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Report from the National Workshop on Recruitment

Edited by M. Sinclair, J.T. Anderson, M. Chadwick, J. Gagné, W.D. McKone, J.C. Rice and D. Ware

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Biological Sciences Directorate
Department of Fisheries and Oceans
Ottawa, Ontario
K1A 0E6

September 1988

Canadian Technical Report of
Fisheries and Aquatic Sciences
No. 1626

Fisheries and Oceans   Pêches et Océans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

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Report from the National Workshop on Recruitment

Northwest Atlantic Fisheries Center
St. John's, Newfoundland
February 23-25, 1988

Edited by

M. Sinclair, J.T. Anderson, M. Chadwick
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Cat. No. Fs 97-6/1626E ISSN 0706-6457

DFO/4160

Correct citation for this publication:

Sinclair, M., J.T. Anderson, M. Chadwick, J. Gagné, W.D. McKone, J.C. Rice, and D. Ware. 1988. Report from the National Workshop on Recruitment. Can. Tech. Rep. Fish. Aquat. Sci. 1626: 261 p.

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ACKNOWLEDGEMENTS

On behalf of the Steering Group (editors), I would like to thank all of the participants for their active participation. It was this participation that made the workshop intellectually stimulating and productive. The contribution of the invited "outside" experts was most beneficial. The Newfoundland hospitality and warmth ensured a most congenial working environment. I would also like to thank D. Burchat for her efforts in typing and collating the document for publication.

ABSTRACT

A National Recruitment Workshop was held by the Science sector of the Department of Fisheries and Oceans (DFO) in response to the request of the Assistant Deputy Minister of Science, Mr. L.S. Parsons. The aim of the workshop was to contribute to the development of a Departmental plan for future research on recruitment. During the first day, overviews of Departmental research of relevance to the recruitment problem were presented with the participation of senior management. During the second day the participants were divided into six multi-disciplinary work teams to address one of three specific recruitment problems. The aim of the work teams concept was to generate increased interaction between scientists of different disciplines. The workshop ended with a general discussion led by comments from each of the non-Departmental invited experts. The Steering Committee (editors) subsequently met and drafted this final report which includes a list of generalizations and recommendations for senior management consideration.

RÉSUMÉ

À la demande du Sous-ministre adjoint (SMA) des Sciences, M. L.S. Parsons, un atelier national sur le recrutement a été tenu par le secteur des Sciences du Ministère des Pêches et des Océans (MPO). Cet atelier avait pour objectif de contribuer à l'élaboration d'un plan ministériel pour la recherche sur le recrutment qui sera réalisée à l'avenir. Des exposés sur la recherche connexe au recrutement effectuée au Ministère ont été présentés au cours de la première journée avec la participation de la haute direction. Au cours de la deuxième journée, les participants se sont répartis en six groupes de travail multidisciplinaires pour traiter de l'un des trois problèmes particuliers au recrutement. Ces groupes ont été formé afin d'accroître les interactions entre les scientifiques des diverses disciplines. L'atelier s'est terminé par une discussion générale animée par les commentaires de chacun des experts invités de l'extérieur du ministère. Le comité directeur (rédacteurs) s'est ensuite réuni et a rédigé le présent rapport difinitif qui comporte une liste des généralisations et des recommandations soumises à la haute direction pour examen.

I. INTRODUCTION

by

M. Sinclair
Director, Biological Sciences
Scotia-Fundy Region

The National Recruitment Workshop was held in response to the request of the ADM Science, Mr. L.S. Parsons. The principle aim of the workshop has been to contribute to the development of a Departmental plan for future research on recruitment. A Steering Group, with regional representation, was formed to organize the workshop. The members were: J.T. Anderson and J.C. Rice of the Newfoundland Region, M. Sinclair of the Scotia-Fundy Region, M. Chadwick of the Gulf Region, J.A. Gagné of the Québec Region, G.B. Ayles and W.D. McKone from Headquarters, and D. Ware from the Pacific Region. The Workshop itself was chaired by M. Sinclair, whilst the Steering Group was chaired by G.B. Ayles.

The first meeting of the Steering Group was held in Toronto in April 1987. At that time, the basic structure of the workshop was defined and requests for written contributions were initiated. A second meeting, to finalize the organizational aspects of the workshop, was held in Halifax in November 1987. Particular emphasis was directed towards ensuring representation of a broad range of disciplines - physical and biological oceanographers, fisheries biologists, and modellers.

The workshop took place at the Battery Hotel in St. John's on February 23 and 24, 1988. During the first day, overviews of departmental research of relevance to the recruitment problem were presented with the participation of senior management. During the morning of the second day, the participants were divided into six multi-disciplinary workteams (9 scientists per team). The teams were asked to address one of three specific recruitment problems. The background documentation (see attached Appendices) for the particular problem had been sent out to each participant several weeks prior to the workshop. Two workteams addressed each problem. One of the workteams comprised members with specific expertise for the assigned problem, and thus could be called the "expert team". Members of the second team lacked detailed knowledge of their particular problem. The aim of the workteam concept was to generate increased interaction between scientists of different disciplines rather than to produce specific recommendations for research. During the afternoon of the second day the chairmen of the workteams presented the results of their deliberations in a plenary session held at the Northwest Atlantic Fisheries Centre. The workshop ended with a general discussion led by comments from each of the non-departmental invited experts. On February 25, the Steering Group met to draft a list of generalizations and recommendations.

II WELCOME AND INTRODUCTION TO WORKSHOP

by

M. C. Mercer
Regional Director, Science
Newfoundland Region

I am pleased to welcome everyone to the second in what is planned to be a continuing series of national workshops on issues of importance to science in the Department of Fisheries and Oceans and by extension to the wider scientific community.

The workshops are intended to give strategic direction to the Department's science efforts, and thus far apparently that intent has been interpreted quite literally. In the first case the direction was west, in this case, it is east.

The subject of this workshop is recruitment. Seven decades ago early prominent fisheries researchers suggested that the recruitment problem was probably the most important one in fisheries. After seven decades we certainly know a great deal more about recruitment, but one still has little trouble finding claims that recruitment is still the most important problem area in fisheries science.

The study of recruitment certainly is still at the core of fisheries science and is important to fisheries management. It has the additional virtue of being fascinating in its own right. Few virtues, however, come without their companion vices - in the case of recruitment, research is not just fundamental and fascinating, but it can be a bottomless pit or "black hole" for resources available for science. Therefore, it is vitally important to plan and design carefully how and where to allocate resources. There is no problem finding something to study about recruitment - the difficulty is identifying problems that are both meaningful and tractable.

We are ready to attack meaningful, tractable problems in recruitment and are probably better prepared and structured than ever before for such efforts. Research on recruitment that is both excellent and useful requires a blend of expertise - in ecology, in oceanography, in statistics, modelling and experimental design. In our various regional laboratories, we have assembled the appropriate types of expertise. Nationally, the desirability of effectively blending physics, fish, statistics, and experimental design has been given renewed impetus. Research programs which will get their start in this workshop, at least as concepts, will serve the Department in two reciprocal ways. A successful workshop, producing effective approaches to blending the various disciplines, will pay back the Department first in the progress made in investigating some of the vitally important problems in recruitment to our aquatic resources, and in the better management which can follow from our enhanced knowledge. But the workshop will pay dividends in a second way as well, integrating people and approaches in individual laboratories, and among laboratories. It is clear that multidisciplinary approaches can broaden the types, and enhance the quality, of a spectrum of research efforts in our science programs that reach far beyond the problems of recruitment.

A cynic might even argue that this will be the more important dividend, as recruitment studies mounted by our colleagues to the south, and in the North Sea will be at scales we in Canada are unlikely to duplicate in the near future. There is a key difference though, because in some areas there is little more to the management of fish stocks than the managing of new recruits. For better or worse (and only someone terribly myopicly interested in recruitment would think it was for the worse), science in Canada still must allocate lots of resources to the assessment and management of past recruits, not just future ones.

The fact that we can study recruitment to improve our knowledge of and ability to manage our aquatic resources, rather than as a last gasp response to collapse and crisis is a laurel for the Department, but not one we should rest on. Rather it is one we should build on. We have the expertise available to do excellent work in the study of recruitment. We have the stocks and much of the knowledge base to implement studies of excellence. Also, with this workshop we have the opportunity to initiate what can become major strides in our understanding of what recruitment processes are and how they should be incorporated in management of our resources. I wish you well in your tasks, and hope the next 2 days are stimulating, fruitful, and enjoyable.

III OPENING REMARKS

by

L.S. Parsons
Assistant Deputy Minister, Science

I am delighted to be here with you today to open this Recruitment Workshop. This occasion marks the launching of the first Biological Sciences Workshop in DFO and follows the very successful Climate Workshop held last spring in Victoria. As you may be aware, there will be a Hydroacoustic Workshop at BIO next week. It is my intention to hold these workshops across the country. I hope they will foster a spirit of scientific cooperation, and contribute to the flow of ideas and information within the newly-integrated Science Sector of DFO. Our challenge is to bring better focus to our Science program by providing clear objectives and by developing mechanisms to better coordinate programs among regions and disciplines.

This question of better coordination among regions and disciplines leads me to stress the self-evident truth that recruitment processes and climatic conditions are interrelated. Understanding of the factors determining year-class variability can only be brought about through an inter-disciplinary approach encompassing all components of the DFO Science Sector and through international collaboration.

The annual variability of year-classes has been a preoccupation of fisheries scientists for about one hundred years. Its manifestation, as catch variability, has been a concern of the fishing industry for a very long time. The flyleaf of a recent book on the Dynamics of Marine Fish Populations by Dr. Brian Rothschild begins with the following statement: "Marine fish populations undergo dramatic fluctuations in abundance over time, a phenomenon that has mystified scientists and laypeople for centuries. These fluctuations obviously have considerable economic and social impact and it is important to understand why they occur". That statement explains why the subject of this workshop was chosen from among a number of important issues that face fisheries science today.

The existence of such year-class variability was vividly demonstrated by one of the first fisheries scientists in the field. I refer to the work of Hjort (1914) who painstakingly followed the large 1904 year-class of a Norwegian herring population as it passed through the fishery.

We have come a long way since Hjort's day but in many ways we can still see only "the tip of the iceberg" when it comes to recruitment. Writing in 1964, David Cushing stated: "The problem of the relationship between parent stock and subsequent recruitment is the hardest one in fisheries biology to solve. Two sorts of data are lacking: (1) long-time series of estimates of stock and recruitment; and (2) a range of measures of larval and juvenile mortality at sea. The proper description of the mechanism will go straight to the root of the dramatic fluctuations in stocks in the great fisheries".

The significance of recruitment variability was first brought home personally to me when I was conducting research on one of the major herring populations of the northwest Atlantic - the southern Gulf-southwest Newfoundland stock. Many of you here today know it only as the southern Gulf stock because it no longer migrates to southwest Newfoundland. But due to two enormous year-classes of the late 1950's, that stock supported a major fishery in the fjords of southwest Newfoundland as well as in the Southern Gulf in the late 1960's-early 1970's. No year-classes of that size have occurred subsequently.

This one example of year-class variability in herring was but part of a broader phenomenon in pelagic fish stocks. This was borne out by the Pelagic Fish Symposium in Aberdeen in 1978. As a participant in that Symposium, I was struck by the extreme variability of recruitment in pelagic fish stocks and their apparent vulnerability to stock collapse.

In the history of fisheries research there have been many conflicts between proposed effects due to fishing and those due to natural causes (recruitment failure due to fishing or to natural causes). Despite this, the Aberdeen Symposium arrived at certain conclusions. I will quote a couple of these:

"In all (of the cases) heavily depleted stocks the events preceding the collapse show similar features. In most cases, the rate of decline has been augmented, in the final states, by <u>recruitment failure</u>."

"In some instances environmental changes may have played a part in the decline but generally their influence would appear to have been minor compared with the effects of the fisheries."

"In all cases considered during the Symposium there is strong positive, or presumptive, evidence that the stock collapse was, in the final analysis, due to reduced recruitment, <u>generated by a decline in spawning stock</u>."

In other species and other stocks large scale changes in abundance have been attributed to the influence of ocean climate factors.

From a management point of view, the long-term average recruitment is important, but so is the variation from the average. Fluctuations in year-classes often translate into 'feast or famine' situations for the fishing industry and for fishermen who, in many cases, are dependent on the resource as their sole source of income. Any improved predictive capability in estimating year-class size would soften the impact of this variability. Managers, along with the industry, would like to be able to plan for large changes, whether positive or negative, for the benefit of all participants in the fishery.

Over the past eight decades there has been slow progress in unravelling the underlying processes that govern recruitment. More recently, in the last 10-15 years, a great deal of effort has been spent internationally on trying to understand recruitment problems.

In the eastern Atlantic, ICES has been actively involved in pursuing solutions to problems posed by the variabilitiy in recruitment. More recently, the International Recruitment Program (IREP) has been formed so that we may look at recruitment over a broader geographic area. A number of ambitious experiments on recruitment have been devised. Our understanding of the underlying mechanisms of stock definition and reproductive biology has progressed. However, our understanding of the processes of survival, from the larval stage to recruitment to the adult population, is still far from complete. Warren Wooster, in his introduction to a recent ICES Mini-Symposium on Recruitment summarized the current situation when he stated: "Events between spawning and eventual attainment of maturity in the next generation are still the most important and least understood in the whole field of fish population dynamics".

In 1983, writing about the outlook for fisheries research over the next ten years, David Cushing predicted that fisheries science would develop in three ways: (1) in polishing procedures associated with cohort analysis; (2) in small but experimental multispecies models; and (3) in continuing the slow progress toward solution of the stock and recruitment problem. He argued that progress would remain slow because the integration of the growth and mortality of larval and juvenile fishes demands expensive work at sea or in artificial enclosures.

More recently, Brian Rothschild has identified the most important constraints as being the fact that only a few components of the entire problem have been studied and that continuing research seems to focus ever more intensively on those few components. Increases in research effort have not resulted in commensurate increases in knowledge. He goes on to state: "What we need to do is to specify or identify the fish's environment. The problem of predicting fish-population variability does not at present rest on our understanding of the behaviour and physiology of any particular group of fish. Rather, it rests on our ability to identify, define and measure the fish's ambient environment".

Brian has reviewed the extensive literature and concluded: "The specific causes of fluctuations in fish-population abundance are supported by a long list of speculations and a short list of facts. The facts are: (1) the abundance of individual stocks has fluctuated for centuries; (2) evident human interaction with most marine stocks is relatively recent; and (3) fish stocks have continued to fluctuate in abundance in the presence of increased toxic-chemical loading, eutrophication, habitat modification and fishing".

He summarizes the numerous hypotheses in six categories:

1) Intraspecific

2) Fishing

3) Natural Environmental

4) Anthropogenic Environmental

5) Interspecific

6) Complexity

He then goes on to provocatively state: "The solution will not be advanced by obtaining more of the same data or replicating research approaches; rather it will be derived from a reformulation of the problem. This should include a systematic search for those parts of the problem that are not well identified and a design of experiments that can illuminate these critical areas".

It is clear that we are only on the threshold of understanding the factors determining recruitment variability. This is an immense scientific challenge. It requires review, dialogue, debate and cooperation. This cooperation must occur among disciplines as well as among individual scientists. Cooperation and collaboration are required both at the national and the international levels. Only through such collaboration can progress be made.

Which brings us back to the reason for this workshop. My expectations from this workshop centre around the development of a Departmental plan for future research on recruitment. In collaboration with colleagues internationally, we must seek a clearer understanding of the underlying processes that influence recruitment and hopefully an improvement in our predictive capability in the longer-term. This requires a commitment to long-term multidisciplinary targetted basic research on this important subject, a commitment that we in DFO are prepared to make. In order to pursue this objective, long-term priorities for the next 5-10 years for DFO research must be developed, recognizing that these will evolve over time. In doing so, we must of course recognize that scientific discovery cannot be premeditated. But it can be facilitated by formulating and debating hypotheses, by sharing experience and insight and by designing future research to shed light on old problems.

Carl Sagan has described science as "a way of thinking much more than it is a body of knowledge". Its goal is to find out how the world works, to seek what regularities there may be, to penetrate to the connection of things. Science is based on a willingness to challenge old dogma and requires the courage to question the conventional wisdom.

I hope that during this workshop you will question the conventional widom on recruitment and point the way to the research necessary for a better understanding of the recruitment process.

Best wishes for a successful workshop.

IV HISTORICAL SKETCH ON RECRUITMENT RESEARCH

by

M. Sinclair
Director, Biological Sciences
Scotia-Fundy Region

The aim of this introductory paper to the National Recruitment Workshop is to introduce the concepts generally shared by those researchers concerned with the so-called recruitment problem in marine fisheries research. This review of concepts is thought to be useful because many participants at the workshop, in particular the biological and physical oceanographers, may not be familiar with the literature and associated specialized vocabulary. A historical approach is taken, and there is some bias towards events in the North Atlantic.

Empirical Observations of 19th Century

Fluctuations in landings (of herring and cod in particular) in northern Europe was a problem of considerable economic and social concern during the 19th century. The empirical observations were straightforward and well documented. The fisheries at that time were limited to coastal waters close to the fishing communities. The landings at particular coastal fishing areas fluctuated on a range of time scales (seasonal, interannual and decadal). It was also noted that there was marked variability in the quality of the fish landed (i.e. relative amount of cod liver oil and the size composition). Thirdly, those people closely associated with the marketing of fish noted persistent slight differences in morphology between fish of the same species coming from different fishing locations. The morphological patterns were not randomly distributed. The most dramatic observation, because of the economic implications, was the decadal fluctuations in the winter herring fishery off Bohuslän, western Sweden. This fishery varied in an extreme fashion, from excess capacity for several years to a total lack of fish in subsequent years.

This overall set of empirical observations was paradoxical. There was an underlying predictable pattern in both the geographic location at which lucrative fishing occurred, and the seasonal timing during which the fish arrived. The timing of the fisheries varied between geographic locations. This was particularly true for the coastal herring fisheries. Superimposed on this orderly natural phenomena of fish migration was considerable variability in local abundance. The fishing communities, given the strict limits to the distance the boats could travel, established themselves in relation to the reproducible patterns in fish distributions in coastal areas. The interannual variability, however, generated feast and famine cycles for the single industry communities.

This set of observations generated the "migration" hypothesis to account for the fluctuations in landings at all time and space scales. The title indicates the essence of the hypothesis which inferred an annual migration of fish from the Arctic Ocean to the coastal waters of northern Europe and North America. During the spring, the fish species of commercial interest were interpreted to begin their migration to diverse spawning locations in coastal waters along both sides of the North Atlantic. A return migration to the Arctic was hypothesized during the autumn. The difference in the timing of the fisheries between geographic areas was considered to be a function of the migration routes. The interannual and decadal fluctuations were thus interpreted to be a function of variability in the migration pattern of a single mass of fish of a particular species. Abundance levels of the exploited species were thought to be relatively constant. The fluctuations in landings at particular coastal fishing locations were, under the migration hypothesis, the result of an edge effect (i.e. variability in the availability along the perimeter of a constant abundance level of pan-oceanic species). The hypothesis did not, however, account for the persistent intra-specific differences in morphological patterns that were observed between geographic locations. Even though by the end of the 19th century this hypothesis had been discredited by many naturalists, the underlying concept that interannual fluctuations in landings at particular geographic locations was a function of changes in migration patterns of the species in question, rather than changes in overall abundance of the species, was still generally accepted. The title of Committee A of the International Council for the Exploration of the Sea (ICES), one of only three standing committees defined in 1902, as the Migration Committee is evidence of the prevalence of this concept at that time. Committee A, the Migration Committee, was specifically established to address the problem of interannual fluctuations in landings. A paradigm shift in the interpretation of fluctuations in landings occurred subsequent to the formation of ICES.

The Paradigm Shift

Several key studies on marine fish species in European coastal waters between 1898 and 1914 resulted in major increases in understanding of the causes of fluctuations in landings. These studies resulted in a paradigm shift.

First Heincke ,(1898), in an extensive monograph, summarized his detailed studies on life cycles and morphometrics of Atlantic herring. He had studied with his colleagues at Kiel, Germany, all aspects of the biology of herring which spawned respectively during the spring and fall in Kiel Bight. It was noted that the duration of the larval phase differed by several months between progeny of the two spawning groups. Also some larvae were retained in the Bight through the larval phase. He noted persistent differences in morphological and meristic characters between the spawning groups (Figure 1). The observations led him to conclude that the species herring was comprised of many component self-sustaining populations, each population having a precise and relatively limited geographical area of distribution. This was a radical conclusion at that time because the extant typological or essentialist species concept inferred that species were panmictic (i.e. comprised a single group throughout the area of distribution). Heincke extended his study by sampling many other spawning fisheries in the Baltic, North Sea and Norwegian coastal waters. He invented rudimentary multivariate statistics to aid in the analysis of the data. His conclusion that herring is comprised of many self-sustaining populations was accepted surprisingly quickly, given the strongly held views prior to its publication and the controversial nature of the new species concept that he introduced.

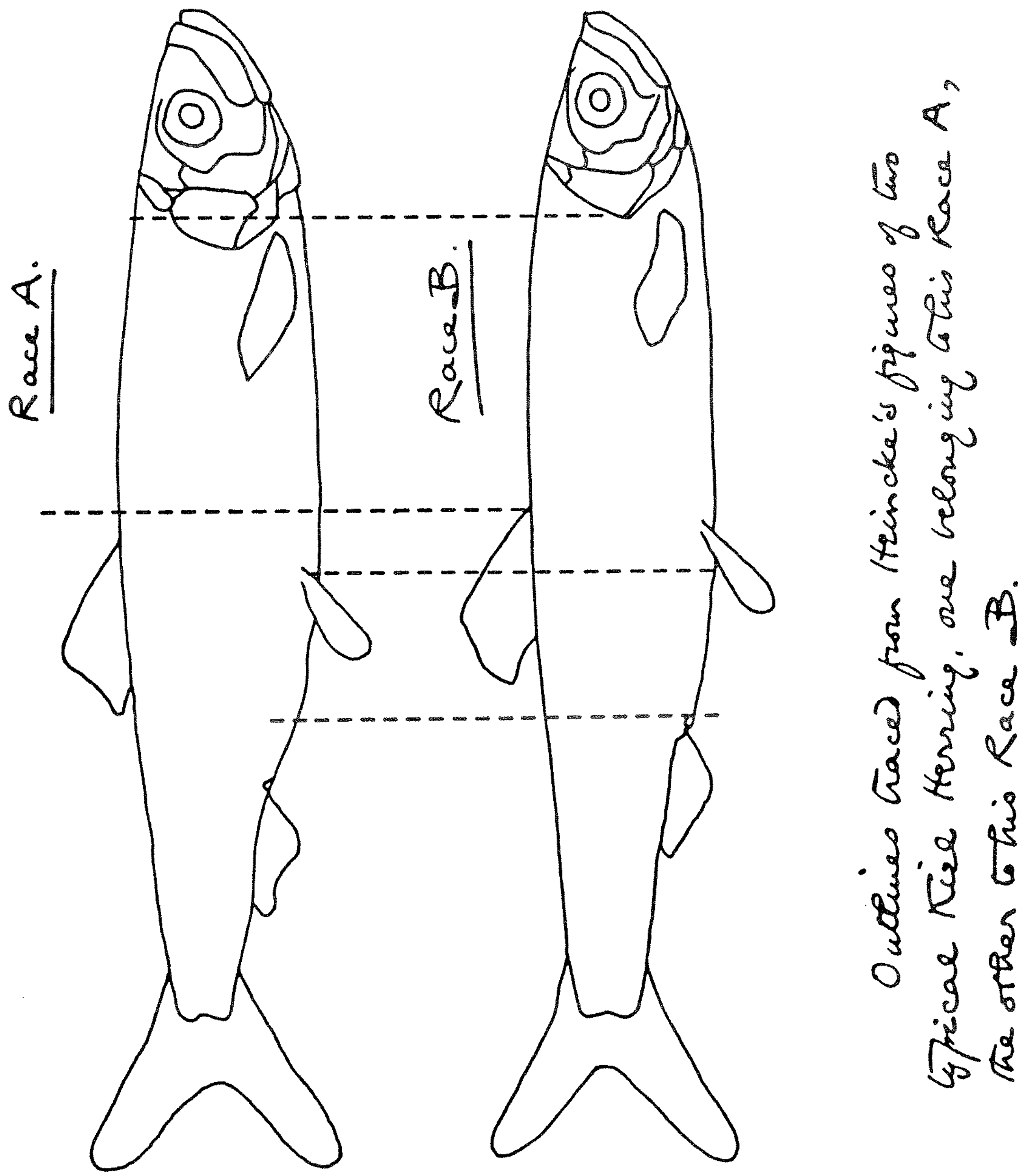

Figure 1. Illustration of morphological differences between two populations of herring spawning in Kiel Bight at different seasons (from an application by Weldon for research funding to the Royal Society in 1894).

The implications on fisheries questions were just as dramatic as on natural history and taxonomy. If the "migration hypothesis" involving a relatively constant massive pan-oceanic aggregation of herring in the high seas migrating seasonally to coastal waters was incorrect, there were obvious implications on fisheries management. The new description of nature and its interpretation suggested the existence of local populations whose abundance levels could be influenced by local fishing activities. If correct, restrictions on fishing effort might be required to allow population persistence. Heincke's work also provided some explanatory power on the problem of interannual and decadal fluctuations in landings of herring. He sampled herring from the Bohuslän "overwintering" fishery (i.e. not a fishery on spawning fish) and compared their shape and meristic characters to various spawning populations in the North Sea and the Baltic. He concluded that the Bohuslän herring fishery exploited the overwintering distribution of a herring population that spawned in the North Sea off Germany. Also, using information on the physical oceanography of the area (Skagerrak and Kattegat) he argued that the overwintering distribution shifted as a function of ocean climate changes. Pettersson (1914) in his classic paper "climatic variations in historic and prehistoric time" argued that the water mass and circulation changes off Bohuslän were caused by tidal processes (18.6 year cycle). Thus the disruptive fluctuations in local abundance in herring in the winter off Bohuslän were interpreted to be due to changes in the overwintering distribution (thus changes in availability of the "German" herring to the Swedish fishery), rather than due to changes in population abundance. In contrast, interannual fluctuations in landings from spawning fisheries were interpreted to be due to changes in the absolute abundance of the population. Heincke did not, however, speculate on what might cause the fluctuations in population abundance. Heincke's (1898) paper fundamentally modified the interpretation of fluctuations in landings. There were two causes: changes in migration patterns of populations, and changes in absolute abundance of populations. Also the geographic scale of the fluctuations problem was changed, from the whole North Atlantic to restricted areas of coastal and shelf waters.

The second major contribution was made by Hjort (1914) based on his studies with colleagues on herring and cod in Norwegian waters. The development of new methods, and some good luck in the timing of his study, were critical to the conclusions that he was able to draw. While helping to introduce an insurance scheme for fishermen, he became aware of age composition statistics and concluded that if fish could be aged, similar statistics could be collected for exploited fish species (Hjort did not appear to have accepted Heincke's conclusions on herring populations during this pre-1914 period, and the "racial" approach of Heincke had not been generalized for other species such as cod). Hjort proposed a port-sampling scheme for the ICES area as a whole in 1907, but the recommendation was not accepted. Nevertheless, his approach was instituted in Norway, where he was the director of fisheries research. As a result, from 1907 onwards, the age composition of the landings of herring and cod were sampled for Norwegian coastal fisheries [the new methods required to permit this development were: (1) an ageing method using fish scales (Figure 2); and (2) development of sampling theory]. An additional methodological tool that was critical was tagging. This provided estimates on the geographic scale of migrations. The good luck was the particular oceanographic conditions of 1904. This year generated a massive year-class of herring in Norwegian waters which was three years old when the port-sampling program began in 1907. It was found

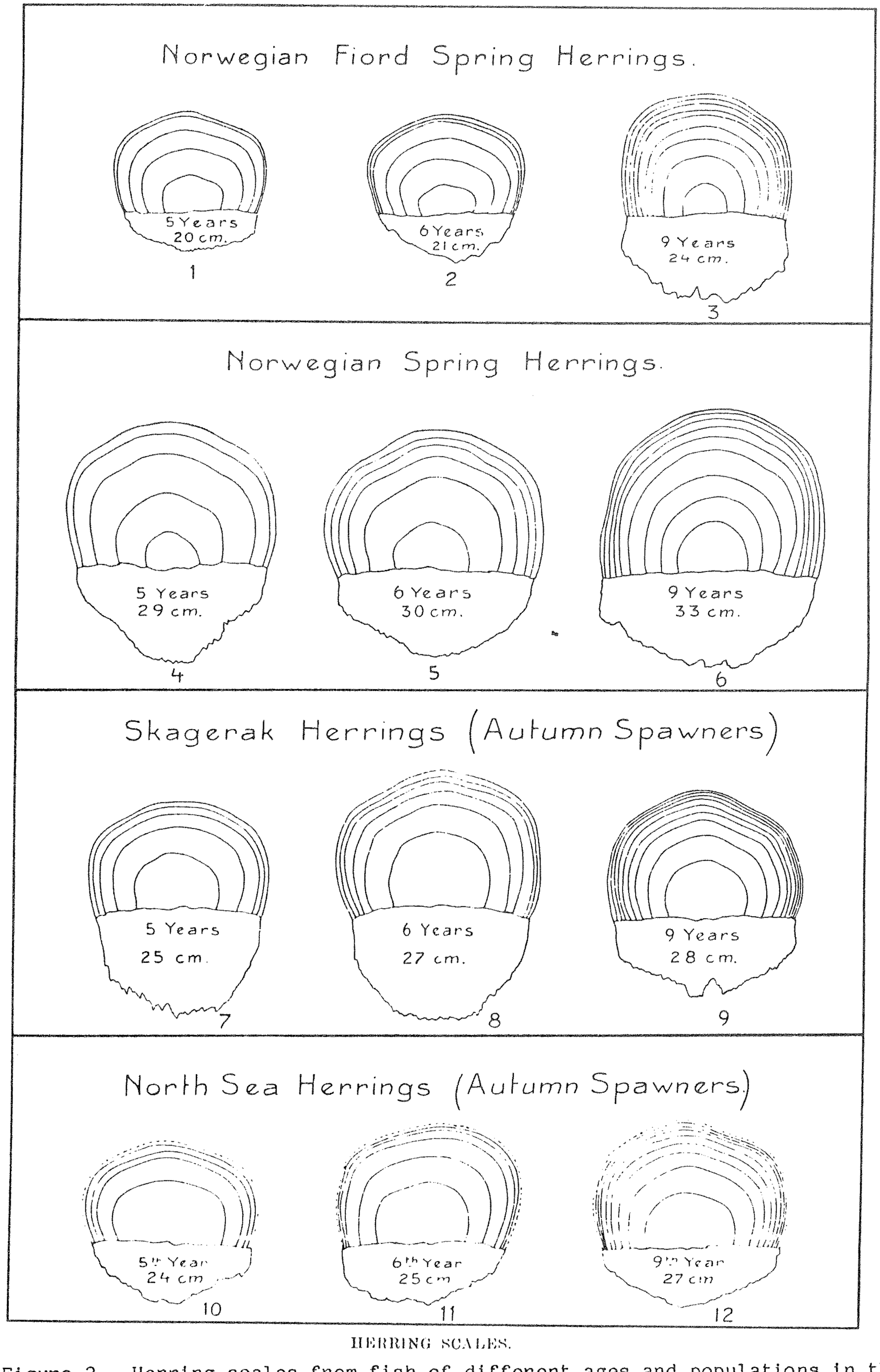

Figure 2. Herring scales from fish of different ages and populations in the northeast Atlantic (from Dahl 1907).

out, subsequently, to be about 30 times larger than the year-classes which bracketed those born in 1904. This strong signal was followed as the year-class progressed through the fishery year by year (Figure 3).

From the results of wide-ranging studies (including the port-sampling results, tagging experiments, egg and larval distributional surveys, timing of phytoplankton blooms and physical oceanographic studies on the circulation of the Norwegian current), Hjort (1914) arrived at exciting conclusions on the causes of interannual fluctuations in landings. They may sound somewhat flat today because his conclusions form the starting point of much of our ongoing research. At the time, the conclusions of his paper generated enormous excitement and considerable explanatory power. The review by Allen (1914) in Nature captures this excitement:

> "There can be little doubt that this report by Dr. Hjort will mark an epoch in the history of scientific fishery investigation. If the arguments upon which its conclusions are based successfully withstand the test of criticism, there has been established a method of predicting the probable future course from year-to-year of some of our most important fisheries, which should be of utmost value both to those engaged practically in the fishing industry and to those responsible for fishery administration" (emphasis added).

Hjort demonstrated convincingly that the fluctuations in landings, both in quantity and quality in the herring and cod in Norwegian fisheries, were a function of extreme variability in year-class sizes (the population concept was not well articulated by Hjort until the 1920's). Thus the problem of fluctuations in landings at particular fishing locations was decomposed into two components (availability changes and year-class size variability).

To sum up, the major contribution of Heincke and Hjort (and thus the paradigm shift itself) was the redefinition of the problem of fluctuations in landings. Age-structured populations persisting on limited geographic scales became the focus of study to resolve the problem, rather than studies of pan-oceanic migration of typological or essentialist species. The paradigm shift involved a change in the unit of study to the geographic population, rather than the species. This shift in thinking by fisheries biologists predated the changes in taxonomy and evolutionary biology by a couple of decades. The migration hypothesis inferred constant abundance levels of pan-oceanic typological species. The new interpretation inferred highly variable abundance levels of the component populations of so-called "biological species". The interpretation of Hjort (i.e. fluctuations in landings due to year-class variability) explained the changes in quality of the landings (i.e. changes in size composition and percent cod liver oil), as well as the quantity.

As well as fundamentally redefining the nature of the "fluctuations" problem, Hjort proposed two hypotheses to account for recruitment variability. During his field studies on cod spawning and subsequent egg and larval distributions in the Lofoten area, Hjort noticed that the events occurred close to the seasonal timing of the spring phytoplankton bloom, the precise timing of which varied between years. From studies on the Norwegian current, he had also estimated with Helland-Hansen and Nansen that there was interannual variability

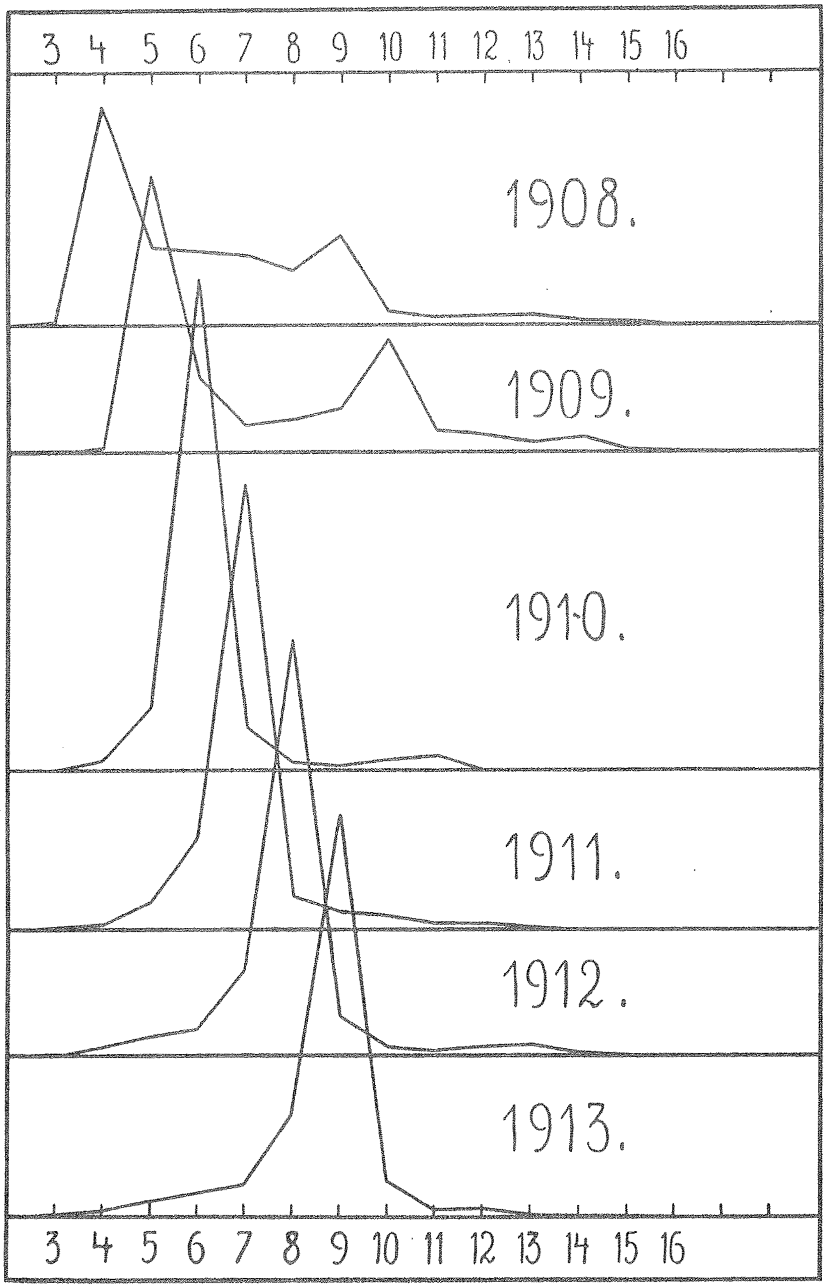

Figure 3. Age composition of the landings of herring caught off Norway from 1908 to 1913 (from Hjort 1914).

in advection. These observations in part led to his two hypotheses that have collectively been linked with the critical period concept. The landings data (such as those shown in Figure 3) indicated that relative year-class sizes were defined prior to recruitment of each year-class to the fishery. Thus the first few years were defined as the "critical period". Hypothesis 1 states that variability in year-class size is a result of between year shifts in the precise timing of spawning and of the phytoplankton bloom (which initiates the seasonal zooplankton production cycle upon which the fish larvae feed). From laboratory culture studies on fish eggs and larvae, it had been observed that first feeding during the few days following final resorption of the yolk sac were critical to larval survival. In the subsequent literature, it has frequently been assumed that the "critical period" defined by Hjort was these few days. A careful reading of the paper, however, indicates that he considered the early-life history stages as a whole (egg, larvae, post-larvae and early juvenile stages) to be the "critical period".

Hypothesis 2 was not very well articulated. In essence, Hjort argued that interannual differences of advection of eggs and larvae away from appropriate geographic areas for feeding and life cycle continuity generates subsequent recruitment variability to the fisheries. He recognized that multiple causes could be important in generating fluctuations in year-class sizes.

A Firming up of the Concepts (1914 to 1948)

After the rapid increases in understanding of the causes of fluctuations in landings between 1898 and 1914, the pace of discovery inevitably slowed. Between 1914 and 1948 (Hjort's death), there was, however, an increasingly better articulated description of the nature of the problem. Hjort's contribution of 1914, the discovery of year-class variability, was linked to that of Heincke (the discovery that species were comprised of geographically defined populations). The recruitment variability question was thus phrased in the context of population regulation. This took some time, and was based on the accumulation of empirical observations on the existence of populations for other fish species, as well as on the existence of year-class variability.

At the 1913 Statutory Meeting of ICES, during which Hjort presented an evening lecture on the major points of his 1914 classic paper, Gran (the phytoplankton ecologist) proposed a multidisciplinary international field test of Hjort's two hypotheses. It was on the books for initiation in 1914, but was stopped due to the outbreak of World War I, and the subsequent reduction of oceanographic research. The state-of-the-art in physical oceanography of continental shelves was probably not adequate at that time to have supported the test of this hypothesis. No field work was carried out on the two hypotheses during the 1914 to 1948 period. During this period there was, however, a substantial amount of study on the description of geographic population patterns for a variety of marine species. Not surprisingly, conceptual progress addressed this aspect of the recruitment variability problem.

A major contribution towards the population question was made by Schmidt in a series of 10 papers entitled "racial investigations" published between 1917 and 1930. He compared population patterns amongst several species (Atlantic herring, Atlantic cod, the eelpout Zoarces viviparous, and the European eel). Several conclusions of his studies were conceptual breakthroughs. He showed conclusively that the numbers of populations of a species varies markedly, from Zoarces sp. (which has dozens of separate populations), to Atlantic cod (which has a moderate number), to European eel (which is a single population or panmictic). He also noted that the characteristic absolute abundance varied considerably between populations of the same species. Thirdly, from experimental studies, he demonstrated that there was a genetic component to the observed differences in shape and meristics between populations. The geographic extent of the distribution of a population, which was shown to vary both within and between species, defines the spatial scale at which the recruitment variability question must be addressed. Schmidt demonstrated that this scale varies between tens and thousands of kilometers.

An additional important contribution during the 1914 to 1948 period were the first statistical studies showing correlations between physical processes (freshwater runoff, wind, temperature, etc.) and indices of fluctuations in abundance of fish populations (for example, the contribution by Sund 1924).

Two Special Meetings were sponsored by ICES in 1928 and 1929 to review progress on, respectively, the geographical patterns in marine fish populations and on recruitment fluctuations within particular populations. Hjort (1930), in his introductory address to the second of these two Special Meetings in London (1929), clearly states the overall importance of the transition from the species to the population as the essential unit of study (as well as its key role in making progress on the recruitment problem). He states (page 5):

> "When we entered upon our international collaboration 30 years ago [i.e. 1899], the biological analysis of the organisms we caught in the sea was in the main confined to the systematic determination of the various species..... However, as the work advanced, the demand for a more refined biological analysis and morphological classification became urgent. It was realized that the terms of species were inadequate to give a clean and orderly grasp of the phenomena in the large field covered by the international cooperation, and that recourse had to be taken to the conception of races or tribes [i.e. populations] as the more natural and convenient morphological and biological units ..... it is a matter of the greatest importance for all our research and deliberations that the existence of these races and their geographical area of distribution have been revealed" (emphasis added).

Hjort (1930) goes on to state the dual aspect of the recruitment problem (year-class variability within geographically defined populations). In a summary of the first 40 years of ICES work (1902 to 1942), Hjort (1945) again indicates the gradual clarification of concepts that had occurred. In a section entitled "Races and Populations" (p. 14-15) he states:

> "In the majority of species, perhaps in all, groups are formed which, so to speak, divide up the distribution area

> of the species among themselves and which, irrespective of size-classes, live separate from each other. They are called races ... The German scientist, Heincke, raised these problems by his years of investigations into the natural history of herring ... Subsequent investigations have confirmed and augmented these observations, not only with regard to herring, but also as regards many other species ...
>
> Out of this view of the geographical limitation of the races to definite areas, there gradually arose the conceptions connected with the words 'population' and 'stock', which denote a group of individuals distinct from all others both geographically and biologically. Thus we speak, for instance, of a herring population and a cod population off the west and north coasts of Norway that are different from the cod and herring populations of the North Sea and the Baltic." (emphasis added).

In summary, during the period 1914 to 1948, the problem of understanding fluctuations in landings of marine fisheries was articulated in terms of population regulation. In retrospect, one can see that this resulted from a linking of Hjort's discovery of year-class variability to Heincke's contribution on the existence of geographically-defined populations. The conceptual advances were firmly based on empirical observations from the North Atlantic. A more detailed historical analysis of fisheries research on the population concept is provided in Sinclair and Solemdal (1987).

The Recruitment Problem and Ecological Theory (1949-1975)

Developments within the field of ecology germane to population regulation were based largely on empirical observations on insects and birds. In general, estimates of temporal fluctuations in abundance were stated in terms of "population density" (numbers of individuals per unit area), rather than absolute abundance of geographically-defined populations in the sense defined above for fisheries studies. This is an important distinction. Theoretical developments concerning population regulation within ecology have not, in general, been based on empirical observations of geographic populations (see Kingsland 1985 for a historical analysis), but rather on density fluctuations at particular locations. Perhaps the most topical question in ecology during the 1950s and early 1960s was that of population regulation, in particular the relative importance of density-dependent and density-independent processes. The key contributions during this time period to the recruitment problem for marine fisheries were linked to this debate on population regulation in the broader field of ecology. Ricker (1954) and Beverton and Holt (1957) introduced mathematical formulations to describe stock/recruitment relationships. These relationships involved some biological feedback between adult abundance and year-class size. Such a relationship was (and still is by many ecologists) considered an essential requirement for stabilization of abundance levels. The fit of the empirical data on year-class sizes and spawning population abundance to the mathematical formulations was generally not sufficiently good to distinguish between the validity of different models based on the data itself. Also, the stock/recruitment relationships did not address the question of control of absolute abundance levels or the variability. The contributions of Ricker and Beverton and Holt did, however, formally state the recruitment problem in terms of population regulation. It appears that the different uses of the term population in respectively ecology and fisheries biology were not always clearly recognized (i.e. the term frequently refers to density differences in local abundance in ecology, whereas it refers to a geographic phenomena involving absolute numbers in fisheries biology).

The other key contributions on the recuitment question during this time period (1949-1975) were the syntheses by R. Harden Jones and D. Cushing of Lowestoft. Harden Jones (1972) in his classic book Fish Migration brought together much of the literature on the distribution of geographic populations and migration patterns at different life history stages. His migration triangle concept for population persistence, which involved larval drift from spawning locations to juvenile nursery areas via the surface layer residual currents, provided a geographical framework for the evaluation of recruitment variability. Events during the larval drift phase were considered to be critical to variability in year-class sizes. Cushing, in a series of papers, gradually developed his elegant match/mismatch theory which was widely read by the oceanographic community as a result of his 1975 book, Marine Ecology and Fisheries. The theory linked Hypothesis 1 of Hjort (1914) (i.e. the variability in timing of spawning and timing of blooming) with the "critical depth" concept of Sverdrup (1953). The critical depth concept itself linked the initiation of the spring bloom of phytoplankton to the seasonal development of thermal stratification. Between year differences in wind events at the time of spawning, and their effect on thermal stratification (and thus on initiation of the plankton production cycle), were packaged together in the attractively-phrased match/mismatch theory. The theory linked oceanographic processes to fisheries fluctuations in a most persuasive manner. Food-chain events during the early larval drift phase, an elaboration of Hjort's first hypothesis, became the focus of study for the recruitment problem. Cushing's food-chain articulation of the issue is perhaps still the leading hypothesis. The papers, and in particular the synthesis in his 1975 book, generated considerable excitement in the marine ecological community. The book, in addition, generated a wave of field studies on the first stages of the life cycle, around first feeding of larvae.

In parallel, particularly during the early period, a separate body of literature accumulated which involved the role of ocean climate (i.e. large-scale changes in physical oceanographic processes) on fluctuations in recruitment. Representative studies are Carruthers et al (1951a, b), Colton and Temple (1961) and Iles (1973). The study by Iles (1973) is particularly noteworthy in that he interpreted the year-class variability in the north Pacific and in western Canadian lakes in relation to large-scale ocean climate changes a decade prior to major increases in understanding of the El Nino/Southern Oscillation phenomena. This literature did not always specify the causal mechanisms generating recruitment variability (i.e., the steps between the physical changes observed and the year-class signal). Some papers, however, elaborated on Hjort's second hypothesis (i.e., variable losses of eggs and larvae from the appropriate distributional area for the population in question due to circulation differences between years). Evidence that the fisheries biologists during the 1950s and 1960s favoured Hjort's second hypothesis is provided in the annual reports of both ICNAF and ICES. In the 1961 Redbook of ICNAF, for example, it was stated (p. 72) that:

> "...there is urgent need for more information as regards year-class strengths in these subareas (SA2 and 3) ... owing to the complex nature of water movements in these and adjacent subareas, and some uncertainties regarding stock identity, there is need for more up-to-date information concerning spawning, larval success and subsequent drift in relation to contemporary environmental conditions. The probable value of studying these in relation to the isolated fishery of Flemish Cap should be considered ..." (emphasis added).

And further on in the report (p. 77):

> "The Working Party gave considerable thought to the problem of investigating the distribution of eggs and larvae of the principal commercial species in each subarea and of plankton studies in general ...
>
> They also recognized that the ICNAF Area, however, in which a series of most valuable fisheries are situated on the edge of a major continental slope, may present particularly important and valuable opportunities for a specially co-ordinated attack on the problem. Special reference has been made above to the value of egg and larval studies in Subareas 1 and 2, over the Flemish Cap and on Georges Bank. From north to south, there are a series of spawning grounds which would appear to be particularly vulnerable to deviations in the normal regime of the waters flowing constantly past them and in meteorological conditions ...
>
> The Working party therefore strongly recommended that the Commission should plan for a co-operative plankton and hydrographic [oceanographic] survey as soon as possible ..."

Part of the stimulation for the 1951 ICES Special Scientific Meeting in Amsterdam to discuss the place of oceanography in fisheries research was the paper presented at the 1950 Statutory Meeting by J. Carruthers and collaborators [subsequently published in Nature (Carruthers et al, 1951b)] in which haddock recruitment in the North Sea was linked statistically to wind-generated physical oceanographic phenomena. In the opening statement of their 1951a paper, they state (p. 6):

> "In this paper brood-strength fluctuations of the North Sea herring, plaice and cod are associated with inferred water movements set up by the local wind" (emphasis added).

In summary, during the early 1950s and 1960s, there was considerable support for the concept that changes in circulation in the egg and larval distributional areas was critical to the definition of year-class variability. The dual contribution of Harden Jones (1968) and Cushing (1975), however, shifted emphasis within the research community in the North Atlantic at least. The match/mismatch concept involving stratification changes and food-chain events generated the leading hypothesis for field studies.

The Decade of Field Studies on Early Life History Stages (1975 to 1985)

Until the mid 1970s, there were few field studies in the North Atlantic specifically designed to evaluate mechanisms involved in generating variable year-class sizes. There was, thus, a surprisingly long drought between Gran's 1913 proposal and the field studies on early life history stages that have proliferated since the mid 1970s. In the North Pacific, the ambitious CalCOFI program was initiated in 1948 to evaluate the importance of oceanographic processes on fluctuations in sardine abundance. For a summary of the historical events leading to the CalCOFI program see Scheiber (1986, Chapter 3). This long-term program has contributed to the recruitment literature, particularly within the 1975 to 1985 decade. For example, Lasker (1975) and Lasker and MacCall (1983) elaborated on Cushing's match/mismatch theory, and Sinclair et. al (1985) linked the CalCOFI data with Pacific mackerel population estimates and argued that the empirical observations support Hjort's second hypothesis (Figure 4).

The field studies on the recruitment question involving <u>Canadian</u> scientists during this decade are briefly summarized, giving emphasis to the particular hypotheses that have been addressed, the geographic scale of the studies and the conceptual advances. To my knowledge, essentially all of the Canadian field studies on recruitment during this period took place in the Atlantic. Grosslein (1987), Lilly (1987) and Grosslein and Lilly (1987) have recently reviewed the ICNAF/NAFO-sponsored multi-national recruitment studies on Georges Bank herring and Flemish Cap cod/redfish. Their reviews include critiques. Sinclair et al (1987), in a review of a broader scope than just recruitment studies, cover much of the same ground, but give particular attention to the adequacy of the physical oceanographic components of these major programs. Given these reviews, there is no need for further soul-searching on their shortcomings. When these two programs are looked at in a historical perspective (i.e. they represent the first serious attempt to investigate recruitment dynamics in the field in the western North Atlantic), the overall approach taken was well-founded.

The first step of the Georges Bank herring program was to describe spawning locations and subsequent larval distributions on a spatial scale considerably larger than Georges Bank itself. The multi-national larval surveys covered the Gulf of Maine area as a whole. The accumulated observations on larval distributions and their spatial shifts seasonally were somewhat contrary to expectations. A persistence in geographic distributions of larvae, rather than a displacement with the residual surface-layer currents, was observed. The recirculation processes on Georges Bank were considered important in limiting the dispersal of larvae from the Bank. The large-scale survey style studies allowed the scientists participating in ICNAF to define the spatial scale at which a Georges Bank herring recruitment study should encompass. The survey series provided the setting for the definition of the research questions involved in the second component.

The aims of the Georges Bank herring recruitment study proper are stated in the 1975 ICNAF Redbook (p. 91-92). Of the eight recommendations, three dealt specifically with Georges Bank-Nantucket Shoals herring. They were:

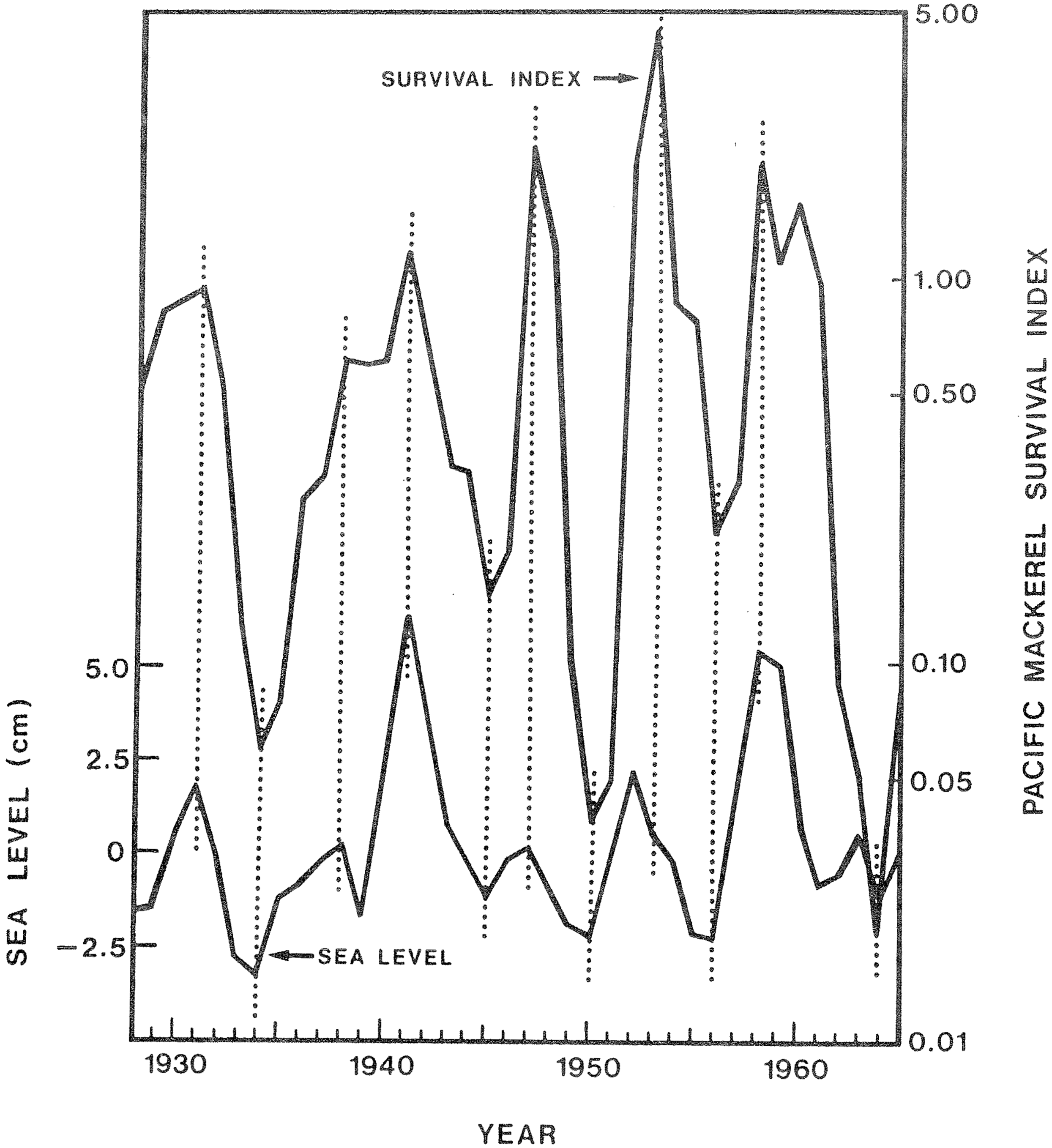

Figure 4. Time series of estimates of Pacific mackerel survival index and an index of the strength of the California current (from Sinclair et al 1985).

"v) that a concerted effort be made to understand the circulation and diffusive processes above and around the Georges Bank-Nantucket Shoals area;

vi) that a special sampling study to follow an isolated patch of larvae on Georges Bank be attempted in 1975 and/or 1976, in addition to the Standard Surveys, with a view to identifying the physical processes responsible for larval loss from the system, and providing information on the finer-scale variations in growth, mortality, dispersion, feeding and vertical distribution, as the basis for evaluating the feasibility of quantitative estimation of these processes and sampling errors inherent in the present data base;

vii) that quantitative studies of primary and secondary productivity should be conducted to provide a better basis for relating these phases of organic production to potential fish production."

International research projects under ICNAF were directed toward Recommendations (v) and (vi) above, but not Recommendation (vii). Although preliminary observations were collected in 1977, the detailed Georges Bank-Nantucket Shoals study did not take place until 1978.

What is of interest is the questions that were asked and their geographic scale. To understand recruitment variability of the Georges Bank spawning population, it was considered necessary to investigate the distributional area for the larval phase of the population, in this case, the bank itself (as indicated from the earlier large-scale surveys). Second, both physical losses from the area and food chain events were considered to be important. Studies on the relevant physics, biological oceanographic production processes, as well as detailed studies on larval behaviour in relation to the physics, were recommended. The approach advocated and taken was descriptive rather than hypothesis testing. For a number of reasons, the program lost momentum and was not brought to a timely conclusion. Thus, conceptual advances from the program itself cannot be considered to be substantive. However, the descriptive data collected and its subsequent analysis have contributed to:

1) a hypothesis on Atlantic herring population patterns and abundance for the northern Atlantic as a whole (Iles and Sinclair 1982, Sinclair and Iles 1985);

2) space- and time-scale characterization of circulation and mixing over submarine banks in general (Loder et al, 1988); and,

3) the conclusion that events during the early life history stages as a whole (rather than the first few weeks of the larval stage) are important in defining year-class stengths (Sissenwine 1984).

This field study in 1978 addressing recruitment dynamics of marine fish in the North Atlantic (65 years after Gran's research proposal at ICES in 1913), in the sense that it involved an enhanced description of the ocean which aided in subsequent hypothesis formulation, can be rated in retrospect as an important program. It is noteworthy that the field study was not a test of Cushing's match/mismatch hypothesis.

The Flemish Cap recruitment study on cod and redfish was more influenced by Cushing's food-chain interpretation of year-class variability. From the early years of ICNAF, Flemish Cap was considered a good geographic area to investigate recruitment dynamics. There was evidence that the Cap supports a self-sustaining spawning population of cod with minimal immigration from contiguous areas. The direct influence of physical oceanographic processes on abundance fluctuations was inferred to be of importance (see earlier quotation from 1961 Redbook of ICNAF).

It was not until 1975 that a major recruitment focus was placed on Flemish Cap by ICNAF. The Flemish Cap International Experiment developed from Recommendation 30(i) of the Environmental Working Group of ICNAF which stated (ICNAF Redbook 1975, p. 100) that:

> "... an attempt be made to identify relationships between the various currents around Flemish Cap, the water temperature at appropriate depths and any other relevant environmental factors with the year-class strengths of cod and redfish on the bank, including the role of predation of cod and redfish, and to identify other major gaps which still exist in knowledge of the area as well as research programs needed to fill them ...".

The reasons why this geographic area was considered amenable to study were listed (1975 Redbook, p. 99). These included:

> "i) both the cod and redfish stocks are relatively isolated from the stocks on the adjacent Grand Bank;
>
> ii) the water circulation patterns are likely to be amenable to study;
>
> iii) the area is restricted in size; and,
>
> iv) the area is one which, because of its major oceanographic features has been of interest to physical oceanographers for many years and there exists a useful historical and physical environmental data base. With respect to the latter, no fully co-ordinated and comprehensive analysis has yet been carried out."

These quotes are of interest for several reasons. Again, it is clear that ICNAF scientists of the time considered that it is critical to study recruitment dynamics in the context of a self-sustaining, geographically identifiable population. The spatial scale of the study must match the distributional limits of the population. Flemish Cap being relatively restricted in size, as well as isolated, offered certain advantages for a field program on recruitment.

Second, a leading hypothesis in 1961 and even 1975 was that interannual differences in circulation generated variable losses of eggs and larvae from the appropriate distributional area for the population, and thus the physics directly influenced year-class sizes. This emphasis on the physics as a leading hypothesis diminished as the progam progressed. The influence of the food-chain events became increasingly important in directing thought concerning the field studies. Lilly (1987, p. 110-111) summarizes the hypotheses that were developed as the program evolved. He states:

> "... they expressed the central hypothesis of the project as follows: 'The year-class strength of the Flemish Cap cod stock varies as a result of specific biological and environmental conditions.' This central hypothesis was divided into four main parts: physical environmental conditions, predation conditions, food abundance conditions and characteristics of the spawning stock. By making references to stages of the life cycle, 12 hypotheses were developed... This document was potentially very useful. It was clearly instrumental in guiding some of the research, particularly the oceanographic program, but its use to date as a framework for gauging progress in the testing of specific hypotheses has been insignificant."

The shift in the leading hypotheses from the direct role of physics to a predominant role by food-chain events paralleled shifts in the published literature dealing with the recruitment question.

As was the case for the Georges Bank herring program, from a historical perspective, the Flemish Cap study has been an important contribution. It was the second field study in the northwest Atlantic that addressed recruitment on the population scale. The study on its own has not contributed to conceptual advances in our understanding of the factors controlling year-class variability, but the empirical observations have contributed to better articulated hypotheses and descriptions of the relevant physics (e.g., Loder et al, 1988).

The third study on similar spatial scales off eastern Canada was the Scotian Shelf Ichthyoplankton Program (SSIP). This program, which was carried out between 1977 and 1982, has received considerable criticism, to a large degree because of a misunderstanding of its goals. As was the case with the ICNAF Georges Bank herring program, it was considered important to conduct a large scale description of the distribution of eggs and larvae on the Scotian Shelf as a whole prior to defining a study on the recruitment dynamics of a particular population. Other than the descriptive work of the 1914/15 Hjort expedition to Canada (published in 1919), there was, in 1975, essentially no information on ichthyoplankton on the Scotian Shelf. The aim of SSIP was to describe the seasonal distribution of egg and larval distributions for all fish species on the Scotian Shelf. An attempt was made to cover each month of the year at least twice over the five-year period (the sampling grid is shown in Figure 5). The surveys provided information on the timing of spawning for different species, the duration of the larval phase and the geographic scales of dispersal from the spawning areas. The empirical observations on spatial distributions were again somewhat surprising, in that they suggested persistence of egg and larval distributions for some species over the banks rather than

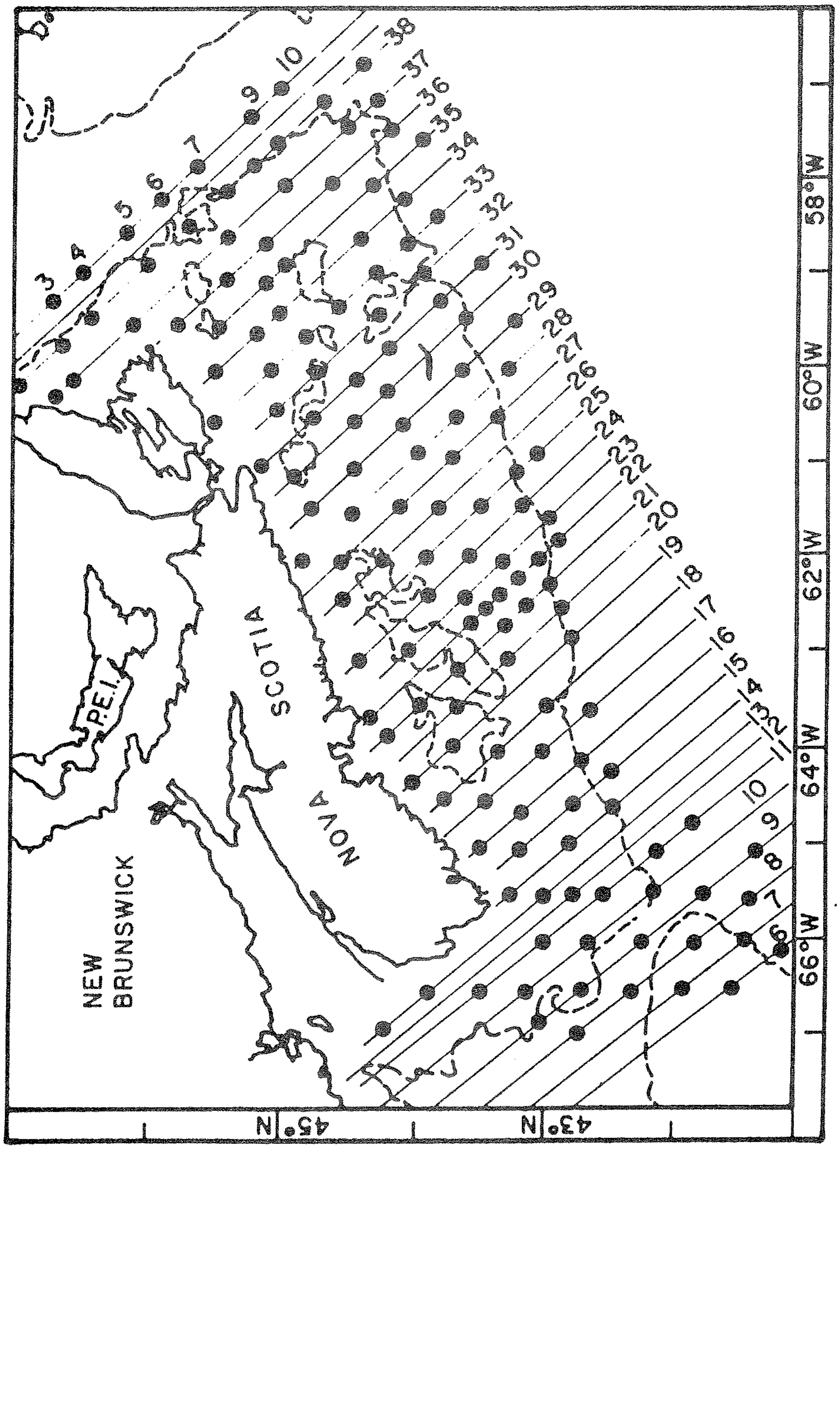

Figure 5. Station locations for SSIP.

drift with the residual surface layer circulation (O'Boyle et al, 1984; Gagné and O'Boyle, 1984). These survey results have provided the setting, and an indication of the appropriate spatial scale, for the follow-up recruitment study on Brown's Bank haddock (part of the Fisheries Ecology Project, FEP). In this sense SSIP was, in my view, the logical first (and necessary) step needed prior to the definition of a recruitment program on the Scotian Shelf. A legitimate criticism is that perhaps more ancillary environmental data was collected than was justified by the limited aims of the program, and that full analysis and publication of the ichthyoplankton data in the primary literature has been slow.

In parallel to these three major expensive large scale field programs of relevance to recruitment, there were two classes of inexpensive small-team studies carried out in eastern Canada during the 1975-1985 decade. The first category is a series of statistical studies initiated by W. Sutcliffe and his collegues in the former Marine Ecology Laboratory (MEL). The study was developed in the early 1970's (Sutcliffe 1972; 1973) but gained momentum and interest by the broader scientific community during the decade in review. The study has involved the analysis of existing time series on year-class sizes (or landings) and physical oceanographic parameters (Sutcliffe et al, 1977, 1983, Koslow 1984, Koslow et al 1987, Drinkwater and Myers 1987). The correlations have generated several site-specific hyptheses, but field tests to date have been minimal. The second category includes the near-shore field studies by W. Leggett and his colleagues on the spawning and early life history of capelin in both the St. Lawrence Estuary and Newfoundland embayments. These studies which were reviewed in the context of the broader literature by Leggett (1986) have focused on smaller spatial and temporal scale processes, not necessarily on the scale of the population (for which there is still considerable uncertainty for this species). The accumulated work has generated a rich set of empirical observations and a number of new hypotheses. The papers have only recently reached the scientific community and their full impact on our thinking about recruitment has yet to be felt. The implications of these studies will undoubtedly be addressed in other review papers of current work in this report. Suffice to say here that the contribution, in terms of both observations on the oceans and on ecological theory, has been substantive and thought provoking.

The recent leading hypotheses that have been generated both by increasing empirical observations (on spawning population abundance, year-class sizes, oceanographic time series and results of process-oriented studies), and a developing theoretical framework, will be introduced in the following papers. It is fair to say that they are still, to a large degree, elaborations of Heincke's geographic population concept and Hjort's two categories of hypotheses (respectively, food-chain events and the direct role of physical oceanographic processes). What has changed since the 1914 paradigm shift dealing with fluctuations in marine fisheries landings is the greater role assigned to predation during the early life history stages in the definition of year-class sizes. In this sense, there are perhaps three categories of hypotheses (direct role of physics in generating losses, food limitation and predation control). In the closing section of this paper, I will take the opportunity to state (or re-state) my conception of the scope of the recruitment problem.

Concluding Remarks

What then do we mean by the recruitment problem or question in fisheries research? First of all, recruitment is a term associated with species having complex life histories (i.e. with egg, larvae, junvenile and adult stages). Secondly it usually addresses age structured populations. The problem involves the causes of the intergenerational variability in abundance of age-clases of geographically persistent populations. In fisheries research the recruitment problem is a euphemism for the fundamental problem of population regulation. It is not to be confused with availability changes which reflect temporal shifts in distribution of populations and thus local abundance rather than changes in absolute abundance. I have found it useful to consider the recruitment problem in the broader context of population regulation. Four components of population regulation can be defined:

i) geographic pattern in the distribution of populations within and between species;

ii) numbers of populations per species, or population richness, and how this characteristic varies between species;

iii) the characteristic mean absolute abundance of numbers of individuals within a population;

iv) the inter-generational variability in age-class strengths that cause temporal fluctuations in abundance.

In brief, the four components of population regulation are pattern, richness, abundance and variability. Most of the research focus in recent years had been on the fourth component. It may well be that substantive increases in understanding of the causes of variability of age-classes within populations depends on a better understanding of the processes regulating the pattern, richness and mean abundance of populations. This involves such problems as understanding why different populations of species spawn in particular locations at different seasons and the degree to which homing exists for mobile animals.

I would prefer that we state the age-class variablility problem (or recruitment problem) in population regulation terms. There is a danger that we may lose sight of the context of the problem by using terminology that emphasizes only part of the natural phenomena. During the workshop we need to consider the research thrusts in oceanography and marine ecology that will generate increases in understanding of population regulation of commercially important species.

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V REVIEWS OF DEPARTMENT OF FISHERIES AND OCEANS PROGRAMS ON RECRUITMENT

A. OCEANIC FACTORS AFFECTING THE DISTRIBUTION AND RECRUITMENT OF WEST COAST FISHERIES

by

R.E. Thomson and D.M. Ware
Pacific Region

INTRODUCTION

Fisheries-oceanographers have long recognized the possible importance of oceanic variability to the distribution and recruitment of North Pacific fish stocks. However, throughout most of this century stock-related research has focused on the migration and survival of salmon in freshwater and the near-shore environment. Until recently, there has been no concerted effort to conduct a coordinated, multi-disciplinary, long-term (decadal scale) program of fisheries and physical oceanographic observations to better delineate the factors influencing the production and recruitment of British Columbia fisheries.

A recent study of the large-scale circulation features and distribution of commercial quantities of marine fish indicates that there are three major production domains in the northeast Pacific Ocean (Fig. 1; Ware and McFarlane 1988). The Coastal Upwelling Domain extends from Baja California (25°N) to the northern tip of Vancouver Island (50.5°N). This domain is defined physically by the normal summer pattern of negative wind stress curl and offshore Ekman transport (upwelling), and by the northward limit of major concentrations of Pacific hake, sardine,and mackerel which migrate into Canadian waters in the summer to feed (when the stocks are abundant), and which return to southern and Baja California where they spawn in the winter and spring (Fig. 2). The Coastal Downwelling Domain extends from Dixon Entrance in northern British Columbia (54°N), along the continental shelf of southeast Alaska to Prince William Sound and then westward along the Aleutian Islands. This domain is defined physically by the poleward flowing Alaska Current, which is an eastern boundary current of the Alaska gyre, and by the buoyancy-driven Alaska Coastal Current. Biologically, the domain is defined by the distribution of major concentrations of Pacific halibut, cod and Walleye pollock (Fig. 3). The third major production domain is the Central Subarctic Domain which is defined by the Alaska gyre and is dominated by Pacific salmon. Ware and McFarlane (1988) also recognized a small Transitional Zone between the Coastal Upwelling and Downwelling Domains. This zone encompasses the coastal waters of central and northern British Columbia, specifically Queen Charlotte Sound and Hecate Strait and is significant because it helps explains why the recruitment patterns differ between northern and southern stocks of Pacific herring, Pacific cod, and Sockeye salmon, and why there are no major commercial halibut fisheries in southern British Columbia.

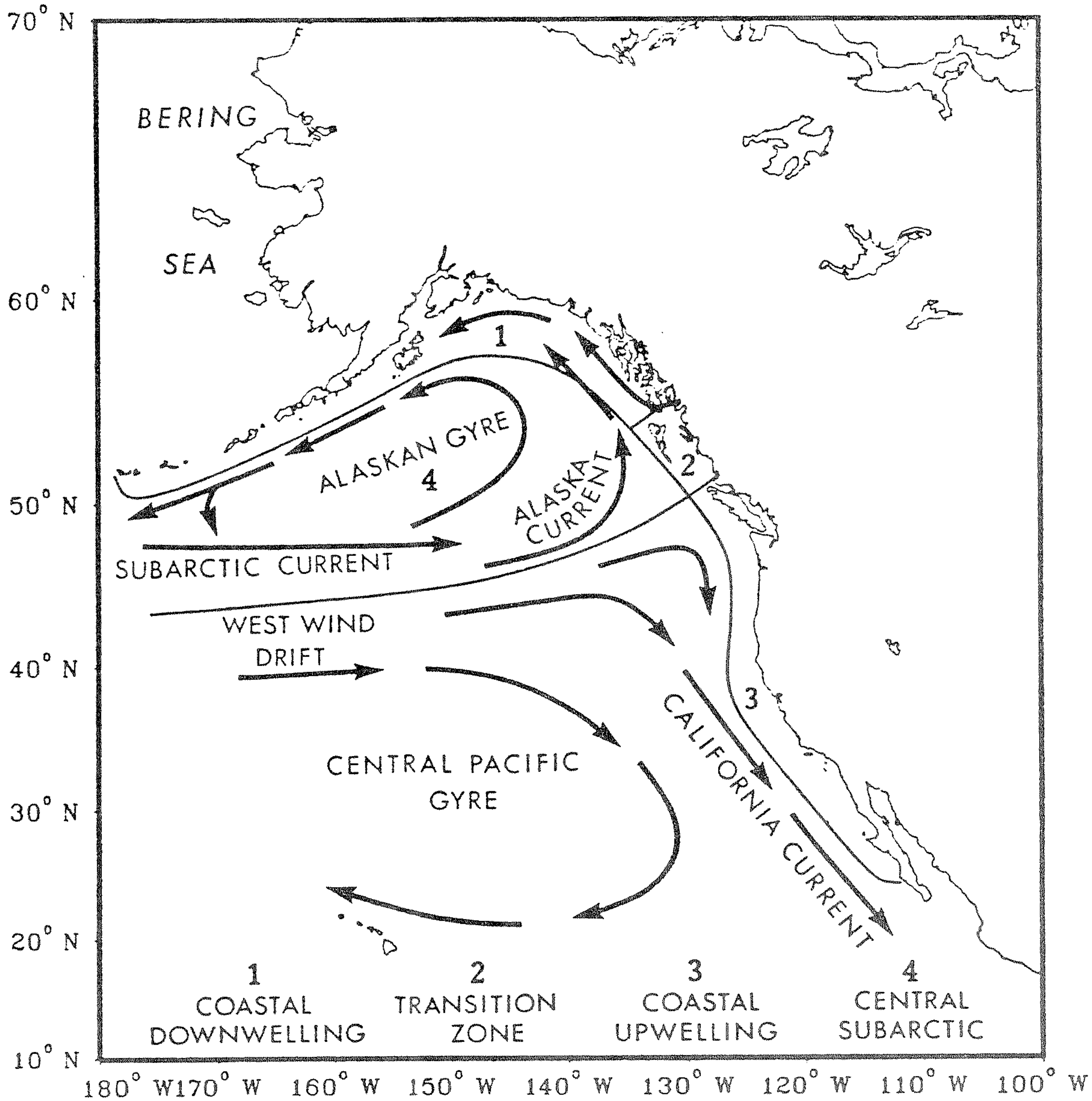

Fig. 1. Approximate areas of oceanic production domains and prevailing current directions in the northeast Pacific Ocean (from Ware and McFarlane 1988).

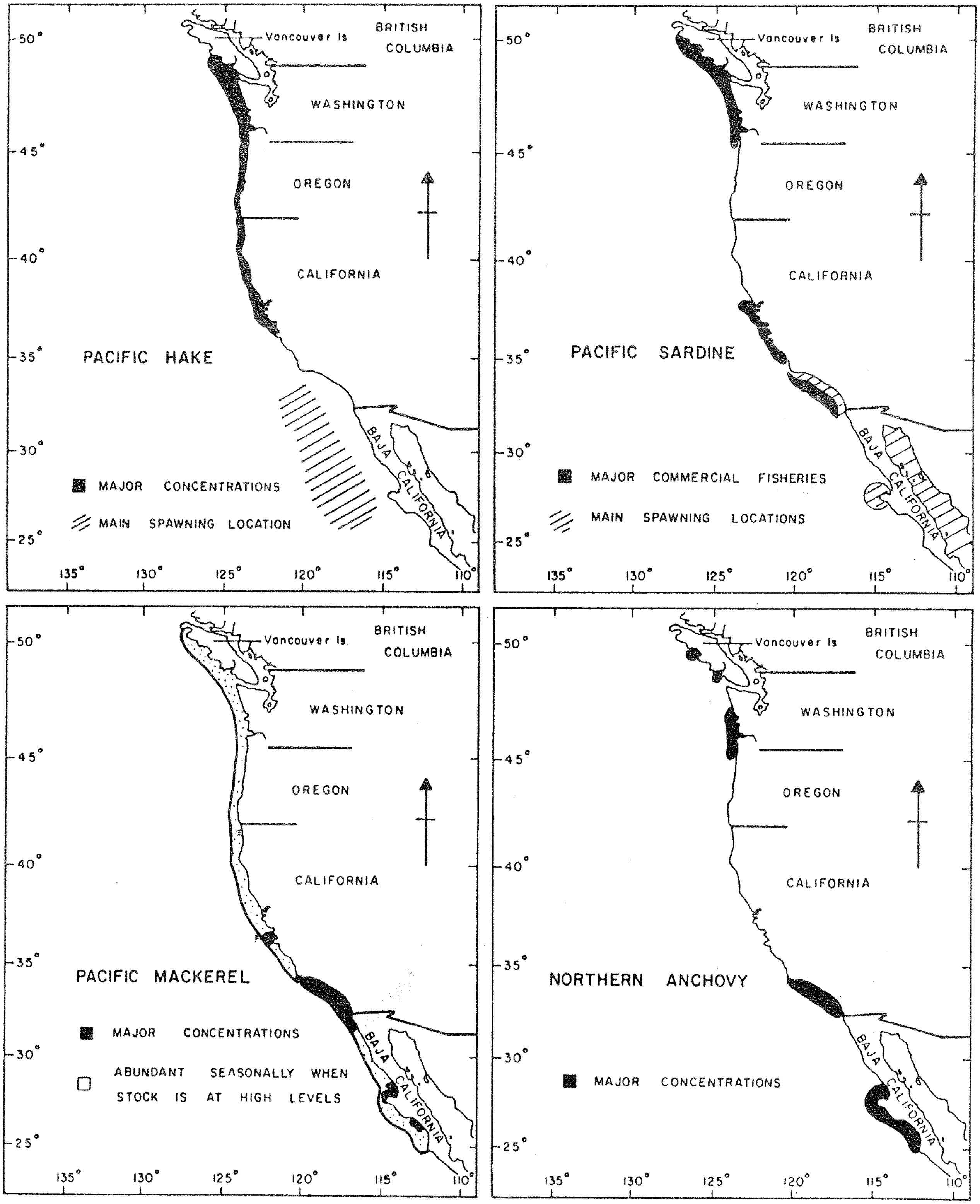

Fig. 2. Major concentrations of the dominant pelagic species in the coastal upwelling domain in summer (from Ware and McFarlane 1988).

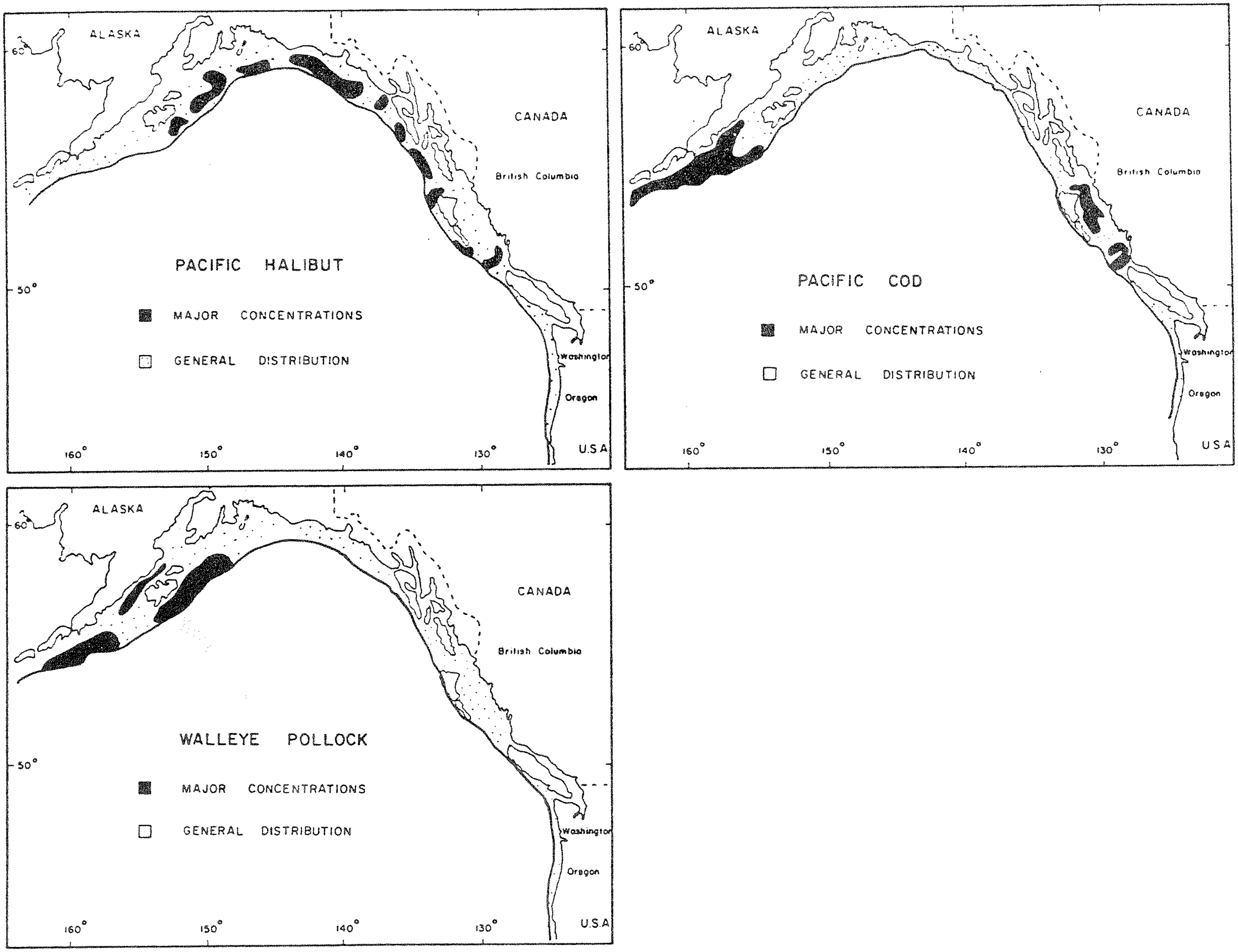

Fig. 3.
Major concentrations of the dominant fish species in the coastal downwelling domain (from Ware and McFarlane 1988).

Most of the continental shelf fisheries in British Columbia fall within two different production regions: the Coastal Upwelling Domain and the Transitional Zone. Historically, the Coastal Upwelling Domain has been the most productive region. Between 1917-66 the West Coast of Vancouver Island (shelf area of roughly 19 thousand sq. km) produced an average catch of 65 thousand tonnes of Pacific herring (from the West Coast and lower East Coast of Vancouver Island stocks; Taylor 1964), and an average catch of 31 thousand tonnes of sardine between 1917-47, which represents an average production rate of 5.1 tonnes/sq. km/yr when the migratory stock of sardine was abundant, and 3.4 tonnes/sq. km/yr when this stock declined. The west coast of Vancouver Island (WCVI) currently produces a catch of some 60 to 70 thousand tonnes of Pacific hake (the potential catch for 1988 is 90 thousand tonnes) and 6 to 8 thousand tonnes of herring. Thus although there is no clear indication that the general level of productivity has changed significantly since 1917, there has been a striking change in the species composition of the catch! The Coastal Upwelling Domain is currently in a state dominated by hake and their principal prey, euphausiids.

In 1985, the Pacific Biological Station and the Institute of Ocean Sciences began a joint, decade-long investigation on the effects of oceanic variability on fish stocks on La Pérouse Bank (Ware and Thomson 1986, 1987). The program was initiated partly in response to the lack of fishery-oceanography data for the west coast following the 1982/83 El Nino-Southern Oscillation (ENSO) event and partly in response to a need for improved regional oceanographic data in the important fishing zones off southern Vancouver Island. The La Pérouse Bank region was chosen for this investigation for several reasons. To begin with, it is a major fishing zone comprising a variety of important fish stocks including Pacific herring, sablefish, Pacific hake, and Pacific salmon. Secondly, the region is fairly well defined (encompassing an area of roughly 100 sq. km at the southwestern end of the Vancouver Island continental margin) and lies entirely within the Coastal Upwelling Domain. Thirdly, the region is one of the most thoroughly studied and best understood physical oceanographic regions on the west coast. Results from a variety of major oceanic programs such as CODE, SuperCODE and the Vancouver Island Coastal Current Experiment have provided us with considerable background information on the major processes affecting the water properties and circulation along the southern continental margin.

BACKGROUND INFORMATION

HISTORICAL PERSPECTIVE

Prior to 1955, much of the regional fishery-oceanography research concentrated on the large-scale oceanic properties in the Gulf of Alaska, with few attempts to investigate the variability of coastal oceanic properties pertinent to fisheries productivity (Fleming 1955). Noteable exceptions for the British Columbia coast include the studies by Tully (1942), Tully and Doe (1953), Pickard and McLeod (1953), Doe (1955) and Hollister (1964). For example, Doe (1955) presented a detailed study of the coastal water properties for the period 1950-51 and concluded that the vertical structure could be divided into a surface zone (0 - 100m depth), a halocline (100 - 150 m depth) and a deep zone (below 150 m depth). The temperature at the top of the lower zone could be considered a conservative property of the lower zone with a salinity of around 33.8 ppt. Fleming's 1955 summary of the physical oceanography of the northeast Pacific appears in Bulletin No. 2 of the International North Pacific Fisheries Commission. The brevity of the document attests to the limited extent of the observed oceanographic data available at the time. Actual time-series information in this document is limited to sea surface temperature and sea level heights obtained from coastal light-stations. This lack of data led Fleming to lump the entire coastal regime from northern California to Kodiak Island into an "American Coastal Region".

Although oceanic research over the following decade continued to concentrate on the Gulf of Alaska, considerably more data were collected on the structure and variability of water properties along the continental margin of British Columbia. In April 1959, the Weathership program at Ocean Station PAPA was extended to include "Line P" oceanographic stations en route to and from PAPA, including three locations over the continental margin of southern Vancouver Island. By early 1969, the program had been upgraded to encompass expendable BT (XBT) and salinity- temperature-depth (STD) observations at the Line P stations. These data, combined with the NORPAC data sets collected through the auspices of the International North Pacific Fisheries Commission (INPFC) and through individual research projects, are summarized by Dodimead et al. (1963). Summarized results revealed seasonal and interannual changes in the complex eddy-like structure in the temperature, salinity and geostrophic velocity fields along the eastern oceanic boundary. The continental margin was still considered part of an extensive "Coastal Domain" but with suggestion of a poleward extension of the California Undercurrent along the coast of British Columbia.

The next in the series of summary reports by the INPFC (Favorite et. al. 1976) summarized the oceanographic information from 1960-71. In addition to observations from the open ocean, the document contains detailed information on the time series variability of coastal sea levels, sea surface temperatures and salinities, atmospheric pressure and large-scale circulation. Moreover, the Coastal Domain was now separated into an "Upwelling Domain" extending from California to southern Vancouver Island and a "Dilute Domain" lying seaward of the British Columbia Coast. A recent summary of the general oceanography of the continental waters off British Columbia is provided by Dodimead (1984). Details of all aspects of the water properties are presented in this comprehensive study, including oceanographic data to 1979 and sea surface conditions at coastal lightstations.

Recent Oceanographic and Recruitment Programs

The first major investigation of the currents and water properties along the southwest coast of Vancouver Island (the Coastal Oceanic Dynamics Experiment, CODE) was undertaken during 1979-81 by the Institute of Ocean Sciences (Freeland 1983, 1987; Thomson et al. 1985a, 1985b, 1986; Huggett et al. 1987). Data from the three cross-shelf mooring lines and more than thirteen CTD/hydro surveys provided new insight into the seasonal variability and mesoscale dynamics of the continental margin flow regimes and paved the way for further research initiatives on the continental margin. Particular aspects of the coastal circulation revealed by this program include: a description of the Juan de Fuca Eddy and associated time-variable upwelling (Freeland and Denman 1982), a detailed analysis of baroclinic diurnal period continental shelf waves

(Crawford and Thomson 1982, 1984), an analysis of mesoscale eddy formation and dissipation (Thomson 1984) and a description of the monthly mean flow structure (Freeland et al. 1984). Data from the SuperCODE program considered the propagation of low-frequency coastal trapped waves along the entire central coast of North America (Yao et al. 1984). A separate study of the vorticity dynamics of the Juan de Fuca Eddy was conducted in 1985 by the Institute of Ocean Sciences.

A study of the Vancouver Island Coastal Current -- a persistent, poleward flowing buoyancy-driven current along the west coast of Vancouver Island -- was initiated in 1984 (LeBlond et al. 1985; Thomson et al. 1985b, 1988). Based on observations from this program, we now have considerable information on the structure, dynamics and seasonal variability of the flow structure over the continental margin of southern Vancouver Island. The North Coast Oceanic Dynamics Experiment (NCODE) for the period 1983 to 1985 is providing similar information concerning the oceanography of the waters adjacent to the Queen Charlotte Islands (cf. Crawford et al. 1985; Thomson 1987; Thomson and Wilson 1987; Thomson et al. 1988).

Since 1982 a number of major research programs in the Pacific Region have been designed to address the recruitment problem in specific fisheries (Table 1). The Hecate Strait program is a multi-disciplinary study which is developing a multi-species approach for managing the complex assemblage of groundfish in Hecate Strait and is attempting to clarify the impacts of oceanic factors on Pacific herring, Pacific cod and rock sole recruitment. Between 1983-86 a companion study of pink and chum salmon surival was conducted in Masset Inlet on the Queen Charlotte Islands. In 1985, the La Pérouse Project was designed to determine what was responsible for the significant fluctuations in herring, sablefish, Dungeness crab and Pacific cod recruitment. This is a multi-disciplinary study designed to identify the dominant physical processes affecting the circulation and water property structure; to quantify the low-frequency, non-periodic variability of the zooplankton; and to formulate and test specific hypotheses concerning how interannual oceanic fluctuations affect recruitment. The Marine Survival of Salmon Project (MASS) was undertaken to investigate the interrelationships between biophysical events and salmon distribution and survival on an annual and interannual time scale. The major objectives of the Project are: 1) to measure the residence time and survival of Barkley Sound sockeye smolts in relation to food, predators, and wind-driven circulation, and to track their northward dispersal along the southwest coast of Vancouver Island; and 2) to measure the residence time and survival of chinook and coho on the offshore banks in relation to local tidal rectification, topographic eddies, and cross-shelf exchange mechanisms that may create favourable feeding conditions. Other recent programs on salmon have focused on the importance of the estuarine phase of the life cycle of chinook on marine survival, and the effect of changes in oceanic conditions on the migration routes and arrival times of maturing salmon in the coastal fisheries.

Annual and Interannual Variability

Until the initiation of the joint PBS/IOS La Pérouse Bank project most modern oceanographic programs on the west coast of Canada have been primarily concerned with understanding the mechanisms affecting the spatial and temporal variability of the coastal ocean. As a consequence, project durations are typically shorter than a few years and provide little insight into possible long-term effects of oceanic factors on fisheries distribution and recruitment. Some long-term data are provided by the Line P data set. However, in general, the stations are too far offshore and widely separated to provide information on the coastal ocean. The most complete records of long-term coastal oceanic variability continue to be sea surface temperature, salinity and sea level from lightstations (Hollister 1964; Hollister and Sandnes 1972; Giovando 1985). These data are supplemented by long-term records of coastal river runoff, atmospheric pressure, precipitation and winds. For the most part, the increase in noise in the salinity data following the change in type of sensor in 1979 has prevented the use of these data for climate-scale investigations.

Lane (1963) presented a detailed analysis of the seasonal cycle in vertical temperature and salinity structure for the region seaward of Amphitrite Point on Vancouver Island. As indicated by Dodimead (1984), this study marked the first attempt to characterize the seasonal variability in the water properties off the outer coast. Fofonoff and Tabata (1966) used the oceanographic time series from Line P to describe long-term fluctuations in temperature and salinities off the west coast. Although mainly concerned with offshore conditions, the study revealed distinct interannual variability in the coastal regime associated with wind-forced upwelling/downwelling dynamics. Using data from coastal oceanic surveys, Dodimead and Pickard (1967) presented evidence for marked year-to-year variability in the "relative area" of coastal water off Vancouver Island whose temperature at the top of the halocline was greater than 7°C in summer. Thomson (1972) suggested that the interannual variations in these intrusions are linked to the average of the meridional wind stress (and, hence to the onshore component of Ekman transport) during the preceeding winter. Ekman transport dynamics forms the basis of the upwelling indices for the west coast of North America published by Bakun (1973) for the period 1946-71. Derived from the longshore component of the frictionally-modified, geostrophic coastal winds, the indices have become an integral factor in determining relationships between oceanic conditions and fish recruitment. Upwelling indices for subsequent years have found general widespread application and have been published on a regular basis for the west coast (e.g. Bakun 1975). Transport computations for the North Pacific provide similar information though on a less detailed scale (cf. Wickett et al. 1977).

Davis (1976) found a significant correlation between the monthly mean anomally patterns of sea surface temperature (SST) and sea level pressure (SLP) in the North Pacific. Regions of anomalously cold (warm) surface temperature tended to coincide with anomalous southward (northward) surface winds. On this basis, it would appear that monthly variations in SST are largely controlled by meridional advection in the surface Ekman layer. Haney (1980) has identified both advection and surface wind-mixing as important factors to the formation of SST anomalies.

Enfield and Allen (1980), Thomson et al. (1984) Emery and Hamilton (1985) and Hamilton (1986) have used long-term lightstation temperature records to investigate El Nino-Southern Oscillation (ENSO) events along the west coast of North America. Oceanic and atmospheric mechanisms affecting these events are summarized in Mysak (1986). Thomson et al. (1984) used nine observation sites on the British Columbia coast dating back more than forty years to investigate the occurrence of ENSO events and long-term warming/cooling periods. Major ENSO events in the equatorial Pacific were found to be strongly correlated with coastal warming along the coast with a return period of 15 to 25 years, although persistent and marked warming can also occur in the absence of equatorial warming events. Similar results are reported by Hamilton (1986) for the coast of northern California to Oregon. The data also reveal pronounced slowly varying, decadal-scale cycles in the water temperatures along the coast. In particular, the years 1925-46, 1957-68 and 1976-present appear to mark periods of anomalous warming while years 1947-56 and 1969-75 mark periods of anomalous cooling.

A study of long-term coastal temperature variability at 100 m depth is presented by Brainard and McLain (1985). Using monthly mean temperature measurements from the U.S. Master Oceanographic Observations data set, they were able to show that the subsurface temperature anomalies of major ENSO events for the period 1951-84 propagate poleward from the northwest coast of South America along the coast of North America at speeds ranging from 10 to 50 km/day. These speeds are comparable to longshore propagation speeds determined for sea level height anomalies and are slower than the theoretical speeds for coastal Kelvin waves (coastally-trapped waves). Unlike surface temperature anomalies for the coastal region, only the 1982/83 warm event and the strong 1954/56 cold event could be traced along the entire length of the observational area from Chile to British Columbia. Major events in 1957/58, 1972/73 and 1976/77 appeared to propagate only as far as northern California. Royer and Xiong (1984) analyzed long-term temperature records from a site off Seward Alaska and found that the subsurface waters of the northeast Pacific have warmed at about 0.1°C per year between 1972-85. The data also indicate that the upper 250 metres at the Seward site warmed in response to the 1977 and 1983 ENSO events.

Long-term variations in coastal sea levels have been studied by a variety of authors including Enfield and Allen (1980), Chelton (1980), Barnett (1984). Sea level fluctuations associated with ENSO events are seen propagating poleward along the entire coast of North America at speeds of several tens of kilometres/day and there is evidence for 5-6 year oscillations in sea level due to long-term variations in atmospheric pressure. Trends in sea level along the British Columbia coast are found to be linked to tectonic processes associated with continental drift and with glacio-isostatic rebound originating with the slow viscous response of the earth to melting of glaciers during the last ice-age (e.g. Barnett 1984; Aubery and Emery 1986; Thomson 1986; van de Plassche 1986).

A study of long-term (twenty-five year) steric sea levels from the Line P data set (Tabata et al. 1986) indicates that salinity effects dominate steric height variations near the coast whereas temperature effects prevail in the offshore region. Near the coast, annual variations in steric sea level are governed by the cycle of winter dilution by precipitation and runoff and summer concentration by upwelling. Local currents such as the Vancouver Island Coastal Current appear to be the primary factor affecting variations in coastal sea level, not variations in the offshore current system. A study of long-term sea level trends in the northeast Pacific is given by Thomson and Tabata (1987).

Using monthly SST and SLP data for the period 1946-82, Emery and Hamilton (1985) have been able to establish a link between atmospheric circulation and interannual variability in SST and coastal sea levels in the northeast Pacific Ocean. In particular, the occurrence of anomalously warm water along the British Columbia coast in winter is coincident with an anomalously intense Aleutian Low in the Gulf of Alaska. These results are consistent with the notion that SST anomalies on seasonal time scales are largely maintained by wind-driven advection in the near-surface waters of the ocean. The results further show that long-term sea level heights along the coast are controlled by large-scale atmospheric circulation in the North Pacific. The authors also argue for an atmospheric link ("telecommunication") between the equatorial region and mid-latitudes during ENSO events. In general, "warm" equatorial winters (strong El Nino episodes) are accompanied by vigorous atmospheric circulation in the North Pacific while "cold" equatorial winters are accompanied by weak mid-latitude atmospheric circulation. Weak winter SLP patterns often precede tropical El Nino events. If an El Nino event is then accompanied by strong North Pacific atmospheric circulation, there is invariably a strong warming of the surface waters in the eastern North Pacific and an increase in sea level along the west coast of North America, such as in 1958 and 1983. However, some ENSO events are accompanied by weak atmospheric circulation and anomalously cold SST along the coast of North America. Conversely, there can be strong winter-time circulation and very warm SST in the northeast Pacific without the occurrence of anomalous conditions in the tropics (e.g. 1961). The mechanism proposed by Emery and Hamilton (1985) did not predict the moderate 1987/88 El Nino event (W. Emery, personal communication).

Recruitment Studies

A variety of studies have suggested links between interannual variability in oceanic conditions and recruitment of west coast fish stocks. For example, Walters et al. (1978) developed a model simulating the first 6 months of ocean life of Pacific salmon. They hypothesized that mortality rates should decrease with body size, so any density-dependent mechanism producing slower growth should result in higher mortalities. They concluded that juvenile salmon are unlikely to be food-limited: there appears to be enough plankton production to support the existing abundance of juvenile salmon without measurable effects on their growth and survival, so the explanation for the observed dependence of marine survival must be sought elsewhere. They suggested density-dependent predation. Recently, Peterman (1987) found some statistical evidence for density-dependent marine survival and growth in some salmonid species; it seems to occur most strongly in the first 14-18 months of ocean life. His analysis of Fraser River pink salmon revealed a significant negative correlation between adult body weight and number of fish per unit zooplankton at ocean station P (in the central subarctic). Contrary to the conclusion reached by Walters et al. (1978), Peterman showed that there may be a period of food limitation during the oceanic phase of the life cycle which has a significant effect on fish weight, and hence the biomass of the returning stock. He also suggested that the form of the relationship describing predation mortality on juvenile salmon may produce complex stock-recruitment curves with multiple equilibria. This possibility has some important management implications in terms of how the stocks should be harvested.

Mysak et al. (1982) conducted a cross-spectral analysis of sea level, sea surface temperature (SST) and salinity off British Columbia with annual Fraser River sockeye catch and west coast of Vancouver Island herring. The cross-spectra indicated that the fisheries time series were highly coherent with the physical data at a period of 5-6 years. Since there are large-scale atmospheric variations and transpacific fluctuations in SST at this period, it seems that these fluctuations may affect the number and average weight of fish through some of the processes hinted at by Peterman (1987). Ware and McFarlane

(1986) extended the work of Mysak et al. (1982), and confirmed that west coast of Vancouver Island herring year-class strength shows a strong negative correlation with annual SST, they also found a negative correlation with the estimated biomass of Pacific hake, which is the key predator of juvenile and adult herring during the summer, when both the predator and prey distributions overlap on the continental shelf. Since both correlations were highest with a zero year lag (for SST), and zero and 1 year lag (for hake biomass), as a working hypothesis this analysis suggests that temperature may reflect the influence of oceanic conditions on herring survival during the first 5-6 months of life, while the predator effect appears to operate most strongly on late age 0+ and 1+ juveniles which are distributed offshore.

In northern British Columbia, Walters et al. (1986) found that Hecate Strait herring have fluctuated in a manner which suggests that their recruitment rates are being forced by Pacific cod predation. In the 1960's and 70's, both populations experienced what appears to be a classical predator-prey oscillation; however, this relationship broke down in the late 1970's indicating the involvement of other, overriding factors. For example, year-class strength of Pacific cod in Hecate Strait is also strongly correlated with water transport and water temperature (Tyler and Westrheim 1986). Poor year-classes tended to be associated with strong northward transport and low temperatures.

With respect to other groundfish species, McFarlane and Beamish (1986) found that good sablefish year-classes tended to occur when spring onshore Ekman transport is strong and water temperatures are high. In British Columbia poor sablefish year-classes predominate during periods of low temperature and reduced onshore transport. Their interpretation of this tendency is that favourable oceanographic conditions may increase the amount of food available to the early larval stages at depth (possibly as early as the half yolk-sac utilization stage) and increase their survival rate. In another statistical study, Fargo and McKinnel (1988) performed a response surface analysis of Rock sole abundance and found a significant dome-shaped relationship between year-class strength and March SST (the period of peak spawning). The optimal temperature was in the range of 5.5-6.5°C, and is believed to reflect optimal hatching success in this species. The response surface analysis also suggested that the stock-recruitment curve for Rock sole resembles a Beverton and Holt asymptotic curve.

A common limitation of the foregoing studies is that the conclusions are derived almost exclusively from correlations; little or no direct, or independent, evidence is presented to support the proposed mechanisms. These exploratory studies therefore mark the first step in the search for understanding, since they attempt to reduce the infinite number of possible factors that may affect recruitment into a smaller set that can be tested directly by making appropriate measurements in the field.

PHYSICAL OCEANOGRAPHY

The purpose of section is to review the key seasonal and interannual variations in water properties and circulation in the La Pérouse Bank region of southwestern British Columbia. Emphasis is on the major temporal changes in the spatial structure and the possible mechanisms affecting these changes. Results rely heavily on the observations obtained from oceanographic field programs conducted over the past decade.

The La Pérouse Bank region falls into the Coastal Upwelling Domain which extends from northern California to northern Vancouver Island (Fig. 1) and is characterized by marked summer upwelling and the presence of a buoyancy-driven coastal current along the inner shelf. Winds in this region are predominantly to the south in summer and to the north in winter. A Coastal Transition Zone separates the upwelling domain from the Coastal Downwelling Domain extending poleward along the Alaska coast from roughly 54°N off Dixon Entrance. The Transition Zone extends from the northern tip of Vancouver Island to Dixon Entrance and is distinguished by low coastal runoff, the absence of an offshore continental shelf and a strong offshore oceanic influence. The Downwelling Domain is characterized by strong downwelling coastal winds, marked land-derived runoff and strong longshore coastal currents (e.g. Royer 1981a, b).

Spring Transition: February-April

The Spring Transition is an annual event that marks a relatively abrupt change from winter to summer water properties and circulation over the continental margin. According to Strub et al. (1987), the transition is a large-scale feature extending from California to southern British Columbia with longshore scales of 500 to 2000 km. The transition coincides with the reversal from southeasterlies to northwesterlies in the prevailing winds and typically propagates from south to north over a period of 3 to 10 days. This poleward propagation is expected to take the form of long coastally-trapped waves or may arise through atmospheric teleconnections. In the former case, estimated propagation speeds range from 50 to 150 km/day. On the coast of British Columbia, the transition occurs over a one- to two-week period sometime between late February to early May with considerable year-to-year variability in the timing and intensity of the reversal. For example, in 1987, observations suggest that the transition occurred in mid-April while in 1983 the transition appears to have taken place in early February.

In addition to the reversal in the prevailing longshore winds, the Spring Transition is accompanied by a reversal in the prevailing shelf-break currents, a lowering of mean coastal sea level, a re-stratification of the shelf/slope waters and the onset of upwelling favourable conditions over the outer shelf (Thomson et al. 1988). The annual cycle in the shelf-break current, from northwestward in winter to southeastward in summer, is quite pronounced and is observed in direct current meter measurements, in surface drogue studies and in calculated geostrophic velocity fields. Typical seasonal variations in mean sea level are of order 10 cm. The Spring Transition also marks an increase in the buoyancy flux from the entrance of Juan de Fuca Strait and an alteration in the primary buoyancy source driving the Vancouver Island Coastal Current. In winter, the coastal current receives relatively low density water from both Juan de Fuca Strait and runoff from the mountain ranges of Vancouver Island; in summer, only Juan de Fuca Strait contributes significantly to the buoyancy flux.

Based on the above summary, it is clear that the Spring Transition delineates an important change in the fundamental structure of the coastal ocean. The timing and intensity of the onset of upwelling favourable winds combined with the establishment of an intense southeastward flowing current centered over the shelf-break and outer shelf could have a significant effect on the currents and water property distribution, and therefore on the regional fisheries. This effect could occur directly through changes in the oceanic environment or indirectly through effects on the distribution of zooplankton and predator populations.

Summer Circulation: May-October

Following the Spring Transition, there is a rapid weakening of the Aleutian Low in the Gulf of Alaska and strengthening of the North Pacific High off California. This leads to prevailing northwesterly winds along central North America and to the establishment of a summer circulation pattern along the coast of Vancouver Island. Increased solar heating leads to increased warming and stratification of the upper 100 m of the water column over the continental margin. Upwelling results in the onshore movement of subsurface slope water onto the outer shelf, leading to an decrease (increase) in near-bottom temperatures (salinity) with an accompanying decrease in dissolved oxygen levels. The combination of shelf-break upwelling and nearshore downwelling (due to the presence of the poleward flowing coastal current) gives rise to a banded longshore structure in the subsurface water properties over the continental margin (LeBlond et al. 1986 and Thomson et al. 1988). In particular, the water properties over the shelf take on a bowed appearance, with relatively high salinity, low temperature (high density) water centered along the 100 m depth contour flanked by relatively low salinity, high temperature (low density) water over the outer and inner portions of the shelf.

The prevailing summer circulation over the continental margin of Vancouver Island is characterized by four main features (Fig. 4; see also Thomson et al. 1988): (1) The poleward flowing inner-shelf Vancouver Island Coastal Current extending from Juan de Fuca Strait to Brooks Peninsula (or beyond to Queen Charlotte Sound); (2) The equatorward flowing Shelf-break Current extending along the entire coast from northern Vancouver Island to northern California; (3) The cyclonic (counterclockwise rotary) Juan de Fuca Eddy situated over the central portion of Juan de Fuca Canyon to the south of La Pérouse Bank; and (4) The generally weak clockwise circulation centered over the central portion of the La Pérouse Bank region. In addition, there appears to be a significant mean flow component generated through rectification of the strong diurnal and semidiurnal tidal currents that dominate the high-frequency variability over the continental margin. Mesoscale eddies with lifespans of a few days to weeks are also common features of the coastal circulation (Mysak 1977; Ikeda et al. 1984a, b,; Thomson 1984; Thomson and Gower 1985; Denman and Freeland 1985; Denman and Mackas, personal communication).

The Vancouver Island Coastal Current is a narrow (15 to 25 km wide), baroclinic current flowing over the inner half of the continental shelf north of Juan de Fuca Strait. The current has typical time-averaged speeds in excess of 10 cm/s and longshore extent of over 150 km. Although it persists throughout the year, the current is most noticeable in summer when it flows poleward counter to the prevailing winds from the northwest. Except over La Pérouse Bank, the core of the current appears to be centered near the 50 m depth contour. In summer, the current is forced primarily by buoyancy flux from Juan de Fuca Strait while in winter it is forced by both coastal precipitation and Juan de Fuca discharge. Since it opposes the prevailing winds in summer, the maximum speed of the coastal current is typically found at depths of a few tens

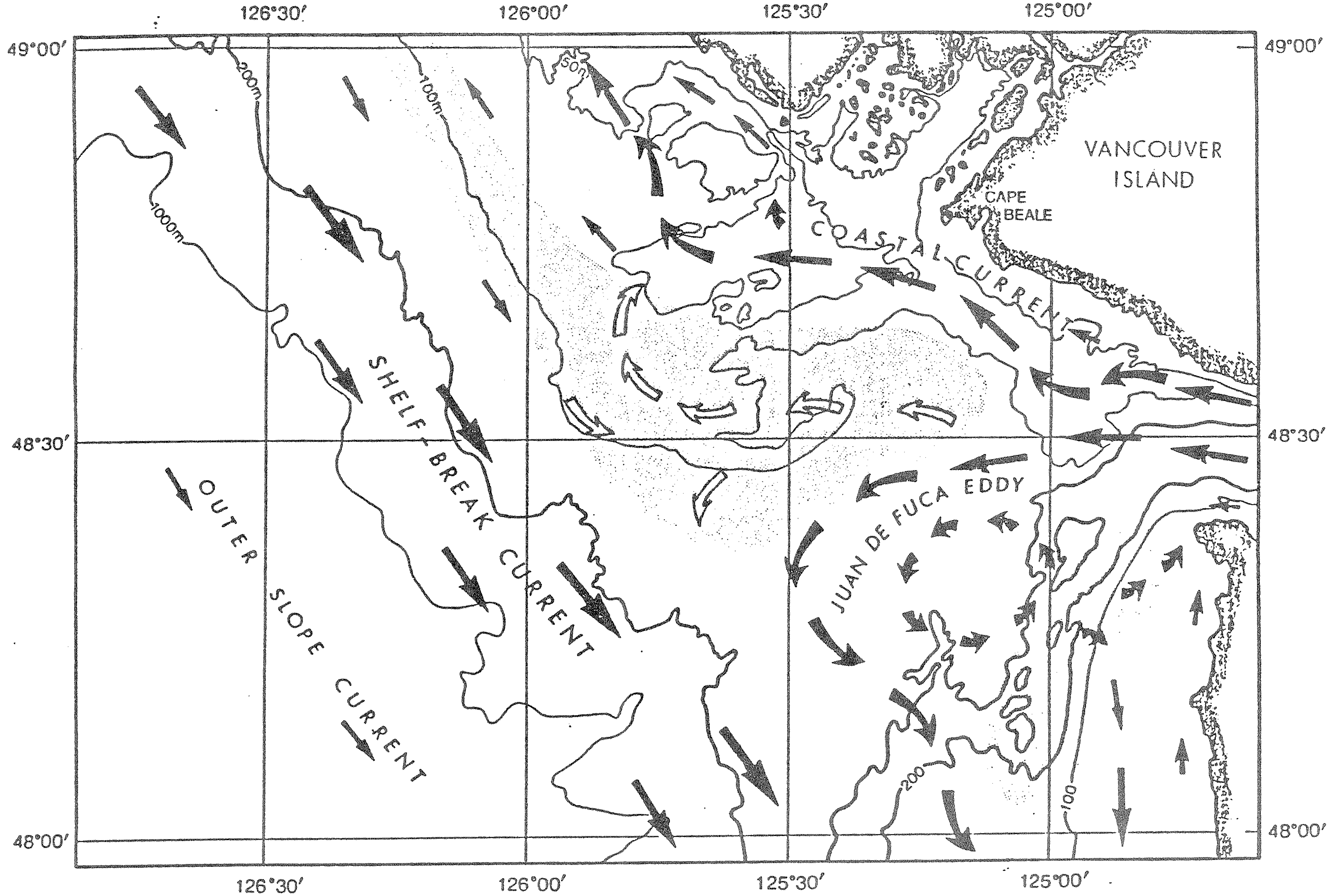

Fig. 4. General summer circulation pattern on La Perouse Bank and surrounding waters. Stippled region denotes an area of confused flow (from Thomson et al. 1988).

of metres rather than at the surface (Thomson et al. 1988). Especially strong northwesterlies (speeds in excess of 15-20 m/s) are capable of reversing the coastal current to considerable depth for periods of a few days.

Throughout its length, the coastal current is separated from a seasonally-reversible Shelf-break Current by an alongshore transition region of relatively weak and variable flow. The transition region is most pronounced in summer and is most extensive over the broad shelf seaward of Barkley Sound. It is assummed that the transition region marks a divergence of the upper layer waters. The Shelf-break Current is an intense wind-driven southeastward flow confined to the upper 150 m with core speeds of order 50 cm/s centered over the outer shelf. In contrast to the coastal current, the shelf-break current reverses seasonally in response to the prevailing winds along the outer coast. The flow is predominantly to the southeast in summer and to the northwest in winter. Flow beneath the shelf-break current appears to be principally to the north in response to oceanic flow conditions over the continental slope. It is assumed that this subsurface poleward flow over the continental slope represents the California Undercurrent Extension, the northward branch of the California Undercurrent thought to carry relatively warm, low dissolved oxygen water northward over much of the slope of North America (Hickey 1979; Mackas et al. 1987).

In addition to the marked cross-shore structure of the shelf circulation, there is an obvious distinction between the circulation to the south and north of Barkley Sound. This spatial distinction is emphasized in summer when the wind and runoff mechanisms produce flows in opposite directions. The buoyancy driven flow emenating from Juan de Fuca Strait loops seaward over La Pérouse Bank before turning northward to form the relatively confined nearshore current north of the Sound. A second branch of this outflow curls southward to form the Juan de Fuca Eddy situated to the south of the La Pérouse Bank region. Looping of the current exiting from Juan de Fuca Strait leads to a weak clockwise eddy centered over the bank. Current meter records from the La Pérouse Bank project indicate that near-surface cross-bank currents gradually intensify through the summer suggesting that the northern boundary of the Juan de Fuca Eddy shifts northward or that there is an intensification of outflow from the strait.

Fall Transition: October-November

The transition from the summer to winter oceanic regime takes place sometime between October and November during the first major autumn storm. As with the Spring Transition, the actual timing and intensity of this event varies interannually. In certain years, the transition can occur as early as late September while in others (e.g. 1987) the transition may take place as late as mid-November. Differences in timing are clearly related to the degree of storm activity in the North Pacific and to positions of storm tracks relative to the coast of North America. In contrast to coastal regions to the south, the Fall Transition along the coast of British Columbia appears to be a reasonably well-defined event.

The Fall Transition is marked by a reversal in the prevailing winds along the coast and is accompanied by a reversal in the Shelf-break Flow, an approximately 10 cm rise in mean coastal sea level, enhanced wind and convective mixing of the surface waters and the cessation of upwelling. Though data are limited, the transition appears to coincide with decreased integrity of the Juan de Fuca Eddy and enhanced strength of the nearshore poleward flow. Currents over La Pérouse Bank are directed more toward the northwest and there is less likelihood of weak, confined circulation over the bank as in summer. Runoff from Vancouver Island begins to contribute to the coastal current which is expected to be more confined to the nearshore regions along the island.

Winter Circulation: November - April

During winter months, the flow is typically to the northwest over the entire continental margin in response to the prevailing southerly winds. Increased runoff from the mountainous regions of Vancouver Island strengthens the buoyancy-driven Vancouver Island Coastal Current while vigorous wind-mixing and convective overturning leads to a deepening and de-stratification of the upper 100 m of the water column. Deceleration of the winter flow regime occurs during brief mid-winter periods when local high pressure systems and accompanying northwesterly winds build over the outer coast. This also leads to strong outflow winds from inlets and channels adjoining the coast and to enhanced cooling of the oceanic surface waters.

ENSO Variability

A variety of studies for the west coast confirm the existence of long-term variability in the water properties and circulation that are partly linked to El Nino-Southern Oscillation events (Enfield and Allen 1980; Thomson et al. 1984; Emery and Hamilton 1986; Mysak 1986; Tabata et al. 1986). All investigations confirm the presence of long-term 15-25 year cycles in the water properties and the influence of major equatorial events on the mid-latitude oceanography (e.g. 1941/42, 1957/58 and 1982/83). In addition, atmospheric pressure and adjusted sea level data suggest the presence of a quasi-six year cycle in the mid-latitude variability (Thomson and Tabata, 1981; Mysak et al. 1982; Tabata et al. 1986). The temperature fluctuations at this period are marginally significant and it is doubtful if there are significant changes in the flow structure at these periods.

Major ENSO events are accompanied by strengthened (weakened) southerly (northerly) winds and a greater bias to poleward transport of upper ocean water along the coast. The combined effect of the modified winds and poleward flow is to diminish the upwelling response and to enhance the integrated temperature of the upper layer. Sea levels rise as a result of the tendency to poleward flow and southerly winds. Depending upon the amount of time-integrated runoff entering the coastal zone, surface salinities can be expected to increase as more saline water is moved northward with the mean circulation.

FISHERIES OCEANOGRAPHY

This section reviews the biological production characteristics and seasonal movements of some of the dominant fish and invertebrate species off the lower west coast of Vancouver Island, and considers how interannual variations in the intensity and timing of seasonal events, and changes in predator and prey distributions may affect marine survival and, hence, recruitment.

SPRING TRANSITION PERIOD

The extant data on phytoplankton and zooplankton biomass are not extensive enough to clearly define the seasonal variability, let alone the interannual variability of the production cycle off the west coast of Vancouver Island. One of the key objectives of the La Pérouse Project is to assemble such a time series. The fragmentary bits of information that exist indicate that the spring phytoplankton bloom begins in late March-early April. The nutrients supporting this bloom tend to be exhausted quite quickly, but are replenished by upwelling which begins in late May. Consequently there may be two peaks in zooplankton abundance: one following the spring bloom and a second in June (Fig. 5). The most abundant copepods in the area in the spring are large bodied forms such as Calanus and Neocalanus spp.; in summer, the dominant copepods are neritic forms like Acartia and Centropages spp. Euphausiids are also locally abundant (3 to 80 g/sq. m). E. pacifica is the dominant species off the west coast of Vancouver Island; it is an oceanic form which tends to spawn intermittently from early May to September in response to plankton blooms (Fulton et al. 1982). E. pacifica grows rapidly following the spring bloom at a rate of about 1.5% of the body weight per day.

The spring transition marks a period when Pacific herring, Pacific hake, and sablefish spawn and the adults of the two former species begin migrating back to the summer feeding grounds. Herring reach their lowest level of abundance on the offshore banks in March; only the pre-recruits occupy the banks then since the adults are inshore near the spawning grounds (Fig. 6). Pacific hake spawn off southern and Baja California from January to March, and then begin their poleward migration back to the rich feeding grounds off the lower WCVI. By early March the main body of hake is off San Francisco (37°N), and progresses northward at an average speed of 16-18 km/day. At this rate of advance hake would not keep pace with the spring transition (which propogates poleward at a rate of 50 -150 km/d) but would lag behind allowing the development of euphausiid stocks along the route. Sablefish spawn from January-March over the continental slope. Their eggs and larvae are most abundant at depths greater than 400 m; hatching and initiation of feeding occurs at depth in late February to mid-March. The larvae migrate to the surface waters late in the yolk sac stage (mid-late March). Measurements are currently being made to test the possibility that favourable oceanographic conditions enhance the amount of food available to sablefish larvae, and increases their survival rate (McFarlane and Beamish 1986).

The seaward migration of Pacific salmon begins around the time of the Spring Transition. On the West Coast of Vancouver Island, sockeye smolts enter Alberni inlet and first appear in Barkley Sound in late April. By mid-June they have largely left Barkley Sound and have begun their poleward migration along the eastern boundary of the Gulf of Alaska. In contrast to the sockeye and coho juveniles, which move out of Barkley Sound quickly, juvenile chinook remain inshore throughout the summer and move to the offshore banks in November. This chinook stock may have sustained heavy predation losses from Pacific mackerel, which were unusually abundant in Barkley Sound in the summers of 1983 and 1984 (Ashton et al. 1985).

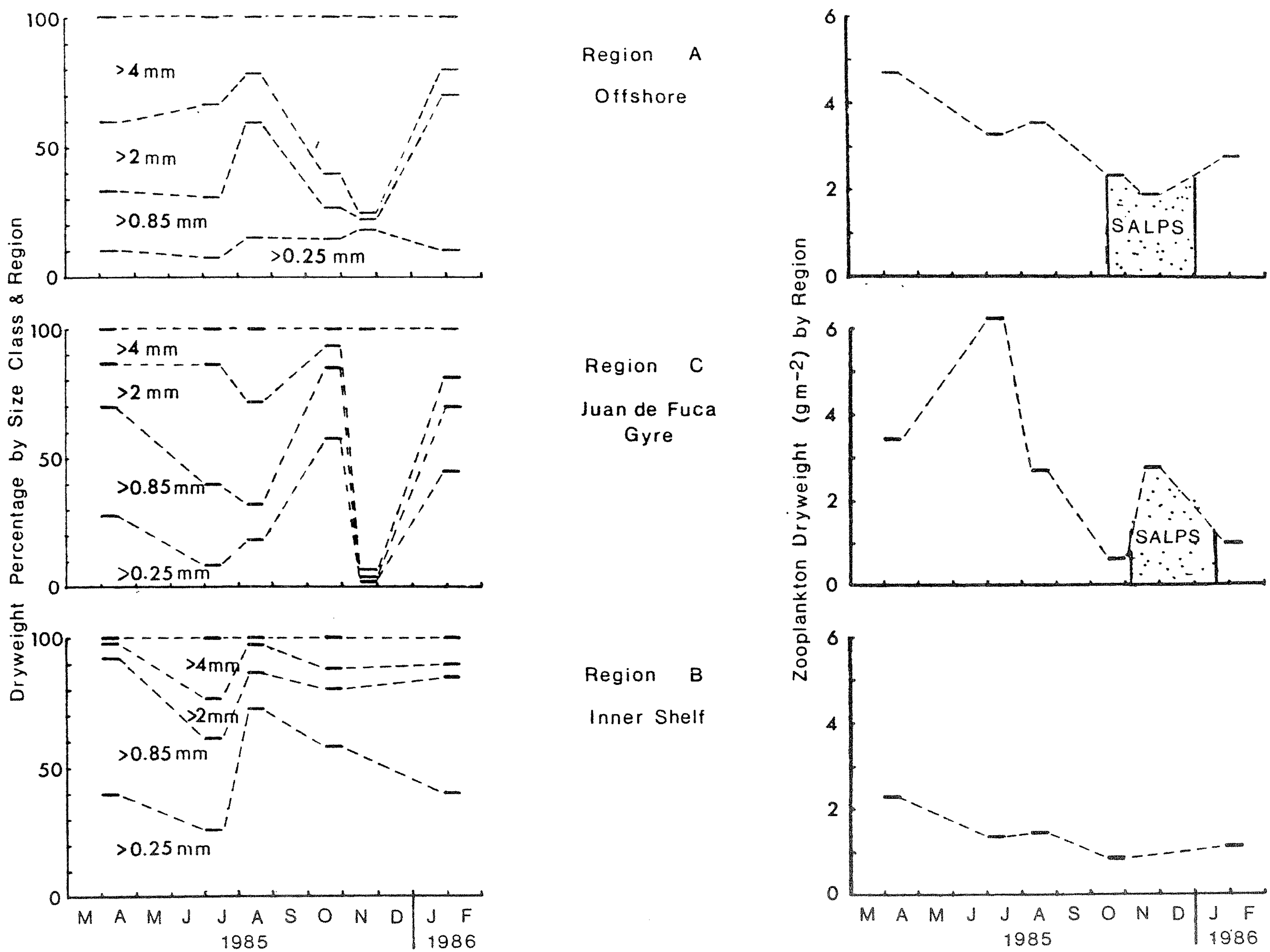

Fig. 5. Zooplankton concentrations, and dry weight percentage by size class in the offshore, inner shelf and Juan de Fuca eddy regions (courtesy of D. Mackas, Institute of Ocean Sciences, Sidney, British Columbia).

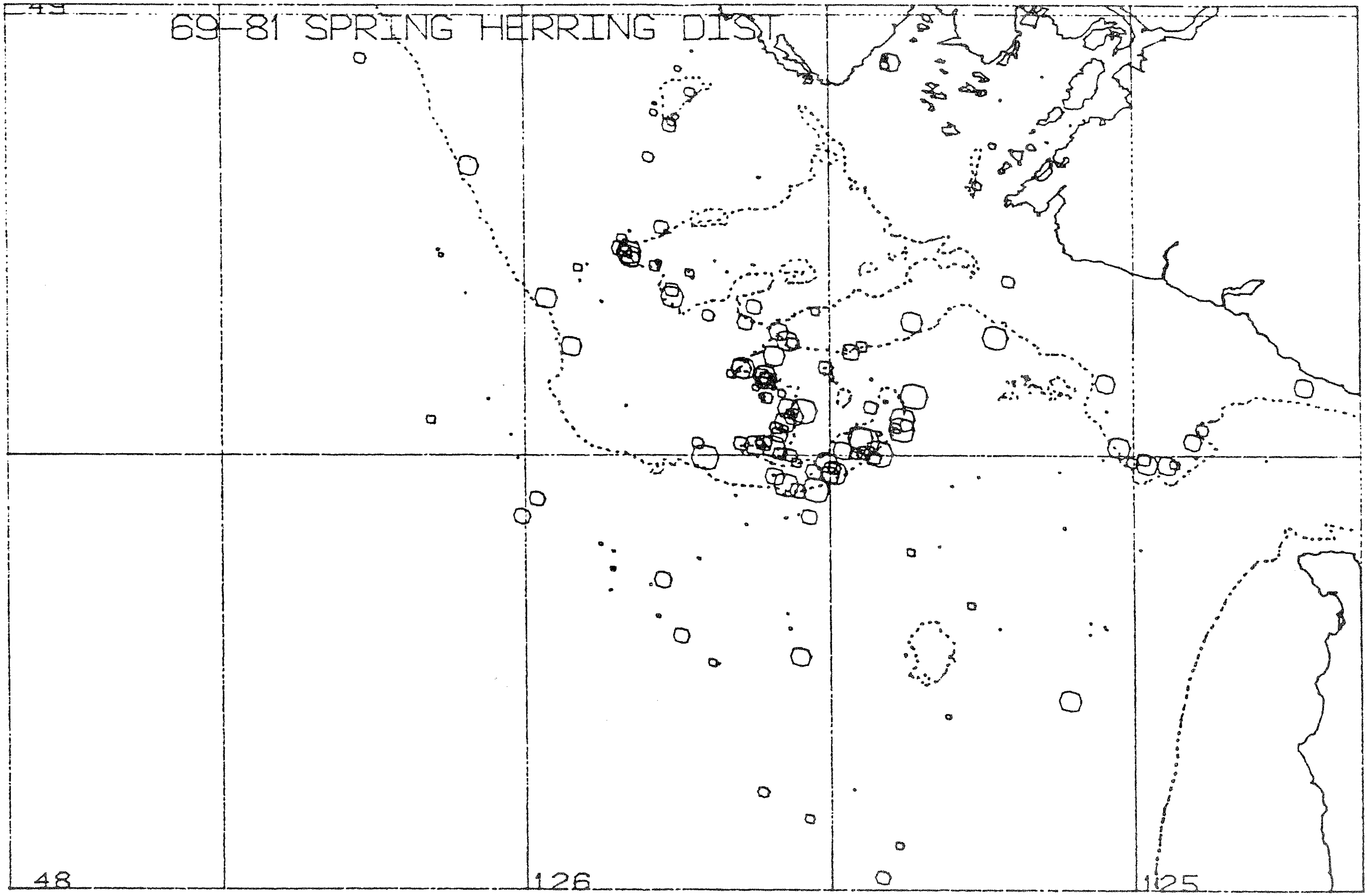

Fig. 6. Offshore distribution of herring observed during spring (March-May) surveys between 1969-81. The size of the octagon is proportional to the logarithm of the catch rate (kg herring/min). The 100 m isobath is shown.

SUMMER PERIOD

Continental Shelf

The summer circulation period (May-October) is characterized as a time of moderate to high zooplankton biomass and production, and is the main feeding period for most offshore fish species, particularly herring and hake. During May, June and July the highest average biomass of zooplankton is associated with the Juan de Fuca Eddy (Fig. 5). Zooplankton concentrations decline sharply in this region in August, thereafter, the highest zooplankton concentrations are found on the outer shelf (Region A, Fig. 5). Euphausiids are particularly abundant along the northern flank of the Juan de Fuca eddy and the shelf-break. In contrast, zooplankton concentrations tend to be low over the inner banks and consist of a high proportion of small bodied forms.

In summer, herring from the lower west coast of Vancouver Island stock are distributed primarily over La Pérouse bank and the nearby basins, out to the shelf-break (200 m isobath). They are particularly abundant along the eastern edge of the 100 m isobath (Fig. 7). Some components of this stock may remain offshore until a just a few weeks before spawning (March). In contrast, herring spawning in the lower Strait of Georgia (lower east coast stock), tend to be distributed south of the US-Canada border (Tester 1948). This stock leaves the summer feeding grounds for overwintering areas in the lower Strait of Georgia in November. Juvenile herring (0+) begin moving out of Barkley Sound for the offshore banks and basins in late summer (Hart 1973).

Pacific hake begin arriving off the lower west coast Vancouver Island (WCVI) in June when the summer circulation pattern is well established. The migratory stock of hake is normally present in large quantities from mid-June to late October; the highest catches typically occur in August (Beamish 1981). Major concentrations are found along the northern edge of the Juan de Fuca Eddy and from the 100 m isobath out to the shelf-break (Fig. 8). Both areas have high standing stocks of euphausiids and smaller zooplankton, so the summer distribution of hake tends to match the distribution of euphausiids. The hake distribution also overlaps components of the offshore herring stocks that are scattered over the inner basins and outer shelf.

With respect to the theme of this recruitment workshop, one of the main ideas being tested within the context of the La Pérouse Project is that the survival of both pre-recruit and adult herring is determined largely by the amount of spatial and temporal overlap in the herring distribution field with the fields of their main offshore predators, like hake, during the summer and fall. Interannual variations in the amount and duration of overlap in the prey andpredator fields are probably related to oceanic conditions and are believed to be responsible for significant variations in predation losses. Preliminary estimates by Ware and McFarlane (1986) indicate that offshore predators have the potential to remove considerable numbers of pre-recruit herring and, on average, between 30-50% of the biomass of adult herring. Within this range there is some circumstantial evidence that the predation rate may be higher in warm summers.

Two specific avenues are being explored to evaluate this idea: The first question is why is there a significant biomass of hake off the lower WCVI? We believe the answer is because the surface outflow from Juan de Fuca tends to concentrate significant numbers of euphuasiids in a band between the

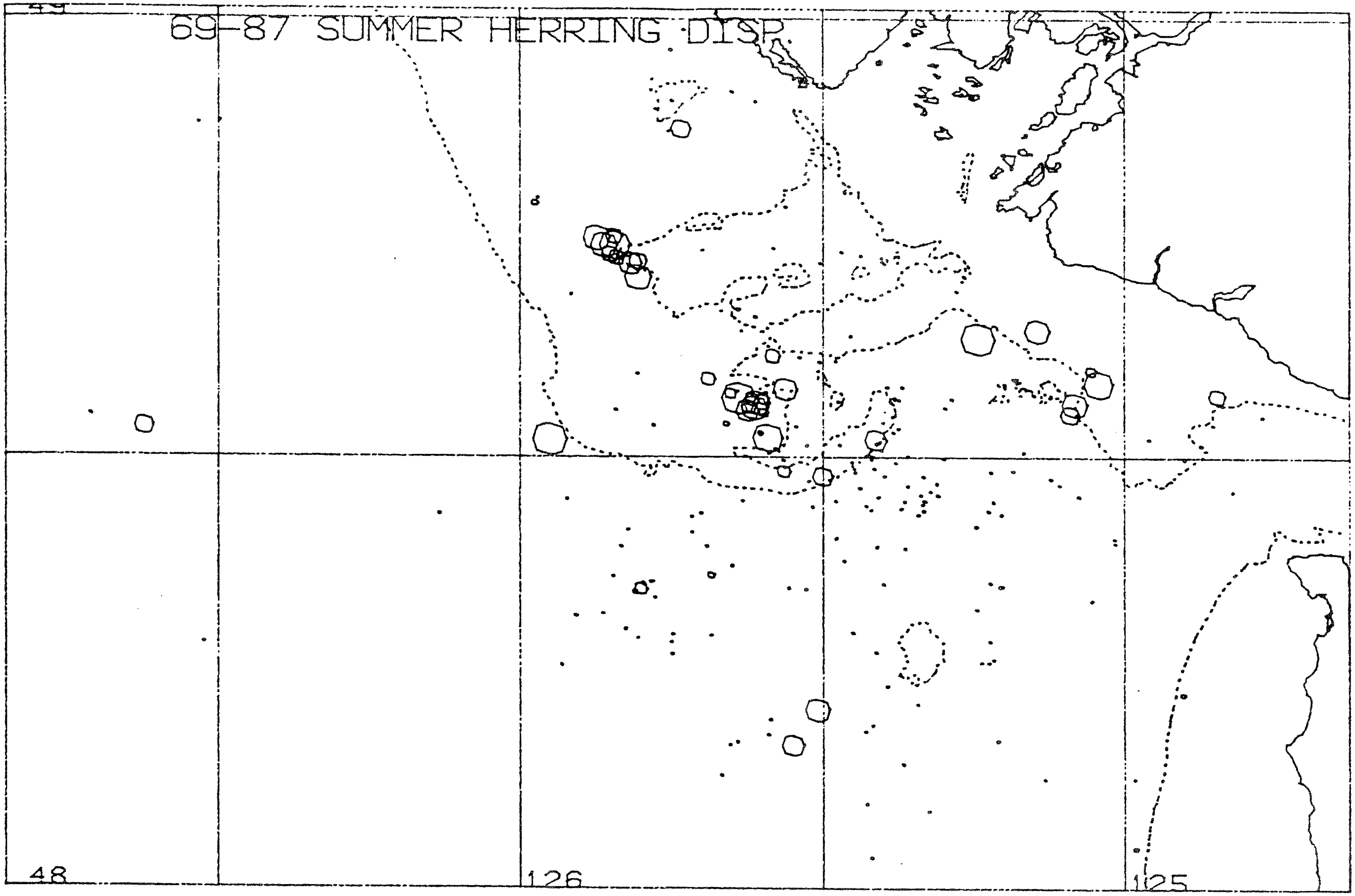

Fig. 7. Offshore distribution of herring observed during summer surveys (June-August) between 1969-1987. The symbols are defined in Fig. 6.

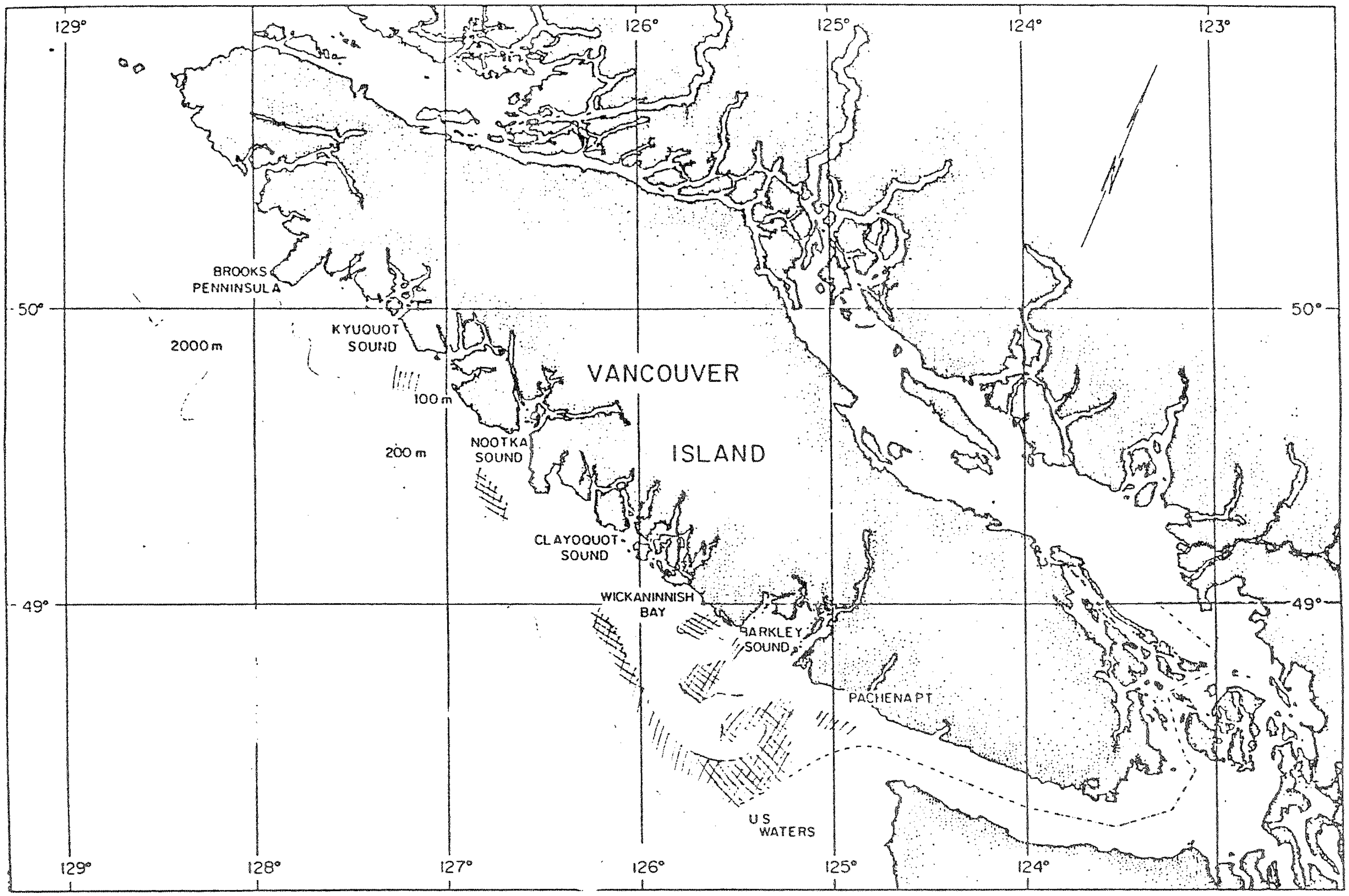

Fig. 8. Distribution and relative concentration patterns of Pacific hake off the west coast of Vancouver Island between 1967-87. Areas with cross-hatching indicate where hake have been found every year; areas with diagonal lines indicate where hake have been observed, but not consistently (courtesy of W. Shaw, Pacific Biological Station, Nanaimo, B.C.).

edge of the inner banks (100 m isobath) and the outer edge of the Juan de Fuca Eddy. A hydro-acoustic survey by Yvan Simard and Dave Mackas in June and August, 1986 established that there were high concentrations of euphausiids in this area which extended across the shelf, and then northward in a narrow band along the shelf break. Dave Mackas has suggested that the equatorward flow of the Shelf-break Current may transport euphausiids from the northern part of Vancouver Island, along the shelf-break and into the vicinity of the Juan de Fuca Eddy (the latter part of this transport mechanism has yet to be clarified). As we noted above there seems to be almost a perfect overlap in the euphausiid and hake distribution fields. This oversimplified picture, however, is complicated by variations in the speed and direction of the cross-bank currents which may move, or temporarily break up the euphausiid concentrations. This may explain why the hake concentrations periodically "melt away" during the summer and become highly dispersed in aggregations that cannot be fished profitably. During this dispersed phase hake may be actively searching for food. Measurements will be made to see if herring have a higher risk of hake predation when the direction and intensity of the cross-shelf currents changes.

The second question is why are herring concentrated along the southern and eastern edges of the inner banks? Surveys are being designed to determine if the cross-shelf currents tend to concentrate copepods and euphausiids along the southern edges of the banks. In addition, it seems possible that under favourable conditions upwelling may lift zooplankton up onto the eastern margins of the banks. Part of the reason why herring are distributed the way they are in the summer, therefore, may be determined by the distribution of the plankton, (Fig. 5); another piece of the puzzle may involve offshore predators. Since both the plankton and predators are more abundant over the inner shelf basins, the summer distribution of herring may reflect a trade-off that has been selected to provide adequate feeding opportunities with minimal predation risk.

The processes that we suspect are important for concentrating plankton along the edges of the inner banks, may also explain the offshore distribution of juvenile coho and chinook salmon. The distribution of large chinook, not suprisingly, seems to match some of the main concentrations of herring.

Coastal Current

The Vancouver Island Coastal Current is a narrow, poleward flowing region of low density water, bounded by a zone of downwelling at the inner edge of the shelf. This may be an important feature which blocks the cross-shelf transport and successful recruitment of Dungeness crab off the lower west coast of Vancouver Island. Jamieson et al. (1988) found that crab megalopae were abundant along the outer boundary of the coastal current and seaward out to 180 km in May and June 1985; but were not abundant in nearshore waters. They speculate that successful recruitment (i.e. settlement) of crab larvae along the lower west coast may only occur when the coastal current is weak. When the coastal current is strong, which it normally seems to be, they speculate that in summer the Shelf-break Current may carry crab megalope southward off Washington where some may eventually settle. There is no coastal current off Washington and the megalopae are abundant there right to the coast. The reason why major crab recruitments seem to occur following ENSO periods off the lower WCVI may be associated with an increased northerly transport of crab larvae from Washington. Some of these larvae may be entrained by the coastal current and consequently make their way shoreward. The strength of the coastal current varies interannually in response to variations in winds, coastal runoff and the outer shelf-slope circulation.

The coastal current may also be an important transportation conduit for juvenile sockeye salmon (Thomson et al. 1988). Hartt and Dell's (1986) analysis of purse-seine catches indicates that juvenile sockeye, chum and pink salmon were caught in the Strait of Juan de Fuca and off the WCVI from June-Sept/Oct. The data are not extensive enough to resolve the offshore distribution, but the MASS Project is testing the possibility that the coastal current may be used preferentially by northward migrating sockeye salmon juveniles. It is not clear what happens to the coastal current in the vicinity of Brooks Peninsula which presents a major barrier to the flow. Cross-shelf filaments are formed intermittently by upwelling north of Brooks Peninsula and tend to move offshore or southward along the outer shelf at speeds of 15-70 cm/sec. These features interrupt the coastal current and may pose a significant barrier to migrating juvenile salmon. Most marine mortality of salmon is believed to occur in the first 6-18 months of sea life, and is highly size-selective. The most probable sources of mortality of migrating juvenile sockeye salmon are marine fish (like hake, dogfish, salmon, rockfish etc.), and birds. Sockeye salmon are a common prey of Rhinocerous auklets in the summer near the northern tip of Vancouver Island (Vermeer and Westrheim 1982). A major objective of the MASS Project is to identify the significant sources of mortality, and to quantify the relative losses sustained during the 1-2 months sockeye juveniles take to migrate along the WCVI.

The coastal current may also be a significant factor determining which route Fraser River Sockeye salmon take into the Strait of Georgia. This is an important concern of DFO personnel responsible for managing the commercial fisheries. The problem is that there is significant interannual variability in the fraction of Fraser River Sockeye that return around the northern end of Vancouver Island through Johnstone Strait (the northern diversion) compared to the fraction that normally returns via the southern route through Juan de Fuca Strait. What is particularly disturbing is that the diversion rates have been unusually high since 1978 (Fig. 9). In a comprehensive study, Hamilton (1985) found a significant correlation between the northern diversion rate and the temperature change in the coastal waters off the WCVI during the last 18 months of the salmon's ocean residence. Strong temperature changes normally accompany large ENSO events, and large northern diversions have occurred after these events (e.g. 1915, 1926, 1958, 1983). Hamilton speculated that ocean temperatures could affect the distribution of salmon, and if the number of fish using the northern route is enhanced under these conditions then warmer temperatures would lead to a high diversion through Johnstone Strait. This explanation accounts for about 33% of the variance, which is encouraging, but it does not explain why the diversion rate was low during the warm years of 1941, 1963 and 1967; nor why it was so high during 1972, which was more or less a normal year. Another factor that might explain these anomalies is the integrity of the Vancouver Island Coastal Current, which in summer is frequently prevented from rounding Brooks Peninsula by the equatorward-flowing Shelf-break Current. The large cross-shore current shears created in this narrow shelf region by the opposing shelf-break and coastal current regimes leads to flow instability and the formation of seaward penetrating filaments. Assuming that this blockage of the coastal current is a quasi-permanent feature of the Brooks Peninsula region in summer, then in warm ENSO event years when the sockeye make a landfall north

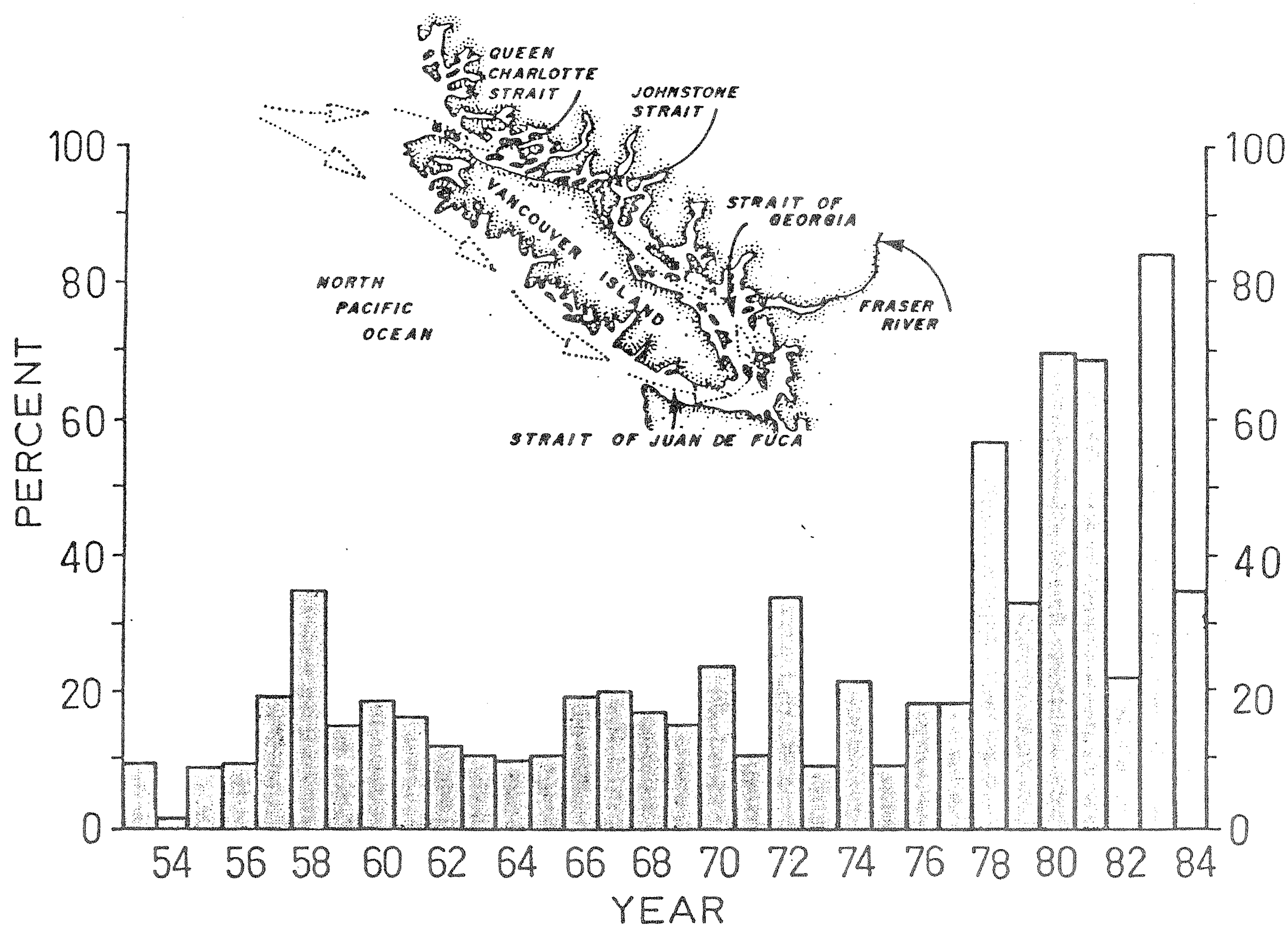

Fig. 9. Percentage of sockeye salmon approaching the Fraser River through Johnstone Strait during 1953-84. The inset shows the migratory routes of adult sockeye bound for the Fraser River and other southern British Columbia rivers (from Mysak 1985).

of the peninsula they may sense a weak Fraser River signal coming out of Queen Charlotte Sound and follow it through Johnstone Strait. Conversely, in normal years when they make a landfall south of the peninsula or in years when the coastal current is particularly successful in negotiating Brooks Peninsula, sockeye may sense Fraser River water in the coastal current and follow it southward through Juan de Fuca. Although the northern diversion problem doesn't appear to affect the marine survival and recruitment of Fraser River sockeye, it merits mentioning here because it provides a clear example of how changes in oceanic conditions can alter salmon migration routes.

FALL TRANSITION PERIOD

The Fall Transition may be a southward progressing event corresponding with a reversal of the coastal wind patterns, which marks the end of the upwelling season and the beginning of the downwelling season. During this period both the zooplankton (Fig. 5) and herring (Fig. 10) seem to be more abundant on the outer shelf than they were in the summer. This tendency may be related to the fact that the strength of the cross-shelf flow increases throughout the summer and reaches maximum strength just prior to the Fall Transition. There is some indication that hake are also more concentrated along the outer shelf in the fall. Thus herring may be particularly vulnerable to hake predation in the late summer-fall period, when there is potentially the greatest overlap in their distributions. Some hake begin migrating south in October but the availability of hake to bottom and mid-water trawls does not usually drop sharply until November (Alverson and Larkins 1969), when the main body of fish migrates southward, presumably in the equatorward flowing California Current (Bailey et al. 1982). In 1987, the Fall Transition was delayed until November and could account for the extended hake fishery off British Columbia. Adult herring begin leaving the offshore banks and move to overwintering areas in the lower Strait of Georgia. Juvenile herring remain on the offshore banks throughout the winter.

SUMMARY

Until recently most oceanographic programs on the west coast of Canada have been concerned with understanding the mechanisms affecting the spatial and temporal variability of the coastal ocean. These short-term projects have provided little insight into the long-term effects of oceanic factors on fisheries distribution and recruitment patterns. The plankton data are in the same state: the existing time series are barely long enough to define seasonal changes, let alone the amount of interannual variability in species composition and biomass. Long-term sea surface temperature records indicate that there pronounced, decadal-scale cycles along the coast. The years 1925-46, 1957-68, and 1976-present mark periods of anomalous warming, while the years 1947-56 and 1969-75 mark periods of anomalous cooling. Both these slowly varying and higher frequency cycles appear to affect the distribution and recruitment of major commercial fish stocks. However, the processes are poorly understood. As a consequence, two multi-disciplinary research programs involving oceanographers at the Institute of Ocean Sciences and fisheries biologists at the Pacific Biological Station were designed to clarify the effects of ocean variability on west coast fish stocks. The MASS project was undertaken to investigate the interrelationships between biophysical events and salmon distribution and survival, on an annual and interannual time scale. The major theme being

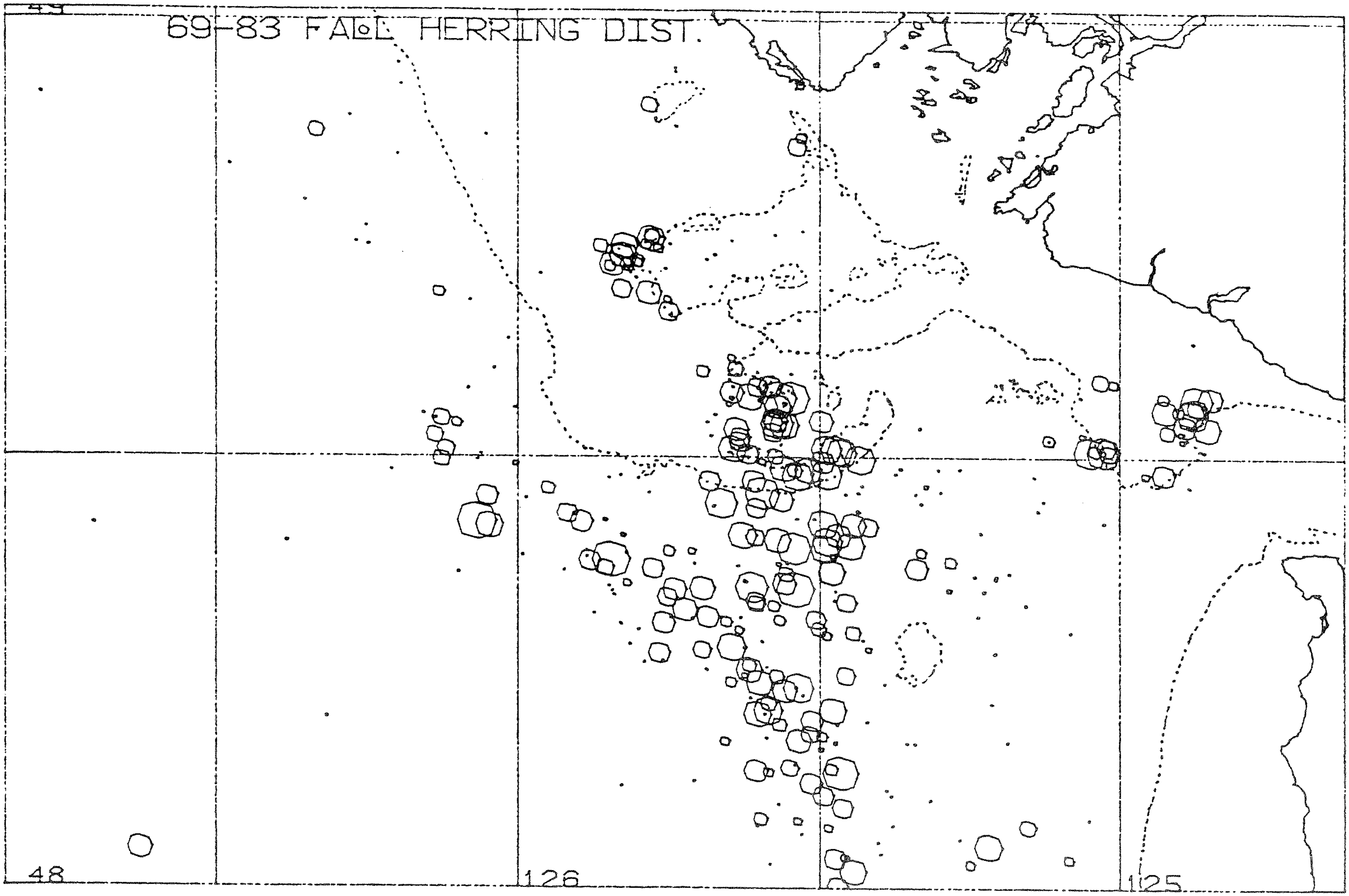

Fig. 10. Offshore distribution of herring observed during fall (September-November) surveys between 1969-83. The symbols are defined in Fig. 6.

investigated is that local circulation patterns affects the seaward migration routes and consequently the survival rate of juvenile salmon.

The La Pérouse project is a decadal-scale, multispecies study designed to identify the dominant physical processes that affect the circulation and water property structure; the low frequency variability in the zooplankton; and to formulate and test specific hypotheses concerning how interannual oceanic fluctuations affect fish distributions and survival. A major theme of current studies is that biophysical events affect the amount, and duration, of overlap in the prey and predators distribution fields, which in turn affects the survival rate of important commercial species like Pacific herring, and sablefish.

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Table 1. Summary of recent studies investigating effects of oceanic factors on recruitment of B.C. fish stocks. Code indicating type of study: S = Statistical analysis of time series; ELH = Early life history studies; JLH = Juvenilie life history studies; RB = Reproductive biology.

Species	Duration of program		Principal investigators
	A. Hecate Strait/Queen Charlotte Sound		
Pacific cod	1984	S	A. TYLER (Coordinator), W. CRAWFORD
Pacific herring	1984-1987	S	M. STOCKER, D. NOAKES
Rock sole	1985-1987	S	J. FARGO, S. McKINNELL
Pink and chum	1983-1986	JLH	R. LeBRASSEUR, B. HARGREAVES
	B. West Coast Vancouver Island/Strait of Georgia		
LaPerouse Project			
Pacific herring	1985	S, JLH, RB	D. WARE, R. THOMSON (Coordinators) K. DENMAN, D. MACKAS
Sablefish	1984	S, ELH	G. McFARLANE, R. BEAMISH
Dungeness crab	1986	ELH	G. JAMIESON, W. HUGGETT W. CRAWFORD
Pacific cod	1988	S, RB	A. TYLER, J. FARGO, R. FOUCHER
MASS Project			
Sockeye, coho, chinook salmon	1986-1989	S, JLH	M. HEALEY (Coordinator), K. DENMAN A. GARGETT. K. GROOT, B. HARGREAVES H. FREELAND, K. HYATT, D. MACKAS R. THOMSON, K. VERMEER, J. GALLOWAY
Chinook salmon (Campbell River)	1982-1986	JLH	C. LEVINGS, C. McALLISTER
Pink, sockeye, chum	1976	S	D. BLACKBOURN

V REVIEWS OF DEPARTMENT OF FISHERIES AND OCEANS PROGRAMS ON RECRUITMENT

B. A REVIEW OF RECRUITMENT RELATED STUDIES AND RELEVANT PHYSICAL OCEANOGRAPHY PROGRAMS RECENTLY UNDERTAKEN BY THE DEPARTMENT OF FISHERIES AND OCEANS IN THE NEWFOUNDLAND AND SCOTIA-FUNDY REGIONS

by

K.T. Frank
Scotia-Fundy Region

INTRODUCTION

This paper is a synopsis of the major recruitment related studies undertaken by scientific staff of the Department of Fisheries and Oceans that are currently in progress or have been recently completed in the Newfoundland and Scotia-Fundy Regions. Relevant physical oceanographic studies are also reviewed. The paper fullfills a request by the Steering Committee for the National Workshop on Recruitment. This document is largely a compilation of summaries provided by the principal investigators of each study. I wish to thank them all for a rapid and concise response to the request for input to this document.

1. NEWFOUNDLAND REGION

A. FRESHWATER AND ANADROMOUS FISHES

Optimum Spawning Requirements and Juvenile Production Studies

This project involves a number of research studies on several Atlantic salmon stocks in insular Newfoundland.

The focus of salmon research is in two areas:

1. Investigate optimum spawning requirements to maximize smolt output as it relates to carrying capacity of different habitats and environmental conditions. This involves increasing egg deposition until carrying capacity is reached. From these data a stock-recruitment relationship will be developed.

2. Investigate salmonid biomass production capacity of different habitats as it relates to biological, physical, chemical, and climatic parameters.

The research is conducted on four river systems. A systematic approach has been taken to study the entire freshwater ecosystem in two of these streams. In a third river, adult salmon stocks are monitored and brood stock are removed for experimental stocking. A fourth river provides control stations for interaction studies with brook trout. An inventory of the biological, physical, and chemical parameters has been undertaken. Emmigrating and immigrating salmon are monitored near the outlet of two streams. Egg deposition undergoes natural variation on one stream at approximately 600 eggs/100 mp^{-2} and is fixed at 240 eggs/100 mp^{-2} on another stream. Changes in smolt and adult production are observed. Juvenile production is monitored in representative types of habitat, and changes in growth, proportion of maturing male parr, and year-class interactions in relation to parr densities and habitats are monitored using electroseining and underwater observations. Competitive interactions with brook trout are being followed. Collaborative research is encouraged with researchers from Memorial University of Newfoundland to investigate aspects of the ecosystem which would not be studied by DFO (eg. in areas of hydrology, geomorphology, primary and secondary production, benthic studies and fish biology; investigations are coordinated by DFO).

I. NEWFOUNDLAND REGION RECRUITMENT RELATED STUDIES

A. Freshwater and Anadromous Fishes

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Optimum Spawning Requirements and Juvenile Production Studies	1985-2000	Ongoing	Trepassey Bay, S.E. Newfoundland	Atlantic Salmon (juvenile)	Stocking of adult salmon to enhance egg deposition, population estimates of juveniles using depletion and mark-recapture techniques, measurement of habitat variables and potential competitors, survival analysis.	R. John Gibson
2. Optimum Spawning Requirements and Juvenile Production Studies	1985-2000	Ongoing	Trepassey Bay, S.E. Newfoundland	Atlantic Salmon (adults)	Fecundity estimates.	M.F. O'Connell

B. Develop and Apply New Methods for Projection of Recruitment from Stock

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Development of Estimation Algorithms	N/A	1986-	N/A	N/A	Non-parametric statistics and simulation modelling; project long series; try to reconstruct series with various estimation algorithms applied to data subsets; test fits of projection to series.	G. Evans, J. Rice
2. Application of Algorithms to Management of Stocks	N/A	1986-	2J+3KL	(Northern) Cod	Pose a series of typical management questions about the stock; apply non-parametric estimation algorithms and project the probability distributions of future recruitment and/or stock sizes; use probability distributions to evaluate management options.	J. Rice, G. Evans
3. Application of Algorithms to Investigating Impact of Environmental Attributes on Recruitment	N/A	1986-	2J+3KL	(Northern) Cod	Extract major tends from Station 27 data; relate these environmental attributes to gross recruitment and residuals from stock analysis (above) using non-parametric estimation algorithms; interpret results.	J. Rice, G. Evans, S. Akenhead

Associated Publications:

Evans, G.T., and J.C. Rice. 1988. Predicting recruitment from stock size without the mediation of a functional relation. J. Cons. int. Explor. Mer, 45: 15-26.

Rice, J.C., and G.T. Evans. In Press. Tools for embracing uncertainty while managing cod in NAFO Divisions 2J+3KL. J. Cons. int. Explor. Mer, (14 p + 5 Fig.). (Accepted March 1988)

C. REPRODUCTIVE ECOLOGY OF HERRING AND CAPELIN

Trinity Bay Recruitment Study

From 1982 to 1986 a series of spring-fall surveys, aimed at herring and capelin larvae, were carried out in Trinity Bay. Prey for larvae were evaluated by sampling zooplankton with a fine mesh net, and measures of dry weight biomass of 5 size fractions were obtained. Temperature and salinity profiles were collected at each station. Correlation analysis is being carried out to examine assocations between larval abundance and measures of the biological and physical environment. Preliminary results are quite variable. Some significant assocations were identified although trends are not consistent throughout the data sets. Further analysis will focus on aspects of the environmental and meteorological conditions prevalent during the sampling period when significant assocations were identified.

The project is also concerned with biases in estimation of larval population parameters. A manuscript has been submitted for publication on changes in length of larval capelin due to preservation in formalin and anhydrous alcohol. Another manuscript is in preparation pertaining to estimates of larval population size frequency distributions using two different types of sampling gear. In 1987 field sampling was aimed at identifing patterns of vertical distribution, and also at ascertaining diel variability in standard oblique bongo tows. This information will be used in interpreting data collected during the surveys. No data collections are being made in 1988.

In 1984 a study of Trinity Bay was contracted to describe circulation and other aspects of the physical oceanography. This description is intended to aid in the interpretation of larval distribution and abudance data particularly as it relates to dispersal/retention.

C. Reproductive Ecology of Herring and Capelin

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Trinity Bay Recruitment Study	1982-1987	Ongoing	Trinity Bay	Herring/Capelin	Larval fish surveys, coincident monitoring of biological and physical environmental; juvenile survival.	Edgar Dalley

D. FLEMISH CAP PROJECT

Feeding and Growth of Redfish Larvae in Relation to Survival and Timing of Production

Planning began for these projects in the mid-1970s and initial field sampling began in October 1977, with the final directed studies ending in July 1983. Field sampling was most intensive during 1979-81. This was a joint project between Canada and the U.S.S.R. carried out under the auspices of ICNAF/NAFO with preliminary results being reported each year through NAFO. Recent results of the project were discussed during the NAFO Special Session on recruitment (Lilly 1987) and a major review of the project was summarized by Grosslein and Lilly (1987). Presently, data collected as part of the project are being analyzed with completion expected within two years.

The major findings of the project to date centre on the growth and survival of redfish larvae. Larval survival between April and August 1978-81 varied widely and initially this can be linked directly to growth rate. Modelled estimates of physical dispersal can account for approximately one half of the average estimated larval mortality, but yearly comparisons have not been done. Analyses are presently underway summarizing the chlorophyll and nutrient relationships on Flemish Cap, analyzing the differences in larval redfish feeding between years. Future work planned includes: analysis of regional differences in feeding, growth and condition of larval redfish in relation to physical and biological factors; analysis of prey availability on the production of the cod stock, analysis of the influence of predation by cod on mortality of juvenile redfish and cod; information on fecundity and the percentages of females which spawned each year; and a more accurate estimate of the cod spawning stock size.

Physical Oceanographic Component of Flemish Cap International Experiment

The Flemish Cap International Experiment was an ICNAF study aimed at identifying the relationships of currents, water temperature, and of the environmental factors with the year-class strengths of cod and redfish on the Cap. The physical oceanographic component of the study was crippled by the loss of moored equipment. Preliminary analyses of most of the current and hydrographic data have been published, and more detailed interpretation of the hydrographic data and their implications for larval dispersion is underway as part of a doctoral thesis (Akenhead 1988).

D. Flemish Ca Project

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Feeding and Growth of Redfish Larvae in Relation to Survival	1977-1983	1980-	Flemish Cap	Redfish	Field collections of food, feeding, size, growth and condition in relation to zooplankton community structure, physical oceanography, predators and corrected for physical advective losses. Relationships analyzed statistically and through simulations.	J. Anderson
2. Timing of Production	1977-1983	1985-	Flemish Cap	Cod and Redfish	Analysis of chlorophyll, nutrients, T-S and invert. zooplankton to examine timing of spring production in relation to survival and eventual recruitment.	J. Anderson, J. Booth, R. Keeley
3. Physical Oceanographic Component of Flemish Cap International Experiment	1979-1981	1979-	Flemish Cap	N/A	Hydrographic surveys; moored current and hydrographic measurements, drifter tracking.	S. Akenhead, C.K. Ross

E. RECRUITMENT STUDIES ON SQUID AND CRAB

Squid Recruitment Studies

Studies of squid recruitment in Newfoundland consist of two annual surveys, both of which are aimed at developing time series of recruitment indices based on catch rates. The earlier annual survey was initiated in 1984. It is carried out during February-March, about 2 months later than when the peak winter spawning activity is believed to take place. Sampling with midwater trawl is carried out in the northern Gulf Stream and Slope Water between 55°W and 60°W. The index of pre-recruit abundance is an overall catch rate of juveniles which at the time, range in size between 1-3 cm mantle length. To date, four annual surveys have been completed (1984-87), all of which occured during years of very low squid abundance at Newfoundland.

A second annual survey occurs during early June on the southwest slope of the Grand Bank. Squid are sampled by bottom trawling within Slope Water, which intrudes into the survey area during spring. The catch rate abundance index is generated only about one month before the inshore fishery commences. This survey was initiated in 1978 but incidental catches from groundfish surveys are available from the survey area as early as 1947. It is apparent that large concentrations on the Grand Bank in June do not always appear later inshore.

Crab Recruitment Studies

Attempts to develop a means of assessing snow crab biomass in Conception Bay using photographic techniques were initiated in May 1987. A portion of the commercial biomass results from within-season molting and recruitment. Prediction of absolute recruitment is attempted by enumerating the immediate pre-recruits from bottom photography. Molt-stages of biological samples are determined using mouthpart-staging techniques to estimate the proportion of immediate pre-recruits which would molt and recruit within the current fishing season.

E. Recruitment Studies on Squid and Crab

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Squid Recruitment Studies	1978-	1985-	Northern Gulf Stream and Slope water between 55°W and 60°W S.W. Slope of Grand Bank	Squid	Midwater trawl, index of pre-recruit abundance, hydrographic data.	E. Dawe
2. Crab Recruitment Studies	1987-	1987-	Conception Bay	Snowcrab	*In situ* photography for pre-recruit enumeration, index of pre-recruit abundance, molting rate determination.	E. Dawe

II. SCOTIA-FUNDY REGION

A. POPULATION STUDIES OF HERRING IN GULF OF MAINE/BAY OF FUNDY

Bay of Fundy Larval Herring Survey

A survey of approximately 150 stations in the Bay of Fundy and eastern. Gulf of Maine has been undertaken annually (Oct./Nov.) since 1972. Oblique bongo tows (0.505 and 0.333 mesh) provide a synopsis of the distribution of larval herring and of associated macrozooplankton abundance. An annual larval abundance index has been used in comparison with spawning stock biomass (i.e. hindcast) to tune the VPA in assessments since 1981 (Iles et al. 1985, Stephenson et al. 1987). The autumn larval herring abundance has shown little relationship with eventual recruitment. The persistence of annually predictable patches of larvae, observed in this survey, was key evidence in the development of the larval retention hypothesis (Iles and Sinclair 1982).

Site-Specific Studies of Larval Herring

The coastal waters of southwest Nova Scotia support a large herring population which is the basis for the largest herring fishery in the western Atlantic. The patch of larvae which results from spawning of this population is the largest and best defined of those in the Bay of Fundy and Gulf of Maine. Observations on this group of larvae were critical to development of the larval retention hypothesis, and annual surveys of abundance are used to tune stock assessments. This larval patch has been observed for site-specific studies to test portions of the larval retention hypothesis and other aspects of larval herring dynamics of relevance to recruitment. A study in November 1985 involving repetitive discrete depth samples (using MININESS) at 3-h intervals over 49 h indicated a definite semidiel vertical movement of herring larvae through as much as 50 m. A recent study (November 1987) sampled herring larvae in a similar manner over 6 depths to test further aspects of vertical movement, including timing and the relationship with prey and potential predators. Additional samples were designed to define the scale of horizontal patchiness of larvae.

Recovery of Georges Bank Herring

Spawning Atlantic herring (Clupea harengus L.) have been recorded on Georges Bank for the first time since the collapse in 1977 of what had once been the largest herring fishery in the northwest Atlantic. The reappearance after almost a decade raises the question of whether there has been resurgence of a residual extant Georges Bank population or recolonization by fish from neighbouring spawning groups. Three independent lines of evidence (biochemical attributes, age composition, and timing) indicate resurgence and support the discrete population concept in herring. There is no indication that stochastic events influenced the genetic structure of the herring population at Georges Bank after the collapse. The period directly after collapse, with the Georges Bank population showed no evidence of recovery, coincided with several years of low or average recruitment in neighbouring populations; only recently has there been generally good recruitment (as documented in neighbouring SW Nova Scotia) providing a chance for the Georges Bank population to recover. Larval abundance data (autumn surveys) are being collected to monitor recovery.

II. SCOTIA-FUNDY REGION RECRUITMENT RELATED STUDIES

A. Population studies of Herring in Gulf of Maine/Bay of Fundy

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Bay of Fundy Larval Herring Survey	1972-	Ongoing	Bay of Fundy/ eastern Gulf of Maine	Atlantic Herring (larvae)	Annual synoptic field survey of approximatly 150 stations using oblique bongo.	R. Stephenson, T.D. Iles
2. Site-Specific Studies of Larval Herring	Nov. 1985 Nov. 1987	1986-1988	S.W. Nova Scotia	Atlantic Herring (larvae)	Repetitive depth stratified sampling in relation to time, tide, and prey.	R. Stephenson
3. Recovery of Georges Bank Herring	1977-	1987-	Georges Bank	Atlantic Herring (spawning stock)	Research surveys (Oct/Nov) define larval abundance and distribution, and sample spawning adults for age structure and stock identification.	R. Stephenson, T.D. Iles
4. Stock Recruitment Theory	N/A	Ongoing	General	Atlantic Herring	Comparative studies of Atlantic herring and other marine fish stocks. Historical analysis of the dynamics of recruitment in the 4WX herring stock.	T.D. Iles

B. ST. GEORGES BAY (SGB) FISHERIES AND ENVIRONMENTAL OCEANOGRAPHY PROGRAM

Reproductive Strategies of Marine Fishes

Studies of the early history of pelagic fish species were initiated in St. Georges Bay (SGB), Nova Scotia, in the early 1970s. As a study site this bay showed great potential in that it appeared reasonably representative of the southern Gulf of St. Lawrence yet was a manageable size from the point of view of sampling. More importantly there was evidence in the form of post-storm suspended sediment trails of a clockwise circulation within the bay. Such a circulation could act as a retention mechanism which would greatly increase the accuracy of estimates of larval growth and mortality. Subsequent physical oceanographic studies confirmed the presence of a semi-permanent gyre within St. Georges Bay (Petrie and Drinkwater 1977). In the absence of low frequency events such as storms, flushing time for the bay is about a month (Petrie and Drinkwater 1978); about the time required for a mackerel to hatch and attain a size of 25 mm.

a) Ichthyoplankton studies aimed at Atlantic mackerel (Scomber scombrus) revealed a close coupling between size and abundance of zooplankton and larval mackeral (Ware 1977). In addition to information on distribution of eggs and larvae, larval diet and timing of spawning, estimates of egg and larval mortality and of larval growth were made for four years.

   Mackerel egg production estimates within St. Georges Bay for six years indicated the possibility of using the bay as a proxy for total southern Gulf of St. Lawrence egg prodution, for the bay seems to regularly receive a proportional (based on area) share of total Gulf production. A 10 year time series of data is now being examined to see if this trend continues.

b) The presence of larval cohorts in the plankton (Lambert 1984) stimulated a study of reproductive strategies of marine fish (Lambert and Ware 1984) and led eventually to a detailed study of the spawning dynamics of Atlantic herring (Figures 6 and 7, Lambert 1987). At present a manuscript is being prepared detailing a hypothesis which links age structure and pattern of spawning to recruitment.

Larval Lobster Ecology

In addition, larval lobster studies begun in St. Georges Bay (Harding et al. 1982) led to a general recruitment model for Nova Scotia Atlantic coast lobster stocks (Harding et al. 1983).

Physical Oceanographic Component of SGB Program

Physical oceanographic investigations were undertaken concurrently with the biological studies in SGB. Early measurements included extensive temperature and salinity data as well as moored current meter arrays in the summers of 1974 and 1975 (Petrie and Drinkwater 1977a, b). Initial analyses of these data indicated a mean clockwise eddy with velocities near 0.1 m/s in the surface waters (Petrie and Drinkwater 1978a). Although energy was equally partitioned between the mean circulation, the tidal currents and the low-frequency velocity events, the latter determines the rate of exchange between the Bay and the Gulf of St. Lawrence. Estimates of the flushing time for the tides and mean circulation is of the order of a month while low-frequency events could flush the Bay on a time scale of days. Petrie andDrinkwater (1978b) developed a numerical model of the mean circulation whichsuggested that the eddy was driven by a steady northeastward flow past the mouth of the Bay.

The dynamics of wind-forced motions in the Bay have been investigated by Drinkwater (1987, 1988) based on the 1974-75 current meter data and additional thermistor and current data collected in 1979. Wind events have been shown to influence the biological processes, e.g. a 2-fold decrease in lobster larvae abundance observed between successive ichthyoplankton surveys of the Bay in July, 1975, was attributed to wind-induced advection (Petrie and Drinkwater 1978). Also, lobster catches appear to be affected by wind driven temperature fluctuations (Drinkwater 1987).

B. St. Georges Bay (SGB) Fisheries and Environmental Ocenography Program

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Reproductive Strategies of Marine Fishes	1973-1978 1981-1986	Ongoing	St. Georges Bay, N.S.	Mackerel	Egg and larval survey.	D.M. Ware, T.C. Lambert
	1973-1976	1976-1980	St. Georges Bay, N.S.	Herring	Egg and larval survey.	T.C. Lambert
2. Larval Lobster Ecology	1978	1981-1982	St. Georges Bay, N.S.	Lobster	Egg and larval survey.	G.C. Harding
3. Physical Oceanographic Component of SGB Program.	1973-1980	1980-	St. Georges Bay, N.S.		Hydrographic survey, moored current and hydrographic measurements, event analysis.	K. Drinkwater, B. Petrie

C. SCOTIAN SHELF ICHTHYOPLANKTON PROGRAM (SSIP)

Scotian Shelf Ichthyoplankton Survey Results

The intitial objectives of the Scotian Shelf Ichthyoplankton Program (SSIP) were:

(a) to discriminate the seasonal and geographic distribution of eggs and larvae of fish stocks on the Scotian Shelf;

(b) to estimate fish larval growth and mortality rates and how these change with developmental stage, season, and area; and

(c) to collect a wide spectrum of both physical and biological oceanographic parameters upon which to construct predictive stock-recruitment models.

Over the period 1977-82, objectives (a) and (c) were addressed by means of ichthyoplankton surveys using a grid of 150 stations covering the Scotian Shelf. A total of 34 surveys were conducted over this period so that there was an accumulated coverage of at least two surveys for each month of the year. In addition, three larval silver hake patch study surveys were conducted as part of objective (b). Further work towards objectives (b) evoloved into species specific process-oriented studies such as the Fisheries Ecology Program (FEP).

Stock Structure of Scotian Shelf Flatfish as Inferred from Examination of Ichthyoplankton Survey Data and Distribution of Mature Females

Data on egg distributions and timing of appearance of maximum egg densities were examined to determine the stock structure of three commercially important flatfish occurring on the Scotian Shelf: American plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*), witch flounder (*Glyptocephalus cynoglossus*). Distributions of sexually mature females obtained from research vessel surveys were used to further support inferences concerning spawning location. Using such information, more than one stock of both American plaice and yellowtail flounder appear to occur on the Scotian Shelf, but no conclusions could be drawn concerning witch flounder. In the case of American plaice and yellowtail flounder, the existing means of geographic aggregation of data do not appear to adequately represent stock structure. Little or no advection of eggs and larvae of those species appear to occur on the Scotian Shelf, supporting the hypothesis that current-driven retention areas promote stock discreteness in that region.

C. Scotian Shelf Ichthyoplankton Program (SSIP)

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Scotian Shelf Ichthyoplankton Survey Results	1977-1982	Ongoing	Scotian Shelf	Marine fish species with planktonic egg and larval stages	Ichthyoplankton surveys using bongo, IKMT, neuston and meter net samplers; physical and chemical oceanography sampling on most surveys.	R. O'Boyle, Y. deLafontaine, P. Hurley, P. Kohler, P. Lett, J. Gagné
2. Stock Structure of Scotian Shelf Flatfish as Inferred from Examination of Ichthyoplankton Survey Data and Distribution of Mature Females	1979-1983	Completed	Scotian Shelf	American Plaice, Yellowtail, Witch Flounder	Examination of SSIP database for distribution and abundance of flatfish eggs and larvae. Also examination of MFD groundfish surveys database for distributions of mature flatfish.	J. Neilson, E. deBlois, P. Hurley

D. SOUTHWESTERN NOVA SCOTIA FISHERIES ECOLOGY PROGRAM

The common goal of this program is improved management advice through the study of factors affecting the productivity of an economically important groundfish stock. The haddock and, secondarily, the cod stock of the Southwest Scotian Shelf was considered most appropriate for this study. Some studies initiated during this program are continuing to evolve and are detailed below. The choice of the area and stocks is based on several reasons:

1. There are a number of interacting fisheries for haddock, cod, pollock, herring, scallop, and lobster allowing for consideration of multispecies approaches to research problems.
2. Baseline data existed for ichthyoplankton, circulation, and primary productivity.
3. Fish and shellfish stocks in the region are economically very important to the Nova Scotian fishing industry.
4. The history of the stocks (especially haddock) is well defined.

Fine Scale Analysis of Larval Survival

Analysis of the fine-scale vertical distribution of haddock eggs and larvae has revealed that: 1) density (sigma-t) characteristics of the water column determine the depth and vertical variance of late stage (=Stage IV) haddock eggs; 2) the centre of mass (depth, m) of the vertical distribution of haddock eggs increases with age such that Stage II eggs occur in the upper 20 m and Stage IV eggs occur between 30 and 40 m, this may explain the tendency for early stage haddock larvae to be associated with the depth range associated with the pycnocline; 3) age-dependent increases in the centre of mass do not produce divergent spatial distributions among eggs and larvae, rather temperature acting on development rate provides a simple explanation for the observed distributional patterns of haddock eggs and larvae from year-to-year; 4) food abundance and the intensity of stratification determines the condition of haddock larvae and possibly survival; 5) larvae in poor condition tend to show either bi-modal or surface-skewed depth distributions whereas larvae in good condition show a spiked, uni-modal depth distribution centred about the pycnocline; 6) pro-rating of larval abundance data by a proxy variable such as a stratification index (= suitability of the larval feeding environment) may yield a better projection of recruits than unadjusted, early larval abundance data commonly used to estimate spawning biomass; and 7) variability of the spring stratification may be a leading candidate in explaining interannual variability in larval survival and, possibly, recruitment.

Dispersal Strategies of Marine Fish Larvae

Broad-scale, horizontal patterns of distribution of the egg larval, and pelagic juvenile stages of cod and haddock have revealed that: 1) the early life stages of cod and haddock larvae originating from Browns Bank appear to be transported northwards along the 100 m isobath towards the Bay of Fundy; 2) the transport of larvae may result in enhanced feeding conditions for larvae because food concentrations are higher nearshore compared to food availability on the bank. This interpretation was supported by the tendency for larval haddock condition to be relatively high in the nearshore and lower in the offshore; 3) although very high densities of larval haddock were evident in 1986, their condition was low compared to 1985 and this mirrored the low microzooplankton levels measured at the same time; 4) use of a single, small gear type precludes the quantitative assessment of larval drift during the entire pelagic phase because of net avoidance by the larger, rarer and more evasive larvae and pelagic juveniles; 5) pelagic juvenile cod, originally spawned offshore, are commonly found in the nearshore, shallow waters off southwestern Nova Scotia whereas haddock juveniles remain further offshore; 6) variable displacement from the spawning site from year-to-year is a characteristic of haddock egg and larval distributions and this applies to cod as well, and 7) other species, (such as Liparis, sculpins, gunnels, etc.) having spawning times similar to haddock in the region but differing in their location of spawning and egg type (demersal vs pelagic eggs) show strongly overlapping larval and juvenile patterns of distribution in direct contrast to those of haddock and cod.

Fisheries Ecology Program: Physical Oceanographic Component

The primary goal of the Browns Bank physical oceanographic study was to investigate physical processes influencing haddock recruitment. Emphasis was placed on the egg and larval stages of haddock. Earlier studies (The Cape Sable Experiment, 1978-80; Cape Sable Extension, 1980-83) had determined that a permanent clockwise gyre, driven by non-linear tidal forces, exists over the western cap of Browns and that the inshore currents off Cape Sable are directed into the Gulf of Maine, with a maximum in winter and strong seasonal cycle. The hypothesis guiding the initial steps of the Browns Bank study (based on SSIP conclusions) was that retention of haddock eggs and larvae on the Bank by the gyre is conducive to their survival, or conversely, that breakdown of the gyre and consequent loss of eggs and larvae from the Bank leads to poor haddock year classes.

The major elements of the physical oceanographic field experiment were: 1) year-long moored current meter measurements at three levels (mid-depth and 10-15 m from surface and bottom) centred around the western cap; and 2) a series of surface-layer dispersion studies using clusters of satellite- tracked drogues deployed at various locations on the Bank (eg. western cap, saddle). As expected, the moored measurements revealed a mean circulation consistent with a closed clockwise gyre in the upper layers over the western cap, but with strong low-frequency variability, driven by wind and tide, superimposed. The trajectories of the satellite-tracked drifters generally supported the gyre circulation, but also showed a high degree of temporal and spatial variability. In April and November, 1983, these observations suggest that the gyre may be broken down by wind-forced currents. In the absence of strong wind events (July/September 1983), drogues placed on the western cap were found to exit the Bank from the northern flank after an average "residence" time of 14 days and subsequently follow the coastal flow into the Gulf of Maine. This estimate of the "residence" time is roughly comparable to the time required for a drifter to circulate around the western cap in the gyre (10-20 days). On the other hand, estimates of the isotropic dispersion coefficient from the drogue cluster experiments are in the range of 100 m^2/s, which suggests that the time scale for horizontal dispersion processes alone to remove particles from the Bank is 25 to 45 days.

Spring Distributions of Plankton in the Browns Bank Area

The purpose of this project is to determine the general temporal and spatial pattern of the spring phytoplankton bloom in waters off southwest Nova

Scotia, and to determine possible underlying mechanisms for these observed patterns. This analysis includes data from Feb.-June 1983 and 1984; a final paper will include data from 1985.

The peak in chlorophyll biomass (based on monthly cruises) occurred at the end of March and beginning of April in both 1983 and 1984. It was followed by a decrease in May, coinciding with a maximum in zooplankton displacement volume, and an increase in June. There was little difference in timing across the area, although the magnitude of the bloom was greatest over Browns Bank and its northern flank. It had been expected that variations in bottom depth would serve to initiate the bloom earlier in shallow areas. However, a model of the vertically averaged mean light intensity suggested the bottom depth even in the shallowest regions was generally too deep, and that stratification was required to initiate a bloom. This condition was met in 1983 by early April.

Rapid changes in water masses on the order of a few days were also noted in late April 1983. The area underwent changes from warm to cold to much warmer (6°C) water over a period of 14 days, with a possible intrusion of oceanic water into the trough north of Browns Bank causing upward doming of isohalines. The result was a rapid decrease in chlorophyll biomass and increase in NO_3. Reasons for the water mass replacement are unknown at present.

Larval Drift

Drift vs retention of larval cod and haddock is the research topic under consideration. Through use of extensive collections of ichthyoplankton made off of SW Nova Scotia in 1985, a test of the competing hypotheses concerning larval drift/retention is nearing completion. Both cod and haddock are suspected to spawn offshore, on or around Browns Bank. The age of each of the larvae collected was estimated through the use of validated otolith microstructure techniques, which produces an age (in days) of extreme accuracy and precision. The distribution of these aged larvae is now being mapped and analyzed with spatial autocorrelation models. If the larvae do indeed drift inshore to a "nursery ground", the age-structured distributons should show a preponderance of younger larvae offshore, and older larvae inshore. The age-structured maps are just now being prepared.

Cohort Survival

The current paradigm suggests that year class strength is determined in the first year of life. As a first step towards testing this hypothesis, an entire year class of cod has been monitored successively from the egg stage through to the settled juveniles. The study was conducted off of SW Nova Scotia in 1985. Indices of relative egg and larval abundance are available from a variety of surveys, as are abundance indices for the pelagic and settled stages. Hatch date distributions have been calculated for each of the life history stages through otolith microstructure examination. Variations through time in the hatch date distribution of the cohort survivors will indicate the presence of a size- or age-selective mortality process. The relative abundance indices will then be used to infer the date and age at which the mortality events occurred.

D. Southwestern Nova Scotia Fisheries Ecology Program

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Fine Scale Analysis of Larval Survival	1983-	1984-	SW Scotian Shelf, Gulf of Maine, Browns Bank	Haddock (egg-juvenile)	Empirical, diet analysis, egg staging, quantititave sampling of microzooplankton and macro-zooplankton, development of proxy variabiles for suitability of feeding environment.	K. Frank, J. McRuer
2. Dispersal Strategies of Marine Fish Larvae	1985-	1985-	SW Scotian Shelf, Gulf of Maine, Browns Bank	Haddock, Cod, Sand Lance, forage fish (egg-juvenile)	Concurrent nearshore/offshore sampling, BIONESS and TUCKER trawl, flourensce, morphometric and biochemical conditions indices, age and growth based on otolith microstructure analysis.	K. Frank, J. McRuer, I. Suthers
3. Fisheries . .ology Program: Physical Oceanographic Component	1983-1985	1984-	SW Nova Scotia	Haddock	Moored current meter measurements, satellite tracked drogues, hydrographic surveys, doppler current profile, physcal modelling.	P. Smith
4. Spring Distributions of Plankton in the Browns Bank Area	1983-1985	1986-1988	Browns Bank, SW Nova Scotia	Phytoplankton and Zooplankton (related to haddock ecology)	Hydrographic and plankton data were collected in conjunction with sampling for larval haddock. Comparisons will be made of timing and distributions of plankton and larval fish production.	I. Perry, P. Hurley, T. Koslow, R. Fournier

D. Southwestern Nova Scotia Fisheries Ecology Program (Continued)

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
5. Larval Drift	1983-1985	1984-	SW Nova Scotia, Browns Bank	Cod, Haddock	Otolith microstruture: Spatial autocorrelation models.	S. Campana, P. Hurley, S. Smith
6. Cohort Survival	1984-1985	1984-	SW Nova Scotia, Browns Bank	Cod	Otolith microstructure: Hatch date distribution.	S. Campana, P. Hurley, I. Suthers

E. LARVAL AND JUVENILE GADID POPULATION STUDIES

Juvenile Fish Surveys on the Scotian Shelf: Implications for Year-Class Size Assessments

The potential for using juvenile fish surveys to estimate year-class strength was assessed from data collected during midwater trawl surveys in the Northwest Atlantic for cod, haddock, silver hake, and herring. Problems encountered in the development of juvenile fish abundance estimators included changes in availability to survey gear caused by diel or ontogentic vertical migrations. Data on the vertical and geographical distribution of juvenile fish illustratees the need for careful, species-specific survey design based on adequate knowledge of juvenile fish behaviour. For example, a change in methodology of a juvenile silver hake survey on the Scotian Shelf predicated on the results of a diel distribution study was associated with an increase in the precision of the abundance estimates. While the use of midwater trawl surveys for abundance estimates must be approached with caution, their use in general biological studies of distribution, behaviour, and even stock structure is advocated. In fact, such preliminary investigations are prerequisite to their practical application in juvenile abundance estimation.

Condition of Atlantic Cod After Transition to Exogenous Feeding: Morphometrics, Buoyancy and Predator Avoidance

The condition of Atlantic cod Gadus morhua L. larvae reared under food densities of 0, 2, 5, and 10 zooplankton m^{-1} was examined after the transition to exogenous feeding. Fulton's K (weight/length3) was not correlated with prey density in which larvae were reared, indicating that this index of condition is inappropriate for larvae immediately after yolk sac absorption. Fulton's K was also not positively correlated with the ability to avoid a simulated predator. However, predation avoidance was positively correlated with higher prey density. A second measure of condition, body height standardized for length, appeared to be a more sensitive indicator of condition but also did not correlate with the ability of larvae to avoid predation. The results of a buoyancy experiment indicated that poorly fed larvae may occur higher in the water column, and thus may be more vulnerable to predation or cause a sampling bias in ichthyoplankton studies.

Assessment of Histological/Biochemical Indices of Condition for Larval Gadids

Using a microbomb calorimeter capable of measuring the energy content of larvae weighing as little as 0.1 g dry weight, and histological techniques developed for Pacific coast species, the condition of gadid larvae reared under various prey regimes in the laboratory is being assessed. Preliminary histological results indicate that of 13 structures examined, the hindgut (the criterion for healthy larvae was a large portion of cells containing one to a few spheriod eosinophilic bodies) is the most sensitive indicator of nutritional well-being in haddock larvae. While the proportion of fed vs starved larvae correctly classified was high using such criteria, considerably lower success was obtained in differentiating larvae fed varyng denstities of prey. Using the techniques developed in the laboratory, the study is being extended to include larvae caught in the field (Georges Bank).

Interactions of Caligid Ectoparasites and Juveniles Gadids on Georges Bank

The role of the ectoparasite (*Caligus* sp. Copepoda: Caligidae) in the northeast Georges Bank cod-haddock ecosystem was examined. The vertical distribution of the free-living adult stage and host-parasite relationships was described at two sites of contrasting hydrographic conditions, one being thermally stratified and the other isothermal. Cod had both a greater prevalence and number of *Caligus* sp. ectoparasites than did haddock. Preferred sites of ectoparasite attachment also differed. While no evidence of reduced fish condition was found as a function of parasite burden, circumstantial evidence is offered in support of the hypothesis that *Caligus* sp. ectoparasitism is a source of mortality for young haddock.

ELH Growth and Year-Class Strength

This project was designed to be a direct test of the relationship between early life history growth and year-class strength. For each of 5 years, samples of juvenile cod have been collected from Georges Bank. The otolith microstructure has been used to reconstruct the age and relative growth rate of each of the fish. Estimates of year-class strength will be derived from VPA after the year-classes enter the commercial fishery. If year-class strength is found to be correlated with larval and/or juvenile growth rate, the relationship could be used to predict recruitment to the fishery at a very early stage.

Diet Changes in Scotian Shelf Haddock During the Pelagic and Demersal Phases of the First Year of Life

The diet of haddock *Melanogrammus aeglefinus* from the southern Scotian Shelf was studied during their first year of life. While haddock were pelagic, copepods were the numerically dominant component in the diet, with a significant benthic contribution (amphipods, polychaetes) first ocurring in late summer. Examination of gut contents indicated that the transition from pelagic to demersal life occurred relatively suddenly. Catch rates did not vary with diel periodicity and gut contents of demersal fish had few occurrences of pelagic prey, indicating that diel migration was likely not an important aspect of the ecology of age-0 fish during the demersal phase of their lives. Dietary changes during the months subsequent to the pelagic- demersal transition were minor relative to those associated with the transition itself, although some trends in importance of dietary items were observed, notably with copepods and mysids. Such trends did not appear to be related to the size of age-0 haddock.

Comparison of Distributions of Age-0 Groundfish with Benthic Food Resources

Using data from MFD groundfish surveys, the distributions of age-0 groundfish will be compared with those of benthic invertebrates known to be of significance in fishes' diets. The area of concern will be Browns Bank.

Age-0 Silver Hake Feeding Ecology

The feeding of age-0 silver hake, a numerically dominant member of the juvenile fish community on the Scotian Shelf, was examined with respect to fish length, time of day and depth caught. Feeding patterns were also used to substantiate patterns of vertical migration previously postulated to occur.

Juvenile Fish in Scotian Shelf Basins

Previous investigations (Sameoto, Herman) of zooplankton productivity on the Scotian Shelf have indicated that basins supported denser populations of zooplankton than did banks, a result contrary to previous beliefs. Acoustic studies associated with those investigations indicated that small fish were also present in large numbers. The intent of this investigation is to identify the species of fish residing in these comparatively deep habitats and to ascertain the trophic interactions with the high concentrations of zooplankton found there.

Trawl Surveys for Juvenile Groundfish in the Sable Island Area

Annual groundfish trawling surveys for juvenile (two year old or less) fish in the shallow waters around Sable Island from 1981-1985 yielded 36 fish species of which the combined totals of haddock, silver hake, cod, and yellowtail flounder alone comprised 98, 95, 90, 96, and 78% or the total catches in the respective years. 0-group haddock, abundant in 1981 and 1982, were virtually absent from 1983-1985. This corresponded to diminution of abundance of age-1 and age-2 fish in the subsequent years. Juvenile cod were also an important constituent of catches but 0-group cod were rare in all years. Silver hake, yellowtail flounder and winter flounder were common but not as juveniles. Length-frequency distributions showed year-to-year changes in relative year-class strength and were also used with catch rates to show that there was no absolute segregation of age-groups in relation to depth or geographic sector but catch rates indicated differences in geographic distributions between age-groups, which varied in most cases from year to year.

Catch rates of 0-group haddock did not show good correlation with estimated population size from independent sources, but age-1 haddock and age-2 cod catches did. Such correlation indicates the value of the surveys as a possible means of providing indices of abundance of haddock and cod stocks of the central Scotian Shelf.

Ecology of Age-0 Cod and Haddock on Georges Bank

Diel changes in the vertical distributions of age-0 pelagic cod and haddock were examined in isothermal and stratified waters of Georges Bank in June 1985. Discrete depth collections every 4-hr indicated cod had more extensive changes in depth than haddock. At both sites, cod were predominately near bottom during the day and in midwater at night, although at the stratified site this upward migration may have been limited by the thermocline. Age-0 haddock occurred about the thermocline at the stratified site, with little diel change of depth. At the mixed site, haddock were distributed near bottom, but were caught throughout the water during the periods before noon and midnight. For both cod and haddock, small fish (30 mm standard length for cod, 40 mm for haddock) were also distributed at shallower depths and undertook less extensive migrations than larger fish. Time-dependent vertical distributions clearly demonstrate overlap at the mixed site, and the separation of distributions at the stratified site. To investigate factors potentially contributing to these diel changes in depth, distributions of temperature, salinity, light, preferred zooplankton prey, and tidal current speed were examined. Vertical migrations of cod were related to the diel light cycle at both sites. At the mixed site, the number of haddock caught, a function of their distribution off the bottom, was inversely related to the mean tidal current speed during the sampling period. This relationship may have been mediated through the effect of current speed on the distribution of the preferred prey.

Physiological condition of cod and haddock, and zooplankton biomass, was significantly greater at the mixed site. Electivity indices indicated *Neomysis americana*, which ocurred at high densities, was the preferred prey of both fish species at this stie. At the stratified site, cod overlapped in deep water with the distribution of its preferred prey *Tisbe* sp., while distributions of haddock and its preferred prey *Limachina* sp. overlapped in upper waters. The ability of cod and haddock to co-occur when prey are plentiful, and separate when prey are scarce, may provide a means to reduce interspecific competition. It also implies that prediction of haddock vertical distributions for survey purposes may depend on the thermal structure, distributions of prey, and tidal current speed.

E. Larval and Juvenile Gadid Population Studies

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Juvenile Fish Surveys on the Scotian Shelf: Implications for Year-Class Assessments	1978-1986	Complete	Scotian Shelf, Bay of Fundy, Georges Bank	Cod, Haddock, Silver Hake, Herring	Examination of time series of surveys.	P. Koeller, P. Hurley, P. Perley, J. Neilson
2. Condition of Atlantic Cod After Transition to Exogenous Feeding: Morphometrics, Buoyancy and Predator Avoidance.	1985	Complete	Biological Station, St. Andrews	Cod	Laboratory-based study.	J. Neilson, I. Perry, P. Valerio, K. Waiwood
3. Assessment of Histological Biochemical Indices of Condition for Larval Gadids	1986-1988	Ongoing	Georges Bank	Cod, Haddock	Combination laboratory/field study.	J. Neilson, I. Perry, K. Waiwood
4. Interactions of Caligid Ectoparasites and Juvenile Gadids on Georges Bank	1985	Complete	Georges Bank	Cod, Haddock	Field study reporting serendipitous findings.	J. Neilson, I. Perry, J. Scott, P. Valerio
5. ELH Growth and Year-Class Strength	1984-1988	Ongoing	Georges Bank	Cod	Otolith microstructure and time series analysis.	S. Campana
6. Diet Changes in Scotian Shelf Haddock During the Pelagic and Demersal Phases of the First Year of Life	1983-1985	Complete	Scotian Shelf	Haddock	Field study.	R. Mahon, J. Neilson

E. **Larval and Juvenile Gadid Population Studies** (Continued)

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
7. Comparison of Distributions of Age-0 Groundfish with Benthic Food Resources	1978-1982	1988	Browns Bank	Cod, Haddock, Plaice, Yellowtail, Pollock	Field study.	D. Wildish, J. Neilson
8. Age-0 Silver Hake Feeding Ecology	1980-1983	1988	Scotian Shelf	Silver Hake	Field study.	P. Koeller, J. Neilson, D. Markle
9. Juvenile Fish in Scotian Shelf Basins	1988-	1988-	Scotian Shelf (Emerald, LaHave basins)	Gadids	Two-vessel study.	D. Sameoto, A. Herman, J. Neilson
10. Trawl Surveys for Juvenile Groundfish in the Sable Island Area	1981-1985	Complete	Sable Island area	Groundfish	Multi-year survey.	J. Scott
11. Ecology of Age-0 Cod and Haddock on Georges Bank	1985-1987	1985-1989	Georges Bank	Cod, Haddock	Investigates the distributions relative to tidal fronts, vertical migratory behaviour, and trophic interactions of age-0 pelagic phase cod and haddock. This information is crucial to the design of surveys for advance estimates of abundance and recruitment.	J. Neilson, I. Perry

F. SHELLFISH RECRUITMENT STUDIES

Recruitment into the Coastal Lobster Fishery Along the Atlantic Coast of Nova Scotia

The lobster landings along the Atlantic coast of Nova Scotia, from Richmond to Lunenburg County, have fluctuated drastically since the turn of the century with a perioicity of approximately 20 years. The most recent decline bottomed-out in the late 1970s with landings 1 to 10% of those during the previous peak years in the mid-1950s and the subsequent recovery in the mid-1980s.

There have been a number of hypotheses proposed on the causes behind this cyclical fishery (eg. construction of Canso Causeway, fishing pressure, various predator/prey hypotheses, climatic changes). Our approach to studying recruitment along the Atlantic coast of Nova Scotia has concentrated on the larval ecology. Huntsman observed that warm water (16°C) stimulates rapid growth of the planktonic larvae, and he proposed that this is necessary for successful molt completion and bottom settlement before cooler temperatures slow or halt development in the fall. Optimal temperatures of sufficient duration for the successful completion of larval developmnt are probably only found in inlets along this coast. Furthermore, the appropriate prey spectra for larval survival is also only found in coastal waters (Harding et al. 1983). Larval lobster surveys were undertaken in and slightly offshore of St. Margaret's Bay, N.S., with the ultimate goal of estimating production and mortality for comparison with the well-studied and stable lobster fishery in the southern Gulf of St. Lawrence.

During the period of the lobster larvae studies (1982-84) a physical oceanographic study was undertaken which included moored thermistor chains in 1984. The data reveal periods of intense upwelling when the upper layer waters were completely replaced. Comparison with temperature data collected as part of a long-term monitoring program using Ryan thermographs (Dobson and Petrie 1985) shows that these upwelling events occurred simultaneously along most of the Atlantic coast of Nova Scotia. This is driven by the alongshelf wind stress in the classical Ekman sense (Petrie et al. 1987). We are presently developing an Ekman model using geostrophic wind data from 1946 to 1986 to test the hypothesis that increased alongshelf winds may reduce lobster recruitment along the Atlantic coast through greater offshore transport.

Recruitment of Larval Lobsters Along SW Nova Scotia, Bay of Fundy, and Gulf of Maine

In a recent reinterpretation of Stasko and Gordon's (1983) larval surveys, it was calculated that between 92 and 97% of the larval recruitment off southwest Nova Scotia occurred in the offshore region from Stage I and IV production estimates, respectively (Harding and Trites 1988).

Lagrangian measurements (from surface and bottom drifter releases) were taken at the same time as the larval surveys. To investigate the hypothesis that inshore stocks receive larval recruits from the offshore we estimated current patterns and velocities (3-16 cm/s) from these drifter releases(Harding and Trities 1988). Limits of larval dispersion were then estimated from surface currents and the physiological and ecological traits of the larval lobster. It would appear that offshore lobster could make an importantcontribution to recruitment throughout the eastern sector of the Gulf of Maine.

Studies planned in the near future will examine the degree of retention of larvae on offshore banks by physical forces or a combination of the interactions between physical oceanography and the behavioural traits of the larvae. Larval release seems to be largely confined to shoal waters. Substaging of molts will be used to improve estimates of larval drift time from the banks. Changes in survival from the condition of these expatriates, using either total lipid content or lipid types as an indicator will be examined. A more comprehensive estimate or larval production off southwest Nova Scotia will be undertaken given the improved knowledge of the vertical distribution of the four planktonic stages of the lobster and more sophisticated collecting gear (Harding et al. 1987).

Scallop Population Studies

The spatial and temporal distribution of sea scallop larvae in relation to (i) concentrations of recruited scallops; and (ii) the physical and biological environment is presently under investigation. The study has evolved considerably since 1984 when the horizontal and vertical distribution of sea scallop larvae was studied in three fall cruises.

In 1986 and 1987 the horizontal and vertical distribution of larvae on Georges Bank was studied and the analysis is in progress. The vertical distribution of larvae was shown to be a function of water column stability in 1986; whether or not this is food related was investigated in 1987.

In October of 1988, larval sea scallop distribution in the frontal zone on the northern flank of Georges Bank will be studied. This is in conjunction with a physical oceanographic study taking place on cross-frontal exchange.

Simultaneous to the field studies, methods to assess larval age and condition in animals from nature have been developed in the laboratory. Initial results of using growth rings to age the larvae were promising (see Hurley et al. 1988) but further lab study indicated that the rate of growth line deposition is a function of temperature and recent feeding history. It may still be possible to assess the relative growth rates of larvae in nature but estimating the true age of the larvae remains problematic.

A lipid index to assess the energy stores of sea scallop larvae in nature appears more promising. In 1987 larvae from different food regimes were stained and prelimianry results suggest that there is food limitation of energy storage.

The Role of the Georges Bank Tidal Front on Plankton Dispersal or Retention

Tidal mixing fronts in continental shelf areas are regions of strong gradients in physical properties and currents. Variations in physical and transport processes in such regions may define recruitment of marine species by influencing the distributions of early life-history stages in relation to the appropriate location for the population. A study of the relative roles of physical and biological/behavioural processes that determine zoo- and ichthyoplankton distributions and physiological condition about the strong tidal front on the northern flank of Georges Bank is proposed. The hypothesis to be tested is that physical processes, and differences in biological processes such as vertical migration or water mass preferences, are responsible for potential dispersal of lobster larvae to southwest Nova Scotia, and retention of scallop and fish larvae on Georges Bank. The generally strong convergence at tidal fronts will also allow us to test whether elevated concentrations of potential zooplankton prey lead to enhanced physiological condition of fish larvae. This program will be closely coordinated with a detailed physical oceanographic study of this front to be conducted by Physical Chemical Sciences Branch at BIO.

F. Shellfish Recruitment Studies

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Recruitment into the Coastal Lobster Fishery Along the Atlantic Coast of Nova Scotia	1982-1984	1984-	Atlantic coast of Nova Scotia	Lobster	Larval survey, moored thermistor, hydrographic survey, spectral analysis of temperature and wind data.	G. Harding, K. Drinkwater, J. Pringle
2. Recruitment of Larval Lobsters Along SW Nova Scotia, Bay of Fundy, and Gulf of Maine	1984-	1984-	Gulf of Maine	Lobster	Analysis of historical data, larval survey, and depth distribution. Lagrangian studies based on drift bottles and satelite tracked drogues.	G. Harding, J. Pringle, R. Trites, K. Drinkwater
3. Scallop Population Studies	1983-1988	1990-1992	Gulf of Maine, especially Georges Bank and Bay of Fundy	Sea Scallops	Discrete depth sampling (i.e. pump), hydrographic data, laboratory age and growth studies, lipid index evaluation.	M.J. Tremblay, M.M. Sinclair
4. The Role of the Georges Bank Tidal Front on Plankton Dispersal or Retention	1988-1989 summer	1988-1991	Georges Bank (northern flank)	Lobster, Scallop, Finfish (silver hake, redfish, yellowtail founder)	In close cooperation with a detailed physical oceanograhic study of the tidal front on northern Georges Bank, this study will examine along-front and cross-frontal distributions of zoo- and ichthyo-plankton. It will examine the relative roles of physical and biological processes in the frontal region on the retention or dispersal of larvae on Georges Bank or into the Gulf of Maine.	I. Perry, G. Harding, J. Tremblay, M. Sinclair, J. Pringle, K. Drinkwater

III. INTER-REGIONAL AND MULTI-NATIONAL STUDIES

A. INTER-REGIONAL

Labrador Shelf Fish Production Studies

The eastern entrance to Hudson Strait is characterized by intense tidal mixing which reduces stratification and results in nutrient-enriched surface waters during the summer (Drinkwater and Jones 1987). Sutcliffe et al. (1983) found evidence that these surface waters are advected onto the Labrador Shelf by the residual circulation and hypothesized that the resultant nutrient influx leads to increased primary production on the shelf. This, in turn, drives a developing food chain as the watermass is carried further southward by the mean currents. The abundance of the 2J3KL cod stocks was related to changes in salinity with higher salinity promoting increased production. It was argued that in years of high freshwater-outflow from Hudson Bay, the increased stratification suppresses mixing in eastern Hudson Strait which reduces nutrients and lowers the salinity of the water on the Labrador Shelf. The reduction in nutrients results in lower primary production and eventually less food for the cod. The significance of Hudson Strait outflow on the Labrador Shelf food chain as proposed by Sutcliffe et al. (1983), if true, suggests a relative increase in the biomass of larger-sized organisms from north to south along the Labrador Shelf. In 1985 a cruise was dedicated to testing this hypothesis by measuring particle-size spectra over the Shelf. The sampling grid was designed to evaluate not only the along-shelf gradients in particle size spectra but also cross-shelf gradients and the influence of bathymetric variations. The particle-size range included bacteria and phytoplankton (measured with a Coulter Counter), zooplankton (from vertical net hauls), and fish (estimated using ECOLOG). Additional information was collected on the benthos, bird distributions, temperature-salinity characteristics, currents, nutrient concentrations and chlorophyll. Processing of the data is near completion and the detailed analysis is ongoing.

Warm-Core Ring and Ekman Transport Effects on Fish Recruitment

Warm-core rings formed from meanders in the Gulf Stream can entrain large volumes of water off of the continental shelf between the Grand Banks and the mid-Atlantic Bight. Several authors have suggested that the shelf water entrained by these rings may transport enough fish eggs and larvae to significantly reduce marine fish recruitment. This hypothesis has recently been tested by Myers and Drinkwater (1986, 1987, 1988) using entrainment indices derived from 14 years of satellite imagery and recruitment indices for 25 commercially important stocks of fish and shellfish. The Slope Water area adjacent to the continental shelf was divided into nine regions which were chosen to correspond to the approximate limits of the fish stocks. An entrainment index including the position and number of warm-core rings was derived for each of these regions from weekly satellite images during the period 1973 through 1986. These data were then combined with estimates of spawning time and the duration of the larval stages to create stock-specific annual indices of ring activity. The results showed strong evidence that a reduction in recruitment of groundfish in the Northwest Atlantic is associated with warm-core ring activity. Recruitment variation in 15 of the 17 groundfish stocks examined was negatively related to ring activity. There was, however, no consistent relationship between recruitment of pelagic stocks and warm-core ring activity. Some of the pelagic species that wereincluded in the analysis spawned sufficiently far from the edge of the shelf that they may not be susceptible to the effects of the rings.

Recently efforts have been directed towards an investigation of the hypothesis that offshore Ekman transport reduces recruitment on the Scotian and Labrador shelves. Data-driven simulations are being carried out of egg and larval cross-shelf transport for the years 1946-86 on 10 separate stocks and will be compared with the observed recruitment. In the model, eggs are released on the spawning grounds each day during the spawning season. The cross-shelf position of the eggs and subsequent larvae are tracked assuming advection through alongshelf wind-generated Ekman transport. The stress estimates are based on six hourly geostrophic winds. Eggs or larvae that are transportd beyond the continental shelf are assumed to die. The result from each years simulation will be the integral of each individual day, weighted by the proportion of eggs estimated to be spawned on that day. The model also includes the influence of vertical migration of the larvae and the time-dependent nature of the Ekman layer depth.

Climate Variability and Recruitment

The physical oceanographic effects of the freshwater discharge from the St. Lawrence River are not limited to the Gulf of St. Lawrence but were shown from temperature and salinity data to extend to the Scotian Shelf and into the Gulf of Maine (Sutcliffe et al. 1976, Drinkwater et al. 1979). Sutcliffe et al. (1977) investigated the catches of 17 commercial marine species of fish and shellfish from the Gulf of Maine and found through exploratory analysis that 10 were significantly correlated with local coastal sea surface temperatures as well as the St. Lawrence River discharge. Maximum correlations again occurred when the fish was lagged by a time approximately matching its age at commercial size. Northern-oriented species were found to be negatively correlated to temperature while southern species were positively correlated. Recently the time series used by Sutcliffe and co-workers in their correlative studies were updated and the relationships re-examined (Drinkwater 1987, Drinkwater and Myers 1987). Using linear regressions based on data from the earlier work, predictions of fish catch or abundance were calculated for the intervening years and compared to the actual catch data. For 6 of the 13 stocks investigated correlations over the 9-14 yr of new data remained high and of the same sign; however, individually none was found to be statistically significant after accounting for the loss of degrees of freedom due to the high autocorrelation in the data (Drinkwater and Myers 1987). The hypothesis of an overall environmental effect on landings in general could not be substantiated as the correlation coefficient for 5 of the 13 stocks reversed sign using the new data, but changes in fishing effort are believed to mask detection of environmental effects in the landings of several stocks. The use of landings, uncorrected for fishing effort, in correlative studies with environmental variables can cause problems in interpretation and later confirmation of relationships (Drinkwater and Myers 1987), however, it is encouraging to note that environment-fish relationships also exist using VPA estimates (Drinkwater 1987).

Northwest Atlantic Capelin Recruitment Studies

Large-scale wind forcing events are known to affect recruitment in beach-spawning capelin and it is hypothesized that similar events affected recruitment of capelin spawned on the SE Shoal of the Grand Brank, a discrete spawning area 350 km from the nearest spawning beach. Specifically we are testing the hypothesis that larvae required a destabilization of the density stratification from storms for effective transport from the spawning beds to the surface waters.

Results of ichthyoplankton surveys conducted in September of 1986 and 1987 were similar in several respects: 1) high concentrations of capelin larvae occured in areas where dense spawning concentrations were observed by hydroacoustic methods in June/July; 2) a mixture of different sizes of larvae (range: 4-26 mm) was observed indicating that larvae hatching at different times were retained in the spawning area; 3) Nov./Dec. surveys conducted in both years showed the concentration of larvae had remained stationary but increased in size consistent with known growth rates; and 4) all sizes of larvae showed evidence of vertical migration behaviour, the daily range increasing with larval size. The dominant larval cohort formed in 1986 coincided with the passage of Tropical Storm Charley which had a pronounced affect on the hydrographic structure of the water column. Other, less abundant cohorts were formed in the absence of such events and what, if any, ecological advantages larvae might accrue from a selective emergence timing mechanism are being investigated. The study in ongoing and several cruises are planned for 1988 and 1989 to address the problem.

SE Shoal Capelin Recruitment Study: Physical Oceanographic Component

The physical oceanographic component of the SE Shoal larval capelin study originated as the SE Shoal Exchange Study. Its aims were to determine the origin and temporal variablity of the relatively-warm bottom water on the Shoal, and infer horizontal and vertical exchange rates from the warm water, seasonal evolution. The field program consisted of hydrographic observations (largely on a ship-of-opportunity basis) in 1985-87, pilot moored measurements in 1986, and detailed moored measurements in 1987. The preliminary results indicate substantial interannual variability in hydrographic properties on the Shoal, and significant influences on currents and water temperatures by atmospheric forcing.

Continued physical oceanographic field measurements on SE Shoal are planned for 1988 and 1989 as part of the larval capelin study, in collaboration with McGill University and the Biological Sciences Branch of Newfoundland and Scotia-Fundy Regions.

Greenhouse Effect on Canadian Atlantic Fisheries

In a scenario with a doubling of present day atmospheric CO_2 concentrations, Wright et al. (1986) predicted several qualitative changes in the physical oceanographic features and properties of the continental shelf waters off eastern Canada. In turn, we have speculated on the impact of such changes on the location, composition, and recruitment of fish populations inhabiting the Gulf of Maine to the Labrador Shelf. For example, a general warming and freshening of the continental shelf waters is anticipated. This may lead to shifts in the geographic distribution of several commercially important groundfish stocks that are presently at the limit of their range. Earlier arrival times and later departures are expected for pelagic speices, which undergo extensive seasonal migrations, under a warmer oceanic regime. Temperature dependent changes in the relative magnitudes of energy flux through the planktonic and benthic components of the food web is one possible mechanism underlying structural changes in fish stock composition. Higher temperatures and increased stratification may result in lesser amounts of organic material reaching the bottom and tend to favour the proliferation of a pelagic fish community. Several published studies exist that use physical data as proxy variables for nutrient flux, advection, and stratification to predict species recruitment patterns in the Northwest Atlantic. These models are being used in conjunction with the specific physical oceanographic sceanario devised to speculate on the most probable consequences to the fisheries of Atlantic Canada.

Time-Scale Characterization of Circulation and Mixing Over Submarine Banks

A time-scale characterization of circulation and mixing is being used to intercompare and interpret physical oceanographic observations from Atlantic coast banks where the Department of Fisheries and Oceans has conducted or is conducting recruitment studies. The characterization consists of intergral time scales for passive-scalar exchange in three orthogonal directions: a residence time (TR) for cross-bank exchange, a recirculation time (TG) for advection by any residual around-bank gyre, and a vertical diffusion time (TV) for the water column. The absolute and relative magnitudes of these times can then be used to estimate changes in scalar distributions on specified biological time-scales, and identify the relative importance of exchange in particular directions. For example, the significance of a residual gyre should be assessed by comparing the associated recirculation time with the bank's residence and vertical diffusion times.

The characterization has been applied to Browns Bank, Flemish Cap, Georges Bank, and the SE Shoal of the Grand Bank, primarily using moored current and drifter measurements. The results for horizontal exchange are shown in Table 1. In general, the residence times are less than (but of the same order of magnitude as) the recirculation times, implying a limited (but some) significance for the gyres. The ratio of residence to recirculation time is largest for Georges Bank and the western cap of Browns Bank, suggesting that the gyres on those banks have the greatest influence on the spatial distribution of properties. The residence and recirculation times are shortest for the smaller Browns Bank, but the greatest interbank difference is in the vertical diffusion time: on the tidally-energetic Browns and Georges Banks, properties are vertically redistributed much more quickly than horizontally exchanged, whereas the reverse is true on Flemish Cap.

It is suggested that the characterization could be extended to describe temporal (eg. interannual) variability in circulation and mixing on banks, as well as expected distributional changes of organisms with simple behavioural patterns (eg. vertical migration).

III. INTER-REGIONAL STUDIES

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
1. Labrador Shelf Fish Production Studies	Sept. 1985	1986-1988	Labrador Shelf, 2J3KL	Cod	Particle-size spectra, Coulter Counter, zooplankton net hauls, ECOLOG, nutrients, CTD, BIONESS.	K. Drinkwater, G. Harding, L. Dickie, R. Sheldon, D. Schneider
2. Warm-Core Rings and Ekman Transport Effects on Fish Recruitment	N/A	1987-1988	NW Atlantic	Many species of commercial value	Statistical analysis of recruitment, wind, and thermal imagery data.	R. Myers, K. Drinkwater
3. Climate Variability and Recruitment	N/A	1972-1987	NW Atlantic	Many species of commercial value	Statistical analysis of catch, SST, and river discharge data.	W. Sutcliffe, K. Drinkwater, R. Myers
4. Northwest Atlantic Capelin Recruitment Studies	1985-	1986-	Southern Grand Bank, SE Shoal	Capelin (larval stage: 4-50 mm)	BIONESS, Tucker trawl, IYGPT, Pisces (submersible), optical plankton counter, fine-scale sampling in frontal region, otolith microstructure analysis.	K. Frank, J. Carscadden, J. Loder, J. McRuer, W. Leggett, C. Taggart
5. SE Shoal Capelin Recruitment Study: Physical Oceanographic Component	1985-1989	1987-	Southern Grand Bank, SE Shoal	Capelin	Hydrographic surveys, moored current and hydrographic measurements, analysis of historical hydrogrpahic data, heat budget computation, meterological data.	J. Loder, C. Ross, S. Akenhead

III. **INTER-REGIONAL STUDIES** (Continued)

Title	Duration		Study Area	Target Species	Techniques/Approaches	Principal Investigator
	Field	Analysis				
6. Greenhouse Effect on Canadian Atlantic Fisheries	N/A	1985-1988	Continental Shelf waters from Gulf of Maine to Labrador Shelf	Several finfish and shellfish species of commercial value in NW Atlantic	Application of several published models that use physical data as proxy variables for nutrient flux, advection, and stratification to predict recruitment patterns from physical changes resulting from doubling of atmospheric CO_2	K. Frank, I. Perry, K. Drinkwater, H. Lear, G. Conan
7. Time-Scale Characterization of Circulation and Mixing Over Submarine Banks	1977-1986	1987-1988	Browns Bank, Georges Bank, SE Shoal, Flemish Cap	Possible extension: a posteriori matching of physical description to biological pattern and structure	Inter-bank comparison based on characterization of time-scales for residence, recirculation, and vertical mixing.	J. Loder, C. Ross, P. Smith

Table 1.

SUMMARY OF RESIDENCE (T_R) AND RECIRCULATION (T_G) TIME ESTIMATES FOR NEAR-SURFACE WATER

	T_R (days)	T_G (days)	
	Lagrangian	Lagrangian	Eulerian
FLEMISH CAP	32 ± 17	67 ± 20	
SOUTHEAST SHOAL	>28 ± 10	56	
BROWNS BANK			
- whole bank	12 ± 9	25 ± 12	>40
- western cap	9 ± 5	8 ± 5	10
GEORGES BANK	54 ± 26	44 ± 11	56

B. MULTI-NATIONAL

Georges Bank Larval Herring Study: Physical Oceanographic Component

As part of the ICNAF-sponsored Gulf of Maine herring program, a larval patch study was planned for the fall of 1978 on Georges Bank. Its aims were to understand the circulation and diffusive processes above a spawning area, and follow a patch of larvae to determine the physical and biological factors influencing its evolution. In collaboration with American physical oceanographers, preliminary physical oceanographic observations were collected in 1977 and more detailed measurements taken in the fall of 1978, focussing on the northern side of the Bank.

Eight research vessels from several countries participated in the patch study. However, larval herring were not sufficiently abundant on Georges Bank to allow successful execution of the program. Some of the biological effort was diverted to larval herring studies on Nantucket Shoals, and the focus of the Georges Bank study switched to a patch of chaetognaths. This patch was found to have a relatively persistent location in spite of the strong residual current, apparently because of the chaetognath's vertical migration in the presence of the vertically-sheared tidal current.

Juvenile Herring Recruitment Studies

Juvenile herring in the coastal waters of eastern Maine (USA) and southwestern New Brunswick (Canada) pose a unique set of management problems. First, the persistent transboundary movements of these fish have made it difficult to establish management authority. Second, landings from the traditional fixed weir and stop seine catch in the area have recently declined, raising questions about the continued viability of the fishery and emphasizing the need to determine the stock origin of the fish on which this fishery has been based. Finally, there is the question of the relationship between these aggregations of juveniles and recruitment to adult spawning stocks of the Bay of Fundy and Gulf of Maine. A variety of studies are underway. Coastal surveys of larvae and juveniles in waters of Maine and New Brunswick (with the Maine Department of Marine Resources; see Chenoweth et al. MS) are addressing the abundance and movements of the juvenile stage. Historical analysis of weir records is being analyzed with the view to understanding fluctuations in juvenile abundance and the relationship with recruitment to adult fisheries. Finally, a stock identification program is comparing spawning populations in the hope of being able to establish the stock affinity of juveniles from mixed schools.

Short-Finned Squid Recruitment Dynamics

Until 1979, little was known of the early life of the short-fined squid *Illex illecebrosus* or of the role played by the Gulf Stream in transporting the larval and juvenile stages. In the winter of 1979, a series of Canadian/USSR cooperative research cruises discovered and mapped the distribution of large concentrations of small juveniles (15-80 mm dorsal mantle length) and a number of larvae between the Gulf Stream and the edge of the Scotian Shelf (Amaratunga *et al.* 1980, Fedulov and Froerman 1980). This was the first strong evidence that the Gulf Stream might play a major role in the life-cycle of *I.*

illecebrosus. Trites (1983) developed a larval dispersion model that would predict an idealized distribution of larval and early juvenile stages over a 1-2 month period after spawning. Under this model, egg massess, larvae, and possibly juveniles are entrained by the Gulf Stream and transported at variable speed northeastward to areas seaward of the Continental Shelf along the northeastern USA, the Scotian Shelf, and Grand Banks. Between January 1983 and February 1986, Canada conducted a series of four research cruises to examine this advection scenario as a mechanism for the transport of larvae and juveniles from areas over the Blake Plateau or areas further to the south (Rowell et al. 1985, Trites and Rowell 1985, Rowell and Trites 1985). Analysis of data from the 1986 cruise is still underway. The results of the previous cruises in this series are summarized by Rowell and Trites (1985), the primary conclusions being:

1. Larvae and early juveniles are caught mainly in a narrow but very long strip of water centred in the Slope Water/Gulf Stream Frontal Zone extending from Floria to an beyond Cape Hatteras.

2. The presence of newly hatched larvae south of Miami, indicates that spawning also ocurs south of the Cape Canaveral area.

3. The physical environment is probably a major factor determining larval/juvenile distribution in that: a) the Gulf Stream provides a rapid transport system (as much as 1000 km/week); b) Frontal Eddies eject surface-layer Gulf Stream Water shoreward into Slope Water, which is subsequently re-entrained into the Stream; c) Frontal Eddies produce upwelling of nutrient-rich water between the filament and the Gulf Stream proper, which in turn increases primary production in the Slope/Gulf Stream Frontal Zone; and d) downstream from Cape Hatteras the formation of Warm-Core Gulf Stream Eddies eject large quantities of Gulf Stream Water into the Slope Water area south of Nova Scotia and the Grand Branks with eddy duration times typically of several months.

4. Recruitment success of failure may be critically dependent on the timing, location, and number of Gulf Stream frontal eddies and warm-core eddies developing when larvae and/or juveniles are present.

It is anticipated that enhanced oceanographic sampling during the 1986 cruise will further clarify some elements noted in the above summary.

Habitat Associations of Age-0 Gadids on Georges Banks

Using a submersible and surface vessels, a detailed investigation of age-0 gadid habit preferences, vertical distributions, and feeding was completed on Georges Bank in 1987. The project was a joint investigation of staff of National Marine Fisheries Service (Woods Hole) and Department of Fisheries and Oceans (MFD, St.^Andrews). Further aspects of the joint work have included a comparison of the two principal nets used by Canada and the United States (International Young Gadid Pelagic Trawl and MOC-10 opening/closing net, respectively).

IV. MULTI-NATIONAL STUDIES

Title	Duration Field	Duration Analysis	Study Area	Target Species	Techniques/Approaches	Principal Investigator
1. Georges Bank Larval Herring Study: Physical Oceanographic Component	1977-1978	1977-1986	Georges Bank, Nantucket Shoals	Herring	Hydrographics surveys, moored current and hydrographic measurements, drifter and dye tracking.	R. W. Trites
2. Juvenile Herring Recruitment Studies	1986-1988	1986-	Bay of Fundy, Gulf of Maine	Atlantic Herring (juveniles)	Analysis of historcial catch data (weir fishery). Coastal surveys. Stock identification of herring spawning populations.	R. Stephenson, DMR Maine
3. Short-Finned Squid Recruitment Dynamics	1979-1986	Ongoing	North and South Atlantic	Short-Finned Squid	Larval and juvenile surveys, hydrographic surveys, integrated biological and physical modelling, extensive university based laboratory research on reproductive biology (O'Dor, Balch, et al.), remote sensing.	T. Rowell, R. Trites, T. Amaratunga, M. Roberge, R. O'Dor
4. Habitat Associations of Age-0 Gadids on Georges Bank	1986-1987	1987-1988	Georges Bank	Silver Hake	Field study using a submersible.	J. Neilson, I. Perry, U.S. National Marine Fisheries Service staff

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V REVIEWS OF DEPARTMENT OF FISHERIES AND OCEANS PROGRAMS ON RECRUITMENT

RECRUITMENT RESEARCH IN THE GULF OF ST. LAWRENCE AND NORTHERN QUEBEC

by

J.A. Gagné and D. Lefaivre
Quebec Region

This report summarizes current research projects conducted by DFO-Quebec scientists to study various aspects of the question of recruitment variability in marine fish and invertebrate populations. The populations investigated inhabit the St. Lawrence system or the waters of northern Quebec.

Major Physical Features of Interest in the St. Lawrence System

Three major features control the hydrodynamics at the head of the Laurentian Trough near the mouth of the Saguenay River (Figure 1): tidal mixing due to bottom stress and internal wave activity; upwelling along the north shore due to wind stress; advection of surface waters due to tidal forcing. All these contribute to maintain a stratification front in the area of Ile Verte.

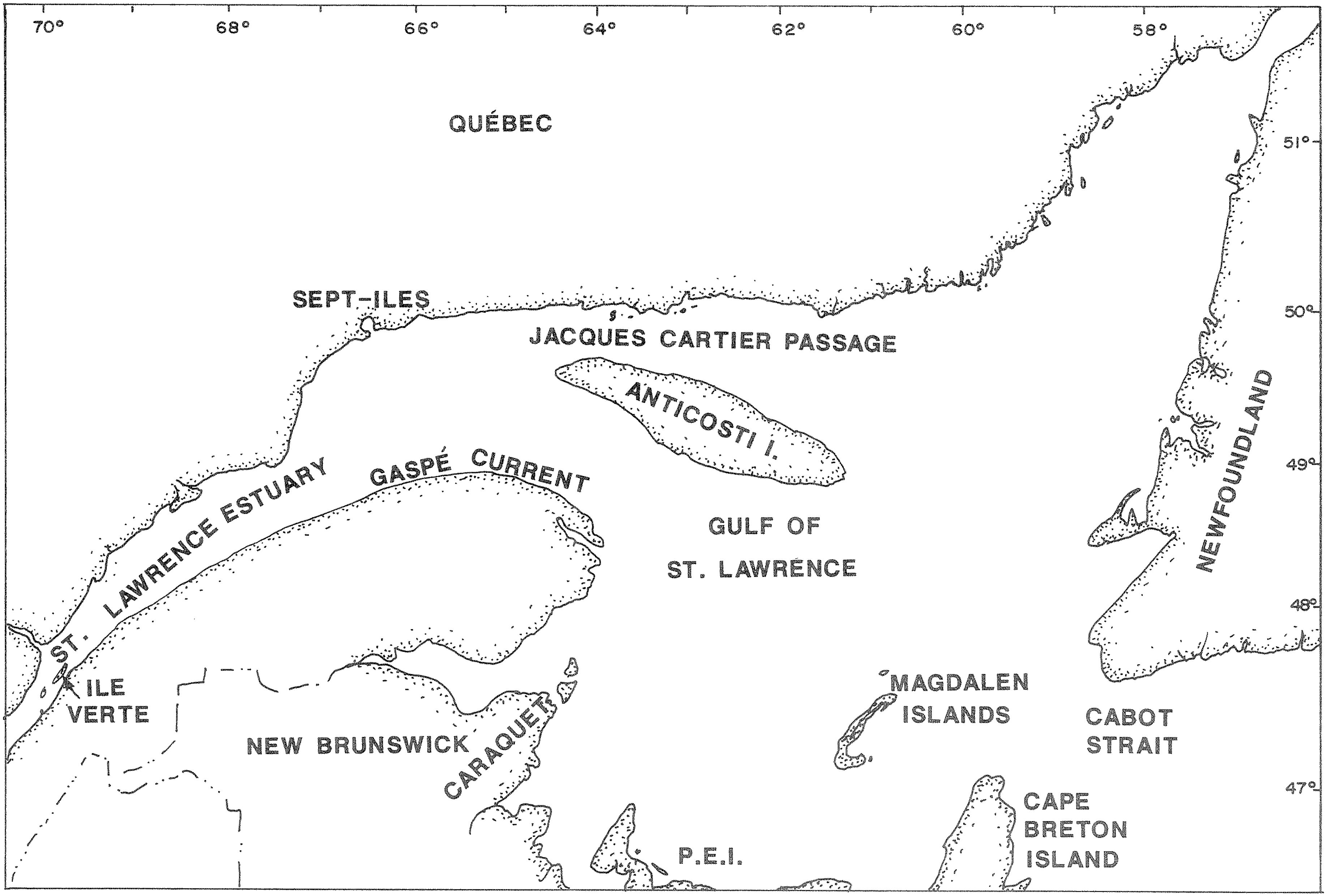
At the mouth of the St. Lawrence River Estuary a cross channel front persists under the influence of fresh waters from upstream and wind patterns in the northwestern part of the Gulf. Along the south shore the Gaspé current advects water out of the estuary towards the southwestern Gulf areas.

The predominant feature in the northwestern part of the Gulf of St. Lawrence is a persistent gyre extending from the shoreline of Sept. Iles to Anticosti Island. This gyre acts as a retention mechanism in the centre but also advects suspended material southward along its sides. In the northern regions, wind-driven upwelling events are common. Mixing is important in shallow areas, especially in the Jacques Cartier Passage. In the spring, freshwater run-off from several large rivers exerts a strong influence on the region by stabilizing the water column.

Along the southern shores of the Gulf wind-generated vertical mixing and freshwater flushing are the main driving forces in numerous small lagoons and estuaries.

Research Projects

Project #1 was initiated when hydrographers, physical and fisheries oceanographers identified a common interest in better understanding various processes operating in the region of the Jacques Cartier Passage, northern Gulf of St. Lawrence (Figure 1). Three objectives reflecting the concerns of the main participants were identified. The first was to understand the influence of freshwater inflow, winds and tides on the circulation and mixing of the northern Gulf waters. In preparation of a survey of the area by the Canadian Hydrographic Service, a second objective was to establish a suitable cotidal map of the water level as well as an atlas of the corresponding tide-induced surface


70°
68°
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48°
47°
QUÉBEC
SEPT-ILES
JACQUES CARTIER PASSAGE
ANTICOSTI I.
NEWFOUNDLAND
ST. LAWRENCE ESTUARY
GASPÉ CURRENT
GULF OF
ST. LAWRENCE
ILE
VERTE
NEW BRUNSWICK
CARAQUET
MAGDALEN
ISLANDS
CABOT
STRAIT
CAPE
BRETON
ISLAND
P.E.I.

Figure 1.

currents. These two objectives are particularly important considering that all the rivers of the Lower North Shore will soon be harnessed for hydroelectric power. Results from this study will be very useful to predict the relative influence of changes in river regimes.

The following specific hypotheses were formulated:

1. The presence of a sill at the western end combines with the lateral constriction imposed by the shores to perturb the tides and induce a rapid phase change through the Passage.

2. The sill and constriction act as a natural barrier for water mass exchanges between the gyre in the northwestern Gulf and the Strait itself.

3. The strong freshwater inflow from the spring melt induces density-driven currents that promote a western flow over the sill and through the Passage. This mechanism induces water mass exchanges and possibly larval advection from one region to another.

4. The topography between Anticosti Island and the continent sustains a gyre that provides a larval retention mechanism.

Moorings of three current meters will measure the currents in the top, mid-depth and bottom layer of the water column. Temperature and salinity profiles will be used to identify local water masses and to determine how the freshwater from the spring melt mixes and disperses in the surrounding waters. These measurements will also allow the inter-calibration of the temperature and salinity sensors on the current meters. Moored and shore tide gauges will be used to evaluate the sea surface slope along and across the Passage. Summer sea-surface temperatures from satellites will be compared to those measured at depths and their temporal evolution linked to current measurements if possible. This should simplify considerably the interpretation of the large-scale circulation.

This region also supports the major shrimp (Pandalus borealis) stocks in the Gulf of St. Lawrence. These stocks are currently managed as independent units even though the genetic integrity of at least the three largest ones is still debated. To determine the degree of isolation between them and better understand their recruitment patterns, it was decided to identify the areas of emergence of larval shrimp and to describe the distribution of the first early life history stages of the species.

A grid of 112 stations positioned on north-south transects 20 miles apart was designed to map the distribution of larval shrimp concentrations over the entire northern Gulf. This grid was sampled with Bongo nets and CTD probes twice in 1986 and once in 1987. Preliminary results for the 1986 cruises indicate the existence of several larval emergence areas in agreement with the known distribution of egg-carrying females. Although the highest level concentrations are always found in some specific locations, stage I and II larvae are dispersed over the entire study area with the exception of a discontinuity between the eastern and western halves of the northern Gulf.

In 1987, the vertical distribution of young larval shrimp was investigated with a multiple opening and closing plankton sampler (BIONESS). This information, coupled with the knowledge of the current patterns in the water column, should provide a better understanding of the factors controlling the direction and extent of larval transport.

Hydrodynamics and Recruitment Variability: Direct Relationships

The influence of hydrodynamic processes on the dynamics of exploited populations constitutes one of the major themes of recruitment research. Sutcliffe (1972) showed that landings of various commercially exploited species can be statistically correlated with broad scale environmental phenomena. For instance, highly significant relationships were obtained with lobster catches in the Gulf of St. Lawrence (Sutcliffe 1972, 1973). Several projects conducted by DFO-Quebec scientists are investigating various aspects of such relationships.

Project #2 was designed to critically examine the likelihood of successfully relating environmental variables to "n"-year-lagged lobster landings in a predictive fashion in the northern Gulf. This study uses lobster landing statistics from six sub-areas of the northern Gulf in an attempt to relate them to environmental factors. The major hydrographic features were identified from NOAA satellite images and related to climatic conditions on the ground. Regional environmental conditions and their potential effects on the growth, survival and advection of lobster larvae were assessed over the period of occurrence of planktonic larvae (months of July, August and September). The exchange of larvae among regions via advective processes was described using a Markov matrix. A conceptual model integrating the expected effects of variations of surface water temperature, wind force and direction, and freshwater outflow on the 9-year-lagged landings of each region was then developed.

The statistical relationship identified by Sutcliffe for the Magdalen Island lobster population is one of the few that held up until recently (Drinkwater 1987). The underlying mechanisms responsible for the association between the runoff from the St. Lawrence River and the landings nine years later needed to be identified. Relevant fundamental information on the basic biology and ecology of that population was gatered by Hudon et al. (Project #3).

Aspects related to egg and larval production, embryonic development and energetic investment in egg production were studied for female lobsters off the Magdalen Islands (Attard 1985; Attard and Hudon 1987). It was found that large females produce eggs in higher numbers, with higher calory content and which hatch faster than eggs from smaller individuals. The higher energy content and earlier hatching time are probably factors that enhance larval growth and survival (Figure 2). If so, larger females would contribute relatively more to recruitment than smaller ones. Larvae produced by small females having molted and extruded their first clutch of eggs in the same summer (Ib) were found to have a low chance of survival due to their late hatching date and low energetic content (Attard and Hudon 1987). These results demonstrate the value of setting an upper size limit to the fishery.

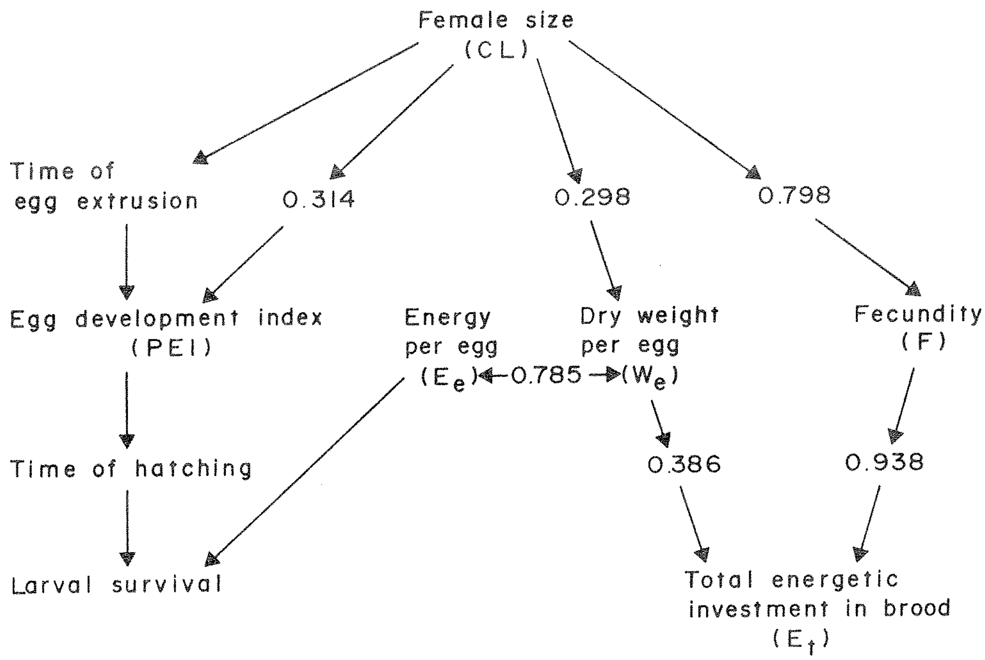

Female size
(CL)
Time of
egg extrusion
0.314
0.298
0.798
Egg development index
(PEI)
Energy
per egg
Dry weight
per egg
Fecundity
(F)
(Ee)←0.785→(We)
Time of hatching
0.386
0.938
Larval survival
Total energetic
investment in brood
(Et)

FIGURE 2

To evaluate larval lobster production and survival off the Islands, 39 stations were sampled with plankton nets during the summers of 1978, 1980 and 1981 (Figure 3). The horizontal and vertical distributions of each of the four planktonic stages of Homarus americanus were assessed from surface tows with simple neuston and meter nets (1978 and 1980) as well as a three-compartment plankton net (Figure 4) (1981). The results indicate that the general pattern of larval abundance is determined by the current regime; the larvae are flushed around Point de l'Est and concentrated in Baie de Plaisance by a gyre (Hudon et al.).

On a smaller scale, 12 stations arranged in a 3 x 4 grid in Baie de Plaisance were sampled for 12 weeks in the summer of 1980. Stage IV larval abundance was found to be significantly correlated with the distance from rocky bottoms favorable to benthic life, suggesting the occurrence of active directional movements on the part of the larvae. The maximum abundance of stage I larvae was synchronized with the period of most rapid increase in summer temperature, thus ensuring that larvae achieve highest net growth rates through their planktonic phase (Figure 5).

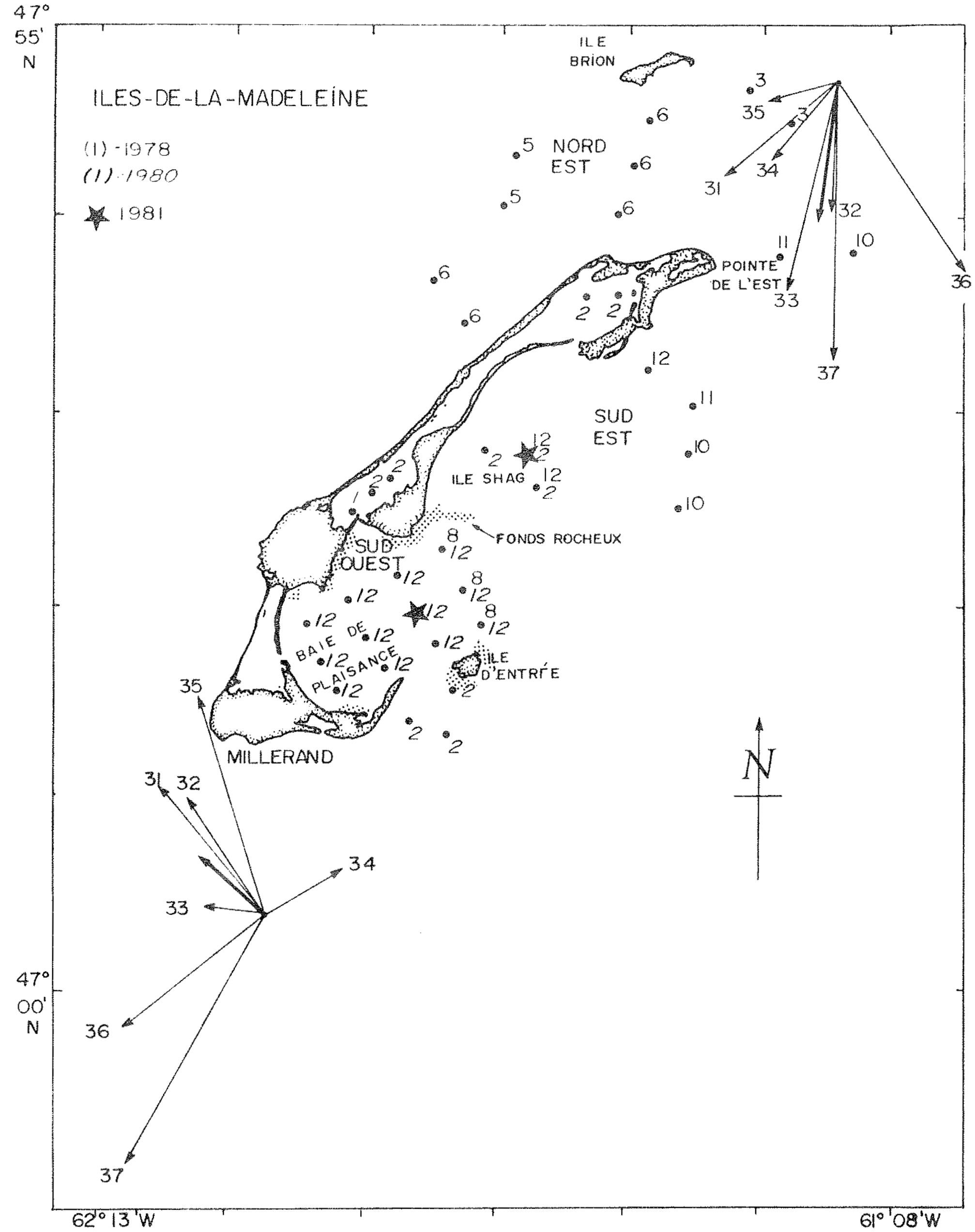
The peak of planktonic larval abundance occurred in mid-July when summer temperatures were maximal, thus ensuring rapid larval development to the benthic stage. This mechanism was hypothesized to minimize the duration of planktonic life in order to avoid the heavy predation likely to occur at this stage (Hudon and Fradette 1987).

These results suggest that summer sea-surface temperatures might play an important role in determining the success of a lobster year-class on the Magdalen Shallows. Simard et. al. (Project #4) want to investigate the role played by summer sea-surface temperatures in the relationship found by Sutcliffe (1972, 1973) between the St. Lawrence river runoff and Magdalen lobster landings. Their objective is to test the following hypothesis:

> Lobster recruitment on the Magdalen Shallows is determined by the intensity and pattern of drift and warming of the sea-surface waters around the Islands during the larval stage. These patterns of drift and warming fluctuate between years under the influence of meteorological conditions and freshwater runoff from the St. Lawrence River.

Historical data on freshwater runoff and meteorological and oceanographic conditions are utilized to model the influence of the St. Lawrence River runoff and wind patterns on the circulation around the Islands. If a relationship is found between these factors and lobster recruitment, the project will proceed to evaluate the respective importance of warming and circulation patterns as causal mechanisms.

The interactions of larval lobster with crab larvae and other macro-zooplanktonic organisms collected simultaneously are also being investigated (Project #5). The peak of larval crab occurrence in Bai de Plaisance occurs during the same period as that of lobster, and is accompanied by biomasses of up to 15 g/1000 m^3 (d.w.) of copepods and other potential preys for both crustacean species. Larval crabs, which are also preyed upon by


47°
55'
N
ILES-DE-LA-MADELEINE
(1) -1978
(1) -1980
1981
ILE
BRION
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EST
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EST
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OUEST
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MILLERAND
N
47°
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62° 13'W
61° 08'W

FIGURE 3

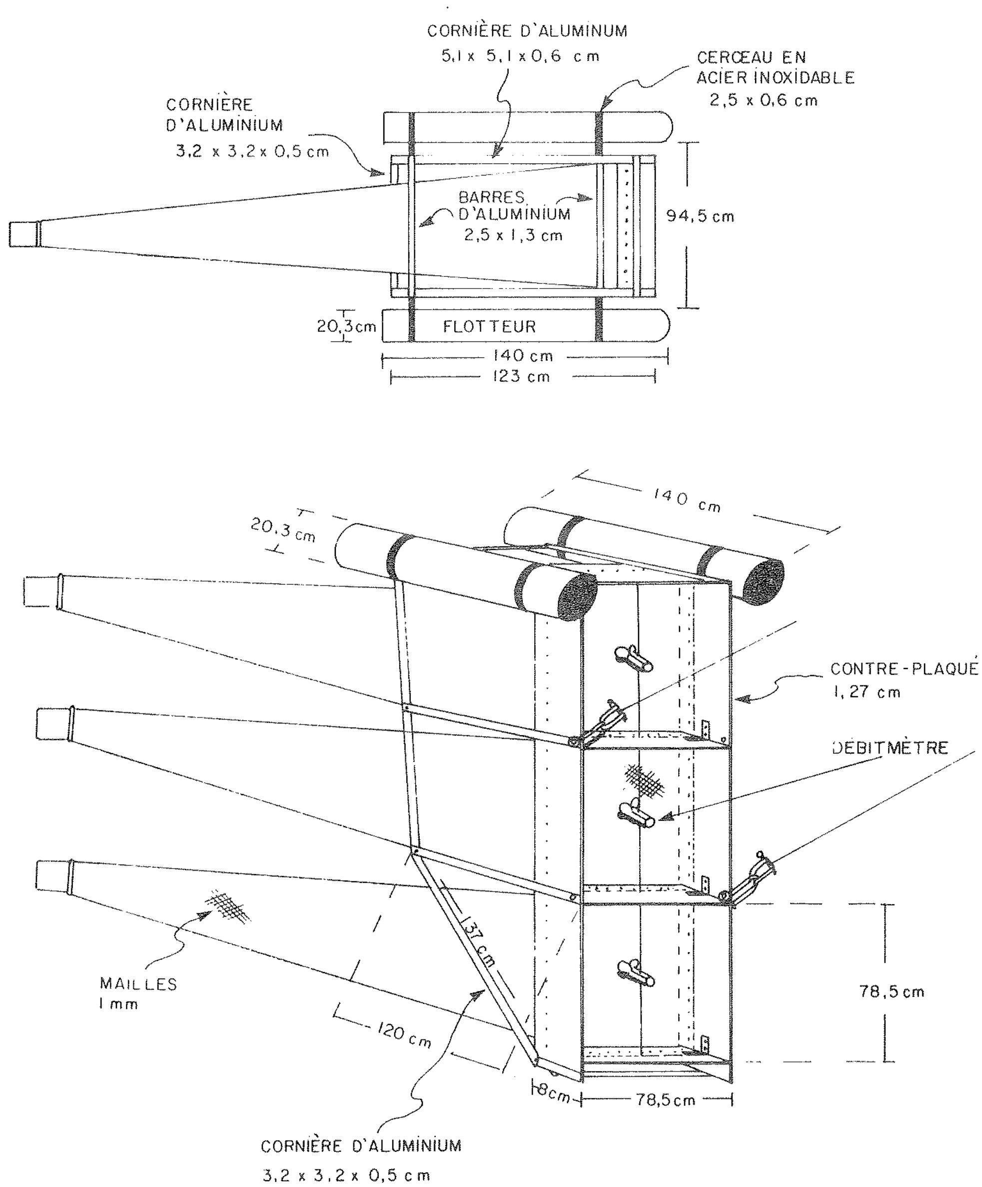
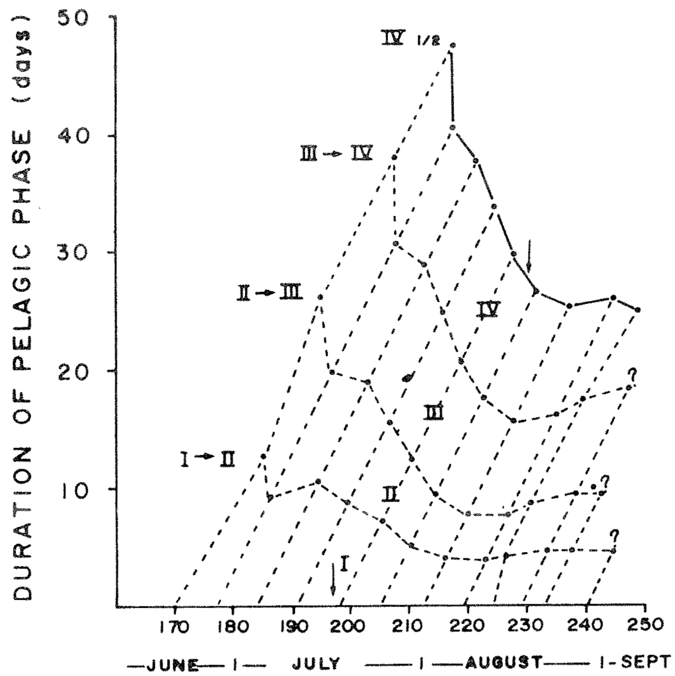

CORNIÈRE D'ALUMINUM
5,1 x 5,1 x 0,6 cm
CERCEAU EN ACIER INOXIDABLE
2,5 x 0,6 cm
CORNIÈRE D'ALUMINIUM
3,2 x 3,2 x 0,5 cm
BARRES D'ALUMINIUM
2,5 x 1,3 cm
94,5 cm
20,3 cm
FLOTTEUR
140 cm
123 cm
140 cm
20,3 cm
CONTRE-PLAQUÉ
1,27 cm
DÉBITMÈTRE
MAILLES
1 mm
137 cm
120 cm
78,5 cm
8 cm
78,5 cm
CORNIÈRE D'ALUMINIUM
3,2 x 3,2 x 0,5 cm

FIGURE 4



DURATION OF PELAGIC PHASE (days)
50
40
30
20
10
IV 1/2
III → IV
II → III
I → II
IV
III
II
I
?
170 180 190 200 210 220 230 240 250
—JUNE— I — JULY —— I —AUGUST—— I - SEPT

FIGURE 5

lobster larvae, are 1000 times more abundant than larval lobsters. It appears that lobster larvae were not food limited in Baie de Plaisance during the study since the duration of the first three planktonic stages was comparable to that measured in laboratory experiments (24 vs 21 d), the growth rates were high and potential prey organisms abundant.

Hydrodynamics and Recruitment Variability: Food Web Effects

Two of the projects summarized so far investigated direct effects of hydrodynamical processes on recruitment variability. Such processes can also influence larval survival indirectly through the food web (Sutcliffe 1972, 1973; Cushing 1975, 1982; Dickie and Trites 1983; Legendre and Demers 1985). In coastal and estuarine environments frontal zones are generally characterized by high primary production rates and large phytoplankton biomasses (Kahru et. al. 1984; Richardson 1985; Richardson et. al. 1986). This promotes the reproduction and growth of herbivorous zooplankton (Kiorboe and Johansen 1986) which are preyed upon by carnivorous organisms such as fish larvae. Such conditions should promote larval fish growth and survival. High abundance of larval fish can therefore be expected in frontal zones either as a result of adapted reproduction strategies promoting transport of larvae into these areas or simply because larvae growing in such areas survive better.

Project #6 was designed to describe the vertical and cross-frontal distribution of phytoplankton, zooplankton and fish larvae in a frontal area and to evaluate specific mechanisms possibly responsible for transferring primary production products to fish larvae. The study was conducted in the frontal zone defined by the Gaspé current and the Anticosti gyre in the northwestern Gulf of St. Lawrence (Figure 1). Stations were sampled along a transect across the front with various plankton nets, including a multiple opening and closing 1-meter ichthyoplankton net (BIONESS), to determine the horizontal and vertical distributions of various plankton groups. Preliminary results indicate that large diatoms and dinoflagellates, which favour herbivorous production and reproduction, as well as copepod eggs and nauplii, the food of larval fish, are concentrated on the stratified side of the front. Small capelin larvae were also much more abundant there, whereas larger capelin and redfish larvae were more widely distributed across the study area. This suggests that the occupation of an exceptionally rich area is less critical for the survival of more robust larvae. While frontal zones might be essential for a massive survival of young larvae, they could play a much lesser role in the ecology of older ones.

Physical processes are expected to have a dramatic influence on food web dynamics in northern areas where ice covers the surface of the sea for extended periods of time. A preliminary sampling program was carried out in the spring of 1986 (Project #7) to evaluate the possible relationship between the timing of ice break and the survival of larval fish in northern Quebec rivers. Several species of anadromous (*Coregonus clupeaformis*, *C. artedii*, *Lota lota*) and marine (*Boreogadus saida*, *Gadus ogac*) fish larvae were previously reported to hatch just prior to, or at the time of ice break-up in James and Hudson Bay. Anadromous fish larvae were shown to be flushed from the rivers into Hudson Bay during the period of increased river flow at ice-break, and could thus benefit from the increased zooplankton biomass associated with the marine epontic flora.

It was hypothesized that the persistence of the ice cover in the Bay after the expulsion of anadromous fish larvae would be favourable to their survival. The absence of wind-induced vertical mixing would allow the maintenance of the integrity of the freshwater plume under the ice. Anadromous fish larvae would then be physically isolated from marine predators and be allowed a more gradual osmotic adaptation to marine conditions, while benefitting from high food supply.

The organisms occurring in the drift were sampled before, during and after the ice break in the Great Whale River. After the ice break, the plume of the river was sampled along a transect in Hudson Bay and compared with the organisms occurring in the marine layer located underneath it. In the absence of wind, the waters in the bay remained heavily stratified and exhibited distinct animal assemblages and physical and chemical properties. Anadromous fish larvae (mostly Lota lota) were restricted to the freshwater upper layer, while marine fish larvae (mostly Boreogadus saida) and predators were found in the underlying marine waters.

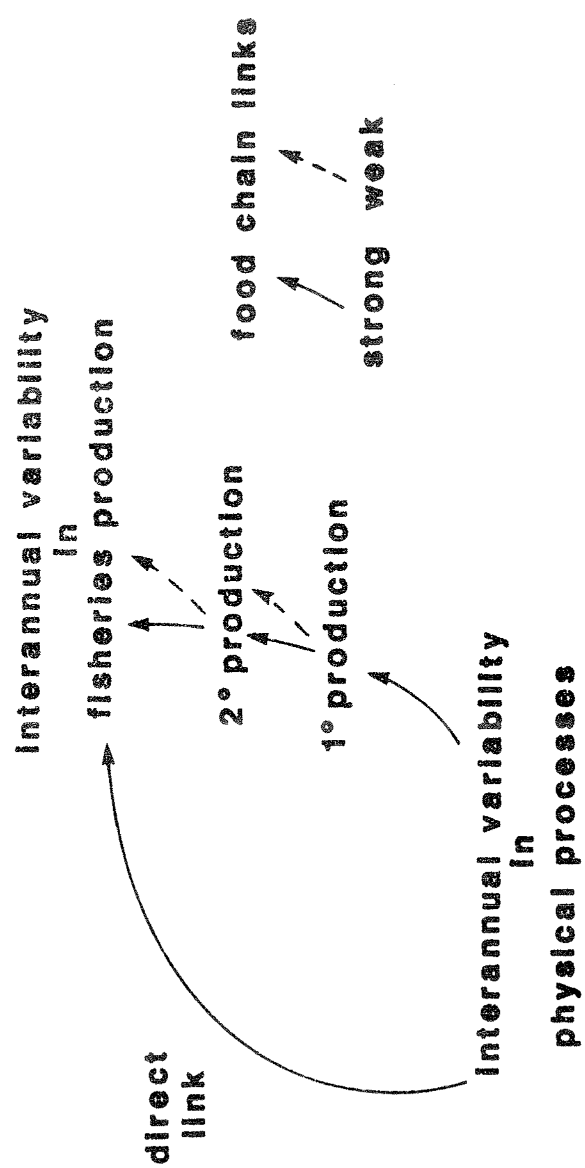
More elaborate work will be initiated in the spring of 1988 (Project #8). Current meters and CTD profiles will be used to identify circulation patterns and describe the evolution of the freshwater plume from winter to spring conditions. The food web from epontic algae to fish larvae will be monitored to determine the food resource available to the larvae. Larval growth and condition will be followed to identify favorable survival conditions.

Food Web Dynamics

A central theme in present-day studies of marine plankton dynamics is the efficiency and variability of linkages in the cycles of marine biological production. Productivity at each step in the marine pelagic food chain has been observed to vary at a number of spatio-temporal scales. How this variability at one tropic level relates to fluctuations in another is still not understood. A key question is how 3- to 4-fold variability in annual primary production is magnified to result in 10- to 100-fold variability in fish or benthos recruitment.

Project #9 concerns linkages in the marine food web of the lower Estuary and the northwestern Gulf of St. Lawrence. It focuses on the role that planktonic copepods may play in the transfer of materials and energy from phytoplankton to larval fish and invertebrates. Two alternative concepts about the interconnection between primary producers, planktonic copepods and invertebrate and fish larvae are proposed. They can be termed the "weak filter" and "strong filter" hypotheses (Figure 6), referring to the extent to which the dynamics of zooplankton populations and the feeding behaviour of the larvae filter out the effects of fluctuations in primary productivity on recruitment (Runge 1988).

The weak-filter hypothesis states that there is a significant link between interannual variability in the magnitude and pattern of primary production and fish recruitment. This would be the case in ecosystems where Calanus finmarchicus dominate the zooplankton community since Calanus egg production rates are strongly related to variability in phytoplankton standing


Interannual variability
in
fisheries production
2° production
1° production
Interannual variability
in
physical processes
direct
link
food chain links
strong
weak

stock (Runge 1985a; 1985b). In such systems, the strength of a fish year-class may be determined by the availability of planktonic food at the time of yolk-sac resorption as proposed by Hjort (1914) and Cushing (1969).

The alternative, the strong-filter hypothesis, proposes that in systems where zooplankters other than Calanus dominate, the impact of fluctuations in primary productivity is filtered by the dynamics of the zooplankton community and by the feeding behaviour of the larvae. There are several variations of this hypothesis, but the essential point is that food may not limit the first feeding larvae because they can eat alternative prey if Calanus eggs and nauplii are not available. Alternative food sources may include tintinnids and nauplii of smaller copepod species (Last 1980). The productivity of these prey populations is much less affected by phytoplankton variability (McLaren 1978; Runge 1984; Ohman 1985; Frost 1985). Consequently, the link between fluctuations in phytoplankton production and prey availability to larval fish and invertebrates is damped. Project #9 will begin to examine the importance of Calanus finmarchicus and the validity of the "weak filter/strong link" hypothesis for redfish (Sebastes sp.) larvae in the northwestern Gulf of St. Lawrence in the spring of 1988.

Project #9 proposes that an abundant supply of prey items of the right size can be critical to the success of a fish or invertebrate year-class. Much of the emphasis of recruitment research has been and still is focused on quantitative characteristics of various larval fish and invertebrate food resources. Much less effort is devoted to the quality of those prey items available to feeding larvae. Project #10 is addressing one aspect of this problem by investigating the sensitivity of marine fish and invertebrate larvae to the toxins produced by the dinoflagellate Protogonyaulax tamarensis.

The frequency and distribution of toxic algal blooms have been increasing in various parts of the world since the mid-seventies (Anderson et. al. 1985). The paralytic toxins responsible for the catastrophic consequences of these blooms have been studied mainly in relation to human food poisoning. However, it is well established from research work conducted in Europe, Japan and North America that these toxins can be lethal for commercially important fish species intoxicated either directly by feeding on the toxic organisms or indirectly through a contaminated food chain (Adams et. al. 1968; White 1980; Mortensen 1985). Recent work indicates that the survival of larval fish can also be compromised by these toxins (White et. al. 1987).

P. tamarensis is the dominant toxic organism in the St. Lawrence system and is abundant in several coastal areas (Therriault et. al. 1986). Such areas are often colonized by early life history stages of marine fish and invertebrates which use them as nursery grounds. In order to verify that the survival of marine fish larvae is reduced in presence of P. tamarensis toxins, herring and capelin larvae were exposed to various concentrations of the toxic dinoflagellate in laboratory experiments. Larval mortality was between 60 and 100% higher in the treatments than in non-toxic controls. Further experiments are being conducted but these initial results suggest that recruitment of various species could be affected by annual or longer-term variations in the distribution and timing of toxic blooms. These effects could become catastrophic for several coastal regions of the world in general, and of Eastern

Canada in particular, if the current increasing trends in time, space and frequency are maintained. Field work will be initiated in the summer of 1988 to investigate the relationships between the dynamics of toxic dinoflagellate blooms and the ecology of larval fish and invertebrates. Particular attention will be devoted to the transmission of dinoflagellate toxins through the planktonic food web.

While it is widely hypothesized that the success of year-classes is influenced by the quantity and quality of food available to the early life history stages of fish and invertebrates, experimental studies have reached the consensus that both starvation and predation are the proximate factors responsible for the mortality rates observed during larval stages (Rothschild and Rooth 1982). Project #11 was devised to test the general hypothesis that the survival of young fishes is a function, at least partially, of the speed at which they grow through those size intervals when they are most susceptible to predation (Schoener 1971). This implies that young fishes growing at various rates will also exhibit various survival rates.

To test this prediction, relationships between the age of young fishes and the size of reference growth structures will be analyzed (Healey 1982). Atlantic mackerel (Scomber scombrus) is an ideal species for such studies. In the southern Gulf of St. Lawrence young mackerel grow to about 180 mm during their first five months of life and daily increments are visible on their otoliths (Dr. B. Côté, INRS, Rimouski, Quebec, Canada, unpubl. data). Young mackerel will be sampled throughout the summer of 1988 and relationships between age and the size of a reference area on the otoliths will be investigated. This represents the first step in the assessment of the influence of mortality during the early life history on recruitment variability in mackerel.

Survival of young fishes appears to revolve around the issue of "eating or being eaten . . .". It is, therefore, generally assumed that larvae benefit largely from feeding and that they should always attempt to eat at maximal rates since fast growth would also reduce their overall vulnerability to predators. Gut contents are customarily used as an index of feeding performance, with low levels implying food limitation, sub-normal growth and higher risk of starvation and/or predation. Using this scenario, it has been argued that larval fish are food limited, that the key to survival is to encounter patches of dense prey organisms (see Houde 1978), and that these patches are formed mainly through physical processes. It then follows that physical phenomena are responsible for the inter-annual variability of survival in populations of marine larval fishes.

This argument is based on a simplistic view of feeding and it ignores the fact that feeding activities also increase the risk of being captured by predators (Giguère and Northcote 1987). This is a non-energetic cost of feeding which must be balanced against its energy benefits (Dill 1986). Unfortunately, formal solutions have not been derived for the lack of a proper common currency.

A unified feeding model has been derived for Project #12 using transparent larvae as model organisms for which volume of ingested food brings together energetic and non-energetic costs of feeding into a unique framework. This formal model allows one to answer a fundamental question of optimal foraging: "How much to feed?". According to this model, the feeding rate which maximizes the survivorship of larval fishes is much less than the physiological maximum. Laboratory and field evidence obtained to date support this view. The amount of food present in the gut is, therefore, not necessarily a good indicator of survival since it appears that larval fish "trade-off" predation risk against energetic benefits and growth. Gut content data should be interpreted with great caution. The role played by food patchiness in determining patterns of survivorship in marine fish larvae should be re-evaluated.

Population Studies

As exemplified in the present report, most recruitment studies concentrate on the ecology and dynamics of young fish and invertebrates. This is mandatory to evaluate the importance of trophodynamic processes (predation and starvation) operating during the early life history as regulatory mechanisms of year-class strength. For instance, it is sufficient to test predictions derived from the hypothesis rooted in the pioneering work of Hjort (1914) and elegantly formalized by Cushing (1969). The "Match-Mismatch Hypothesis" proposed that variations in recruitment are determined by interannual variations in the degree of spatio-temporal coincidence between larvae and their food resource. The timing and location of spawning would, therefore, be selected as to optimize this spatio-temporal coincidence.

Studies of both the adult and larval phases are, however, necessary to evaluate a new hypothesis introduced by Iles and Sinclair (1982) and fully developed by Sinclair (1988). The "Member/Vagrant" hypothesis challenges the importance of trophic interactions during early life history as recruitment regulatory mechanisms. It states that temporal variability in abundance of marine species with a complex life cycle is a function of the inter-generational losses of individuals (vagrancy and mortality) from the appropriate distributional area that will ensure membership within a given population. For species with a planktonic stage oceanographic processes may dominate in generating this variability in losses (Sinclair et Iles 1987). This implies that absolute abundance could be largely independent of reproduction, growth, or other biological parameters.

This might be the case, for instance, for Atlantic herring (*Clupea harengus*) where the number of genetically distinct populations would be determined by the number of distinct, geographically stable larval retention areas (Iles and Sinclair 1982). The hydrodynamic processes specific to a retention area would dictate the mean size as well as the year-to-year variability in recruitment of its associated population. The genetic isolation between populations would result from homing of mature individuals back to their native retention area to reproduce. This homing instinct would be focused on the hydrographic features of the retention area.

Project #13 was designed to test various aspects of the "Member/Vagrant" hypothesis and evaluate its merits relative to those of the "Match-Mismatch" hypothesis. It concentrates on the Ile Verte herring population of the St. Lawrence Estuary which presents the following advantages: it is relatively isolated from adjacent populations and easily accessible which simplifies sampling and decreases the uncertainty as to the origin of the individuals sampled, especially for early life history stages and mature fish. It is commercially exploited which facilitates data collection on the adults. Finally, it has been the object of several population dynamics studies and is often used in the work of Sinclair and collaborators as evidence to support their theory.

According to the "Match-Mismatch" hypothesis, the spawning of a marine population should occur at a time and location such as to maximize the chance of coincidence between first-feeding larvae and their food (Cushing 1969). The "Member/Vagrant" hypothesis predicts that spawning will take place within a retention area defined by hydrodynamic processes (Iles and Sinclair 1982). Herring from a genetically isolated population will spawn at a moment in the season such as to ensure that the larvae will have enough time to grow and reach metamorphosis either during the same or at the onset of the following productive period of the year, for spring and fall spawners respectively (Sinclair and Tremblay 1984). Because the St. Lawrence Estuary is a tidally energetic sea of low productivity (Therriault and Levasseur 1985) it is predicted that spawning will occur only in the spring (Sinclair et Tremblay 1984). The poor growing conditions in the Estuary would result in the larvae methamorphosing at a smaller size which would explain why the adults of this population are particularly small at age (pygmy) (Côté et. al. 1980). That this population retains its pygmy characteristics is seen as a proof of homing in herring, an essential element of Iles and Sinclair's stock structure hypothesis (Sinclair and Iles 1985).

To test these various predictions ichthyoplankton surveys were conducted in 1985 and 1986. Spawning herring were sampled in both years for various biological characters and morphometric, meristic and biochemical analyses.

The results available to date indicate that spawning occurred in the spring and fall of both years. In 1985, spring and fall larvae emerged within the limits of the predicted retention area (Iles and Sinclair 1982). The spring cohort appeared in the retention area two weeks prior to the maximum concentration of particles in the size range of suitable prey organisms. The fall cohort emerged after the fall peak in particle concentration and its abundance in the samples decreased relatively faster than that of the spring larvae. Analyses of the data collected on adult fish revealed that pygmy herring did not constitute more than 50% of the spawning stock and that genetic isolation from adjacent populations was much less than expected. In the light of these incomplete results, it now appears as though a hierarchy of factors is controlling herring spawning in the St. Lawrence Estuary. Spawning location would be determined by the location of hydrodynamical processes delineating a retention area as predicted by Iles and Sinclair (1982). However, timing and possibly interannual variability in year-class success could depend on trophic processes within the retention area. Homing certainly does not appear as strict as proposed by Iles and Sinclair (1982) and tidally energetic seas can support more than one herring population.

Special Projects

CIRESOL: A Canada/France Collaborative Effort on Recruitment

France recently launched a National Recruitment Program with the general objective of better understanding the factors determining recruitment variability in marine organisms. One of the goals of this multidisciplinary program focusses on the early life history of the flatfish *Solea vulgaris*. A specific objective of CIRESOL (Circulation et Recrutement de la Sole) is to assess the respective role of transport and mortality in the decrease of larval sole abundance with age. Another one is to describe the mechanisms whereby sole larvae are transported from the open sea spawning grounds to the coastal nursery areas.

In a concerted effort to address the transport problem, French and Canadian scientists conducted a joint research cruise in the Bay of Biscay in April 1987 (Project #14). The vertical distribution of the zooplankters and fish larvae and the structure of the water column were investigated along three transects and during a 72-hour fixed station with a BIONESS. The plankton samples are currently being sorted and results are not yet available.

An Inter-regional Joint Project

Project #15 is a joint project with the DFO-Gulf region designed to acquire a better understanding of the processes involved in the self-sustainment of *Crassostrea virginica* populations, a dominant oyster species in Caraquet Bay and adjacent areas of the western Gulf of St. Lawrence. Another objective is to examine the dispersal and settlement mechanisms of oyster spat. The following questions will be addressed: how does the circulation pattern influence larval distribution? What are the possible larval retention mechanisms in the bay? Since it is hypothesized that most larvae are swept out of the bay by wind action and tidal exchange, how does the circulation pattern influence the observed differences in growth rates between areas at the north and south sides of the bay? Is this strictly a function of algal food supply?

This project is expected to commence in July and August 1988 depending on the timing of spawning in natural beds. Current meters, drogues, tide gauges and CTD's will be used to study baywide water movements and transport capabilities over a 3-5 week period at the time of maximal larval abundance. Plankton surveys will be conducted every 2-3 days over the course of the project to describe the horizontal distribution of the larvae and monitor various biotic and abiotic variables. Spat collectors will be used as well.

Symposium on Food Quality

Technical limitations constitute the principal reason why food quality is only rarely investigated in planktonic food webs. New technologies recently introduced in biological oceanography such as High Pressure Liquid Chromatography and Flow Cytometry open up new research avenues. An international symposium aimed at identifying and evaluating these new possibilities as well as addressing the more general problem of evaluating the quality of planktonic food organisms is in preparation at the Maurice Lamontagne Institute (Project #16). Its general objectives would be to:

1. evaluate which parameters are most effective at quantifying the nutritive value of primary producers;

2. determine the consequences of feeding on certain types of particles; possible effects of taxonomical differences, physiological states, etc.;

3. seek a better interpretation of the relations between food abundance and larval fish and invertebrate condition factors.

This symposium is now planned for the summer of 1989.

Conclusion

The 16 projects summarized in this review cover the entire range of topics found in modern recruitment research. Most of them are multidisciplinary and several involve collaboration between scientists from two or even all three research branches of DFO-Quebec (biological sciences, chemical and physical sciences, and Canadian Hydrographic Service). Several scientists from various Quebec universities are often involved as well. This demonstrates that recruitment research constitutes a major investment in the region. It also represents an impressive example of research integration within the youngest Fisheries and Oceans region in the country.

Acknowledgements

We are grateful to Denis D'Amours, Louis Giguère, Christiane Hudon and Patrick Ouellet for providing us with special reports on their research. They were very useful in preparing this summary. We, however, assume full responsibility for the way these, as well as any other information, were incorporated in this document.

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ANNEXE I - List of Participants for Each Project

1. The COHJAC project: Circulation, oceanography and hydrography of Jacques Cartier Passage. D. Lefaivre (D), V. Koutitonsky (G), P. Ouellet (A), D. Hains (E), A. Condal (I).

2. Effects of climate and hydrography on the recruitment of Northern Gulf of St. Lawrence lobster. C. Hudon (B), A. Lavoie (K), J.M. Dubois (K), G. Vigeant (L).

3. Distribution of lobster larvae around the Magdalen Islands. C. Hudon (B), P. Fradette (M), P. Legendre (N).

4. Lobster recruitment around the Magdalen Islands: influence of climate and hydrography. Y. Simard (A), D. Gauthier (A), E. Bourget (J).

5. Distribution and growth of rock crab (Cancer irroratus) larvae in Pleasant Bay, Magdalen Islands. C. Hudon (B), B. Ste-Marie (A), L. Gendron (A).

6. Planktonic trophic relationships in a cross-frontal area of the Gaspé current: production and larval distribution. L. Fortier (J), J.C. Therriault (C), M. Levasseur (C).

7. Relationship between the timing of ice break and the survival of larval fish in southeastern Hudson Bay. C. Hudon (B).

8. Recruitment of anadromous fish in Canadian Arctic waters: regulation by underice hydrodynamics and microalgal production. L. Fortier (J), L. Legendre (J), R.G. Ingram (O), J.A. Gagné (A), J.C. Therriault (C), S. Demers (C).

9. Role of copepod dynamics as a filter of trophic variability. J.A. Runge (C), Y. Delafontaine (C), L. Giguère (C).

10. Recruitment of commercial species in the St. Lawrence: sensitivity of the larvae to Protogonyaulax tamarensis toxicity. L. Fortier (J), J.A. Gagné (A), A. Cembella (C), A. Cardinal (J).

11. Selective mortality in juvenile Atlantic mackerel (Scomber scombrus). D. D'Amours (A).

12. Optimal feeding rates in transparent zooplankton. L. Giguère (C), R. Dunbrack (P).

13. Population dynamics and recruitment of the St. Lawrence Estuary herring population. J.A. Gagné (A), L. Fortier (J), Y. Gratton (H).

14. Hydrodynamics and distribution of larval sole (Solea vulgaris in the Bay of Biscay, France. J.A. Gagné (A), L. Fortier (J), C. Koutsikopoulos (Q), A. Herbland (Q).

15. Study of oyster larval distribution and retention in Caraquet Bay and adjacent areas of the western Gulf of St. Lawrence. D. Booth (D), T.W. Sephton (F).

16. Symposium on the quality of primary producers as a food source for zooplankters. J.C. Therriault (C), S. Demers (C).

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ANNEXE 2

The following list represents recruitment-oriented research projects currently conducted by DFO scientists from the Gulf Region (Department of Fisheries and Oceans, P.O. Box 5030, Moncton, New Brunswick, E1C 9B6). These projects are not included in the review presented here.

1. Recruitment of salmonids in western Newfoundland. M. Chadwick.
2. Herring spawning bed surveys in the southern Gulf of St. Lawrence. S. Messieh.
3. Distribution of juvenile herring in the southern Gulf of St. Lawrence. D. Cairns, M. Chadwick.
4. Production of juvenile salmon in the southern Gulf of St. Lawrence. R. Randall.
5. Production of juvenile gaspereau in the southern Gulf of St. Lawrence. R. Alexander.
6. Distribution of juvenile cod in the southern Gulf of St. Lawrence. G. Chouinard.
7. Feeding ecology of hake in the southern Gulf of St. Lawrence. D. Clay.

A list of relevant, recent publications, is given below.

Chadwick, E.M.P. 1987. Causes of variable recruitment in a small Atlantic salmon stock. In Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Scoiety Symposium 1: 390-401.

Chadwick, E.M.P. 1987. Relationship between Atlantic salmon smolts and adults in Canadian rivers. P. 301-324. In Mills, D. and D. Piggins (Eds.) Third International Atlantic Salmon Symposium. Timber Press, Oregon. 587 p.

Chadwick, E.M.P., R.R. Claytor, C.E. Léger and R.L. Saunders. 1987. Inverse correlation between ovarian development of Atlantic salmon (*Salmo salar*) smolts and sea age. Can. J. Fish. Aquat. Sci. 4: 1320-1325.

Chadwick, E.M.P. and R.G. Randall. 1986. A stock-recruitment relationship for Atlantic salmon in the Miramichi River, New Brunswick. North American J. Fish. Mgmt. 6(2): 200-203.

Chadwick, E.M.P., R.G. Randall and C. Léger. 1986. Ovarian development of Atlantic salmon (*Salmon salar*) smolts and age at first maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89: 15-23.

Messieh, S.N. 1987. Some characteristics of Atlantic herring (*Clupea harengus*) spawning in the southern Gulf of St. Lawrence. NAFO Sci. Coun. Studies 11: 53-61.

Messieh, S.N., D.S. Moore and P. Rubec. 1987. Estimation of age and growth of larval Atlantic herring as inferred from examination of daily growth increments of otoliths. In The Age and Growth of Fish, Edited by Robert C. Summerfelt and Gordon E. Hall. 1987. The Iowa State University Press, Ames, Iowa 50010. p. 433-442.

Randall, R.G. and E.M.P. Chadwick. 1986. Density as a factor affecting the production of juvenile Atlantic Salmon (*Salmo salar*) in the Miramichi and Restigouche Rivers, New Brunswick. Polskie Archivum Hydrobiologii 33: 392-409.

Randall, R.G., M.C. Healey and J. Brian Dempson. 1987. Variability in length of freshwater residence of salmon, trout and char. Amer. Fish. Soc. Symp. 1: 27-41.

V REVIEWS OF DEPARTMENT OF FISHERIES AND OCEANS PROGRAMS ON RECRUITMENT

D. RECRUITMENT STUDIES - CENTRAL AND ARCTIC REGION

by

J. Craig
Central and Arctic Region

A number of Canadian freshwater fish populations, in particular percids, such as walleye and yellow perch, and coregonids such as whitefish and cisco, provide important commercial fisheries even if this importance is somewhat local. Sport fisheries have higher returns in economic and social terms that commercial fisheries. Other fisheries are vital as domestic or subsistence fisheries. Several detailed studies on population dynamics have been performed as a result of the necessity to manage these freshwater fish stocks. These studies have resulted in the production of predictive models such as the morphoedaphic index (Ryder 1965) relating fish production to total dissolved solids and mean depth of lake, and fish yield prediction from total phoshorus (Hanson and Leggett 1982) and from mean annual water temperature (Schlesinger and Regier 1983). Models to predict year class strengths from density independent (in particular temperature and volume of spring run off) and density dependent (number or biomass of adult spawners and predators) have often explained a high proportion of the variability involved (Craig and Kipling 1983; Lysack 1986; Shuter and Koonce 1977). None of these models have defined the direct causative reasons for mortality on the potential recruits to a stock.

In most cases the highest mortality rates take place during the early, larval stages and detailed studies on factors controlling this mortality are being carried out at the Freshwater Institute (see Mathias below). Man induced perturbations such as those causing eutrophication, acidification and pollution (by organics and metals) and their effects on recruitment are being investigated at the Experimental Lakes Area (see Mills below), Habitat changes, such as the building of reservoirs, on fish recruitment have also been studied (see Bodaly below). The limits of response of fish populations to changes in environmental conditions can be measured by comparing fish which are severely perturbed by over-exploitation to unexploited populations. The allocation of energy resources to reproduction and thus potential recruitment can be observed in terms of growth, age of maturity, fecundity and longevity (see Craig below). Over-exploitation can also lead to species shifts in lake communites and this is under investigation in the Dauphin Lake Project (see Flannagan et al. below).

Many freshwater systems in North America are stocked with indigenous and exotic fish. In Canada there has never been a quantitative measure of the success of this stocking in terms of recruitment to the commercial catch. This is at present being done in the Dauphin Lake Project by stocking the lake with genetically distinct walleye larvae.

Freshwater lakes, in particular in the undisturbed regions of Northern Canada, present opportunities for the study of the relationships betwen stock and recruitment that are seldom available elsewhere (see Johnson below). This is particularly the case with certain Arctic charr, Salvelinus alpinus, populations that occur as the single fish species present. This has the advantage that all population structure that may develop can be ascribed to intraspecific interactions.

The most significant fact to emerge from examination of these undisturbed stocks, and this applies in both single species stocks and multi species stocks, is that juvenile, or pre-recruitment stock is virtually absent in even the most meticulously taken samples. This is evidently a case of suppression of the juveniles by the adults, since continued exploitation does increase the number of juveniles in the sample. This increase may be effected over the course of a single year, if the fishing is extremely heavy, or over the course of a number of years if the fishing is light. Thus there are evidently some juveniles present even though they do not appear in the samples. There is therefore some inverse relationship between stock and juveniles. However these juveniles do not necessarily become recruits. It is frequently observed that large "waves" of pre-recruits appear in one or two years and then disappear before attaining actual recruitment to the "adult" or "establishment" mode.

Long-term, detailed studies on population changes at the Chitty Lakes Station have shown that there is apparently little direct relationship between stock and recruitment (Figs 1 and 2). Baptiste Lake shows the results of continuous observation on an unexploited lake, Drygeese Lake was a) unexploited 1971-73, b) heavily exploited 1973-74 and c) allowed to recover without exploitation 1974-85. Figure 3 shows the effect of exploitation on the sucker population of Heming Lake over a long period of time a) in the pristine state, b) under increasingly heavy exploitation and c) during a period of recovery. Evidently this population is extremely responsive to changes in population density as modulated by fishing pressures. When fishing ceases the population quickly returns to a bimodal size distribution.

Investigations of Arctic marine fish are still at a preliminary stage and are mainly concerned with stock identification. Stock and recruitment studies are planned for the future.

Projects involving recruitment studies that are at present ongoing in the Central and Arctic Region

Name of Scientist: Rodaly, A. Species: Whitefish, Coregonus clupeaformis. Area of work: South Indian Lake, Manitoba. Start of project: 1976. Type of project: A study of the commercial whitefish fishery with respect to the development of a dam at South Indian Lake and the diversion of the Churchill River.

Name of Scientist: Craig, J.F. Species: Walleye, Stizostedion vitreum. Area of work: Dauphin Lake, Ungor Lake and Lake Winnipegosis, Manitoba. Date of start of project: 1984. Type of project: A study of growth, fecundity, age or maturity, longevity and enery allocation between somatic growth and reproductive effort in exploited and unexploited populations.

Name of Scientists: Flannagan, J.F., J.F., Craig, W.D. Franzin and J.A. Mathias. Species: Walleye and other lake species. Area of work: Dauphin Lake, Manitoba. Date of start of project: 1982. Type of project; A study of methods of

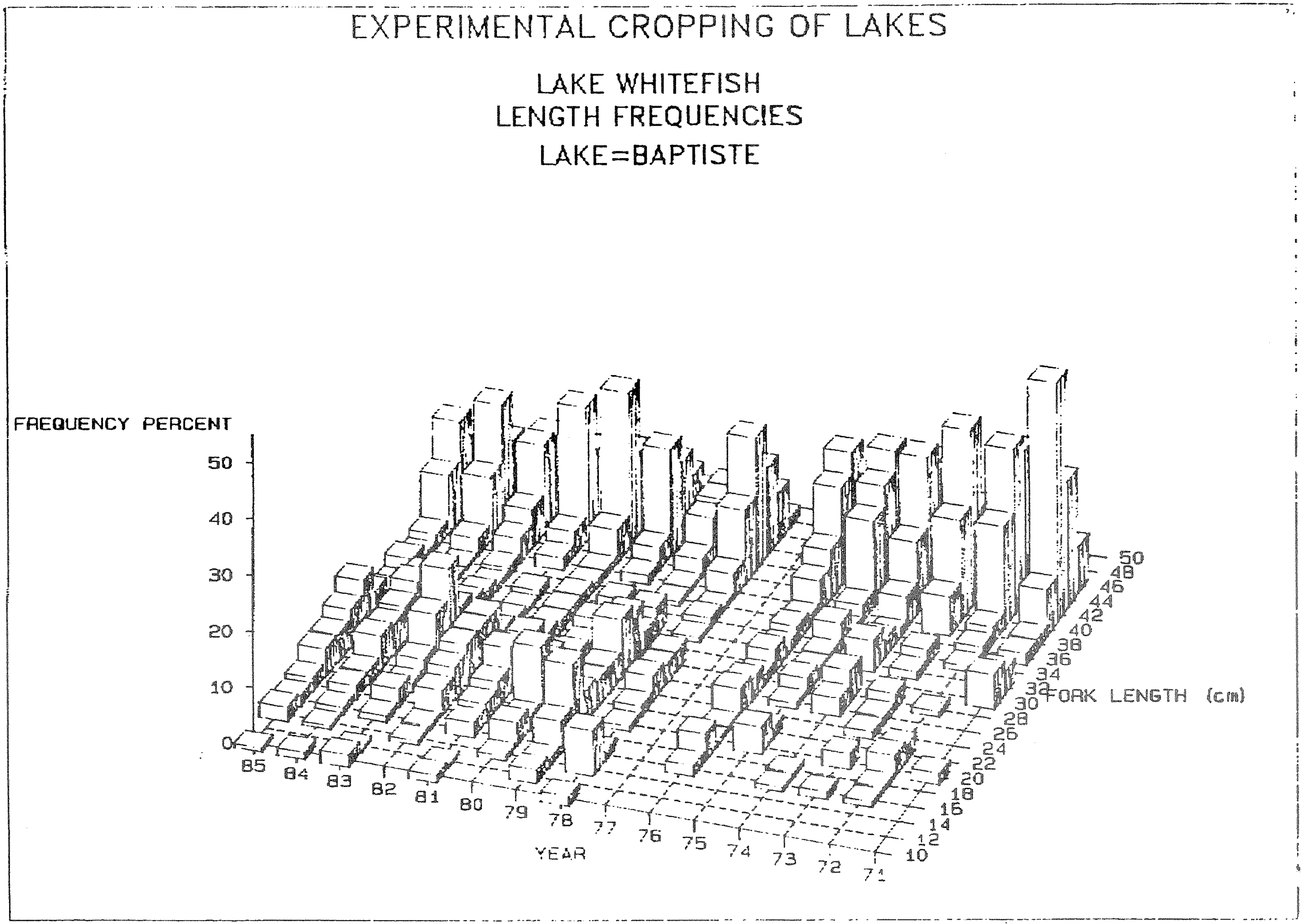
EXPERIMENTAL CROPPING OF LAKES
LAKE WHITEFISH
LENGTH FREQUENCIES
LAKE=BAPTISTE
FREQUENCY PERCENT
0
10
20
30
40
50
YEAR
85 84 83 82 81 80 79 78 77 76 75 74 73 72 71
FORK LENGTH (cm)
10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50

FIGURE 1