heezen.

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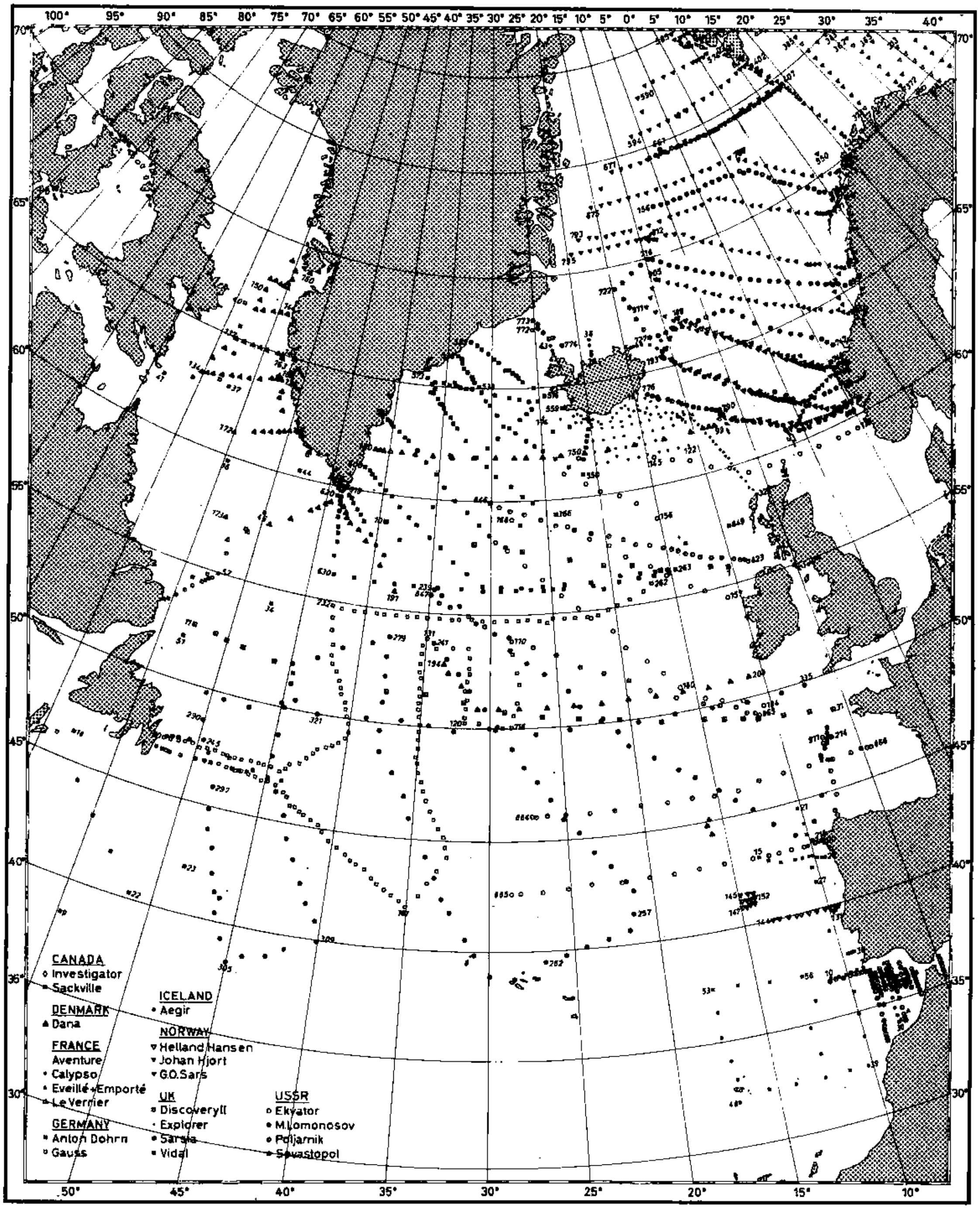

Fig. 1. Oceanic Polar Front Survey in the IGY 1958. Oceanographic stations in the northern North Atlantic (outside adjacent seas); July-December 1958, mainly late summer. Repetition of the cruises made in this program in late winter 1958.

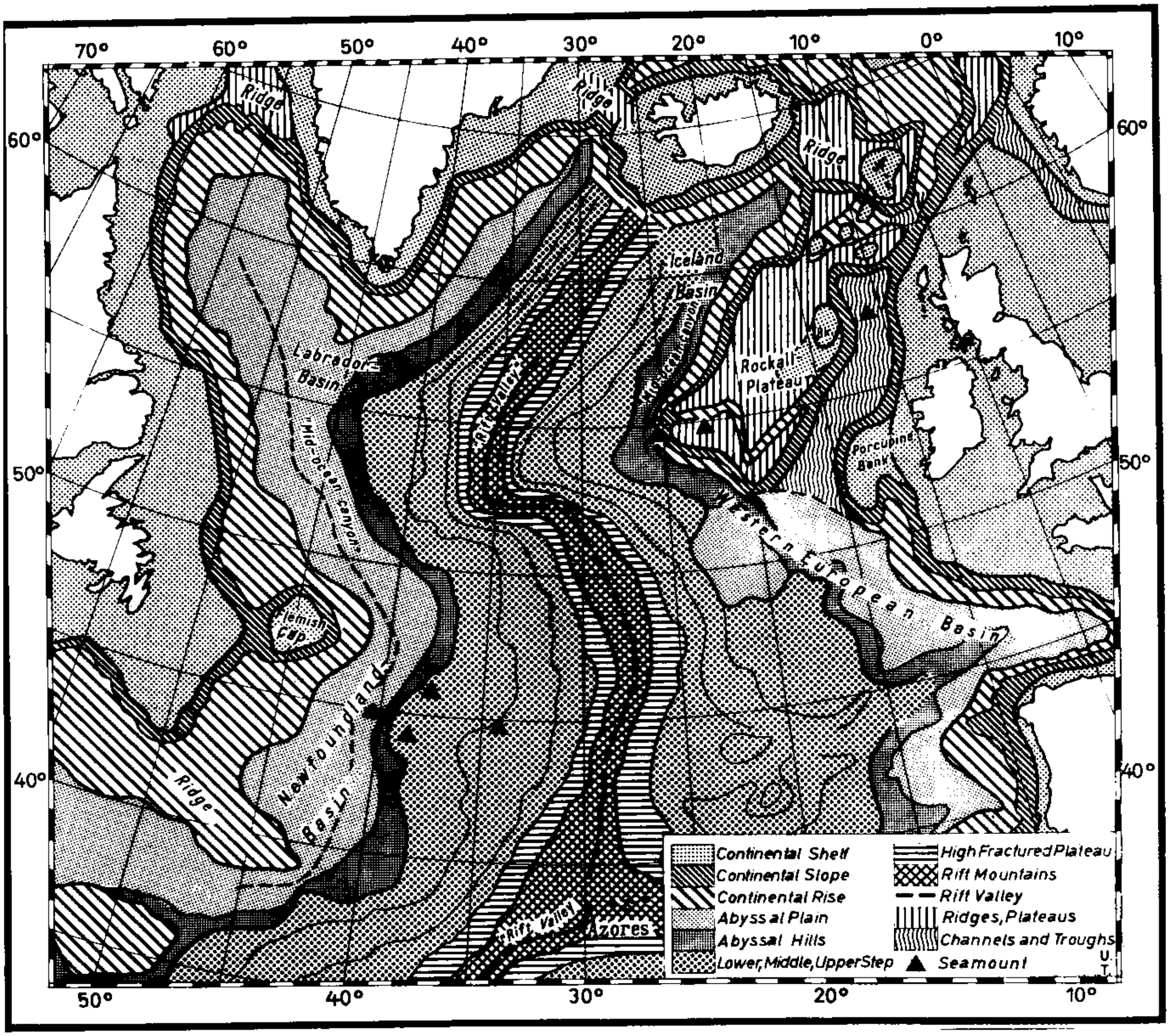

Fig. 2. Bottom morphology of the northern North Atlantic (After Ulrich, 1963).

The Mid-Atlantic Ridge partly separates the deep Northwest Atlantic Ocean from the deep Northeast Atlantic Ocean. It is distinguished by the deep rift valley which begins in 57°N and turns with the ridge to the east in about 52°N and to the south in about 30°W. These bottom features are of great importance for the water circulation, especially for the main branches of the Gulf Stream, as will be demonstrated later. The Mid-Oceanic Ridge is flanked by a high fractured plateau, further by the upper, middle and lower step of this fractured plateau. It follows the abyssal hills and the flat abyssal plains which cover the central part of the Labrador and Irminger Seas. These plains are distinguished by a mid-ocean canyon in the Labrador Sea, but not in the Irminger Sea as maintained by Heezen. The abyssal plains pass over to the continental rises, indicated by the wide hatched areas. These are surrounded by the steep continental slope and finally follow the continental shelf, differing greatly in their width. The shelf is narrow around southern Greenland, but broadens along the coasts of Labrador and Newfoundland. Without entering into details I wish to illustrate the nature of the morphological provinces with some examples. Figure 3 shows the echo sounding profiles made from *Anton Dohrn* during the IGY 1958. The area of sections I to III has no rift valley in the Mid-Atlantic Ridge. It follows the different steps of the fractured zone, the abyssal hills, the abyssal plains, the continental rise and the continental slope.

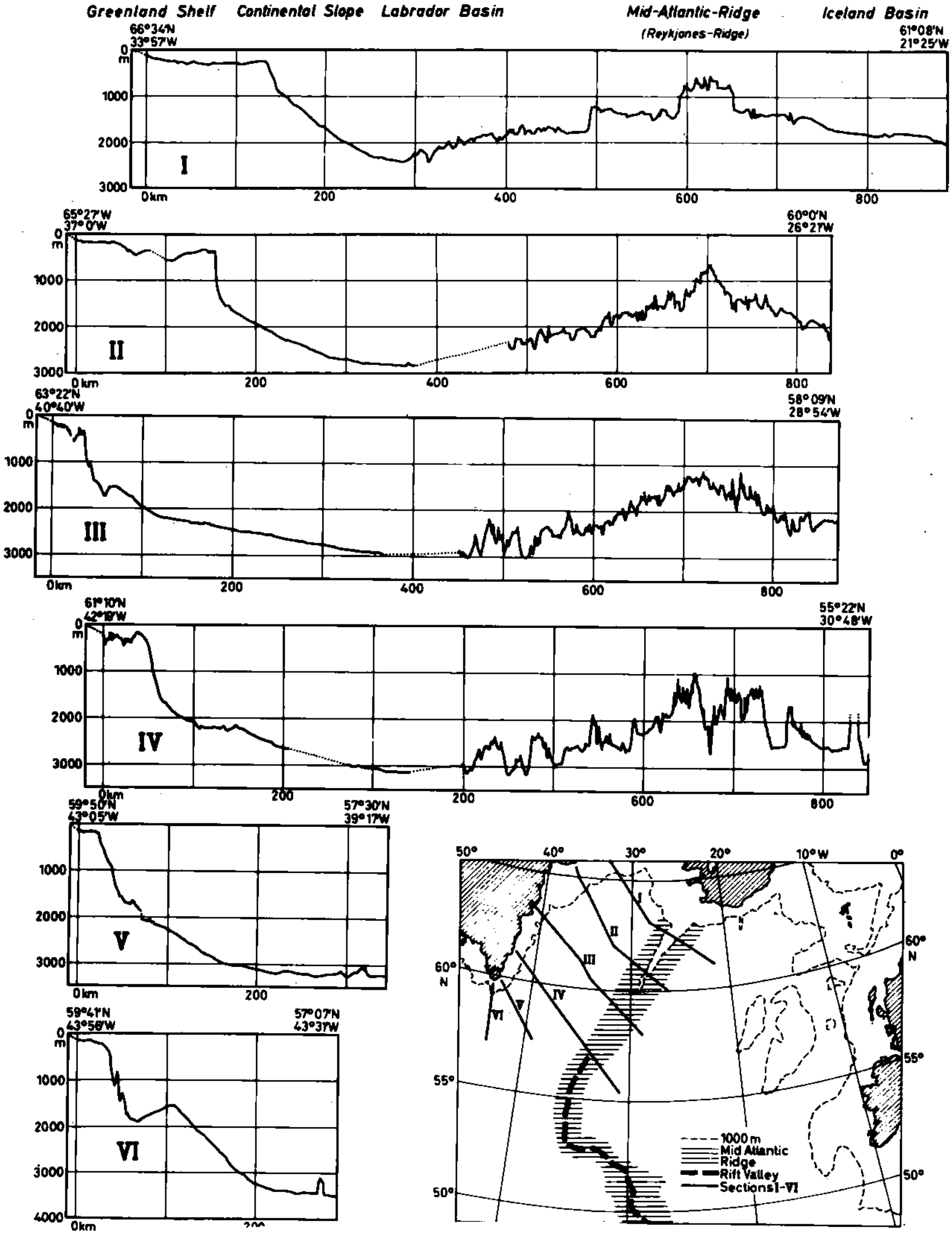

Fig. 3. Six bottom profiles normal to the East Greenlandic slope made by *Anton Dohrn* late summer 1958 (After Ulrich, 1962) (x 50).

The main point of discussion at this symposium will be the environment of the commercial fish. The main interest, therefore, is directed not to the deep sea, but to the shelf areas. These shelves are distinguished by special features which have become of great interest for the fisheries in the Northwest Atlantic Ocean during past years. In the well-known profile of the shelf in the world ocean, the water becomes deeper and deeper as we move away from the continental coast. Suddenly,

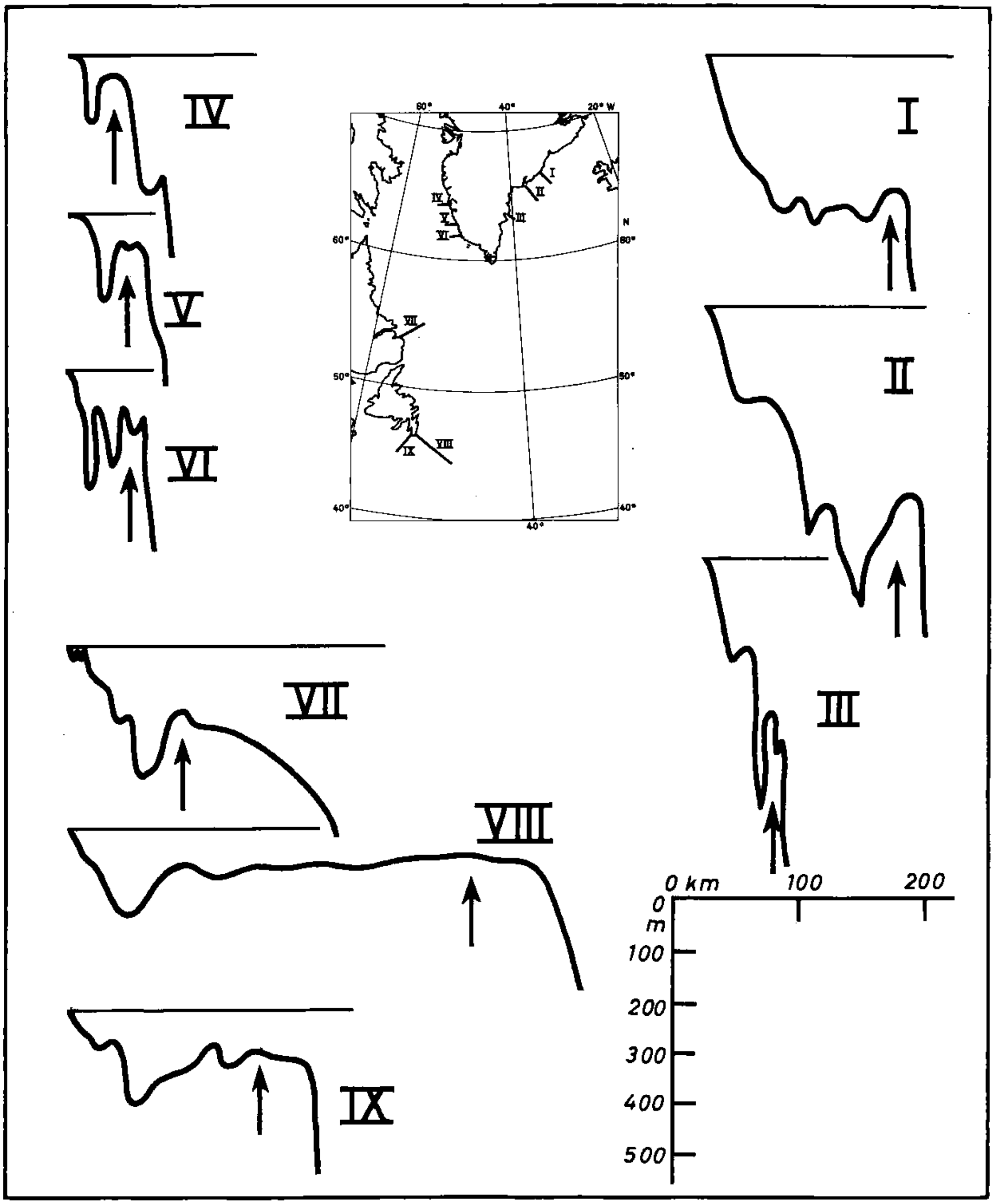

Fig. 4. Examples of bottom profiles across the Northwest Atlantic shelf. (Arrow indicates the sill of the shelf (magnification of profiles 400 times).

on the shelf edge in about 200 m depth, the steep continental slope goes down to the deep sea. This is the rule in the oceans, but not so in the Northwest Atlantic. Here one finds a small rise close to the shelf edge. This rise is well-marked even in the small scale profiles. It becomes more distinct when a larger scale is used and also when examples are taken from other parts of the Northwest Atlantic shelf. This special feature is illustrated in Fig. 4. It is an exception if one of the bottom profiles is without such a shelf rise. A topographic map may show this shelf rise more convincingly than the single profiles. Two examples of well-surveyed areas are the East Greenland shelf (Dietrich, 1957*a*) and the East Labrador shelf (Litvin and Rvachev, 1962). In the first example (Fig. 5) the waters over the shelf rise are 50 to 100 m shallower than the neighbouring waters nearer to the coast. The crest of the shelf rise is indicated by the broken line. Even the prolongations of the East Greenland fjords, crossing the shelf are closed by a rise against the deep sea.

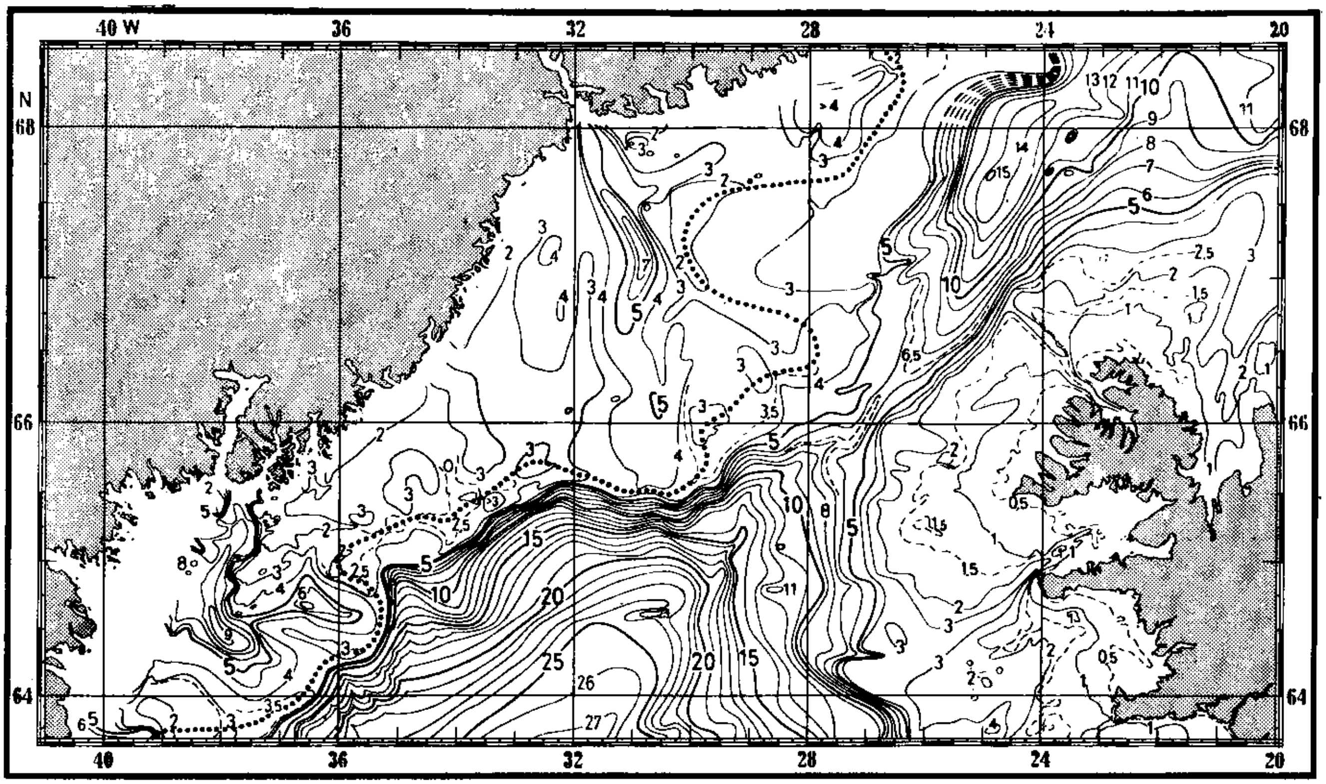

Fig. 5. Topographic map off East Greenland (depths in hectometer) and the crest of the shelf rise (dotted line) (After Dietrich, 1957*a*).

The second example (Fig. 6) off East Labrador shows principally the same features, namely a sill running along the shelf edge and closing also the deep channels crossing the shelf against the deep sea.

The surprising fact, that the shelf has a distinct rise just near the edge and is shallower there than nearer to the coast, must have a special cause. These rises are obviously terminal moraines of the pleistocene glaciers of Greenland and Labrador. Having established the shelf sill as a fact in many parts of the Northwest Atlantic, it is not difficult to imagine its importance for the near bottom water on the shelf coastwards of the sill. Before considering these facts, let us review, generally, the hydrographic conditions based on the IGY work in 1958.

LAYERING AND CURRENTS

The IGY work was known as the Polar Front Survey. How is this Polar Front defined in North

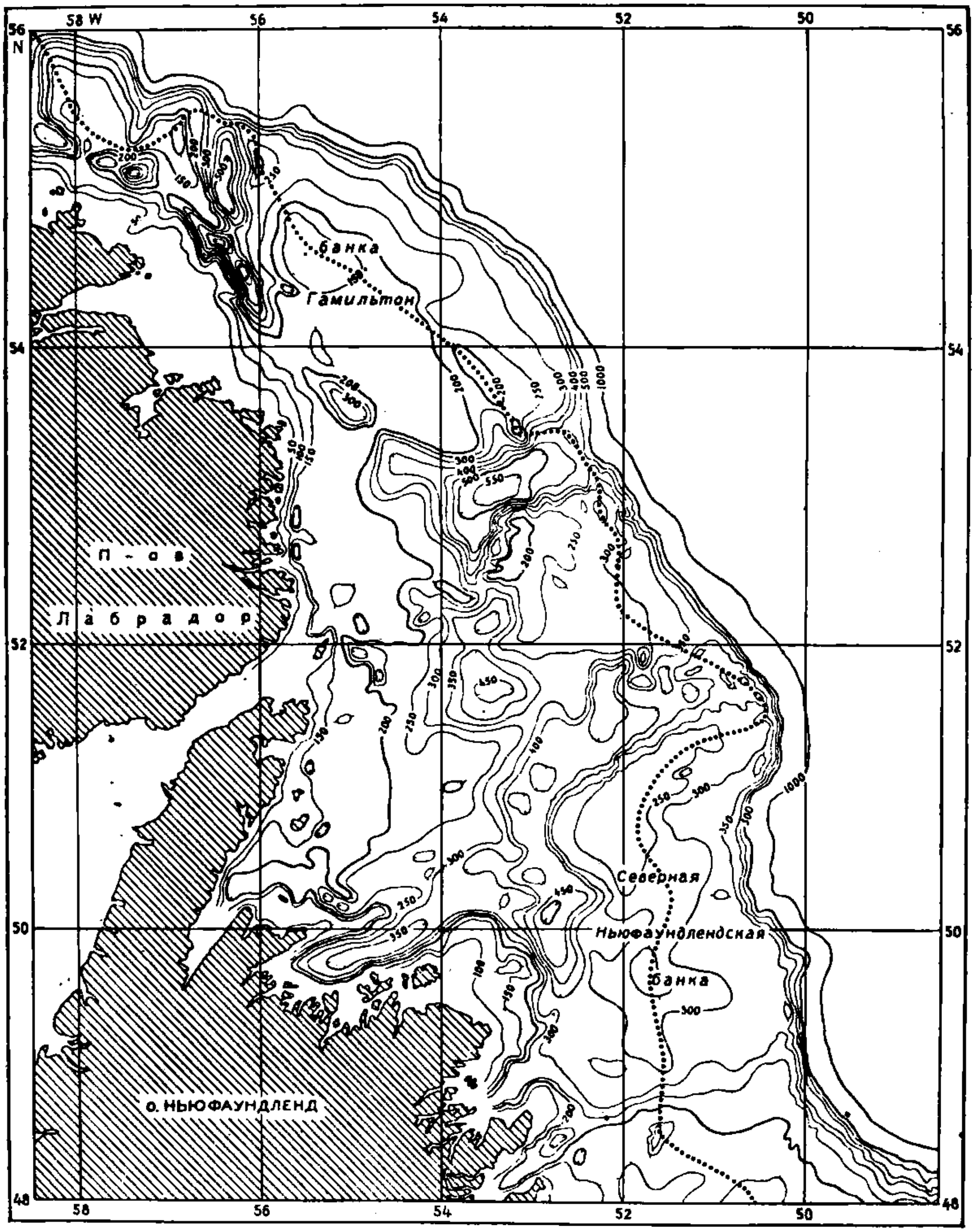

Fig. 6. Topographic map off East Labrador and the crest of the shelf rise (dotted line) (After Litvin and Rvachev, 1962).

Atlantic waters? No long explanation is needed when one looks on the maps showing the distribution of the two most important hydrographic factors - temperature and salinity. These maps are part of the ICES Atlas which is in preparation and which shows the distribution of temperature, salinity, oxygen and density at several levels during the winter and summer of 1958.

Let us consider, for example, the temperature distribution at 200 m depth (Fig. 7). No personal interpretation of the distribution is necessary because the stations are in a close net (Fig.1). Figure 7 shows that the cold and warm water lie side by side. The thermal front from Cape Hatteras to the Grand Banks is well known as the Gulf Stream. It extends to the north along the Flemish Cap and to the east to a point in 30°W and 52°N. This is the point shown on the physiographic map (Fig.2) where the Mid-Oceanic Ridge changes direction. This area is known for its very complicated topography, with deep depressions and high peaks. One can recognize a second thermal front in the Norwegian Sea, along East Greenland, Baffin Island and Labrador. Comparing this map with Fig. 8 which shows the summer distribution of salinity at 200 m depth, the thermal front appears as a haline front which also weakens remarkably over the Mid-Atlantic Ridge. The definition of the Oceanic Polar Front is now obvious. It is the boundary between cold, low haline, subpolar water and warm, high haline, subtropical water. As the Polar Front also separates waters with different oxygen and nutrient content, it is one of the most important and singular oceanographic features in the North Atlantic.

As mentioned previously, two surveys of the northern North Atlantic were made during the IGY. Thus one can compare the situations in the winter and the summer of 1958. Figure 9 shows the temperature distribution at 200 m depth in the winter of 1958. The thermic front is apparent with the 10° isotherm as its centre. Comparing the geographic positions of the fronts in IGY surveys in both winter and summer of 1958 (Fig. 10), the displacement of the front is evident. One can distinguish between the main front in the open Atlantic Ocean and the secondary fronts in the Norwegian and Greenland seas. The fronts in winter and summer show great horizontal meanders, but in different positions. In some places the winter and summer fronts cross each other. It is difficult to decide whether these crossings happen accidentally or regularly. However, it seems that there are two places which are distinguishable by bottom features; one being east of Flemish Cap and the other in 52°N, 30°W on the Mid-Atlantic Ridge. The front, meaning the main branch of the Gulf Stream, looks like a ribbon hanging from these two fixed points and swinging between with great horizontal displacement. The strong current splits east of the Mid-Atlantic Ridge where the weak and broad water movements in the Portugal Current, in the Northeast Atlantic Current and in the Irminger Current are found.

The horizontal displacement of the front between Flemish Cap and the Mid-Atlantic Ridge must have a great influence on the circulation system in the Northwest Atlantic. The water in the bay must react when the water in the mouth shows great displacements. However nothing is known about these relationships. Only the very first step has been taken to show the nature of the strong current system in the open Northwest Atlantic. It will be a task for the future to improve these statements and to investigate this current system which must have great influence on ocean and atmosphere not only in this area, but also in the Northeast Atlantic Ocean. I should be very happy if the audience picks up these new facts about the Northwest Atlantic Ocean and if the institutes find a way of coordinating further international investigations of this part of the ocean.

Since this symposium concerns the environment for life in the sea, we will have only a short look in the deep sea. I have chosen the distribution of salinity at 1,000 m depth as observed in the IGY 1958 (Fig. 11). Three facts may be pointed out:

1. There were no remarkable differences in the salinity winter and summer of 1958 at 1,000 m. Therefore, all observations from the IGY cruises were used in preparing Fig. 11.

2. The distinct salinity and temperature fronts have vanished at a depth of 1,000 m.

3. The influence of high haline water from the Mediterranean is evident and can be followed on four main courses, one leading to the Azores, another to the west-north-west, a third to north-west and a fourth along the European continental slope moving around the northern North Atlantic, crossing the Mid-Atlantic Ridge and entering the Labrador Sea. A central low salinity patch characterizes the Northwest Atlantic Ocean. It has the lowest salinity in the whole open northern Atlantic at this level.

The current velocity at 1,000 m is not known and can only be estimated. It should, however, be small compared with that in the near-surface layers. Therefore, the dynamic topography of the sea

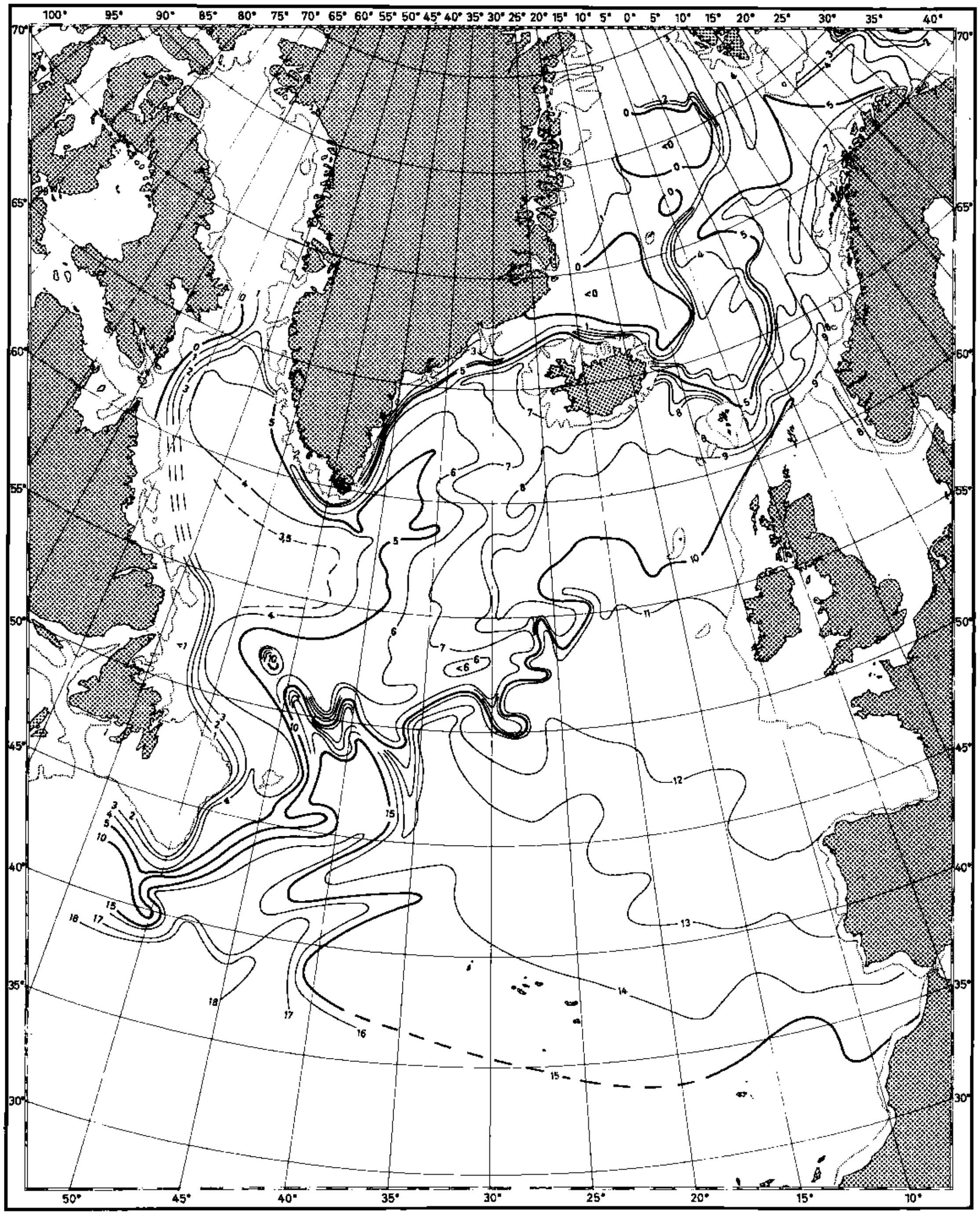

Fig. 7. Temperature in the northern North Atlantic in 200 m depth in late summer 1958 (Oceanic Polar Front Survey in the IGY).

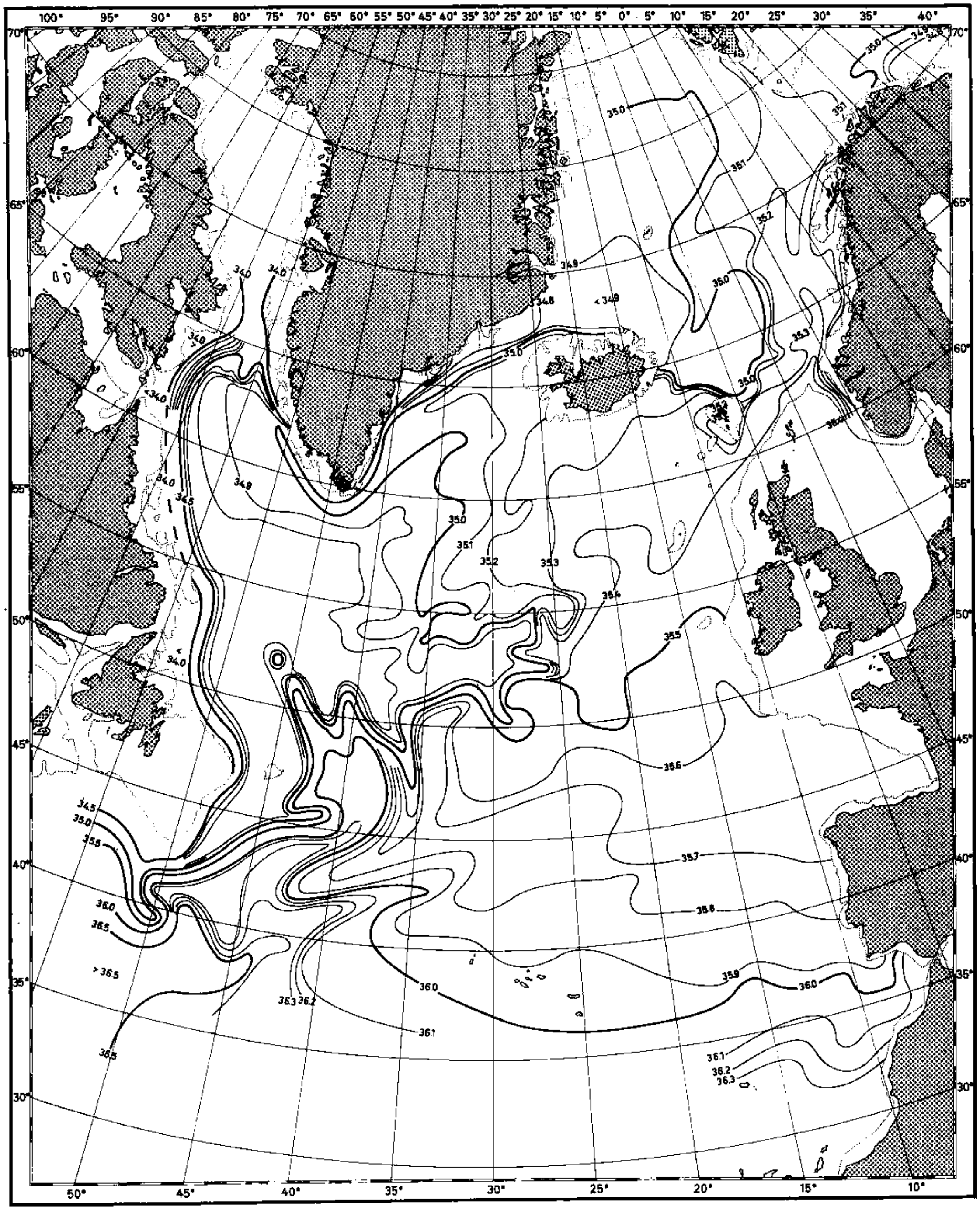

Fig. 8. Salinity in the northern North Atlantic at 200 m depth in late summer 1958 (Oceanic Polar Front Survey in the IGY).

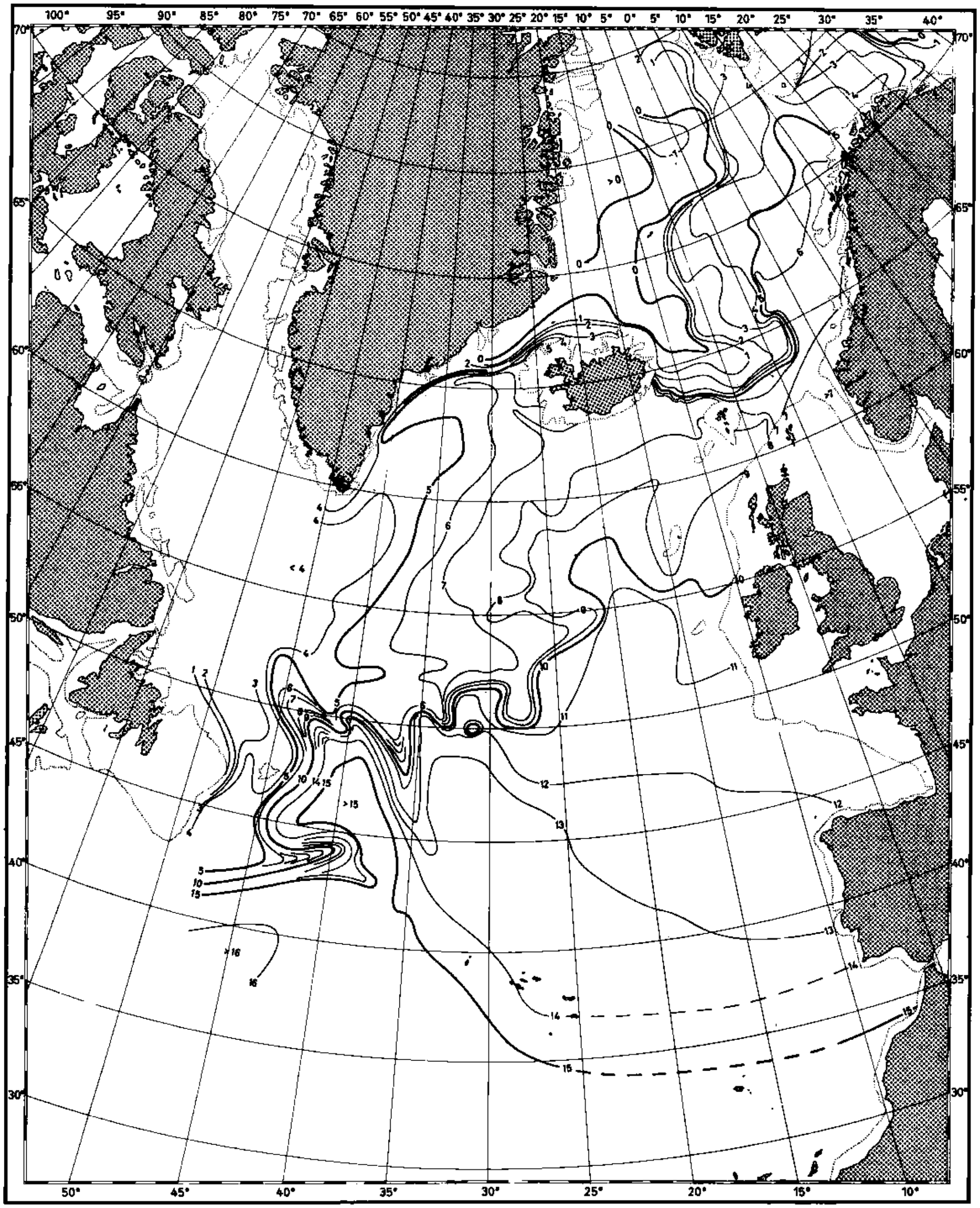

Fig. 9. Temperature in the northern North Atlantic at 200 m depth in late winter 1958 (Oceanic Polar Front Survey in the IGY).

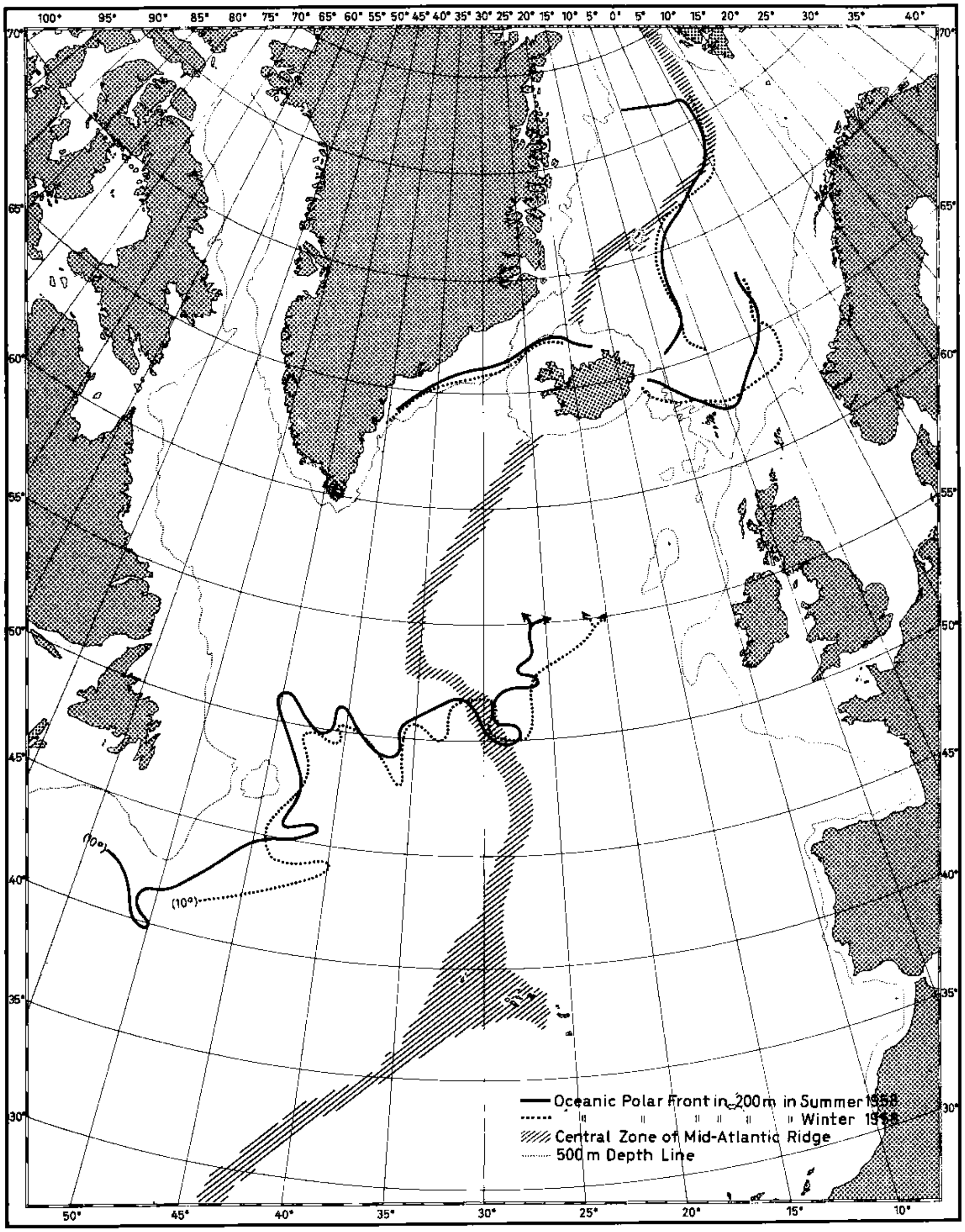

Fig. 10. The Oceanic Polar Front in the northern North Atlantic at 200 m depth in late winter and late summer 1958.

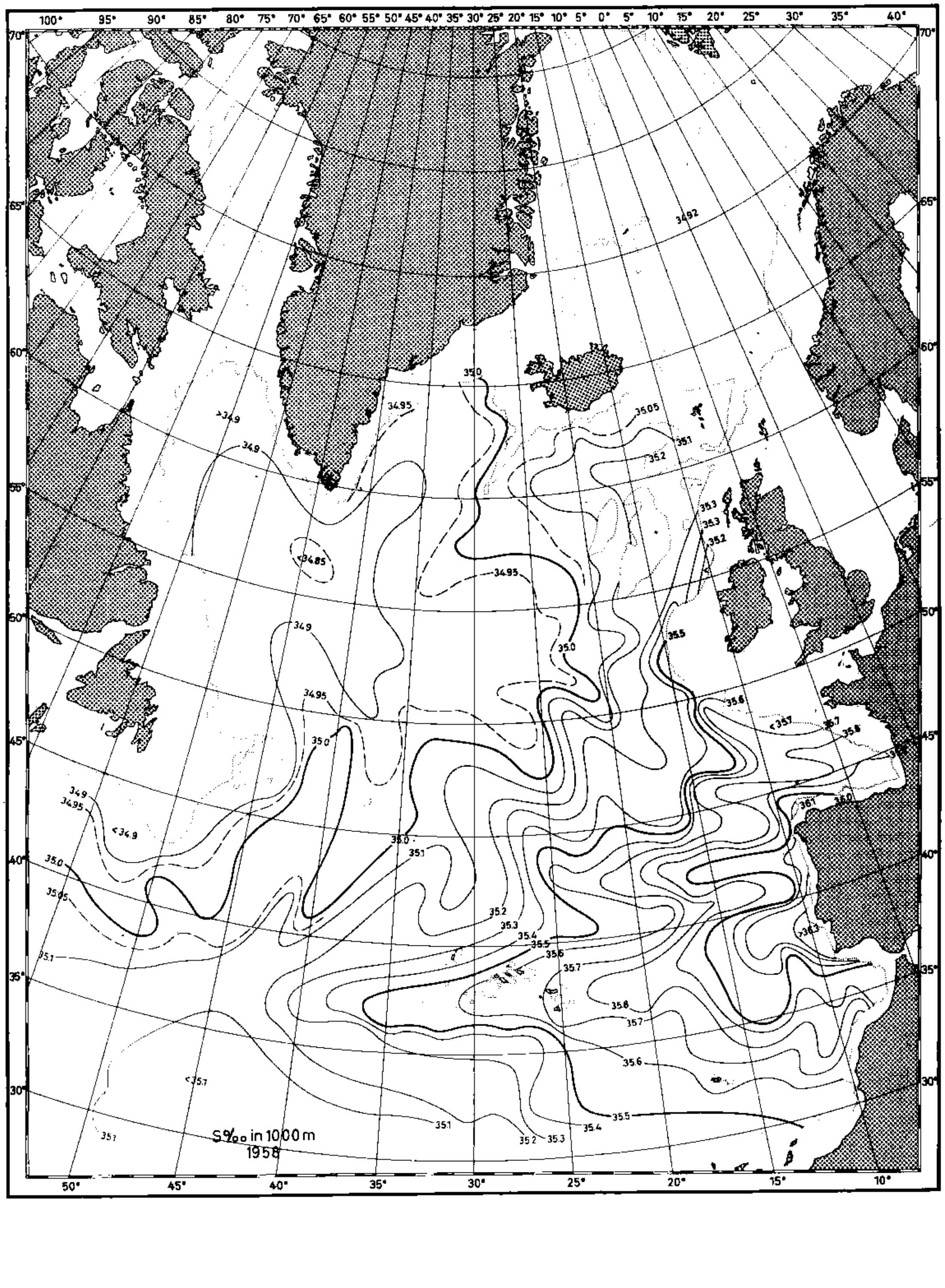

Fig. 11. Salinity distribution (in o/oo) in the northern North Atlantic at 1,000 m depth based on all IGY observations 1958.

surface over the 1,000 decibar surface gives an approximate review of the system of the geostrophic currents on the surface, in this case, for the summer of 1958. In Fig. 12 the Oceanic Polar Front appears again, this time as a jetstream, a very narrow ribbon, but with high velocities. It parts into a broad and a weak current system at about 52°N, 30°W, the distinguished point on the Mid-Atlantic Ridge that we know from the bottom topography and the Polar Front. Summarizing the different facts, one sees that the Gulf Stream system crosses the Northwest Atlantic Ocean as a meandering jetstream and separates the subtropic anticyclonic movement from the subpolar cyclonic movement. These two big cells determine the oceanic conditions of the northern North Atlantic Ocean.

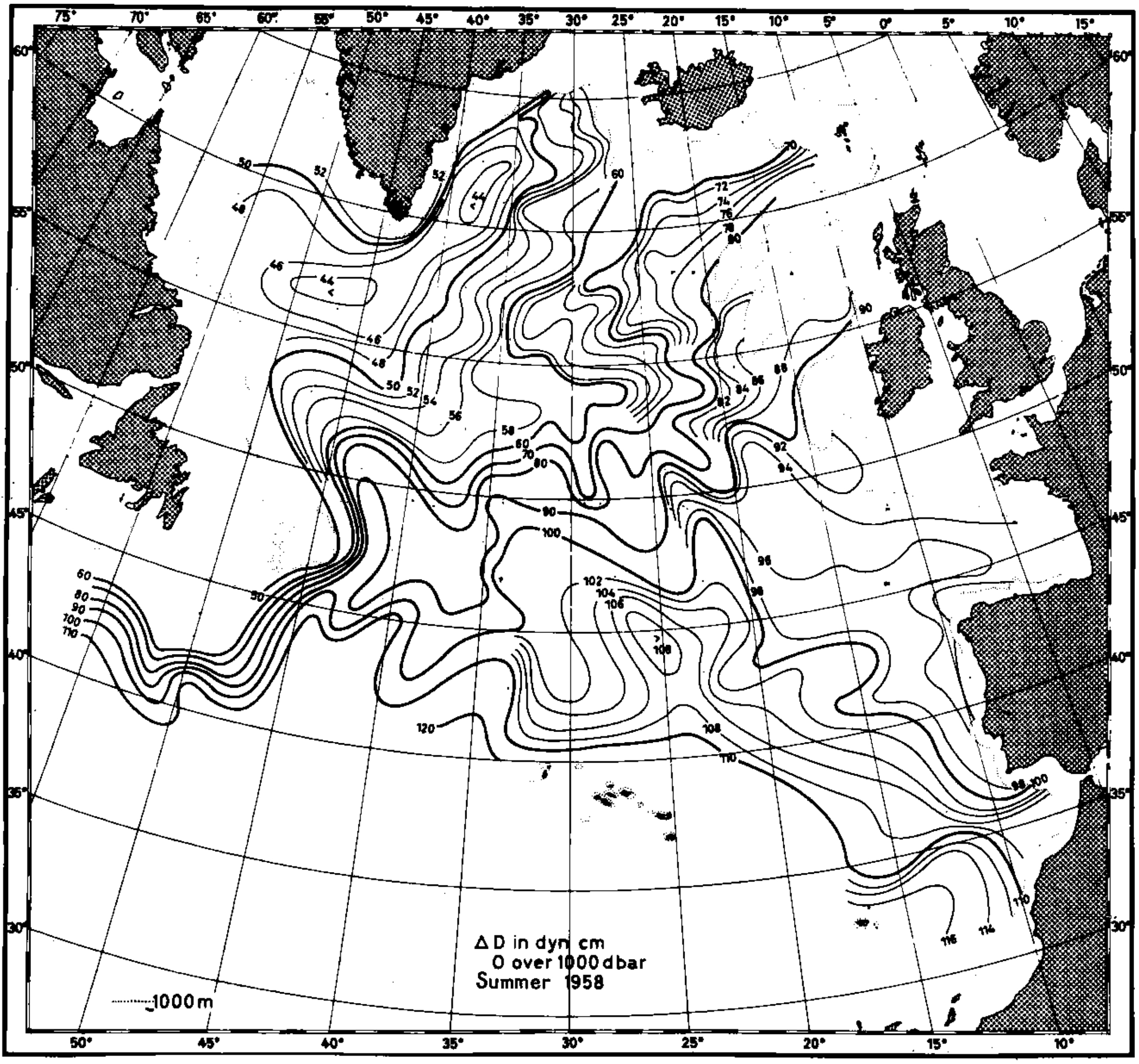

Fig. 12. Dynamical topography of the sea surface (0 over 1,000 decibar) in the northern North Atlantic in late summer 1958.

The general consequences of the vertical component of the water movement are known. Cyclonic movements in the ocean and atmosphere on the rotating earth are combined with upwelling in the centre of the cyclone, while anticyclonic movements are combined with downwelling in the centre of the anticyclone. This means that, in a cyclonic movement, cold, deep water, rich in nutrients is brought up near the surface. This can be seen in Fig. 13 which shows a section from Greenland to the Azores and represents the temperature and the oxygen distribution in the early spring of 1958. Note that the vertical scale is reduced four times at depths below 1,000 m. When in the

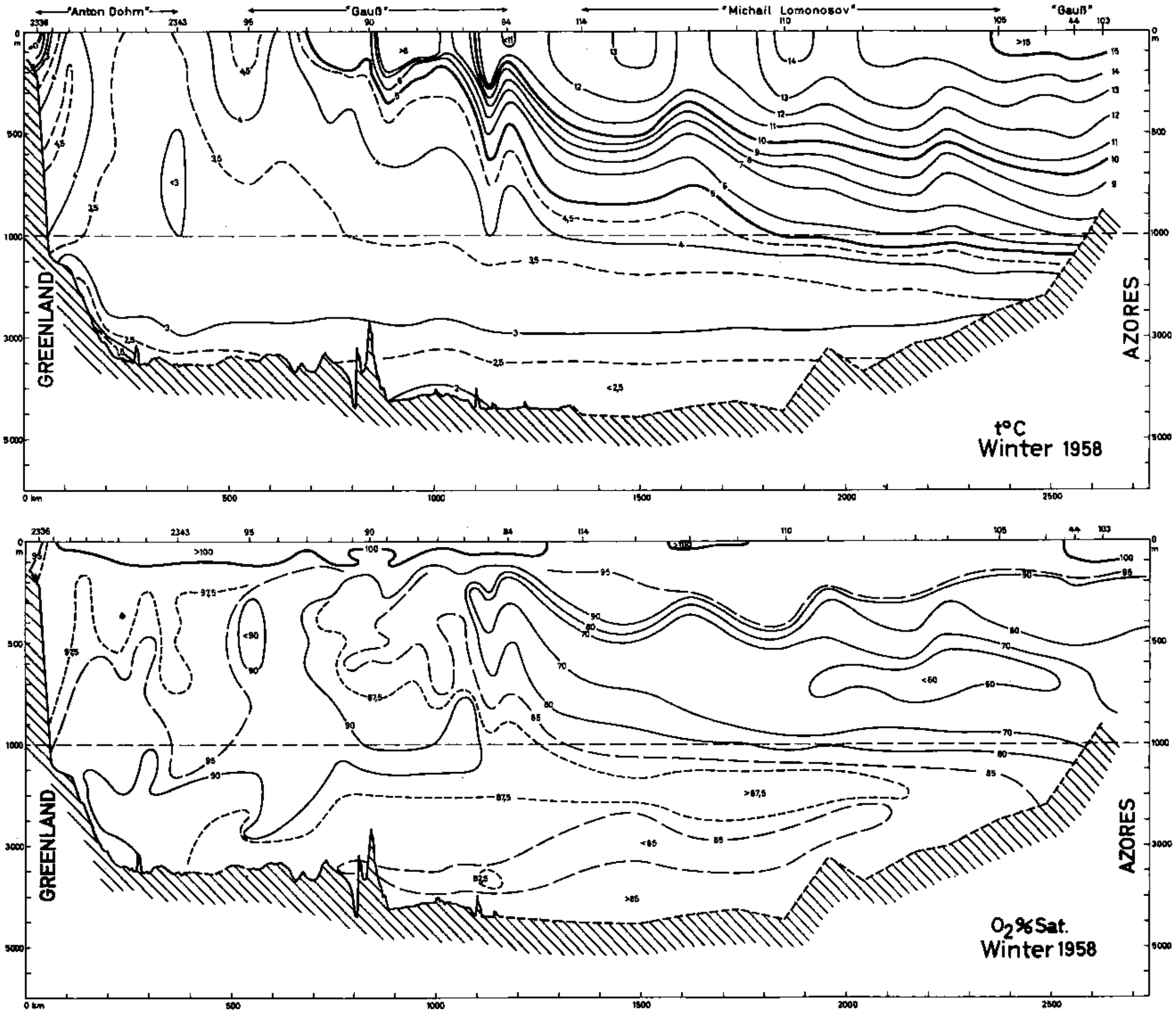

Fig. 13. Temperature and oxygen (in % of saturation) distribution on a section, South Greenland (Cape Farewell) to Azores, in late winter 1958.

centre of the cyclone, *i.e.* in the central Labrador Sea, the surface water cools in winter and a deep-reaching vertical convection starts. The water is nearly homothermal and the oxygen-rich surface water reaches the deep layers. The vertical renewal goes down to 3,000 m making the Labrador Sea one of the best aerated areas in the world oceans and the most effective source for the deep water circulation of the whole Atlantic Ocean. These cold water masses with high oxygen content can be traced through the whole Atlantic southward to the Antarctic waters. The Atlantic deep water breathes like a pair of lungs, but the frequency of breathing is small. It happens only once each year in winter, when the thermocline has vanished. In the North Atlantic Ocean proper this happens only in the Labrador Sea. It is mouth and air tube for oxygen for the deep Atlantic Ocean. Thus, the Northwest Atlantic, this rough, unpopular, part of the Ocean, holds a key position in the deep water circulation.

The convection processes in the Labrador Sea which are of great importance for the renewal of the surface layer and, therefore, for the environment of the eggs, larvae and fish, have already been mentioned. When this vertical convection was first studied 30 years ago by Hermann Wattenberg and myself on the old *Meteor* in the winter of 1935 between Farewell and Newfoundland, I thought the water column was homogeneous. The same conclusions were made in the winter of 1958 during the IGY cruises. Looking critically at the single observations they often seem to be an oversimplification of the processes. I was happy, therefore, to send some of my co-workers on the *Anton Dohrn* in 1963 to the NORWESTLANT Program in the same area. This was in April and it was expected that isothermal and isohaline water would be found. A new "in situ salinometer", developed in Kiel, recorded the temperature and electrical conductivity and, with its help, the salinity from the surface down to 1,400 m was computed. This new recording instrument, the bathysonde, was used at all stations.

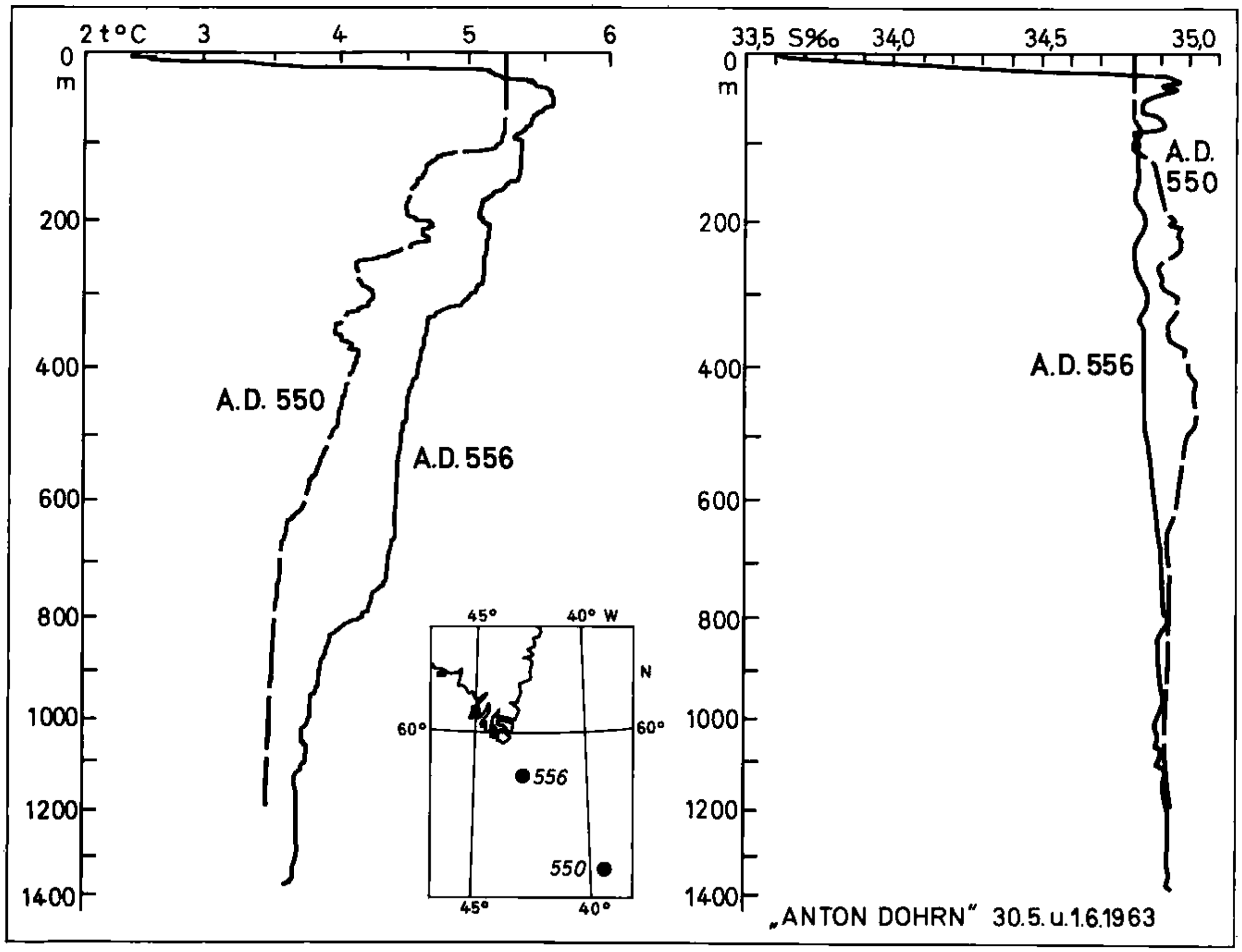

Fig. 14. Recording of temperature and salinity (based on recordings of electrical conductivity) with the bathysonde on two *Anton Dohrn* stations in the Labrador Sea 1963 (After Holzkamm, Krause and Siedler, 1964).

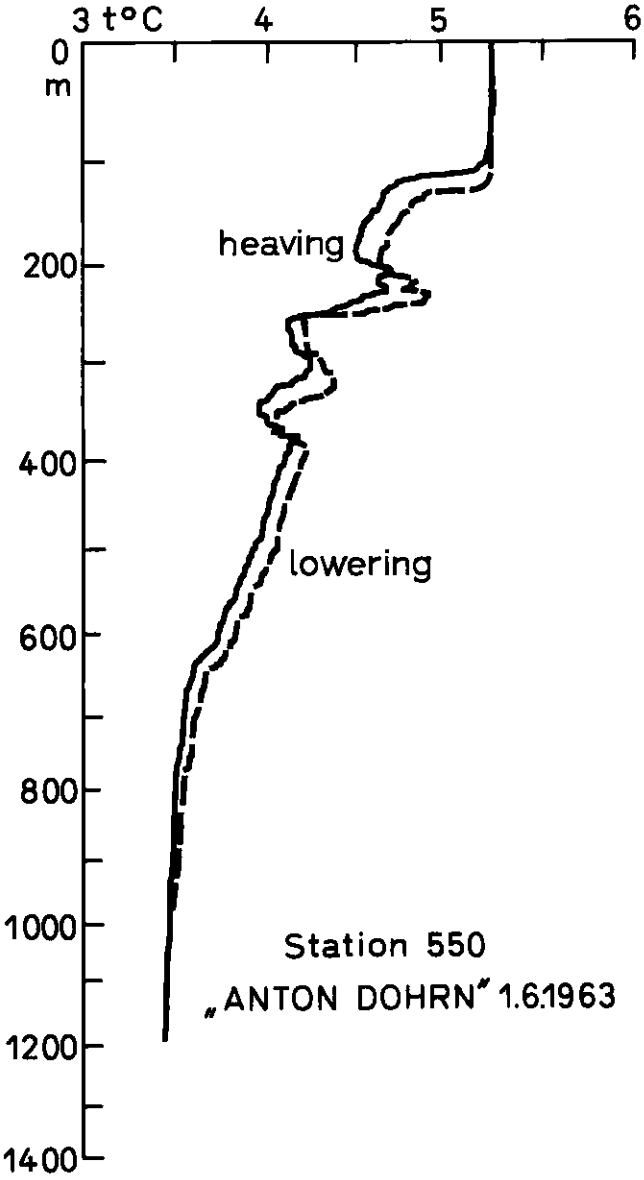

Fig. 15. Recording of temperature at the *Anton Dohrn* station 550 during lowering and raising of the bathysonde (After Holzkamm, Krause and Siedler 1964).

Figure 14 shows the typical results from two stations. The temperature, accurate to 0.01°C, shows a fine structure of layering. The differences are not great, some 0.1 to 0.3°C, but the vertical gradients are remarkable. The new recording instruments demonstrate in the cases of temperature, salinity, oxygen or transparency, that the ocean water is much more inhomogeneous than is suggested from the water sampling and the temperature measurements with reversing thermometers. From our observations, it seems that there is no vertical convection, but rather an inclined convection along density surfaces. Attempts to find characteristic layers in the recordings from neighbouring stations (the distance between our stations in the Labrador Sea was 20 nautical miles) were made without any definitive relations. A relatively small inclination of the layers is enough to prevent finding it again in a station 20 miles away. The situation appears even more difficult when examined in some detail. The temperature curves recorded at *Anton Dohrn* station No. 550, during the lowering and raising of the instrument, (Fig. 15) shows that in the isothermal surface layer the curves are identical, although the time between lowering and raising is about 30 min. But below the surface layer, the curves show that temperature differences are great. Most of the differences can be explained by internal waves. The water layers rose between the time of lowering and raising about 20 m, but there are also differences which cannot be explained by vertical changes, *i.e.* by internal waves, but which might be explained by horizontal differences in the layers. This is the local inhomogeneity with which the oceanographer is confronted, even in the open ocean. The consequences are far-reaching. On the one hand, it is stimulating for the scientist; on the other hand, it is discouraging to see how complicated the sea is. Reference stations for comparing the methods are useless in such a situation.

To this point, we have considered the bottom topography of the Northwest Atlantic, beginning in the open ocean and finishing on the shelf, as well as some new aspects of the ocean water starting in the open ocean. The last step is to consider the shelf waters. These waters are most important for the commercial fish. Our general knowledge of them is relatively good and is based on many expeditions. The current system includes the East Greenland Current, the West Greenland Current, the Baffin Current and the Labrador Current, all distinguished by their cold, low haline water. Some points of our knowledge can be summarized from a series of selected sections extending over the shelf from Denmark Strait to the Grand Banks. The general features of the shelf are found in many publications (Smith, *et al.* 1937; Dietrich, 1957*b*, 1960; Krauss, 1958; Hermann, 1961; Adrov, 1962). Two facts concerning the temperature features (Fig. 16, 17) should be mentioned.

1. The four currents are not one system, but two, namely the East and West Greenland Current system with its origin north of Denmark Strait and the Baffin and Labrador Current system with its origin north of Baffin Strait picking up only a weak branch of the West Greenland Current.

2. Each of the four currents is in some regions divided into two parallel currents, while in other regions the two branches are joined, depending on the width of the shelf and on the shelf rise, which I have mentioned as the characteristic feature of the Northwest Atlantic shelf.

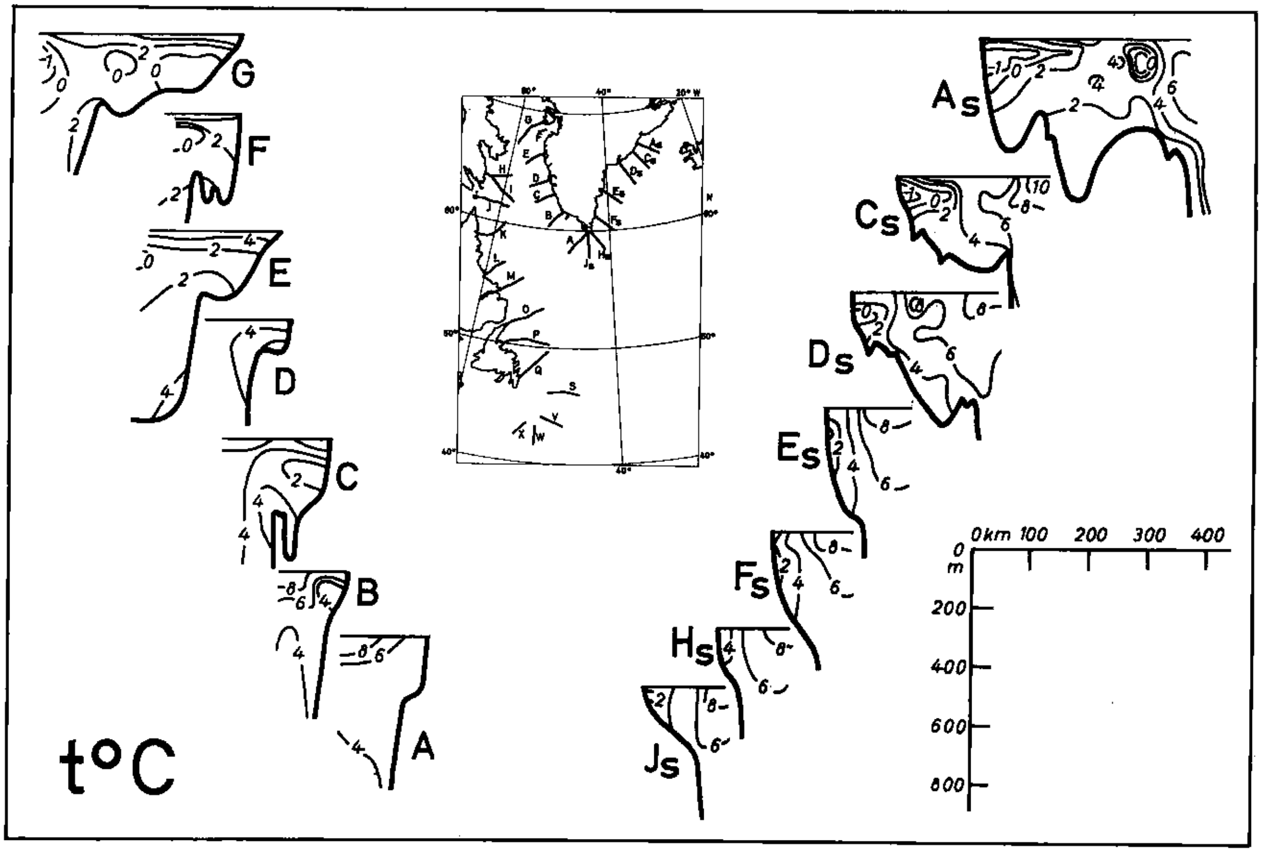

Fig. 16. Series of selected temperature sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

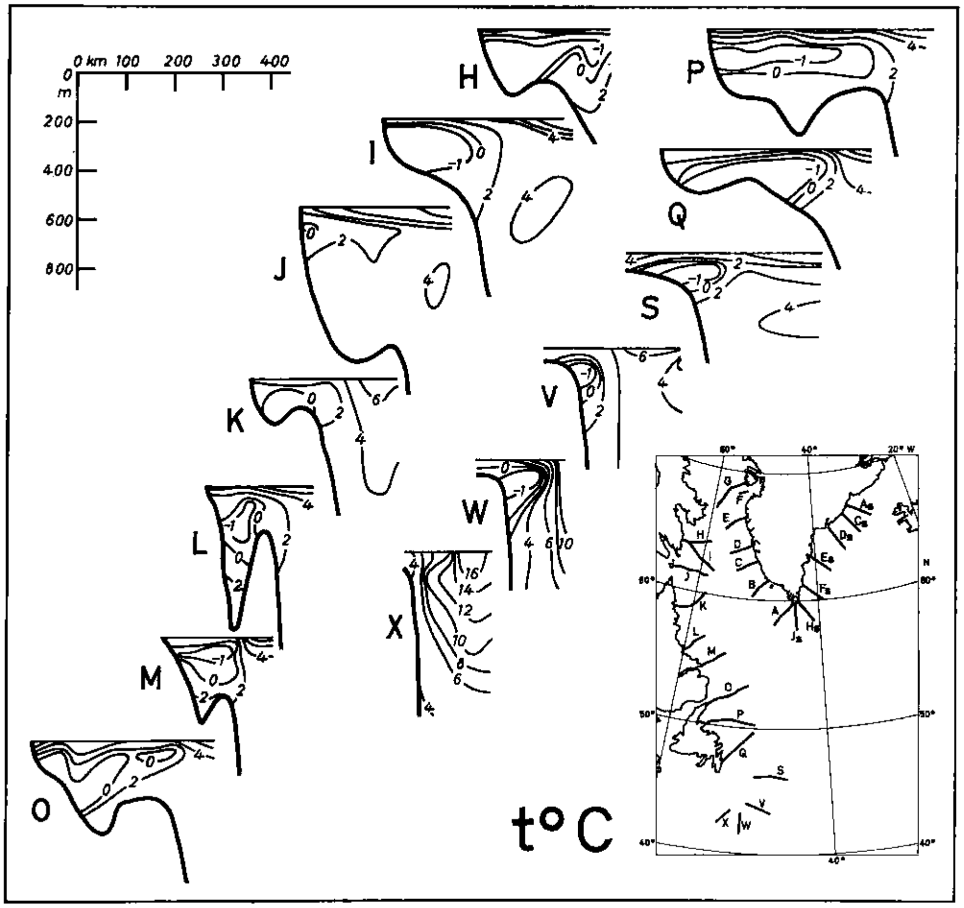

Fig. 17. Series of selected temperature sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

It may be added that the cold water cores do not represent the currents but are their borders. The density gradients are highly influenced by the salinity. Therefore, let us look at the same series of salinity sections in Fig. 18, 19. If we consider the sections carefully, we confirm the statements, namely two currents in some regions, on the whole decreasing along Southern Greenland and renewed in the Baffin Strait.

Many investigations have shown that the velocity of the currents is high (up to 1 m/sec and more) that the velocity and hence water transport changes in time and also that the axis of each current shows horizontal displacement. The changes of the currents in place and time make it evident that great changes in the natural environment, which the biologists want to know about, are taking place in temperature, salinity, oxygen and nutrients. The hydrographers therefore are in a very difficult position, because just the rises on the edge of the shelf, which belong to the main fishing places, are under the influences of great changes in the characteristics of the water masses. Satisfactory forecasting is nearly impossible unless we undertake systematic investigations of the dynamics of these strong ocean currents. Such work cannot be neglected. The hydrographic sections cannot be abandoned, but new research methods which are adequate to the problem must be used.

The following review of the natural situation may help to explain my proposed new method of research. In August 1956 we made a topographic survey of the new fishing grounds found by the *Anton Dohrn* and *Gauss* in 1955 in East Greenland waters and observed the surface temperature along the narrow echosounding sections. Figure 20 shows the quasi-synoptic map of surface temperatures obtained.

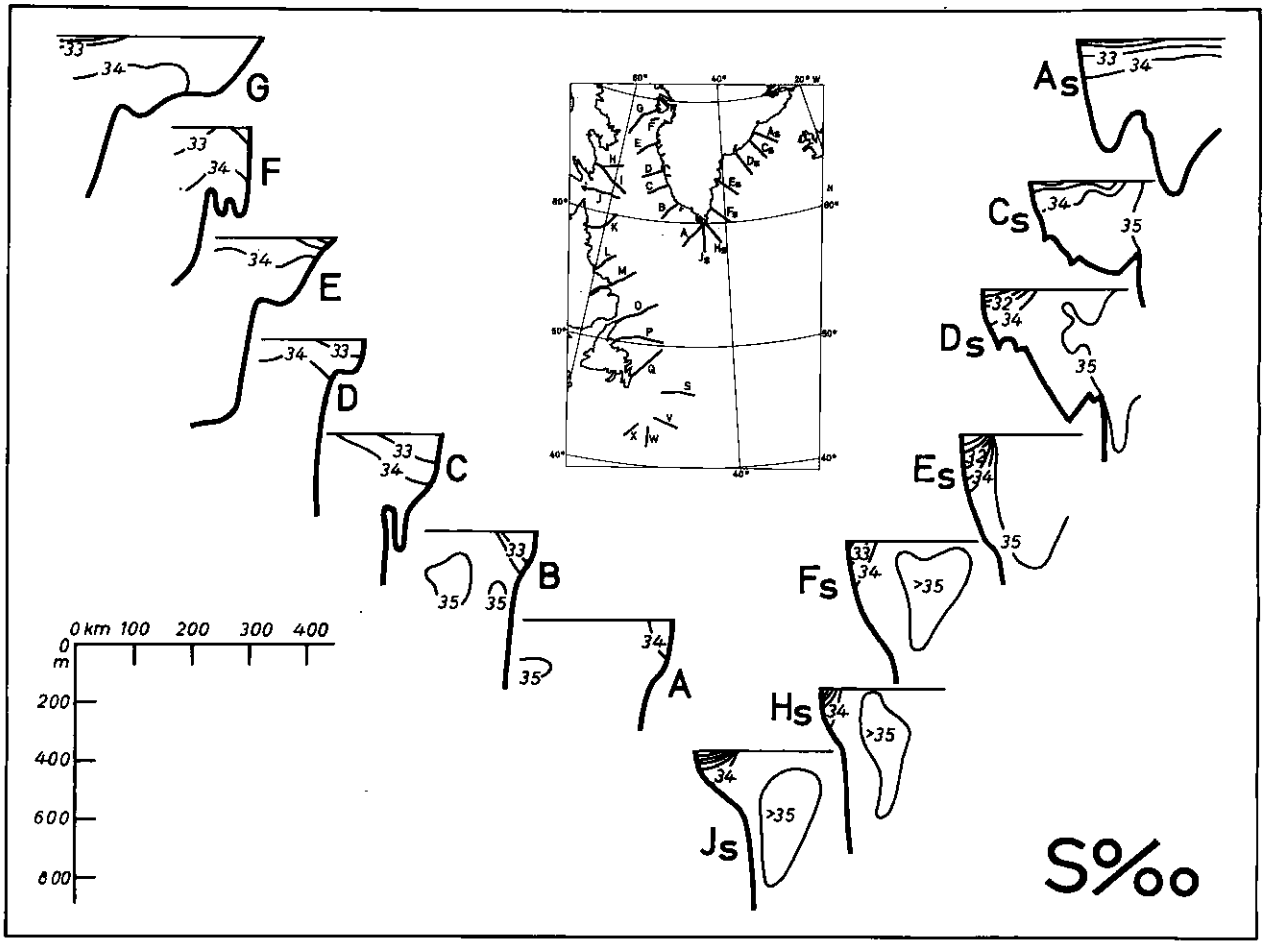

Fig. 18. Series of selected salinity sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

The East Greenland current is the thermal front where the temperature changes abruptly about 6 to 8°C. This front meanders and, although observations do not show it, the meanders are likely drifting in the main direction of the current. The front follows the shelf edge but with the horizontal displacements of the current axis also influencing the deeper water of the shelf. One method of following the displacement of this front is not with a ship, but with the use of an aircraft to measure the infra-red radiation from the sea surface. I made this proposal to the US Weather Bureau in 1957 but I have seen no results. Today, a new method is available and again I have a proposal for our American colleagues. We know that in springtime this thermal front is also the edge of the pack ice.

This edge of the pack ice can be distinguished in the pictures taken by the weather satellites. Photographs of the ice distribution in the Gulf of St. Lawrence taken from the first weather satellite "*Tiros I*" are very encouraging (Wask, and Popham, 1960). My guess is that the pack ice border in the Labrador Sea in springtime will also follow the thermal front. Perhaps our American and Canadian colleagues can find a way to use these outstanding technical devices to study the fishes' environment from outer space. It should be possible to take pictures of the ice edge repeatedly in order to evaluate changes in its position with time and to establish its general

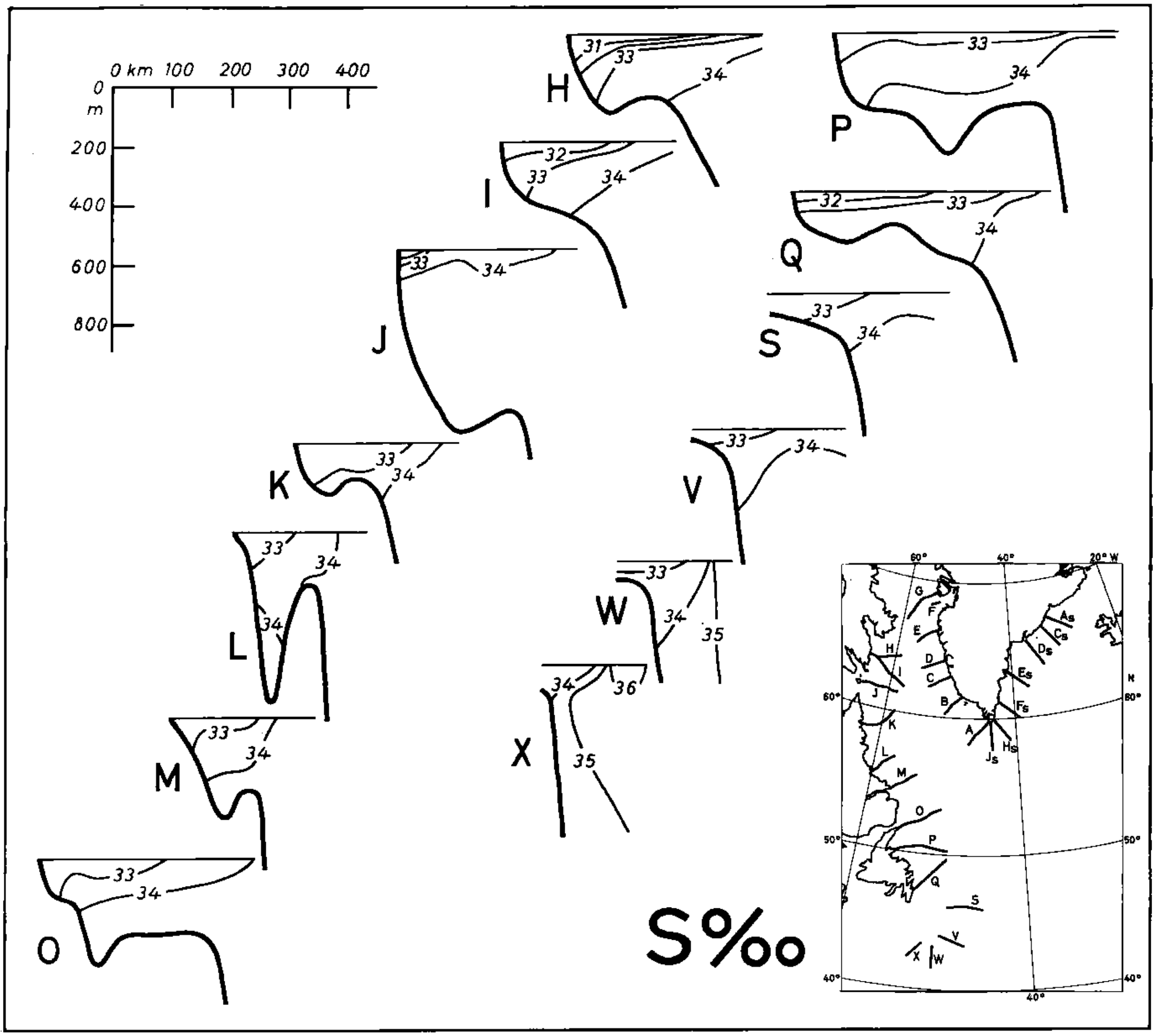

Fig. 19. Series of selected salinity sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

relationship with the meandering of the current.

The other method of investigation is to anchor recording instruments in the most interesting areas. This cannot be done by using surface buoys because of the pack ice and the icebergs. But it can be done by using instruments anchored near the bottom. The instruments can be released from the anchor by a signal and floated to the surface. This method of investigation has many difficulties, but these have to be overcome, because without continuous recordings for weeks and months, we cannot understand the dynamics of water movements and cannot make a decisive step forward in providing the marine biologist with the information he is asking for about the environment.

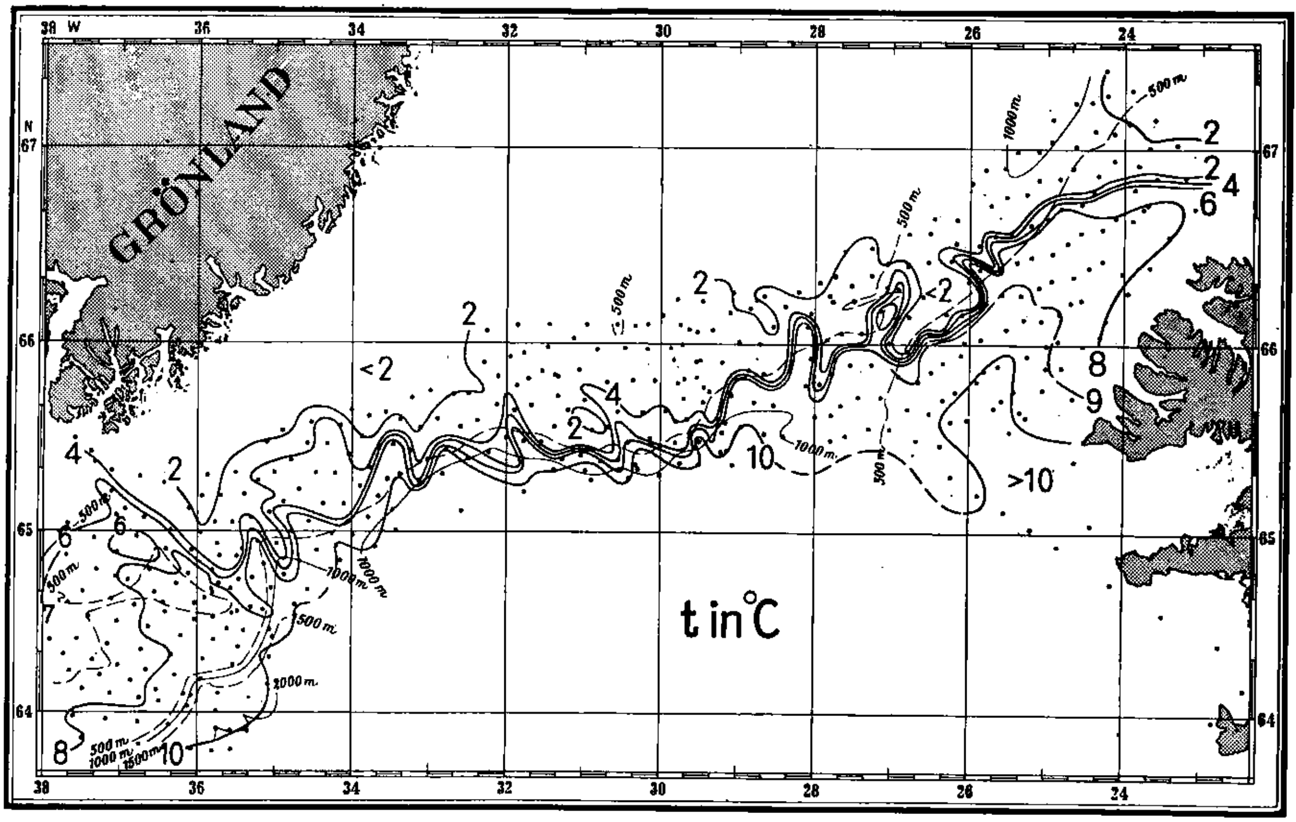

Fig. 20. The thermal front of the East Greenland Current in August 1956 (After Dietrich,1957*b*).

REFERENCES

ADROV, M.M. 1962. Hydrologic investigations off West Greenland. *Soviet Fish. Invest. in North-Western Atlantic*. Moscow. VNIRO and PINRO.

BÖHNECKE, G. and A. BÜCKMANN. 1959. Edit: Die Expeditionen von F.F.S. *Anton Dohrn* and V.F.S. *Gauss* im Internationalen Geophysikalischen Jahr 1957/1958. Erg. Heft Nr. 3, *Dtsch. hydrogr. Z.*

DIETRICH, G. 1957*a* Ozeanographische Probleme der deutschen Forschungsfahrten im Internationalen Geophysikalischen Jahr 1957/1958. *Dtsch. hydrogr. Z.*, 10: 39-61

1957*b*. Schichtung und Zirkulation der Irminger-See im Juni 1955. *Ber. dtsch. Komm. Meeresforsch*, 14: 255-312.

1960. Temperatur-, Salzgehalts- und Sauerstoffverteilung auf den Schnitten von F.F.S. *Anton Dohrn* und V.F.S. *Gauss* im Internationalen Geophysikalischen Jahr 1957/1958. Erg. Heft Nr. 4, *Dtsch. hydrogr. Z.*

1964. Oceanic Polar Front Survey in the North Atlantic in the IGY. US Nat. Acad. Sc., Spec. Vol. for IGY. (in press).

DUNBAR, M.J. 1951. Eastern Arctic Waters. *Bull. Fish. Res. Bd. Canada*, 88, 1-131, Ottawa.

HACHEY, H.B., F. HERMANN and W.B. BAILEY. 1954. The Waters of the ICNAF Convention Area. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4: 67-102.

HEEZEN, B.C., M. THARP and M. EWING. 1959. The floors of the oceans. I. The North Atlantic. Geol. Soc. Amer. Spec. Paper 65.

HERMANN, F. 1961. Danish hydrographic observations under the Polar Front Programme. *Rapp. et Proc. Verb.*, 149: 118, Copenhagen.

HOLZKAMM, F., G. KRAUSE and G. SIEDLER. 1964. Observations of the vertical fine structure of water layers in the Irminger Sea. (In press).

INTERNATIONAL COUNCIL FOR EXPLORATION OF THE SEA. 1961. Contributions to special IGY Meeting 1959. *Rapp. et Proc. Verb.* 149, Copenhagen.

KRAUSS, W. 1958. Die hydrographischen Untersuchungen mit *Anton Dohrn* auf dem ost- und westgrönländischen Schelf im September-Oktober 1955. *Ber. dtsch. Komm. Meeresforsch*, 15: 77-104.

LITVIN, V.M. and V.D. RVACHEV. 1962. A study of bottom relief and types of ground in the fishing areas of Labrador and Newfoundland. *Soviet Fish. Invest. in North-Western Atlantic*. Moscow. VNIRO and PINRO. P. 9-111.

SMITH, E.H., F.M. SOULE and O. MOSBY. 1937. The Marion and General Green expedition to Davis Strait and Labrador Sea. *Bull. U.S. Cst. Guard*, 19.

ULRICH, J. 1962. Echolotprofile der Forschungsfahrten von F.F.S. *Anton Dohrn* und V.F.S. *Gauss* im Internationalen Geophysikalischen Jahr 1957/1958. Erg. Heft Nr. 6, *Dtsch. hydrogr. Z.*

1963. Zur Gestalt des Meeresbodens im Nordatlantischen Ozean. *Erdkunde* 17, 190-205.

WASK, D.Q., and R.W. POPHAM. 1960. *Tiros I* observations of ice in the Gulf of St. Lawrence. *Month. Weath. Rev.* 88, 182-186.

A REVIEW OF THE EFFECTS OF THE ENVIRONMENT OF THE PACIFIC SARDINE

By

E. H. Ahlstrom[1]

Four and a half years ago a sardine symposium was held here in Rome. The chief theme of that symposium was the marked fluctuations that occur in abundance of clupeid stocks. It, also, was basically an environmental symposium. My contribution to that symposium, a background paper on "Fluctuations and Fishing" has only an oblique relevance to our present symposium. Two sections of the sardine symposium dealt more directly with environmental factors; these were titled: "Fluctuations in abundance and availability caused by biotic factors" by Ramon Margalef, and "Fluctuations in abundance and availability of sardine populations caused by abiotic factors" by Zinziro Nakai.

Some points raised in the sardine symposium will reappear in my presentation, but the bulk of the material I wish to present is of more recent vintage.

When considering what I should include in my talk, I decided that primary emphasis should be placed on our recruitment studies. Our sea surveys combine oceanographic and biological observations, and thus permit us to relate environmental variables to the distribution and abundance of the younger stages of sardines and other pelagic fishes.

We are also concerned with the effect of physical environmental conditions on the distribution of the adult sardine population. A variable portion of the sardine population has been available to the U.S. fishery; this varying availability has constituted one of our major problems.

Our laboratory has spent a major part of its research effort on the problem of year-class strength in the Pacific sardine. Much of our research has been done in cooperation with the Scripps Institution of Oceanography. It covers the years 1939 to 1941, and 1948 to the present. Since 1949 the investigations have formed part of the California Cooperative Oceanic Fisheries Investigations, which we abbreviate into CalCOFI.

Systematic hydrographic-biological surveys have been made since the inception of CalCOFI. Surveys between 1949 and 1960 were made at approximately monthly intervals; since 1961 surveys have been spaced at quarterly intervals. The region being surveyed has as its dominant feature the southward flowing California Current, which is the eastern limb of the clockwise circulation in the North Pacific. Stations in the survey pattern are arranged in lines which are normal to the general trend of the coastline, hence cut across the California Current. The pattern that is routinely surveyed at present on the quarterly survey cruises extends from San Francisco, California, to Pt. San Juanico, Baja California, a north-south extent of 920 miles. Station lines are spaced 40 miles apart, stations on lines are spaced at 20 or 40 miles intervals, except near shore where the spacing is closer. Most of the 24 lines of stations in the pattern surveyed routinely extend 200 to 250 miles seaward, but two of the cardinal lines of stations off California extend over 600 miles to sea in order to completely delimit the offshore extent of the California Current.

Some cruises made during the 1950's had more extensive coverage than that just described, extending from Cape Mendocino, off northern California, to below Cape San Lucas, Baja California—a north-south extent of 1,320 miles. Our surveys have had the advantage of co-ordinated hydrographic and biological observations.

We have put more effort into investigating the distribution and abundance of the young stages of fishes than any other research group, so it becomes pertinent to ask, has it been worth the time and money expended?

If I were to single out one aspect of egg and larval surveys as of prime importance, it would be their use in fish resource evaluation. This is especially true off California, where our fish resources are but partially exploited. It is a most fortunate circumstance that most of our marine

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fishes spawn in the open sea, and their egg and larval stages may be quantitatively sampled by plankton gear. It was through our surveys that we found out how widely distributed the jack mackerel resource is at time of spawning, how consistently abundant and widespread are hake eggs and larvae, rockfish larvae, etc. But of more consequence to our research has been the information gathered on the northern anchovy. Without this body of information it would not be possible to document the marked increase in abundance of this resource that has occurred since 1950. The anchovy appears to have filled most of the ecological niche formerly occupied by the sardine.

I discussed various aspects of the use of larval surveys for resource evaluation in the talk I gave at the larval fish symposium we held as part of our CalCOFI Conference at Lake Arrowhead, California, in October of 1963.

A number of European biologists participated in the larval fish symposium including Gotthilf Hempel, Jim Shelbourne, John Blaxter, Fred Holliday and Wilhelm Einsele. The contributions to the symposium will be published in Vol. X of our CalCOFI Reports, so I will not enlarge further on the use of larval surveys in resource evaluation, except as they apply to the competition between sardine and anchovy.

We have also demonstrated that it is possible to delimit the spawning range of a widely distributed pelagic species and to follow the year by year variations in the time and place of its spawning.

Too much emphasis and concern has been placed on the precision with which the amounts of spawning can be determined. We estimate that the 95% fiducial limits of our yearly estimates of egg abundance are approximately half or double. The consistency of our results are compatible with this judgement. Furthermore, if surveys were limited to sampling of eggs alone, it would be possible to devise sampling techniques that would greatly increase the reliability of our estimates. In a paper on a high speed sampler, designed by John Isaacs, and co-authored by Ahlstrom, Isaacs, Thrailkill and Kidd, 1958, we demonstrated that horizontal strip sampling along cruise tracks using a series of high speed samplers is an excellent way of integrating the patchy distribution of sardine eggs over area. This technique was not used routinely because our high speed samplers did not collect sufficient larvae—the volume of water strained was just too little to get an adequate size representation of larvae. Hence, to avoid using two kinds of sampling gear, one for eggs, one for larvae, we have continued to sample with obliquely-hauled plankton nets.

We have found that estimates of larval abundance are more consistent than estimates of egg abundance. This is an interesting point, as it is often assumed that the reverse is true (*e.g.* in Saville's (1964) contribution to the 1963 ICES Symposium on the Measurement of Abundance of Fish Stocks). When I present our estimates of larval abundance of the anchovy in a later section, this point will become quite clear.

There are two contrasting approaches that can be followed in investigating the effect of environmental conditions on year-class strength. One approach considers that the environmental effect is a widespread, primary effect such as a marked warming or cooling of ocean temperatures throughout the spawning range, changes in the intensity or flow of major current systems, changes in productivity, and the like. The other approach is to consider that good survival is related to local, more transient effects—that we are, in point of fact, dealing with patchiness in survival—the coincidence in certain areas of high availability of food organisms at times that larvae begin to feed, or of low predation on the developing larvae, and so forth.

Most of the workers dealing with the effect of environmental conditons on year-class strength assume that the former is the correct approach to follow—that even if survival is patchy, there will be more areas of good survival under certain widespread environmental conditions such as high productivity or favourable transport.

There is good rationale behind this approach. In order to correlate environmental factors with year-class strength, the factors have to have certain consistency in their effects from year to year, and they have to be of the kind that can be quantitated.

For example, if there is a relation between temperature and survival, we carry out the correlation by having a single value for survival rate and for temperature for each year in a series. The same would apply to a correlation involving basic productivity, or the intensity of upwelling, or the amount of water carried by currents, etc. It is necessary to express some values in relative rather than absolute terms. With quantitative data, multiple correlations can be carried out as well as simple correlations.

On the other hand, if we should be investigating the more transient conditions that favour good survival, our problem becomes a more difficult one, perhaps by orders of magnitude. For one thing, it is difficult to locate and recognize transient phenomena. Their effective study would require more resources for sea surveys than are available to us. A more important consideration is that it is difficult to quantitate transient phenomena.

A good example of a successful application of this approach on a small scale is Shelbourne's (1957) paper dealing with,"The feeding and condition of plaice larvae in good and bad plankton patches".

I read Gulland's contribution to the symposium on "Survival of the youngest stages of fish and its relation to year-class strength" (B-9) with great interest. He points up the weaknesses in the correlation approach and he adds this pungent sentence, "Though many correlations between year-class strength and environmental factors have been suggested, few, if any, have stood the test of time."

Perhaps there have been several difficulties in the approaches followed to date. Fishery biologists, along with other scientists, like to simplify their problems. They know that the environment is complex, but they are nevertheless hopeful that some factors are of over-riding importance, and that it may be possible to find a straightforward relation between environmental variables such as wind, temperature or productivity and year-class strength.

Simplification is an essential technique in science, but it so easily leads to over-simplification. We begin to investigate a species as if it were living in vacuo, entirely separate from other species. Further, the environmental conditions looked at are often those that come easiest to hand, data collected over a series of years for other purposes, such as meteorological data, light ship data, or sea surface temperatures. These over-simplified approaches have not stood the test of time, and they lead inevitably to the conclusion that year-class strength is not mediated by any one factor alone.

One of the early correlations relating year-class strength to an environmental variable was Walford's (1946) correlation between year-class strength in the Pacific sardine and salinity. Walford used year-class strength as determined from the fishery and the summer salinity at Scripps Pier. The relation was interpreted as one between productivity and survival--high salinity was the resultant of more intensive upwelling with attendant transport of inorganic nutrients, which increased the phytoplankton production and which in turn was reflected in the other parts of the productivity chain. It has been pointed out by various investigators (*e.g.* Marr, 1960) that the correlation did not hold for subsequent years.

One of the difficulties with Walford's simplified analysis is that high salinity can result from causes other than upwelling. There are better indices of upwelling than salinity alone, indices that take temperature, oxygen and nutrient content of the water into account as well as salinity.

There is an implication in a correlation between general productivity and year-class strength that most fishery scientists have overlooked, mainly because they have been looking at a single species rather than the complex of species in an ecological assemblage. If the relation is a simple cause and effect relation between productivity and survival, then we would expect the effect to be reflected in all species in a trophic level. We should have good survival of anchovies in the same years when we have good survival of sardines, for example, along with good survival of jack mackerel and Pacific mackerel, etc.

It is very easy to demonstrate that this is just not so. There is no consistent relation between good year classes of sardines and good year classes of anchovies. In fact, as I will point out later, the reverse appears to be true. Neither is there a coincidence between good year classes of sardines and Pacific mackerel.

Furthermore, we have found that there is no consistent relation between one measure of productivity, the standing crop of zooplankton, and year-class strength of sardines. Here again, some of the poorest survival years have been years of high productivity.

I am fully cognizant of the fact that more sophisticated measures of productivity are needed than measures of general productivity. It has been pointed out by various scientists that what is needed is information on the kinds of food organisms important in the diet of fish larvae, determined in the areas where larvae occur over the time period of their development.

Arthur (1956) studied the sizes and kinds of food particles eaten by sardine, anchovy, and j mackerel larvae. He found that body shape and particularly head and mouth size determined the siz of particles that could be engulfed. Sardine and anchovy larvae are, of course, elongated, thread-like larvae with small heads. Newly feeding larvae can engulf only very small food particles—up to about 80μ in length. These are the sizes of organisms that have to be sampled by water bottle rathe than by nets. As the larvae of both species increase in length, they consume increasingly larger food particles, hence have a wider spectrum of choice. Even so, copepods in various stages of development formed the bulk of the diet of both species. Jack mackerel larvae have a much larger head and gape in relation to length, and as a consequence, have a greater choice of food items. The studies, as we will see later, show that sardine larvae are very directly competitive for food with anchovy larvae, much less so with jack mackerel larvae.

The CalCOFI surveys have sampled microplankton only intermittently, so we do not have the body of information needed for correlating larval survival with abundance of larval food. However, because the food requirements of sardine and anchovy larvae are so similar, and the larvae of the two species tend to co-occur, as I will show later, the two species should in general respond similarly, if abundance of larval food is a controlling mechanism in year-class strength. As I have noted earlier, there is no such correspondence.

Environmental conditions are often thought of in terms of primary physical parameters, such as temperature or drift. The only biological factor usually considered is food. This is too restricted a view. The thesis I wish to develop is that the primary environmental condition can in some situations be other fish—especially species occupying the same trophic level. I am not going to ignore other environmental factors, although I must confess that some of them have lost their glamour.

In developing my point, I will go into our sampling procedures and problems in enough depth to establish that we can sample eggs and larvae of sardines and anchovies with some precision. This is a necessary requirement if one is to deal with the effects of competition within a trophic level. As a prelude, may I say that we early established the depth distributions of sardine and anchovy eggs and larvae, to insure that our sampling at all stations more than covered this parameter.

First, I would like to discuss some of our observations on the distribution and abundance of sardine eggs during the decade of the 1950's. During these years sardine spawning occurred mainly between Pt. Conception, California and Pt. San Juanico, Baja California. Even within this area, the distribution of eggs was quite different from year to year. In 1952 and 1953, for example, very little spawning occurred off southern California and northern Baja California while heavy spawning took place off central Baja California. In 1954 there was an explosive spread northward to waters off northern Baja California and southern California. The 1954 distribution of both sardine eggs and larvae constituted the most widespread distribution encountered during the decade. I am including a figure (Fig. 1) to contrast the distribution of sardine eggs in 1953 and 1954.

There were no marked changes in oceanographic conditions between 1953 and 1954 that would account for the dispersion of sardines that occurred. A moderate increase in temperature is the only obvious difference. A plausible explanation is that sardines spread out in response to an increase in population abundance, resulting from the recruitment of the fairly successful 1952 year class. During 1954 approximately 38.5 % of sardine eggs were obtained off northern Baja California and southern California in contrast to the 1% obtained in these areas during 1953.

Sardines that came to California waters to spawn in the spring of 1954 remained in the area during the commercial season. The catch jumped from 4,000 tons in the 1953-54 season to 68,000 tons in the 1954-55 season. The change in spawning distribution preceded the change in catch,hence demonstrated that egg surveys could furnish advance information on availability, that is, on the portion of the sardine population likely to be accessible to the U.S. fishery. Distributions of sardine spawning in the immediately succeeding years, 1955, and 1956, were similar to 1954, although less widespread.

While the change in distribution that occurred between 1953 and 1954 has no obvious relation to oceanographic conditions, changes that occurred in the time and place of sardine spawning in 1958 were obviously influenced by the warmer regime then prevailing. During the years between 1950 and 1956, ocean temperatures off California were below the long term average. Professor John

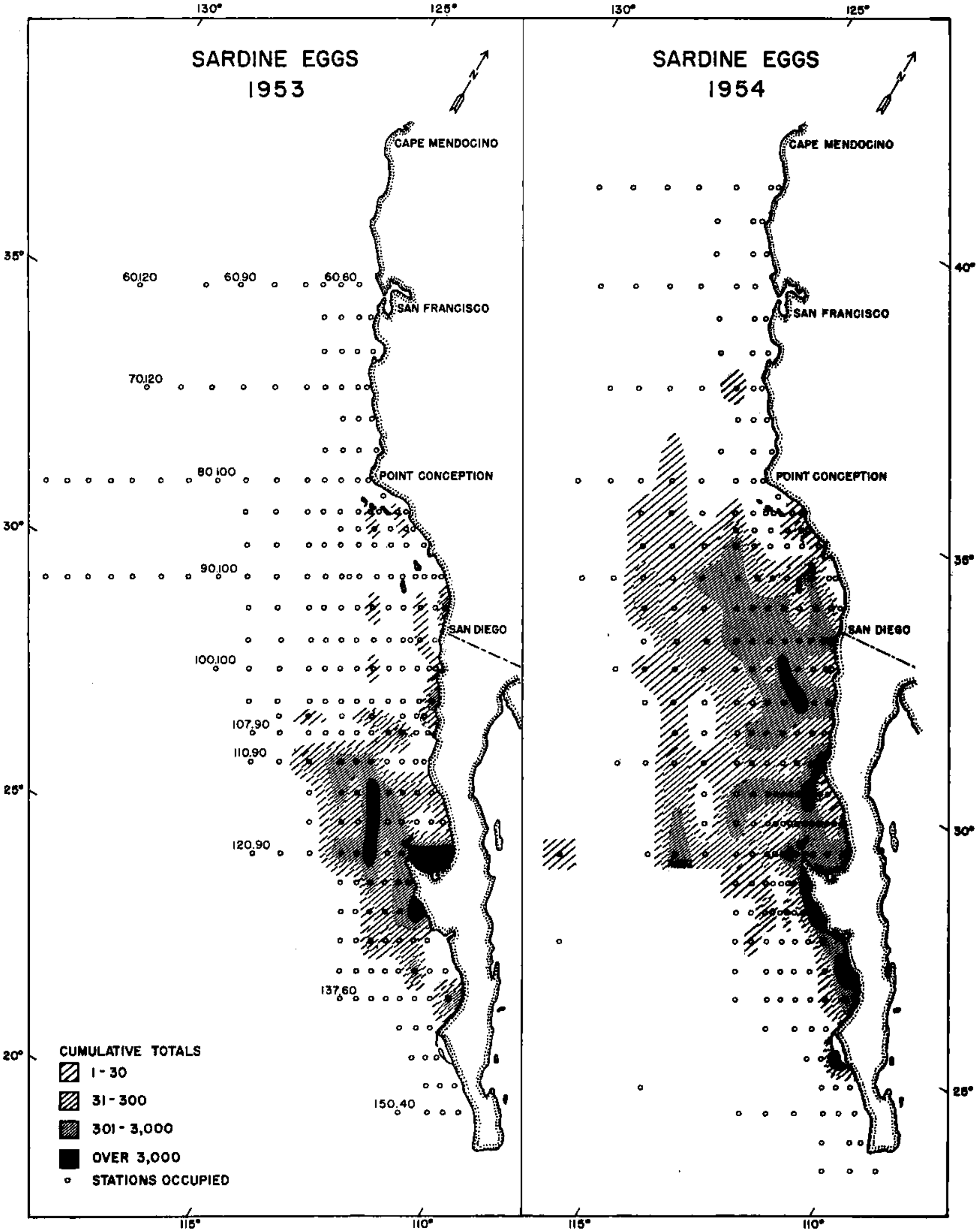

Fig. 1. Distribution and relative abundance of sardine eggs in 1953 and 1954. Selected station numbers of the CalCOFI survey grid are given on the chart for 1953.

Isaacs (MS) of Scripps refers to these years as the "soggy years". Warming in the region of the California Current began in 1957 and reached its height in 1958. There was a marked warming of several degrees centigrade in many parts of the California Current region. As a result, sardine spawning off southern California which had been mostly confined to the months of May and June during 1950-56 was both markedly earlier and more prolonged in 1958 (Table 1).

TABLE 1. PERCENT OF SARDINE EGGS COLLECTED IN EACH MONTH OFF SOUTHERN CALIFORNIA

	1951-1956	1958
January	0.01	51.33
February	0.03	1.61
March	1.93	17.16
April	5.59	5.06
May	44.59	16.06
June	35.89	1.59
July	11.96	7.12
August-December	0.08	0.08

John MacGregor (1957) of our laboratory has followed the maturation and fecundity of sardines over a number of years. He has found that sardines off southern California in most years reached an advanced stage of maturity by late February. Spawning, however, occurred mostly in May and June. Apparently, the fish held back the final phase of maturation until favourable conditions prevailed in the environment.

We have investigated the distribution of sardine eggs in relation to water temperatures. The lower temperature limit for sardine spawning is about 13°C. This appears to be a critical temperature for sardine eggs. Our physiologist, Dr Reuben Lasker (1964), has found from controlled laboratory experiments that sardine eggs do not develop normally at temperatures below 13°C.

There were extensive areas off southern California with temperatures below 13°C during the first four calendar months of 1951-56, especially during March and April. When spawning took place, largely in May and June of these years, it occurred at temperatures between 13°C-18°C, averaging 14.7°C. The earlier spawning of 1958 took place within the same temperature range, and averaged 15.3°C. Temperature appears to influence both the time of spawning and the length of the spawning season.

The sardine potentially can mature several batches of eggs during a season (MacGregor, 1957). The developing ovaries contain several size modes of yolked eggs. This type of ovarian development is found in many pelagic fishes. It seems logical to assume that more batches are matured during an extended spawning season, such as that of 1958, than during a shorter season, such as prevailed off southern California during much of the 1950's. We do not have definite evidence to prove or disprove this assumption. MacGregor did find that smaller fish, including a portion of the one-year olds, were maturing in 1958; these fish were precocious by about one year. One of the major needs in fecundity studies is an adequate method of determining the number of batches of eggs that are spawned per female and the relation of frequency of spawning to size and age of fish and to environmental conditions.

In considering conditions that might favourably influence the survival of a year class, I have theorized (Ahlstrom 1959*b*, p.203) that the extent of the area over which spawning was spread was probably one of the more important ones: the larger the area, the greater the chance of good survival. The 1954 distribution was the most widespread of any we have encountered in our surveys. As such it affords a test, of sorts, of this hypothesis.

I have given in Table 2 the estimated relative areal extent of sardine eggs for 1952 through 1959. The value for each year is the summation of the areal distributions of eggs on monthly cruises. Similar values for sardine larvae are also included.

The areal extent of sardine eggs in 1954 was nearly 1.5 times as great as in the next best year, 1955, and nearly 5.5 times as great as in 1957. The best survival years in the series are 1952, 1956, and 1957. Areal extent in 1954 was 2.4 times as great as in 1952 and 2.1 times more than in 1956. There does not appear to be any obvious relation between extent of spawning and rate of survival.

TABLE 2. RELATIVE AREAL EXTENT (ΣMONTHLY DISTRIBUTIONS) OF SARDINE EGGS AND LARVAE, IN SQ MILES, 1952 TO 1959

	Northern center (Sta. lines 107 and above)		Southern center (Sta. lines 110-157)		All areas	
	eggs	larvae	eggs	larvae	eggs	larvae
1952	27,800	41,600	89,900	174,900	117,700	216,500
1953	14,600	11,900	98,500	165,400	113,100	177,300
1954	149,900	135,400	137,700	187,900	287,600	323,300
1955	120,900	98,800	76,200	151,200	197,100	250,000
1956	80,400	57,200	55,100	98,600	135,500	155,800
1957	24,600	44,900	28,200	100,400	52,800	145,300
1958	57,500	68,300	21,500	73,600	79,000	141,900
1959	63,300	59,500	26,800	55,700	90,100	115,200

Sardine larvae in all years had a greater areal extent than the eggs. This is not at all surprising, for a larval sample potentially can contain an accumulation of sizes that span approximately 45 days, while a sardine egg sample, on the average, represents an accumulation of only 3 days' spawning.

In our publications we have subdivided the spawning distribution of the sardine in various ways, depending upon what feature we wished to emphasize. Our broadest grouping is a division into northern and southern spawning centers. The northern center comprises all of California and northern Baja California from the international border to Pt. San Quintin. The southern spawning center comprises central and southern Baja California. The areal extents of sardine eggs and larvae in the two centers are shown in Fig. 2. The marked change in distribution of sardine eggs and larvae that occurred in the northern center between 1953 and 1954 is nicely illustrated by this figure. Another reason for its inclusion is to call attention to differences in the distribution of eggs and larvae in the two centers. In the northern center the areal extent of sardine eggs is as great, on the average, as the areal extent of larvae. In the southern center, however, sardine larvae always have a greater areal distribution than eggs, and the difference is most marked below Pt. San Eugenio. The California Current carries developing larvae southward of the area where they were spawned. This happens in all seasons. We have not been able to discern any consistent relation between the strength of the California Current and the extent of larval transport on the one hand, and the rate of larval survival on the other.

Sette (1960) has proposed a rather complex model to explain successful year classes of sardines, especially in the area of the California fishery. To discuss his model in any detail would require more time than I have available. He hypothesized that with weaker winds in winter, the waters on the southern California spawning grounds more often warm earlier in the spring, permitting a longer period of spawning. As a further consideration weaker summer winds were conductive to the better development of the inshore counter-current, permitting the larvae hatched from the eggs to be retained in the southern California area, and to be carried to inshore feeding grounds. Thus successful year classes were likely to be produced during periods of weaker than average winds and warmer than average temperatures. These also would be years with weaker than average flow of the California Current and with reduced amounts of coastal upwelling. This is an attractive model in which the strength of the winds influence both water temperature and the transport of larvae. This pattern did not prevail, however, in 1939, when our most successful year class of sardines was produced. Winter and spring winds were stronger than usual in 1939, but winds were weak during the summer period. Perhaps the essential part of the model is the mechanism that assures the inshore transport of larvae to the feeding grounds.

The population of the Pacific sardine has been shown by Sprague and Vrooman (1962) and Vrooman (In press) to be made up of at least three genetically distinct stocks, two occurring in the Pacific off California and Baja California, the other in the Gulf of California. The stocks in the Pacific are referred to as "northern" and "southern" stocks. Not enough sardines have been tested serologically during the spawning season to definitely establish the spawning distributions of the two Pacific stocks. Enough "fall" spawning sardines have been tested to show that this group is

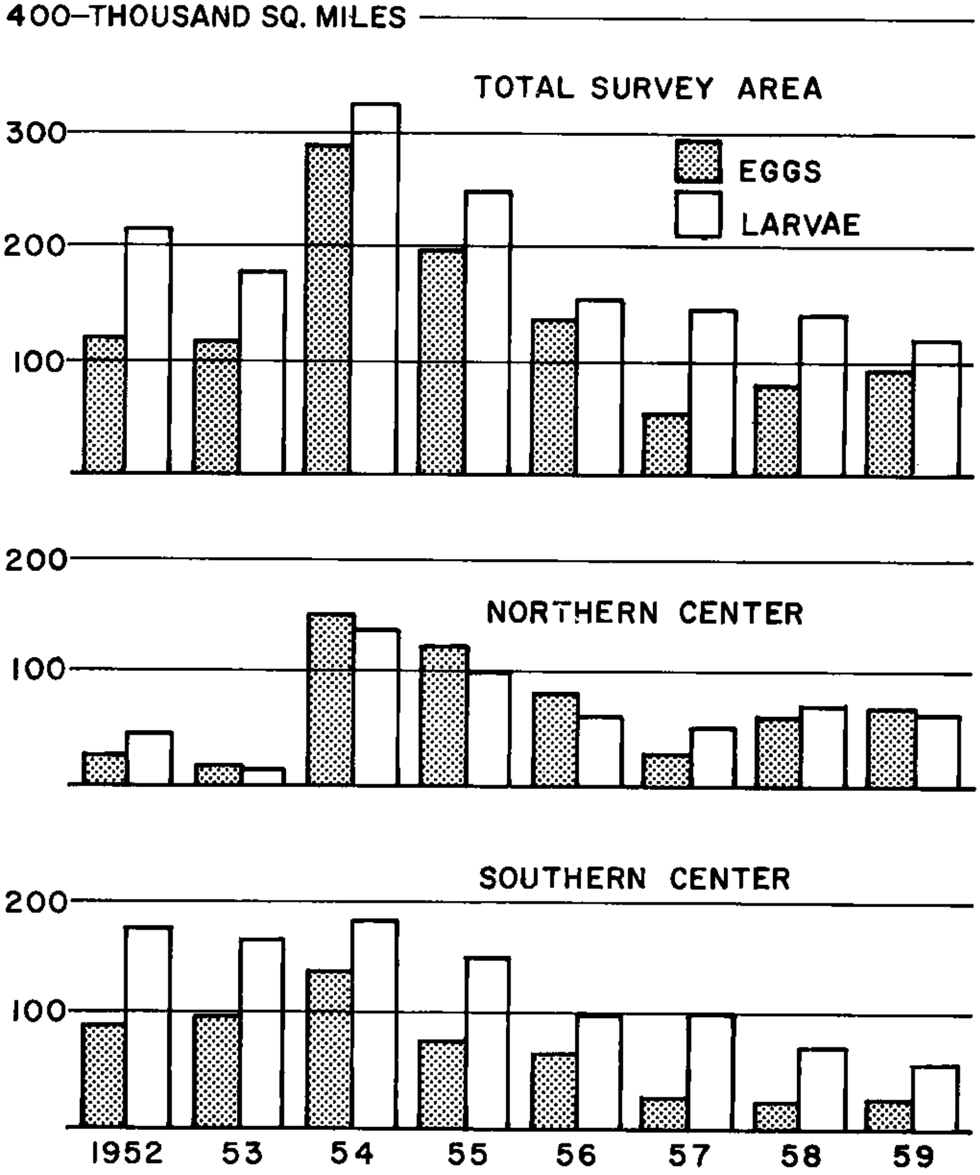

Fig. 2. Areal extent of sardine eggs and larvae, 1952 to 1959. Upper graph, total survey area; middle graph, northern center (station lines 107 and above); lower graph, southern center (station lines 110 - 157).

"southern" fish. Whether all the sardines spawning during the main spawning period belong to the other stock has not been clarified. Since the offseason spawning occurs at temperatures which average 2 to 3°C higher than the spring spawning, we would like to believe that the "southern" stock is a physiologically distinct group of fish.

We obtain an abundance estimate for sardine eggs, which is an estimate of the total number of sardine eggs spawned during a year, exclusive of the Gulf of California. We can determine rather precisely the number of days' spawning represented in each egg collection, either actually or potentially, hence can put each sample of eggs on a spawned per day basis (Ahlstrom, 1943). By integrating these values over time and area, we derive our estimates (Ahlstrom 1954, 1959*b*). Various studies have been made of the reliability of our egg estimates (Silliman, 1946; Sette and Ahlstrom, 1948; Taft, 1960). The fiducial limits of a season's estimate appear to be approximately half or double.

In a paper dealing with the 1950 and 1951 seasons, I also derived abundance estimates for sardine larvae by size (Ahlstrom, 1954). This was, in part, an exercise to demonstrate that such estimates could be derived. The principal weakness was an inexact knowledge of the growth rate of larvae.

Information about the time required to grow through any given unit of larval length is a requisite to meaningful integration of larval data over time. Average values for growth are probably not too meaningful. The rate of larval growth may be as much influenced by temperature as is the rate of embryonic development.

For the present I have given up the attempt to derive abundance estimates of larvae, and am content with a lesser estimate that I call a "census" estimate. The larval data for each collection, by size category, are integrated over area, but not over time. The yearly estimate is simply a summation of the monthly "census" estimates.

We have programs in progress to try to remedy this lack of information about larval growth and how it is affected by environmental variables. These include physiological studies of the nutritional needs of larvae, behaviour studies of sardine and anchovy larvae, and a concerted team attack on the problem of rearing larvae of pelagic marine fishes.

Because of the inadequacies of our growth data, there is little point in taking other than a rough and dirty look at larval survival. A simple way of looking at differences in survival during the larval period from year to year is to relate the number of larger larvae obtained to total eggs or total larvae (Table 3). A year class with good survival should have a larger proportion of larger larvae than a year class with poor survival.

TABLE 3. RELATIVE PROPORTION OF LARGER SARDINE LARVAE (15.26 mm AND LARGER) TO EGGS AND TO TOTAL SARDINE LARVAE COLLECTED DURING THE YEARS 1951-58.

	Estimated abundance eggs ($\times 10^{11}$)	Census estimates larvae ($\times 10^{9}$)	Census estimates larger larvae ($\times 10^{9}$)	Relative proportion larger larvae to eggs	Percentage larger larvae is of total larvae
1951	6108	5773	172.5	2.82	2.99
1952	1360	5465	108.6	7.99	1.99
1953	4402	4020	89.7	2.04	2.23
1954	3554	7298	97.8	2.75	1.34
1955	1626	4341	76.6	4.71	1.76
1956	2560	3897	134.5	5.25	3.45
1957	1108	2431	63.7	5.75	2.62
1958	896	2832	30.4	3.36	1.07

In relating larger larvae to eggs, we are attempting to look at differences in survival between the time of spawning and the late larval period.

I have explained earlier that the egg and larval estimates are not exactly comparable. The egg estimates are abundance estimates. They are an estimate, albeit a minimal one, of the number of eggs spawned during a season. The larval estimate takes only area into account, not time, hence is a partial estimate. In comparing eggs and larvae, therefore, we are concerned only with the proportion of larger larvae to eggs. It is a relative estimate, but a comparable one from year to year.

The values have a range of about four times. In this comparison the 1952 class has the best survival, the 1957 ranks next, and the 1956 class is third. The same three year classes were the most successful of any during the 1950's, based on their contribution to the commercial catch, but with a different ranking—1956, 1952, and 1957 classes in that order. The fact that there is a close correspondence between the rate of survival between the egg and late larval stages as determined from survey data, and year-class strength as determined from the fishery is encouraging. The range in survival to the late larval stage is only 4 times during the eight years being considered, however, and this value has an error of estimate which may be as great as half or double, hence it would be difficult to establish statistical significance.

In relating larger larvae to total larvae, we are attempting to look at differences in survival during the larval period itself. I am considering as larger sardine larvae, all larvae that are over 15.25 mm in length. During the 8-year period, 1951-1958, these sizes of larvae made up from 1.07% to 3.45% of the sardine larvae collected. This is a range of a little over three times.

In a word, the values from year to year are too similar. The bright spot is that the highest percentage of larger larvae occurred in 1956, and this year class was the best in this series, based on commercial landings. The next best, the 1952-class, does not show up as such in this analysis, but the third best, the 1957-class does. There is an error of estimate associated with these values, which we cannot be precise about, but which may have a noise level about as wide as the range of values shown.

Our anchovy larval data are so much more extensive than the sardine, that we like to check on observations, such as the above, by looking at the same features in the anchovy data. For this purpose I have used standard haul totals of anchovies, and in the category of larger larvae I have included all anchovy larvae larger than 14.26 mm (Table 4). The results are even more consistent than for sardine larvae. Seven of the eight years have almost identical percentages of larger larvae, 0.94% to 1.07%. Only one value is divergent, and this only moderately.

TABLE 4. RELATION OF LARGER ANCHOVY LARVAE (>14.26mm) TO TOTAL ANCHOVY LARVAE, 1951-1958.

	Total anchovy larvae (standard haul totals)	Number 14.26 mm larvae	Percentages that larger larvae are of total larvae
1951	29,076	280	0.96
1952	59,528	894	1.50
1953	99,020	928	0.94
1954	161,056	1,556	0.97
1955	140,019	1,476	1.05
1956	134,913	1,394	1.03
1957	146,551	1,494	1.02
1958	205,376	2,200	1.07

This consistency poses a real problem. It is generally assumed that survival during the larval period is quite variable, and that this period may be the determinant one as regards year-class strength. Our data do not support this. Despite the heavy mortality that occurs during the larval period, about the same percentage of larvae attained the late larval stage year after year. During the 1950's the sardine population was decreasing in abundance, the anchovy population markedly increasing. At the moment I am concerned with the increase in anchovy abundance as it related to rate of survival. The standard haul totals for anchovy larvae, given in Table 4, show a greater difference between 1951 and 1958 than do our census estimates, (Table 5) but even the latter show a tripling in the abundance of anchovy larvae between 1951 and 1958. We interpret the increase in larval abundance to reflect a similar increase in abundance of the adult population. Despite this marked increase in population abundance, the rate of larval survival remained remarkably constant, hence appeared to be independent of the density of larvae.

Obviously this consistency pulls the rug out from under any attempts to relate variation in larval survival to environmental conditions. It would be an understatement to say that we never anticipated this result.

I have considered the possibility that this seeming consistency is an artifact of sampling. There are two obvious problem areas in the quantitative sampling of clupeid larvae. One of these is the marked undersampling of larger larvae that occurs during daylight hours, a phenomenon that has been well documented in the literature (Russell, 1926; Bridger 1956; Ahlstrom, 1959, etc.).

TABLE 5. CENSUS ESTIMATES OF SARDINE AND ANCHOVY LARVAE, 1951-59.

	Census Estimates ($x 10^9$)		
	Sardine larvae	Anchovy larvae	Ratio: sardine to anchovy larvae
1951	5,773	15,104	1 to 2.6
1952	5,465	17,072	3.1
1953	4,020	23,680	5.9
1954	7,298	38,416	5.3
1955	4,341	37,660	8.7
1956	3,897	38,508	9.8
1957	2,431	40,441	16.6
1958	2,832	56,928	23.6
1959	1,158	54,167	46.8

The other problem is more directly related to the mesh size we employ in our CalCOFI nets. We construct our nets of No. 30 xxx grit gauze, which has openings of about 0.7 mm before use, and about 0.55 mm after the initial shrinkage. Some of the very small sizes of larvae escape through these mesh openings. We do not consider net selectivity a serious sampling problem except in one respect; anchovy eggs also are not completely retained, hence we cannot make a critical egg-larva comparison for anchovies.

I presented a day escapement graph for sardine larvae in a paper published in 1954. In deriving the graph, I utilized day and night catches for 1940 and 1941, and 1950 and 1951. We now have a much larger mass of data, and it appears that there are some differences between the 1940-41 data, collected by coarser-meshed nets, and the more recent data obtained with the CalCOFI net. Hence, the following discussion is based on the latter data only, covering the years 1950 through 1958.

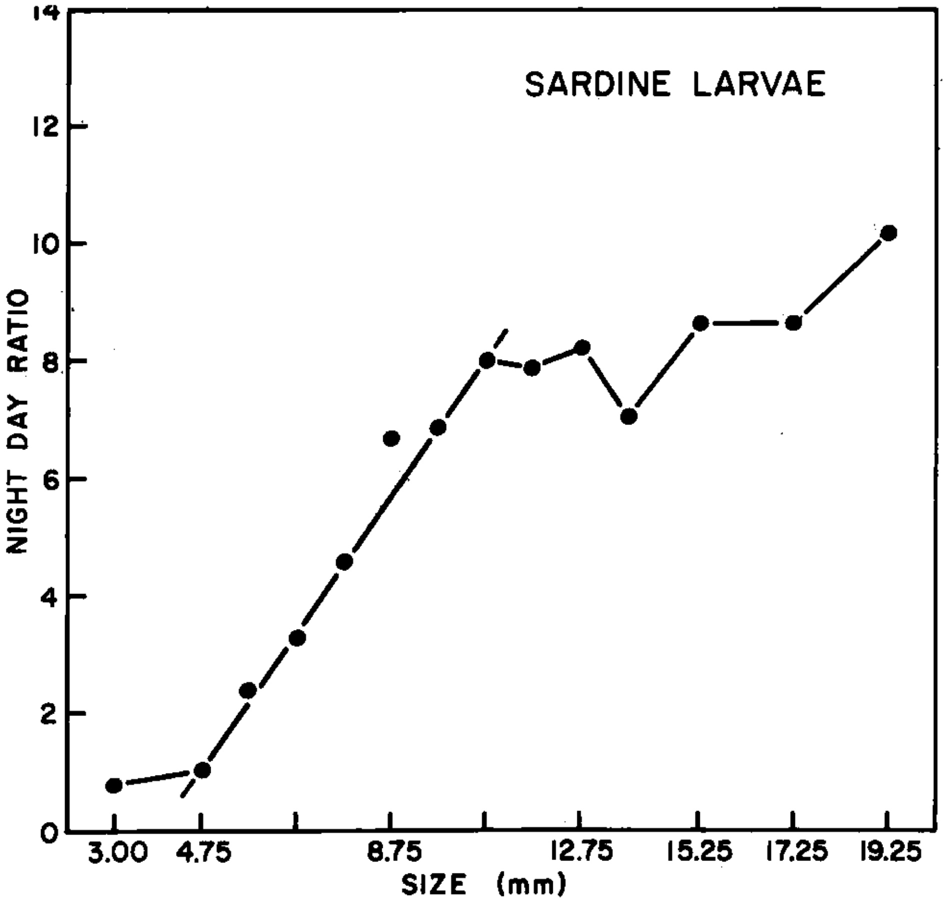

Fig. 3. Extent of undersampling of sardine larvae in day hauls as compared to night hauls, as a function of larval size, based on collections made 1950 to 1958. (All samples containing sardine larvae were used in this comparison, except those collected within one-half hour of sunrise or sunset.)

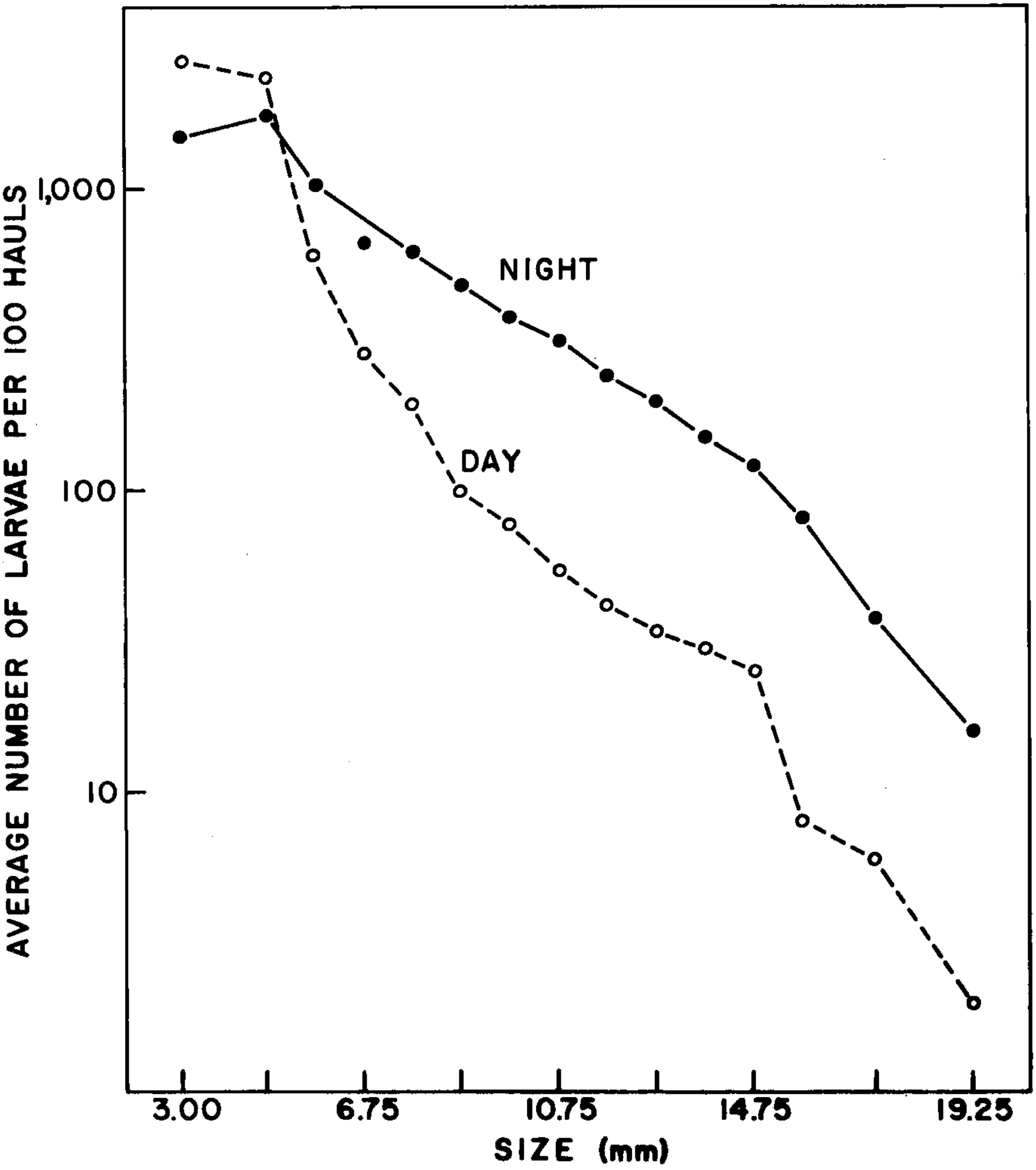

Fig. 4. Relative abundance of day-caught and night-caught sardine larvae, by size, based on the average number of larvae per 100 positive hauls during 1950 to 1958.

TABLE 6. AVERAGE NUMBER PER HAUL (X 10^2) OF NIGHT-CAUGHT AND DAY-CAUGHT SARDINE LARVAE, AND THE DIMINUTION IN NUMBERS OF NIGHT-CAUGHT LARVAE, 1950-58.

Size category	Night-caught larvae	Difference	Diminution in numbers of night-caught larvae	Day-caught larvae
5.75	1,050			602
		380		
6.75	670		208	282
		35		
7.75	635		92	192
		150		
8.75	485		125	99
		100		
9.75	385		85	77
		70		
10.75	315		72	54
		74		
11.75	241		57	42
		40		
12.75	201		44	34
		48		
13.75	153		40	30
		31		
14.75	122		36	25
		40		
15.75	82		42	8
		44		
17.25	38			

I am illustrating undersampling of sardine larvae in daylight hauls in two different figures. In the first, (Fig. 3) the ratios of night-caught larvae to day-caught larvae are shown as a function of larval size. The ratio is close to 1 to 1 at a larval length of 4.75 mm; rapidly increases to about 8 to 1 at 10.75 mm; and then more or less levels off.

The second figure (Fig. 4) is a semi-log plot. The average numbers (x 10^2) of larvae in day and in night hauls are given as a function of size. The difference between day and night hauls is also well shown by this type of plot. The decrease in numbers of larvae with size in the night hauls has a linear relation over the size range from 5.75 to 14.75 mm. This is not a mortality curve: growth rate is not taken into account. Sette (1943) analyzed available information on growth of fishes during the larval period and concluded that a simple logarithmic curve fitted the growth data for the few species about which he had information. The net effect of correcting the 10 size categories involved for logarithmic growth would be to change the slope of the straight-line relation. Obviously these are the sizes of sardine larvae that we sample most adequately. A similar plot is shown for anchovy larvae (Fig. 5).

John Isaacs of Scripps Institution of Oceanography has been intrigued by our sardine and anchovy larval data. He presented a paper on this subject at the Larval Fish Symposium held at Lake Arrowhead last October (Isaacs, MS). One of his novel suggestions is that day-caught sardine larvae are in some way a measure of the mortality of larvae. He concluded from an inspection of day and night records that day-caught larvae in each of the size categories between 5.75 and 15.75 mm are numerically almost equal to the diminution of the numbers of night-caught larvae over the same intervals.

I have plotted the average numbers of sardine larvae (x 10^2) in the day catches and the diminution in numbers in night catches for size categories between 6.75 and 14.75 mm in length (Fig. 6). The data are given in Table 6. It can be seen that day-caught larvae exceed the diminution in numbers of night-caught larvae for the two smaller size categories shown (6.75 and 7.75 mm), and thereafter are uniformly lower in numbers. Although the trends are similar, I would hesitate to conclude that day-caught larvae could be used as a measure of larval mortality of the Pacific sardine.

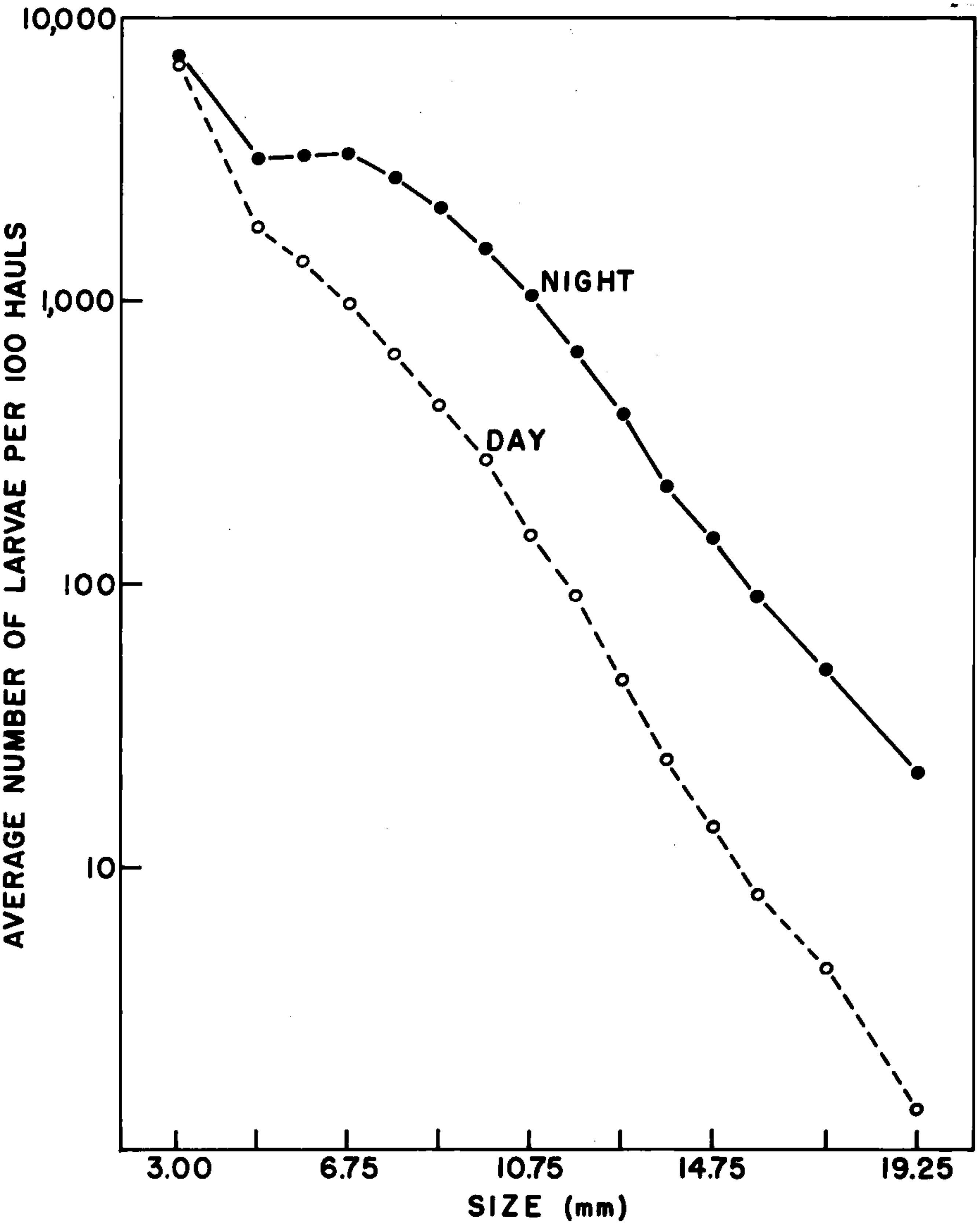

Fig. 5. Relative abundance of day-caught and night-caught anchovy larvae, by size, based on the average number of larvae per 100 positive hauls during 1950 to 1959.

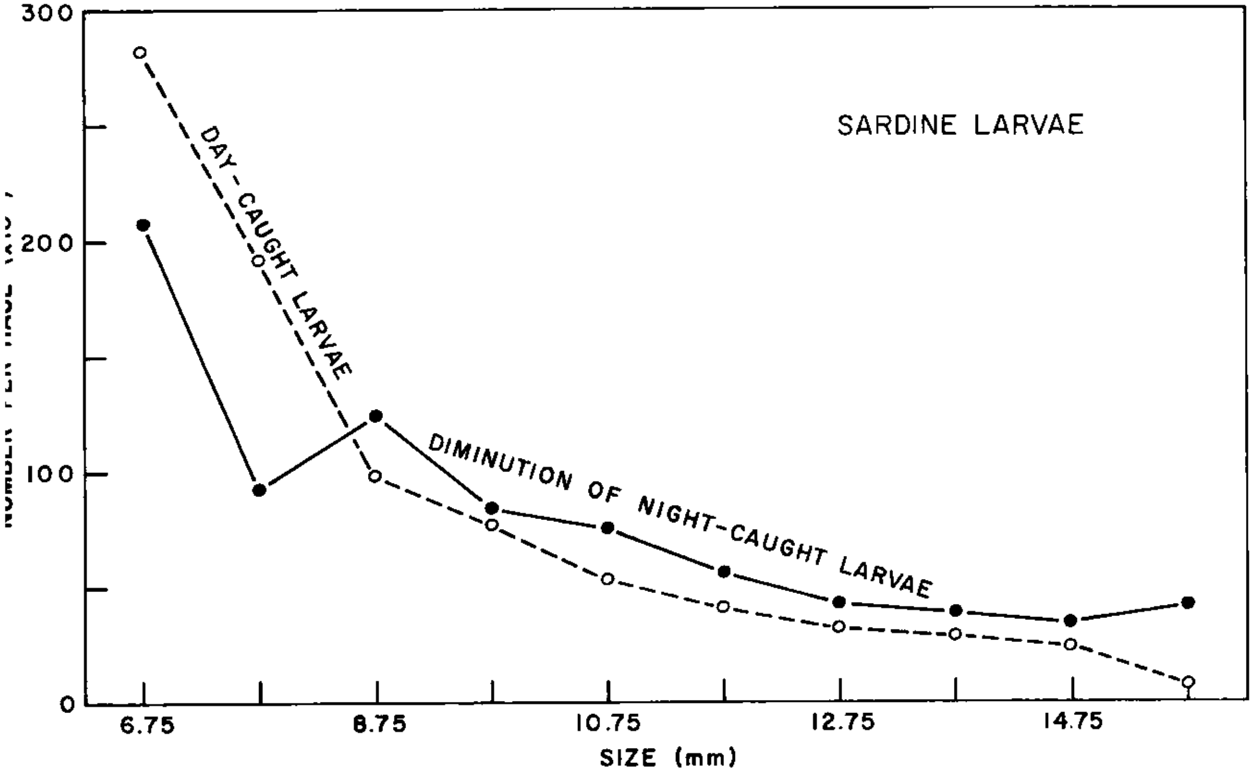

Fig. 6. Average number per standard haul (x 10^2) of day-caught sardine larvae for each 1.0 millimeter size interval between 6.75 and 15.75 mm, compared to the diminution in numbers of night-caught larvae per millimeter of length over the same size range.

TABLE 7. AVERAGE NUMBER PER HAUL (X 10^2) BY SIZE OF NIGHT-CAUGHT AND DAY-CAUGHT ANCHOVY LARVAE, AND THE DIMINUTION IN NUMBERS OF NIGHT-CAUGHT LARVAE, 1950-1959.

Size category	Night-caught larvae	Difference	Diminution in numbers of night-caught larvae	Day-caught larvae
6.75	3,320			973
		535		
7.75	2,785		570	647
		605		
8.75	2,180		606	423
		608		
9.75	1,572		506	273
		512		
10.75	1,060		454	151
		396		
11.75	664		328	90
		260		
12.75	404		216	46
		173		
13.75	231		128	24
		83		
14.75	148		70	14
		57		
15.75	91		48	8
		40		
17.25	51			

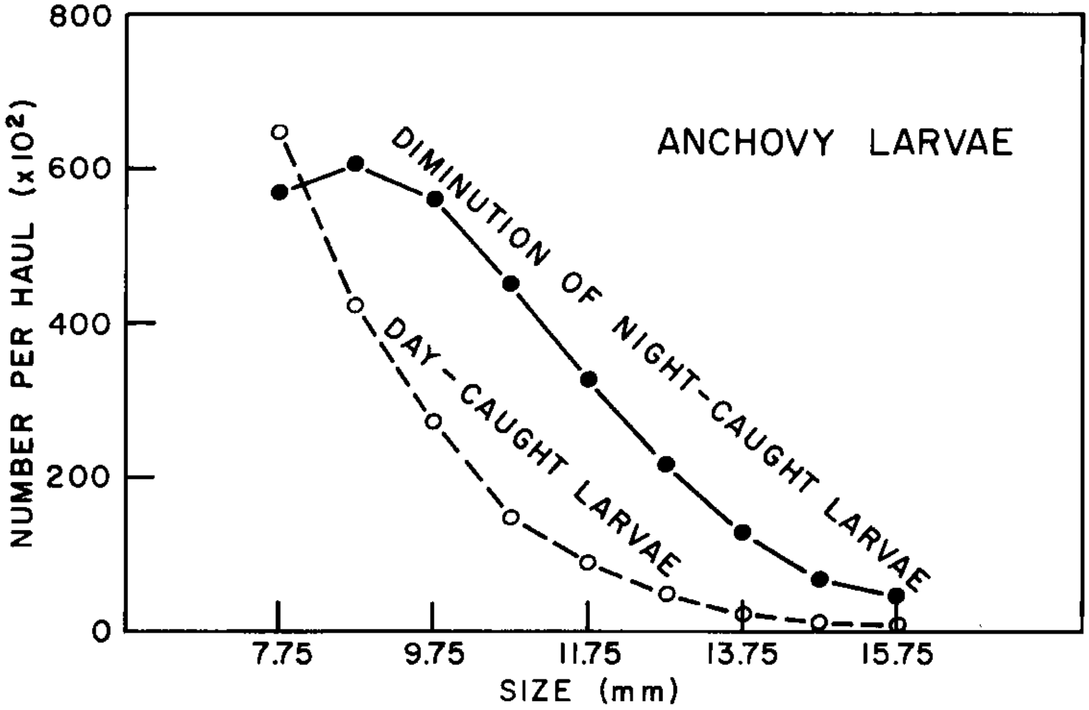

Fig. 7. Average number per standard haul (x 10^2) of day-caught anchovy larvae for each 1.0 millimeter size interval between 7.75 and 15.75 mm, compared to the diminution in numbers of night-caught larvae per millimeter of length over the same size range.

Similar graphs have been prepared for the anchovy (Fig. 7 and Table 7). The disparity between night and day hauls is greater for the anchovy than the sardine. There are proportionately fewer day-caught larvae, and consequently one would never be led to assume that they could represent a meaningful measure of larval mortality.

The picture that is emerging from our investigations is that the primary environmental condition affecting the sardine population is the flourishing anchovy population. I briefly commented in an earlier section about the marked increase in anchovy abundance that has occurred during the period of our CalCOFI surveys. I would like to use my remaining time in looking at the problem of competition between species within a trophic level.

Unfortunately we do not have much information about the comparative strength of the sardine and anchovy populations during the years when the sardine was at a high level of abundance. We made sardine egg and larval surveys in 1939 to 1941, but these were mostly limited to the waters off southern California. During these years the sardine population was in a fairly healthy state. The 1939 year class was the largest of which we have record, for example. At that time anchovy larvae were slightly more abundant than sardine larvae (Marr and Ahlstrom, 1948). We collected 1.2 times as many anchovy larvae as sardine in 1940, 1.7 times as many in 1941. In terms of biomass we know from John MacGregor's investigation that a kilogram of spawning female anchovies will produce twice as many eggs as an equivalent weight of spawning sardines. We also know that anchovies are shorter-lived than sardines.

The relative strength of the sardine and anchovy populations may not have changed much during the decade of the 1940's inasmuch as anchovy larvae were only 2.2 times as abundant as sardine in 1950.

During the decade of the 1950's the picture is quite otherwise. There has been a continuing increase in the size of the anchovy population relative to the sardine as deduced from larval abundance. In 1951 anchovy larvae were 2.6 times as numerous as sardine, by 1955 they were nearly 9 times as numerous. The disparity widened in succeeding years. By 1959 anchovy larvae outnumbered sardines by about 46 to 1, and in 1962 the difference may be as great as 80 to 1.

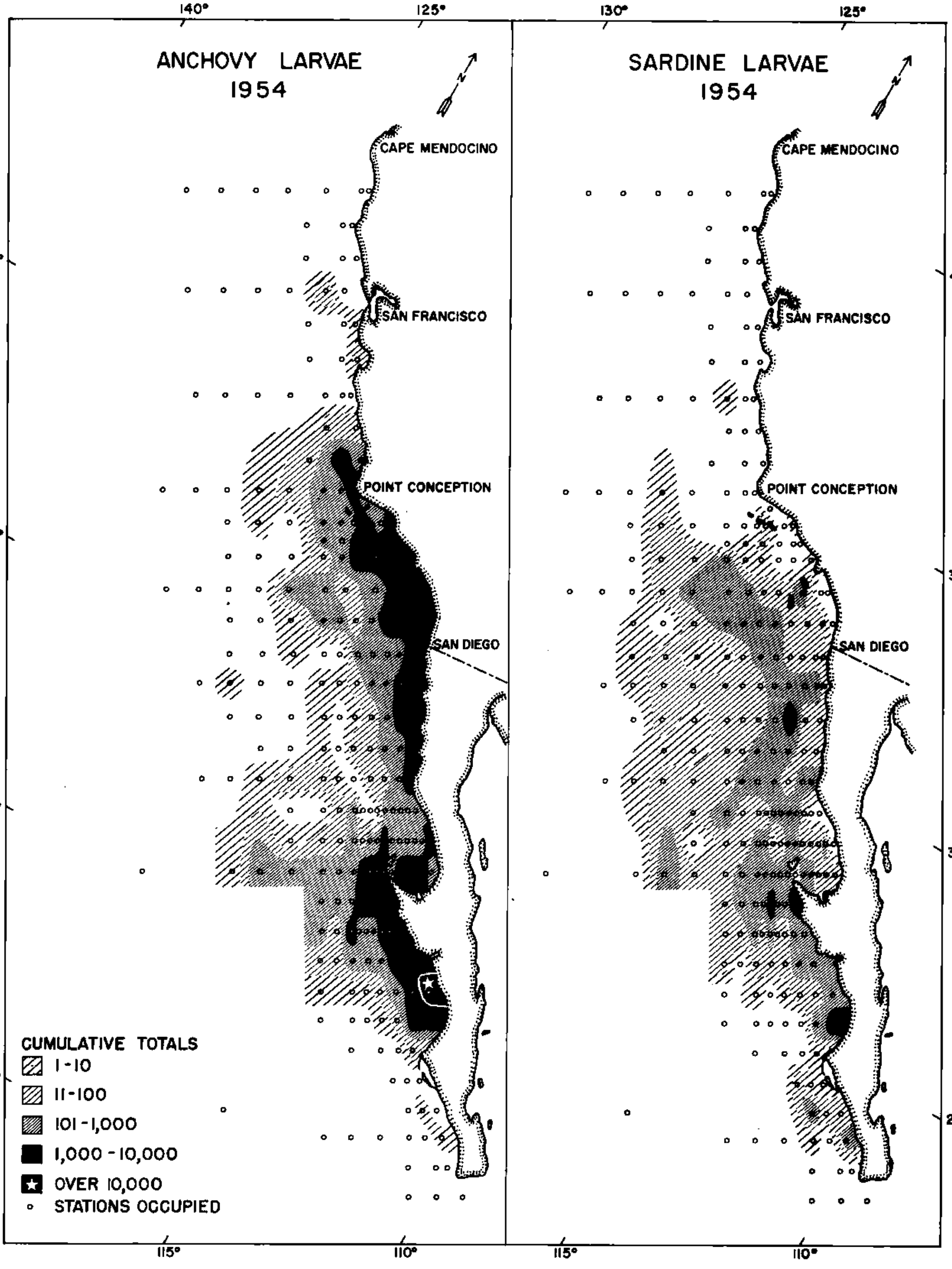

Fig. 8. Distribution and relative abundance of sardine and anchovy larvae in 1954.

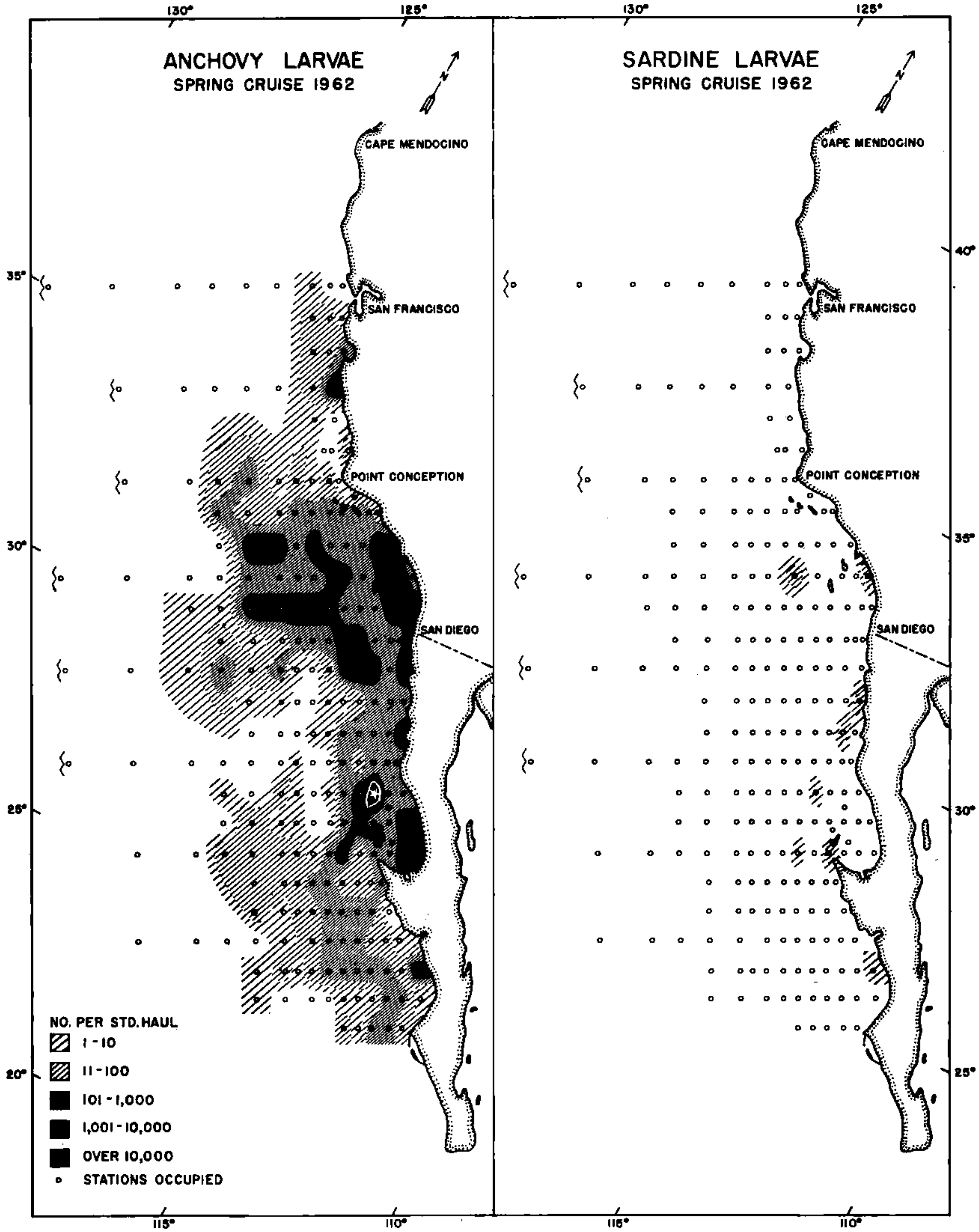

Fig. 9. Distribution and relative abundance of sardine and anchovy larvae during the spring 1962 CalCOFI survey cruise.

Ratios such as the above are striking but also tend to be misleading. The anchovy population, based on census estimates of larvae, more than trebled between 1951 and 1958 (Table 5).

During the same period the sardine population had a brief resurgence in 1954 and then declined to barely one-sixth of this abundance by 1959.

In more recent years, such as 1962, the abundance of anchovy larvae is considerably greater than in 1959, and the abundance of sardine larvae considerably less.

It is interesting to look at some aspects of this change. I have previously contrasted the distribution of sardine eggs in 1953 and 1954. I also wish to contrast the distribution of sardine and anchovy larvae in 1954 (Fig. 8). Note that sardine larvae are even more widespread than anchovy, and that anchovy larvae do not extend as far seaward off southern California as do the sardine larvae. However, note that both species have widespread distributions.

Anchovy larvae, as they increased in abundance, were spread over a larger area. This is strikingly shown in the spring survey cruise of 1962 (Fig. 9). Anchovy larvae are now abundant in offshore waters off southern California where they were barely represented in 1954. Sardine larvae, on the other hand, are exceedingly sparse. Furthermore, they are mostly distributed along shore. The number of anchovy larvae taken on this one cruise was as great as the total number taken in all cruises of 1956, and greater than the combined totals of anchovy larvae for 1950, 1951, and 1952, so great has been the increase in abundance of this species.

As the anchovies have become more widespread, they have tended to co-occur more frequently with sardines. In 1958, 94% of sardine larvae were taken in hauls containing anchovy larvae. A significant reason why the anchovies now have a competitive advantage is their sheer numbers. There were 10 anchovy larvae, on the average for each sardine larva in hauls where they co-occurred in 1958. In the spring cruise of 1962, the few occurrences of sardine larvae were in hauls swarming with anchovy larvae (Fig.9): sardine larvae averaged 19 per haul, anchovy larvae in the same hauls averaged 900. Sardine larvae seldom had the opportunity to see one of their own kind.

As noted above, we do know the time sequence of the increase in anchovy abundance. It began about 1951. The reasons why it occurred are somewhat speculative, but three factors seem to be quite important: 1) a decrease in the abundance of the sardine population due to the coincidence of two exceptionally poor year classes, the 1949 and 1950 classes, 2) a selective fishery which exploited one element of the trophic level, the sardine population, and left the anchovy resource almost alone, and 3) the prevalence of oceanographic conditions that favoured anchovy spawning.

The sardine spawning stock is made up principally of three age groups, two through 4-year old fish. The occurrences of three very poor year classes in succession could have a disastrous effect on the population and even two poor classes in succession could reduce the population to a low level of abundance. The 1949 and 1950 year classes were exceptionally poor ones. Survival during these years was at a rate which was barely an eighth of the average rate for sardine year classes. The increase in anchovy abundance began at about the time that these sardine year classes were recruited. The anchovies were able to fill a hole that developed in their trophic level; there is no evidence that they helped create the hole. The effect of the selective fishery was to give the anchovy a competitive advantage over the sardine. Oceanographic conditions also favoured the anchovy during much of the 1950's. (Marr, 1960, has discussed this problem at some length). Anchovies can spawn at somewhat lower temperatures than sardines. For the sardine, 13°C has been shown to be a limiting temperature; sardine spawning does not ordinarily occur below this. The threshold temperature is lower in the anchovy, being about 11.5° or 12°C.

The difference may not seem large, but it was enough to permit anchovies to spawn earlier off southern California—in some years as much as three months earlier and to spread the spawning over a longer spawning season.

We can quite definitely establish that sardine and anchovy larvae co-occur. We assume from this that the two species compete. The mechanisms of competition are less clear. I have earlier noted that the young stages of sardine and anchovy larvae compete for food. When food is inadequate, this could be a source of mortality. However, the chief source of mortality appears to be predation rather than competition—predation of adults on their own young and the young of other species with planktonic eggs and larvae. Filter-feeding fish are indiscriminate feeders—they feed on whatever they can strain from the water. We have the basic problem that many pelagic fishes have a planktonic phase in their life history, yet depend on plankton for food. Their young are part of this food. This seems to be the mechanism of population control, and it does not really matter whether the predator is a sardine or an anchovy or some other filter-feeding fish.

I have purposely avoided the problem of the relation of survival to spawning stock size. This is a problem that could have taken all the time available to me. Radovich (1962) pointed out that there is a relation between stock sizes and survival, with best survival at middling stock sizes (refer especially to his Fig. 8 on p. 134). Workers on sardines now generally concede this (MacGregor, in press). The spawning stock cannot be dismissed as unimportant. Fishery biology is full of wishful thinking and none more so than in the area of the non-importance of stock size. We in California now know that small spawning stocks produce only small year classes. A year class, on the average, is only about 4/10 as large as the spawning stock. An exceptional year class may be 3 x as large as the parent stock, but a very poor year class may be only 1/20 or 1/25 as large as the parent stock. We have had three abundance regimes, and this relation has held in all three.

And so to conclude. We have found that the chief environmental conditions in our area are biological, not physical or chemical, and that they concern other fishes in the same trophic level with the Pacific sardine. One of the prime accomplishments of CalCOFI surveys has been the documentation of changes in abundance of the younger stages of pelagic fishes in the California Current System during the decade of the 1950's. The value of systematic egg and larval surveys for resource evaluation cannot be overemphasized. On the other hand, we have found an unanticipated uniformity in the survival pattern of sardine and anchovy larvae from year to year.

REFERENCES

AHLSTROM, ELBERT H. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish and Wildlife Service, Special Scientific Report No. 23, 26 p.

1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull., U.S.* 93, 56: 83-140.

1959*a*. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *Fish. Bull., U.S.* , 161, 60: 107-146.

1959*b*. Distribution and abundance of eggs of the Pacific sardine, 1952-1956. *Fish. Bull. U.S.*, 165, 60: 185-213.

1960. Fluctuations and Fishing. Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 1353-1371.

MS. Kinds and abundance of fishes as determined from larvae. Paper delivered at Larval Fish Biology Symposium of the 1963 California Cooperative Oceanic Fisheries Investigations Conference. To be published in CalCOFI Reports, vol. X.

AHLSTROM, ELBERT H., J. ISAACS, J. THRAILKILL, L. KIDD. 1958. High-speed plankton sampler. *Fish. Bull. U.S.*, 132, 58: 187-214.

ARTHUR, DAVID K. 1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Doctoral Dissertation, University of California, Scripps Institution of Oceanography.

BRIDGER, J.P. 1956. On day and night variations in catches of fish larvae. *J. Cons.* 22(1): 42-57.

GULLAND, J.A. 1964. Survival of the youngest stages of fish, and its relation to year-class strength. This Symposium, p.363-371.

ISAACS, JOHN D. MS. Larval sardine and anchovy interrelationships. Paper delivered at Larval Fish Biology Symposium of the 1963 California Cooperative Oceanic Fisheries Investigations Conference. To be published in CalCOFI Reports, vol. X.

LASKER, REUBEN, 1964. Effect of temperature on incubation time, development and growth of embryos of the Pacific sardine, Copeia, No. 2: 399-405.

MACGREGOR, JOHN S. 1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). *Fish.Bull. U.S.*, 121, 57: 427-449.

1964. The relation between anomalies of spawning stock size and year-class size for the Pacific sardine, *Sardinops caerulea* (Girard). *Fish. Bull. U.S.*, 63 (2): 477-491.

MARGALEF, RAMON. 1960. Fluctuations in abundance and availability caused by biotic factors. Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 1265-1285.

MARR, JOHN C. 1960. The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard). Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 667-791.

MARR, JOHN C. and ELBERT H. AHLSTROM. 1948. Observations on the horizontal distribution and the numbers of eggs and larvae of the northern anchovy (*Engraulis mordax*) off California in 1940 and 1941. U.S. Fish and Wildlife Service, Special Scientific Report No. 56, 13 p.

NAKAI, ZINZIRO, 1960. Fluctuations in abundance and availability of sardine populations caused by abiotic factors. Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 1327-1352.

RADOVICH, JOHN. 1962. Effects of sardine spawning stock size and environment on year-class production. *Calif. Fish and Game*, 48 (2): 123-140.

RUSSELL, E.S. 1926. The vertical distribution of marine macro-plankton. III. Diurnal observations on the pelagic young of teleostean fishes in the Plymouth area. *J. Mar. biol. Ass. U.K.*, 14: 387-414.

SAVILLE, ALAN. 1964. Estimation of the abundance of a fish stock from egg and larval surveys. *Rapp. Cons. Explor. Mer.* 155: 164-170.

SETTE, OSCAR E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I. Early life history, including growth, drift and mortality of the egg and larval populations. *Fish. Bull. U.S.*, 38, 50: 149-237.

1960, The long term historical record of meteorological, oceanographic and biological data. California Cooperative Oceanic Fisheries Investigations Reports, VII: 181-194.

SETTE, OSCAR E. and ELBERT H. AHLSTROM. 1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. *J. Mar. Res.*, VII (3): 511-542.

SHELBOURNE, JAMES E. 1957. The feeding and condition of plaice larvae in good and bad plankton patches. *J. Mar. biol. Ass. U.K.*, 36 (3): 539-552.

SILLIMAN, RALPH P. 1946. A study of variability in plankton tow net catches of Pacific pilchard (*Sardinops caerulea*) eggs. *J. Mar. Res.*, VI (1): 74-83.

SPRAGUE, LUCIAN and ANDREW M. VROOMAN. 1962. A racial analysis of the Pacific sardine (*Sardinops caerulea*) based on studies of erythrocyte antigens. Annals of the New York Academy of Sciences, 97, article 1: p. 131-138.

TAFT, BRUCE A. 1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. *Limnol. & Oceanogr.* 5 (3): 245-264.

VROOMAN, ANDREW M. 1964. Serologically differentiated subpopulations of the Pacific sardine. *J. Fish. Res. Bd. Canada,* 21 (4): 691-701.

WALFORD, L.A. 1946. Correlation between fluctuations in abundance of the Pacific sardine (*Sardinops caerulea*) and salinity of the sea water. *J. Mar. Res.* VI (1): 48-53.

A REVIEW OF THE EFFECTS OF THE ENVIRONMENT ON THE TUNA

By

Vernon E. Brock[1]

INTRODUCTION

Tuna are among the most pelagic and mobile of fishes. Their distribution and movements mirror the oceanic regions of favourable environment and changes in these with an apparent precision, now largely beyond the human oceanographer, but slowly coming within his reach.

The present review is concerned with the results of recent work which have added significantly to our understanding of the effects of the environment on this interesting and important group of fishes. A short lecture, such as this, is not suitable for an exhaustive review.

The environment is considered as all the external or internal foreign elements that may affect the tuna. However, one complex of elements, the tuna fisheries and their effects on tuna populations, is not dealt with here.

Attention has been given to those species of tuna for which environmental effects have been reported in some detail. Mention is made of other species of tuna which include altogether, following nomenclature of Collette and Gibbs (1963), the albacore (*Thunnus alalunga*), the Atlantic bluefin tuna (*T. thynnus thynnus*), the Pacific bluefin tuna (*T. thynnus orientalis*), the yellowfin tuna (*T. albacares*), the bigeye tuna (*T. obesus*), and the skipjack (*Euthynnus pelamis*).

Environmental changes that may affect tuna include its physical deterioration or improvement, availability of prey, suitability of a region for the survival of eggs and larvae, and the competition or predation of other species. Other changes in the quality of the environment may occur relating to parasites, diseases, and subtle changes in the marine community of which the tuna are a part.

Environmental effects to be significant must, of course, evoke a response. The response may be either active or passive. Active responses may involve translocation, schooling, or other behavioural changes. These may also change with changes in size and maturity.

The passive responses are ones of endurance, and are detectable by changes in mortality or recruitment rates. Survival in these cases is not through appropriate patterns of behaviour or movement, but by the reproductive, physiological, or ecological resilience of the species.

The problems of obtaining adequate data on environmental changes together with the accompanying responses of the tunas have not been frequently solved. The effects of the environment on the tuna have been deduced largely from data concerning tuna fisheries, studies of the fish landed, and work at sea, both aboard fishing and fisheries research vessels. Environmental data have also been obtained from fishing and fisheries research vessels. However, most of these data are from a diversity of sources such as sea surface temperatures from merchant ships; oceanographic observations from oceanographic research and survey ships, weather station ships, naval ships, and others; and data from shore stations.

Not much of the data on the environment and on the tuna are collected simultaneously in space and time. To varying degrees the adequacy of their juxtapositioning is inferential. In addition, the major source of data concerning the effects of the environment on the tuna, the tuna fisheries, provides information that is also largely inferential in character. A recent contribution by Shibata (1963) suggests that the inferences made from catch data may sometimes not be true. He reported on the comparison of catch rates by long-line gear and density of tuna estimated from a sonic fish finder operated at the same times and places where fishing was done. He found no relationship between the two methods for estimating abundance.

Regardless of what fishing success measures, it can sometimes be related to changes in a given

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environmental parameter. However, it may be only inferential that changes in the environmental parameter measured are directly responsible for changes in fishing success. The existence of a chain of causal relationships between the cue to which the fish respond and the measured property will make the observed relationship of unknown reliability depending upon the invariability of the causal linkages involved. These are some of the sources of error in the data.

The environment of the tuna is the pelagic realm of the temperate and tropical ocean. The complex of ocean currents composing the equatorial circulation and the great current gyres poleward of the equator are the important habitats. Various species also occur in seas located at suitable latitudes.

The distributions and abundances of tuna and changes in these are related to the pattern of ocean currents and their changes. The basic pattern of surface currents for the major ocean basins at low and mid latitudes is a transport of water to the western side in the equatorial region, a flow towards the poles along this side, a return flow across the ocean basin to the east at middle latitudes, and a flow towards the equator on the eastern side. Various portions of these great gyral currents have various names such as the Gulf Stream, the North Atlantic Current and the Canary Current in the North Atlantic. Corresponding current segments in the North Pacific are the Kuroshio, the North Pacific and the California Currents. The flow of these currents, by the movement of tropical water poleward on the western margin of the ocean basin and by the movement of temperate water towards the equator on the eastern margin, broadens the band of tropical water in the western oceanic regions and narrows it in the eastern oceanic regions. The depth of the isothermal surface layer of warm water in the tropics is also greatest in the west, and least in the east. The broad band of cool water of the temperate latitudes in eastern oceanic regions is further cooled and enriched by coastal upwelling of greater or lesser intensity. The seasonal temperature change of the surface waters in this part of the ocean is not great, while in contrast the relatively narrow band of cool water in temperate latitudes on the western margin of the oceans shows a marked change in temperature between winter and summer. This description of the major features of the oceanic surface circulation of the temperate and tropical regions is a great simplification of the situation obtaining, but should suffice as a background for considering the effects of the environment on the tuna.

The availability of some species of tuna to various fishing gears may depend upon transitory or permanent features of the ocean. Brock (1959) suggested that the relatively shoal thermocline in the eastern tropical Pacific may be related to the success of surface and near-surface fishing methods such as purse seining. This suggestion implies that the thermocline may serve as a floor to the vertical distribution of the tropical species. Conversely it may also serve as a ceiling for the albacore in the tropics where this species is available to long-line gear, but never apparently in evidence on the surface.

Laevastu and Rosa (1963, Fig. 10) summarize data regarding the temperature tolerance of tunas. The yellowfin appears to tolerate the highest temperatures, and the bigeye, the greatest temperature range. Since this latter species seems to rarely occur at the surface, the surface water temperatures for its fishing areas may not provide a good indication of that of its normal habitat. The albacore and bluefin tunas are considered as temperate water species and possibly the bigeye too, while the skipjack and yellowfin are tropical species. All of these species occur, however, in the tropics to some degree.

THE ENVIRONMENT AND VOLITIONAL RESPONSES OF THE TUNA

During the summer months the poleward movement of many tuna species is a characteristic occurrence which sustains important fisheries. The summer occurrence of albacore and Pacific bluefin tuna off California, skipjack and the Pacific bluefin off Japan, the Atlantic bluefin off northern Europe and New England are examples of this poleward movement. There is no evidence relating these excursions to reproductive activities; in fact, the albacore and Pacific bluefin in California waters are adolescent, immature fish. The most probable hypothesis is that such movements are invasions of a habitat which for reasons of water temperatures or some other is only available seasonally but which affords a more abundant source of prey. In the tropics the seasonal cycle is less evident, at least as far as temperature changes are concerned. However, evidence exists that biologically productive areas have associated higher abundances of tuna. Schaefer (1960) reviews much of this evidence for the eastern and central Pacific, pointing out the association between oceanic processes that stimulate biological productivity such as upwelling and the effects of the equatorial current and countercurrent interaction in bringing nutrient salts into the enphotic zone. The temperature structure of the tropical ocean, with a permanent warm surface layer separated by a density difference from the cooler underlying waters, leads to a depletion of the nutrient salts in the surface layer and its consequent biological impoverishment. The cooler subsurface waters are potential sources of nutrient salts, and any process that moves water of this layer into the illuminated surface layer will stimulate biological productivity.

Blackburn (1963) investigated the association of tuna with variations of biological productivity in the Gulf of Tehuantepec on the west coast of Mexico. He found that the consistent and vigorous northerly winter winds result in the entrophication of the waters of a portion of the Gulf and that the abundance of yellowfin tuna, as estimated by the fishery, was significantly associated with this portion some three months later. A similar association was not found for skipjack; however, the possibility that this species may be excluded during the spring and summer of warm years, thus interfering with the detection of the association, was mentioned but not investigated.

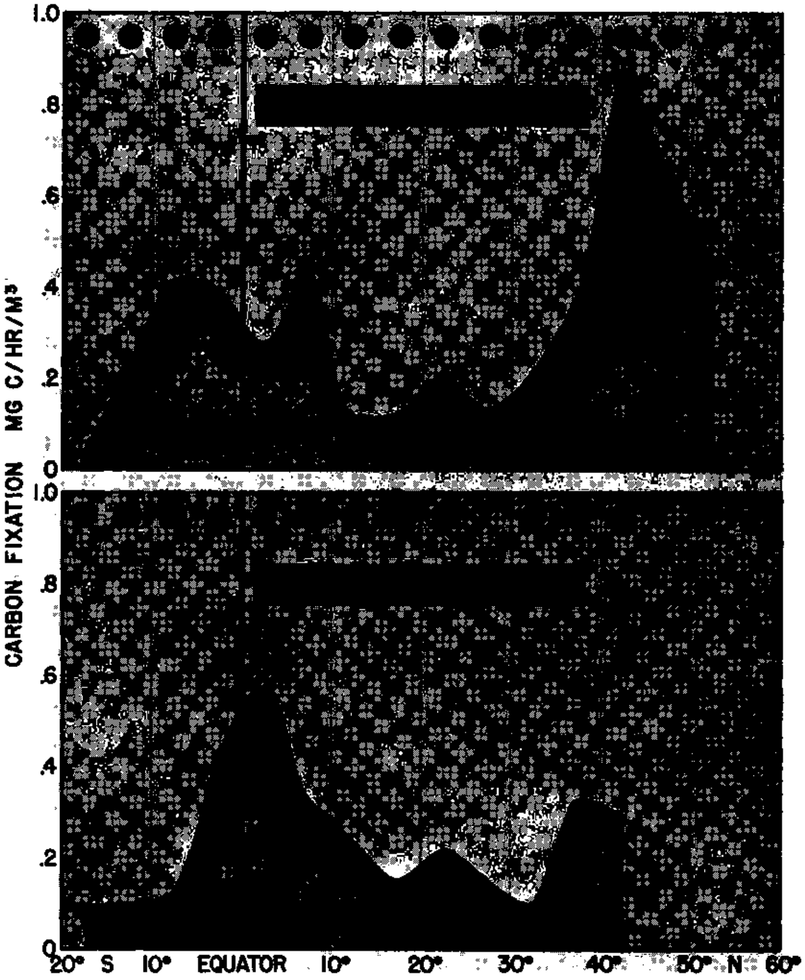
The time lag in the association between the entrophication of a portion of the waters of the Gulf and the abundance of yellowfin tuna was attributed to the time required for the results of entrophication to appear as an increased abundance of tuna prey.

The association of tuna with sea mounts and banks suggests that these features are productive of food for tuna, a suggestion that has not yet been clearly demonstrated to be true. While tuna appear to be more abundant in the vicinity of oceanic islands, a major effect of islands on offshore productivity thereby attracting tuna has not yet been clearly proven. However, an island effect on the composition of the zooplankton for a considerable distance offshore has been shown (Jones, 1962). There is some evidence that yellowfin tuna near islands in the central Pacific are smaller in average size than those further offshore (Shomura and Murphy, 1955).

Austin and Brock (1959) examined the relationships among primary productivity as estimated by C-14 uptake, the standing crop of zooplankton, the standing crop of zooplankton predators from mid-water trawl hauls, and of climax predators from long-line catches from lat 20° S to 40° N. Productivity was high in the equatorial and mid latitude regions, low in lat 10° - 20° band as measured at these trophic levels (Fig. 1, 2). The tuna provided an identical pattern when all species were lumped except for the high latitude stations. However, in the equatorial region the only species whose abundance coincided with the regions of highest biological productivity was the yellowfin; the greatest abundance of albacore and bigeye was at higher latitudes where primary productivity was less (Fig. 3). While these data may reflect some artifacts of gear selectivity or differences in vertical distributional patterns among these species, there is a suggestion of differences in habitat requirements which do not, in all cases, coincide with the region of highest biological productivity. The equatorial distributional patterns of albacore may be related to the habitat requirements of the eggs and larvae rather than that of the adults. The ready availability of skipjack to the local Hawaiian fishery during the summer months appears to be a departure from the relationship between the abundance of tuna and their prey. While it can be hypothesized that the skipjack appear in the Hawaiian region, which is in the subtropical belt of low marine productivity, to spawn, they appear to grow rapidly during their season of abundance (Shippen, 1961).

The seasonal poleward movements of some species of tuna are apparently quite sensitive to anomalies of the ocean climate. These anomalies, being unexpected to a degree, and causing shifts in the customary times and places where tuna occur, may occasion serious economic loss to tuna fisheries. An understanding of their effects and predictions of their occurrence are, therefore, greatly desired. Uda (1962) discusses anomalous events in the ocean climate on both sides of the North Pacific and in the North Atlantic together with the linkage mechanisms provided by the atmosphere. Changes in the deep-water circulation in the western North Pacific which may shift the position of the Kuroshio off Japan are also discussed. The possibility of a periodicity in these events related to the sunspot cycle is considered. The apparent reciprocal relationship between the yields from skipjack and albacore fisheries off Japan and the west coast of the United States is discussed in relation to these anomalous situations.

Radovich (1963) discusses the anomalous warming of the ocean off California and the associated poleward movements of warm water fishes including various species of tuna which brings them into regions far beyond their normal ranges. Radovich concludes that these movements are a direct response to temperature change. It is of interest, in this connection, that skipjack appear to leave the warmest areas in the eastern tropical Pacific, when summer temperatures exceed 28° C, during the warm years (Anon., 1963).



CARBON FIXATION

Fig. 1.

Hester (1961) made a study of the areas of seasonal catch of albacore and Pacific bluefin tuna off the coasts of California and Lower California. He found, during years of below normal sea surface temperatures, a large part of the catch came from the waters south of California, off Lower California. Bluefin tuna are taken south of the best albacore fishing localities ordinarily, apparently preferring somewhat warmer water than the albacore. The center of the fisheries for both species move northward as the season advances. Hester's Fig. 1, recopied here as Fig. 4, shows the center of the seasonal bluefin fishery for a selected cold period (1952-53) largely south of Point Eugenia, about midway along the coast of Lower California, and in contrast for a warm period (1957-58) off Southern California, a latitudinal shift of 350 - 400 miles.

Johnson (1963) also studied the eastern North Pacific Ocean albacore landings during the 1952 cold period and the 1958 warm period on the basis of sea surface temperatures and salinities for a large part of the eastern North Pacific Ocean. During the 1952 albacore season the coastal zone where fish were found was from lat 27° to 45° N. The 1958 coastal fishing ground was from lat 31° to 48° N. The fishery began at the southern end of the ground, usually in June, progressing northward as the season advanced. Johnson related the more southerly occurrence of albacore at the beginning of the fishing season in 1952 to the more vigorous flow and consequent stronger southern penetration of the California Current. In 1958, when the fishery began further to the north, the California Current flow was weaker. The water type characteristic of the California Current could be identified by a combination of lower temperature and salinity, and the general area where the

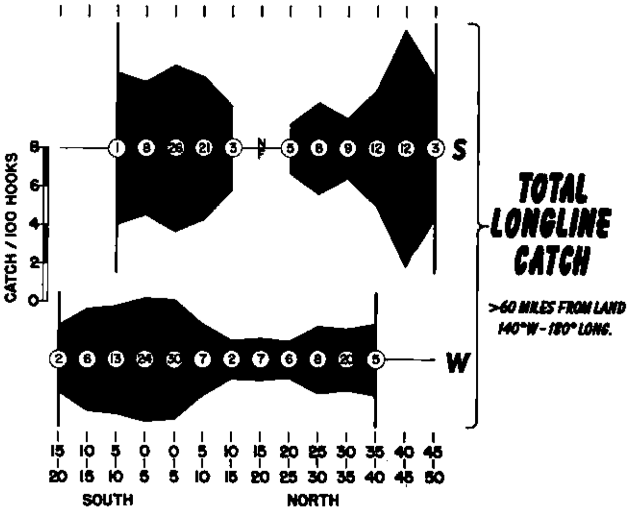

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Fig. 2.

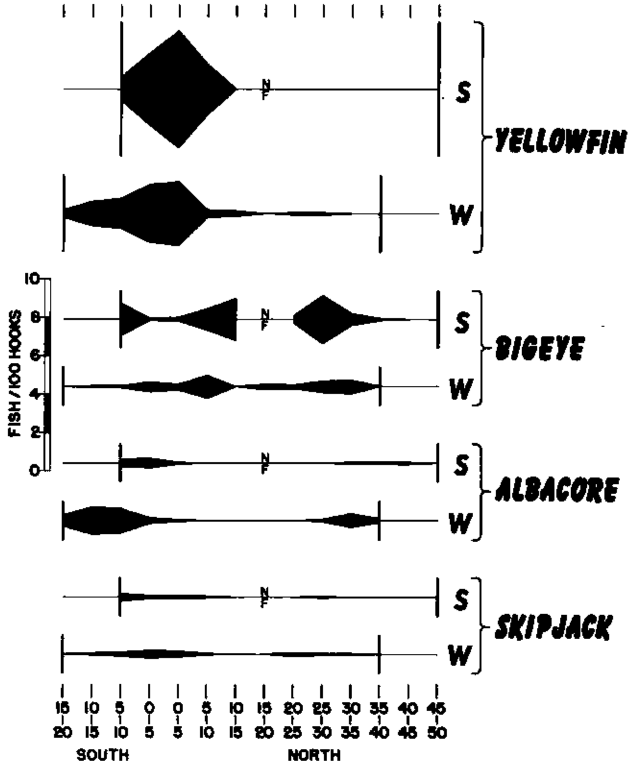
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Fig. 3.

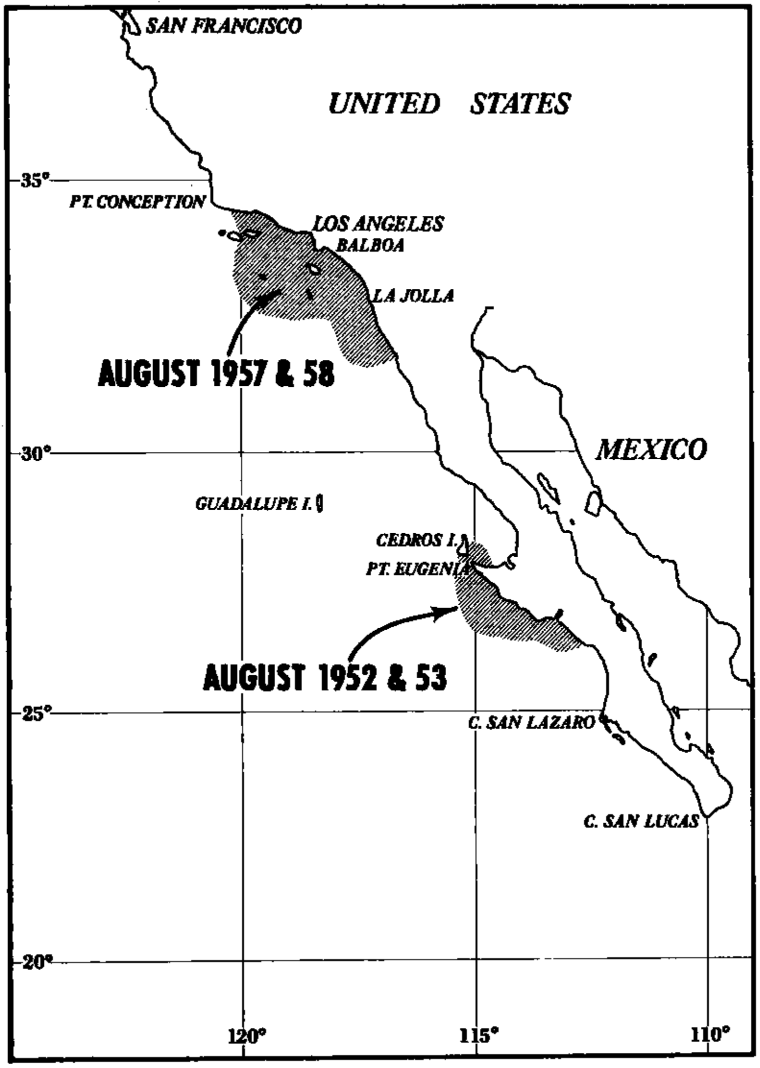


Fig. 4, from Hester, 1961

coastal fishery could be anticipated to begin corresponded to that where this water type approached the coast. The distribution of isotherms in this part of the eastern north Pacific tends to roughly parallel the coast, approaching it obliquely in the south. The movement of albacore, judging from tagging experiments (Otsu, 1960), begins in the central north Pacific in spring towards the American coast in the 13° to 18° C band of water of the Transition Zone lying between the Subarctic and Subtropic Zones. As the fish approach the coast they migrate in the California Current.

Johnson found the anomalously cold conditions for 1952 characterized a large part of the eastern north Pacific and could be related to a more vigorous pattern of wind flow which strengthened the flow of the California Current and increased the degree of coastal upwelling. These associated phenomena were evident several months prior to the beginning of the albacore fishery. He also found in 1958, the wind patterns were such as to weaken the flow of the California Current and that an anomalously warm period was also in evidence several months in advance of the albacore fishing season.

The area where albacore would first appear could be anticipated to a degree by the spring sea surface temperature and salinity distributions in the Southern California - Lower California region. The California Department of Fish and Game has made spring cruises in this region and used the sea surface temperature data as a basis for predicting the locale of the initial albacore catches of the season (Clemens, 1961).

The shifts in the coastal fishing grounds for albacore as related to shifts in ocean climate suggest that the species can detect and remain in a particular water type. The success of the seasonal fishery may depend in part on the relation of the position of the water type, the location of the fishing ports, and the range of the fishing vessels.

The albacore fishery of the eastern north Pacific has experienced major fluctuations in yield in the past, including a virtual disappearance of landings for a time. The mean annual California landing for the years 1916 - 25 was about 17,000 tons; for 1926 - 41, about 2,400 tons; and for the subsequent period, 1942 - 61, about 31,000 tons. During this latter period an additional 10,000 tons or so was landed annually in Oregon and Washington ports to the north of California. Whether the period of scarcity following 1925 was related to major anomalies in the ocean climate or changes in the abundance of the north Pacific albacore stock is not known. Beginning in 1936, an albacore fishery developed to the north of California which continued following the resurgence of the fishery in California. Uda (1962) reported that the 1930 - 40 period was one of good fishing off Japan, and the 1941 - 49 period as one of poor fishing. Figure 5 depicts the albacore fishing areas for the North Pacific.

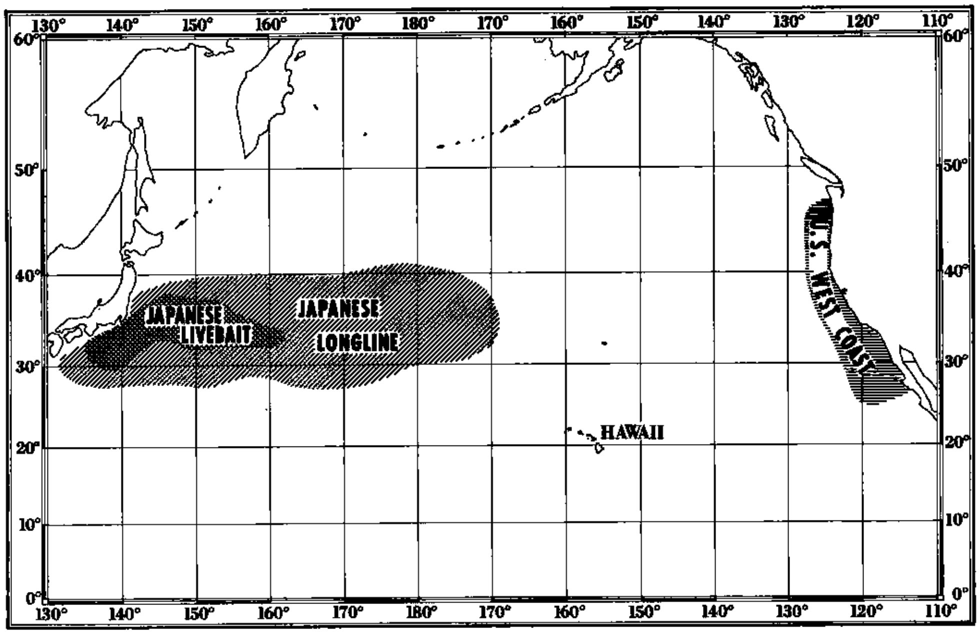


Fig. 5, from Otsu, 1963.

In addition to the bluefin tuna and albacore, there are seasonal fisheries for skipjack in the middle latitudes. The duration and developmental pattern of the large skipjack fishery off Japan is strongly affected by the Kuroshio system and its dynamic interaction with the Oyashio (Anon., 1963). A fishery for this species is also beginning in the analogous current systems in the western north Atlantic.

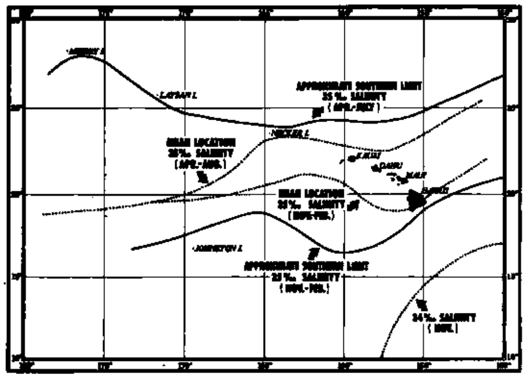


Fig. 6, from Seckel, 1963.

While the seasonal association of tuna with summer warming is well known, studies of the seasonal changes in abundance of skipjack in Hawaiian waters and their anomalies suggest the possibility of more subtle environmental responses. Seckel (1963) described the seasonal cycle in the ocean climate for the Hawaiian region, its anomalies, and the associated changes in the availability of skipjack. The seasonal change at the latitude of the Hawaiian Islands is a gentle one, and the marine environment never becomes unsuited for skipjack which is, indeed, a resident species. Nevertheless, the summer catch may exceed that of winter by as much as twenty times, and the proportion of large fish in the landings greatly increases during the summer.

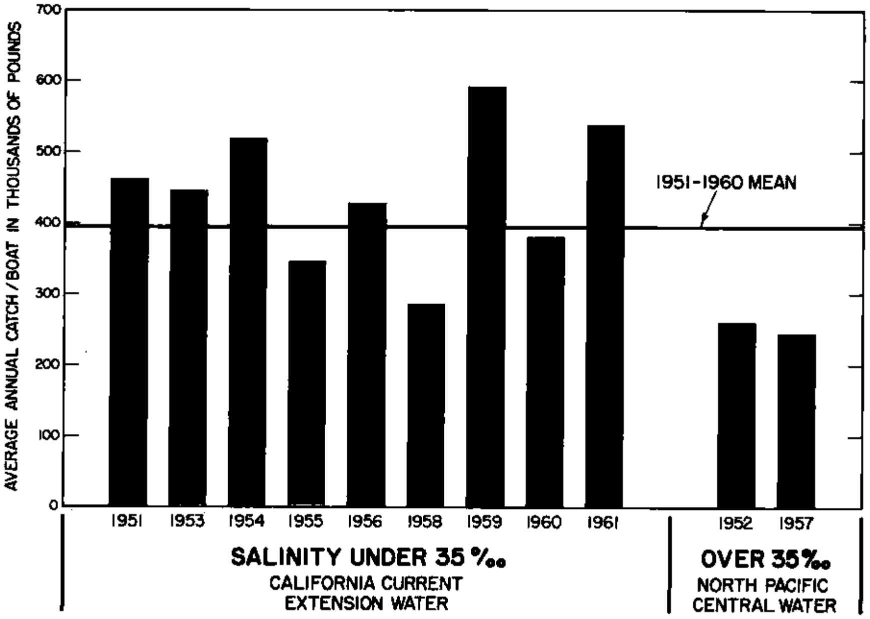


Fig. 7, from Seckel, 1963.

Coincident with the seasonal changes in the availability of fish is a change in the origin and character of the water in the Hawaiian region. During the summer period of good fishing, the water is of transitional character between the North Pacific Central and the North Pacific Equatorial Water Types. This transitional water type has been referred to as the California Current Extension by Seckel. It is separated from the North Pacific Central Water Type by a well defined salinity gradient. This salinity gradient (from 34.8°/00 to 35°/00) is located to the north of the main islands from April through August or September, and to the south from November through February (Fig. 6). At other seasons of the year it is in transit through these islands. This rhythmic seasonal movement of the salinity gradient through the Hawaiian Archipelago, marking the replacement of one water type by another, varied from year to year in the precise time of the advance and retreat and in the vigor of the change. In some years, the more saline waters remained in the Hawaiian area through the summer, and during such years the catch of skipjack was roughly half that of the best years (Fig. 7).

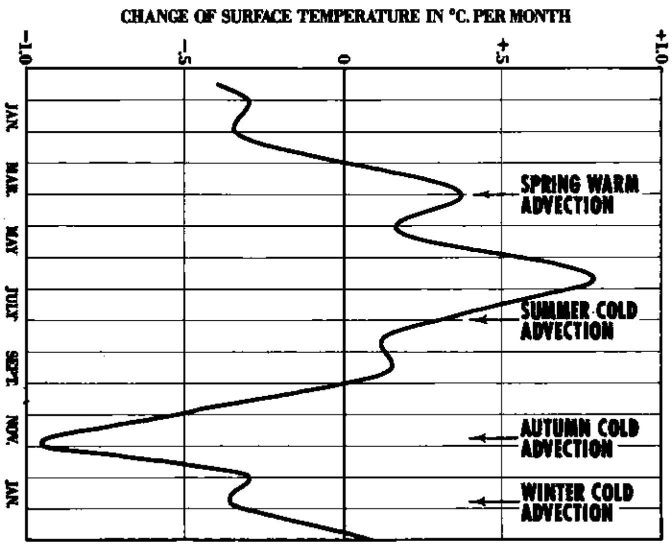


Fig. 8, from Seckel, 1963.

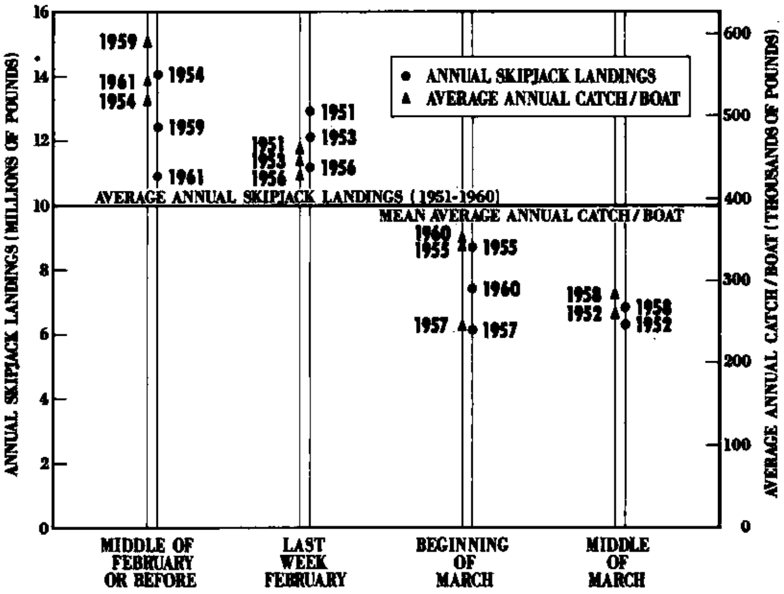


Fig. 9, from Seckel, 1963.

The change in the water types was detectable not only by salinity changes, but by temperature changes also. The seasonal change of sea surface temperatures followed a characteristic pattern, best expressed as a rate of change of temperature with time (Fig. 8). The changes in the observed temperatures reflected, in part, the advection of water through the Hawaiian region, and the time when the rate of temperature change reversed direction from negative to positive indicated a reversal in the direction of advection and provided an advanced notice that the California Current Extension had begun its seasonal march towards Hawaii (Fig. 6). The reversal of advection usually occurred between the latter half of February and the middle of March. The earlier it did occur, the earlier was the beginning of summer in the sea and the appearance of large skipjack in abundance, characteristic of this season. In this situation was the means of predicting during the early spring the probable quality of the fishing for the next summer. Such predictions have been made on this basis since 1959 by the staff of the Honolulu Biological Laboratory, Bureau of Commercial Fisheries. Figure 9 shows the relationship between the time of the reversal in the temperature trend and the annual average catch by boat and that for the year. The reversal from cooling to warming of the ocean surface layers had been followed, as previously mentioned, when this change occurred early in the spring, with a correspondingly earlier replacement of the high salinity North Pacific Central Water by that of the lower salinity California Current Extension for the period for which data were available. In 1963, although the early spring reversal in the trend of sea surface temperatures did occur, it was not followed with the replacement of the first mentioned water type by the second. Apparently the dynamic seasonal processes began with vigor, but became much weaker, for some reason, prior to summer. The substantially lower than average yield of skipjack for the Hawaiian fishery for 1963 also indicated that the availability of skipjack responded to the anomalous development of the season as might have been anticipated.[1] Interestingly enough, the two water types did not differ significantly in their standing crops of zooplankton or other evidence of productivity aside from that provided by the fishery.

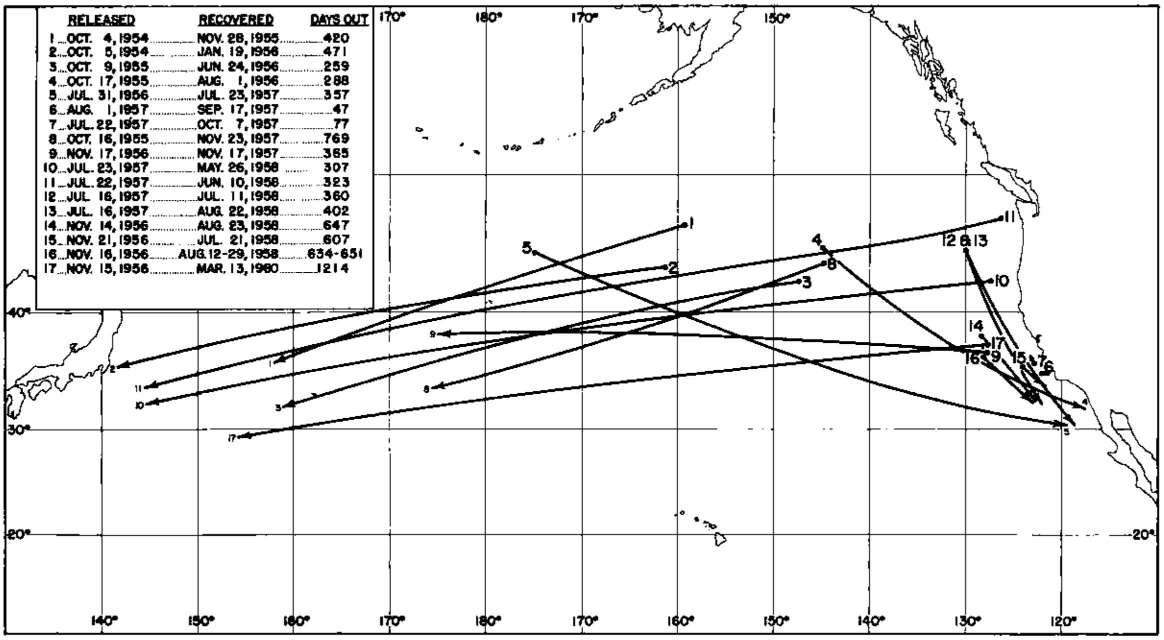
The stock of skipjack associated with the California Current Extension in Hawaii has not exhibited any immunological differences, based on serological tests, from those of the Mexican coast (Dr Lucian Sprague, personal communication). The skipjack present in Hawaiian waters during the winter months do exhibit differences in this regard, suggesting the occurrence of two independent stocks of this species replacing each other seasonally, each associated in Hawaiian waters with a different water type. A related bit of evidence, the recovery of two skipjack in the summer Hawaiian fishery two years after being tagged off Mexico, further strengthens the possibility that the summer Hawaiian skipjack and the skipjack of the eastern Pacific belong to the same stock.

SIZE CONNECTED ACTIVE ENVIRONMENTAL RESPONSES

Studies of the environmental responses of some species of tunas have suggested a change in such responses with growth. These produce a differential distribution of the fish by size or age. In the Pacific this appears to be the case for albacore, bluefin and skipjack tunas.

Brock (1943) found that the albacore fishery of the eastern Pacific off Oregon took adolescent fish and reported that the Hawaiian longline fishery took much larger fish including an occasional mature one. He suggested the possibility that the spawning stock may be in the tropical central Pacific with the adolescent fish entering the temperate eastern Pacific on a feeding migration.

Subsequently the successful tagging of albacore by the California Department of Fish and Game (Wilson, 1953) and later by the Honolulu Biological Laboratory of the Bureau of Commercial Fisheries (Otsu, 1960) (Fig. 10) suggested a complex pattern of migration across the Pacific, with the smaller fish reaching the central north Pacific during the winter months but returning to the eastern side during the summer. To an increasing degree the larger fish continued across the Pacific, being taken



	RELEASED	RECOVERED	DAYS OUT
1	OCT. 4, 1954	NOV. 28, 1955	420
2	OCT. 5, 1954	JAN. 19, 1956	471
3	OCT. 9, 1955	JUN. 24, 1956	259
4	OCT. 17, 1955	AUG. 1, 1956	288
5	JUL. 31, 1956	JUL. 23, 1957	357
6	AUG. 1, 1957	SEP. 17, 1957	47
7	JUL. 22, 1957	OCT. 7, 1957	77
8	OCT. 16, 1955	NOV. 23, 1957	769
9	NOV. 17, 1956	NOV. 17, 1957	365
10	JUL. 23, 1957	MAY. 26, 1958	307
11	JUL. 22, 1957	JUN. 10, 1958	323
12	JUL. 16, 1957	JUL. 11, 1958	360
13	JUL. 16, 1957	AUG. 22, 1958	402
14	NOV. 14, 1956	AUG. 23, 1958	647
15	NOV. 21, 1956	JUL. 21, 1958	607
16	NOV. 16, 1956	AUG. 12-29, 1958	634-651
17	NOV. 15, 1956	MAR. 13, 1960	1214

Fig. 10, from Otsu, 1963.

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[1] Article in Commercial Fisheries Review, Vol. 25, No. 12, pp. 24-25.

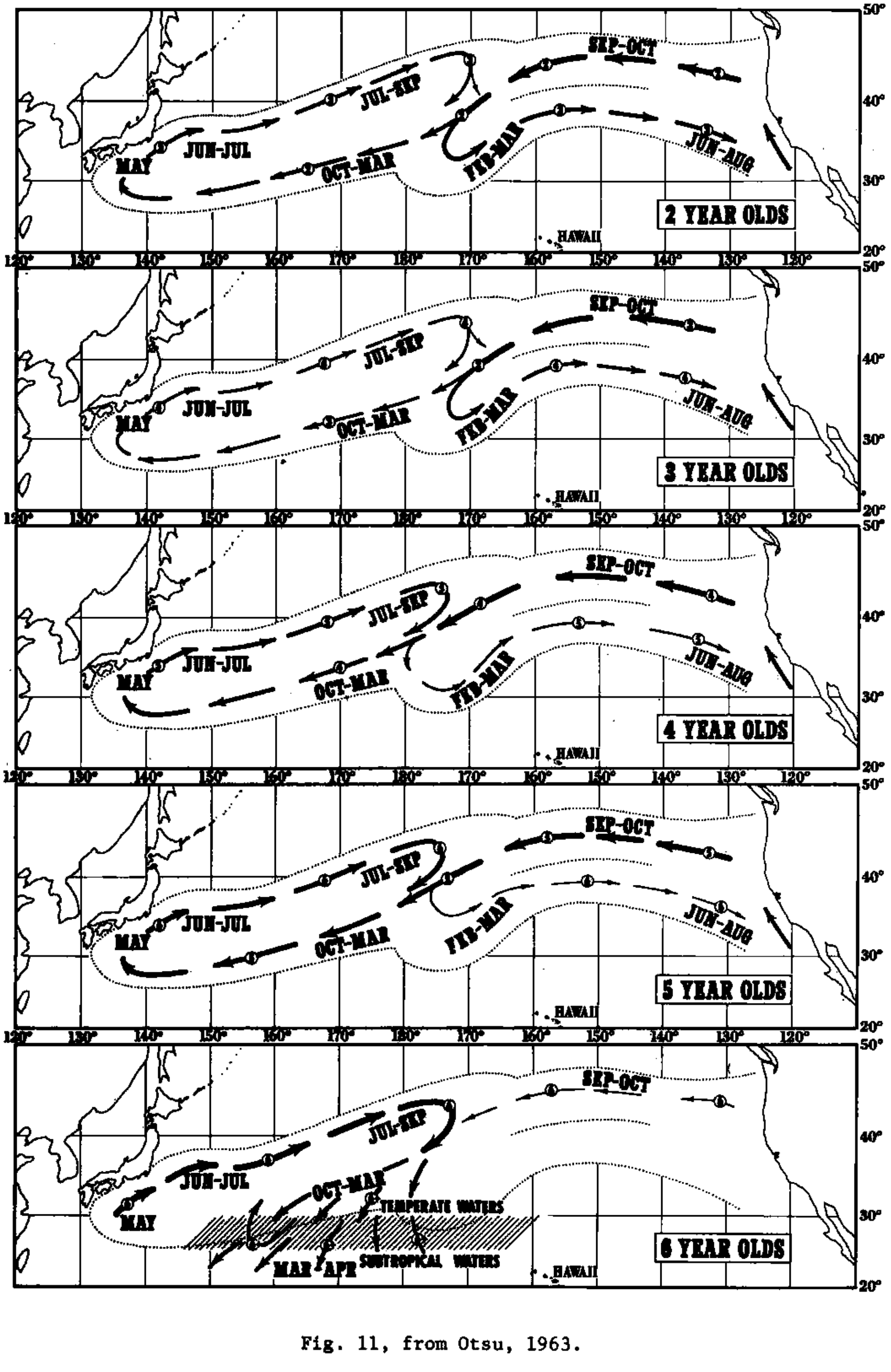

Fig. 11, from Otsu, 1963.

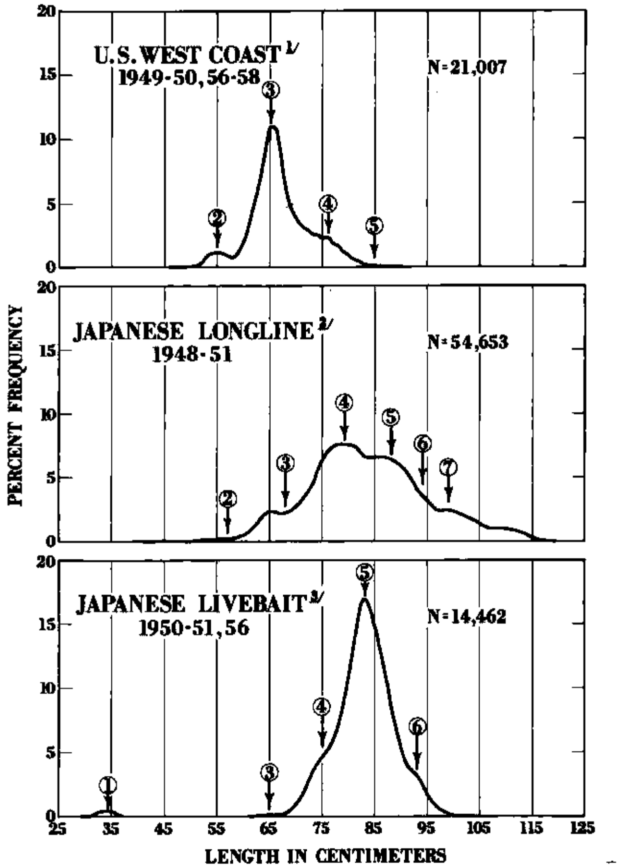

Fig. 12.

in the Japanese fishery and finally appearing in the North Equatorial Current below the surface water from the central to the western side where spawning apparently occurred. Otsu (1960 and 1963) (Fig. 11) described the back and forth migrations in terms of the ages of the fish; both Clemens (1961 and 1963) and Suda (1963) published essentially similar accounts. This migratory pattern did not involve the whole of the north Pacific albacore stock since fish of all sizes did occur in the western Pacific (Fig. 12).

Japanese data on the latitudinal variation in the sizes of albacore taken in the South Pacific suggests a similar pattern there with the adolescent fish in temperate latitudes in the mixed layer and the mature fish in the tropics below the thermocline. The albacore stock of the South Pacific appears to be distinct from that of the North Pacific (Suda, 1963).

The stock of bluefin tuna of the Eastern Pacific is also composed of immature fish. Unlike the bluefin tuna of the Western Pacific and of both the eastern and western North Atlantic, the fish are not large, the abundant sizes being from 4.5 to 20 kg (Roedel, 1953). Recently Orange and Fink (1963) reported the recapture of a bluefin tagged off Lower California about 300 miles south of Tokyo. It was presumably about 16 kg in weight when tagged, and about 121 kg when recaptured some five years later. Of course, the trans-ocean movements of bluefin tuna in the Atlantic were found earlier than those reported by Mather (1963). Here the direction of movement was from west to east.

The coastal stocks of skipjack in the Pacific are composed of individuals usually less than 7 or 8 kg in weight. The fisheries for these species in both Hawaii and Tahiti take, predominately during the summer seasons, a high proportion of large fish from 10 to 20 kg in weight. As previously indicated, there is evidence, including the capture of tagged fish, that the skipjack stock of the West Coast of Mexico and Hawaii, in the summer, are identical. This suggests that an unusually high proportion of the largest individuals in the stock are concentrated at the western or offshore boundary of the range.

The act of translocation is, of course, one of a number of possible responses to environmental changes. It is, through the effects on yields of fisheries, an easily inferred response. Some of the apparent effects of growth or age on this response have been discussed. The effects of changes in size or age on other responses to environmental changes may be less readily detected, depending upon the nature of the response. However, other responses should occur simply by reason of the shift in trophic level that major changes in fish size bring. Such responses may be detected through an appropriate analysis of fishery data if, on theoretical grounds, the nature of the response can be anticipated.

Brock and Riffenburgh (1960), through the use of a simple model, explored certain aspects of prey-predator relationships as these may be affected by schooling. They concluded that, for a given number of schooled prey, the encounter rate with a predator would be greatly reduced as compared to an equal number of scattered prey. If the reduced encounter rate were not to result in a reduced consumption of schooled prey, the predator would need to consume more prey on the occasion of an encounter. This could occur by consuming a large enough quantity immediately on encounter or remaining with the school for an extended period. Considering the quantities of prey that a predator would need to consume to negate the schooling advantage, estimated from reasonable models of school sizes, a strong possibility existed that schooling did confer a real survival advantage, at least in terms of the simple model used. The same model, considered in reverse, suggested that predation would be more efficient by scattered rather than by schooled predators.

The Brock-Riffenburgh hypothesis suggests that predators which are also prey of another predator would be subjected to a survival pressure to school, and a hunger pressure to scatter. With abundant food resources and heavy predation pressure, large schools should occur which should decrease in size as the food resources became less or predation was reduced, or both.

Tunas, like many other groups of fishes, rise through a number of trophic levels during their growth. As larvae they are part of the zooplankton and feed on a selected portion of it. With increasing size they feed on zooplankton predators, including their own young, and on higher predators, until for the larger species, they may approach or become members of the small assemblage of climax predators in the sea. With increasing size, the number of predators for which they are prey diminishes. However, as they become larger their prey may be, to an increasing degree, made up of larger organisms too. These, being in part at least members of higher trophic levels, may be relatively less abundant, requiring in turn more efficient predation by the larger tunas. Such considerations, together with the conclusions drawn from the schooling model, suggested that school size should be an inverse function of fish size within some limits of fish size and school size.

Some of the fishing methods for taking tuna, such as purse seining and live-bait fishing, depend upon schooling fish at or near the surface of the water. The longline method does not depend upon fishermen finding schools by sight. Longline fishing gear is a floating set line with, in some common versions, a hook spacing of 30 fathoms. The hooks are ordinarily baited with frozen fish or squid of appropriate size and the gear set for a day or a sizable portion thereof. Sets of the gear from a large longline vessel may involve upwards of a thousand baited hooks. The wide spacing of the hooks suggests that this gear should be particularly effective for scattered fish, but since no more than a single fish can occupy a hook, not as effective for schooled fish. Additionally, longline gear seems to fish selectively for the larger tuna which in a stable population should be less

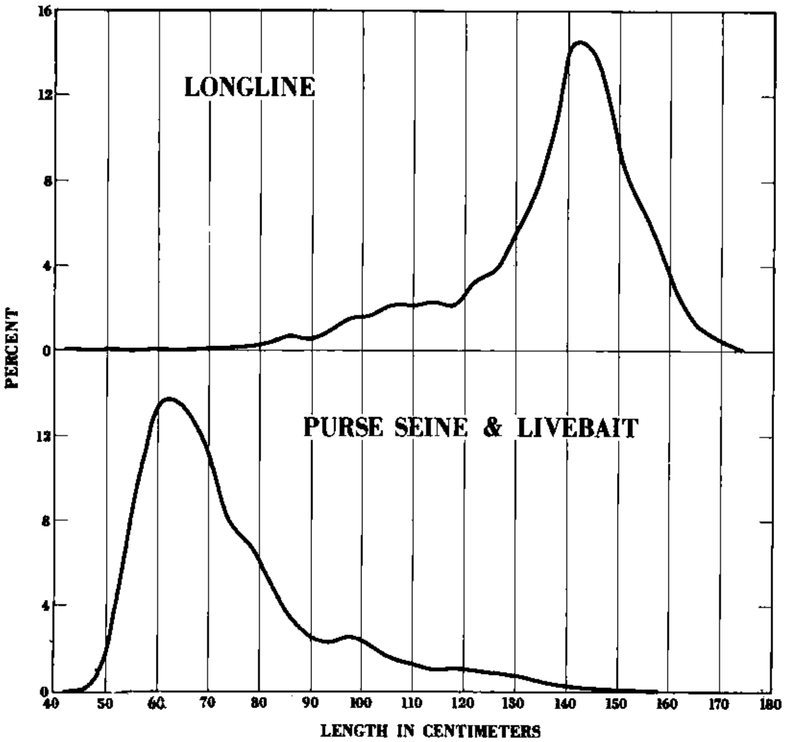

Fig. 13, from Brock, 1962.

numerous than the smaller ones (Fig. 13). However, the gear is ordinarily set to fish well below the surface, depending upon the principal species sought, between 20 and 70 fathoms.

Brock (1962) in a study of the nature of the size selectivity of longline gear for yellowfin tuna analyzed the relation between the size of fish hooked and the number hooked in a run. Runs were defined as fish of the same species taken on adjacent hooks in an uninterrupted sequence. The likelihood of getting runs of various numbers from scattered, solitary fish was computed and compared with that found in longline catches of yellowfin tuna taken in the central equatorial Pacific by the Bureau of Commercial Fisheries Laboratory in Honolulu where accurate records were kept of the species and size of each fish hooked and the hook position in the set of gear. The number of runs was found to occur more frequently than could be accounted for on a chance basis, assuming that the fish were scattered. This suggested that runs of fish may occur as a result of a school of fish encountering a set of longline gear and that the number of fish in a run and the size of the school from which they came would vary in the same direction. If both this and the Brock-Riffenburgh schooling model hold, the average size of the fish in a run should vary inversely with the number of fish in the run. This proved to be the case for the yellowfin catch data employed in the study.

The use of longline catches is an awkward way to investigate the relationship between the number of fish in a school and their size. I suggested to Dr M.B. Schaefer, then Director of Investigations of the Inter-American Tropical Tuna Commission, that this may be conveniently investigated using selected purse seine catches where presumably the entire school was captured. He reported (1963) such an analysis for the yellowfin tuna purse seine catches in the Eastern Pacific Ocean which clearly showed the predicted inverse relationship between the number of schooled fish and their size (Fig. 14).

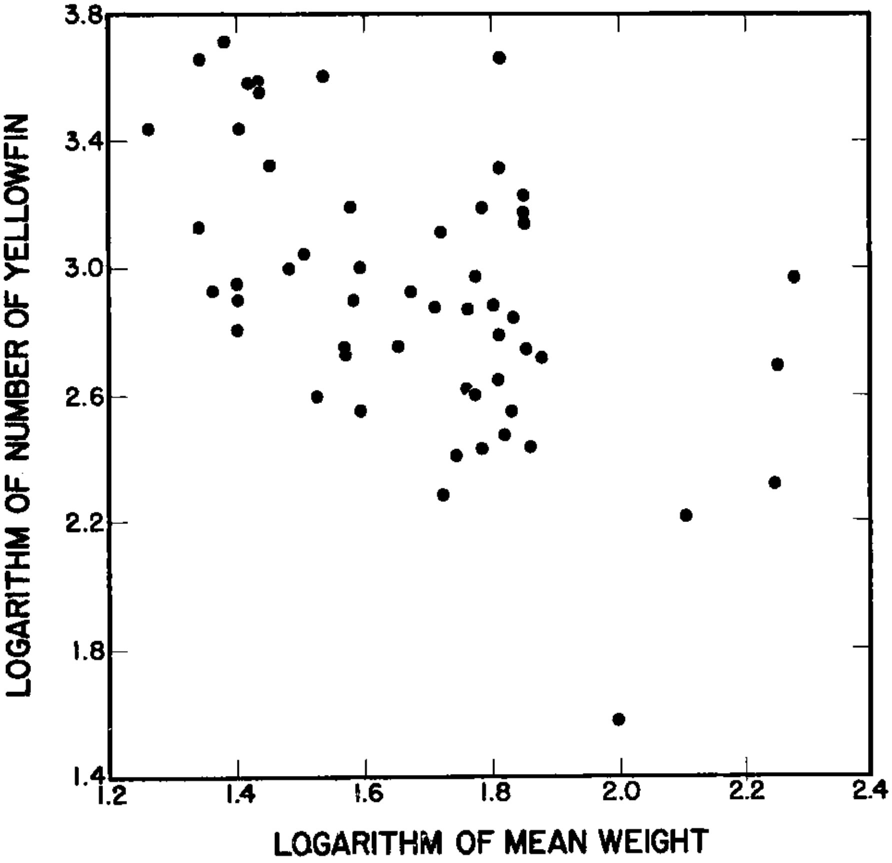

Fig. 14; from Schaefer, 1963

PASSIVE RESPONSES TO THE ENVIRONMENT

These may be difficult to distinguish from active ones, or, in the absence of good records relating to the fisheries, from fishery caused changes.

The predictive success of the model used by Dr Schaefer in estimating the effects of the fishery on the stocks of yellowfin tuna in the eastern Pacific, considering yields and fishing effort, but not environmentally induced changes in recruitment, suggests that these latter changes are not of great magnitude or significance for this species, at least over the extensive fishing grounds of the fishery.

Suda (1963), using primarily the catch and effort data for the winter longline fishery for albacore in the north Pacific, concludes that variations in recruitment are the most significant element in determining the magnitude of the catch per unit effort. He noted that large year classes were associated with a smaller mean size of recruits, and suggested that this was related to competition for sustenance. There was little evident relationship between the estimated number of spawners and resulting recruits. Large year classes of albacore and bigeye tuna seemed to occur during the same years. These relationships suggested that environmental factors were of substantial importance in determining the number of annual recruits to the population. He found no relationship, however, between the apparent abundance of albacore as measured by the fishery in the eastern north Pacific and by the Japanese fisheries, suggesting as a cause that the former fishery did not encompass the whole range of the fishable stock.

A number of workers have used tuna length frequency data as a means of estimating age and growth. Evidence that size groups were age groups was often not complete, but was difficult to interpret on other grounds. In general, tuna growth studies have indicated a rapid growth rate and a short life span for the tropical species and a longer life for bluefin tuna and albacore and a slower growth rate for the latter species. The age determination of these latter two species has also been done by the use of presumed annual marks on hard parts. Some differences have been found in estimates of age and growth of eastern Pacific albacore for the two methods.

The distinct modes and relatively modest range in size of a presumed age group in length frequency distributions for some species of tunas suggests the possibility of a short period of effective spawning. Brock (1943) found that the increase in modal length between the first major group in the length frequencies of albacore landed at San Pedro and the second major group in the landings for the following year was much alike for a number of years of these data, while this same difference for these length groups in the same years was decidedly more variable. This effect would be expected if the first group for one year were sampled from the same year class as that of the second group sampled a year later. Hamre (1963) suggested that the difference found here in the modal position of length of fish of the same age but belonging to different year classes may represent a difference in spawning time. However, Suda (1963) considering the inverse relationship between the mean size of recruits and the magnitude of the year class from which they came for Japanese data, concluded that a difference of this kind may be the result of an initially reduced growth rate through competition for food among the fish of the larger year classes.

Brock (1954), using modes of length frequency curves for the summer Hawaiian skipjack fishery, estimated the growth rate of this species. Recoveries of tagged skipjack showed somewhat less growth but substantially confirmed these estimates. He also found that spawning appeared to occur during the summer months with no evident short period of high intensity. Yet the sharp modes occurring in the length frequency curves, which considering the high rate of growth, suggested a relatively short period of effective recruitment from the apparently extended summer spawning. The possibility existed that the spawning season effectively blanketed an environmental situation that favored a high survival of the young for only a brief period. If this were true, and if the brief period of good survival occurred at different periods of the summer for different years, fish belonging to different year classes should exhibit correspondingly different average lengths at the same nominal ages. This has not yet been investigated.

THE NAVIGATION PROBLEM

The extensive movements of some species of tuna and their apparent ability to detect and associate with specific water types raise some interesting problems concerning how these fish navigate. Albacore, for example, appear in the eastern Pacific off the west coast of Lower California, the three Pacific coast states of the United States, and Canada during the summer as adolescent fish. They move offshore to the north central Pacific during the winter, and some of the older members of this group of adolescent fish continue on to the western Pacific while others return to the eastern Pacific during the following summer. As the older fish that move to the west approach maturity, which occurs at a length of 90 cm, they move towards the equator into the water of the North Equatorial Current where presumably spawning occurs. While the albacore of the North Pacific remain in the great current gyre between the middle latitudes and the equator, they do not simply ride the flow of the current. At times they move with it and at other times against it in a regular pattern related to the age of the fish and the season.

For the albacore to successfully orient themselves to the waters of this gyral current system would imply that they can identify its water by some cue. What the cue may be has yet to be demonstrated. However, Bull (1952) found that some species of marine fish could detect temperature differences of 0.03°C and salinity differences of 0.2 o/oo. Hasler (1960) and others found that fish can detect very slight changes in the odor or taste of water.

Navigation by the location of water masses would seem to play an important role since the anomalous movement of these seems to result in the anomalous movements by the tuna. The nature of gradients in the properties of the ocean suggests that their sole use as a means for navigation and orientation may be difficult, and certainly confusing and inefficient. Due to the effects of local air-sea interaction processes, gradients will not be uniform and may be reversed in a given area for a time. It is difficult to see what properties of the water itself would reveal the direction of current motion. While current boundaries are often sharply defined, their position and direction may be erratic and changeable with islands of water from one water mass becoming isolated in the other (Iselin, 1960).

The ability of many animals, including fishes, to use the azimuth of the sun as a compass has been demonstrated by a number of workers. Hasler (1960) and his co-workers, Braemer (1960), Schwassmann (1960), and Schwassmann and Braemer (1961) have published results of their work on the sun compass, utilizing several species of freshwater fishes and an anadromous one. Since the azimuth direction changes not only during the course of the day, but seasonally and with latitude, a complex response is involved, requiring an accurate time sense, and a change in the orientation pattern seasonally and latitudinally if movements of sufficient length to change latitude significantly are involved. Crossing the equator also involves a reversal of these. Birukow (1963) has provided a short general review of the problem. Adler (1963) studied the accuracy of the sensory abilities of a few species of birds, involved in the use of the sun's azimuth for navigation, the psychophysical limits. His results suggest that navigation may not be by sun compass alone, but may depend to some degree on landmarks or other cues.

There is little information on the abilities of tuna to detect changes in the properties of the ocean and none on their ability to use the sun's azimuth as a compass. However, evidence does exist concerning their ability to orient to the structure of the ocean in a complex way which suggests that they may be able to detect slight changes in the ocean, to navigate great distances accurately, and to anticipate the march of the seasons by appropriate earlier responses. Their means of accomplishing these feats would be of great interest, and their investigation, a challenge.

REFERENCES

ADLER, H.E. 1963. Psychophysical limits of celestial navigation hypothesis. *In* Animal Orientation. *Advances in Biology,* Vol. 26, Berlin.

ANONYMOUS, 1963. Skipjack - a world resource. Cir. 165. Fish and Wildlife Ser. May 1963, pp. 1-28.

AUSTIN, T.S. and V.E. BROCK. 1959. Meridianal variations in some oceanographic and marine biological factors in the central Pacific. Internat. Ocean. Cong. Preprints, pp. 130-132.

BIRUKOW, G. 1963. Time-compensated sun orientation in animals. Proc. 16th Internat. Cong. Zool., Vol. 4, pp. 346-350.

BLACKBURN, M. 1960. Distribution and abundance of tuna related to wind and ocean conditions in the Gulf of Tehuantepec, Mexico. Proc. World Sci. Meet. Biol. Tunas Rel. Sp., *F.A.O.Fish.Rep.*, (6) Vol. 3: 1557-1582.

BRAEMER, W. 1960. A critical review of the sun-azimuth hypothesis. Coldspring Harbor Symp. Quant. *Biol.*, 25, pp. 413-427.

BROCK, V.E. 1943. Contribution to the biology of the albacore *Germo alalunga* of the Oregon coast and other parts of the North Pacific. *Stanford ichthyol. Bull.* 2(6), pp. 199-248.

1954. Some aspects of the biology of the aku; *Katsuwonus pelamis* in the Hawaiian Islands. *Pacif. Sci.* 8 (1), pp. 94-104.

1959. The tuna resources in relation to oceanographic features. In Tuna Industry Conference Papers, May 1959, U.S. Fish and Wildlife Service., Cir. 65, pp. 1 - 11.

1962. On the nature of the selective fishing action of longline gear. *Pacif. Sci.* 16 (1), pp. 3-14.

BROCK, V.E. and R.R. RIFFENBURGH. 1960. Fish schooling: a possible factor in reducing predation. *J. Cons. Explor. Mer*, 25(3), pp. 307-317.

BULL, H.O. 1952. An evaluation of our knowledge of fish behaviour in relation to hydrography. *Rapp. Cons. Explor. Mer*, 131, pp. 8-23.

CLEMENS, H.B. 1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951-1958. Dept. Fish and Game Fish. Bull. 115.

1963. A model of albacore migration in the North Pacific Ocean. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1537-1548.

COLLETTE, B.B. and R. H. GIBBS. 1963. A preliminary review of the fishes of the family Scombridae. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 1: 23-29.

HAMRE, J. 1963. Size and composition of tuna stocks. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1023-1039.

HASLER, A.D. 1960. Guideposts of migrating fishes. *Science*, 132 (3430), pp. 785-792.

HESTER, F.J. 1961. A method of predicting tuna catch by using coastal sea-surface temperatures. *Calif. Fish. Game*, 47(4), pp. 313-326.

ISELIN, C. O'D. 1960. The Gulf Stream system. *Oceanus*, 6(4), pp. 20-23.

JOHNSON, J.H. 1963. Changes in availability of albacore in the eastern Pacific Ocean. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1227-1235.

JONES, E.C. 1962. Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Island, Central Pacific. *Jour. du Cons.*, 27(3), pp. 223-231.

LAEVASTU, T. and H. ROSA, Jr. 1963. Distribution and relative abundance of tunas in relation to their environment. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6) Vol. 3: 1835-1851.

MATHER, F.J., III. 1963. Game fish migrations. *Oceanus*, 10(2), pp. 16-19.

ORANGE, C.J. and B.D. FINK. 1963. Migration of a tagged bluefin tuna across the Pacific Ocean. *Calif. Fish Game*, 49(4), pp. 307-308.

OTSU, T. 1960. Albacore migration and growth in the North Pacific Ocean as estimated from tag recoveries. *Pacif. Sci.*, 14(3), pp. 257-266.

OTSU, T. and R.M. UCHIDA. 1963. Model of the migration of albacore in the North Pacific Ocean. *Fish. Bull., U.S.* , 63(1), pp. 33-44.

RADOVICH, J. 1963. Effects of water temperature on the distribution of some scombrid fishes along the Pacific coast of North America. Proc. World Sci. Meet. Biol. Tunas and Rel.Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1459-1475.

ROEDEL, P.M. 1953. Common ocean fishes of the California coast. *Fish. Bull. 91, State of California*, Department of Fish and Game.

SECKEL, G.R. 1963. Climatic parameters and the Hawaiian skipjack fishery. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1201-1208.

SCHAEFER, M.B. 1960. Tuna oceanography programs in the tropical central and eastern Pacific. Calif. Coop. Oceanic Fish. Invest. (CalCOFI) 8, 1 July 1959-30 June 1960, pp. 41-44.

1963. Report on the investigations of the Inter-American Tropical Tuna Commission for the year 1962.

SCHWASSMANN, H.O. 1960. Environmental cues in the orientation rhythm of fish. Coldspring Harbor Symp. Quant. *Biol.*, 25, pp. 443-450.

SCHWASSMANN, H.O. and W. BRAEMER. 1961. The effect of experimentally changed photoperiod on the sun-orientation rhythm of fish. *Physiol. Zool.*, 34(4), pp. 273-286.

SHIBATA, K. 1963. Analysis of the fish finder records II some acoustic and ecological information on tuna and others. *Bull. Fac. Fish. Nagasaki*, No. 14, February 1963, pp. 15-24.

SHIPPEN, H.H. 1961. Distribution and abundance of skipjack in the Hawaiian fishery, 1952-53. *Fish Bull.* 188, Vol. 61.

SHOMURA, R. and G.I. MURPHY. 1955. Longline fishing for deep-swimming tunas in the Central Pacific. *Sp. sci. Rep. Fish.* 157, September 1955, pp. 1-70.

SUDA, A. 1963. Structure of the albacore stock and fluctuation in the catch in the North Pacific areas. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1237-1277.

UDA, M. 1962. Cyclic correlated occurrence of world-wide anomalous oceanographic phenomena and fisheries conditons. *J. oceanogr. Soc. Japan*, 20 Ann. Vol. 1962. pp. 368-376.

WILSON, ROBERT C. 1953. Tuna marking, a progress report. *Calif. Fish Game*, 39 (4) pp. 429-442.

A REVIEW OF THE EFFECTS OF THE ENVIRONMENT ON THE HERRING

By

B. B. Parrish[1]

NOTE:

"The substance of Mr Parrish's paper will be included within a longer review which is being **prepared in conjunction with** Mr A. Saville of the Marine Laboratory in Aberdeen, under the title **"The biology of north-east** Atlantic herring populations", for publication in the review journal **"Oceanography and Marine Biology"**, edited by Dr H. Barnes (published by George Allen and Unwin **Ltd.). It is expected that** Parts 1 and 2 of this joint review will appear in volume 3, to be **published in 1965, and other parts** subsequently".

---

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