Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic

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Year-class formation in beach-spawning stocks of capelin (*Mallotus villosus*) in eastern Newfoundland is strongly influenced by the frequency of large-scale wind-forcing events that regulate the timing and frequency of larval drift. Coastal wind forcing causes abrupt increases in water temperature and wave turbulence which in turn trigger larval emergence. Recent analysis of capelin age-composition data revealed that the strong year classes in the beach-spawning stocks also occurred in a discrete, offshore stock of capelin on the Southeast Shoal of the Grand Bank some 350 km from the nearest spawning beach where capelin spawn annually during June/July at water depths averaging 50 m. The hypothesis tested from the observations described in this paper is that essentially the same kinds of environmental factors, operating during the immediate post-hatching period, are responsible for strong year classes in both stocks.

Field sampling conducted in 1986 revealed several patterns relevant to the evaluation of the hypothesis. In September, the length-frequency distribution of capelin larvae was at least bimodal, indicative of the production of more than one cohort. The formation of the dominant cohort coincided precisely with a storm event and sharp increases in both bottom temperature and currents in the area. This sequence of changes in the water-column structure appeared to reflect an episode of de-stratification due to *in situ* mixing. A second cohort, produced in the absence of any abrupt change in the surrounding physical environment, did not fare as well as the first as evidenced by its poor showing in a later larval survey. The areal distribution of larval capelin in 1986 was similar for all sizes and coincided with the distribution of spawning capelin, indicating that larvae hatching at different times remain in approximately the same geographic location. Capelin larvae smaller than 8 mm showed a diel vertical migration but were generally confined by the pycnocline to the upper 20 m. Larvae larger than 8 mm were almost always below the pycnocline by day and above it at night. These time-dependent patterns of vertical distribution could have contributed to the retention of larval capelin over the Southeast Shoal.

Emergence timed to periods of destratification is argued to be beneficial to larval survival for two reasons: (1) rapid ascent of larvae from the bottom waters while normally high predator densities that occur during stratified conditions are diluted, and (2) enhanced feeding conditions during the initial stages of larval drift associated with the passage of storms.

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Introduction

Capelin (*Mallotus villosus*) is a cold-water, pelagic schooling species closely related to smelt and is considered one of the most important forage species in the Northwest Atlantic. There are five major stocks of capelin in the Newfoundland area (Fig. 1), with most of the commercial fishery aimed at three of the stocks (Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3K, 3L, 3NO). Carscadden (1983) should be consulted for a historical review of the commercial fishery for capelin and its management. Capelin spawn on or near beaches of Newfoundland and Labrador and at water depths averaging 50 m on the Southeast Shoal
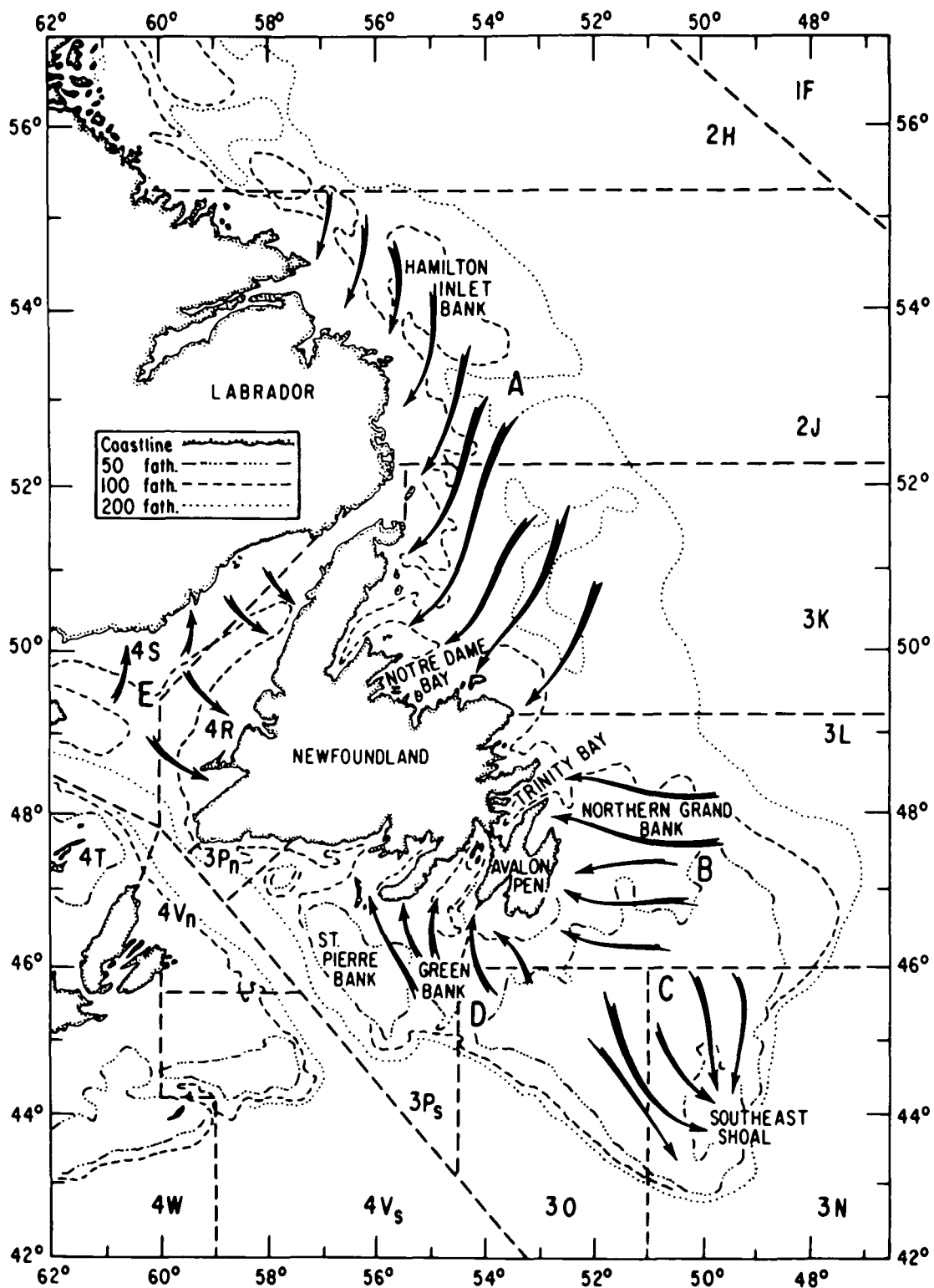
Figure 1. Map showing major stocks (A − E) and spawning migration routes of capelin in the Northwest Atlantic. Alpha-numeric designations (e.g., 2H, 2J, etc.) are NAFO Divisions. Key: A) Labrador/Northeast Newfoundland (NAFO Divisions 2J3K) stocks; B) Northern Grand Bank/Avalon (NAFO Division 3L) stock; C) South Grand Bank (Southeast Shoal − NAFO Divisions 3NO) stock; D) St. Pierre−Green Bank (NAFO Division 3Ps) stock; and E) Gulf of St. Lawrence stock.
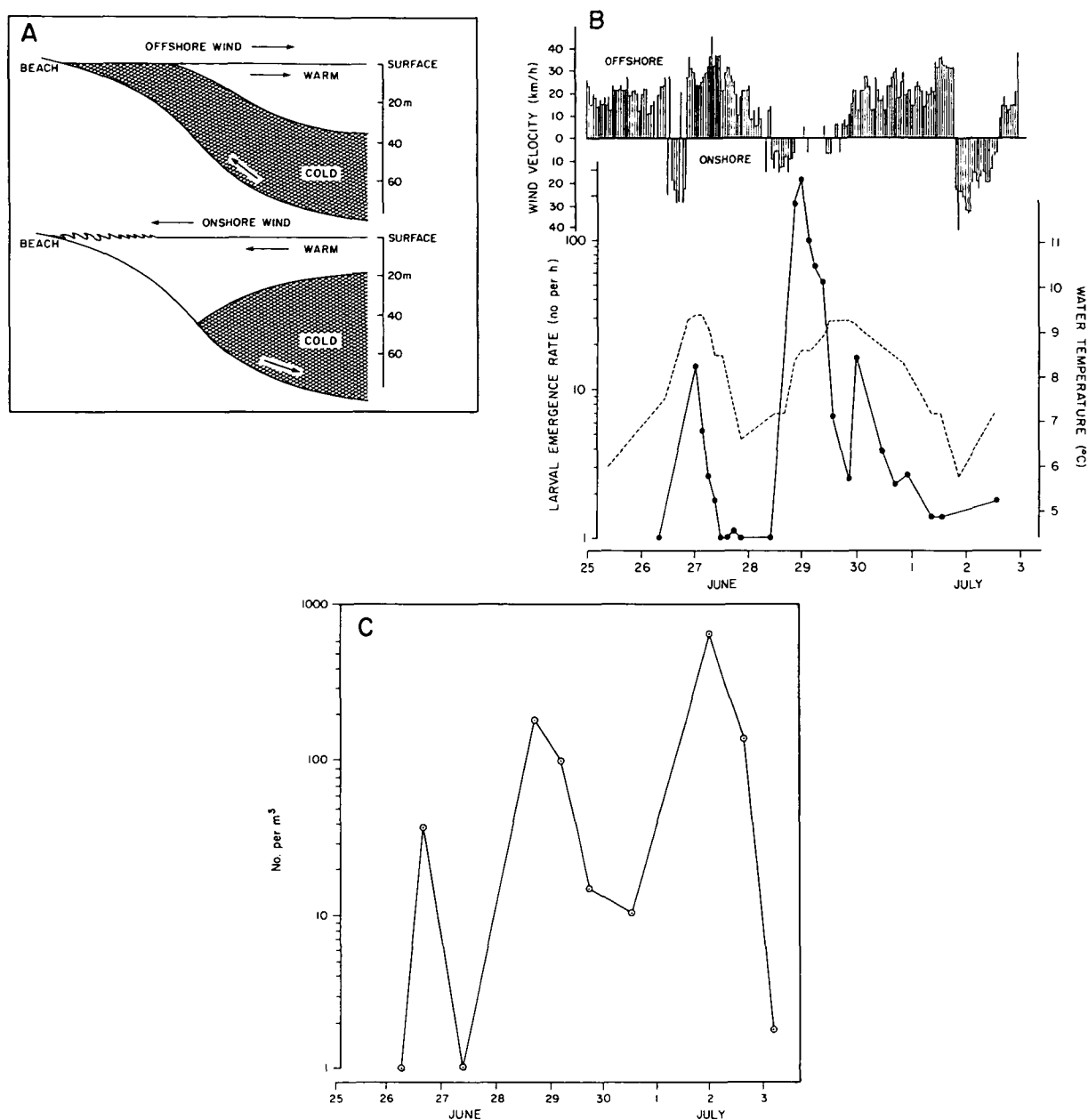
Figure 2. A) The effect of winds on the water-mass characteristics in the nearshore region of eastern Newfoundland. B) Experimental evidence showing that in the absence of physical disturbance of the beach gravel by waves, larval emergence coincided with sharp increases in water temperature associated with onshore winds. Data are means based on larval emergence from five aquariums in a seaside laboratory at Bryants Cove during June/July 1981 (see Frank and Leggett, 1983, for details). C) Larval emergence from the spawning beach at Bryants Cove during the same time period as B).

of the Grand Bank. The Shoal is the shallowest area on the Bank and is located approximately 350 km from the nearest spawning beach.

In this paper we report on an investigation of the environmental factors affecting recruitment in the Southeast Shoal capelin stock. We have chosen to focus our studies on the early life stages of capelin for two compelling reasons: first, year-class strength among

beach-spawning stocks of capelin is influenced by the frequency of large-scale wind-forcing events that regulate the timing and frequency of larval drift (Leggett et al., 1984), and second, preliminary analysis of capelin age-composition data indicates that the strong year classes (1969, 1973, 1979, 1980, 1983) in the beach-spawning stocks also occurred in the Southeast Shoal stock. We hypothesize that the mechanism underlying

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the synchronous production of strong year classes between the beach-spawning and offshore stocks is a similar suite of environmental effects linked to wind-forcing events acting during the immediate post-hatching period.

Capelin eggs are negatively buoyant and adhesive, and during incubation they gradually mix with the substratum to depths of 15 cm in both the beach- and offshore-spawning locations. The environmental signals triggering emergence and subsequent drift of beach-spawned larvae are sharp increases in water temperature and wave turbulence associated with warm surface waters forced into the nearshore region by intermittent onshore winds (Fig. 2). Post-emergence survival is also believed to be influenced by air/sea interactions because the warmer surface waters are typically food rich and predator poor (Leggett et al., 1984).

Capelin spawning commences during mid-June to early July on the Southeast Shoal (Pitt, 1958). Post-spawning, mean bottom-water temperatures on the Shoal range between 2 and 4°C and under these conditions, an incubation period of about 30 days is to be expected based on field and experimental observations of beach-spawning capelin (Frank and Leggett, 1981b). Egg layering, which is commonly observed in other demersal spawners, could prolong the incubation period owing to reduced oxygen levels in the interior of the egg mass (Bowers, 1969). Consequently, we expected the principal hatching and larval emergence times to occur during August and September, periods when the water column is usually strongly stratified.

The hypothesis that the timing of larval emergence is linked to periods of temporary destabilization of the density stratification is examined in this paper. Höglund (1968) and Dubravin et al. (1976) have shown that strong density stratification prevented vertical movements of yolk-sac herring larvae from near bottom to the surface waters. Mann (1982) postulated that fall spawning by the pelecyod Arctica islandica would be most conducive to high larval survival because the vertical movement of larvae would not be limited by the intense thermocline of summer. Also, peak hatching of herring larvae off the north coast of Scotland and around the British Isles in general coincides with the breakdown of thermal stratification and increases in zooplankton biomass (Cushing, 1986; Heath et al., 1987). Prolonged confinement of capelin larvae to sub-pycnocline waters could reduce survival either through predation or food-limitation. We also explore these possibilities in the paper.

Temporary destratification could result from mixing by storms or spatial shifts of water masses adjacent to the bank. Only in situ mixing caused by storms would generate both a thermal signal and bottom turbulence similar to that created by wind-driven water-mass exchange in beach-spawning areas. Sub-surface intrusions of warmer slope water onto the bank are not uncommon (Templeman and Hodder, 1965). A much weaker ther-

mal signal relative to in situ mixing, increased density stratification, and no acceleration of bottom currents are the most probable consequences of slope-water intrusions.

Analysis of historical data

Before starting our field studies we examined two historical series of physical data for the Southeast Shoal region. Surface- and bottom-water temperatures were analysed to determine whether destratification had ever occurred during the postspawning period. Wave data were used with theoretical relationships and preferred spawning substrate sizes to evaluate the potential for physical agitation of the sediment due to surface wave activity. The temperature data available were based on Nansen bottle and bathythermograph data extracted from the region bounded by 43°56'N—44°50'N 49°20'W—50°40'W. Surface wave data were generated from a waverider accelerometer buoy deployed from 27 July to 30 August 1973 where the total depth was 58 m.
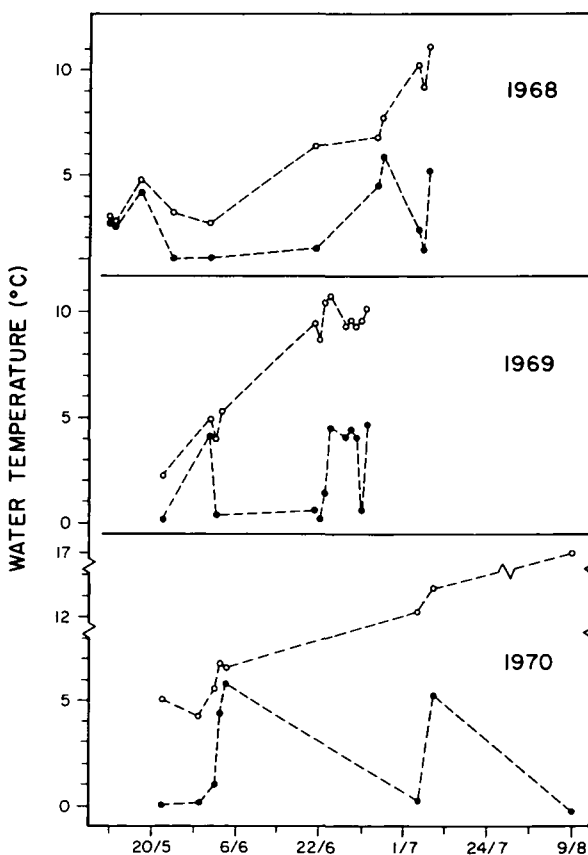

Figure 3. Composite of some historical water-temperature data taken from the Southeast Shoal. Surface (open circles) and bottom (closed circles) temperatures on each date are from the same locations.

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Figure 4. A) Surface wave characteristics generated by a waverider accelerometer buoy positioned at 44°43'29"N 49°27'23"W during July–August 1973 in the vicinity of the Southeast Shoal. Numbers refer to frequency of occurrence. B) Resultant frequency histogram of calculated oscillatory bottom-current velocities (cm/s) at 50 m. Number of observations: 228.
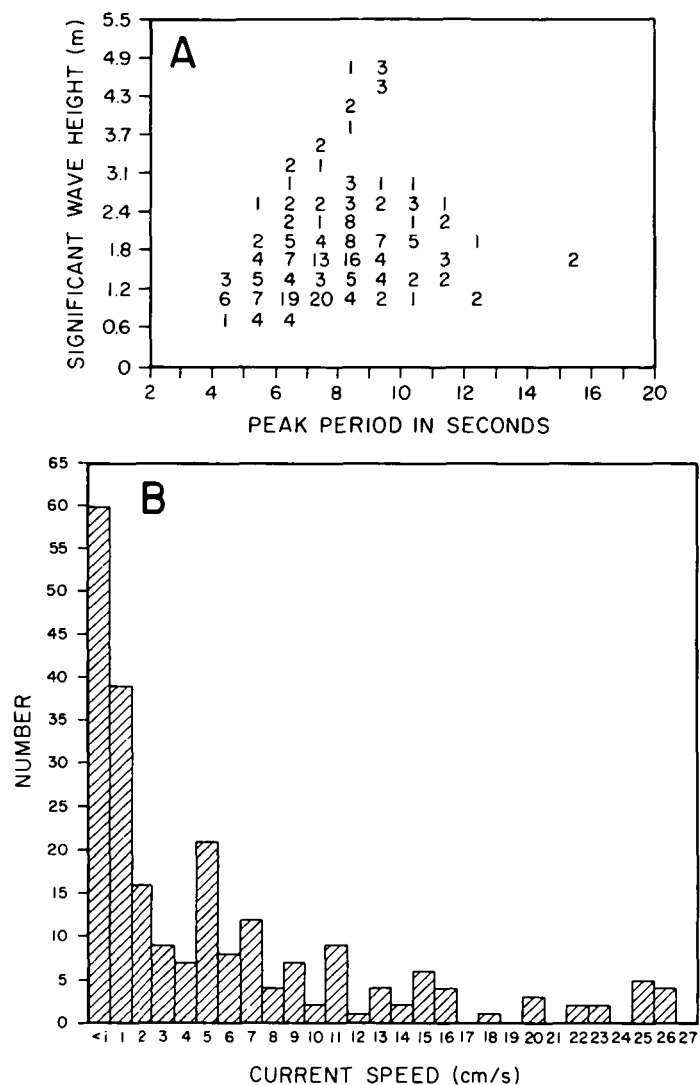
All physical data were archived by the Marine Environmental Data Service, Ottawa, Canada.

Temperature data approximating a time series was extremely limited because no systematic monitoring scheme has ever been conducted there. Given this qualification a composite temperature record was developed for 1968, 1969, and 1970. There were occasions when bottom-water temperatures increased abruptly during the June–August period (Fig. 3); this could have resulted from in situ mixing or spatial shifts of a warmer water mass such as slope-water intrusions. The latter effect was documented by Templeman and Hodder (1965), who showed that during May/June in some years, particularly 1955, haddock followed intrusions of warm slope water onto the bank from the southwest slope region (between 53° and 51°W). The 1955 haddock year class was the most successful on record, and the authors suggested that "the extent, shape, temper-

ature, and other characteristics of this warm water mass during the spawning season in May and June and the resulting distribution of haddock at spawning time should have a considerable influence on the survival and retention on the bank of haddock eggs and larvae". We conclude from this analysis that the Shoal waters are subject to short-term increases in bottom-water temperature.

The wave characteristics (Fig. 4) were used to calculate the maximum horizontal orbital velocity (cm/s) at the bottom. Horizontal oscillatory bottom currents (U_m) were calculated from the theoretical relationship

$$U_m = \pi \, H/T \, \sinh kh$$

where H is the wave height in metres, T is the wave period in seconds, h is the water depth in metres (=50 m), and k is the wavenumber (=$2\pi/L$). The wave-

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length (L_d) for a deep-water wave was calculated from the expression $L_d = gT^2/2\pi$ where g is the acceleration due to gravity = 9.8 m/s^2. The final approximation of L in water of any depth was derived from $L^2 = L_d^2$ tanh $k_d h$ (Inman, 1963). Resulting estimates averaged 5.4 cm/s, and only infrequently (8 %) was the velocity $\geq$20 cm/s when maximum wave heights and long period surface waves prevailed (Fig. 4).

Sediment size selected by capelin on spawning beaches in eastern Newfoundland is much larger (size range: 5−25-mm diameter; Templeman, 1948) than the substrate selected for spawning on the SE Shoal (size range: 0.5−2.2-mm diameter; Pitt, 1958). The possibility exists that the sediment size selected for spawning is related to the mixing energy at the sediment/water interface and that capelin select sediments which are large enough to prevent transport of the eggs under the prevailing energy regime, but sufficiently small to allow for current- or wave-induced burial during incubation and erosion during emergence.

The relationship between the velocity needed to move a particle, the erosion velocity, and its size is known as the Hjulström (1935) curve. Low erosion velocities of about 15 cm/s are required to move sand (0.25−0.5-mm diameter) and increase thereafter with increasing grain size. The calculated maximum speeds of wave-induced currents likely to be encountered on the sea bottom during the July−August period of 1973 were occasionally sufficient ($\geq$20 cm/s) to cause erosion of the preferred spawning substrate on the Southeast Shoal and weak enough, on average, to prevent displacement during the incubation period (Fig. 4).

We conclude from the analysis of the historical temperature and wave data available for the Southeast Shoal that this region is conducive to supplying intermittent physical signals to newly hatched larvae to leave the bottom sediment and enter the water column. By analogy with beach-spawned capelin, stimulation by abrupt increases in temperature causing active larval emergence and/or passive displacement of larvae via sediment erosion are the most likely biological consequences of such events. If emergence timing is linked to intermittent storms we would expect to find one or more distinct modal size groups of larvae in our field collections whose time of formation coincided with an obvious physical signal. Should larval emergence timing be independent of storms a unimodal and probably broad distribution of larval sizes centred about the median hatching date is expected. We address these possibilities in the analysis of the data generated from our ichthyoplankton surveys.

Methods

Field observations

Beginning in September of 1985 we initiated preliminary field studies on an opportunistic basis to collect cape-

lin larvae and associated organisms using a 0.75-m diameter 80-μm mesh net towed vertically from near bottom to the surface at nine stations in the Southeast Shoal region. This work was the forerunner of a dedicated ichthyoplankton study that was successfully executed during September of 1986. The sampling area was centred on 44°30'N 50°00'W because the results from acoustic surveys conducted annually by the Science Branch, Department of Fisheries and Oceans, St. John's, Newfoundland, since the early 1980s showed consistently high concentrations of spawning capelin in this vicinity. The procedures used to conduct the acoustic surveys of the Southeast Shoal spawning stock during 1985 and 1986 are described in Stevens et al. (1985), Miller (1986), and Miller and Carscadden (1987). We use these data to examine the distribution of spawning capelin relative to the distribution of their larvae from the September survey in each year.

A rectangular grid of 39 stations spaced at 10-nautical-mile intervals along six (I−VI) east−west transects was established for intensive biological sampling during September 1986 (Fig. 5). The spatial distribution of capelin larvae and macrozooplankton was determined from discrete sampling at seven depths at each station using a small-scale version of the BIONESS (Sameoto et al., 1980). Sampling depths were 5, 10, 15, 20, 25, 30, and 40 m. Each depth was sampled for 10 minutes and about 200 m^3 of water was filtered through each of seven 333-μm mesh nets. A CTD positioned on the top of the net frame provided real-time measurements of temperature, salinity, depth, pitch, roll, and flow rate. A horizontal surface tow of 10 minutes' duration at a depth of 1 m was made during the middle of each BIONESS tow using a 0.75-m diameter, 333-μm mesh net. XBT casts were also made at each station.

All samples were preserved in 4 % formalin buffered with sodium borate. All fish larvae and macrozooplankton were sorted from the samples and counted. Total length measurements were made of all capelin larvae using an ocular micrometer. A random subsample of capelin larvae was selected from a few stations and transferred to alcohol within one week of collection for enumeration of otolith rings. Fish larvae and macrozooplankton densities were expressed as number per 100 m^3 of water filtered.

Capelin larvae were grouped into 1-mm size categories from 4 to 15 mm, and variation in their vertical distribution was evaluated by calculating the depth of the centre of mass of the distribution, Z_{cm} (in m):

$$Z_{cm} = \sum_{i=1}^{8} (P_i * Z_i)$$

where P_i is the proportion of larvae in the (i)th depth interval and Z_i is the average depth of the (i)th stratum. Stations occupied between 20:00 and 06:35 h were considered night collections and all other times were day. Physical oceanographic studies were initiated by J.
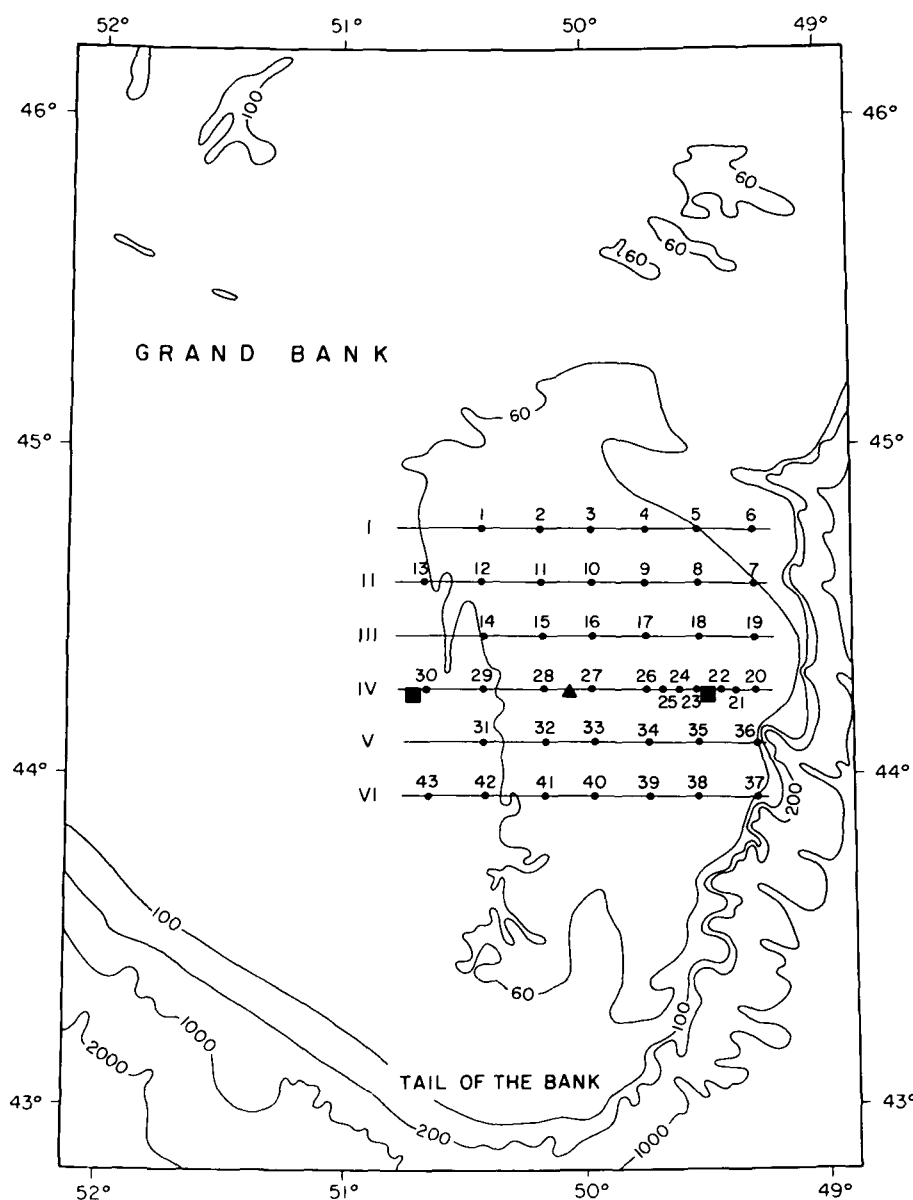
Figure 5. Map showing transects (roman numerals I–VI) and stations (circles) sampled during the September 1986 survey. Locations of moorings (current meters, thermistor chain, and Hermes buoy (triangle); Ryan thermographs (squares)) are shown. Depth contours in metres.

Loder and C. Ross (Physical and Chemical Sciences Branch, Department of Fisheries and Oceans) during 1986 to monitor the current and temperature fields of the Southeast Shoal. Moored sensors (current meters, a thermistor chain, and a surface buoy that measured barometric pressure and sea surface temperature) were deployed in April and recovered in October of 1986 (Fig. 5).

Results and discussion

Adult distribution

High concentrations of capelin (>100 g/m^2) were frequently encountered during the June/July acoustic survey in 1986, with 51 % of the fish spent and only 9 % immature. This situation contrasts markedly from the 1985 survey when there were no spent fish and a large proportion of the fish (42 %) were immature (Fig. 6). The Southeast Shoal capelin stock experienced much colder bottom-water temperatures in 1985 relative to
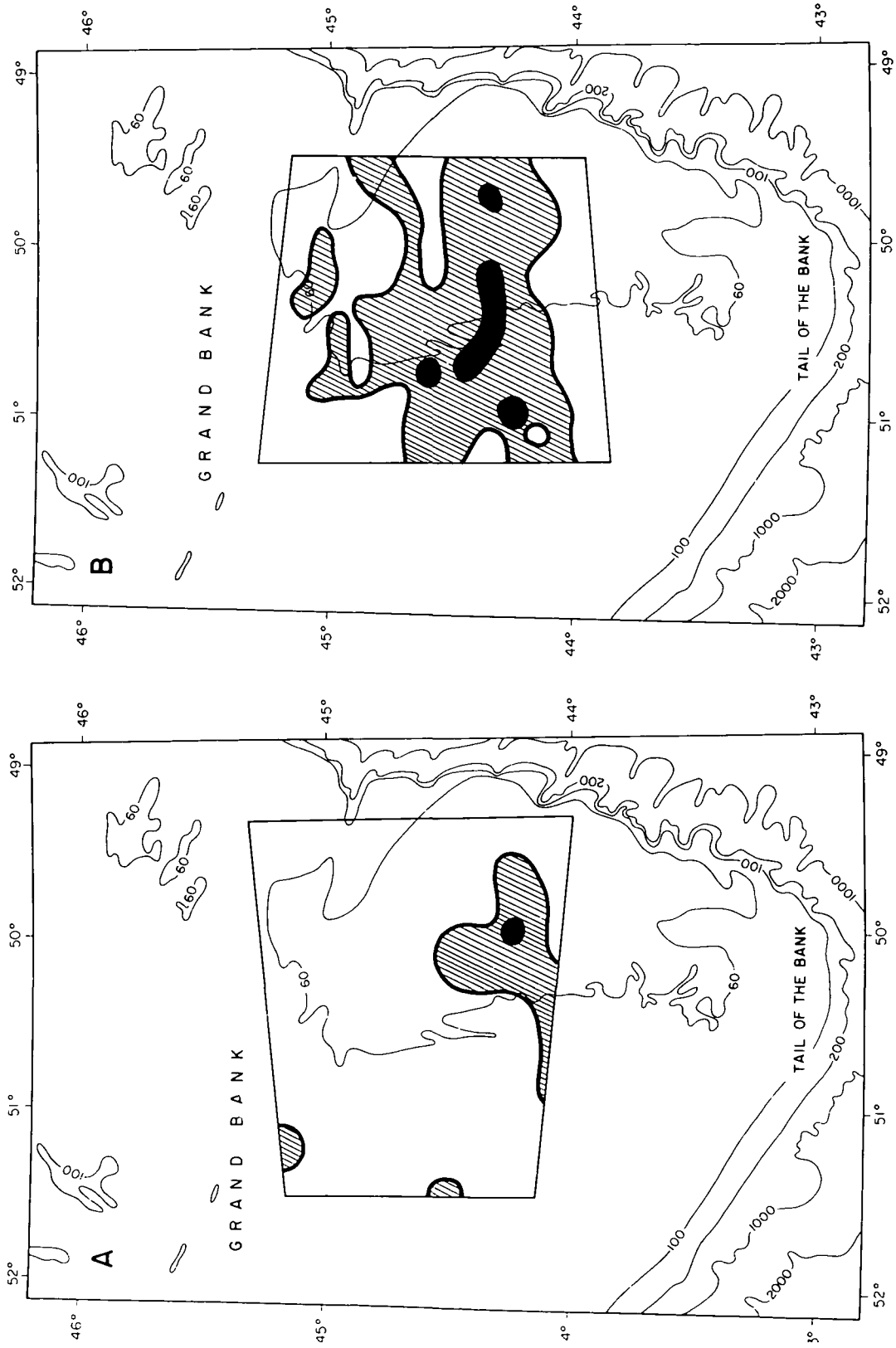
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Figure 6. Distribution of capelin biomass on the Southeast Shoal during A) 22–26 June 1985 and B) 26 June–2 July 1986. Key to contour levels: 10 g/m² (open); –100 g/m² (hatched); >100 g/m² (solid). Survey area enclosed by a polygon.
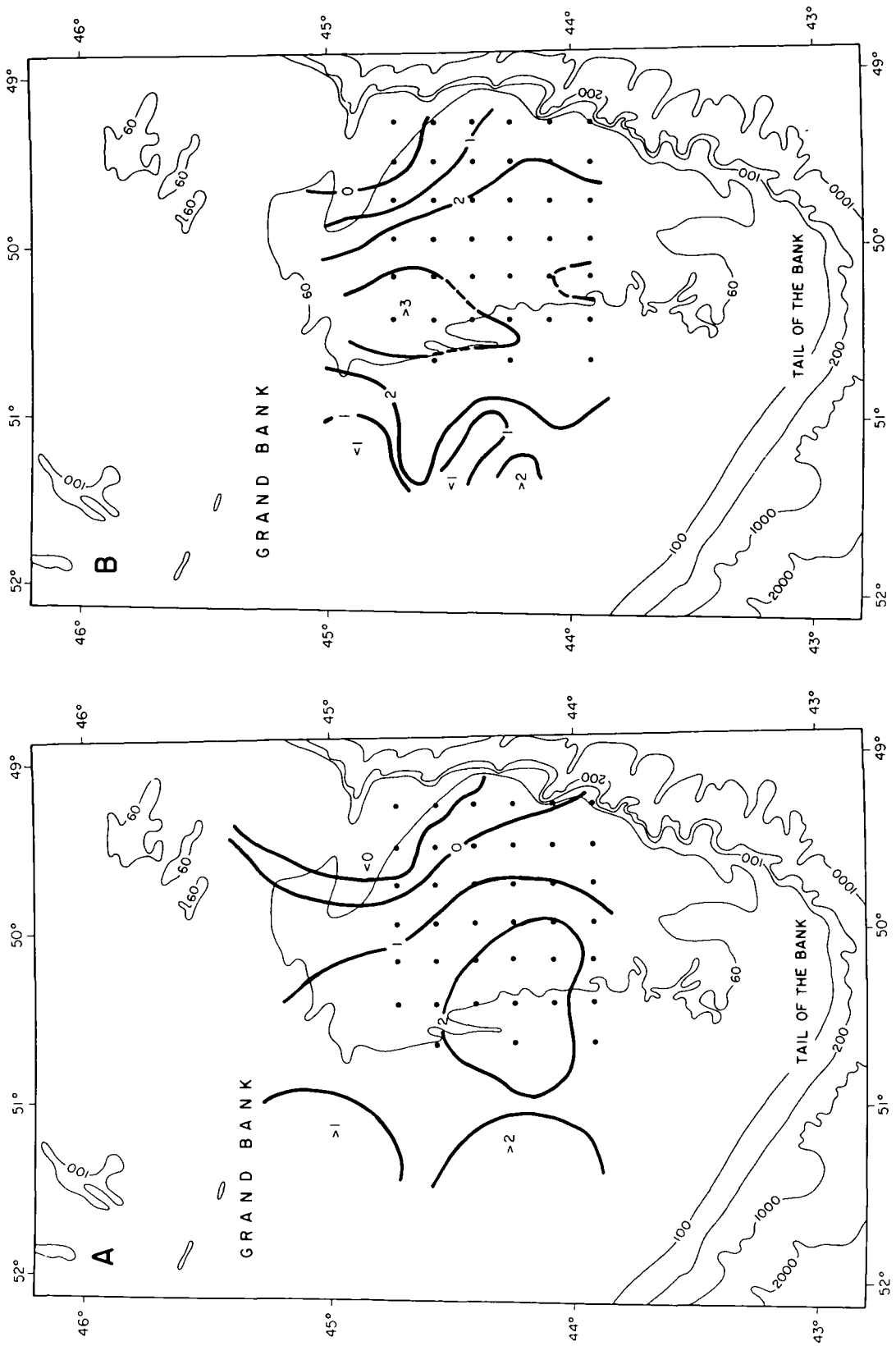
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Figure 7. Bottom-water temperatures derived from XBT casts taken during the June/July capelin hydroacoustic survey in A) 1985 and B) 1986.
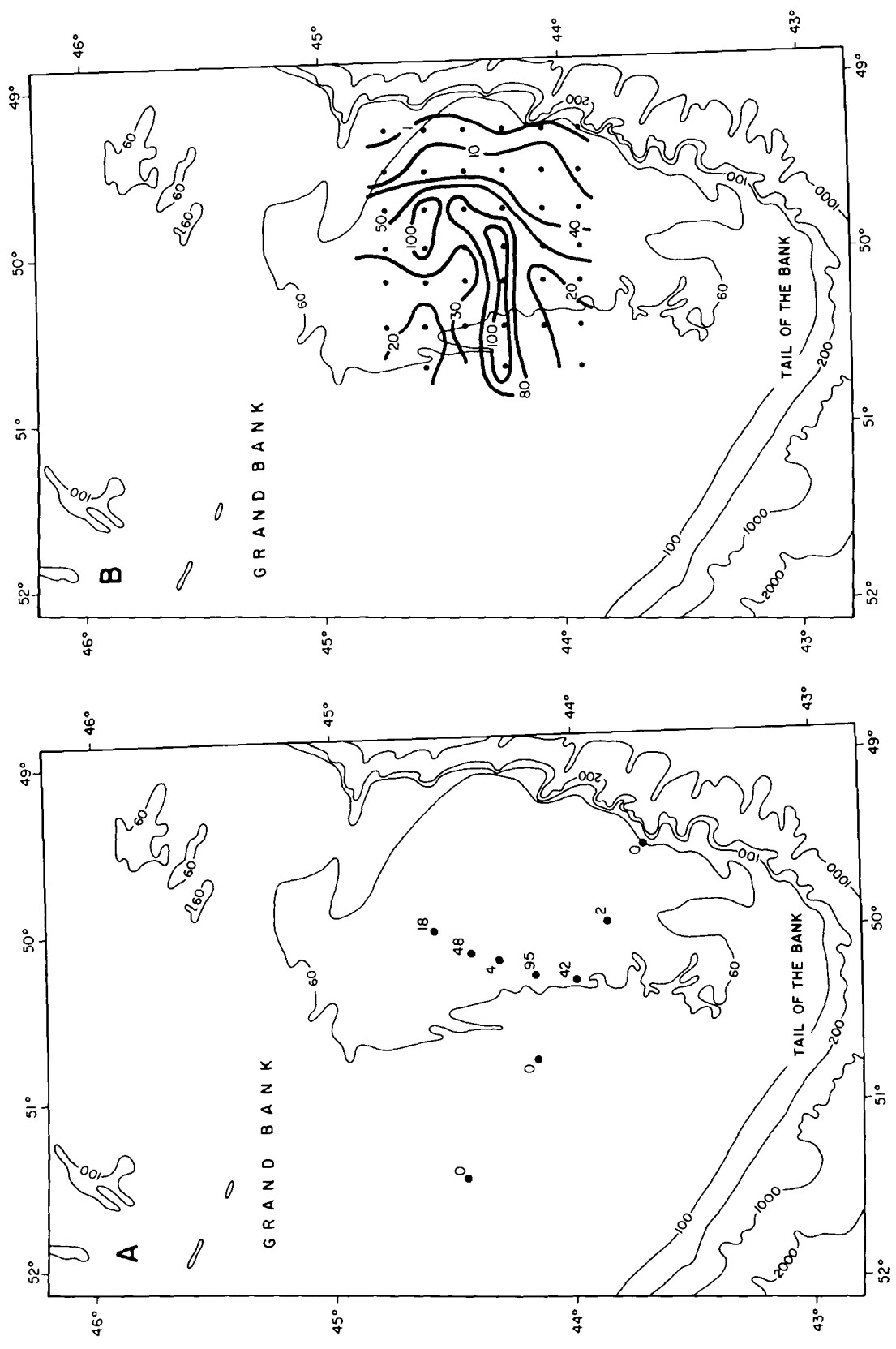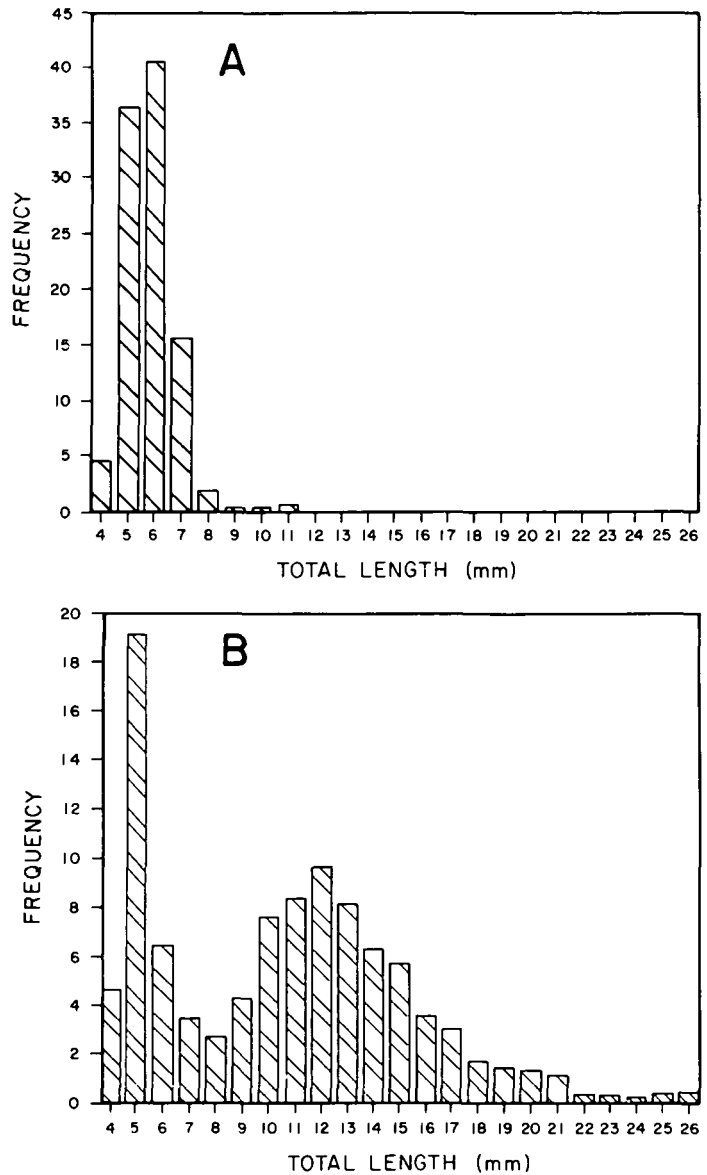
Figure 8. Distribution of capelin larvae (all sizes) collected in September of A) 1985 (units: larvae/m^3) and B) 1986 (units: larvae/100 m^3).

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Figure 9. Length-frequency distribution of capelin larvae collected during September of A) 1985 and B) 1986.

1986 as indicated by the XBT data collected during the acoustic survey (Fig. 7). Large expanses of the bottom over the Shoal during June/July of 1985 were 2°C and lower, which may have delayed spawning because capelin spawning on the Southeast Shoal normally occurs at bottom temperatures between 2 and 4°C (Pitt, 1958). Below-normal temperature anomalies extending over the entire water column were prevalent throughout most of eastern Newfoundland during most months of 1984 and 1985, while in 1986 a general increase in water temperature was evident (Petrie et al., 1987).

Larval distributions and size composition

High concentrations of capelin larvae occurred in the same locations during the September survey in both years (Fig. 8) and, in 1986, the areas of peak larval concentration coincided with the adult capelin concentrations witnessed in June/July. More than 90 % of the capelin larvae collected in 1985 fell within the 4–7-mm total length range, indicating recent hatching and emergence (Fig. 9). The extremely high densities (maximum: 95/m³) of newly hatched larvae collected in 1985 support our suggestion of delayed spawning. It is possible to calculate the approximate spawning date from the development rate/temperature relationship for capelin eggs (Frank and Leggett, 1981b). At bottom temper-

atures between 2 and 3°C, time to hatching is about 35 days, which suggests that peak spawning occurred in late July – a delay in spawning of about one month compared with 1986.

Two modes were evident in the length-frequency distribution of capelin larvae in September 1986, one at 12 mm and the other at 5 mm. The average total length was 10.6 mm (Fig. 9). The broad range of sizes (4–26 mm) encountered in the same area as the spawning adults and in high concentrations relative to those observed for other species in other areas (Able, 1978; O'Boyle et al., 1984) indicates that larvae hatching at different times remain within the same approximate geographic location. Published information on the growth rates of larval capelin (range: 0.25–0.35 mm/d, Jacquaz et al., 1977; Frank and Leggett, 1986) and size at hatching (approximately 5 mm, Frank and Leggett, 1981a) provides a preliminary estimate of the minimum residence time of larvae on the Shoal after hatching. The average and largest size of larvae collected would be equated with individuals about 14 and 60 days old respectively. Retention of larvae in this region may be a reflection of the general circulation characteristic of the Shoal. Using geostrophic calculations and drifter tracks, Petrie and Isenor (1985) suggest that a weak anticyclonic gyre may exist in the area.

Information on the age of capelin larvae collected was available from the 1986 survey. Gjøsæter and Monstad (1985) examined otoliths from known-age capelin larvae and found a significant correlation (r = 0.75, p < 0.001) between ring number and age with a slope not significantly different from one, suggesting the formation of one ring per day during the larval stage of capelin. Examination of the otoliths from capelin larvae was restricted to individuals 14 to 21 mm in total length, because poor ring clarity prevented larvae under 14 mm from being accurately aged and too few larvae over 21 mm were collected. Nevertheless, at the extremes of the size range evaluated (14 and 21 mm), the age of capelin larvae was 24 and 50 days respectively. The relationship between total length (X, in mm) and ring number (Y) was

$$Y = 2.936X - 16.03, \quad r = 0.89, \quad p < 0.01.$$

Extrapolation of this relationship to day zero yielded an intercept of 5.4 mm, which is close to the hatching size for beach-spawned capelin larvae (Frank and Leggett, 1981a). This suggests that the length-at-age relationship developed from the narrow observed range of capelin sizes may apply well enough to a wide range of capelin sizes, especially those less than 14 mm. Using the length-at-age data we derived a growth rate estimate of 0.35 mm/d for Southeast Shoal capelin larvae, a result consistent with a published study from the Gulf of St. Lawrence for capelin larvae growing over a six-month period (Jacquaz et al., 1977).

The same length-at-age relationship was used to cal-culate the time of formation of the dominant cohorts in both years of the survey. In 1985, the one and only larval cohort in our samples should have been formed in early September (day of the year = 246), shortly before the 6–9 September field survey conducted in that year. In 1986, the length modes at 12 and 5 mm corresponded to individuals approximately 20 (day 236) and 1–2 (day 254) days old respectively. Capelin larvae were abundant in the size categories surrounding the 12-mm mode, with the proportion of larvae in the 10–15-mm size interval relative to all sizes collected exceeding 45 % (Fig. 9). Given that substantial mortality had probably occurred during the approximately 20 days of its existence (e.g., in the St. Lawrence estuary Fortier and Leggett (1985) estimated larval capelin mortality rates of 44 % per day during the immediate post-yolk-sac absorption period), we conclude that the cohort of capelin around 12 mm was the dominant cohort in 1986.

Physical data and cohort formation

Geostrophic wind data, calculated from 6-h atmospheric pressure maps for 1985 and 1986, were provided by the Atmospheric Environment Service (Downsview, Ontario) for 44°06'N 50°30'W. The wind records (direction and speed) are shown in Figure 10 for the period 15 July (day 196)–13 September (day 256). In 1985 we looked for a strong wind event around day 246 corresponding to the time of formation of the dominant larval cohort. Near to this time an upswing in the wind speed record to 20 m/s (or 40 knots) was evident; however, there were no other physical data available so we hesitate to pursue the 1985 analysis any further.

It was shown above that in 1986 the time of formation of the dominant larval cohort occurred around day 236. The wind record shows a dramatic increase in wind speed on day 233, with speeds in excess of 30 m/s occurring on days 234 and 235. This event marked the passage of Tropical Storm Charley (Lawrence, 1987) and, as Figure 11 shows, it had a great impact on the hydrographic structure of the water column. The surface-water temperatures dropped from 15° to 5°C while temperatures at mid-depth and near the bottom rose sharply. This sequence of changes in the water-column structure appears at least partly to reflect an episode of destratification due to in situ mixing that coincided with the time of formation of the dominant larval cohort produced in 1986. Current speeds approaching 45 cm/s (averaged over 30-minute intervals) at a depth of 45 m also coincided with the storm event (Fig. 12). This velocity is sufficient to cause erosion of material from the spawning bed and could cause the synchronous emergence of large numbers of larvae, particularly if larvae hatching at different times accumulate in the sediment in a manner similar to that occurring on beaches (Frank and Leggett, 1981a). The passage of Tropical Storm Charley near to the study area was not an unusual
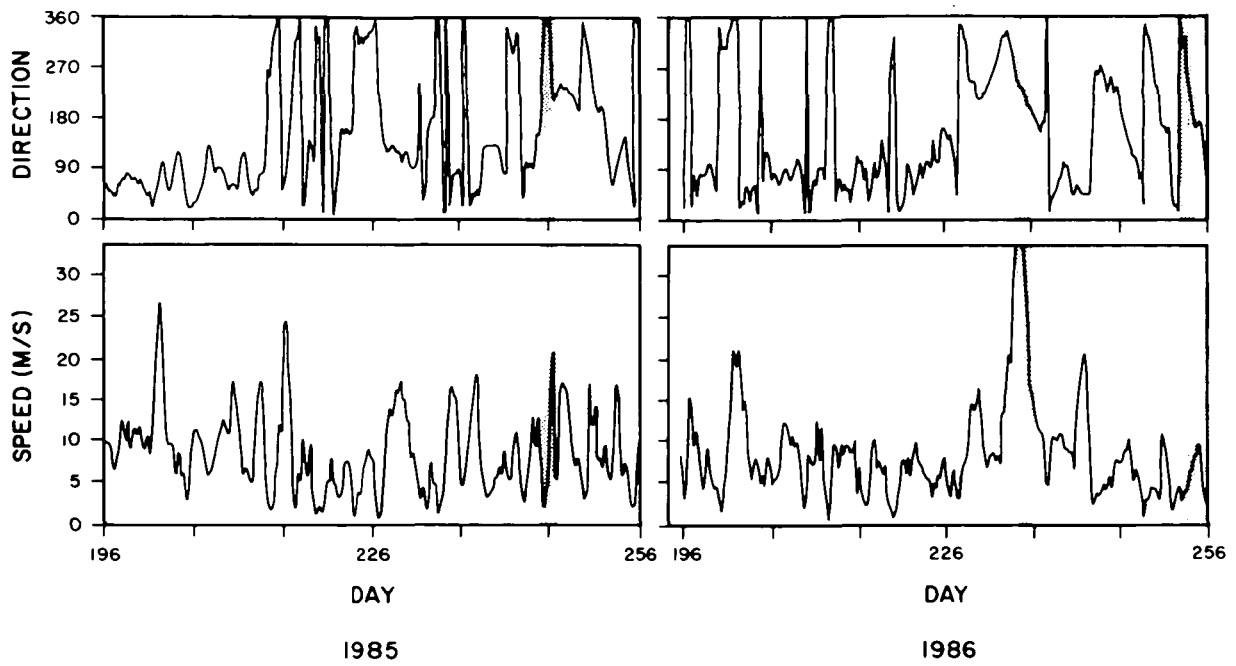
Figure 10. Geostrophic wind data calculated from 6-h atmospheric pressure maps at 44°06'N 50°30'W for the period 15 July (day 196)–13 September (day 256). Stippling shows estimated larval cohort formation times.
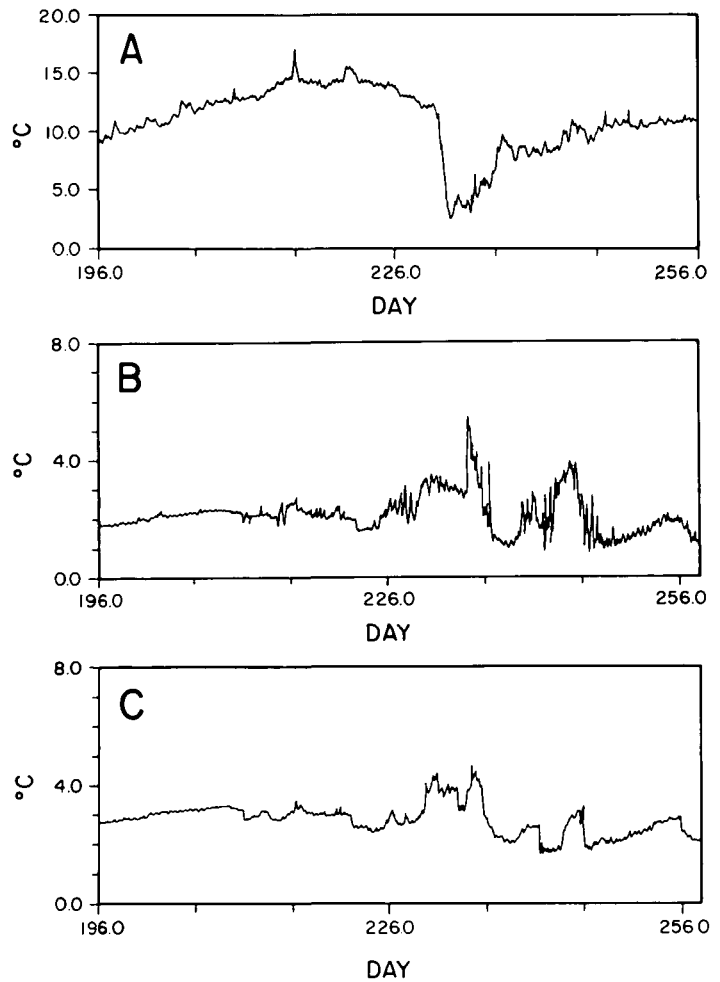

Figure 11. Hydrographic data showing 1986 time series of water temperatures at three depth levels at the central mooring site (see Fig. 5) on the Southeast Shoal. A) Surface, B) 34 m, and C) 52 m.
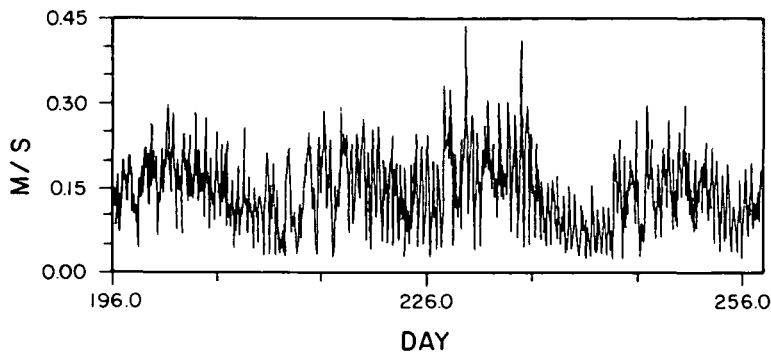
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Figure 12. Current-meter data, averaged over 30-minute intervals, obtained from the instrument at 45-m depth located at the central mooring site on the Southeast Shoal during 1986.
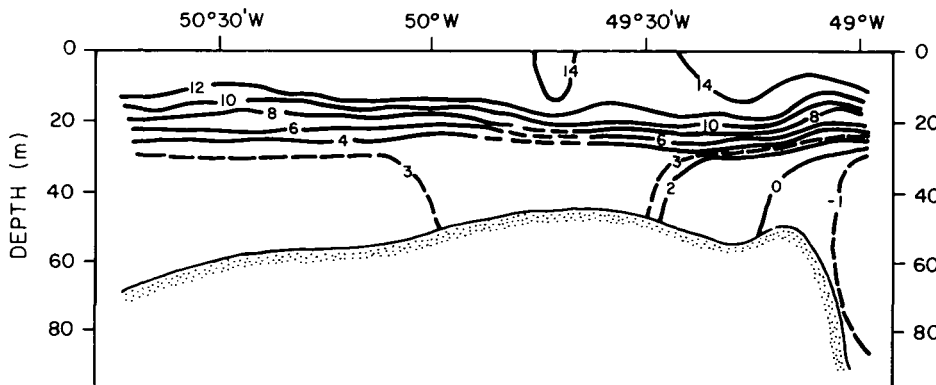

Figure 13. Vertical section of temperature derived from XBT casts across transect IV (44°15'N) during the September 1986 survey. The thermocline was well developed at 20 m, and it generally coincided with the pycnocline depth.

event, considering that the annual occurrence of tropical cyclones during the period 1969–1986 was between 3 and 12 (Neumann et al., 1978; Annual Summaries of Atlantic Hurricane Seasons 1978–1986, Monthly Weather Review). Not all of these storms passed over the southern Grand Bank, but between 1 and 5 did so

annually, primarily during August and September of the 18-year period considered.

The second cohort evident in September of 1986 was composed of recently hatched larvae produced near to day 254 in the absence of any abrupt change in their physical environment. Wind speeds were below 10 m/s

Table 1. Published studies comparing post-storm structure and biomass of plankton communities at fixed oceanic station relative to pre-storm conditions. Except for the study by Lough (1984) enhancing feeding conditions for larval cohorts formed coincident with storms are expected.

Source	Location	After-storm result
Walsh et al. (1978)	New York Bight	Biological responses to storms drawn from 20 cruises under mixed/stratified conditions; injection of 2 µgat NO_3/litre/storm generally leading to doubling of phytoplankton standing stock.
Hayward and McGowan (1979)	North Pacific Gyre	Doubling of 1° productivity and zooplankton biomass increased by a factor of 2.
Lough (1984)	Georges Bank	3–5-fold reduction in prey density of larval haddock; prey uniformly distributed over water column (range: 5–10 prey/l).
Mullin et al. (1985)	California Current	Naupliar copepods, chlorophyll, and some phytoplankton more abundant; several zooplanktonic taxa were more concentrated in the upper layers of the water column.
Cowles et al. (1987)	Gulf Stream WCR 81-D	Microzooplankton biomass (64–333 µm) doubled with cyclopoid copepods showing largest increase in numbers; 1° productivity and chlorophyll a increased.

at that time and the water-column structure showed no marked deviation from the normal pattern of stratification (Fig. 13). Current speeds at 45-m depth were less than 20 cm/s (Fig. 12).

Bakanev (1987) conducted sampling of pre-recruits on the Southeast Shoal during late 1986, so a preliminary assessment of the survival rates of the two cohorts that were produced under radically different environmental conditions can be made. No such survey data are available for 1985. Assuming a constant growth rate of 0.35 mm/d the expected size of larvae originating from the two cohorts should have been about 34 and 41 mm

during the first week in December. Yet, only 10 % of the larvae collected were smaller than 36 mm (minimum size collected was 32 mm), whereas nearly 30 % of the larvae were in the 38−42-mm size range. Thus, it appears that the second cohort formed in 1986 did not fare as well as the first.

Several recent studies have shown that production and standing stocks of phytoplankton and zooplankton increase dramatically after the passage of storms (Table 1). Enhanced feeding conditions coincident with the formation of the first cohort may have been responsible for its dominance in the 1986 ichthyoplankton surveys.
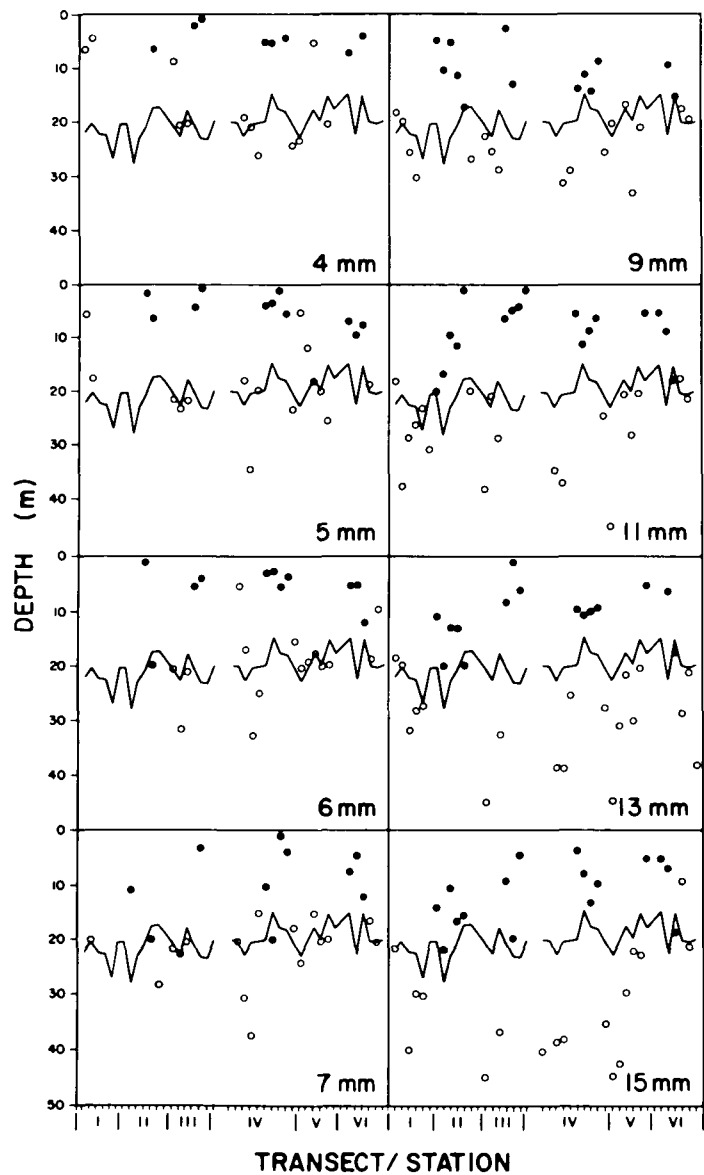
Figure 14. The centre of mass of capelin larvae of various sizes relative to the depth of the pycnocline at each station. Data are presented in chronological order as collected during the September 1986 survey. Daytime (open circles); nighttime (closed circles).
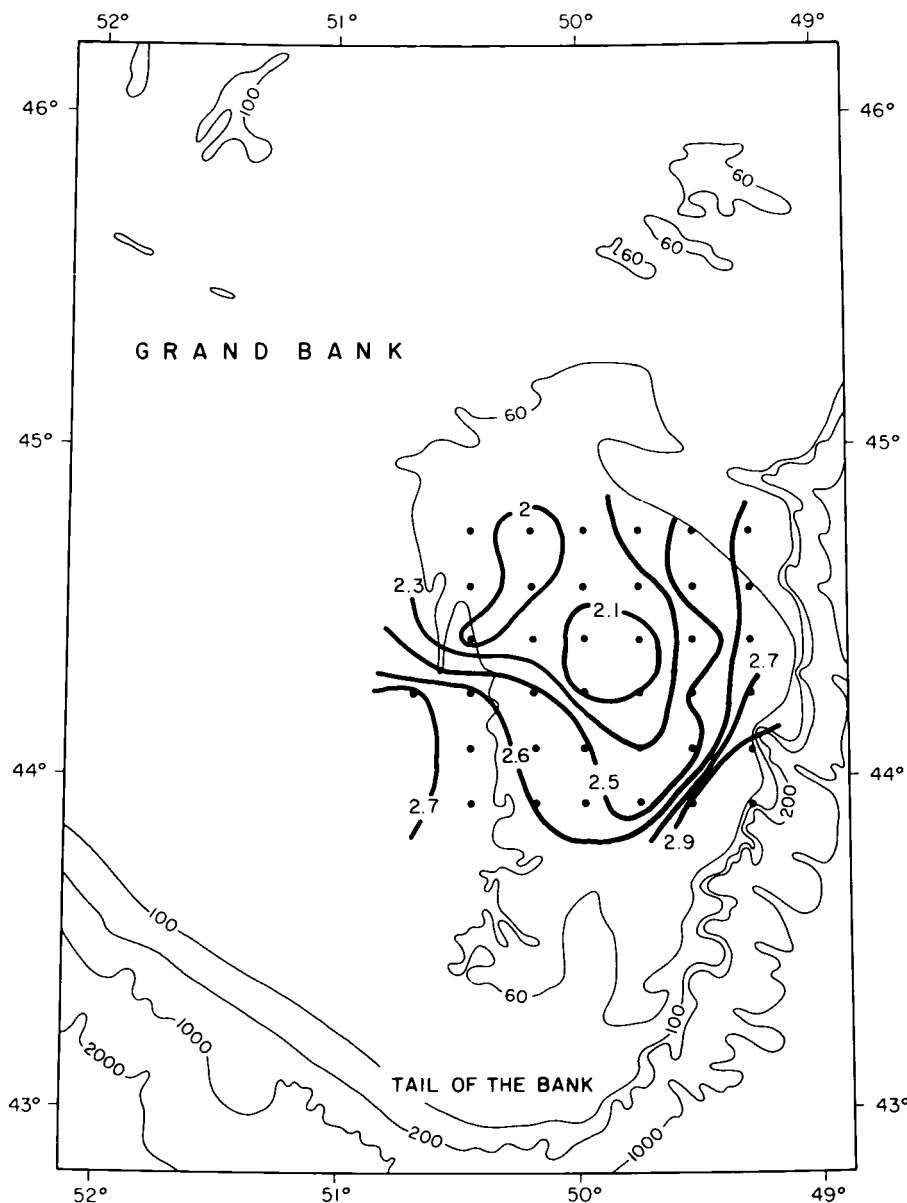
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Figure 15. Isolines of the difference in sigma-t between 5 and 40 m during the September 1986 survey.

Vertical distribution of capelin larvae

We further explore our original hypothesis by considering the vertical distribution of different sizes of capelin larvae collected during our September 1986 survey. The presence of a sharp pycnocline is believed to act as a barrier to vertical movement or, possibly, to reduce the rate of vertical ascent by yolk-sac larvae from the spawning bed to the surface waters. If true, then the second cohort of newly hatched larvae collected in September of 1986 should have been confined mainly to the waters beneath the pycnocline. A plot of the centre of mass of larvae 4, 5, 6, and 7 mm in total length versus the pycnocline at each station shows this expectation to

be false (Fig. 14). Rather, at 60 to 70 % of the stations sampled, larvae ≤7 mm were generally confined by the pycnocline to the *upper* 20 m of the water column. Among these four size groups of larvae, diel depth variation was apparent with a daily vertical range of movement of about 12 m (Fig. 14). Larvae over 8 mm were almost always found below the pycnocline by day and above it at night, and their daily vertical range of movement frequently exceeded 20 m (Fig. 14).

If the pycnocline restricts the vertical movement of small capelin larvae as it appears to do for herring larvae (Höglund, 1968; Dubravin *et al.*, 1976), the question remains as to how recently hatched larvae reached
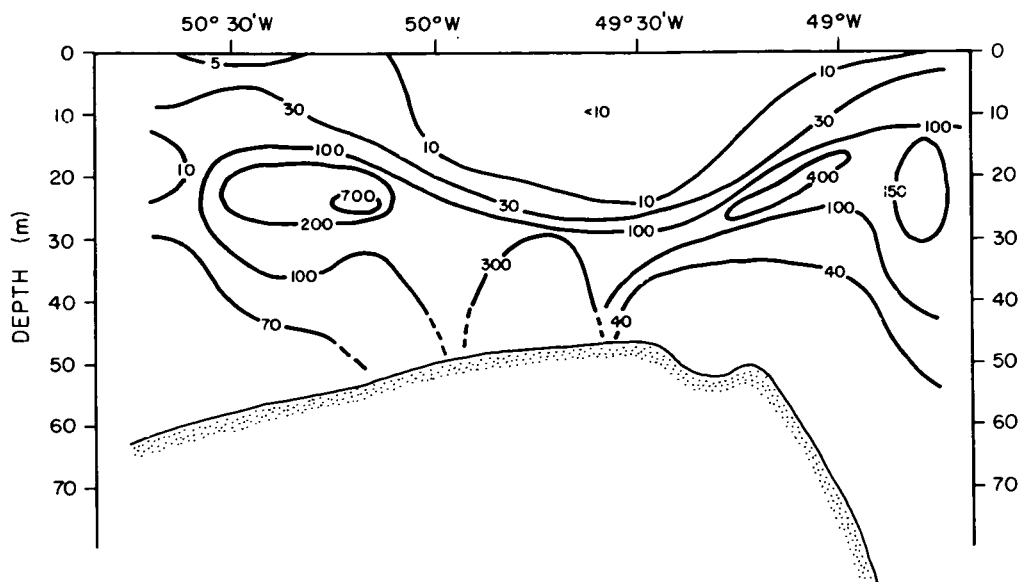
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Figure 16. Depth distribution of hyperiid amphipods (individuals/100 m³) along transect IV (44°15'N) during the September 1986 survey. Note the difference in amphipod concentration above and below 20 m which corresponds to the thermocline depth shown in Figure 13.

the surface waters from the bottom in the absence of a destratification event.

Here we draw on reports of buoyancy changes in several marine fish larvae to speculate on a possible mechanism to explain the observation that some cohorts of larval capelin were formed independently of abrupt changes in the surrounding environment. Increases in buoyancy related to starvation have been noted in plaice and herring larvae (Blaxter and Ehrlich, 1974), and Henri *et al.* (1985) have argued that under field conditions natural increases occur in the buoyancy of yolk-sac to post-yolk-sac herring larvae. Neilson *et al.* (1986) showed that both starved and poorly fed cod larvae exhibited significant increases in their buoyancy from hatching to shortly after the end of yolk-sac absorption. This buoyancy change amounted to greater than 2.0 sigma-t units among starved larvae and slightly less than 0.5 in well-fed larvae. During our September 1986 survey, the average difference in water density between 5 and 40 m was 2.5 sigma-t units (Fig. 15). If capelin larvae underwent similar buoyancy changes while inhabiting the sub-pycnocline waters, then sufficient lift would be generated to overcome the confining effect of the pycnocline.

While we have hypothesized that there is an advantage for larvae to reach the warmer, post-storm, food-rich surface layers as quickly as possible, it may also be an advantage to leave the sub-pycnocline waters because of high concentrations of predators. Our sampling has indicated that there are high concentrations of predators of fish larvae in the form of hyperiid amphipods (recognized as voracious predators of fish larvae: West-

ernhagen and Rosenthal (1976)) in the sub-pycnocline waters (Fig. 16). We noted that the abundance of newly hatched larvae collected in 1986 was approximately 100× less than in 1985. Many factors could be contributing to this difference, including a prolonged transit from the bottom to the surface waters. During this time capelin larvae may have experienced poor feeding conditions relative to cohorts formed coincident with storm events (Table 1) and/or intense predator pressure below the pycnocline.

Preliminary examination of the data derived from our September 1987 ichthyoplankton survey has yielded some insight into the significance of warm slope-water intrusions to larval capelin emergence. August and September of that year were relatively quiet in terms of storm activity, with no abrupt changes in the hydrographic structure of the water column comparable to that in 1986. There was, however, a large tongue of warm (>4°C), salty (>34.00) sub-surface water originating from the southwestern slope region covering an extensive portion of the study area. Larval abundances (all sizes) were nearly one order of magnitude lower than in 1986, and there were no dominant cohorts beyond the post-yolk-sac stage. For some of the reasons alluded to previously, spatial shifts of warm water masses may not be as effective as destratification events for generating dominant larval cohorts and, possibly, strong year classes.

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Conclusion

This paper contains the first results of a multi-year study designed to identify factors affecting recruitment of capelin on the Southeast Shoal of the Grand Bank. Because it is based on only one full year of sampling, some of the conclusions are preliminary and subject to confirmation with more data; however, some observations can be made based on the data presented here.

1) In September 1986, the length-frequency distribution of capelin larvae was at least bimodal – indicative of the production of more than one cohort.

2) The formation of the dominant cohort coincided precisely with a storm event and sharp increases in both bottom temperatures and currents in the area.

3) The areal distribution of larval capelin in 1986 was similar for all sizes and coincided with the distribution of spawning capelin, indicating that larvae hatching at different times remain in approximately the same geographic location.

4) Capelin larvae ≤7 mm showed diel vertical migration but were generally confined by the pycnocline to the upper 20 m. Larvae over 8 mm were almost always below the pycnocline by day and above it at night.

5) Emergence timed to periods of destratification is argued to be beneficial to larval survival for two reasons: (a) rapid ascent of larvae from the bottom waters while normally high predator densities that occur during stratified conditions are diluted, and (b) enhanced feeding conditions during the initial stages of larval drift associated with the passage of storms (Table 1).

Acknowledgements

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