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Summary Report of the Special Session on Recruitment Studies

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Introduction

The Special Session on "Recent Advances in Understanding Recruitment in Marine Fisheries of the Northwest Atlantic, with Particular Emphasis on Georges Bank Herring and Flemish Cap Cod and Redfish Stocks", convened by the first author with the assistance of the second, was held at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, during 3-5 September 1986. Twenty-six papers and two oral reports were presented. The first day was devoted chiefly to papers dealing with Atlantic herring (*Clupea harengus*) recruitment on Georges Bank and in adjacent waters, and the second day focused on the results of recruitment-related research on the cod (*Gadus morhua*) and redfish (*Sebastes* sp.) stocks of the Flemish Cap region. On the third day, papers were presented on general recruitment studies, which were not directly related to those of the two major international research projects. Discussion periods followed the presentation of papers on each of the 3 days.

The papers represented a wide range of topics which covered the entire reproductive life cycles of herring, cod and redfish in the study areas, with particular emphasis on empirical correlations between recruitment and various physical and biological factors, including spawning stock size, and processes affecting abundance, distribution, dispersal, survival and growth of egg and larval stages. Knowledge of these processes was reviewed in relation to the principal historical and current hypotheses about timing and mechanisms which control year-class strength. Also, the effectiveness of research approaches, represented by the Georges Bank and Flemish Cap programs, was considered in relation to their objectives and to achievements in the understanding and predictability of recruitment, and ways of improving research strategy were discussed at length.

Georges Bank

Synopsis of research on herring recruitment

A review paper by Grosslein (1987) traced the development of the International Commission for the Northwest Atlantic Fisheries (ICNAF) larval herring program and subsequent studies relevant to herring recruitment and provided a synopsis of knowledge to date on the recruitment process in herring. The ICNAF larval herring surveys began in 1971 and were initially designed to delimit the principal spawning grounds of the various stocks of the Gulf of Maine region, to provide fishery-independent estimates of the relative sizes of the stocks, and to document the dispersal of larvae during their first several months as a means of obtaining information on possible interrelationships between the populations of adult and juvenile herring. The objectives were expanded in 1974 to investigate the factors which control variability in year-class success, particularly on Georges Bank, and this led to a much broader research program, which ultimately contributed to a more comprehensive description of the ecology of herring larvae and associated ichthyoplankton and zooplankton on Georges Bank as well as the primary production and hydrography of the region.

The overview (Grosslein, 1987) demonstrated that the ICNAF larval herring program had succeeded in providing estimates of spawning biomass, larval dispersal and larval mortality for a series of years prior to the disappearance of the population from Georges Bank. A westerly shift in spawning from Georges Bank to Nantucket Shoals was observed, coincidental with the shift in fishing activity after the disappearance of herring from the eastern part of the bank. A review of the herring stock structure in the entire Gulf of Maine region confirmed that the stocks are discrete at the time of spawning (and for the first several months of larval

life) but that juveniles and adults intermix at other times of the year.

During the 8 years of the ICNAF program (1971–78), timing and location of spawning on Georges Bank and Nantucket Shoals were documented, larval growth, feeding and mortality were described, and egg and larval productions were calculated for each year. Although accurate estimates of confidence limits were not possible for egg and larval abundance and subsequent year-class size, some interesting patterns emerged. Initial larval production was correlated with spawning stock size, but larval abundance (to 6 months of age) was not correlated with recruitment, implying that year-class strength was not set before the late larval stage. Knowledge of the late larval and postmetamorphosis stages from the ICNAF larval herring surveys was extremely limited. However, other evidence pointed to determination of year-class size at least by the end of the first year of life (age 1) but probably earlier near the time of metamorphosis.

Mortality in postlarval and juvenile stages (late larvae to age 2) appeared to be roughly comparable in magnitude to that of the first 6 months (eggs to late larvae), which indicates that both periods may be of equal importance in controlling year-class size. In any case, neither the classical "critical period" hypothesis nor the "match-mismatch" hypothesis appears to explain recruitment variability in Georges Bank herring. It was noted that overwinter mortality of larvae may exert significant control over recruitment variability, and there was some evidence during several winter seasons that this mortality was inversely correlated with temperature and larval abundance. However, the collapse of the herring stock on Georges Bank in 1978 interrupted the data series, and the significance of overwinter mortality could not be confirmed.

Other contributions

In addition to the overview paper on the first day, six other contributions were relevant to recruitment of herring on Georges Bank and in adjacent areas.

Smith and Johnson (MS 1986) reviewed the historical literature and the results of MARMAP (Marine Monitoring, Assessment and Prediction) surveys which have monitored larval fish production since 1977. The historical review indicated that herring, although present, was probably not a dominant species on Georges Bank during the first half of the 20th century. The MARMAP data indicated virtual extinction of spawners on Georges Bank (absence of larvae) during the 1978–85 spawning seasons, although limited spawning still occurs on Nantucket Shoals.

Bolz and Lough (MS 1986) described three zooplankton faunal zones on Georges Bank and related them to different water masses of the region. A seasonal cycle and the interannual variability of these zones were linked to ichthyoplankton faunal zones (Bolz and Lough, 1984), which in turn appeared to be linked to retention of shelf larvae on the bank.

In the last year of the ICNAF larval herring program (1978), a multinational larval herring patch study was planned for Georges Bank. Although no herring were found, a dense patch of chaetognaths served as a model for larval herring (Lough and Trites, MS 1986). The analysis indicated that the mean drift and dispersion of the patch was inconsistent with the mean flow, but the observed dispersal was considered to be plausible if vertical structure in the water column (both physical and biological) is taken into account.

Campbell and Graham (MS 1986) described a model of recruitment to the herring fishery along the Maine coast. It took account of spawning stock size, overwintering temperature, and exchange rates of herring larvae from east to west and between coastal waters and estuaries. Further development of the model and its validation were noted as being in progress.

In a study of recruitment to the Gulf of St. Lawrence herring stocks, Messieh (MS 1986) noted the predation of mackerel (*Scomber scombrus*) on herring eggs and the unusual mortality in patches of herring eggs which were deposited in extremely thick layers. This unusual spawning behavior may have been triggered by oscillations in temperature due to storms.

An exploratory analysis of satellite imagery was undertaken to develop indices of the exchange of shelf water and slope water in the Northwest Atlantic (Myers and Drinkwater, MS 1986) insofar as they affect recruitment. Hypotheses which were developed from the exploratory analysis will be tested on independent data.

Critique of Georges Bank larval herring program

Although the initial objectives of the ICNAF larval herring program on Georges Bank were largely met (except for the limitations imposed by the untimely collapse of the stock), there were several constraints on the program which prevented rigorous testing of hypotheses about factors controlling variability in recruitment success. In particular, postlarval and early juvenile stages were not adequately sampled, thereby precluding any evaluation of the distribution and relative abundance and mortality profiles of those stages for comparison with the larval stages. Also, the demersal egg stage (with unknown mortality due to predation) and the very uncertain estimates of spawning stock size prevented accurate estimation of egg production for each cohort. Finally, it was noted that lack

of adequate resources led to a slow rate of processing zooplankton samples, which resulted in prolonged delay in analysis of the "patch study" survey in the final year of the program. For future large-scale programs, adequate resources should be committed to ensure the collection of all data which are critical to evaluation of key hypotheses, and to provide for timely processing of samples and reporting of results.

Flemish Cap

Synopsis of research on cod and redfish recruitment

The second day of the Special Session began with a paper (Lilly, 1987) which reviewed the development of the Flemish Cap project, the hypotheses posed, the research conducted and results reported prior to the Session. Flemish Cap was chosen for the study of recruitment mechanisms in demersal fish because fluctuations in year-class strength of both cod and redfish had been observed, the cod stock was discrete, the area was not too large, the circulation patterns were likely to be amenable to study, and a historical database existed for both physical oceanography and fish production. Objectives of the project were very broad: to study the effect of water circulation patterns on the retention of larvae and the influence of abundance and size composition of the food supply on the survival of larvae; to determine the effect of intraspecific and interspecific predation on the survival of juvenile fish; and to improve the assessment of the size of the spawning stocks in order to study the relationship between stock size and recruitment. When it became clear that only two countries (Canada and USSR) would participate in the research program, the frequency of ichthyoplankton surveys was much reduced from the original proposal of a survey every 2 weeks, and special surveys for juveniile fish were eliminated. Most of the sampling was conducted from 1978 to 1983, with less frequent surveys continuing to the present time.

With respect to the above-noted hypotheses, it was thought that breakdown of the clockwise gyre on Flemish Cap might cause a loss of eggs and larvae, but there has been no documentation of such a breakdown being followed by loss of larvae, and subsequent poor recruitment. Spatial and temporal patterns in the life cycle of copepods have been described, but relationships between prey availability and feeding of fish larvae, and between feeding and survival of larvae, have not been described. Cod are known to consume smaller cod and a large number of small redfish, but the contribution of predation on juveniles to variability in year-class strength has not been assessed. Recruitment in cod appears to be unrelated to size of the spawning stock. Further analysis and synthesis of the available data may yield valuable insight, because some significant events were recorded during the course of the investigations. For example, a strong year-class of cod arose from a small spawning stock, two relatively strong year-classes of redfish were born, one year-class of redfish virtually disappeared at the larval stage and another was greatly reduced in abundance at the juvenile stage, and annual differences in growth of redfish larvae were observed.

Knowledge of the physical oceanography and the biology of the major species on Flemish Cap has been considerably improved by the analyses which have been reported to date. The ichthyoplankton community has been described. Most attention was devoted to the larvae of redfish, with reports on the time and location of spawning, the vertical and horizontal distributions of larvae, and the growth and mortality of larvae. Study of the early life history of cod was greatly limited by small catches of eggs and larvae. There have been reports on the horizontal distribution of juvenile redfish, the occurrence of juvenile redfish and cod in the stomachs of larger cod, and the abundance and feeding of cod from bottom-trawl catches. Reported progress in methodology included development of techniques for ageing redfish larvae by interpreting rings in otoliths, and examination of frequency distributions of cod catches during stratified-random bottom-trawl surveys.

Other contributions

Following the synopsis paper, eleven papers and one oral report were presented. These dealt with various research aspects which were considered to be relevant to recruitment of cod and redfish on Flemish Cap.

In a review of hypotheses concerning recruitment variability in marine fishes, Anderson (MS 1986) concluded that there was little evidence to support most of the hypotheses but that a comprehensive growth and mortality hypothesis deserved greater attention. This hypothesis, stating that conditions which determine growth rate during specific life history stages such as the larval phase will ultimately determine survival, is based on sound biological principles, incorporates aspects of several other hypotheses, and leads to predictions which are testable. The growth-mortality hypothesis was supported by observations on growth and mortality of larval redfish on Flemish Cap.

Anderson and Webster (MS 1986) described the results of a study which was designed to identify and measure certain sources of error in data from ichthyoplankton surveys. The abundance and mean length of redfish larvae were determined every 2 hr over a 24-hr period at a single station on Flemish Cap. There were significant between-tow differences in abundance (coefficient of variation, CV = 45.3%) but not in mean length (CV = 4.7%). A negative correlation between

volume of water filtered and number of larvae per m^2 was attributed to the occurrence of larvae in the near-surface layer only and the presence of strong subsurface tidal currents.

A numerical modal of water movement on Flemish Cap was described in an oral presentation by S. A. Akenhead (Northwest Atlantic Fisheries Centre, St. John's, Newfoundland). The progressive shift of redfish larvae from the edge of the bank where spawning occurs toward the center of the bank can be attributed to diffusion. Furthermore, it may be possible to distinguish between apparent mortality caused by loss from the bank and mortality caused by other factors on the bank.

Lilly (MS 1986) described the abundance and growth of juvenile redfish which were caught on Flemish Cap during bottom-trawl surveys in 1978-85. Number and mean length by age-group were estimated by fitting normal distributions to the length compositions of catches.

Lilly and Evans (MS 1986) described the number, length and weight of juvenile redfish (ages 1 to 4) in the stomachs of cod which were caught during bottom-trawl surveys on Flemish Cap in 1978-84. These data were used in a sequential population analysis (SPA) to estimate the number of redfish by age-group on the bank at the time of the survey in each year. The calculated numbers of small redfish (ages 1 and 2) from SPA were much higher than the estimates from trawl surveys.

Histological analysis of gonads of female cod which were caught during the prespawning period on Flemish Cap (Walsh *et al.*, MS 1986) confirmed earlier visual observations at sea that the ovaries of many mature females, having spawned in the previous year, did not show signs of development for spring spawning in the ensuing season. During the winter surveys of 1978-85, approximately one-third of mature female cod present in each year evidently did not spawn in the usual period, thereby reducing the number of eggs that might have been spawned. There is no evidence to indicate that spawning occurs in the autumn on Flemish Cap.

Data on fecundity, gonad weight and maturity of cod from winter surveys on Flemish Cap in 1978-85 were presented by Wells (MS 1986a, 1986c). The percentage of females which were maturing to spawn in the year of observation increased with length in most years, but, in 1978 and 1979, the percentage of mid-sized maturing cod was lower than the percentages of both smaller and larger maturing fish.

The overall variation in condition factor for cod on Flemish Cap was low (Wells, MS 1986b). However, the factor tended to be higher in January-February than in March-May. There was annual variation in the values for January-February, and the annual pattern varied with fish length.

The quantity of redfish, available as prey of cod in each winter of 1978-85, was estimated from the length compositions of redfish and cod in bottom-trawl survey catches on Flemish Cap and from estimates of the maximum length of redfish which can be eaten by cod of specified lengths (Wells and Power, MS 1986). They concluded that the available redfish biomass was high for large cod (>70 cm) throughout the period. For smaller cod (<50 cm), the available redfish biomass varied, being low in 1978-81 and much higher in 1982-83. The analysis did not take account of the apparent, very low catchability of small redfish in bottom trawls.

Further examination of the available data for the 1958-64 and 1969-76 periods detected no relationship between recruitment of cod on Flemish Cap and either spawning stock size or temperature and salinity (Rice and Evans, MS 1986). In contrast, recruitment of cod to the Labrador-East Newfoundland (Div. 2J+3KL) stock was found to be clearly influenced by the size of the spawning stock.

A dome-shaped stock-recruitment curve was fitted to Flemish Cap cod data for the 1959-77 period (Gomez-Munoz, MS 1986), and estimates of sustainable yield at various exploitation rates were derived.

Critique of the Flemish Cap project

Some aspects of the Flemish Cap project which reduced the probability of success were consequences of decisions during the planning phase. Although Flemish Cap was a good study site for the reasons stated above, its considerable distance from land (southeastern Newfoundland) made it inconvenient for Canadian research vessels to make brief diversions during cruises to other areas, and observations tended to be greatly restricted in time. The project went into a monitoring phase without the benefit of a pilot study to describe such things as the annual zooplankton production cycle, spawning times, horizontal and vertical distributions of eggs, larvae, juveniles and adults, and the growth patterns of larvae and juveniles. The hypotheses remained so numerous and broad that research effort was not sufficiently focused on specific questions. The decision to proceed with the project, when it became clear that only Canada and USSR would participate, required that the frequency of sampling be reduced well below the originally-proposed level, and there was no documented consideration of the adequacy of the reduced effort to address the hypotheses. Clearly, the research effort was inadequate, particularly with regard to the construction of annual survival curves for the early life history stages of cod and red-

fish. The decision to eliminate autumn surveys for juveniles meant that the success of each cohort could not be assessed until juveniles were caught during standard bottom-trawl surveys in the following winter, and even these catches were unsatisfactory because the juveniles were not highly susceptible to capture by the trawl. The choice of survey tools also presented some problems. For example, the Canadian surveys utilized the bongo sampler which was quite useful for measuring ichthyoplankton abundance but much less useful for examining various aspects of the biology of larvae, such as distribution in the water column. In addition, Canada and USSR used different gears for sampling plankton and different trawls and survey methods for assessing abundance of demersal fish, necessitating intercalibration studies in both cases. The time required for some analyses was seriously underestimated, and the results from many phases of the study were reported so slowly that progress could not be monitored adequately. For example, results of the intercalibration studies were not reported at an early stage and, consequently, the results from Canadian and USSR surveys were not combined. Also, there were failures to collect certain kinds of information. Even when it became clear that most of the ichthyoplankton work would be devoted to redfish, very little attention was given to redfish juveniles and adults. The number of redfish larvae extruded each year could not be estimated, partly because fecundity was not measured. The ageing of juvenile redfish received very little attention. Redfish cannibalism could not be measured because there were no quantitative feeding studies on redfish. Other serious problems were created by factors beyond the control of the scientists involved in the project. Inadequate biological sampling of the commercial catches and inadequate reporting of catch and fishing effort made it difficult to measure recruitment and spawning stock size. The intensive fishery kept the size of the cod stock at such a very low level that the influence of varying stock size on recruitment could not be studied. The lack of success in keeping moored current meters in place caused the early curtailment of the special oceanographic program.

Much data analysis remains to be completed. It may be possible to account for annual variability in mortality of larvae by examining the dynamics of water circulation or (and) by analyzing spatial variation in food availability, feeding and condition. A more accurate estimate of the size of the cod spawning stock may be forthcoming from new information on fecundity and the percentages of females (by size-groups) which spawned in each year. There will also be further analysis of the influence of prey availability on the production of the cod stock and analysis of the influence of predation by cod on mortality of juvenile redfish and cod. It will also be possible to use the results from the groundfish surveys to describe the demersal fish assemblage and to look for changes over a period of at least 8 years.

Other Recruitment-related Studies

Seven papers on studies which were not specifically associated with the Georges Bank and Flemish Cap research programs were presented. Those pertaining to fish included temperature-induced effects on survival of Arcto-Norwegian cod larvae (Ellertsen *et al.*, MS 1986); recent surveys of 0-group pollock (*Pollachius virens*) off the Norwegian coast (Nedreaas, MS 1986); effects of temperature and severe advective events on survival of haddock (*Melanogrammus aeglefinus*) eggs and larvae on Georges Bank (Cohen *et al.*, MS 1986); correlation between recruitment and spawning stock biomass of cod in Div. 2J+3KL and several environmental factors including temperature and salinity (Vazquez and Larraneta, MS 1986); and conceptual evaluation of the evidence for internal behavioral capabilities of early life stages of fishes, which allow them to "direct" their movements contrary to passive drift (Iles, MS 1986). Two papers on sea scallops (*Placopecten magellanicus*) involved a description of the dispersal of larvae in the Bay of Fundy, Georges Bank and Scotian Shelf areas (Tremblay and Sinclair, MS 1986), and a method for identifying daily growth increments on the shells of larval sea scallops (Hurley *et al.*, MS 1986). Following the presentation of these papers, there was general discussion on the issues which were raised during the course of the Special Session.

General Discussion

The paper stimulated discussion on a number of key topics, including stock structure, density-dependent and density-independent processes, age at which year-class strength is established (i.e. predictable), and adequacy of estimates (i.e. accuracy, precision and independence of variables). It was apparent that no single dominant physical or biological process determines recruitment and that critical events can occur at almost any stage in the early life history. Because of the multiplicity of possible factors that can operate over this broad time-scale, it will be difficult to develop useful predictive models to explain interannual variability. It was concluded that density-dependent processes are most relevant to long-term fishery management strategies, because they involve biological mechanisms which can be influenced by fishing. Although greater research emphasis on density-dependent processes seems desirable, it is clear that these processes cannot be isolated from physical factors which have a density-independent effect. There-

fore, both types of processes must be incorporated into a definitive research strategy on the recruitment problem.

Evidence of density-dependent effects on growth, maturation and fecundity was discussed relative to herring, and several hypotheses were considered regarding depensatory processes that might explain the nearly complete extinction of Georges Bank herring and the failure of the stock to recover after almost a decade. If the demise of the stock was due to depensatory processes (e.g. predation by marine mammals) which began to operate after the population was reduced to a very low level by fishing, a slow recovery (if at all) may be expected. Recovery of the herring stock may also be inhibited by increased abundance of several species, most notably sand lance (*Ammodytes* sp.). The replacement may have resulted from the response of opportunistic species which filled the void that was left when the herring stock was overexploited, or from a change in the climatic regime that favored the replacement species, or both.

Another explanation for the failure of the Georges Bank herring stock to recover relates to the historical occurrence of herring on the bank. One hypothesis is that Georges Bank is a suboptimal habitat which is occupied when the population expands its distribution due to crowding of the optimal habitat (e.g. coastal waters). If this hypothesis is correct, recovery of the Georges Bank herring stock will not occur until the coastal populations increase substantially. Further evaluation of alternative hypotheses concerning recovery of the Georges Bank stock is desirable, because they have important implications for management. In addition, the possibility of experimental introduction of herring onto Georges Bank was considered.

There was general agreement among participants that the recruitment process is so complex that even large logistic efforts, such as the ICNAF Georges Bank and Flemish Cap projects, may not provide a sufficient level of understanding of mortality causes and predictive capability to justify their overall costs. In order to improve the chances of success in future recruitment studies, it will be extremely important to ensure that sampling design and scope of the research plan provide all essential data which are relevant to the hypotheses being tested. In particular, it is important to conduct appropriate "pilot" studies in advance of a standard monitoring series (or at least concurrently) in order to document critical biological characteristics (e.g. vertical distribution of pelagic life stages) and to develop and (or) test the sampling gear for all important life stages. In general, it is desirable to incorporate selected fine-scale studies into the framework of larger-scale field studies in order to improve knowledge of basic biology of the species and to improve measures of the nature and magnitude of sampling errors. Also, it is important to select species and stocks which are amenable to an extended and definitive research effort (i.e. clearly discrete stocks which are expected to maintain reasonable spawning populations and not be overfished), and for which good data on annual recruitment and stock size are available. It was emphasized that, during the initial planning stages, more importance should be given to assuring adequate resources for timely processing and dissemination of data.

Despite recognition that, on the basis of the Georges Bank and Flemish Cap studies, significant progress had been made in understanding some aspects of the recruitment process, there was general concensus that new approaches are needed. Some suggestions are listed below.

(a) **Genetic models relating diversity of populations to stock size and vulnerability to fishing and environmental perturbations**. The influence of genetic mechanisms on recruitment requires more attention. If environmental conditions within a year select for a specific genotype, reduction of the number of year-classes in a population through fishing pressure will reduce genetic diversity and thereby reduce resiliency of the population to environmental variability.

(b) **Experimental laboratory work on selected behavioral responses of fish (especially early life stages) to clarify the scope for response to environmental cues and stresses, and to explore other behavioral characteristics, particularly those which could help to explain non-passive drift**.

(c) **Search for growth-history indicators (e.g. daily growth rings and associated biochemical tags on otoliths) in juvenile stages of fish, which may reconstruct the early growth history of the cohort population**. This type of approach may hold promise for sorting out causes of interannual variations in recruitment success without large-scale logistic sampling of various developmental stages of each cohort.

(d) **Studies of annual maturation and spawning to determine the range of "condition" of adults and possible effects on egg viability and subsequent recruitment**. This is an example of a process where density-dependent effects might be expected.

(e) **Comparative studies among different stocks, including geographic patterns of population distributions and production (particularly stock-recruitment relationships) relative to exploitation levels and environmental characteristics of population habitats**. Fishing reduces spawning biomass both in total and on a "per recruit" basis. Spawning biomass per recruit (S/R) must be sufficiently large

that the year-classes replace (on the average) the spawning biomass of their parents in order for a population to persist. It would be useful to compare the levels of S/R, as percentage of the unexploited population level, for various fisheries throughout the world. Consistent patterns might emerge in the levels of S/R that are needed to sustain fisheries within species, taxonomic groups, habitat types and climatic regimes. Such patterns could provide useful guidelines for fishery managers, even if the controlling ecological mechanisms are not fully understood.

(f) **Improved analytical and statistical procedures to reduce incidence of bias and spurious correlations that may arise from lack of independence among variables in complex and interrelated data sets.**

In general, the participants agreed that there was a need to take a more comprehensive and retrospective view of the recruitment process by looking at all available clues within a more holistic framework, ranging from experimental studies on individual organisms to global-scale patterns of geographic distribution and population "richness" of exploited species or stocks. A more integated approach should improve our understanding of the recruitment process from the standpoints of both ecology and fishery management, and it may even provide new advances in ecological theory.

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