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A Synopsis of Research Related to Recruitment of Cod and Redfish on Flemish Cap

by

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SPECIAL SESSION ON RECRUITMENT

INTRODUCTION

A cooperative international program of research into the causes of variation in year-class strength of demersal fish was initiated by ICNAF in the mid-1970's. The area selected for an intensive study was Flemish Cap (47°N; 45°W), a plateau east of the northern Grand Bank and separated from it by the deep (>1000 m) Flemish Pass. This isolated bank has supported major fisheries for only two species: cod (*Gadus morhua*) and redfish (*Sebastes* spp.). Other groundfish 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 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).

II. Overview of the Flemish Cap Project

Proposal for a Flemish Cap 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 controlling 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 Environmental Working Group met later in 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 1975a). 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 herring in the Georges Bank - Gulf of Maine area and cod (and redfish) on Flemish Cap. Flemish Cap was chosen for the groundfish study for the following reasons (ICNAF, MS 1975a):

1) Fluctuations in year class strength of both cod and redfish were regularly observed in this area.

2) The stocks of cod are discrete and confirmed as separate from those of the Grand Bank.

3) The circulation patterns are likely quite amenable to study.

4) The area is reasonably restricted in size.

5) 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 spring 1975, reviewed biological data on Flemish Cap groundfish stocks and major features of the oceanography of Flemish Cap, and confirmed those advantages of Flemish Cap cited above (ICNAF, 1975b). The only recommendations were that there be further reviews and analyses of the available data. (This slow progress contrasted with the numerous detailed proposals for research on herring.) Because some of the data requested in 1975 were still not available in 1976, no progress toward a research proposal could be made (ICNAF, 1976). Accordingly, a 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 Redbook 1977. p. 43).

Hypotheses and proposed research

The Working Group meeting in Murmansk in 1977 "identified three major problems that should be considered in order to predict the survival of different year-classes:

i) the effect of water circulation patterns and the abundance and size composition of the planktonic food supply on the retention and the survival of fish larvae on Flemish Cap;

ii) the effect of intraspecific and interspecific predation on the survival of juvenile fish; and

iii) improved assessment of the size of the spawning stocks" (ICNAF, 1977).

To address larval survival, it was proposed that a grid of about 50 oceanographic and simultaneously-occupied ichthyoplankton stations be occupied every two weeks throughout the period of spawning and larval development (February to June). 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 juvenile survival, it was proposed that a pelagic and bottom trawl survey be conducted in both March and September.

To address assessment of adults, 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 continue. Participating countries should conduct joint cruises to calibrate fishing gear and other instruments. Participating countries were urged 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, Canada and the USSR planned to undertake a less extensive program if participation by other countries were insufficient to implement the full program. The reduced program would involve surveys in late March, in April, and in May to estimate the size of the cod stock and to identify the drift pattern of eggs and larvae. The pelagic survey for juvenile fish would have low priority. There was no statement of what accomplishments were anticipated from a program reduced well below that considered necessary to ensure a reasonal probability of success.

In September 1977 a group of Canadian scientists met to expand upon the proposals developed at the Murmansk meeting (Akenhead, MS 1978). They decided that the experiment should focus on cod and 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 divisions: physical environmental conditions, predation conditions, food abundance conditions, and characteristics of the spawning stock. By making reference to the stage of the life cycle involved, a total of twelve hypotheses were developed (Table 1). These hypotheses were more explicit than those arising from the Murmansk meeting, and included some hypotheses not proposed in 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 also provided detailed lists of the data required to test each hypothesis, and 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 to date it has been little used as a framework for gauging progress in the testing of specific hypotheses.

Sampling and reviews of progress

With the exception of a Polish plankton survey in April 1978 (Grimm et al., MS 1980), all research specific to the Flemish Cap Project was conducted by Canada and the USSR. That is, the reduced program of research came into effect. Canada conducted one plankton survey in 1978, three or four surveys each year from 1979 to 1981, and single surveys in 1982 and 1983. The USSR 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 USSR bottom-trawl surveys have continued into 1986. There were no surveys using gear specifically designed to catch juveniles. The special oceanographic program involving satellite-tracked buoys and current meter arrays was initiated in 1979 but discontinued in 1980 because of excessive loss of moored instruments. A summary list of data collected on Flemish Cap from 1949 to 1979 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, meeting in May 1978, reviewed new analyses of historic data and noted the start of sampling in early 1978 (ICNAF, 1978). Meetings in April 1979 (ICNAF, MS 1979a) and May 1979 (ICNAF, 1979b) recorded work that had been performed to that date, and 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. This meeting, held in January 1980, accomplished its goals and concluded that no major changes in approach were necessary (NAFO, MS 1980a). A meeting in September 1980 reviewed additional new data and recommended that participants give high priority to the analysis of all existing information (NAFO, 1980b). 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 may be summarized as follows:

1) 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.

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

3) 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 juvenle fish program, there were uncertainties 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.

4) The oceanographic program was crippled by the curtailment of the moored current meter program.

5) Fishing effort on Flemish Cap was high, and monitoring of catch and effort was poor.

There followed a recommendation for a reappraisal of the aims of the Flemish Cap project.

Discussions in June 1982 were guided by a prospectus on future research 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 listed in Table 1, the recommendation was for a change in emphasis from hypotheses C2, C3, and D2 to hypothesis A1 (and possibly A2).

There followed one more meeting in June 1983 (NAFO, 1983). 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.

III 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 has frequently been found over the central portion of the bank.

The records from current meters moored on Flemish Cap in 1979 support the hypothesis of a weak anticyclonic gyre (Ross, MS 1980). They also indicate a strong semi-diurnal tidal signal and a 4-day periodicity in the current pattern, particularly in the spring. The drift patterns of six satellite-tracked buoys deployed on Flemish Cap at intervals between January 1979 and May 1980 show a general sluggish circulation over the central part of the bank, with a trend toward an anticyclonic rotation (Ross, 1981). All buoys exited from the southeastern 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 the Cap itself 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 top 100 m on the Cap to demonstrate that Flemish Cap water is derived exclusively from Labrador Current water. About 50% of Flemish Cap surface waters are 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 1982b). From all available temperature and salinity data in April and May it was possible to detect six regions. 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) provide monthly means of temperature and salinity for five regions on Flemish Cap plus Flemish Pass. 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 3-4°C throughout the year, whereas the temperature at 20 m varies from about 4° in March-April to about 12° in September. The most rapid warming of near-surface waters 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 (1982a) presented an analysis of anomalies of water temperature and salinity at selected stations on the 47°N oceanographic section for the decade 1970-79. Akenhead (MS 1981) provided monthly (March to September) means of surface (0-20 m) temperature and salinity for the years 1955-80. Only stations from depths less than 400 m were chosen. Bailey (MS 1982) obtained temperatures for Flemish Cap from weekly synoptic sea-surface temperature charts, prepared from data provided in weather reports by "ships of opportunity" during 1962-81. The annual cycle has a mean of 7.5°, with a minimum of 3.2° in February and a maximum of 13.0° in August. Annual and seasonal departures from normal were presented.

IV Biology of redfish

Redfish: species composition and stock isolation

Three species of redfish (*Sebastes mentella*, *S. fasciatus*, *S. marinus*) occur on Flemish Cap (Ni, 1982; Ni and McKone, 1983). Common names recently assigned by Robins et al., (1986) are deep-water redfish (*S. mentella*), Acadian redfish (*S. fasciatus*) and golden redfish (*S. marinus*).

Adult *S. mentella* and *S. fasciatus* cannot be distinguished readily in the field, but can be separated on the basis of 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 (see review in Penney, 1985). Redfish larvae caught on Flemish Cap have been identified simply as *Sebastes* spp. (Anderson, 1984; Serebryakov et al., MS 1984; Penney and Evans, 1985).

There appear to have been no studies of the isolation of the redfish stocks since Templeman (1976) concluded that "the redfish stocks on Flemish Cap, at least of 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."

Redfish: 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 plus 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 caught in 14 tows on line transects occupied during 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 proportions 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.

A high proportion of the commercial catch of redfish on Flemish Cap is caught with midwater trawl (Chekhova and Konstantinov, 1978) indicating that much of the redfish are pelagic. Chekhova and Konstantinov (1978) found differences in biological characteristics between beaked redfish caught with midwater trawl and individuals caught with bottom trawl, 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, about 30cm by age 12, and 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), ages estimated from otoliths tend to be greater than those estimated from scales. Females grow more quickly than males (Sandeman, 1969).

Maturity and fecundity

Redfish start to mature at a length of 27-28 cm and most are mature by 33-35 cm. Males mature at a smaller size than females (Chekhova and Konstantinov, MS 1979). There are no published reports on fecundity.

Food and feeding

Redfish on Flemish Cap are primarily pelagic feeders (Konstantinov et. al., 1985). The most frequently occurring prey in 1979-82 were pelagic invertebrates (copepods, hyperiid amphipods and euphausiids), shrimp (Pandalus borealis), and fish, the dominant group being myctophids. Young redfish are found occasionally. Stomach fullness is highest in summer (June-August).

Redfish: extrusion time and area

Estimates of extrusion time are available from three sources: maturity stages of adult redfish, abundance and size of larvae caught in ichthyoplankton surveys, and estimation of date of extrusion of individual larvae from counts of circuli in otoliths.

Penney et al., (MS 1984) observed the state of maturity of redfish caught in February and March 1983. Using estimates from the literature for the length of time from fertilization to hatching and from hatching to extrusion, they estimated that extrusion of larvae by S. mentella and S. marinus would peak in mid to late April and extrusion by S. fasciatus would peak in early to mid-May. Observations of maturity stages are also provided by Serebryakov et al. (MS 1984) for beaked redfishes and S. marinus.

The abundance of recently extruded larvae reaches a peak in late April (Anderson, 1984) or mid-to-late April (Serebryakov et al., MS 1984). There is evidence from length frequencies of larvae caught in July and August of a second but much smaller extrusion peak occurring during the second to third week of June (Anderson, 1984). Serebryakov et al. (MS 1984) state that the second peak occurs in July-August.

Penney and Evans (1985) obtained ages of larval redfish collected from late June to July by counting increments in otoliths. Back-calculation to the date of extrusion indicated an extrusion peak during the last two weeks in April and a decline through May with some residual extrusion still occurring into July. There is evidence of a very small peak in late June.

The distributions of recent extruded larvae in March and April, as determined during surveys by Canada (Anderson, 1984), Poland (Grimm et al., MS 1980) and the USSR (Serebryakov et al. MS 1984; Akhtarina and Chechenin, MS 1985) illustrate that extrusion begins in March in the southwest and by mid-April has spread to all areas in depths greater than 200 m.

Redfish: biology of larvae

Distribution

After April redfish larvae become widely distributed over Flemish Cap, with highest densities in June and July often occurring near the centre of the bank (Anderson, 1984; Serebryakov et al., MS 1984; Akhtarina and Chechenin, MS 1986). Serebryakov et. al. (MS 1984) state that this change in distribution is 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 a very high total mortality so, 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.

Larvae tend to be concentrated in the upper 10 or 20 m of the water column (Serebryakov et al., MS 1984).

Growth rate

Estimates of growth rates of redfish larvae in 1980 and 1981 are available 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 daily growth rate was 0.156 mm/d in 1980 and 0.109 mm/d in 1981". "Individual growth histories ...varied considerably with age and extrusion date. Larvae typically grew slowly for 10-15 days after extrusion and then rapidly for 60-70 days before slowing as they entered the pelagic juvenile stage". Anderson estimated a growth rate of 0.037 mm/day for early May to late May 1981 and 0.146 and 0.163 mm/d for late May to late July - early August, 1980 and 1981, respectively. Estimates from the two techniques are similar for 1980, but very different for 1981. Possible reasons are discussed by Penney and Evans (1985).

Mortality

Anderson (1984) examined the numbers at length estimated from Canadian surveys in 1980 and 1981, and isolated that portion of the population assumed to be derived from the late April peak in spawning. From abundance estimates for this group only, he calculated mortality rates in 1981 of 0.04 between early May and late May, 0.06 between late May and late June, and 0.13 between late June and early August. In the period from late May to late June-early August, the mortality rate was twice as high in 1981 (0.093/day) as in 1980 (0.043/day).

Estimates of larval abundance are also available from USSR surveys in 1978-81 and 1983 (Serebryakov, et al., MS 1984) and can be calculated for surveys in 1984 and 1985 (Akhtarina and Chechenin, MS 1985, MS 1986). Although many of the estimates are close to the curve in Fig. 2, there are two instances in which sampling was coincident and the Canadian estimates 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 Canadian and USSR estimates, especially for 1980 and 1981, by applying the results of the ichthyoplankton gear calibration study conducted in 1981 (NAFO, 1980). Results from USSR surveys may not be very useful for redfish, however, because all surveys but one (July 1978) were conducted before or during early June, and are therefore confined to the early larval period.

Food and predators

Preliminary results of feeding studies indicate that copepod eggs and nauplii were the major prey in April 1979, and adult Oithona similis, a herbivorous copepod, was the major prey in July 1979 (Anderson and Akenhead, 1981). There are no reports on the predators of redfish larvae.

Redfish: biology of juveniles

Distribution

There were no surveys designed specifically to catch juvenile fish, and no bottom-trawl surveys were 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 winter (Atkinson, MS 1985) and by the USSR in spring-summer (Chumakov et al., MS 1986). The smallest juveniles caught have been 7-8 cm. In years of high abundance these are 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 11-12cm tend to have the same distribution. Distribution of larger juveniles has not been reported.

Growth rate

The age of 7-8cm redfish caught in winter-spring remains uncertain (Lilly and Gavaris, 1982; NAFO, MS 1986). They are estimated by Canadian interpretation of otolith annuli to be 2-year-olds (Gavaris & Legge, MS 1981; Power and Atkinson, MS 1986), whereas an interpretation of the progression of modes would indicate they are 1-year-olds (Lilly and Gavaris, 1982). USSR age interpretation indicates they are 1-year-olds (Chumakov et al., MS 1986). Resolution of this problem is essential for determining the correspondence between larvae caught in spring-summer and juveniles caught in winter-spring.

The growth rate of juvenile redfish is slow, but estimates of growth rate vary. Based on age reading of otoliths collected in July 1956 and November 1958 (Templeman, 1976), Sandeman (1969) found that redfish attain a length of about 19-20 cm by late age 5. Based on age reading of otoliths collected from juveniles caught in the early 1980's, Power and Atkinson (MS 1986) found that juveniles attain a length of only about 14 cm by winter of age 5. Based on the progression of modes in length-frequencies of the catches studied by Power and Atkinson (MS 1986), Lilly (MS 1986) estimated that juveniles attain a length of about 20 cm by winter of age 5.

Mortality

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

Food and predators

The food of juvenile redfish has not been reported.

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).

Redfish: recruitment

Population numbers at age estimated from Canadian stratified-random bottom-trawl surveys from 1979 to 1985 are provided by Power and Atkinson (MS 1986). The assignment of ages is based on ageing of otoliths. As noted above, most 7-8 cm individuals are aged as 2-year-olds. There are very few 1-year-olds in the series. In addition, peaks in the length frequency are assigned to older year-classes as the redfish age. The historical pattern from this analysis is that there trend 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 only occasional year-classes are strong (Templeman, 1976; Lilly and Gavaris, 1982). 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) expect that specimens 17-21 cm long at age 4-5 in 1985 will constitute a considerable part of the commercial catch at a length of 19-24 cm in 1987. Thus, if the USSR age interpretation is correct, redfish on Flemish Cap are at least partially recruited to the fishery by age 7, and perhaps even earlier.

V Biology of cod

Cod: stock isolation

The many studies demonstrating the discreteness of the Flemish Cap cod stock are reviewed by Templeman (1976) and Lear et al., (1981).

Cod: biology of adults

Distribution

Most cod are found in depths of 360m or less (Wells, MS 1980a, MS 1983b). Highest catch rates during Canadian surveys in winter 1977-83 were not consistently confined to any region of the bank (Wells, MS 1983b). The average weight of cod tends to increase with depth (Wells, MS 1980a).

Growth rate

Cod on Flemish Cap attain a length of 10-13cm by January-February of age 1 (Wells, MS 1986), and then grow about 10cm per year (Wells, MS 1983c). Mean length at age increased from the period 1949-51 to the mid-1960's (1964, 1968), and then increased again by the early 1980's (Wells, MS 1983c).

Maturity and fecundity

In winter 1979, the lengths at which 50% of males and females were mature were about 50cm and 52 cm, respectively (Wells, MS 79). Measures of fecundity have not been published.

Food and feeding

The prey spectrum of cod on Flemish Cap is relatively narrow, and most 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, 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).

Cod: spawning time and area

Observation of maturity stages of gonads of cod caught during USSR bottom-trawl surveys confirm previous reports that the peak of cod spawning is in March (Serebryakov et al., MS 1984). Spawning females have been found in most parts of the bank in depths between 200 and 500 m (Serebryakov et al., MS 1984). At the low stock spawning biomass of recent years, one would probably not find dense spawning concentrations such as were found in the 1960's (see review in Templeman, 1976).

Very few eggs were caught during Canadian and USSR ichthyoplankton surveys (Anderson, MS 1982a, b; Serebryakov et al., MS 1984), so very little information on timing and location of spawning can be inferred from egg distribution.

Cod: biology of eggs and larvae

Very little was learned during this study about the biology of cod eggs and larvae because both were caught in extremely low numbers. In Canadian surveys larval abundance was highest in 1981 (Anderson, MS 1982b). Growth rates calculated for three periods in this year 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 were no reports concerning either predation on cod eggs and larvae or the prey of cod larvae.

Cod: biology of juveniles

Distribution, growth rate and mortality

The first opportunity for catching each cohort of juvenile cod was the bottom-trawl survey in winter. In some years good numbers of age 1 cod and large numbers of age 2 cod were caught (Wells and Baird, MS 1985). The distribution of these juvenile cod has not been described. Growth rates may be calculated from mean lengths at age (eg. Wells, MS 1983a). Reliable mortality rates cannot be calculated from the catch at age because cod of ages 1 and 2 are not fully recruited to the research trawl (Wells, MS 1983a).

Food and predators

The food of young juveniles (age 0 and 1) has received little attention. Older juveniles (age 2,3) feed on calanoid copepods, hyperiid and gammarid amphipods, euphausiids, shrimp, and small fish, particularly myctophids and 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).

Cod: recruitment

Indices of recruitment are available from both survey data and cohort analysis.

Population numbers at age estimated from Canadian stratified-random bottom-trawl surveys in 1978-85 are provided by Wells and Baird (MS 1985). Mean catch/tow of cod of ages 1-3 is available from USSR bottom-trawl surveys (e.g. Bulatova, MS 1984).

Numbers of recruits at age 3 are available from cohort analysis (Wells, MS 1980). Biological sampling of the commercial catch from Flemish Cap has always been poor, but it was particularly weak in some years between 1964 and 1971. As a result, stock size estimates are available for 1959-68 and for 1972-79 (Wells, MS 1980). 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 presented until Wells et al., (MS 1984) attempted a cohort analysis. STACFIS had little confidence in the estimates of population numbers for the last few years, but put more confidence in the estimates for 1978-80 (NAFO Council Reports, 1984: p. 41). Cohort analysis was not attempted in 1985 and 1986. Thus, estimates of population numbers span the period from 1959 to 1983, but are not available for some years and are suspect for many.

For the purpose of this study the index of recruitment was the number of 4-year-olds on January 1 (Akenhead, MS 1978; NAFO, MS 1980a). Derivation of an adequate index for year-classes 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 Council Reports, 1984 (p. 40), 1985 (p. 53)).

VI. Correlation studies

There have been only two recent analyses of the relationship between year-class strength and variation in the physical environment.

Konstantinov (MS 1981) found an inverse relationship between the abundance of juvenile cod (ages 1 and 2) in USSR bottom trawl surveys in 1968-79 and mean water temperature in the 0-50 m layer on USSR hydrographic section 4A. The analysis could be repeated with recent years added, but it may be noted that indices of year-class strength from USSR surveys are not well correlated with indices from cohort analysis, the hydrographic section is southwest of Flemish Cap, and the relationship is highly dependent on a single point.

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. Significant correlations were not found. Akenhead (loc. cit.) also examined relationships between year-class strength and wind direction, and found significant correlations 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.

VII. Causal mechanism studies

This section will briefly review studies directly related to investigating the twelve major factors proposed to explain variation in year-class strength (Akenhead, MS 1978) (Table 1).

1) The size of the spawning stock

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

In 1982 the Flemish Cap Working Group 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) at age and maturity at age. A problem at present is that the cod stock has been at very low levels since the project started, so data have been collected for only the low range of possible stock size.

There have been no studies of the relationship between recruitment and spawning stock size in redfish.

2) The condition of the spawning stock.

Variation in the energy available per cod may be reflected in change in both fecundity at weight and quality of eggs produced. No information on changes in fecundity have been presented. 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, b). There are no reports of such data being collected for redfish.

3) Predation upon juveniles

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 coincides with the appearance of a large year-class in 1981. In winter 1983 cod preyed on both 1-and 2-year-old cod (Lilly, MS 1984) and in winter 1984 cod preyed on cod age-classes 1-3 (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 age-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 predation on redfish in 1979 and very low incidence in 1980, although they did not state which redfish age-classes were involved. The rapid decline of the 1978 year-class between age 1 and age 2 indicates that juvenile mortality 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 on juveniles to variability in year-class strength will be difficult to assess with the information available. We need better information on gastric evacuation rate, which can be obtained. We also need more complete seasonal information on predation, particularly in the autumn when 0-group juveniles are first becoming 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.

4) Predation upon eggs and larvae

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

5) Predation upon adults (fishing)

This hypothesis is important because of the effect of fishing on spawning biomass. See hypothesis 1.

6) Influence of physical environment on adults.

This was not studied, and has been considered unimportant.

7) Influence of physical environment upon eggs and yolk-sac larvae.

The major physical effect considered 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 a multiple correlation analysis relating mean catch/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.

As described in Section III, Kudlo et al., (1984) described the pattern of water movement at the time of 26 oceanographic surveys on Flemish Cap in the period 1977-1982. They did not try to relate the patterns to year-class strength in 1978-82. They did say: "Year-to-year variation in retention of ichthyoplankton is undoubtedly one of the reasons for variability in year-class strength... . In particular, good year-classes of cod and redfish would be expected to 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. 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".

8) Influences of physical environment upon swimming larvae

The potential of being washed off Flemish Cap, as described under hypothesis 7, exists for swimming larvae as well. By late May redfish larvae are usually found over the shallower areas of the bank, but during the last week of May 1983 a large catch of larvae was taken on the southeastern edge of the bank over a depth of 800 m (Serebryakov et al., MS 1984). It is not known if these larvae were subsequently lost from Flemish Cap, but the southeast is the region from which all six drogued buoys left the bank in 1979-80 (Ross, 1981).

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

9) Influence of physical environment upon juveniles

No information on this topic has been reported.

10) Food availability for prespawning mature fish

The food of cod on Flemish Cap has been studied throughout the project (Konstantinov et al., 1985; Lilly, MS 1985), but not with the seasonal coverage desired. 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 from 1978 to 1985 might permit a test of this hypothesis. The food of redfish has also been investigated, but only on a percent occurrence basis (Konstantinov et al., 1984), so the potential for further investigation is limited.

11) Food availability for larval fish

A lot of data were 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 was low in chlorophyll a and was surrounded by a larger area of higher values with greater variability.

Highest values tended to occur in the north and west. Konstantinov et al., (1985) stated that phytoplankton was abundant in the southwest in March 1981 and in 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 overlying Flemish Cap. Surrounding this central area on all sides, but especially to the north and west, is a dynamic boundary area of variable but much higher biomass and production. This boundary area should be subject to considerable mixing, largely from the Labrador Current water impinging on the north and west slopes of Flemish Cap bank, and therefore 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 (Akenhead, MS 1980) and 1981 (Konstantinov et al., 1985). Akenhead (MS 1980) estimated that in 1979 mass spawning began about March 31 and peaked about April 10. In 1981 there was a progresion from nauplii in March to copepodite stages I-III in April to copepodite stages IV-V in May (Konstantinov et al., 1985). In both years copepods were most abundant over deeper waters to the west and north.

To summarize, primary and secondary productivity are highest in the west and north. The extrusion of redfish larvae into this area 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.

12) Food availability for juvenile fish

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.

VIII. Concluding Remarks

As described in Section II, several major problems were identified only three years after the start of sampling in 1978. Despite these problems, much has been learned about the biology of cod and redfish on Flemish Cap, and several significant events were 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 indicates that strong year-classes occur infrequently in redfish.

3) Growth rates of redfish larvae differed considerably between 1980 and 1981. The significance of this for subsequent recruitment is not known.

4) The 1979 year-class of redfish larvae virtually disappeared by mid-summer 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?) and 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 our understanding of factors affecting recruitment in groundfish.

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

A. Spawning stock characteristics

- A.1 The size of the spawning stock determines YCS.
- A.2 The condition of the spawning stock determines YCS.

B. Abundance of predators

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

C. Physical environmental influences

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

D. Abundance of suitable food

- D.1 Food availability for prespawning mature fish determines YCS.
- D.2 Food availability for larval fish determines YCS.
- D.3 Food availability for juvenile fish determines YCS.

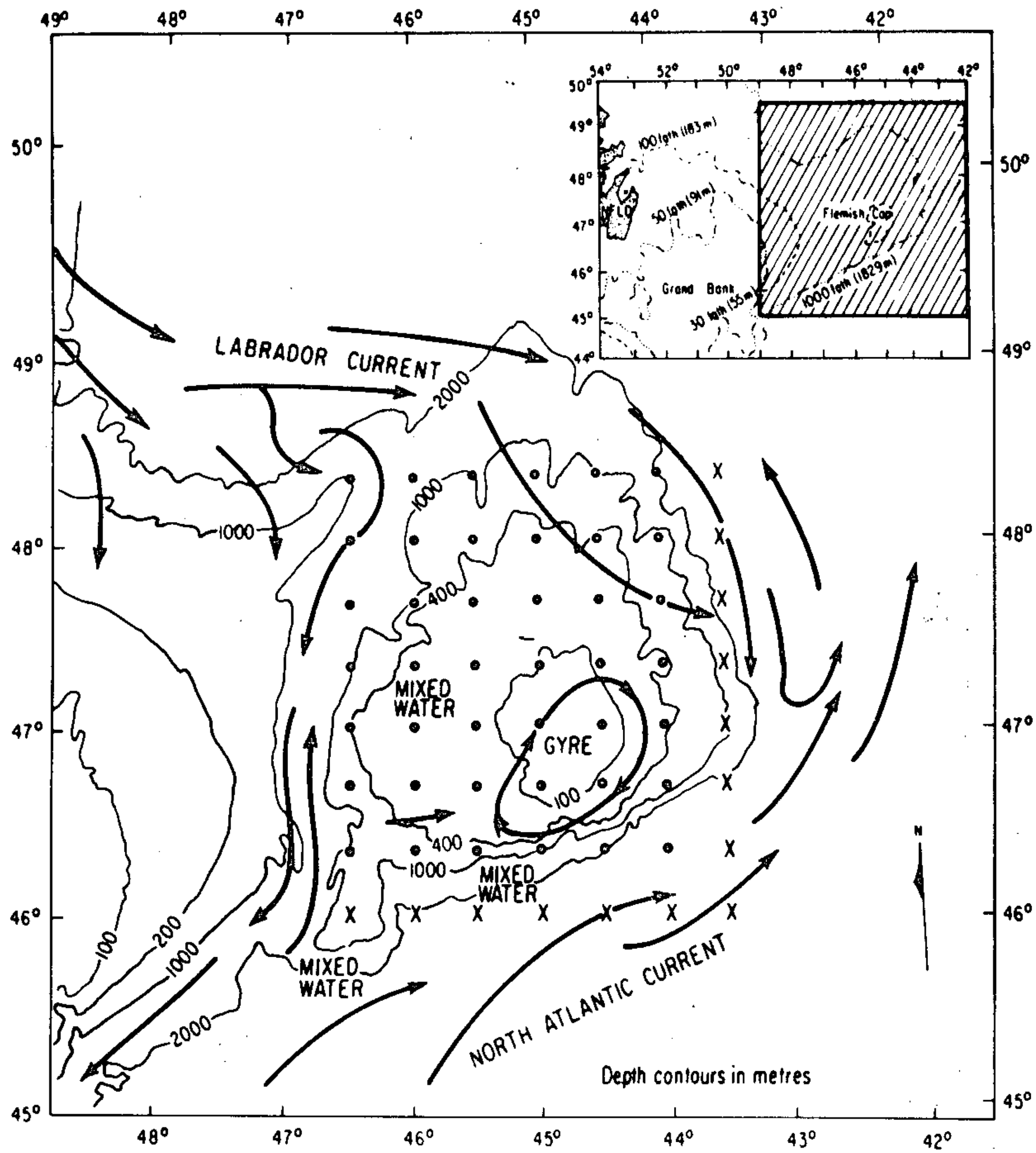

Fig. I. Flemish Cap bank, showing the main oceanographic features of the region and the study sampling grid (from Anderson, 1984).

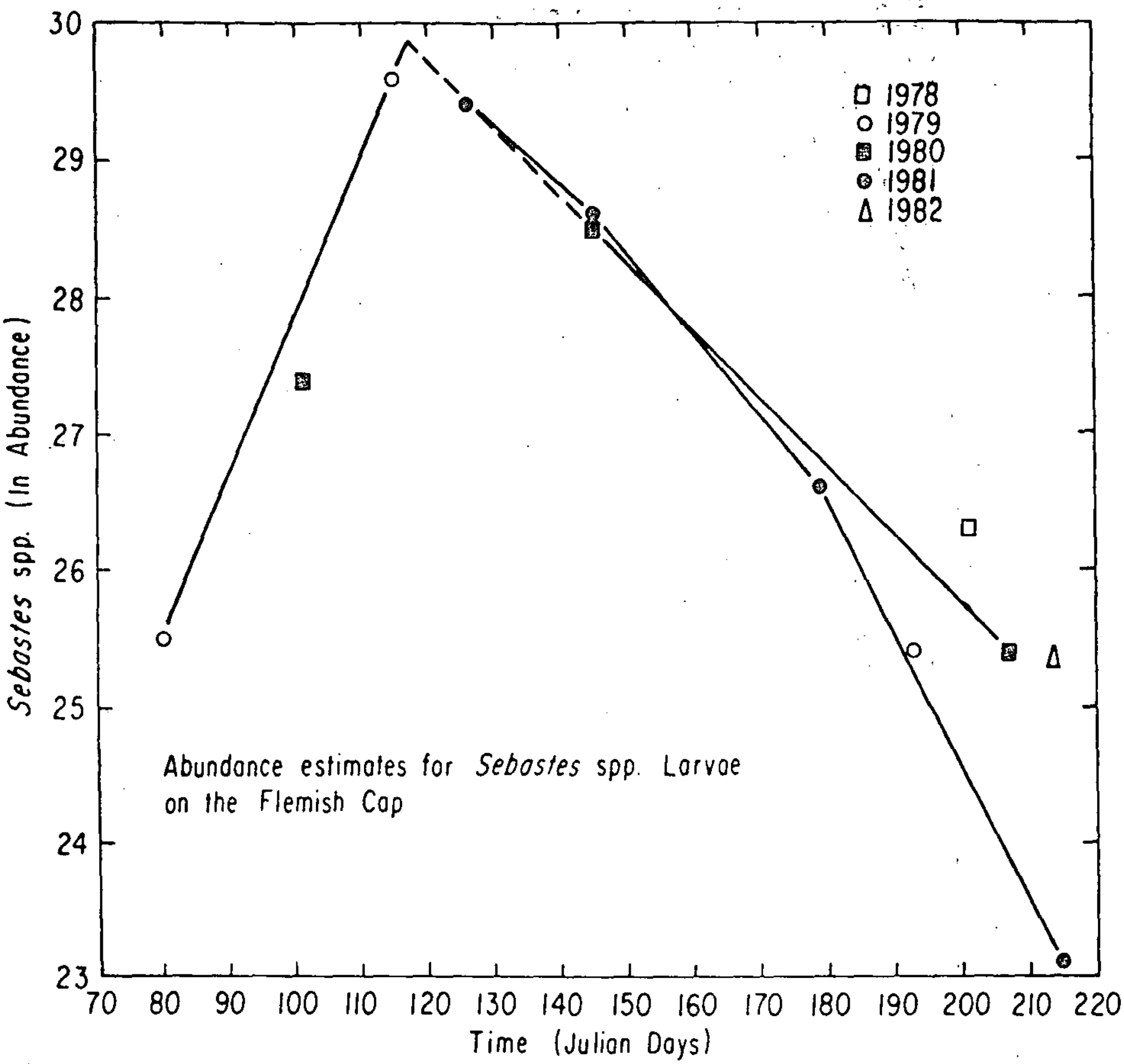

Fig. 2. Abundance estimates for larval redfish (Sebastes spp.) sampled on Flemish Cap during Canadian surveys, 1978-82 (from Anderson, 1984).