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Synopsis of Research Related to Recruitment of Atlantic Cod (*Gadus morhua*) and Atlantic Redfishes (*Sebastes* sp.) on Flemish Cap

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Abstract

Research into the causes of variation in year-class strength of Atlantic cod and Atlantic redfishes was conducted during the late 1970's to the mid-1980's on Flemish Cap, an isolated plateau east of the Grand Bank in the Northwest Atlantic. Objectives of the project were very broad: to study the effect of water circulation patterns on the retention of larvae and the influence of the 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 stock in order to study the relationship between stock size and recruitment. Several factors caused the research effort in all phases of the project to fall below the originally-proposed level, greatly reducing the possibility that the hypotheses could be adequately addressed. The presence of a weak anticyclonic gyre on the central part of the bank was confirmed, and it was shown that this gyre breaks down occasionally. This breakdown, which is associated with the passage of storms, was hypothesized to cause a loss of eggs and larvae, but there has been no documentation of such a breakdown followed by a 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 the feeding of fish larvae, and between feeding and survival, have not yet been described. Cod are known to consume smaller cod and large numbers of small redfish, but the contribution of predation on juveniles to variability in year-class strength has not yet been assessed. Recruitment in cod appears to be unrelated to size of the spawning stock.

The analyses to date have resulted in considerably increased knowledge of the biology of the species found on Flemish Cap. The ichthyoplankton community has been described, with most attention being devoted to the larvae of redfish. Also, the time and loction of redfish spawning, the vertical and horizontal distribution of redfish larvae, and the growth and mortality of these larvae have been described. 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 and on the occurrence of juvenile redfish and cod in the stomachs of larger cod. A major problem has been that, although most of the work on larvae and juveniles has been concentrated on redfish, most of the study on distribution, abundance, growth, maturity and feeding of adults has been concentrated on cod. Because much analysis and synthesis of data remain to be completed, the success of the project cannot yet be assessed.

Introduction

The international program of research into the causes of variation in year-class strength of demersal fishes was initiated by the International Commission for the Northwest Atlantic Fisheries (ICNAF) in the mid-1970's. The area selected for an intensive study was Flemish Cap (centered at 47° N, 45° W), a plateau to the east of the Grand Bank and separated from it by the deep (>1,000 m) Flemish Pass. This isolated bank has supported major fisheries for Atlantic cod (*Gadus morhua*) and Atlantic redfishes (*Sebastes* sp.), hereinafter called cod and redfish. Other demersal fish are not abundant. Capelin (*Mallotus villosus*) and sand lance (*Ammodytes dubius*), the two dominant planktivorous fish on the adjacent Grand Bank, are rare visitors.

The purpose of this paper is to review the history of the Flemish Cap project and the scientific progress that has been reported since the thorough review of the biology of Flemish Cap cod and redfish by Templeman (1976) and the reviews of the physical oceanography of Flemish Cap by Templeman (1976) and Hayes *et al.* (MS 1977). Most of the available analyses are in the form of mimeographed research documents of ICNAF and its successor the Northwest Atlantic Fisheries Organization (NAFO).

Overview of the Flemish Cap Project

Proposal for a research project

In 1974, the Environmental Subcommittee of ICNAF reviewed a proposal for an expanded program of coordinated environmental research on both physical and biological processes which control organic production on the continental shelf. The program would include "intensive short-term studies in selected key areas to determine the smaller-scale (within season) dynamics of processes controlling fish production" (ICNAF, 1974). An environmental working group was established to prepare "a proposal aimed at determining the factors involved in the production of good and poor year-classes in some of the main fisheries of the ICNAF area". The working group met in September 1974 and agreed on a two-pronged approach: a "correlation approach in which emphasis is placed on predictability without necessarily understanding the causal mechanisms involved", and a "causal mechanism approach which leads to a real predictability and which attempts to understand the real processes and mechanisms included in fish production" (ICNAF, MS 1975). The working group also agreed that the study should be limited to an important stock or substock of a pelagic species and a groundfish species and recommended that research be focused on Atlantic herring (*Clupea harengus*) in the Georges Bank–Gulf of Maine area and on cod and redfish in the Flemish Cap area. Flemish Cap was chosen for the groundfish study for the following reasons (ICNAF, MS 1975): (a) fluctuations in year-class strength of both cod and redfish were regularly observed in this area; (b) the stock of cod is discrete and has been confirmed as separate from those of the Grand Bank; (c) the circulation patterns are likely to be quite amenable to study; (d) the area is reasonably restricted in size; and (e) 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 data-base of fish production and physical environmental data.

The environmental working group, meeting again in May 1975, reviewed biological data on the groundfish stocks and the major features of the oceanography of Flemish Cap, and confirmed the advantages of Flemish Cap as a suitable study area (ICNAF, 1975). The only recommedations at that meeting were that there be further reviews and analyses of the available data. (The slow progress in initiating the Flemish Cap project contrasted with the numerous detailed proposals for research on herring in the Georges Bank–Gulf of Maine area.) Because some of the data which were requested in 1975 were still not available in 1976, no progress toward a research proposal could be made (ICNAF, 1976). The next meeting of the environmental working group was convened in Murmansk, USSR, in May 1977, specifically to address the Flemish Cap proposal (ICNAF, 1977). This meeting reviewed available information on Flemish Cap, developed hypotheses, proposed research for addressing these hypotheses, and made preliminary plans for research in 1978. The ICNAF Standing Committee on Research and Statistics accepted the recommendations of the working group and finally recommended in May 1977 "that a coordinated international research project be launched on the factors determining year-class success for Flemish Cap (Div. 3M) groundfish, with emphasis on cod and redfish" (ICNAF, 1977).

Hypotheses and proposed research

The Murmansk meeting the environmental working group (in May 1977) identified three major problems that should be considered in order to predict the survival of different year-classes: (a) effect of water circulation patterns and the abundance and size composition of the planktonic food supply on retention and survival of fish larvae on Flemish Cap; (b) effect of intraspecific and interspecific predation on survival of juvenile fish; and (c) improved assessment of the size of the spawning stocks (ICNAF, 1977). To address the problem of studying larval survival, it was proposed that a grid of about 50 oceanographic and simultaneously-occupied ichthyoplankton stations be sampled every 2 weeks throughout the period of spawning and larval development (February to June), and that an enhanced oceanographic program, including current-meter arrays and drifting buoys, should be initiated. Careful intercalibration of methods and instrumentation of the various countries was considered essential. To address the problem of studying juvenile survival, it was proposed that pelagic and bottom-trawl surveys be conducted in both March and September. To address the problem of assessing the spawning stocks, it was proposed that the bottom-trawl survey for juveniles in early March be used to assess the abundance of spawning cod, and that the USSR groundfish surveys be continued. Participating countries were urged to conduct joint cruises to calibrate fishing gear and other instruments and to make a special effort to sample catches of their commercial fleets.

The above proposals were considered "necessary in order to ensure a reasonable probability of a successful outcome from the studies" (ICNAF, 1977). However, Canadian and USSR scientists planned to undertake a less extensive program if participation by other countries was insufficient to implement the full program. The reduced program would involve surveys in late March, April and May to estimate the size of the cod stock and to identify the drift pattern of eggs and larvae, with the pelagic survey for juvenile cod and redfish having low priority. There was no statement of what accomplishments were anticipated from a program which was reduced well below the level considered necessary to ensure a reasonable probability of success.

In September 1977, a group of Canadian scientists met to expand upon the proposals that were developed at the Murmansk meeting (Akenhead, MS 1978). They decided that the experiment should focus on cod and 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 reference to stages of the life cycle, 12 hypotheses were developed (Table 1). These hypotheses were more explicit than those arising from the Murmansk meeting and included some that were not proposed at the former meeting, most notably that predation upon eggs and larvae determines year-class strength. Year-class strength was defined as the number (and weight) of fish that became 4-year-olds. The report (Akenhead, MS 1978) also provided detailed lists of the data that would be required to test each hypothesis, with some consideration of the sampling strategies that might be required. 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.

Sampling and review of progress

With the exception of a plankton survey by Poland in April 1978 (Grimm *et al.*, MS 1980), all research, specific to the Flemish Cap project, was conducted by Canada and USSR (i.e. the reduced program of research was implemented). Canadian scientists conducted one plankton survey in 1978, three or four surveys each year in 1979, 1980 and 1981, and single surveys in 1982 and 1983. USSR scientists conducted two or three plankton surveys each year in 1978–81 and 1983, and single surveys in 1984 and 1985. Bottom-trawl surveys were conducted by Canada in January-February 1977–85, and the USSR bottom-trawl surveys have continued into 1986. There were no surveys with specifically-designed gear to catch juveniles. The special oceanographic program, involving satellite-tracked buoys and current-meter arrays, was initiated in 1979, but it was discontinued in 1980 because of excessive loss of moored instruments. A summary list of data for Flemish Cap in 1949–79 was prepared by Anderson and Chumakov (MS 1980) and a compendium of Flemish Cap research vessel surveys was prepared by Akenhead (MS 1984).

The *ad hoc* working group on the Flemish Cap project, during its meeting in May 1978, reviewed new analyses of historical data and noted the start of sampling in early 1978 (ICNAF, 1978). Meetings in April 1979 (ICNAF, MS 1979) and May 1979 (ICNAF, 1979) recorded work that had been performed to date, and it was recommended that a meeting of a small group of scientists be convened to undertake an in-depth examination of the data obtained in 1978 and 1979 and to assemble a detailed plan for sampling in 1980. That meeting, held in January 1980, accomplished its goals and concluded that no major change in approach was necessary (NAFO, MS 1980). A meeting in September 1980 reviewed additional new data and recommended

TABLE 1. Hypotheses proposed to explain variation in year-class strength of cod on Flemish Cap (from Akenhead, MS 1978).

A. Spawning stock characteristics

- A.1 The size of the spawning stock determines year-class strength
- A.2 The condition of the spawning stock determines year-class strength

B. Abundance of predators

- B.1 Predation upon juveniles determines year-class strength
- B.2 Predation upon eggs and larvae determines year-class strength
- B.3 Predation upon adults (fishing) determines year-class strength

C. Physical environmental influences

- C.1 Environmental influences upon adults determine year-class strength
- C.2 Environmental influences upon eggs and yolk-sac larvae determine year-class strength
- C.3 Environmental influences upon swimming larvae determine year-class strength
- C.4 Environmental influences upon juveniles determine year-class strength

D. Abundance of suitable food

- D.1 Food availability for prespawning mature fish determines year-class strength
- D.2 Food availability for larval fish determines year-class strength
- D.3 Food availability for juvenile fish determines year-class strength

that participants give high priority to the analysis of all existing information (NAFO, 1980). Significant progress in examining data was evident by September 1981, but there were also growing concerns that "the original aim of the Working Group was no longer achievable" (NAFO, 1981). These concerns will be addressed in greater detail in subsequent sections, but they may be summarized as follows:

(a) Cod eggs and larvae were in such low abundance in the Canadian ichthyoplankton surveys in 1979, 1980 and 1981 that there was insufficient material for useful analyses.

(b) The cod stock was at a very low level of abundance, and there was considerable uncertainty about studying recruitment mechanisms at early life history stages when the spawning biomass was so low.

(c) Redfish larvae were abundant in ichthyoplankton surveys and were providing material for study. However, the study of redfish alone was not promising because recruitment to the adult stock would not occur for many (10?) years, there was no study on juveniles, there was uncertainty regarding ageing of juvenile and adult redfish, the three species of redfish could not be distinguished at the larval stage, and changes in spawning stock biomass of redfish were not being measured.

(d) The oceanographic program was crippled by the curtailment of the moored current-meter program.

(e) Fishing effort on Flemish Cap was high, and the monitoring of catch and effort was poor.

These concerns were followed by a recommendation for reappraisal of the aims of the Flemish Cap project. Discussions at the June 1982 Meeting were guided by a prospectus on future research that was prepared by Anderson (MS 1982). There followed recommendations that emphasis be placed on cod and that there be a shift away from examining survival at the larval stage to studying compensatory responses of adult cod at low population levels (NAFO, 1982). With respect to the hypotheses in Table 1, the recommendation was for a change in emphasis from hypotheses C2, C3 and D2 to hypotheses A1 and A2. During a meeting of the working group in June 1983 (NAFO, 1983), it was noted that analysis and presentation of data were progressing at a slow pace, and it was recommended that the next meeting be held only when there was sufficient information available to evaluate the project and plan future research.

Physical Oceanography

Circulation

Flemish Cap is bordered by two major current systems (Templeman, 1976; Hayes *et al*., MS 1977) (Fig. 1). The Labrador Current transports cold low-salinity water southward through Flemish Pass and along the eastern edge of Grand Bank. A branch of this current flows eastward and then southeastward around the northern and northeastern slopes of Flemish Cap. The warm high-salinity North Atlantic Current flows eastward and northeastward near the southern slope of Flemish Cap. A weak anticyclonic gyre is frequently observed over the central portion of the bank.

Records from current meters which were moored on Flemish Cap in 1979 support the hypothesis of a weak anticyclonic gyre (Ross, MS 1980). They also indicate a strong semidiurnal tidal signal and a 4-day periodicity in the current pattern, particularly in the spring. The drift patterns of six satellite-tracked buoys which were deployed on Flemish Cap at intervals between January 1979 and May 1980 showed a general

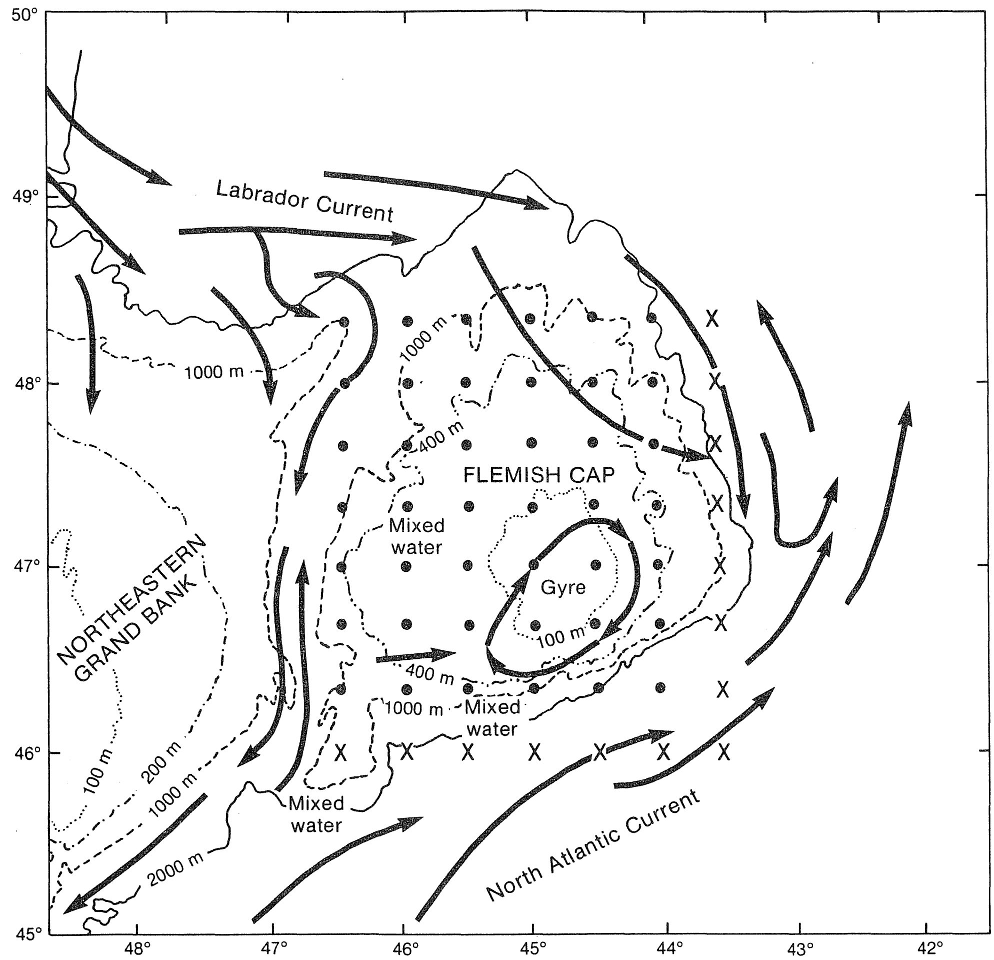

Fig. 1. The main oceanographic features of the Flemish Cap region and the ichthyoplankton sampling grid (adapted from Anderson, 1984).

sluggish circulation over the central part of the bank, with a trend toward anticyclonic rotation (Ross, 1981). All buoys exited from the southwestern sector of the bank and entered the North Atlantic Current.

Analysis of charts of dynamic sea-surface topography, based on 27 oceanographic surveys from December 1977 to April 1982, confirmed that the anticyclonic gyre is the prevailing form of water circulation (67% of observations) (Kudlo *et al.*, 1984). A meandering flow eastward across the bank occurs occasionally (7% of observations) and only in winter. A mixed type of circulation, involving simultaneous local gyres and transient flow across the bank, occurs fairly frequently (26% of observations). The breakdown of the gyre is associated with the passage of storms.

Origin of water

Hayes *et al.* (MS 1977) stated that the water on Flemish Cap is essentially a mixture of the water from the two currents — the Labrador Current and the North Atlantic Current. Akenhead (1986) used a model of salt flux in the upper 100 m on the bank to demonstrate that Flemish Cap water is derived exclusively from Labrador Current water. About 50% of the surface water on Flemish Cap is replaced each month.

Temperature and salinity

Techniques of empirical orthogonal function and cluster analysis were used to discern regional differences in water types in the Flemish Cap region (Keeley, MS 1982). From all available temperature and salinity data in April and May, it was possible to detect six regional types. The approach has not been extended, and the results from the analysis have not been used in examining regional variation in biological variables.

Drinkwater and Trites (1986) provided monthly means of temperature and salinity for the Flemish Pass and five regions on Flemish Cap. The regions do not correspond to those described by Keeley (MS 1982). On the central part of Flemish Cap, the temperature at 100 m remains around 3° to 4°C throughout the year, whereas the temperature at 20 m varies from about 4°C in March-April to about 12°C in September. The most rapid warming of near-surface water occurs in June-July. Near-surface salinities reach a maximum of about 34.2 in March and a minimum of about 33.4 in August-October (see also Akenhead, 1986).

There are several published reports of annual variability in temperature and salinity. Keeley (1982) presented an analysis of anomalies of water temperature and salinity at selected stations on the 47°N oceanographic section for the 1970-79 decade. Akenhead (MS 1981) provided monthly (March to September) means of surface (0-20 m) temperature and salinity for the 1955-80 period. Only stations from depths less than 400 m were chosen. Bailey (MS 1982) derived surface temperatures for Flemish Cap from weekly synoptic sea-surface temperature charts, which were initially prepared from data provided in weather reports by "ships of opportunity" during 1962-81. It was shown that the annual cycle has a mean of 7.5°C, with a minimum of 3.2°C in February and a maximum of 13.0°C in August. Annual and seasonal departures from normal were also presented.

Biology of Redfish

Species composition and stock isolation

Three species of redfish (*Sebastes mentella*, *S. fasciatus*, and *S. marinus*) occur on Flemish Cap (Ni, 1982; Ni and McKone, 1983). While golden redfish has been the common name of *S. marinus* for several years, the common names which have recently been assigned to the beaked species by Robins *et al.* (1986) are deepwater redfish (*S. mentella*) and Acadian redfish (*S. fasciatus*).

Adult *S. mentella* and *S. fasciatus* cannot be distinguished readily in the field, but they can be separated by morphology of the extrinsic gasbladder musculature (Ni, 1981a), meristic and nominal characteristics (Ni, 1981b), and morphometric data (Misra and Ni, 1983). They are grouped in research catches as beaked or sharp-beaked redfishes, in reference to the projection on the tip of the chin which distinguishes them from *S. marinus*. All three species are combined in commercial fishery statistics. Identification of larval redfish remains unresolved (Penney, 1985). Redfish larvae from Flemish Cap have been identified simply as *Sebastes* sp. (Anderson, 1984; Penney and Evans, 1985; Serebryakov *et al.*, 1987).

There appears to have been no study of the isolation of the redfish stocks since Templeman (1976) concluded that "the redfish stocks on Flemish Cap, at least the sharp-beaked forms, are relatively but not necessarily completely isolated from those on the slopes of the adjacent Grand Bank. What relationship there may be with the oceanic stock of *S. mentella* is unknown".

Biology of adults

Distribution. The density of golden redfish (*S. marinus*), as determined from research vessel catches, is highest in depths less than 400 m, whereas the density of beaked redfishes (*S. mentella* and *S. fasciatus*) is low in depths less than 300 m but high in depths greater than 300 m (Chekhova and Konstantinov, MS 1979; Ni and McKone, 1983). From an analysis of meristic characters of the beaked redfishes, Ni (1982) concluded that *S. fasciatus* occurs in relatively shallow water

(<360 m) whereas *S. mentella* occurs from 200 m to the limit of the surveys (750 m).

Penney *et al.* (MS 1984) used morphology of gas-bladder musculature to identify redfish from catches in 14 bottom-trawl tows on line transects in March 1983. They concluded that "*S. marinus* comprised the bulk of the redfish population down to 258 meters, *S. fasciatus* predominated from there to 369 meters, and *S. mentella* was the main constituent in deeper water". The species proportions in five depth zones were applied to the catch-per-depth-zone from a stratified-random survey in February 1983, yielding the following percentages for Flemish Cap as a whole: *S. mentella* (57%), *S. fasciatus* (32%), *S. marinus* (11%). The estimates may be suspect because of the small number of tows in the March survey.

Chekhova and Konstantinov (1978) reported that a high proportion of the commercial catch of redfish on Flemish Cap has been caught with midwater trawl, indicating that a part of the redfish population is mainly pelagic. These authors found differences in biological characteristics of beaked redfish in midwater trawl and bottom-trawl catches, particularly in spring (March-June) during the period of larval extrusion and in autumn (October-November) when mating occurs. They concluded "that a single population of beaked redfish inhabits the Flemish Cap area, differing components of which are exploited by bottom and midwater trawls at various times of the year".

Growth rate. Beaked redfish on Flemish Cap attain a length of about 21 cm by age 6 and 30 cm by age 12, and they grow very slowly thereafter to a maximum of about 40 cm (Sandeman, 1969). This rate of growth is based on interpretation of annuli in otoliths. As discussed in detail by Templeman (1976), estimated ages from otoliths tend to be greater than estimated ages from scales. Females grow faster than males (Sandeman, 1969).

Maturity and fecundity. Chekhova and Konstantinov (MS 1979) reported that maturity of beaked redfish begins in males at 27 cm and in females at 28 cm, with most males being mature at 33 cm and most females at 35 cm. In contrast, Ni and Sandeman (1984) reported that the lengths at which 50% of individuals mature (L_{50}) is 21.5 cm for males and 30.6 cm for females. The difference in the estimates for males is striking (range of 27–33 cm in the first case and mean of 21.5 cm in the other). If the length-at-maturity estimates by Ni and Sandeman (1984) and the estimates of growth by Sandeman (1969) are correct, male beaked redfish mature at about age 6 and females do not mature until about age 11 or 12. Ni and Sandeman (1984) reported that the L_{50} values for golden redfish are 22.2 cm for males and 39.2 cm for females. There are no published estimates of fecundity.

Food and feeding. Redfish on Flemish Cap are primarily pelagic feeders (Konstantinov *et al.*, 1985). From studies in 1979–82, the most frequently occurring prey types were pelagic invertebrates (copepods, euphausiids, and hyperiid amphipods), shrimp (*Pandalus borealis*), and fish (mainly myctophids). Young redfish were found in the stomachs occasionally. Stomach fullness was highest in summer (June–August).

Extrusion time and area

Various methods have been used to estimate the time of extrusion of redfish larvae on Flemish Cap. From observations on the stage of maturity of adults during February–March surveys in 1983 and using estimates from the literature for length of time from fertilization to hatching and from hatching to extrusion, Penney *et al.* (MS 1984) estimated that extrusion of larvae by *S. mentella* and *S. marinus* would peak in the last half of April and extrusion by *S. fasciatus* would peak during the first half of May. Penney and Evans (1985) aged redfish larvae by counting the circuli in otoliths and used these ages to back-calculate the extrusion dates. From larvae caught in late June and July, they estimated that extrusion began in mid-March, peaked during the last 2 weeks of April and declined during May, with some residual extrusion continuing until July.

Results from Canadian ichthyoplankton surveys indicated that the abundance of recently-extruded redfish larvae peaks in late April, with some evidence, from length frequencies of larvae caught in July and August, of a much smaller extrusion peak during the second and third weeks of June (Anderson, 1984). USSR survey results indicated that peak extrusion occurs during the last half of April, with evidence of a second peak in July–August (Serebryakov *et al.*, 1987). The distributions of recently-extruded larvae in March and April, as illustrated by the results of ichthyoplankton surveys (Grimm *et al.*, MS 1980; Anderson, 1984; Akhtarina and Chechenin, MS 1985; Serebryakov *et al.*, 1987), indicate that extrusion begins in March on the southwestern slope of Flemish Cap and spreads to all areas in depths greater than 200 m by the middle of April.

Biology of larvae

Distribution. Redfish larvae become widely distributed over Flemish Cap after April, with highest densities in June and July often occurring near the center of the bank (Anderson, 1984; Akhtarina and Chechenin, MS 1986; Serebryakov *et al.*, 1987). Serebryakov *et al.* (1987) stated that this change in distribution was a result of drift within the anticyclonic gyre on the bank. Clearly, the presence of larvae over shallow depths is a result of drift from the periphery, but the change in relative abundance is accompanied by very high total mortality. Thus, as noted by Anderson (1984), the apparent change in distribution might also be effected by higher survival over the central area. The relative importance of these two possible mechanisms has not been measured.

According to Serebryakov (1987), redfish larvae tended to be concentated in the upper 10–20 m of the water column.

Growth rate. Estimates of growth rates of redfish larvae in 1980 and 1981 have been obtained from otolith increment analysis (Penney and Evans, 1985) and analysis of the progression of modes in length-frequency data (Anderson, 1984). Penney and Evans (1985) found that newly-extruded larvae ranged from 6.2 to 8.9 mm (total length) and that length at extrusion varied with extrusion date. The mean growth rate was 0.156 mm/day in 1980 and 0.109 mm/day in 1981. Individual growth histories varied considerably with age and extrusion date. Larvae typically grew slowly for 10–15 days after extrusion, rapidly for 60–70 days and again slowly as they entered the pelagic juvenile stage. Anderson (1984) estimated growth rates of 0.037 mm/day for early to late May 1981, 0.146 mm/day for late May to early August 1980, and 0.163 mm/day for the same period in 1981. Estimates from the two techniques were similar for 1980 but very different for 1981. Possible reasons were discussed by Penney and Evans (1985).

Mortality. Anderson (1984) examined the length compositions of catches of larvae from Canadian surveys in 1980 and 1981 and isolated that portion of the population which was assumed to be derived from the spawning peak in late April. From abundance estimates for this group only, the calculated mortality rates in 1981 were 0.04/day from early to late May, 0.06/day from late May to late June, and 0.13/day from late June to early August. For the period from late May to early August, the mortality rate was twice as high in 1981 (0.093/day) as in 1980 (0.043/day). Estimates of larval abundance were also available from USSR surveys in 1978–81 and 1983 (Serebryakov *et al*., 1987) and from surveys in 1984 and 1985 (Akhtarina and Chechenin, MS 1985, MS 1986). Although many of the estimates are close to the survival curve in fig. 2 of Anderson (1984), sampling was coincident in two instances, for which the Canadian estimates of larval abundance were about three times the USSR estimates:

	Late May 1981	Mid-July 1978
Canada	2.7×10^{12}	2.7×10^{11}
USSR	0.8×10^{12}	0.8×10^{11}

It is important to determine if a more detailed survival curve can be constructed from the Canadian and USSR abundance estimates, especially for 1980 and 1981, by applying the results of the ichthyoplankton gear calibration study which was conducted in 1981 (NAFO, 1980). Results from USSR surveys may not be very useful for redfish, however, because all surveys except one (July 1978) were conducted before or during early June and are therefore confined to the early larval period.

Food and predators. Early results from a study of the food of redfish larvae indicate that copepod eggs and nauplii were the major prey in April 1979, and an adult herbivorous copepod (*Oithona similis*) was the major prey in July 1979 (Anderson and Akenhead, 1981). There are no reports on the predators of redfish larvae.

Biology of juveniles

Distribution. The surveys were not designed specifically to catch juvenile redfish, and bottom-trawl surveys were not conducted in the autumn. Thus, the first opportunity for catching juveniles from each year-class of larvae was during bottom-trawl surveys by Canada in the following winter (Atkinson, MS 1985) and by USSR in the following spring-summer (Chumakov *et al*., MS 1986). The smallest juveniles in the catches were 7–8 cm. In years of high abundance, these were found primarily in depths of 200–300 m, with major concentrations in an arc on the southern slope of the bank (Lilly and Gavaris, 1982). Individuals of another modal group at 11–12 cm tended to have the same distribution. Distribution of larger juveniles has not been reported.

Growth rate. The age of 7–8 cm redfish in the winter-spring catches remains uncertain (Lilly and Gavaris, 1982; NAFO, 1986). They were estimated by interpretation of otolith annuli to be 2-year-olds (Gavaris and Legge, MS 1981; Power and Atkinson, MS 1986), whereas an interpretation of the progression of modes indicated that they are 1-year-olds (Lilly and Gavaris, 1982). Age interpretation by USSR scientists also indicated that they are 1-year-olds (Chumakov *et al*., MS 1986). Resolution of this problem is essential for determining the correspondence between larvae caught in the spring-summer period and juveniles caught in the following winter-spring period.

The growth rate of juvenile redfish is slow but the estimates vary. From the age reading of otoliths which were collected in July 1956 and November 1958, Sandeman (1969) found that the redfish attained a length of about 19–20 cm by late age 5. However, from the age reading of otoliths of juveniles caught in the early 1980's, Power and Atkinson (MS 1986) reported that juveniles attain a length of only about 14 cm by the winter of age 5. The growth rate of juveniles may also be estimated from the progression of modes in the length frequencies which were reported by Atkinson (MS 1985). If the 7–8 cm redfish were 1-year-olds, the juveniles spawned in the early 1980's attained a length of about 20 cm in the winter when they became age 5.

Mortality. There are no estimates of abundance of juvenile redfish other than those from the bottom-trawl surveys, and these obviously underestimate abundance at early ages. Thus, reliable estimates of mortality are not available.

Food and predators. There are no published reports of studies on the food of juvenile redfish. However, large numbers of juvenile redfish are consumed by cod (Lilly and Gavaris, 1982; Lilly, MS 1985), and small redfish are eaten by larger redfish (Gavaris and Legge, MS 1981; Konstantinov *et al*., 1985).

Recruitment

Population numbers of redfish by age-group, estimated from Canadian stratified-random bottom-trawl surveys in 1979–85, were reported by Power and Atkinson (MS 1986). The assignment of ages was based on ageing by otoliths. As noted above, most of the 7–8 cm individuals were classified as 2-year-olds, there being very few 1-year-olds in the series. In addition, peaks in the length frequency were assigned to older year-classes with increasing size. The inferred historical pattern from this analysis was that there tended to be sequences of several years of good recruitment and sequences of several years of poor recruitment. In contrast, the progression of modes in length frequencies may be interpreted to indicate that recruitment is very poor in most years, and that only occasional year-classes are strong (Templeman, 1976; Lilly and Gavaris, 1982). D. Power and D. B. Atkinson (Northwest Atlantic Fisheries Centre, St. John's, Nfld., pers. comm., 1986) opined that errors in age reading may smooth year-class strengths, and that the progression of modes in length frequencies is probably a more reliable indicator of the frequency of occurrence of strong year-classes. An acceptable series of redfish year-class strengths is not yet available.

Recruitment to the fishery was assumed to occur at age 10 (about 25 cm) (NAFO, MS 1980). Chumakov *et al*. (MS 1986) indicated that 17–21 cm redfish at ages 4–5 in 1985 will be 19–24 cm in 1987 and will constitute a considerable part of the commercial catch in that year. Thus, if this age interpretation is correct, redfish on Flemish Cap are at least partially recruited to the fishery by age 7, and perhaps even younger.

Biology of Cod

Stock isolation

Studies on the discreteness of the Flemish Cap cod stock have been reviewed by Templeman (1976) and Lear *et al*. (1981).

Biology of adults

Distribution, growth and maturity. From winter surveys on Flemish Cap during 1977–83, cod were found mostly in depths less than 360 m, with no consistent confinement to particular areas of the bank (Wells, MS 1980a, MS 1983b), but their average size tended to increase with depth. They attain a length of 10–13 cm at the end of the first year in January–February and then grow about 10 cm per year (Wells, MS 1983c, MS 1986). There has been considerable variation in mean length-at-age, which increased from 1949–51 to the mid-1960's (1964, 1968) and again during the early 1980's (Wells, MS 1983c). Cod sampling in 1979 (winter) indicated that the lengths at which 50% of males and females became mature were 50 and 52 cm respectively (Wells, MS 1979). Estimates of fecundity have not been published.

Food and feeding. The prey spectrum of cod on Flemish Cap is relatively narrow, and most of the food comes from the pelagic food web (Konstantinov *et al*., 1985; Lilly, MS 1985). The major prey are hyperiid amphipods and planktivorous fish (juvenile redfish, myctophids, and juvenile cod). The hyperbenthic shrimp (*Pandalus borealis*) is important in some years. Epibenthic invertebrates, such as crabs, echinoderms, polychaetes and gastropods, are very minor components of the diet. In recent years, the food composition in winter has been dominated by juvenile redfish (Lilly, MS 1985).

Spawning time and area

Observations on maturity stages of gonads of cod during USSR bottom-trawl surveys confirm previous reports that the peak of cod spawning is in March, and spawning females have been found on most parts of the bank in depths between 200 and 500 m (Serebryakov *et al*., 1987). At the low spawning-stock biomass of recent years, one would probably not find dense spawning concentrations such as were found in the 1960's (see Templeman, 1976).

Very few eggs were caught during Canadian and USSR ichthyoplankton surveys (Anderson, MS 1982a, 1982b; Serebryakov *et al*., 1987), and, consequently, very little information on timing and location of spawning can be inferred from egg distribution.

Biology of eggs and larvae

Very little was learned during this project about the biology of cod eggs and larvae, because both were caught in extremely low numbers. During the Canadian surveys, larval abundance was highest in 1981 (Anderson, MS 1982b). With larval size expressed as standard length (SL), growth rates for three periods in 1981 ranged from 0.20 to 0.42 mm SL/day, and mortality rates during the same periods ranged from 0.023 to 0.079/day. The peak of hatching, estimated by back-calculation of length-at-age to a hatching length of 3.5 mm SL, was April 23 (Anderson, MS 1982b). There have been no reports on the predators of cod eggs and larvae or on the prey of cod larvae.

Biology of juveniles

Distribution, growth and mortality. In the absence of specific surveys to sample juvenile cod within the year of hatching, the first opportunity for catching each cohort was the Canadian bottom-trawl survey in the following winter. In some years, good numbers of age 1 and large numbers of age 2 cod were caught (Wells and Baird, MS 1985). The distribution of these juveniles has not been described. While growth rates may be calculated from mean length-at-age data, reliable mortality rates cannot be calculated from the catch-at-age data because 1-year-old and 2-year-old cod are not fully susceptible to capture by the research trawl (Wells, MS 1983a).

Food and predators. The food of young cod (ages 0 and 1) has received little attention. Older juveniles (ages 2 and 3) have been found to feed on calanoid copeods, hyperiid and gammarid amphipods, euphausiids, shrimp and small fish, particularly myctophids and small redfish (Lilly, MS 1979, MS 1985; Konstantinov *et al*., 1985). There is a gradual increase in prey size with increasing predator size. Juvenile cod are preyed upon by larger cod (Lilly, MS 1982, MS 1983, MS 1985).

Recruitment

Indices of recruitment are available from Canadian and USSR surveys on Flemish Cap. Population numbers by age-group have been estimated from Canadian stratified-random bottom-trawl surveys in 1978–85 (Wells and Baird, MS 1985), and mean catch (per tow) of young cod (ages 1–3) has been calculated for USSR bottom-trawl surveys since 1959 (e.g. Konstantinov and Noskov, MS 1978; Bulatova, MS 1984).

Numbers of recruits at age 3 are available from sequential population (cohort) analysis of a time series of catch-at-age data (Wells, MS 1980b). Biological sampling of commercial catches on Flemish Cap has always been poor, but it was particularly weak in some years between 1964 and 1971. Thus, estimates of stock size are available for 1959–68 and for 1972–79. The later series was extended to 1980 by Gavaris (MS 1981). Sampling was inadequate again in the early 1980's, and no analytical assessment was carried out until Wells *et al*. (MS 1984) attempted a cohort analysis. There was little confidence in the estimates of population numbers after 1980, but there was more confidence in the estimates for 1978–80 (NAFO, 1984, p. 41). Cohort analysis was not attempted in 1985 and 1986. Thus, while estimates of population numbers span the 1959–84 period, they are not available for some years and are suspect for many others.

For the purpose of the Flemish Cap studies, the index of recruitment was considered to be the number of 4-year-olds on January 1 (Akenhead, MS 1978; NAFO, MS 1980). Derivation of an adequate index for year-classes which were spawned after 1979 will be difficult because of inadequate sampling, intensive fishing of some year-classes at age 3, and possible substantial discarding of some year-classes at age 2 (NAFO, 1984, 1985).

Correlation Studies

The relationship between year-class strength of cod and variation in the physical environment was analyzed by Konstantinov (MS 1981), who found an inverse relationship between the abundance of juveniles (ages 1 and 2) in USSR bottom-trawl surveys of 1968–79 and mean water temperature in the 0–50 m layer on a USSR hydrographic section across the eastern slope of Grand Bank (45°57'N, 48°30'W to 45°20'N, 47°22'W). The analysis could be extended by the addition of data for recent years, but the indices of year-class strength from the USSR surveys are not well correlated with indices from cohort analysis and the hydrographic section is actually on the eastern edge of Grand Bank southwest of Flemish Cap.

Akenhead (MS 1982) examined the relationship between abundance of 3-year-olds, as determined from cohort analysis, and surface (0–20 m) temperature and salinity on Flemish Cap in the year when each year-class was spawned and found no significant correlation. He also examined the relationship between year-class strength and wind direction and found a significant correlation involving wind direction in March. He discussed possible mechanisms for such early, large-scale meteorological effects but none could be well supported, given the poor level of understanding of oceanography and production cycles on Flemish Cap.

Causal Mechanism Studies

Studies which relate directly to investigating the 12 major factors that were proposed to explain variation in year-class strength (Akenhead, MS 1978) (Table 1) are reviewed in this section.

Size of spawning stock (A.1)

Akenhead (MS 1982) examined the results from cohort analysis of cod catches by age and found no relationship between the number of 3-year-olds and biomass of the spawning stock (ages 5+ or 6+). This was not due to insufficient variability, because both stock size and recruitment varied considerably in the period from the late 1950's to the late 1970's (Anderson, MS 1982b; Akenhead, MS 1982). As noted above, there is considerable uncetainty regarding the estimates of number-at-age. In addition, the proportion of mature-at-age fish is not known for most years and may have varied, for the growth rate increased considerably from the 1960's to the 1980's (Wells, MS 1983c). Sampling of the commercial catch has been very poor since the late 1970's, and, consequently, recruitment and spawning stock size have been poorly estimated from commercial catch data during the period of the Flemish Cap project (1978–86).

In 1982, the working group on the Flemish Cap project recommended that emphasis be placed on the response of the cod stock to a reduction in stock size (NAFO, 1982). This would include looking for changes in length (weight) and maturity of cod by age-group. A problem at present is that the cod stock has been at a very low level since the project started, and the available data represent only the lower end of the range of possible stock sizes.

There has been no study of the relationship between recruitment and spawning stock size in redfish.

Condition of spawning stock (A.2)

Variation in the energy available per cod may be reflected by changes in fecundity-at-weight and quality of eggs, but no information on such changes have been reported. Data on size of gonads, liver, soma and other body parts of cod have been collected since the project began (e.g. Wells, MS 1982a, 1982b), but there are no reports of such data being collected for redfish.

Predation upon juveniles (B.1)

Juvenile cod are preyed upon by larger cod. Lilly (MS 1982) reported that the incidence of cannibalism on 1-year-olds increased in 1982 after several years of low incidence. Konstantinov *et al.* (1985) also reported that the incidence of cannibalism was higher in 1982 than in 1979–81. The increase in 1982 coincided with the appearance of a large year-class in 1981. Cod preyed on cod of age-groups 1 and 2 in the winter of 1983 (Lilly, MS 1983) and on age-groups 1–3 in the winter of 1984 (Lilly, MS 1985).

Large numbers of juvenile redfish have been found in cod stomachs. In 1978, 1979 and 1981, cod preyed primarily on age 1 redfish, but the number of age-classes increased from 2 in 1982 to 4 in 1984 (Lilly and Gavaris, 1982; Lilly, MS 1983, MS 1985). The 1978 year-class of redfish was abundant in cod stomachs in 1979 but was present in very small numbers in 1980 (Lilly and Gavaris, 1982). Konstantinov *et al.* (1985) also reported a high incidence of cod predation on redfish in 1979 and very low incidence in 1980, but they did not state which redfish year-classes were involved. The rapid decline of the 1978 year-class from age 1 to age 2 indicates that mortality of juveniles can be high. The role of cod predation remains speculative (Lilly and Gavaris, 1982). Juvenile redfish are also preyed upon by larger redfish. The incidence of cannibalism was 7% in 1979, nil in 1980, and 5% in 1981 (Konstantinov *et al.*, 1985), reflecting the pattern of predation on redfish by cod.

The contribution of predation of juveniles to variability in year-class strength will be difficult to assess with the information available. There is need for better information on gastric evacuation rate, which can be obtained. Also, there is need for more complete seasonal information on predation, particularly in the autumn when 0-group juveniles first become available to demersal predators. Even if consumption rates can be reliably estimated, the contribution of such removals to the total mortality rate would be difficult to measure without independent measures of abundance.

Predation upon eggs and larvae (B.2)

This hypothesis has received very little attention. It may be possible to estimate the abundance of potential predators in the zooplankton from plankton surveys. Predation by juvenile redfish and cod and by other fish, such as myctophids, is also a possibility.

Predation upon adults (fishing) (B.3)

This hypothesis is important because of the effect of fishing on the spawning stock biomass (see hypothesis A.1).

Influence of physical environment on adults (C.1)

This factor was considered to be unimportant and was therefore not studied.

Influence of physical environment on eggs and yolk-sac larvae (C.2)

The major physical effect under consideration was the possibility that eggs and larvae may be washed off Flemish Cap. Kudlo and Boytsov (1979) obtained a coefficient of multiple correlation of 0.87 from an analysis relating mean catch-per-tow of 2-year-old cod in USSR surveys to two parameters "defining the horizontal and vertical water circulation" on Flemish Cap. Good year-classes were associated with intensified circulation. As noted above, estimates of year-class strength from USSR trawl surveys are not well correlated with estimates from cohort analysis.

Kudlo *et al.* (1984) described the patterns of water movement at the time of 26 oceanographic surveys on Flemish Cap during 1977–82. They did not try to relate the patterns to year-class strength of cod and redfish. They did say, however, that year-to-year variation in retention of ichthyoplankton is undoubtedly one of the reasons for variability in year-class strength, with the expection that good year-classes of cod and redfish would occur in years when a high frequency of anticyclonic circulation types prevailed during the period from spawning until the larvae have acquired the ability to avoid considerable transport by currents. They noted that validation of this hypothesis would require very detailed information on distribution of eggs and larvae during the early stages of development, coincident with reliable information on variation in water movements over the bank.

Influence of physical environment on swimming larvae (C.3)

The potential of being washed off Flemish Cap, as noted in the preceding paragraph, exists for swimming larvae as well. Redfish larvae are usually found over the shallow areas of the bank by late May, but a large catch of larvae was taken on the southeastern edge of the bank over a depth of 800 m during the last week of May 1983 (Serebryakov *et al.*, 1987). It is not known if these larvae were subsequently lost from Flemish Cap, but all six drogued buoys that were deployed on Flemish Cap in 1979–80 left the bank over the southeastern area (Ross, 1981).

The other physical variable which has received attention is temperature. From sampling in May 1980, Anderson (MS 1982c) found that the condition of redfish larvae was positively correlated with water temperature. Anderson (1984) also postulated that high mortality of redfish larvae in certain years may have been associated with temperatures which were not only unusually high but also were increasing at a greater-than-normal rate.

Influence of physical environment on juveniles (C.4)

No information on this topic has been reported.

Food availability for prespawning mature fish (D.1)

The food of cod on Flemish Cap has been studied throughout the project (Konstantinov *et al.*, 1985; Lilly, MS 1985) but not with the desired seasonal coverage. There has not yet been an investigation of how annual variation in quality and quantity of prey might affect the spawning potential of the cod stock. Lilly (1980) postulated that the growth rate of cod might be influenced by the availability of juvenile redfish as prey. Data collected during 1978–85 may permit a test of this hypothesis. The food of redfish has also been studied, but it has been reported only on a percent occurrence basis (Konstantinov *et al.*, 1985).

Food availability for larval fish (D.2)

Much data have been collected on primary and secondary producers and the stomach contents of larval fish, but little has been published to date. Anderson (MS 1980) described the distribution of phytoplankton, measured as chlorophyll a, during April–May 1979. Flemish Cap is an area of relatively high production and biomass, but productivity is not spatially uniform. The central area of the bank was found to be low in chlorophyll a and was surrounded by a larger area of higher values with greater variability. Highest values tended to occur to the north and west. Konstantinov *et al.* (1985) stated that phytoplankton was abundant over the southwestern slope in March 1981 and to the west and north in April of that year. Anderson (MS 1980) speculated that "surface waters are probably limited by some degree of nutrient limitation due to seasonal stratification in waters overylying Flemish Cap". He noted that the central area is surrounded on all sides, especially to the north and west, by a dynamic boundary area of variable but much higher biomass and production, and he suggested that this boundary area should be subject to considerable mixing, largely from the Labrador Current water which impinges on the northern and western slopes of the bank, and therefore is not subject to nutrient limitation.

The zooplankton on Flemish Cap is dominated by copepods, the most important of which are *Calanus finmarchicus* and *Oithona similis* (Konstantinov *et al.*, 1985). The distribution and abundance of the various developmental stages of *C. finmarchicus* have been described for 1979 and 1981. Akenhead (MS 1980) estimated that mass spawning in 1979 began about 31 March and peaked about 10 April. In 1981, there was a progression from nauplii in March to copepodite stages I–III in April and to copepodite stage IV–V in May (Konstantinov *et al.*, 1985). In both years, copepods were most abundant over deep areas to the west and north.

In summary, primary and secondary productivity is highest in the west and north. The extrusion of redfish larvae in these areas in April and early May would seem to be appropriately timed to match the appearance of copepod eggs and nauplii. The degree of "match" or "mismatch" has not been studied. Relationships between prey availability and feeding and between feeding and survival, both within and among years, have not been reported.

Food availability for juvenile fish (D.3)

The food of 0-group juveniles has not been reported, but some stomach-content data are available for older juvenile cod (Konstantinov *et al.*, 1985; Lilly, MS 1985). The relationship between food availability and survival has not been investigated.

Concluding Remarks

Several major problems were identified about 3 years after the start of sampling in 1978. Despite these problems, much as been learned about the biology of cod and redfish on Flemish Cap. Several significant events have been observed.

1. A strong year-class of cod, the 1981 year-class, arose from a small spawning stock.
2. Two strong year-classes (1980 and 1981?) of redfish were born. These have not yet been recruited to the fishery, but they should do so in a year or two. An analysis of length frequencies has indicated that strong year-classes occur infrequently.
3. Growth rates of redfish larvae in 1980 and 1981 differed considerably. The significance of this for subsequent recruitment is not known.
4. The 1979 year-class of redfish larvae virtually disappeared by midsummer after an apparently successful extrusion.
5. A year-class of juvenile redfish (the 1978 year-class?) was relatively strong at an early age (age 1?) but was reduced to very low abundance within a year.

Analyses of unreported data and a synthesis of results may help in interpretation of these and other events and may contribute to an understanding of factors which influence recruitment in the major groundfish species on Flemish Cap.

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