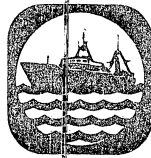


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Early Life History Aspects of Redfish (Sebastes sp.) on Flemish Cap

by

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ABSTRACT

Flemish Cap is an offshore fishing bank lying east of the Newfoundland Grand Banks, being unique in its isolated nature and low fish species diversity. Studies began in 1978 to determine the general nature of fish spawning cycles, distribution and growth during their early life history, and possible relationships of these to environmental factors affecting recruitment. Reported are the results for redfish larvae (Sebastes spp.), by far the most abundant fish larvae found on Flemish Cap. Redfish, as live bearers, began releasing larvae during March, rising to an abrupt peak during the last part of April. This was followed by a second, less abundant, release period that began during June. Larval abundances reached as high as 733 larvae m^{-2} during the last week of April 1979 with peak larval abundance for the study area being $\approx 9.2 \times 10^{12}$ larvae. Redfish larvae first appeared in the S.W. corner of Flemish Cap and soon were found in waters throughout the area over depths > 200 m. By July the survivors were concentrated mostly over central Flemish Cap supporting the concept that Flemish Cap redfish constitute a distinct group. Growth of both April/May and June/July-released redfish larvae was exponential through the periods sampled. However, in 1981 growth rate ranged from 0.40 to 1.66% d^{-1} and 1.48 to 4.52% d^{-1} , respectively. These growth rates are comparable to those reported for many other species of marine fish larvae. Larval growth was significantly correlated to surface water temperatures during most surveys. However, significantly high temperatures appeared to reduce larval growth. In turn this reduced growth during warm years appeared to be related to increased larval mortalities. From these observations it is suggested that larval fish growth on Flemish Cap is under the direct control of the seasonal heating cycle and that the critical period for larval growth and survival occurs during exponentially increasing surface water temperatures in June.

INTRODUCTION

Flemish Cap bank (47°N Latitude; 45°W Longitude) has been the subject of an international fisheries investigation in recent years. The basis of this research, and indeed of existing fisheries theory, is that recruitment in commercial fishes is determined during the first year of life (Gulland 1965; May 1974; Cushing 1975). Studies into the early life history of fishes have been carried out in many areas of the world in an attempt to determine causal factors affecting survival during fish egg and larval stages (e.g. May 1974; Lasker and Sherman 1981). Following the assumption that environmental, or density independent, factors play a key role in larval fish survival, Flemish Cap was identified as a promising area in which to carry out such a study (Anon. 1973).

Flemish Cap is a unique oceanic area lying to the east of the Newfoundland Grand Banks, separated from it by the 1000 m deep Flemish Pass (Fig. 1). Biologically the area is distinct from the adjacent Grand Banks. Only three groups of commercial fish are present: Atlantic cod (Gadus morhua); Atlantic redfish (Sebastes spp.); and, of minor importance, American plaice (Hippoglossoides platessoides). Noticeably absent is a pelagic fish community similar to the adjacent Grand Banks. Capelin (Mallotus villosus) and sandlance (Ammodytes spp.), historically found in abundance on the Grand Banks, are rarely observed on Flemish Cap (Templeman 1976). In addition, Flemish Cap cod form a distinct population (Templeman 1974; Cross and Payne 1978; Lear et al. MS 1979a).

Oceanographically, the area is also distinct. The bank is bounded by two major oceanic current systems; the cold, low-salinity Labrador Current flowing south through Flemish Pass and east along the northern flank, and the comparatively warm, high-salinity North Atlantic Current flowing from west to east along the southern portion of the Cap (Fig. 1). A weak anticyclonic gyre overlies the central portion of Flemish Cap with broad areas of mixed water occurring in intermediate areas (C. Ross, per. comm.). Water temperatures seldom fall below 3°C, which is warm compared to the adjacent Grand Banks.

From a fisheries standpoint, Flemish Cap was considered to be an ideal location to carry out investigative work into factors controlling fish production (Templeman 1976). Among the reasons were the relatively simple fish complex, the discrete cod stock, and a distinct, relatively small oceanographic area that would facilitate sampling. Initial ichthyoplankton and oceanographic surveys were carried out on Flemish Cap during 1978-82 to determine the general nature of these relationships. Reported here are the results of larval redfish (*Sebastes* spp.), by far the most abundant larval fish found on Flemish Cap. The general nature of the timing of larval release, changes in distributions and abundances through the spring-early summer period, and characteristics of larval redfish growth are reported. Finally, interpretation of results is discussed with respect to environmental control and year-class strength fluctuations.

MATERIALS AND METHODS

Eleven ichthyoplankton surveys were carried out during 1978-81 on Flemish Cap. Samples were taken using a survey grid at 20 km (37 km) station spacing, ranging from 20 to 56 stations per survey each survey being 3-7 days' duration (Table 1). At each station ichthyoplankton and physical oceanographic sampling was carried out. During these four years, sampling dates ranged from the last week of March in 1979 to the first week of August in 1981.

Ichthyoplankton sampling was done using 61 cm Bongo nets towed at ~3.0 knots, following standard bongo techniques (Smith and Richardson 1977). Nets were towed obliquely from 200 m depth, or from within 5 m of the bottom, with payout and retrieval rates of 50 m min⁻¹ and 20 m min⁻¹, respectively. Each net was fitted with a General Oceanics flow meter. In 1978 and 1979 paired nets of 0.505 mm and 0.333 mm mesh sizes were used. In all subsequent surveys only 0.333 mm mesh nets were used. The smaller mesh size demonstrably caught more larvae at smaller sizes (<7 mm), whereas there was no difference in the numbers of larger larvae that were caught (up to 26 mm). Maximum depth was monitored, using a pressure sensor fitted above the bongo frame. During one survey, 20-24 March 1979, oblique tows were taken down to only 125 m depth.

Samples were preserved in 5% buffered formalin. All fish eggs and larvae were sorted from each paired sample and identified to species, or lowest taxonomic level possible. Larval fish were counted and measured to the nearest 1 mm, standard length. Abundance was calculated as number of larvae per m²,

$$N = CD/\pi r^2 L$$

where C is the number of larvae collected, D is the maximum sampled depth (m), L is the length of the tow path (m) and r is the radius of the net opening (m). Total abundance for the study area was calculated as the summed abundance for a 42-station grid, where each station was taken to represent approximately 1.37 x 10⁶ m². Where only 20 stations were sampled during July 1979 and August 1981, total abundance for a 42-station area was estimated, assuming 86% of all larvae had been sampled by 20 stations over central Flemish Cap. This was based on a comparison to full areal coverage during 1978 and 1980, and the fact that larvae were concentrated in the central area of Flemish Cap (Anderson, MS 1981).

Oceanographic data were collected at each station, using a Guildline Mark IV CTD probe fitted to a Rosette sampler. Sampling was carried out to within 5 m of the bottom, down to maximum depths of 1000 m. Water temperatures sampled at 10 m depth over central Flemish Cap (47°N/45°W) were taken to be representative of surface water conditions. This was based on a mixed-layer depth of ~20 m during all surveys, and waters at this central location being most representative of the Flemish Cap surface waters (Keeley, MS 1982).

Expected seasonal water temperatures in surface waters over Flemish Cap were calculated as mean monthly values from two data sources. One was estimated sea surface temperatures based on METOC charts for the position 47°N 44° 30'W (Bailey, unpubl. data), while the second was based on the Marine Environmental Data Services' bathythermograph and Nansen bottle data at 0 m and 10 m within the area bounded by 46°40' - 47°20'N by 44°30'W - 45°20'W (cf. Keeley, MS 1982). The METOC data represented data for each mid-month from 1962 to 1981, while the

MEDS data set represented all data available 1910-81, by month. Values from both sources were combined to give mean monthly temperatures and standard deviation.

RESULTS

ABUNDANCE ESTIMATES

Larval redfish (*Sebastes* spp.) were by far the most abundant larval fish sampled during all eleven surveys. In most cases redfish larvae made up 90%, or more, of each sample. Abundances estimated for the survey area ranged through two orders of magnitude during different phases of the release cycle (Table 1, Fig. 2). Values during the early part of the cycle in late March 1979 and early April 1980 were 1.1 and 8.0×10^{11} larvae for a survey area of 42 stations, respectively. Abundance increased quickly to peak values estimated by linear extrapolation to be $\approx 9.2 \times 10^{12}$ larvae occurring at the end of April, first week of May. Observations close to an estimated peak during late April 1979 and early May 1981 were 6.9×10^{12} and 6.1×10^{12} larvae, respectively. Apparent from these values is a very short and precise period of peak abundance due to larval release from adult female redfish. Abundances decreased logarithmically from this peak period to lowest values of $< 3 \times 10^{11}$ larvae observed during July and early August.

The decreases observed in abundance through the May to July period corresponded to larval population mortalities which were in excess of 99%. Instantaneous mortalities calculated through this period ranged from 0.043 d^{-1} to 0.093 d^{-1} in 1980 and 1981 ($Z = (\ln N_0 - \ln N_t) / \Delta t$). In 1981 these mortality rates increased from May to June, and then again into July. Average instantaneous mortality from 2-9 May 1981 to 1-4 August 1981 was 0.070.

Year-to-year comparisons of abundances are difficult due to infrequent sampling throughout March to August each year. The only direct comparison was late May in 1980 and 1981. At this time abundance estimated each year was very similar being 2.2×10^{12} larvae in 1980 and 2.7×10^{12} larvae in 1981 (Table 1; Fig. 2). In addition, samples were taken during July and early August of each of the four years (1978-81). Standardizing abundance estimates each year to Julian day 200 (approximately 19 July) indicated there were significant differences between years. Total larval redfish abundance estimated for 1981 was approximately an order of magnitude less than in either 1978 or 1980 (Table 2). Abundance estimated for 1979 fell between these extremes. However, in 1979 only larvae < 11 mm were observed, which would have been released later than the April/May - release period.

LARVAL DISTRIBUTIONS

The early distribution of redfish larvae was localized in the southwest corner of Flemish Cap in March 1979 over depths > 300 - 400 m (Fig. 3a). Larval redfish at this time were highly unimodal around 6 mm (Fig. 4) and low in abundance (Table 1; Fig. 2). As the season progressed into April and the rate of larval release increased, maximum concentrations of recently released 6 mm larvae were observed around Flemish Cap in waters > 200 m depth (Fig. 3b,c). There was a notable absence of larvae in the shallow waters overlying central Flemish Cap.

Release of new larvae 2-9 May 1981 was past the date of peak extrusion as evidenced by the low numbers of 6 mm larvae (Fig. 4). At this time larval redfish were abundantly distributed throughout the survey area, with a remnant low abundance area still observed in the central area (Fig. 3d). Observations available through the rest of May, June, July and into August demonstrated that larval redfish tended to occur in waters generally within the 400 m contour (Fig. 3 e-k). During June, July, and August these distributions include recently released 6 mm larvae which occur as part of a second larval release. During three years - 1978, 1979 and 1981 - summer distributions were highest in small areas north and west of the 200 m contour (Fig. 3g, h, i and k). In July 1980 larval redfish concentrations were highest in the central area of Flemish Cap over waters < 200 m depth (Fig. 3j).

To summarize, the major area of redfish extrusion appears to take place in waters > 200 m depth, and mostly over the broad area lying immediately to the north and west of the central, shallow area. Following peak extrusion, occurring in late April, there is an apparent shift in the abundance distribution towards the central waters of Flemish Cap. This might be the result of convergence, area of higher survival over the central area.

LENGTH-FREQUENCIES

Length-frequencies of larval fish sampled during March and April were unimodal about 6 mm (Fig. 4). Average size ranged from 5.6 to 6.5 mm (Table 1). It is apparent from these samples that recently extruded redfish larvae, formally preserved, are approximately 6 mm in length. This is true of larvae released during June and July as well (Fig. 4). Even by 23-27 April 1979, it is apparent that mass extrusion of larvae is still ongoing, with little overall population mean size. It was not until May that there was any evidence of overall growth in the population. Samples from May indicated a significantly reduced proportion of 6 mm larvae, with mean population size increasing to between 8 to 10 mm (Table 1).

During surveys in 1981, population size increased from 9.0 mm in late May to 11.3 mm in late June (Table 1). At this time there was an increasing proportion of 6 mm larvae, indicating the onset of a second period of larval redfish release (Fig. 4). During July and August surveys of all four years, the presence of larvae modal about 6 mm standard length is indicative that a second period of larval extrusion begins during June on Flemish Cap, and is ongoing during July and at least into August.

In July and August larval redfish released during peak extrusion in late April, possibly early May, averaged 18.0-21.4 mm in length, with the exception of July 1979 when no larvae > 11 mm were found. The largest larvae caught during all surveys was one specimen 27 mm in length collected in July 1980. During July 1980 there was definitely a third mode in the larval distribution at 10 mm length, ranging from 8 to 12 mm and averaging 11.8 mm. This mode, sampled during 22-28 July 1980, is probably indicative of a peak extrusion occurring sometime during late June or early July. In fact, length-frequency distributions from July 1978 and August 1981 similarly show single peaks at 9 mm and 16 mm, respectively. Assuming these peaks ranged from 8 to 12 mm and 13 to 17 mm, respectively, then mean sizes were 9.2 mm in 1978 and 15.2 mm in 1981. Assumed is that these peaks are produced as a result of a maximum redfish extrusion occurring during June/July.

Year-to-year comparisons are available for some of the data. Comparison of mean larval sizes in late May of 1980 and 1981 indicates larvae in 1981 were approximately the same size (Table 1), with the overall range being 6-12 mm both years. Comparisons during July and early August of all four years indicated sizes of April/May-released larvae were comparable, given the slight date differences in all years, except for 1979. In 1979 no larvae > 11 mm were sampled.

LARVAL REDFISH GROWTH

Mean population size estimated for each sampling date indicated that growth of April-released larvae was exponential from May through July (Fig. 5). Due to ongoing extrusion during April, there was an initial lag, after which mean population size increased. Growth fit the exponential form:

$$L = 2.0 \text{ EXP } [0.011t] \quad (1)$$

where L = standard length (mm) and t = time (Julian day), with $r^2 = 0.95$. Mean population sizes for June through August were based on the largest length-frequency distributions (Fig. 4). Observations for 1981 were joined in Fig. 5, as these represent the year most extensively sampled, as well as the only year with an observation in June. The June observation was well below the line of predicted size for this period in 1981, whereas observations during May and the first week of August in 1981 were close to both the predicted size and observations from other years.

Increases in population mean size following April extrusion in 1980 and 1981 corresponded to exponential growth rates ranging from 0.43 to 1.66% d^{-1} (Table 3). While average growth rates estimated for the May to July period in 1980 and 1981 were similar, growth rate in 1981 was slightly higher (Table 3). Values calculated from the 1981 data indicated increasing growth rate between successive pairs of observations (Fig. 6). The absolute timing of these calculated changes in growth rate is dependent on the sampling dates. Nevertheless, they do indicate that growth rate increased non-linearly through the period sampled. This contrasts with the general exponential equation of growth where % d^{-1} increases between any pair of observations would be a constant (Fig. 5). This appears to be due to the lower than expected size of redfish larvae during June 1981, compared to values before and after.

From the length-frequency data available, it is similarly possible to estimate a mean size of larvae from a second extrusion period beginning during June on Flemish Cap. Here again population growth is exponential, however, the rate of increase was greater (Fig. 5). These data fit an exponential curve of the form:

$$Y = 0.107 \text{ EXP } [0.022X] \quad (2)$$

where Y = standard length (mm) and X = time (Julian day), $r^2 = 0.96$. The value from 1979 was not used in the equation due to the lower-than-expected mean size for that sampling date, and the unusual length-frequency distribution from that date. Conditions during July 1979 did not appear to be normal.

The calculated rate of increase for June/July-released redfish larvae was substantially greater than for April/May-released larvae. Comparison of equations 1 and 2 indicates that larvae would reach the same size on Julian day 272 (~29 September), assuming growth to be exponential through to this time. Thus, larvae released two months later during June/July, would soon catch up in size.

GROWTH AND TEMPERATURE

The long-term average temperature cycle for surface waters on Flemish Cap indicated an exponential increase from May through July (Fig. 7). Water temperatures increased gradually from a minimum of $3.3 \pm 0.3^\circ\text{C}$ in February to $5.0 \pm 0.4^\circ\text{C}$ in May. This was followed by a rapid rise in surface water temperatures to $11.5 \pm 0.3^\circ\text{C}$ in July. Maximum temperatures of $12.7 \pm 0.6^\circ\text{C}$ occurred during the month of August.

There was a close relationship between increases in larval size and surface water temperatures on Flemish Cap. From larval survey data, increases in mean population size of April/May-released redfish larvae closely parallel increases in surface water temperatures on Flemish Cap. This relationship was linear and highly significant ($p < 0.001$, $r^2 =$), excluding the June 1981 observation at 10.25°C which fell substantially below the line (Fig. 8). While obviously compounded by other factors, seasonal heating of surface water temperatures explained most of the increase in population size. This suggests that larval growth is under the control of surface water temperatures and seasonal heating.

Similarly, redfish larvae from the second extrusion during June-July, indicated a linear relationship of increasing size with surface water temperatures. Although limited to four observations, excluding July 1979, the relationship was similarly highly significant ($p < 0.01$) (Fig. 8). For these data the slope was much greater than for April/May-released larvae.

While the general fit of larval size versus surface water temperatures was good during these three years, there were two cases where it did not hold. One was for April/May-released larvae observed during June 1981, and the second was June/July-released larvae during July 1979. In both cases lower than expected mean population sizes were associated with higher than average surface water temperatures.

Comparison of mean monthly temperatures from all available data to the long-term mean for 1979-81 indicated only four significant differences ($p < 0.01$). These occurred during April and June 1979 and May and June 1981 (Fig. 7). While other values were not significant at the 99% level it is worthwhile to note that all mean monthly values during 1979 were greater than the 99 percent C.I. of the long-term mean. In contrast, no values from 1980 were significantly different from the long-term mean.

To summarize these temperature observations, 1979 was a warmer-than-average year throughout the spring-heating cycle, with April and June being significantly warmer. During the March-August period in 1980, temperatures were slightly cooler during March and April, fell within the 99 percent C.I. during May, June and August, and were slightly warmer during July. No values were significantly different from the long-term mean. Finally, in 1981 temperatures were significantly warmer during May and June only, with all other values falling within the 95 percent C.I.

Comparing these temperature data with larval redfish, suggests that warmer than average temperatures are detrimental to larval fish growth. Sampling in July 1979 indicated total mortality of the April/May-released larvae, following what appeared to be a normal release period during April. In addition, the only larvae observed during July 1979 were 5-13 mm,

with a mean size of only 6.3 mm. Compared with the other years, this was less than expected for this time of year (Fig. 5, June-July larvae). Also, the temperature-size relationship was significantly different from the other years (Fig. 8). Thus, during 1979 the April/May-released larvae were lost from the system by July, and June/July-released larvae indicated no overall growth.

During 1981 similar results occurred. Initial growth of larval redfish during May and June appeared to be low after which it had increased sharply through July and into the first week of August. The low growth rates are directly comparable to significantly high temperatures, while increased growth through the July period occurred during seasonally normal temperatures. In addition, abundances estimated for day 200 in 1981 (Table 3) were an order of magnitude less than comparable data from July 1978 and 1980. Compared with 1980, mortalities from May through July in 1981 were almost twice as high, being 0.05 in 1980 and 0.09 in 1981 through this period. Thus, in 1981 higher temperatures during May and June appeared to reduce population growth and increase larval mortality. Following this period growth rates increased, in conjunction with a return to seasonally warm temperatures.

DISCUSSION

REDFISH POPULATIONS

Redfish (*Sebastes* spp.) larval data collected over four years on Flemish Cap demonstrated that there are probably two periods of larval release; one during April-May and a second during June-July. These periods of release correspond with two cycles in maturation of adult redfish on Flemish Cap (Templeman, 1976) and are further characterized by larval growth differences. Whether or not these release periods represent separate populations remains a matter of conjecture. Insemination in redfish takes place many months earlier, probably during the fall (c.f. Westrheim 1975; Jones 1970). However, virtually nothing is known about this aspect of redfish life history; e.g. whether there are different mating times, different locations, or different depth zones. In addition, on Flemish Cap three species of redfish are reported (Templeman 1976). Of these, *Sebastes mentella* is by far the most numerous, and reportedly accounts for larvae released during the April-May period (ibid). The second peak in extrusion comprises of *S. marinus* and *S. fasciatus* larvae. The lack of knowledge regarding the mating of redfish species and the confused nature of redfish species identification, coupled with possible interbreeding between species (ibid), makes it difficult to discuss population differences between these redfish.

The bimodal spawning peak observed on Flemish Cap is identical with that reported in the Irminger Sea a large oceanic area lying S-E. of Iceland, and in contrast to that reported for all areas lying west of Flemish Cap. In the Irminger Sea, redfish first release larvae in April-May, followed by a second, smaller release during June and July (Magnusson 1968). These extrusions are thought to be species-specific, attributed to *S. mentella* and *S. viviparus*, respectively. Nowhere else in the North Atlantic have bimodal release periods been observed. On the adjacent Grand Banks and off Labrador, release first occurs during June (Bainbridge and Cooper 1971). In the Gulf of St. Lawrence release begins in May, with a peak occurring during early June (Steele 1957). On the Scotian Shelf release occurs from April through July with a peak in June (Day 1961; Serébryakov 1962; Henderson 1968; Bainbridge and Cooper 1971), while in the Gulf of Maine release occurs from May through July, with a single peak during late June (Kelly and Barker 1961). In no case has a bimodal release pattern been reported. Thus, throughout the entire area lying to the west of Flemish Cap, from the Gulf of Maine north to the Labrador Shelf, the main release period of redfish larvae is unimodal and occurs significantly later than on Flemish Cap.

This observation raises a number of interesting questions. One question is the uniqueness of Flemish Cap redfish from surrounding oceanic and shelf areas. The pattern of release would indicate the redfish species assemblage on Flemish Cap is distinct from the adjacent Grand Banks, and more closely associated with that of the Irminger Sea. Oceanographically, Flemish Cap is a distinct area, bounded by the Labrador Current to the north and west, and the North Atlantic Current to the south and east. Cod on Flemish Cap constitute a separate stock (Templeman 1976; Lear et al. 1981). Pelagic species such as capelin and sandlance are seldom found here, while being abundant on the adjacent Grand Banks (Templeman 1976). Flemish Cap redfish have been designated as a separate stock complex from other areas (Mead and Sinderman 1961; Bainbridge and Cooper 1971; NI 1982). While delineating Flemish Cap as a separate area, Bainbridge and Cooper (1971) pointed out that redfish there were very similar to that of the Irminger Sea. Results from this study indicated that larvae were concentrated towards central Flemish Cap by June and July of each

year. These redfish-larval concentrations over the Cap were discontinuous with surrounding areas supporting the notion of a distinct larval population unique to Flemish Cap. Whether or not adult redfish migrate in and out of the area is not known. However, the notion that Flemish Cap redfish constitute a separate stock, or stock complex, is supported. As such, the early life history of these fishes will be dependent on the vicissitudes of the Flemish Cap ecosystem.

A second question of interest is why are there different release strategies for redfish distributed at similar latitudes? On the Cap, release is bimodal with most of the annual redfish release occurring in April at the onset of seasonal production cycles. Elsewhere, the second spawning strategy is unimodal, with the main release of larvae occurring about two months later well after spring production peak. In all cases, two or more species reportedly occur in each area. The obvious answer is that the release periods are species specific. On both Flemish Cap and in the Irminger Sea the dominant redfish is reported to be S. mentella and the main release period occurs during April and early May. In the other areas S. fasciatus is reported over the shelf areas and upper slope while S. mentella occurs in deeper waters (NI 1982). On both the Grand Banks (Mobil Oil, unpubl. data) and the Scotian Shelf (R. O'Boyle, per. comm.) redfish release begins in April along the shelf break areas, with redfish larvae appearing in shelf waters only later on in May and June. The apparent conclusion is that the early released redfish larvae are S. mentella with larvae occurring during the June peak being S. fasciatus.

LARVAL REDFISH GROWTH

Mean population size of April/May-released larvae increased exponentially throughout the periods sampled, following an initial lag phase due to ongoing extrusion. With the exception of June 1981, all observations fit this curve well, which is the usual and expected case for fish larvae (Ahlstrom 1954; Nakai and Hattori 1962; Houde 1977). From this study, growth rate ranged from 0.43 to 1.66% d^{-1} in 1981 (0.037-0.255 $mm\ d^{-1}$). At some point, however, growth rate will drop off coincidental with metamorphosis to a juvenile stage. In the Gulf of Maine, for June-released redfish larvae, this was reported to occur at 40-50 mm length during October-November (Barker and Kelly 1961). This occurs from 30 to 55 mm in several species of Pacific redfish, but mostly around 50 mm (Moser and Ahlstrom 1978; Laroche and Richardson 1980; Boehlert 1981, 1982). If this was true for Flemish Cap, similar lengths would be reached about the third week of October. With this assumption, computed average growth rate for larval redfish would be of the order 1.11% d^{-1} from May through October. Similarly, growth of June/July-released redfish larvae was exponential, although the rate of increase was greater than the earlier released larvae. Here again, with the exception of one observation in July 1979, the fit of data was good. Based on the exponential equation for June/July-released larvae, larval sizes of 40-50 mm would be reached towards the second week of October, essentially the same date as April/May-released larvae. In this case average growth rates would be on the order of 2.22% d^{-1} from July 1 to September 30.

Comparison of these growth rates to other studies indicates the ranges are comparable. The only other information available for Flemish Cap is unpublished data collected during May, June and July 1978 (Postolaky MS 1980). From these data, growth rates ranged from 1.25% to 1.32% d^{-1} from May through July. Values for the May-July period (1.25% d^{-1}) correspond well with the observations from this study. However, values calculated for the May and June periods were greater than those observed during 1980, and especially in 1981. The lowest growth rate calculated for June 1981 (0.67% d^{-1} for Julian days 162), was considerably less than the rate of 1.32% for Julian day 161 estimated from the Postolaky's data. Values during May were again higher for USSR data, being 1.29% d^{-1} versus 0.43% d^{-1} for this study. Thus, the low growth rates observed during the early part of the growing season in 1981 do not appear to have occurred in 1978. This is primarily due to the comparatively larger size of redfish larvae sampled during June 1978 (14.5 mm) as compared to May (9.3 mm) and July (20.1 mm) of that year.

Growth-rate data for larval redfish are also available from the Labrador Shelf and the Gulf of Maine. During July-August on the Labrador Shelf, larvae grew from about 8 to 14.5 mm in 30 days (Bainbridge and Cooper 1971). This corresponds to ~1.98% d^{-1} . In the Gulf of Maine, redfish larvae grew at a rate of 1.22% d^{-1} during July-August to September, increasing from 23.6 mm to 38.5 mm in 42 days. These larvae were nearing metamorphosis, and may have been past the period of exponential larval growth. Larvae from these two areas are June/July-released, and therefore may be most comparable to the second group on Flemish Cap. On Flemish Cap, growth estimates of these larvae ranged from 1.5 to 4.9% d^{-1} . In general, the values from Flemish Cap are comparable as mm d^{-1} increases, but range higher as percent increases in exponential growth (cf. Table 3).

Growth estimates for the Pacific redfish, *Sebastes diploproa*, ranged from 0.154 to 0.225 mm d⁻¹ based on otoliths of larval fish ranging from 9.0 to 42.7 mm SL and a variety of surface temperatures which varied from 13° to 22°C (Boehlert 1981). While size-dependent comparisons cannot be made, these growth-rate estimates are very similar to those observed on Flemish Cap, and in particular to the April/May-released larvae (Cf. Table 3).

GROWTH AND MORTALITY

Abundance estimates indicated a rapid rise in the numbers of 6±1 mm redfish larvae on Flemish Cap through the April period, followed by an abrupt decline. This indicates a very pronounced period of maximum larval release of short duration. A similar short duration of peak redfish release has been reported in the Irminger Sea (Jones 1970), indicating a precise timing in the release of redfish larvae. The result is a distinct unimodal peak containing the bulk of larvae released during any one year. The subsequent survival of this cohort will determine eventual year-class production. It is not known how variable the time of maximum release is on a yearly basis, but it appears to occur about the last week in April on Flemish Cap, and may vary around this date by about one week.

Larval mortalities estimated from April through July were high, with less than one percent of larvae estimated at the time of peak release surviving. Such rapid declines in larval fish populations are common. For example, larval studies of N. Sea plaice over a number of years indicated 94.8-99.6% mortality over 140 days (Bannister et al. 1974), while round herring in the Gulf of Mexico had 98.3 and 99.4% mortality during two successive years (Houde 1977). Similarly, mortalities > 99% have been reported for cod, plaice and herring larvae (Cushing 1974). These rapid declines in abundances are usually associated with decreasing rates of mortality, with proportionally more larvae surviving with time (Bannister et al. 1974; Cushing 1974).

An unusual increase in instantaneous mortality rate with time was found on Flemish Cap in 1981. Values rose from 0.04 between May surveys to 0.06 between late May and June, to a high of 0.13 between late June and the first week of August. As well, 1981 mortalities were almost twice as high as mortalities during the same May-July period in 1980.

These increasing mortality rates in 1981 coincided with a decreasing growth rate which occurred during May and June (Fig. 6), suggesting that increasing larval mortalities and decreasing growth rates might be associated. This was certainly the case compared with 1980. Similar observations for growth over the May and June months in 1980 are not available. However, abundances that were almost identical during the last week of May 1980 and 1981 differed by an order of magnitude in July (Table 3). Additionally, growth rates estimated during May 1978 from unpublished data (Postolaky MS 1980) indicated high growth during May and June (1.29% d⁻¹ and 1.25% d⁻¹, respectively). It appears then, that low growth rates during May and June of 1981 may have been significantly low, and that these low and decreasing growth rates led to high larval mortality.

It appears that extremely high larval mortality also occurred during the May-June period in 1979. Following what appeared to be a normal release period in April, with abundances during 23-27 April 1979 close to the predicted maximum on Flemish Cap (Fig. 2), there was a total absence of these larvae (> 11 mm) in July. Between our April and July sampling dates in 1979 there appears to have been 100% mortality of larvae from the first release-period. In addition, there was no increase in population size in the June/July released redfish larvae as compared to other years. This high mortality was somewhat confirmed by cod feeding studies routinely carried out during January of each year. Samples collected in January 1980 indicated an almost complete absence of 7-8 cm redfish in cod stomachs, assumed to be 0-group fish (Lilly MS 1981). This was in contrast to feeding studies in other years, both before and after 1980, in which young redfish 7-8 cm in length comprised a significant portion of the cod diet.

From these data, then, there is evidence of high larval mortality that occurs sometime during the May-June period for larvae released during April-May. In addition, this appeared to be growth related, higher mortality occurring when growth was reduced. Finally, the magnitude of this response varied between years. This suggests if there is a critical period for larval redfish survival on Flemish Cap, it appears to occur sometime during the May-June period.

SIZE DEPENDENT GROWTH AND TEMPERATURE:

Increasing surface water temperatures on Flemish Cap accounted for most of the increase in larval fish size through the exponential phase during the first three months of life. Obviously, such a relationship is compounded by other factors. These would include such things as increasing daylight and hence time available to feed, successional changes in the zooplankton community affecting food supply, and increased water stability which may act to concentrate food. However, it remains that temperature, as a single variable, did explain most of the larval growth through this period. Physiologically there is a good basis for this to be true. Food availability and water temperature are the most important factors controlling fish growth (Fry 1947, 1971; Brett 1969, 1979; Riley 1966; O'Connell and Raymond 1970; Houde 1975). Under non-limited food conditions fish growth responds linearly to changes in water temperature, between upper and lower tolerance limits (Brett 1969, 1979; McCormick et al. 1971; Ryland et al. 1975; Ryland and Nichols 1967). Thus, in temperate latitudes as surface waters are heating seasonally growth in larval fish would be expected to respond linearly - in the case where food was not limiting. If one assumes this to be true, then it is clear that larval redfish growth on Flemish Cap responds directly to the seasonal heating. This was the case for most observations on Flemish Cap sampled over four years (Fig. 8). The exceptions were observations during June 1981 and July 1979; in both cases, mean larval size was considerably smaller than expected at the observed temperatures. However, temperatures for May and June 1981 were significantly warmer than the long-term mean ($p < 0.01$), while during 1979 all temperatures from April to July were above average, with April and June being significantly so ($p < 0.01$). From these data it appears that unseasonably high temperatures reduced growth. In addition, these occurred during June of both years, the period of greatest increase in surface water temperatures.

Perhaps this is worth exploring further. While growth in fish responds linearly between tolerance limits, it decreases beyond these limits and eventually results in death. In particular, higher temperatures are the more lethal, being closer to temperature growth optima in most fish than are the lower lethal temperatures. This is explained by the non-linear nature of the relationship between growth efficiency and temperature. Specifically, as temperature increases, the necessary food ration to maintain basal metabolism increases exponentially (Brett 1979, 1979). The result is that gross growth efficiency decreases above optimal temperatures ultimately reducing growth (Ryland and Nichols 1967; McCormick et al. 1971; Ryland et al. 1975; Williams and Caldwell 1978). Thus, as temperatures increase the cost of metabolic maintenance, and hence the demand for food, increases exponentially to the point where growth rate begins to decrease; and this ultimately results in death. Following this line of argument, the obvious conclusion from Flemish Cap is that growth in redfish larvae was under the control of seasonal heating, when these temperatures did not exceed mean expected values. When temperatures were too high, as in June 1979 and May-June 1981, growth was reduced through metabolic stress. This metabolic stress might well be due to high temperatures pushing food requirements (ration) beyond either what is normally available or what the larvae are able to ingest. The result would be increased larval mortalities; through physiological death, increased predation or some other cause. Implicit in this argument is that food is not limiting growth under normal temperature conditions. Only when temperatures rise too high, exponentially increasing metabolic demands, might food become limiting to growth.

The converse would also be true. Temperatures that were too cold, or did not increase rapidly enough in the spring, would also be detrimental to growth. In this case food would not necessarily be limiting, but the larvae would be subject to metabolic stress and possible feeding limitations due to such things as abnormal jaw development (Lasker 1975; Alderdice and Velsen 1971; Brett 1979). In either case the result is the same, growth efficiency drops off outside optimal temperature ranges eventually decreasing growth rates and larval survival. Effects of temperature affecting survival in marine fish larvae have generally been ignored (c.f. May 1974). Some studies have observed temperature effects but few have studied the functional response in natural systems. Methot and Kramer (1979) found no effects of temperature on anchovy growth, but felt the temperature range may have been too small to affect growth differences. O'Connell (1970) found starvation in larval anchovy was related to warmer temperatures, which he attributed to horizontal variations in surface waters. Colton (1959) observed mass mortality and emaciated larvae on George's Bank due to a warm water temperature intrusion and postulated such events could affect year-class production. Hermann et al. (1965) found surface water temperatures were significantly correlated to West Greenland cod recruitment, with warmer temperatures favouring higher recruitment. Finally, Alderdice and Velsen (1971) stated minor variations in annual temperatures would have profound effects on year-class strength in Pacific herring.

One of the clearest studies relating temperature to year-class strength has been carried out on smallmouth bass in north temperate lakes (MacLean et al. 1981). In this case survival and year-class strength was found to be dependent on two things: fish size following the first summer of growth; and, on the duration of the winter period. In both cases temperature was the primary determinant ultimately affecting survival. It was concluded low survival and year-class strength was the result of low temperatures which lead to exhaustion of metabolic reserves (ibid). Similar results were reported for Gulf of Maine herring during 1964 where winter water temperatures that were too low affected the over-wintering survival of fall-spawned herring (Chenoweth 1970; Graham and Davis 1971).

Seemingly forgotten are rates of change in the larval environment as the first growing season progresses. Averages of temperatures correlated to fish production can be misleading, being especially dependent on the time frame over which they are averaged. Given the non-linear nature of seasonal heating any summation of yearly or seasonal temperature must be weighted. On Flemish Cap, for instance water temperatures reached minima of $3.3 \pm 0.3^\circ\text{C}$ in February and rose to maxima of $13.0 \pm 0.7^\circ\text{C}$ in August. However, approximately 60% of this heating occurs in just 30-40 days, from late May to early July. This is obviously a critical time. Not only will the magnitude of seasonal heating be important, as an integral through time, but as important will be the rate at which this heating occurs over any particular time interval.

This leads me to a final comment on the critical period concept in fisheries research. Much attention has focused on a critical period involving successful first feeding and/or the match of larval/prey production cycles on appropriate time and space scales. However, the validation of a critical, post yolk-sac period in fish larvae has remained elusive (May 1974; Sharp 1980; Lasker and Shermann 1981). I propose the answer may alternatively lie in the magnitude and rate of seasonal heating of surface waters, at least for temperate water species. Given the known importance of temperature, it may be that this particular period through which there is a physiological hurdle imposed by exponentially increasing temperatures may constitute the critical period for larval fish survival; not first feeding.

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Table 1. Summary of larval redfish (Sebastes spp.) data from Flemish Cap, 1978-81. Temperature is that of surface waters at 10 m depth at 47°N latitude, 45°W longitude.

Year	Date	Julian mid-date	Stations (n)	Abundance (larvae m ⁻²)	Population size		Temp. (°C)
					April	June/July	
1978	16-23 July	201	56	2.7x10 ¹¹	18.5	9.2	11.5
1979	20-24 March	80	42	1.1x10 ¹¹	5.6		4.2
	23-27 April	115	42	6.9x10 ¹²	6.3		5.2
	10-14 July	193	20	1.1x10 ^{11a}	-	6.3	12.6
1980	6-13 April	101	41	8.0x10 ¹¹	6.4		3.4
	20-26 May	145	42	2.2x10 ¹²	8.9		6.1
	22-28 July	207	56	1.1x10 ¹¹	17.9	10.3	11.6
1981	2-9 May	126	41	6.1x10 ¹²	8.3		6.3
	22-27 May	145	42	2.7x10 ¹²	9.0		7.3
	26-30 June	179	42	3.6x10 ¹¹	11.3	6.5	10.3
	1-4 August	215	20	1.2x10 ^{10a}	21.4	15.2	12.7

^aEstimate for a 42-station grid assuming these 20 stations sampled 86% of the larval Sebastes (spp.) on Flemish Cap during July.

Table 2. Size and growth for larval redfish (Sebastes spp.) from Flemish Cap.

Year	Period (Julian dates)	Mid- point	Growth Increment (mm)	Growth rate (mm d ⁻¹)	Instantaneous Growth rate (% d ⁻¹)
a) April/May released larvae					
1980	145-209	177	9.04	0.146	1.13
1981	126-145	136	0.7	0.037	0.87
	126-179	153	2.91	0.055	0.56
	145-179	162	2.30	0.068	0.40
	126-215	171	12.10	0.136	1.01
	145-215	180	11.40	0.163	1.05
	179-215	197	9.19	0.255	1.66
b) June/July released larvae					
June '81 & July '78	179-201		2.7	0.114	1.48
June '81 & July '80	179-207		3.8	0.136	1.64
June '81 & August '81	179-215		8.7	0.242	2.36
July '78 July '80	201-207		1.1	0.183	1.88
July '78 & August '81	201-215		6.2	0.443	3.74
July '80 & August '81	207-215		4.9	0.613	4.86

Table 3. Larval Sebastes spp. abundance estimated for July during the period 1978-81. Values were standardized to Julian day 200.

Year	Abundance	In abundance
1978	27.8x10 ¹⁰	26.35
1979	7.6x10 ¹⁰	25.05
1980	15.2x10 ¹⁰	25.75
1981	2.8x10 ¹⁰	24.05

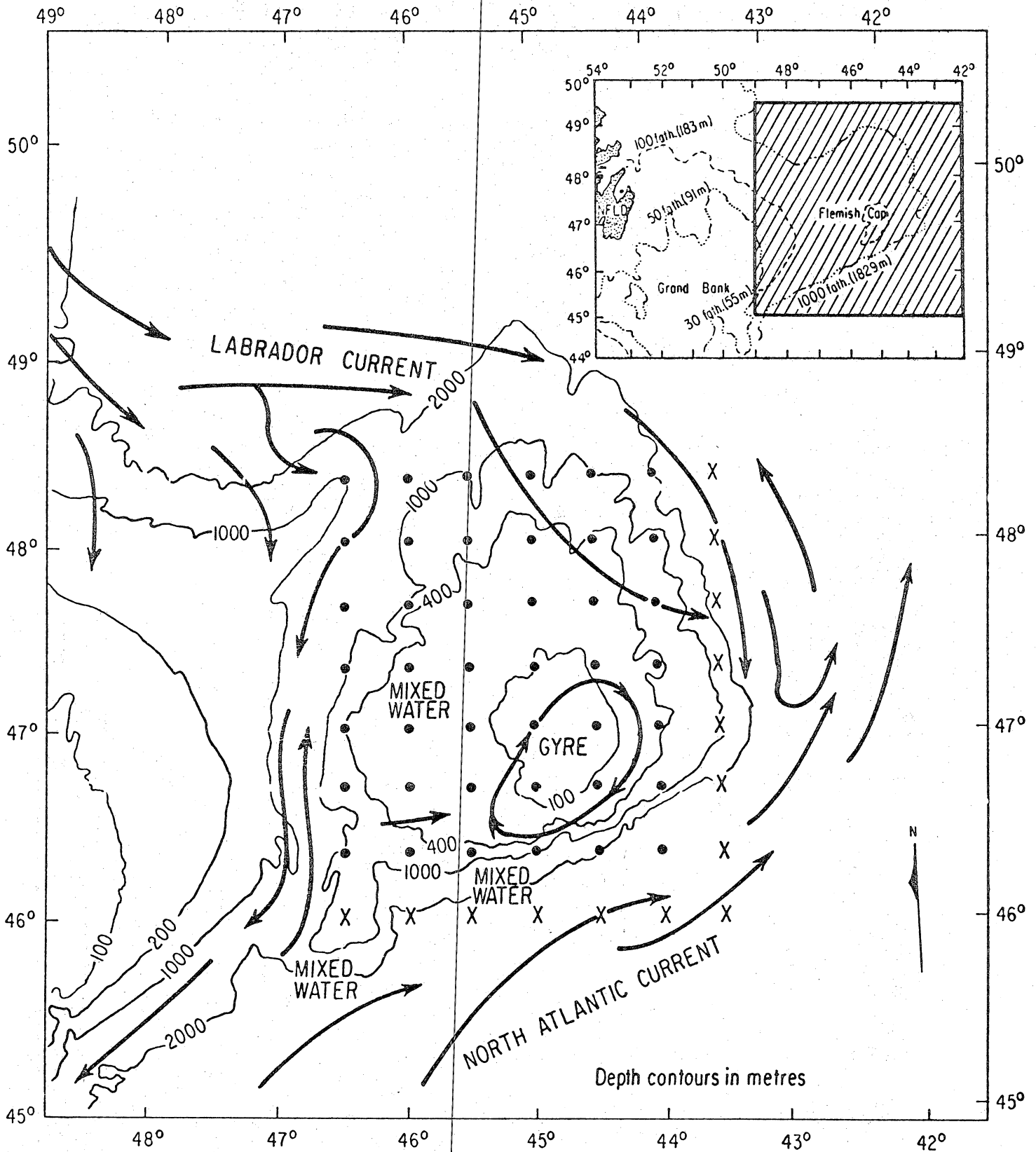


Fig. 1. Flemish Cap bank, lying east of the Newfoundland Grand Banks, showing the oceanographic features of this region.

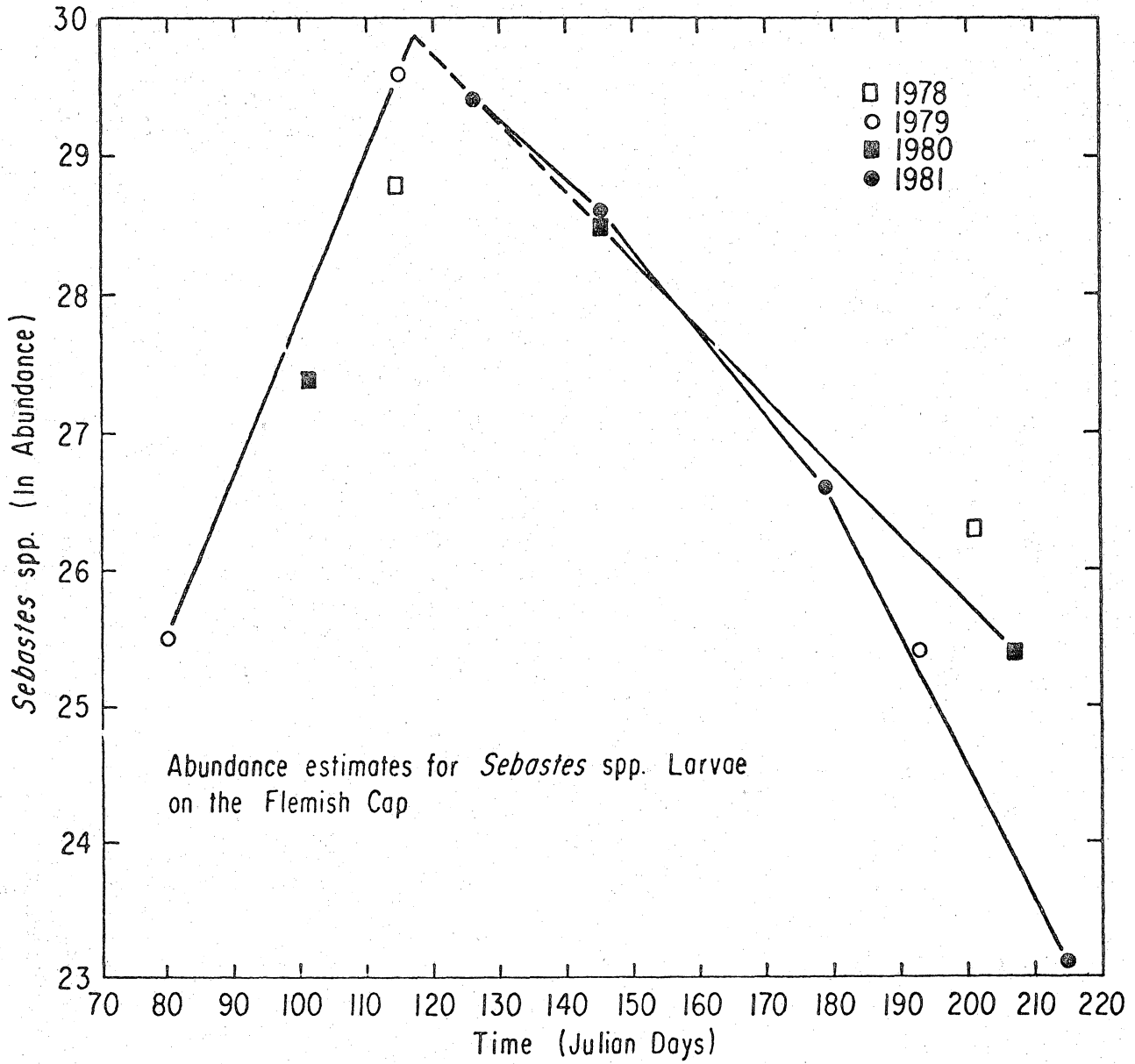


Fig. 2. Abundance estimates for larval redfish (Sebastes spp.) sampled on Flemish Cap 1978-81.

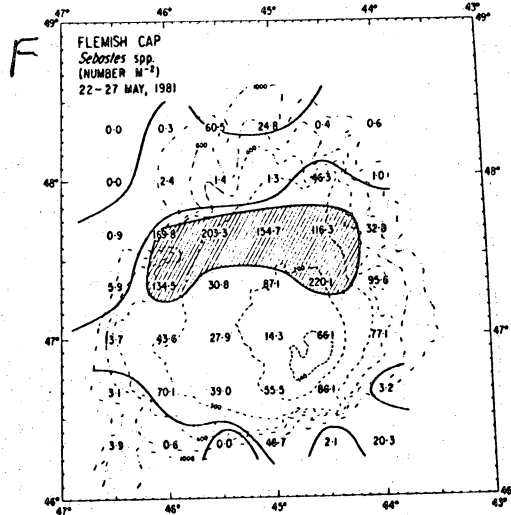
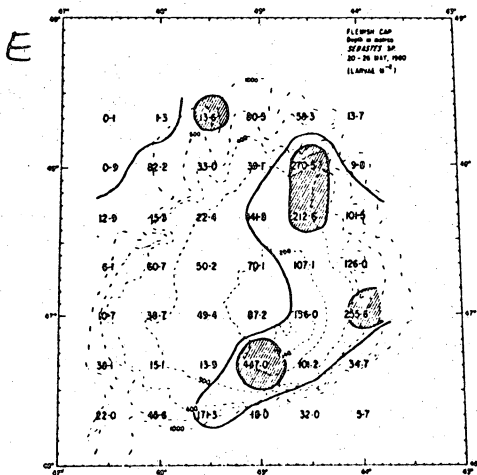
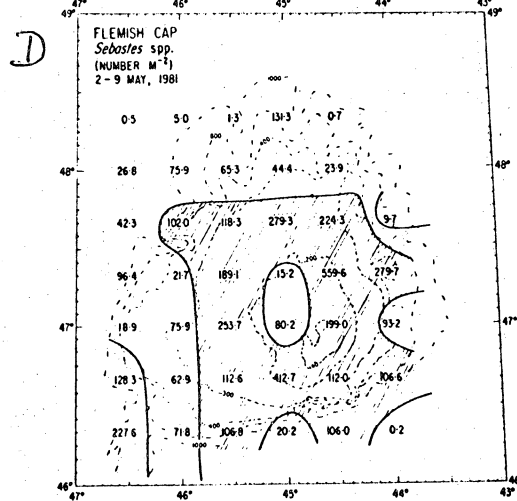
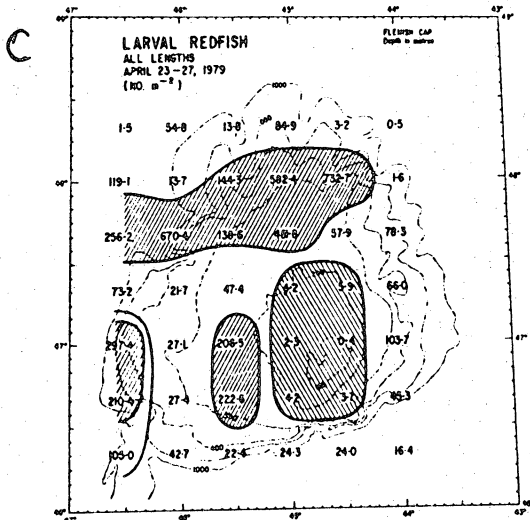
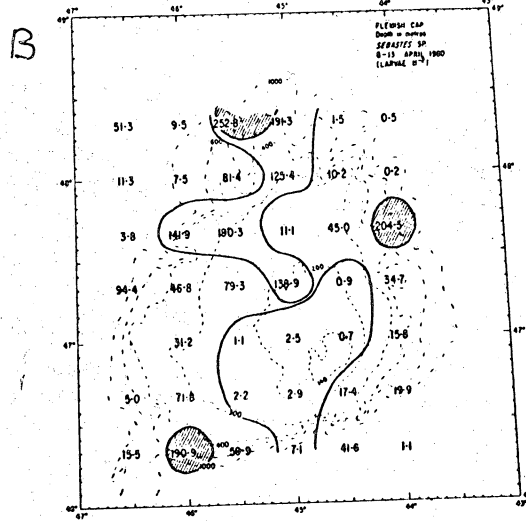
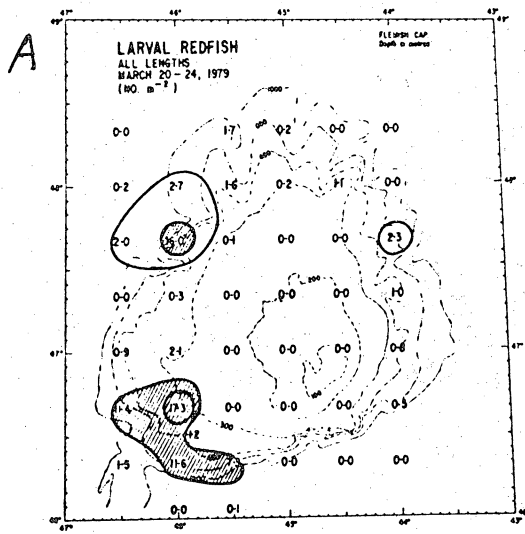


Fig. 3. Abundance distributions of larval redfish (*Sebastes* spp.) sampled on Flemish Cap, 1978-81 (larvae m⁻²).

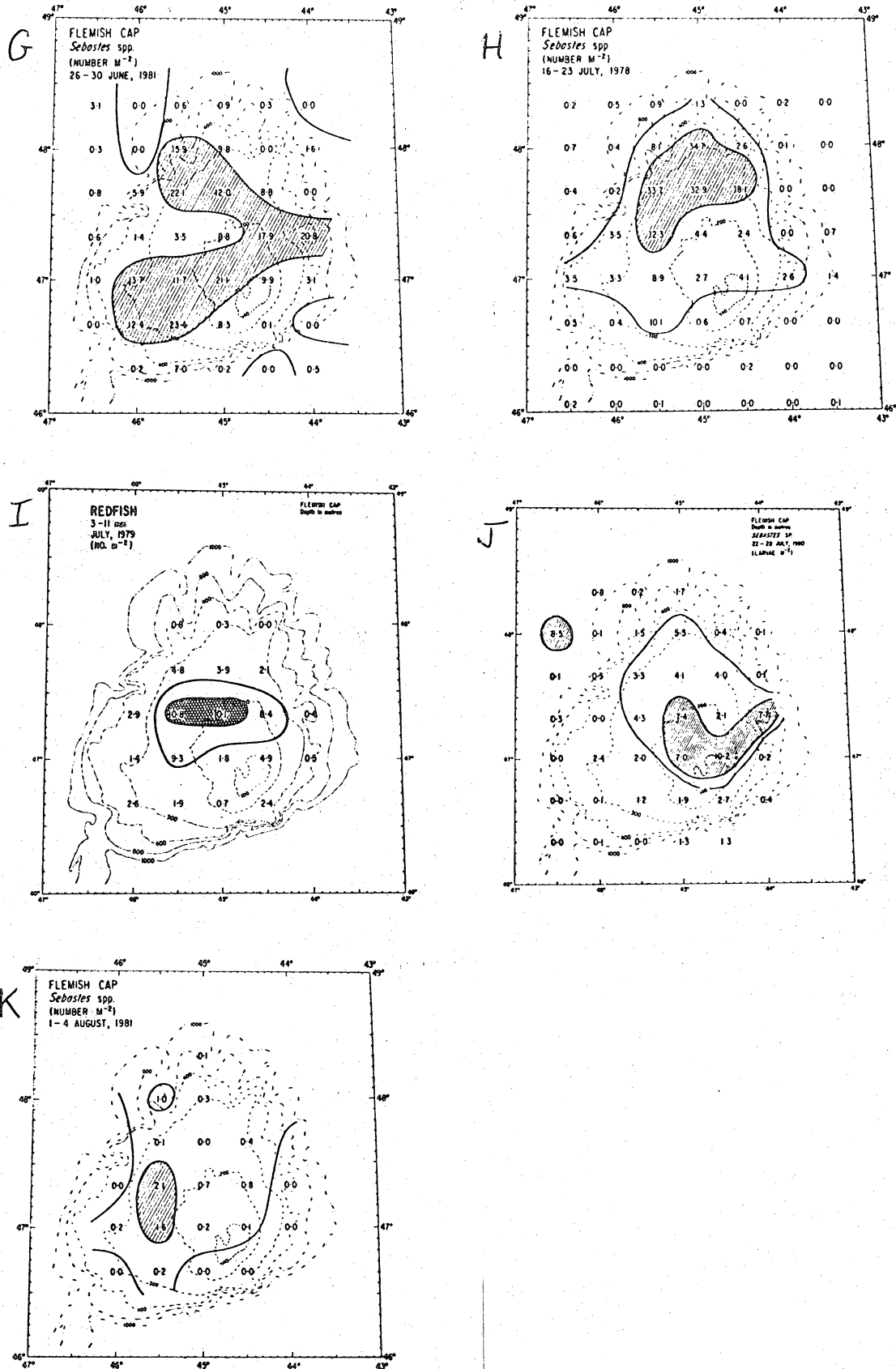


Fig. 3. (cont'd)

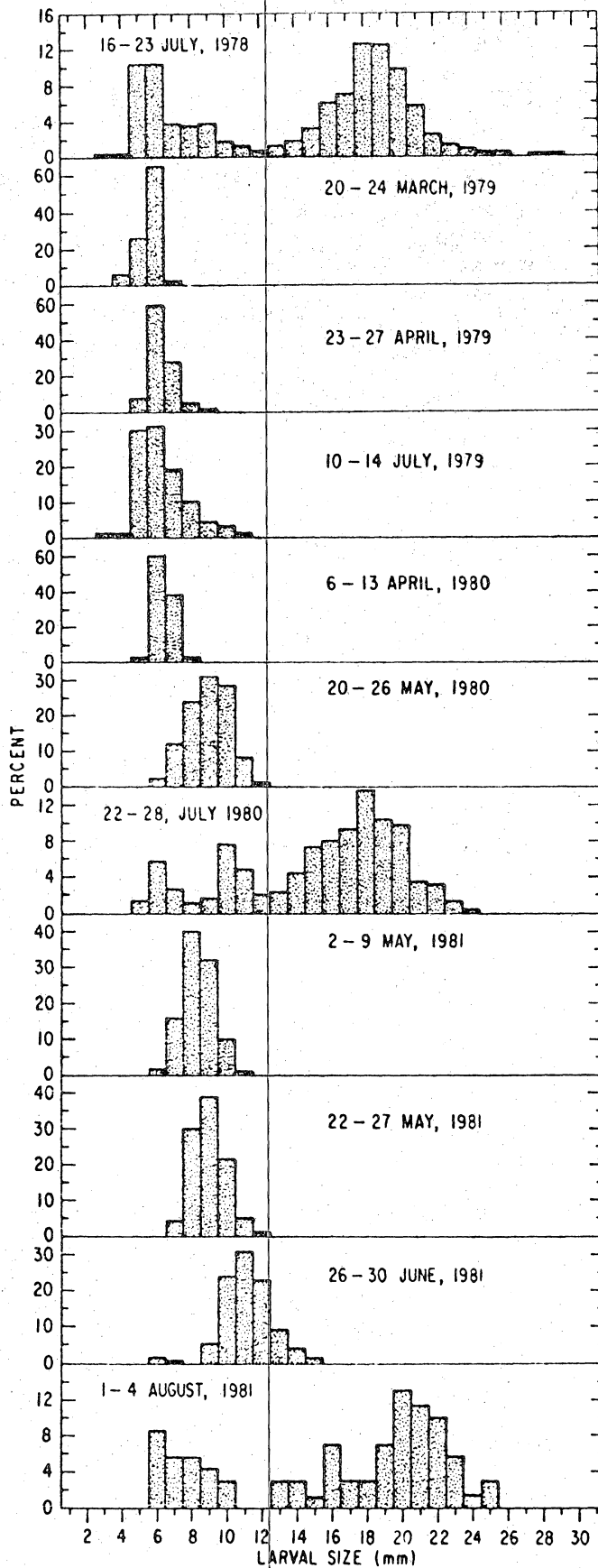


Fig. 4. Length-frequency distributions for larval redfish (Sebastes spp.) sampled on Flemish Cap, 1978-81.

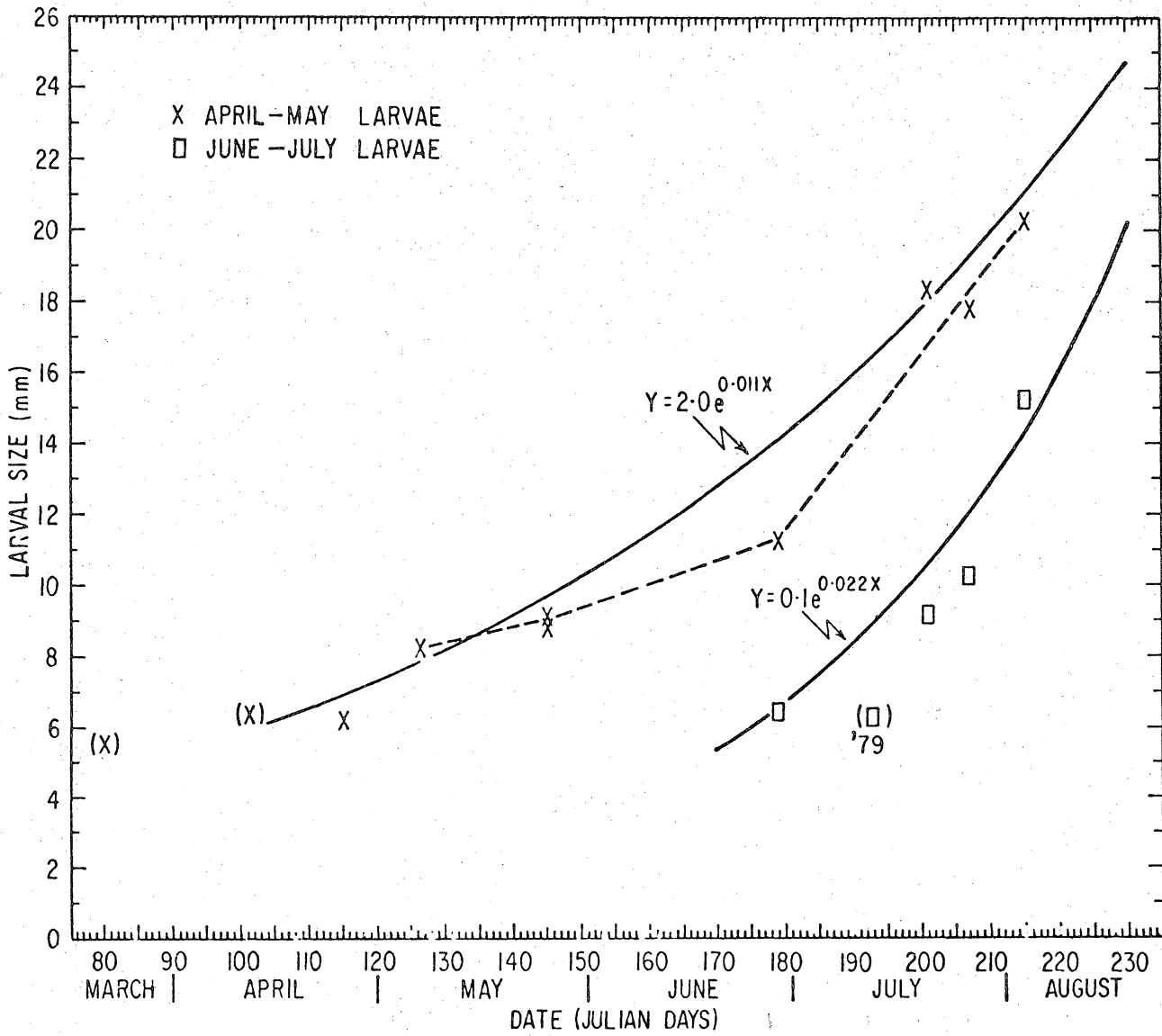


Fig. 5. Population growth estimates during each sampling period on Flemish Cap. Solid lines represent fitted exponential growth curves for April/May and June/July released larval redfish (Sebastes spp.). Dashed line connects 1981 observations for April released larvae. The observation for June/July released larvae in 1979 was not used in estimating the exponential equation.

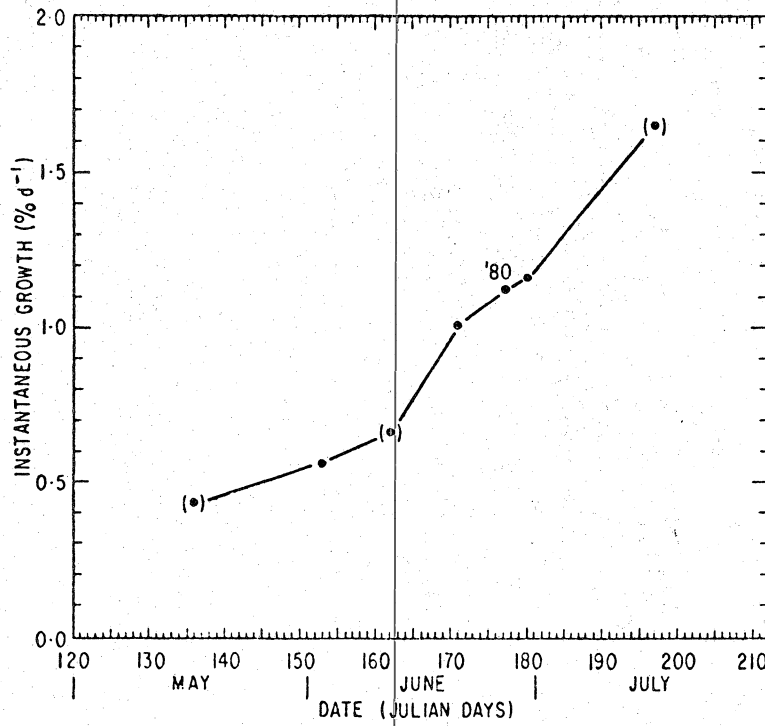


Fig. 6. Instantaneous growth rates (% d⁻¹) calculated for larval redfish (Sebastes spp.) released during April/May 1981. The single observation available during 1980 is also plotted.

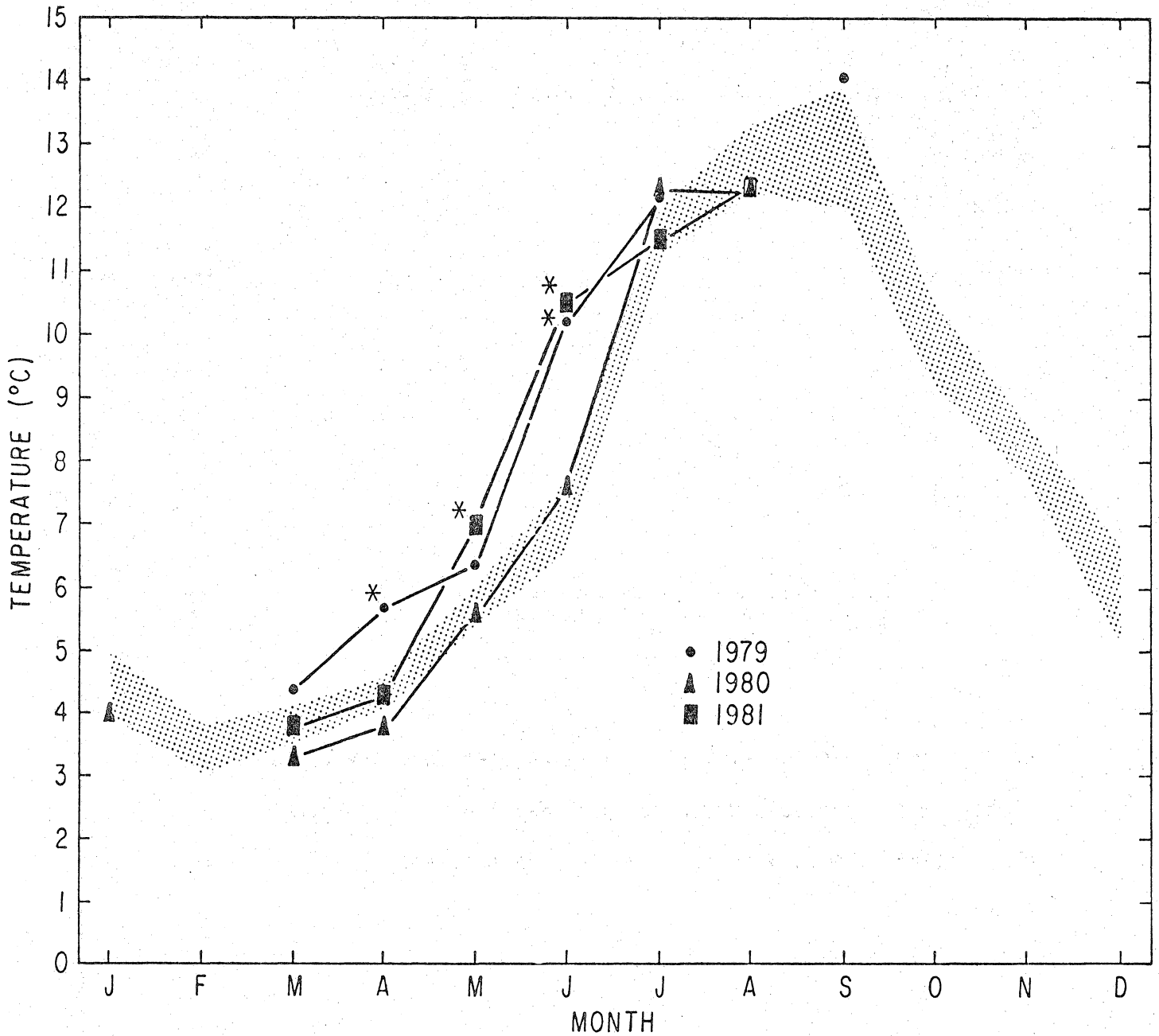


Fig. 7. The 99% confidence interval of the long-term/mean monthly temperatures of surface waters (<15 m) for central Flemish Cap (46°40'N-47°20N by 44°30'W-45°20'W). Plotted also are mean monthly temperatures (<15 m depth) for 1979-81. The star indicates significant differences from the long-term mean ($p < 0.01$).

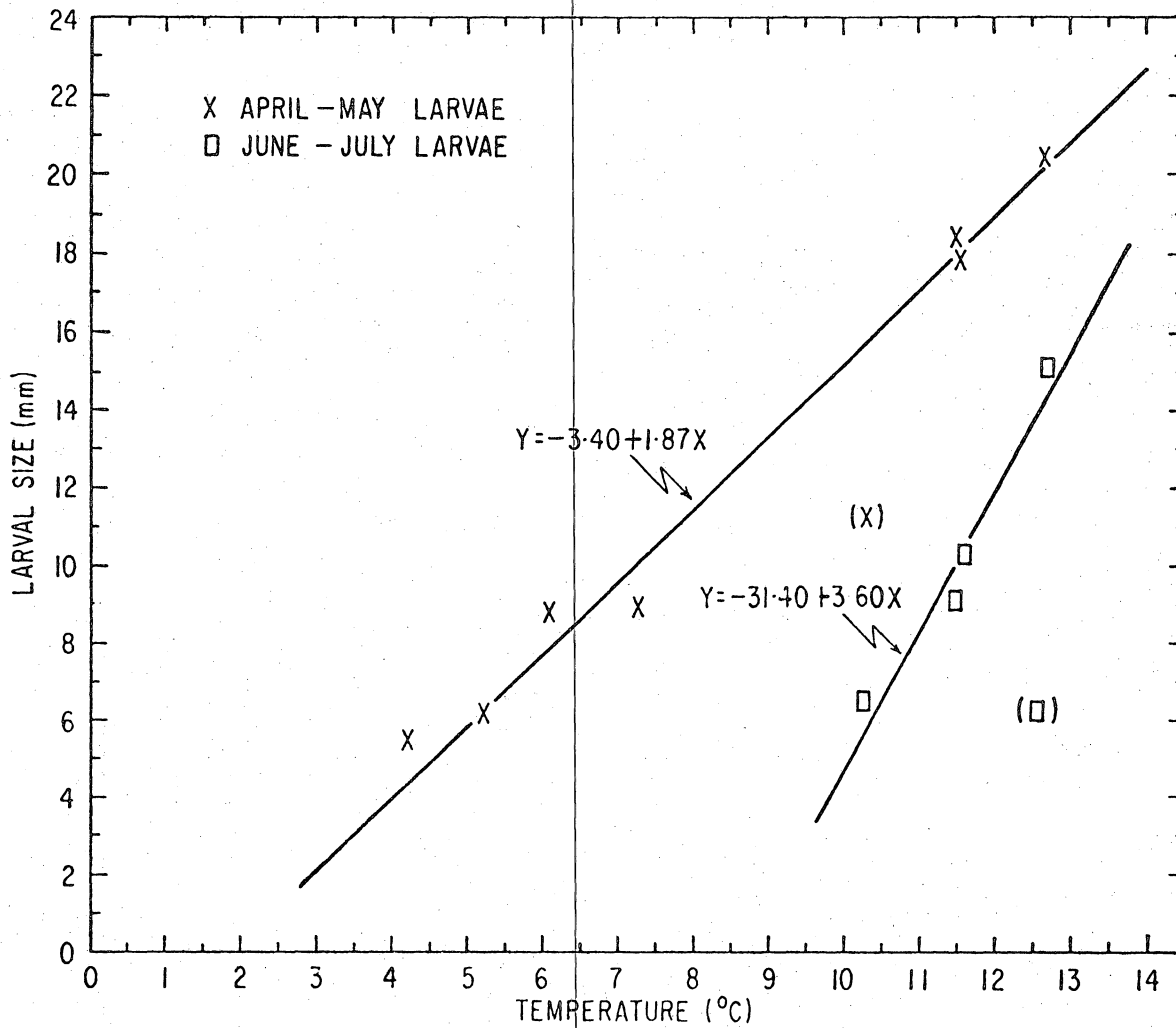


Fig. 8. Temperature versus larval redfish (Sebastes spp.) size for April and June/July released larvae on Flemish Cap. Values in parentheses were not used in the linear regressions.

