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Distribution of Capelin (*Mallotus villosus*) in Relation to Physical Features on the Southeast Shoal

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INTRODUCTION

Capelin (Mallotus villosus) are small, pelagic, schooling fish native to the northern hemisphere. In the Northwest Atlantic, there have been 5 stocks (or stock complexes) identified (Fig. 1, Campbell and Winters 1973, Carscadden and Misra 1980, Misra and Carscadden 1984, 1987) using knowledge of spawning times, patterns of the fishery, meristics and morphometrics. All of the stocks spawn on or near beaches except the Southeast Shoal stock which is the only stock known to spawn in the offshore area. Capelin are demersal spawners and their eggs adhere to the spawning substrate.

Two physical factors previously cited as important for spawning in both environments are water temperatures and gravel sizes, and capelin have been observed to exhibit different preferences for these physical features in both areas (Sleggs 1933, Templeman 1948, Pitt 1958). For beach spawners, Templeman (1948) reported the best spawning beaches had gravel 2 to 15 mm in diameter, but that spawning occasionally did occur in gravel up to 25 mm in diameter. The favourable temperature range for intensive spawning was 5.5 to 7.5°C on the east coast and 6 to 8.5°C on the south coast (Templeman 1948). Sleggs (1933) recorded capelin beach spawning when water temperatures fell between 8.6 and 10.7°C. Capelin spawning on the Southeast Shoal was first reported when capelin eggs adhering to sand grains were collected from haddock stomachs (Pitt 1958) from two collections, one each in 1950 and 1951.

SPECIAL SESSION ON ENVIRONMENTAL CONDITIONS

Bottom water temperatures were 2.8 to 4.7°C and gravel sizes were 0.5 to 2.2 mm in diameter. None of the bottom temperatures recorded by Pitt equaled the minimum temperatures preferred for beach spawning (Templeman 1948).

In spite of the presence of a large commercial capelin fishery in the area during the mid-1970's (catches exceeded 100,000 t) and the continuing interest in monitoring this capelin stock (see ICNAF Redbooks and NAFO Sci. Coun. Repts, 1974 to present), there has been little research on the ecology of this stock (however, see Whitehead and Glass 1985; Frank and Carscadden 1988). Except for occasional references, usually in relation to fishing success (eg. Sangolt and Ulltang 1976), there have been no dedicated studies to augment Pitt's (1958) scanty data relating capelin spawning distribution to bottom temperature and gravel type and size.

It is the purpose of this paper to examine the relationships between the distribution of capelin during the spawning season on the Southeast Shoal of the Grand Banks to physical parameters such as depth, bottom temperatures and substrate. Maturity states of capelin are also analyzed in relation to bottom temperature. We discuss the biological implications of our results, their relevance to the monitoring and management of this capelin stock and the evolution of bottom spawning in this stock in relation to beach spawning.

MATERIALS AND METHODS

Hydroacoustic surveys of the spawning population of capelin have been conducted by Department of Fisheries and Oceans, St. John's since 1981. During 1981-85, surveys of the NAFO Div. 3NØ area were part of a larger survey which also included portions of NAFO Div. 3L. Beginning in 1986, the Div. 3NØ survey was independent of the pre-1985 surveys and of longer duration, thus allowing for better temporal and spatial resolution of the spawning population. During 1981, 1983, 1986 and 1987 XBT casts were made at regular intervals throughout the survey and after fishing sets while in 1982, 1984 and 1985, temperature data were collected only in conjunction with fishing sets. The acoustic surveys are conducted during the end of June and beginning of July and the results have been presented annually in the NAFO Research Document series. Details of the data collection hardware can be found in Stevens (1986) while data analysis techniques are described in Miller (1985) and Miller and Carscadden (1984). During the acoustic surveys, midwater trawling sets are conducted to collect biological information on target species. A number of biological measurements such as length, sex, age, maturity, and stomach fullness are made on capelin but for this paper only maturity stage is considered. A brief description of each of the maturity stages is as follows:

1. immature: gonads appear as thin threads

2. maturing: gonads are beginning to develop and external sexual characteristics of males are becoming visible. Since this process often begins in the fall, this stage can be quite long.

3. pre-spawning: this stage is reached just prior to spawning. Gonads are full and a light squeeze of the fish results in extrusion of sexual products.

4. spawning: ripe and running sexual products. Partially full gonads.

5. post-spawning: capelin at this stage are usually taken on or near the spawning grounds. There may be residual eggs or milt and males will retain secondary sexual characteristics.

We used density ($g.m^{-2}$) estimates averaged during 1 hour of survey time at a constant speed (equivalent to one estimate per 19 km) to construct eye-fitted contours of the capelin distributions on the Southeast Shoal. Bottom temperatures were also contoured by eye to compare with the capelin distribution.

It should be noted that in some instances immature fish were encountered. These fish are usually one or two years old and occur in very low abundance (less than 5% by numbers) in most years. It was not possible to reliably delineate the boundaries of areas where immatures occasionally occurred in fishing sets because these data were obtained from discrete fishing sets in contrast to the hydroacoustic data which are collected continuously. During the estimation of biomass for assessment purposes, all sets are grouped and estimates by age-groups are calculated for the entire survey area. In the years investigated, mature biomass accounted for approximately 95% of the total biomass (range of 77% to 100%). Thus, for purposes of this paper, the densities of capelin are considered to be densities of mature fish.

We also conducted a more detailed examination of the relationship between capelin density and temperature and depth. For this analysis, the average densities of capelin were calculated from data collected from the time period between 20 min. before the XBT cast and 20 min. after for a total time equivalent to about 12 km. Depth was read from the temperature record.

Centroids were calculated from the distribution of capelin densities generated from each hydroacoustic survey. The x co-ordinate ($\bar{X}$) of the centroid was defined by the location (x_i) in a defined grid and corresponding capelin density (N_i) using the following relationship:

$$\bar{X} = \Sigma_{i=1,n} \; N_i \; X_i \; / \; \Sigma_{i=1,n} \; N_i$$

The Y co-ordinate of the centroid ($\bar{Y}$) was calculated in a similar manner. Therefore, this analysis relates density to geographical location, denoted by latitude and longitude, thereby identifying the centre of mass of the capelin distribution. Because latitude and longitude were not automatically recorded on magnetic tape with the acoustic data until 1987, we used the same densities that were used in the temperature and depth analysis (Table 1).

We also related each of the five maturity stages of capelin to bottom temperatures. Capelin were collected with a midwater trawl and may not have been on bottom when captured. However, we feel our analysis is valid for the following reasons: 1) temperature stratification on the relatively shallow Southeast Shoal is weak during the time of our survey (Loder and Ross 1988) and 2) capelin are bottom spawners and their presence in an area is assumed to be ultimately related to spawning and bottom temperature.

RESULTS

Influence of Temperature and Depth

Bottom temperatures on the Southeast Shoal during late June and early July in 1981, 1986 and 1987 (Fig. 2) showed a pattern similar to the long-term monthly means (Fig. 3). Temperatures on the eastern side of the Shoal were colder, usually less than 2°C, because of the influence of the cold Labrador Current. Temperatures on the central and western part of the Shoal were warmer, usually reaching 4°C and occasionally exceeding 6°C, as was evident in 1984. Although there were few bottom temperature measurements made in 1982 and 1984, both years showed that in the central part of the Shoal temperatures exceeded 4°C, and in 1984 colder temperatures of 2°C and less were observed to the east and northeast. In 1983, warmer bottom temperatures were observed throughout the study area. In contrast, during the 1985 survey, bottom temperatures below 2°C extended over a wider area of the Shoal and water above 4°C occurred in only the southern part of the survey area at approximately 44°N.

The distribution of capelin densities ($g.m^{-2}$) varied annually but in general, most capelin were evident in areas where bottom temperatures exceeded 2°C (Fig. 2). In every year except 1984, there were areas where densities of capelin exceeded 100 $g.m^{-2}$ and these areas coincided with relatively warm bottom waters. Densities of capelin plotted against bottom temperatures (Fig. 4) clearly show that high densities of capelin were associated with bottom temperatures greater than 2°C. Low capelin densities were found throughout the range of bottom temperatures measured but high densities occurred only when bottom temperatures exceeded 2°C. The low densities throughout the range of bottom temperatures are not unexpected given the schooling nature of capelin. In addition to capelin, some of these low densities may be "biological noise", that is, other species besides capelin that produce an echo return that exceeds the acoustic threshold. In the case of low densities, the species are not always identified by fishing. In some instances, the low densities of capelin may be composed of immature fish which do not produce a strong echo return or spent fish which are not schooling (see below). On the other hand, most of the higher densities have been confirmed to be capelin by fishing. In addition, these high densities appear to be spawning aggregations given that the distribution of recently hatched capelin larvae coincides with the distribution of high adult capelin densities (Fig. 5). We visually investigated the relationships between capelin density, bottom temperature and depth. On an annual basis there was no apparent relationship between capelin density and depth and bottom temperature and depth; these relationships combining all years are shown in Figures 6 and 7, respectively.

Since capelin exhibit dense aggregations when spawning, the relationships between density and bottom temperatures prompted us to examine in detail the maturity data. The maturity data (% by weight) were superimposed on the bottom temperature distributions (Fig. 2) using the following criteria for the maturity data: >50% at maturity stage 2 = maturing, >50% at maturity stages 3 + 4 = imminent spawning and in the act of spawning or >50% at maturity stage 5 = spent. Using these criteria, there was only 2 instances, one each in 1981 and 1987, when spawning fish occurred in bottom temperatures less than 2°C. Maturing and spent fish were found throughout the entire range of bottom temperatures from below 0°C to approximately 6°C.

A composite relationship between each of the five between maturity stages and bottom temperatures during the seven annual surveys is presented in Figure 8. Low proportions of maturity stages 3 and 4 (i.e. immediately before spawning and during spawning) were found over a wide range of bottom temperatures but higher proportions were almost always encountered at bottom temperatures exceeding 2°C. Fish at maturity stages 1 and 2 occurred over a wide range of bottom temperatures. When high proportions of maturity stage 5 were present in the catches, the fish were found at a wide range of bottom temperatures. The maturity state of capelin appears to influence their distribution on the spawning grounds and this might help to explain the high variance in capelin densities associated with temperatures in excess of 2°C.

Centroids were calculated from point estimates of capelin density and the corresponding latitude and longitude from each of the seven surveys bounded by the box shown in Figure 9. Results of this analysis (Fig. 9) indicated that the centres of mass of the distributions were constant over the seven years. The maximum distance between centroids was about 22 nautical miles and the centre of distribution of the centroids was located at 44°37'N, 50°12'W. Some caution must be exercised in interpreting the results of this analysis because, in years (eg. 1982, 1986 and 1987) where more than one area of dense concentration occurs, the centroid analysis will produce an "average" area of concentration. Nonetheless, the distribution of capelin in the area was almost constant over the period examined.

Influence of Substrate

We have not developed our data from bottom grab samples obtained during July 1985 from dives aboard the submersible PISCES IV over the capelin spawning grounds on the Southeast Shoal, but some insight can be gained from the geological literature. Muller and Milliman (1973) review the results of earlier workers who state that southern and southeastern sections of the Grand Banks contain sand, gravelly sand and muddy sand. Slatt (1974) has produced figures showing distribution of gravel (coarser than 2 mm) and textural types on the Grand Banks (Figs. 10 and 11).

The circles in Figures 10 and 11 denote the distribution of centroids of capelin distribution in Figure 9. Thus, the capelin centres of mass occur in areas which are predominantly sand with grain sizes less than 2 mm, although the detailed figures of capelin distribution indicate that areas of heavy capelin concentrations often occur on or near gravel beds. These figures of substrate types must be viewed as gross interpretations of the actual distribution of bottom types. During our dives aboard the submersible PISCES IV, we observed changes in bottom types from fine sand to coarse gravel and shells on the order of a few hundreds of metres.

DISCUSSION

The results of this analysis indicate that spawning capelin on the Southeast Shoal during June-July most often occur in areas where bottom temperatures exceed 2°C. It is clear that capelin also occur in areas where bottom temperatures are below 2°C but, in these cases, the fish were immature, pre-spawning or spent. Soviet authors (Kovalev et al. 1977) have noted that all mature capelin do not move into the spawning area at the same time; this observation is supported by our results in which we find spawning capelin in a predictable area while pre-spawning capelin occur in areas with different temperature regimes at the same time. The presence of spent capelin in the area at the same time as pre-spawning and spawning capelin also indicates that capelin spawning also occurs over an extended time period (on the order of days to weeks), similar to beach-spawning capelin (Frank and Leggett 1981).

Our results agree with Pitt's (1958) observations of bottom temperature and capelin distribution. Pitt reported that the warmest bottom temperatures he observed on the Southeast Shoal did not reach the minimum temperatures recorded during beach spawning. The Southeast Shoal is the shallowest area of the Grand Bank and during summer, the warmest bottom water temperatures occurs there (Loder and Ross 1988). The warmest temperatures we observed during the capelin spawning period did not exceed 6.3°C. Thus, capelin on the Southeast Shoal may indeed be capable of spawning in warmer water but do not because bottom temperatures greater than 6°C are uncommon in this region throughout the summer (see Fig. 2 in Loder and Ross 1988). On the other hand, Frank and Leggett (1981) reported capelin spawning in temperatures ranging from 2.5 - 10.8°C. Thus, capelin appear to have a much wider temperature tolerance during spawning than reported in earlier literature. While there is probably an optimum (as opposed to the term "preferred" that is often used), this optimum may have broad limits or may differ between beach spawning and the Southeast Shoal spawning populations.

Temperature is undoubtedly an important factor in determining the spawning location on the Southeast Shoal. The location of the highest concentrations of mature capelin appears to be predictable in most years; these concentrations coincide with bottom temperatures in excess of 2°C and usually with the warmest water available in the region. However, temperature is probably not the only factor that has operated in the evolution of this spawning stock and based on available geologic and fossil evidence, we hypothesize that the Southeast Shoal stock was once a beach-spawning stock. Slatt (1977) has provided a descriptive model for the late Quaternary depositional history of the Grand Bank. During the late Wisconsin glaciation (about 20,000 years ago) it is believed that the Avalon ice cap extended over the Avalon Peninsula. Slatt suggests that the rugged topography of the western edge of the Grand Bank acted as a barrier to eastward movement of the glacier by channelizing and dispersing the margin of the ice. As a result, large glacial streams probably did not occur and the only significant melting occurred at the north and south edges of the ice where it met the sea. The end result was that the Grand Bank was probably a barren plain with only small glacial streams. During deglaciation, gravel was deposited in the area now adjacent to the Avalon Peninsula (see Fig. 10). The predominantly sandy area (at present) on the southeastern area of the Grand Banks is of non-glacial origin. It was created by shoreface erosion and coastal retreat, submergence as the glacier melted and reworking by winter storms and summer/fall tropical cyclones. During the glacier melt, a surf zone would have occurred on the shallowest area of the Bank (i.e. the Southeast Shoal), eroding the coastal cliffs and depositing the sand on the shelf floor. Beach-frosted sand has been found in the area (Slatt 1973, 1977) supporting the conclusion that there was a passage of a high-energy surf zone across the Southeast Shoal. Thus, during the last 20,000 years, the Southeast Shoal region (and much of the Grand Banks) was exposed, but as the glaciers melted and receded, the entire Grand Banks became submerged. Being the shallowest area, the Southeast Shoal was the last to become covered with water and during the submergence, the Southeast Shoal or parts of it were an exposed beach.

The fossil history for capelin is discussed by McAllister (1963) and he reports that Pleistocene (most recent 1 million years) or post-Pleistocene fossils from Canada, Greenland, Iceland, Norway and Yugoslavia have been collected. In examining more recent specimens, McAllister concluded that the species in the Pacific and Atlantic are monotypic. Specimens from both areas are different but Arctic specimens are intermediate, indicating a monotypic species with a cline in characters. He suggests that the cline probably arose because of separation of populations by southward depression of isotherms and/or the Bering land bridge during the Wisconsin glaciation. Thus, the late Pleistocene period appears to have been a time of importance in the evolution of capelin in both the Pacific and Atlantic areas. Given the available geologic, fossil and biological evidence we suggest that the Southeast Shoal stock of capelin was once a beach-spawning population (truly "litophilus" = beach loving (McAllister 1963)) which returns each summer to an ancestral beach to spawn. Other areas of the Grand Bank may have suitable substrate but bottom temperatures are probably too cold during late June - early July period to support viable capelin populations. Long-term monthly means of temperature at 50 m depth by subareas defined by specific topographic features (Drinkwater and Trites 1986) supports our suggestion of areas outside of the Southeast Shoal being too cold (<2°C). The Southeast Shoal area provides the correct combination of substrate and bottom temperature characteristics to ensure survival of eggs and larvae. In this respect, it is worthwhile emphasizing the survey of 1985. At this time the warmest bottom temperatures and the heaviest capelin concentrations occurred more to the south. Greater proportions of pre-spawning capelin were also evident in 1985 than in some other years. Thus, temperature may act to fine-tune the exact location of spawning once the general area of the Southeast Shoal has been reached.

Templeman (1965) alluded to the importance of substrate for capelin spawning on the Southeast Shoal. He noted that capelin return annually to the same parts of beaches where the substrate is of a suitable size and capelin appear to return to the same offshore banks, which are probably limited in size. He concluded that heavy echo traces near bottom on the Southeast Shoal were capelin spawning on small patches of suitable substrate. Between 1952 and 1958, haddock trawlers experienced good catches after being directed to capelin spawning areas by personnel from the Biological Station (now DFO), St. John's based on the knowledge of the capelin spawning areas and of the heavy predation of capelin eggs by haddock.

For Barents Sea capelin, Tjelmeland (1987) found a positive correlation between east-west migration and the autumn temperature gradient which he noted was consistent with a theory that capelin seek cold temperatures during the pre-spawning migration. On the other hand, a negative correlation was found between east-west migration and the spring temperature gradient which is consistent with the theory that capelin seek a warm or at least optimal temperature during the month prior to spawning. Tjelmeland's findings and the results in this paper are in agreement and lead us to suggest that temperature during the spawning migration is important in determining the final spawning location within a larger geographical area.

Our conclusions are somewhat in contrast to the conclusions of Borovkov and Kovalev (1976) concerning Newfoundland capelin. They noted that capelin spawning locations were invariable although it seems that they were discussing the Southeast Shoal area as a general spawning location rather than the finer scale that we have identified. They attributed differences in distribution, nature of pre-spawning migrations and spawning times to differences in water temperature. However, the invariable spawning location was determined by the bottom substrate and stable salinity conditions on the Southeast Shoal.

In southern Iceland, water depth and circulation have been identified as the most important factors in the selection of spawning location for bottom-spawning capelin while sediment grain size and water temperature play a secondary role (Thors 1981).

The mechanism(s) used by capelin to return to a restricted geographical area at a predictable time each year are outside the scope of this paper but worthy of future investigation. Capelin are small salmonid fish, members of the suborder Salmonoidei (McAllister 1963). Salmonids have been the subject of intensive studies on homing for decades and it is not inconceivable that capelin are also homing to specific spawning areas. Recognition of home streams by odour has been widely discussed (see, for example, several papers in McCleave et al. 1982) but odour recognition is usually cited as a clue in the final phases of a spawning migration, i.e. when the fish are close to the spawning area and able to detect a stream odour. Capelin are not anadromous but do migrate over long distances in the open sea before they reach the spawning areas on the Southeast Shoal. We have observed that the spawning beaches in Newfoundland are located at the heads of embayments having small freshwater streams percolating through the sediments. Undersea seepages have been postulated to provide clues for homing for other marine fish (Harden-Jones 1981) and there may be a linkage between the small streams on the beaches and undersea seepages (if they exist) on the Southeast Shoal.

The predictable return of spawning capelin to the Southeast Shoal has implications both for scientific monitoring and management. In most years spawning is occurring during late June and early July, but the observation that capelin are arriving in "waves" prior to and during this period indicates that ideally, several surveys of the area over an extended time period would be necessary to provide an integrated estimate of abundance.
Research vessel time is usually allocated several months in advance; in most years, an appropriate time period can be selected but in years with abnormal temperature conditions (such as 1985), long-term allocation of ship-time may not match the best time.

The Southeast Shoal capelin stock supported a fishery of over 100,000 tons during 1973-76 then declined abruptly to about 5,000 tons during 1978. The fishery was closed from 1979 to 1986 inclusive. The capelin stocks in the Northwest Atlantic declined during the late 1970's but the decline in recruitment in the Southeast Shoal stock was greater than in the adjacent Div. 3L stock. Scientists assessing these stocks considered that the intense commercial fishery on the spawning grounds in Div. 3N may have substantially reduced the spawning stock size and that "the possibility of recruitment overfishing should be taken into account" (p. 37, 1979 ICNAF Redbook). Given the predictability of timing and location of spawning capelin shown by this study, these conclusions would still seem reasonable. Many of the vessels operating in this fishery were midwater trawlers >2000 GRT and were towing large trawls. Thus, disruption of spawning activity and possibly even damage to spawning beds may have contributed to the decline of this stock. Total allowable catches on this stock have been advised for 1987 and 1988. It may be prudent to augment future TAC's with area closures to allow capelin spawning to proceed unhindered by commercial activity.

The boundary of Canada's 200-mile fishing zone intersects the Southeast Shoal (Fig. 2). Based on the contours of capelin abundance given here it would appear that in most years the bulk of the spawning stock occurs within the 200-mile zone. The variability in occurrence of mature capelin inside and outside the zone is undoubtedly determined by the bottom water temperatures. At present, there is a lucrative Japanese market for ripe female capelin and this market is very selective in terms of the state of ripeness of the gonads. Our maturity stages are too broad to describe exactly what is acceptable to this market but it would appear that late maturity stage 2 and early maturity stage 3 would be the most desirable. Our results indicate that maturity stage 2 could occur in the full range of bottom temperatures encountered on the Southeast Shoal. Very ripe (late maturity stage 3) or spawning (maturity stage 4) fish, which in most cases would be unacceptable for the roe market, will occur where bottom water tempertures are greater than 2°C with suitable bottom for spawning. According to the centroid analysis, the centres of capelin abundance will occur well within the 200-mile boundary in the Southeast Shoal area and in most years, warmest bottom water temperatures will predominate inside the zone.

The Southeast Shoal area has recently become the focus of intensive studies on the early life history of caeplin (Frank and Carscadden 1988, Frank et al. 1988) and physical oceanography (Loder and Ross 1988). Larval surveys in September 1986 and September and November 1987 have revealed that centres of capelin larval abundance occur in the same area as centres of adult capelin, indicative of larval retention (discussed in detail in Frank et al. 1988). Thus, the evolution of this bottom-spawning stock has implications for larval survival and long-term persistence of the population. Furthermore, there is a link between beach-spawning stocks and the Southeast Shoal stock regarding factors affecting larval survival. Large-scale wind forcing events that are known to influence larval emergence timing and recruitment in beach-spawning capelin have recently (Frank and Carscadden 1988) been shown to similarly affect larval capelin on the Southeast Shoal. Specifically, it appears that the destablilization of the density stratification from a storm in 1986 resulted in the formation of the dominant larval cohort. The suspected similarity of factors affecting recruitment in both areas does not necessarily support our contention that the Southeast Shoal capelin were once beach spawners; nevertheless, it is intriguing to investigate the linkages between beach and bottom spawners at both the adult and larval stages.

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Table 1 . Maximum and minimum values and sample sizes (n) of bottom temperature (°C), depth (m) and capelin density ($g.m.^{-2}$), 1981-87 used in analysis.

	Temperature		Depth		Density		
Year	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	n
1981	-0.5	4.5	39	90	0.17	111.57	38
1982	1.0	4.6	50	65	20.97	306.25	9
1983	2.7	5.8	40	61	0.21	457.95	28
1984	1.8	6.3	44	64	2.04	139.30	8
1985	-0.3	4.5	52	75	1.53	41.25	12
1986	-0.7	3.4	41	69	0.04	269.86	34
1987	-1.2	4.8	41	71	0.02	91.39	54

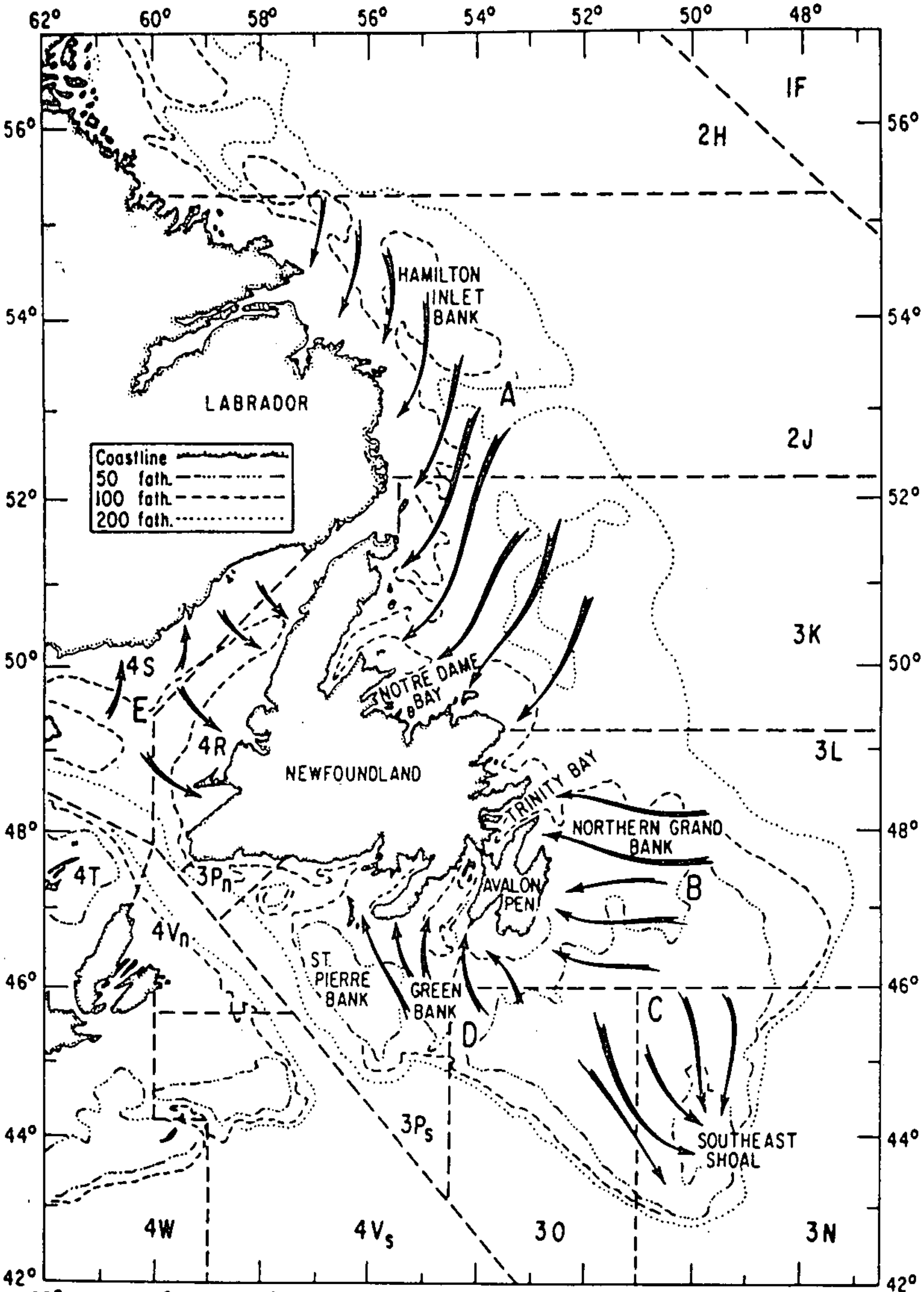


Fig. 1. Map showing major capelin stocks (A-E) and spawning migration routes of capelin in the Northwest Atlantic. Key to stocks: A - Labrador/Northeast Newfoundland (NAFO Div. 2J3K) stock; B - Northern Grand Bank/Avalon (NAFO Div. 3L) stock; C - South Grand Bank (Southeast Shoal - NAFO Div. 3NO) stock; E - Gulf of St. Lawrence stock.

Fig. 2. Densities ($g.m^{-2}$) of capelin from hydroacoustic surveys, bottom temperature (°C) contours during the surveys, and maturities of capelin in fishing sets, 1981-87. Dashed line is approximate location of 200-mile limit.

Legend

Capelin densities: <10 $g.m^{-2}$

10-100 $g.m^{-2}$

>100 $g.m.^{-2}$

Temperature: Temperature contours not drawn for 1982 and 1984 because of small sample size but actual bottom temperatures are shown. Contours are drawn for 1985 although sample sizes are relatively small, and locations of samples are shown by dots (●).

Maturities: Maturity stage(s) is plotted if it exceeded 50% in the sample.

>50% maturity stage 2 (prespawning)

>50% maturity stage 3 + 4 (imminent spawning and spawning)

>50% maturity stage 5 (spent)

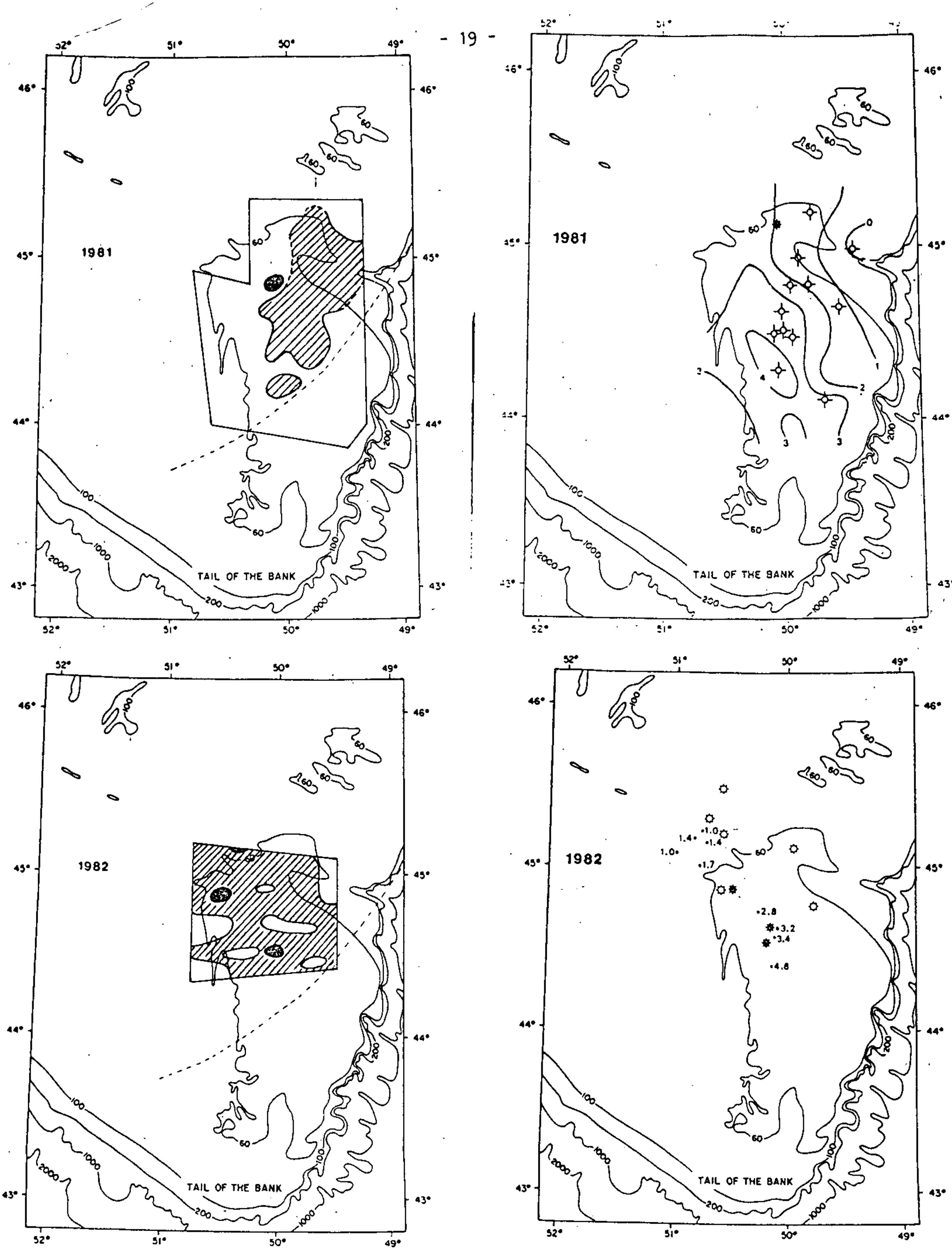

1981
TAIL OF THE BANK
1981
TAIL OF THE BANK
1982
TAIL OF THE BANK
1982
TAIL OF THE BANK
52°
51°
50°
49°
46°
45°
44°
43°
60
100
200
1000
2000
1.0
1.4
1.7
2.8
3.2
3.4
4.8

Fig. 2

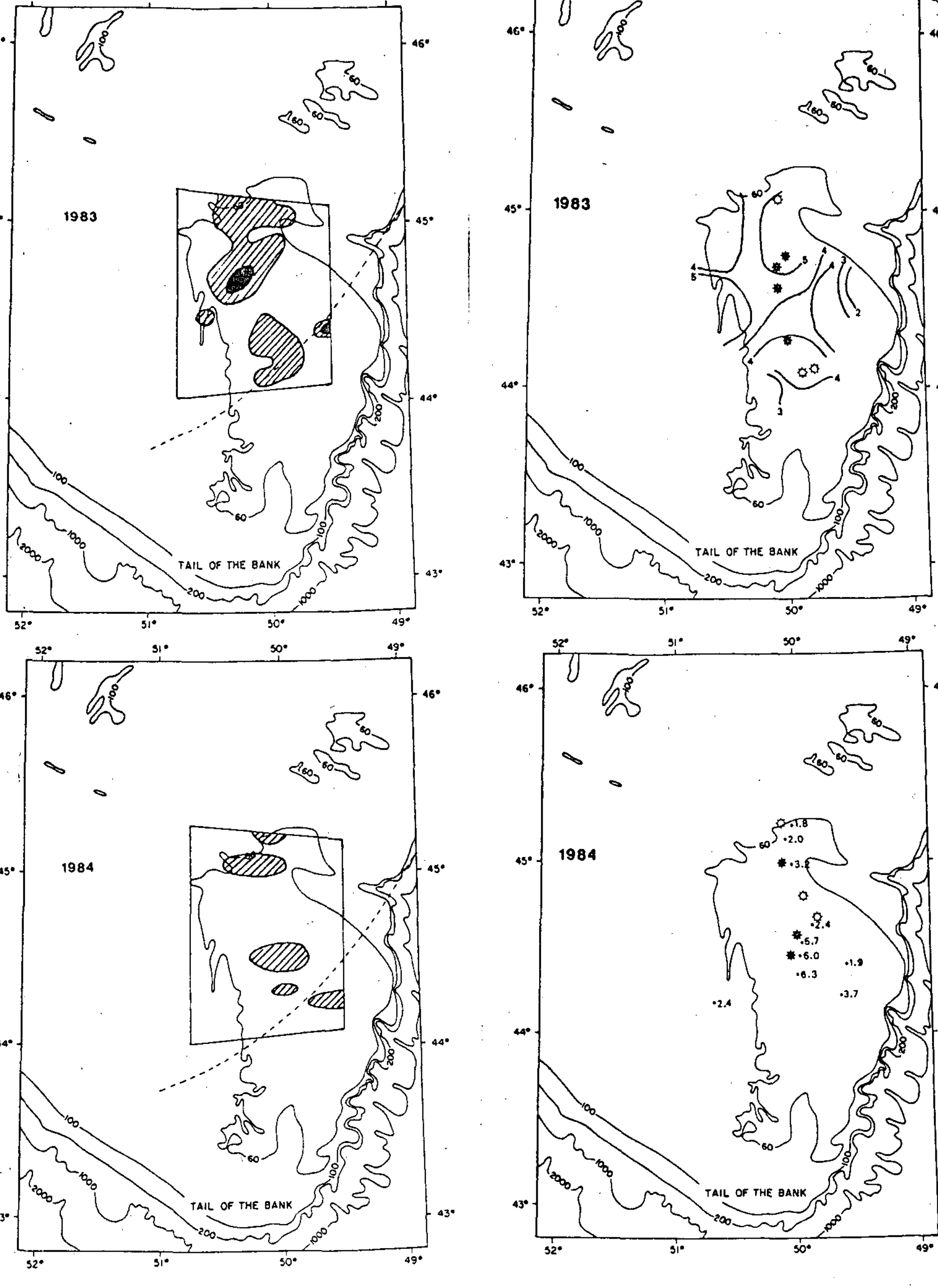

1983
TAIL OF THE BANK
1983
TAIL OF THE BANK
1984
TAIL OF THE BANK
1984
•1.8
•2.0
•3.2
•2.4
•5.7
•6.0
•6.3
•1.9
•3.7
•2.4
TAIL OF THE BANK
52°
51°
50°
49°
46°
45°
44°
43°
60
100
200
1000
2000

Fig. 2.

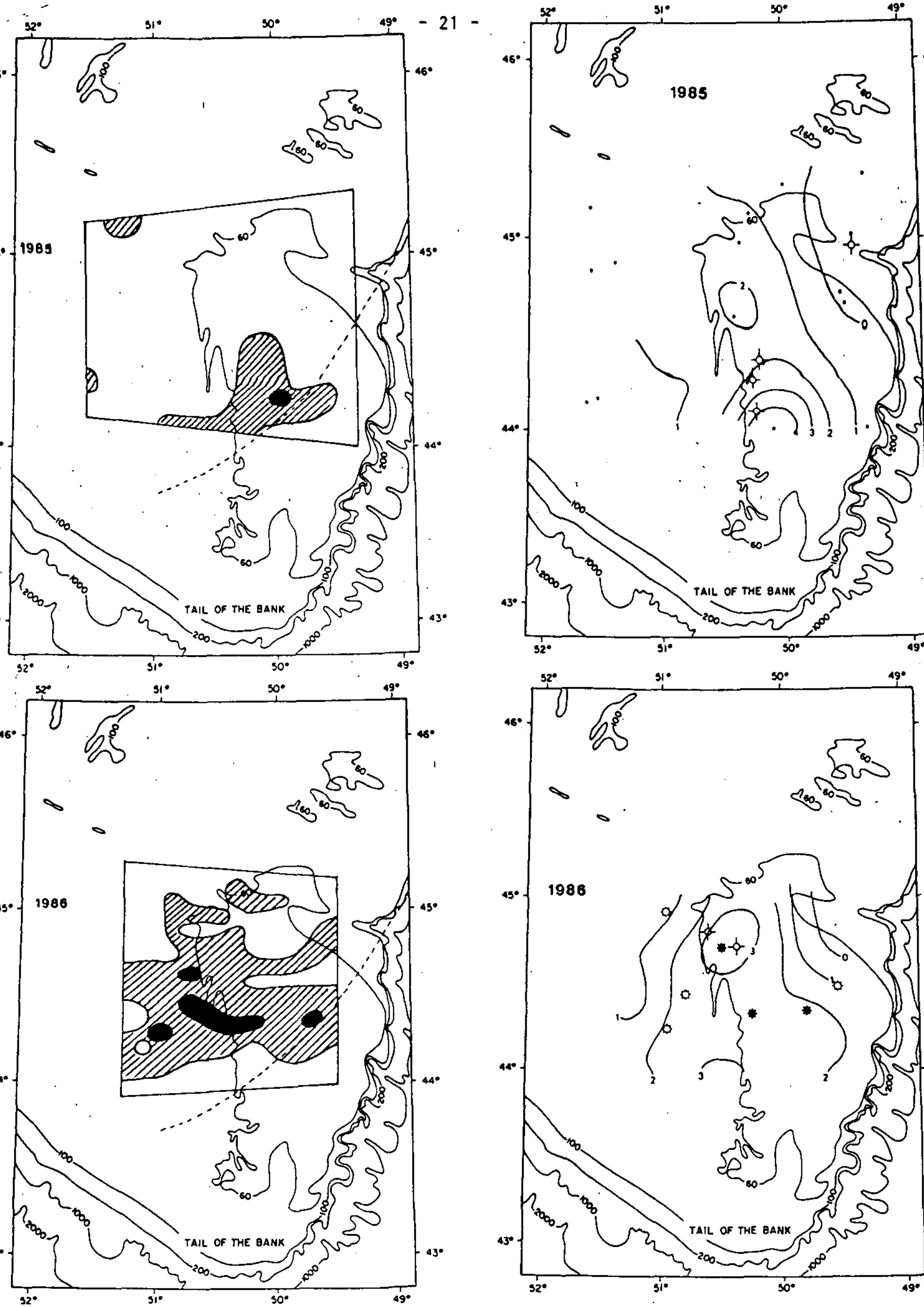
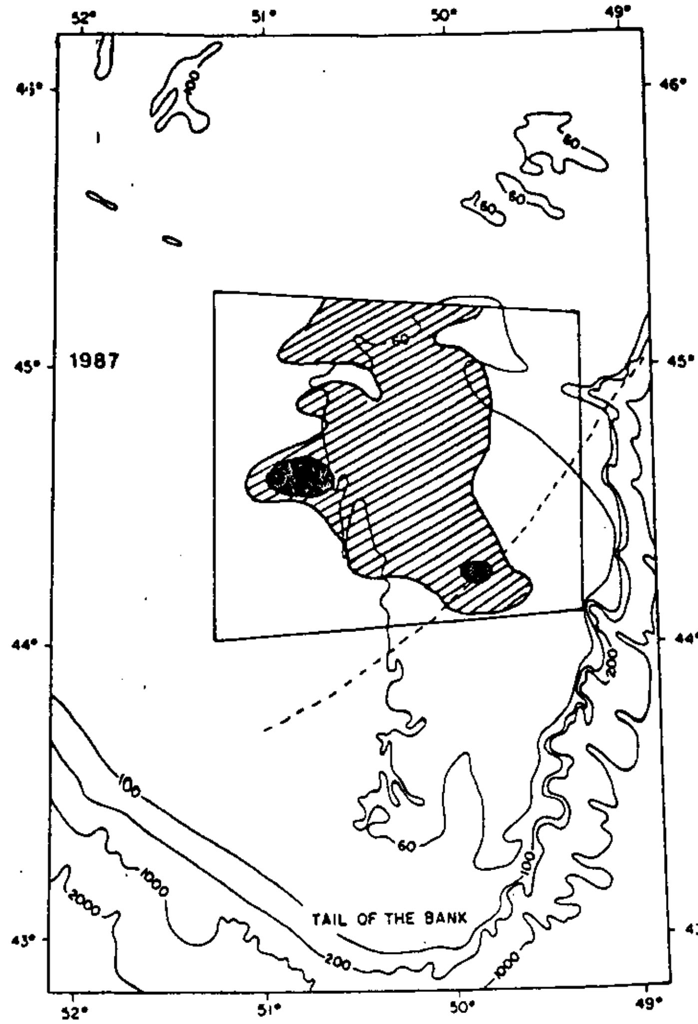

52°
51°
50°
49°
46°
45°
44°
43°
1985
1986
TAIL OF THE BANK
60
100
160
200
1000
2000

Fig. 2



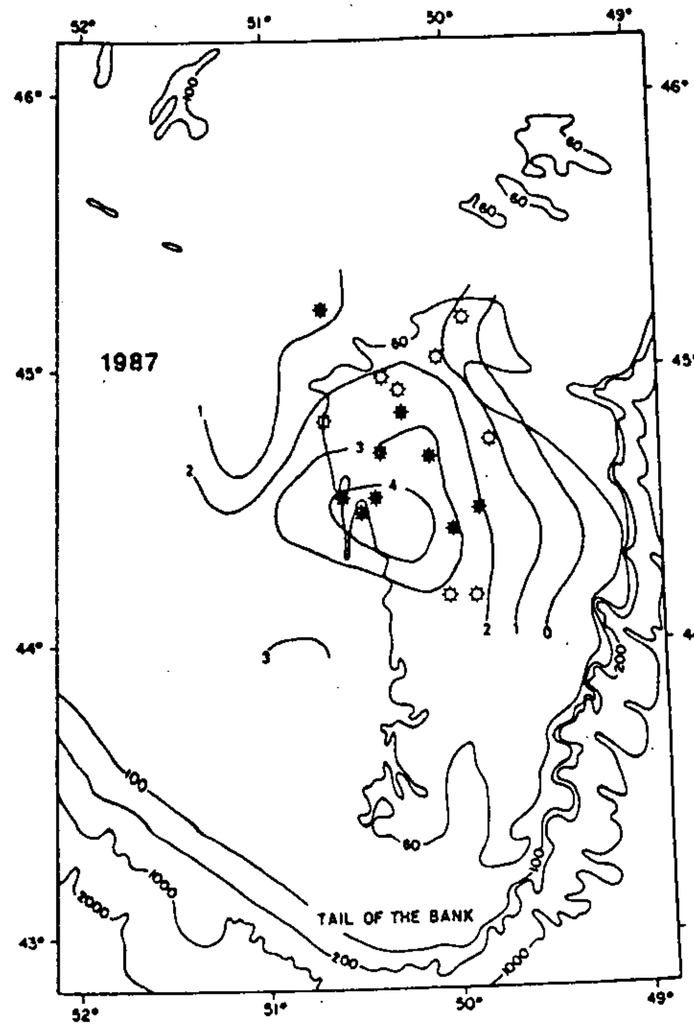


Fig. 2.

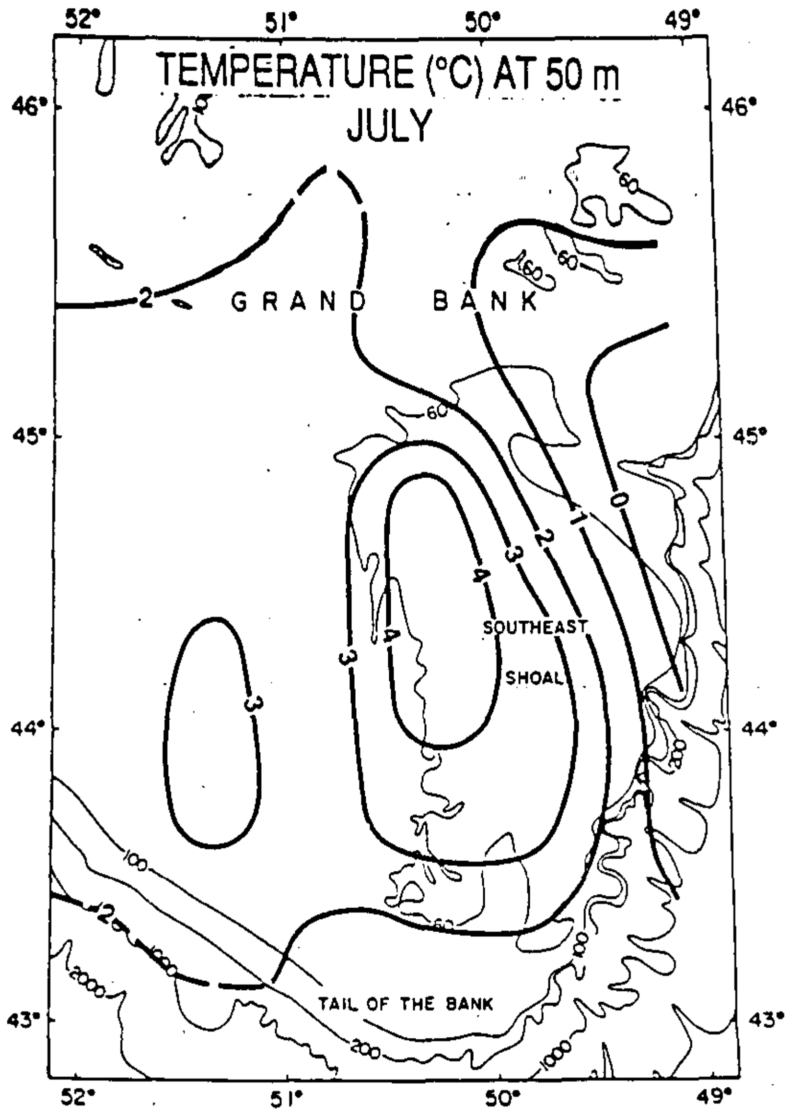


Fig. 3. Temperature distributions from long-term monthly means at the 50-m level in the Southeast Shoal area during July (from Loder and Ross 1988).

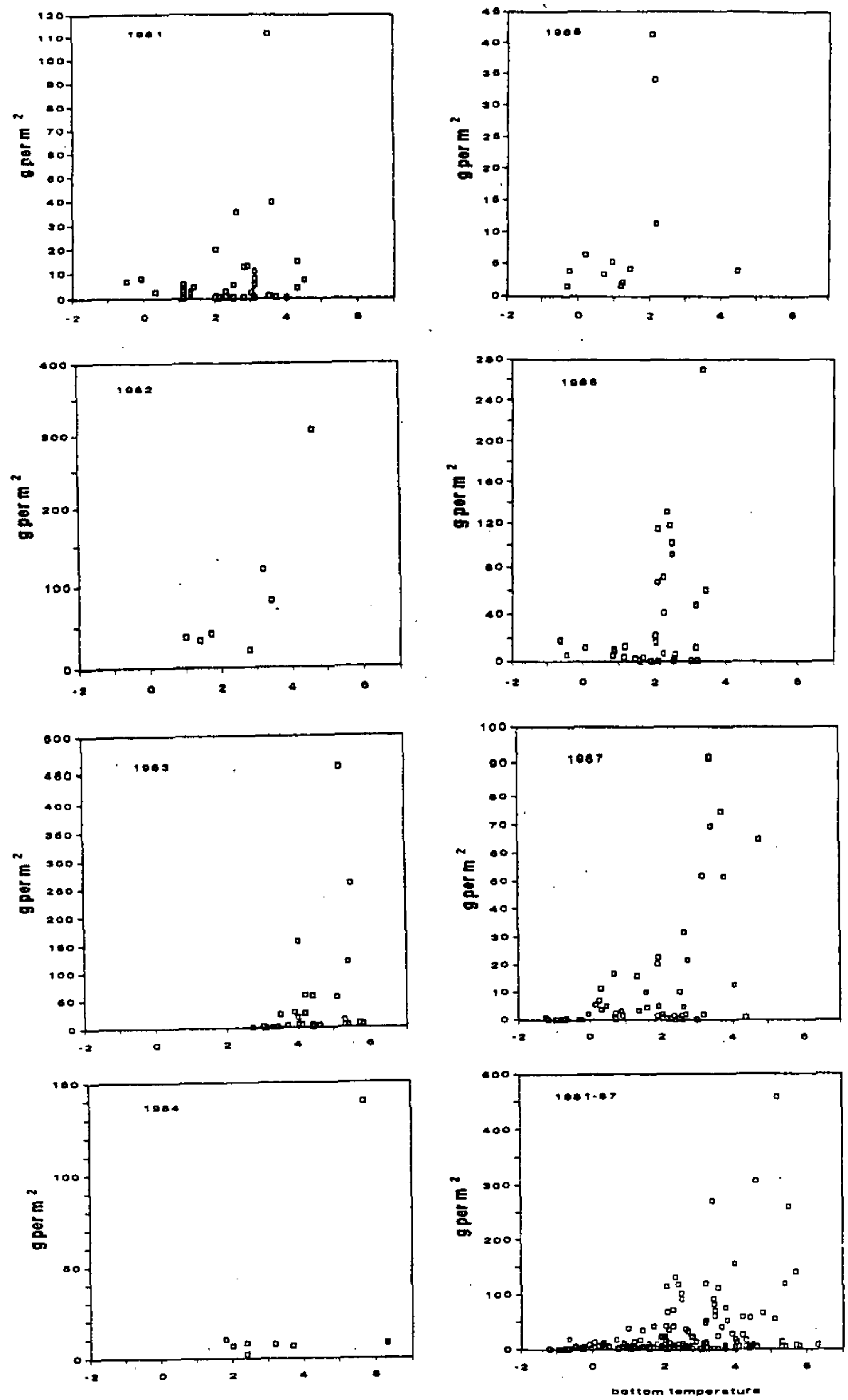


Fig. 4. Densities ($g.m^{-2}$) of capelin in relation to bottom temperatures (°C) on the Southeast Shoal 1981-87 and all years combined.

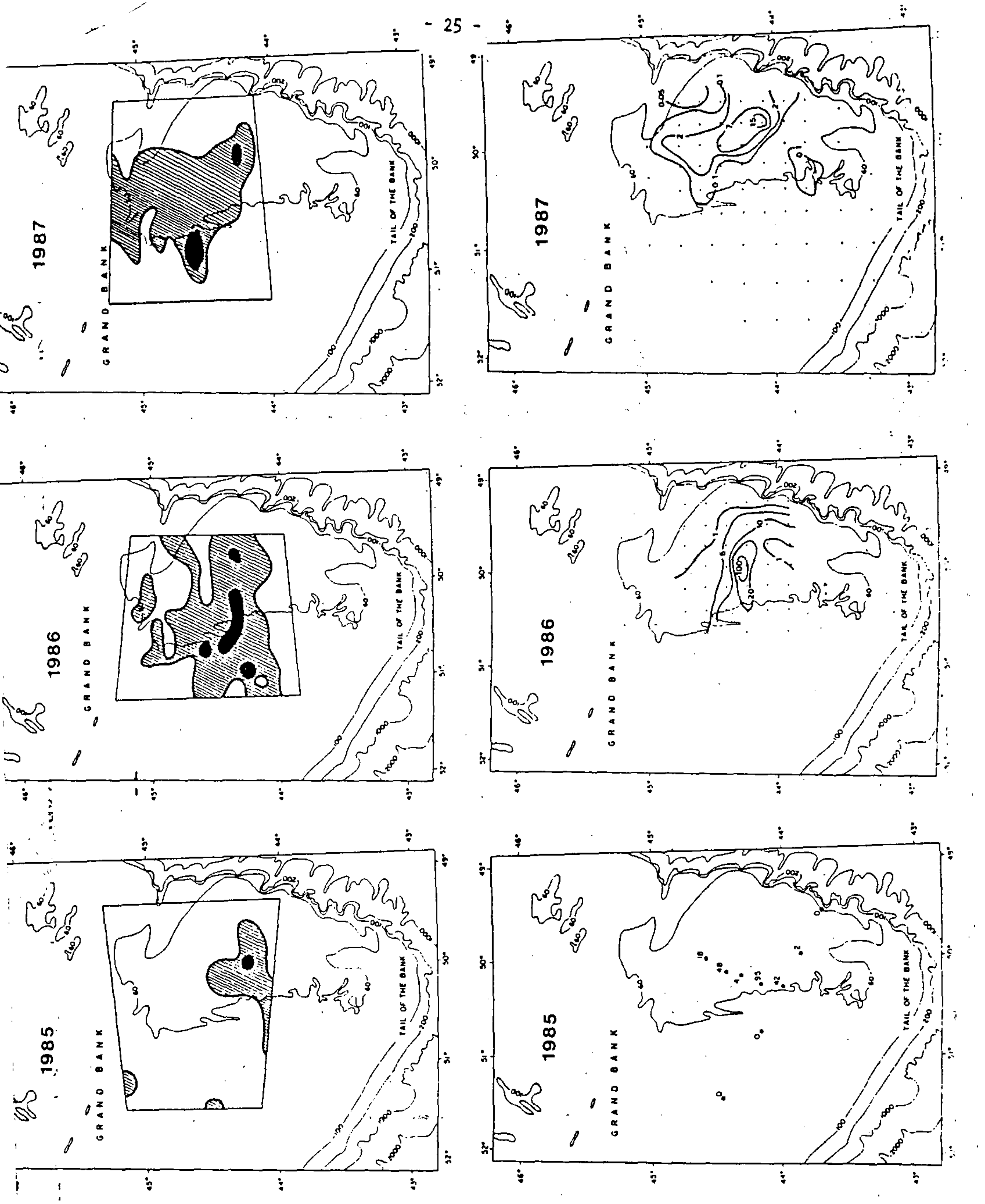


Fig. 5 Densities ($g.m^{-2}$) of adult capelin (top panel) from hydroacou

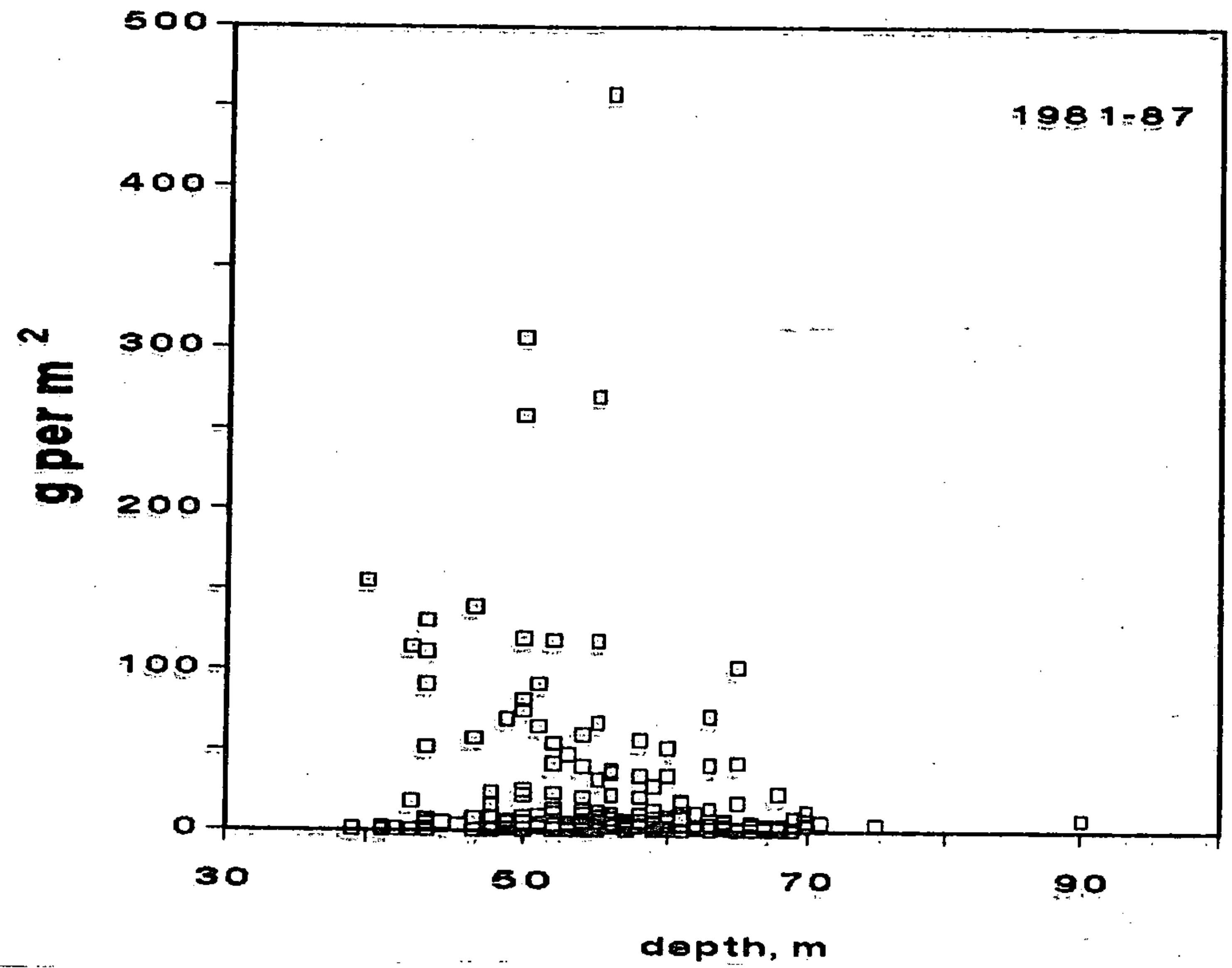


Fig. 6 Densities of capelin (g.m.$^{-2}$) of capelin in relation to depth (m) on the Southeast Shoal 1981-87 combined.

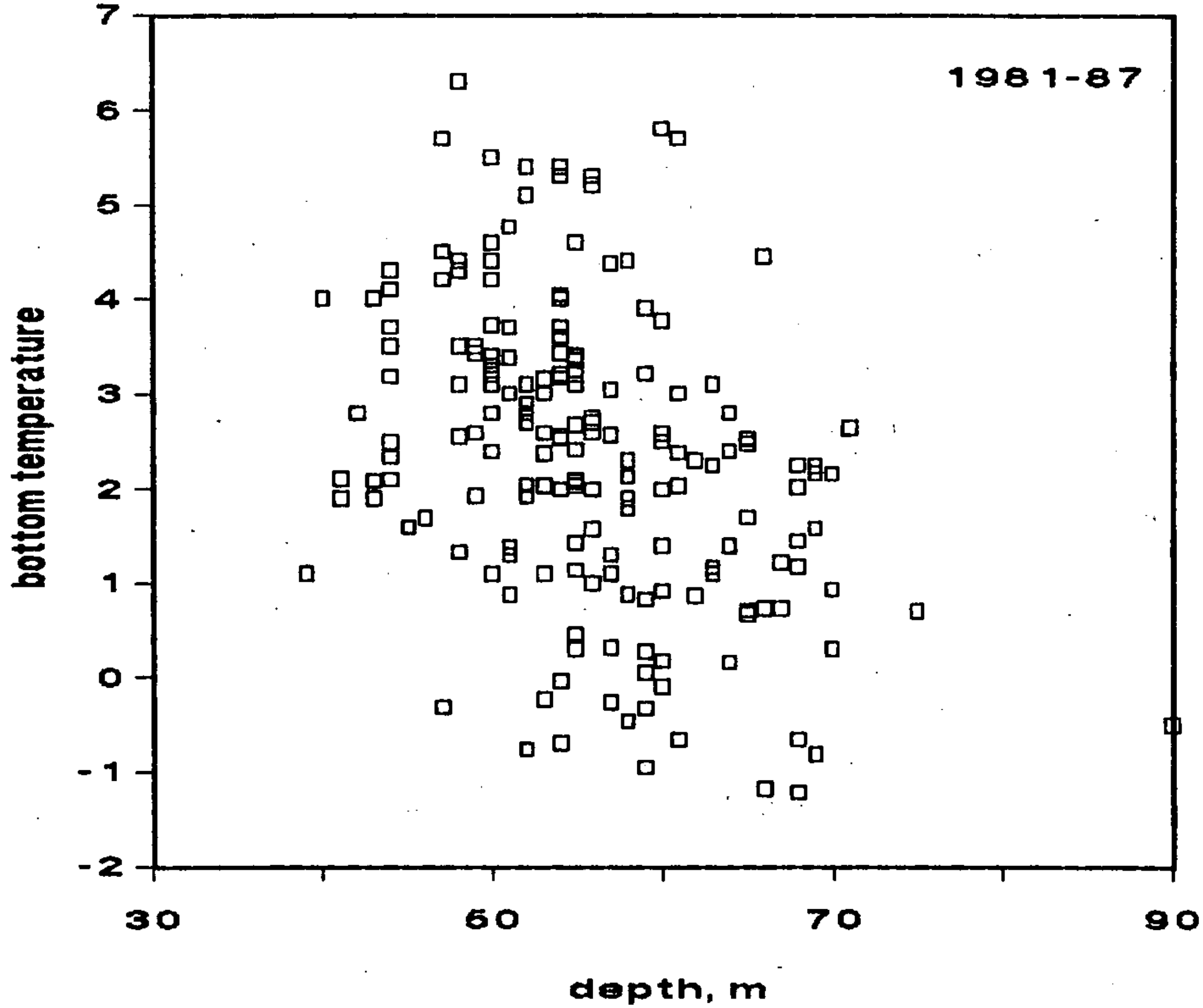


Fig. 7 Bottom temperature (°C) in relation to depth (m) on the Southeast Shoal 1981-87 combined.

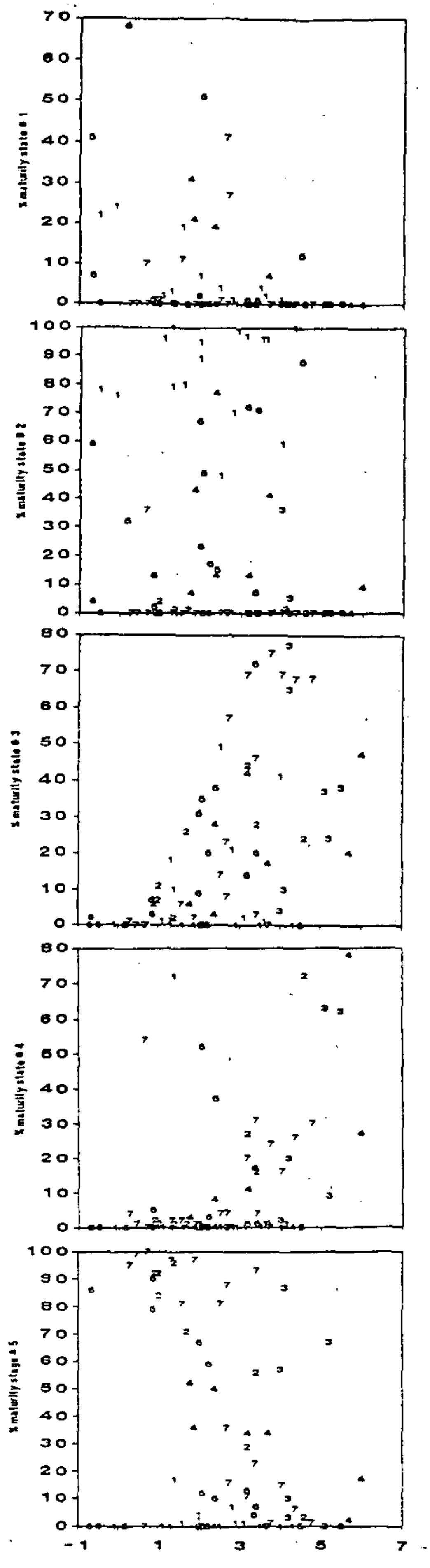
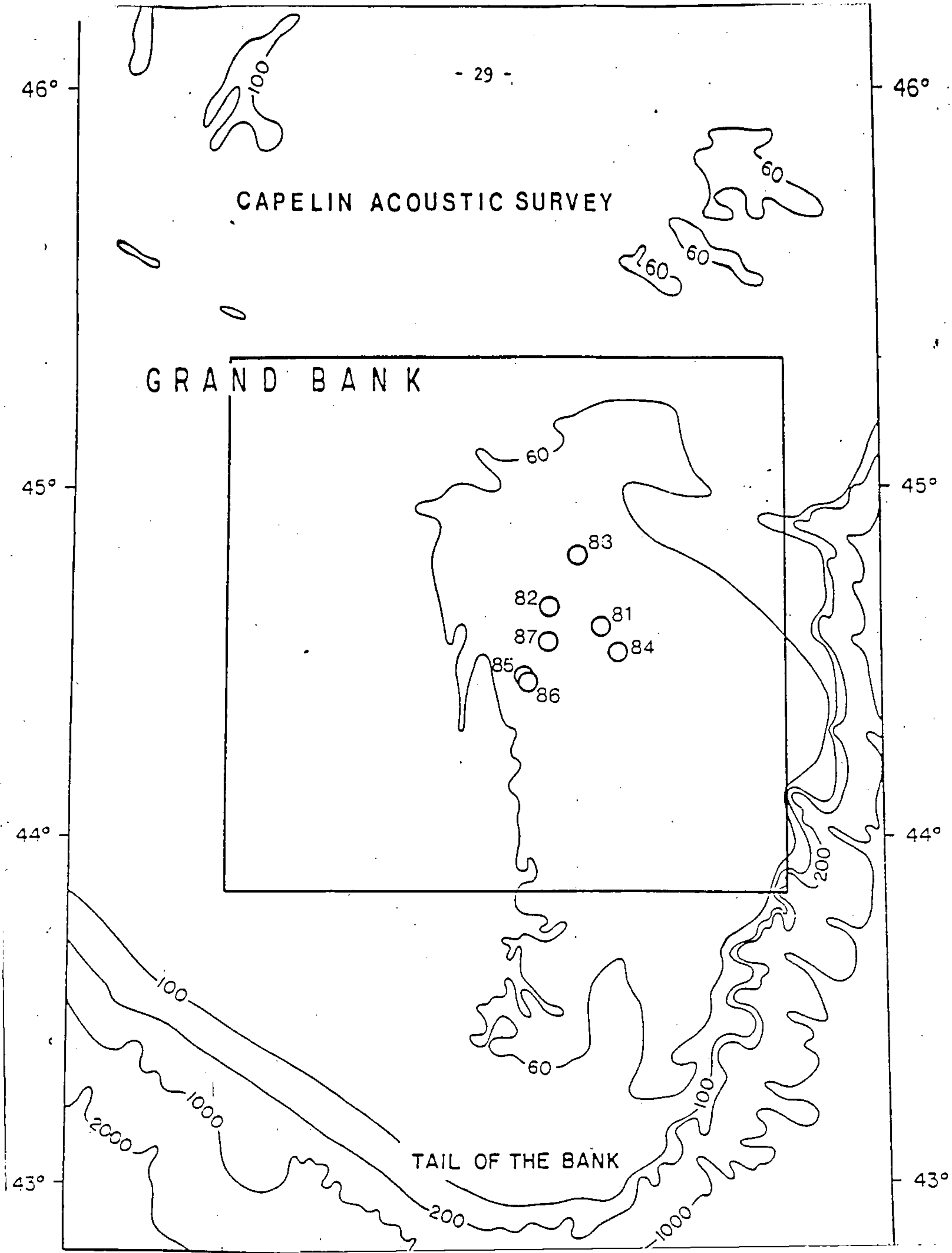
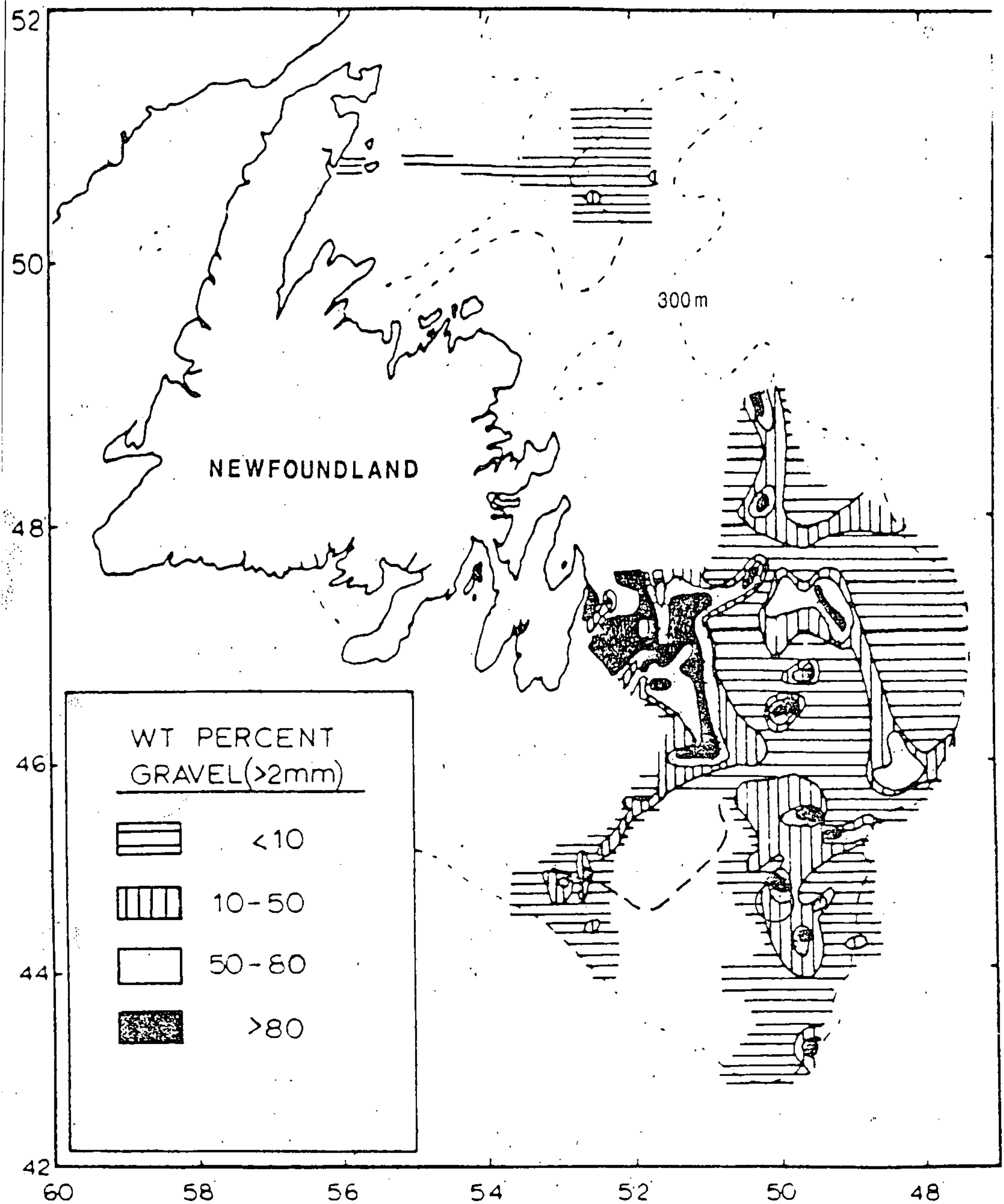


Fig. 8. Maturity stages (%) of capelin in relation to bottom temperature (°C) 1981-87 combined. Numbers are last digit in year, i.e. 1 = 1981.


CAPELIN ACOUSTIC SURVEY
GRAND BANK
TAIL OF THE BANK
46°
45°
44°
43°
100
60
60
60
60
83
82
81
87
84
85
86
200
100
1000
2000
60
100
200
1000


NEWFOUNDLAND
300m
WT PERCENT GRAVEL(>2mm)
<10
10-50
50-80
>80
52
50
48
46
44
42
60
58
56
54
52
50
48

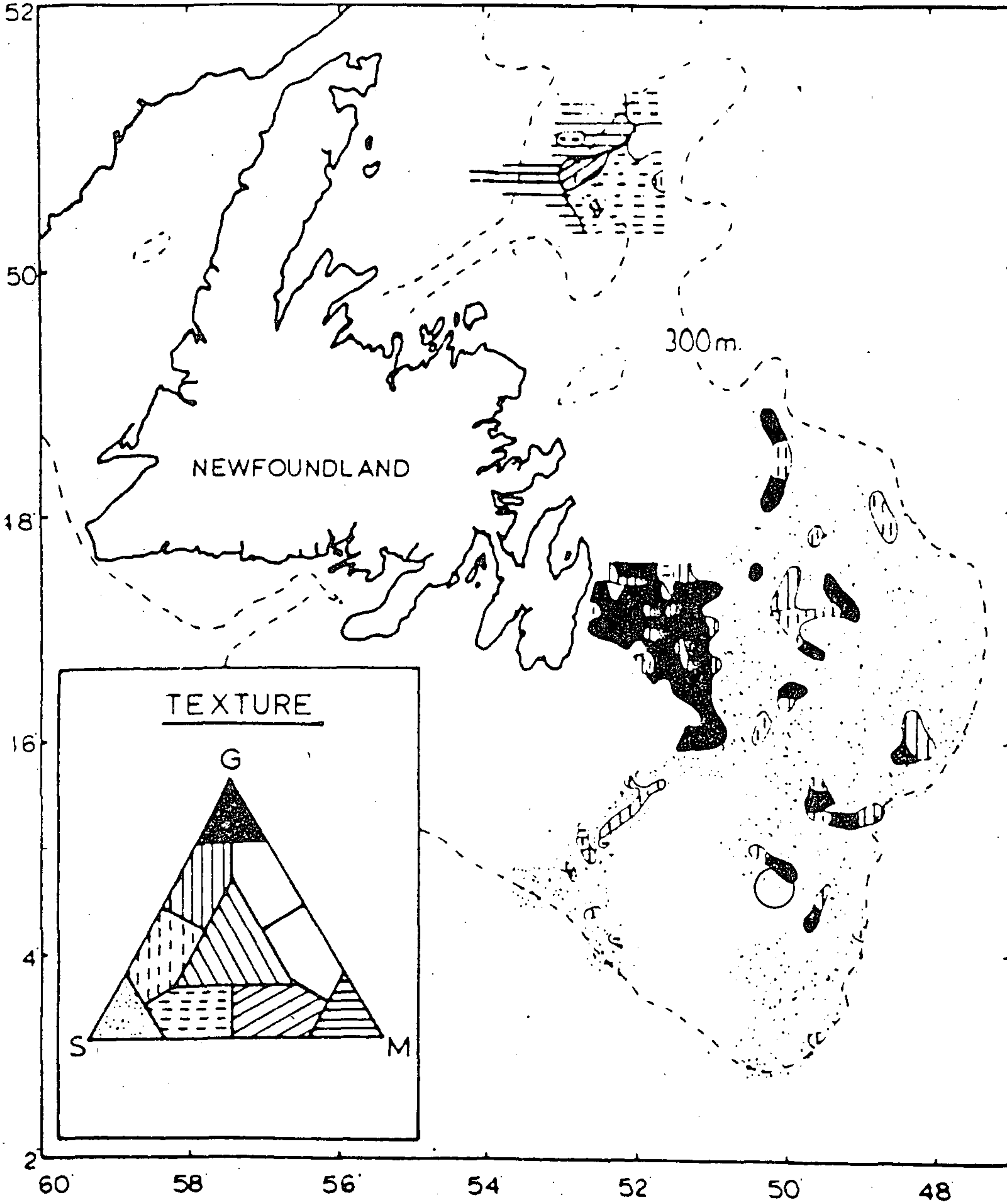


Fig. 11. Distribution of textural types on the Grand Banks (from Slatt 1974).