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Long-term Variations in Cod Distribution and Feeding on the Newfoundland Shelf in Spring and Summer

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Abstract

Hydrographic and cod (*Gadus morhua*) biological data collected over the period 1978–91 on the Shelf of Newfoundland enabled four regions to be distinguished which are occupied by water masses of different origin and quality. These were labelled as the main, inshore, intermediate and shallow water masses. It was found that the areas of cod concentrations and feeding did not coincide completely with these, with the main portion of the stock (nearly 80%) concentrated in the main and shallow water masses. The most intensive feeding occurred in the inshore and intermediate water masses. In warm years the proportion of the cod stock in the shallow water mass increased. Sand lance, shrimp and planktonic crustaceans (mainly hyperiids) dominated the cod diet on the study area in warm years. In contrast, the proportion of the cod stock in the main water mass increased in cold years, and the cod diet in the study area was dominated by capelin and bottom crustaceans (mainly crabs).

Keywords: cod, distribution, feeding/food, hydrography, Newfoundland Area,

Introduction

For hundreds of years cod (*Gadus morhua*) has been the most important species for fisheries on the Newfoundland Shelf, and for this reason it has been the subject of much research. Many papers have reported on the feeding of cod. Their food spectrum is wide. It includes more than a hundred species of bottom and pelagic fish and crustaceans, as well as molluscs, polychaetes, coelenterates and echinoderms (Popova, 1962; Lilly and Rice, MS 1983). Capelin (*Mallotus villosus*), sand lance (*Ammoditus dubius*), shrimp (*Pandalus borealis*, *P. montagui*) and crabs (*Hyas araneus*, *H. coarctatus*, *Chionoecetes opilio*) are among the most important prey species of cod.

Sometimes euphausiids (mainly *Thysanoessa raschii*) and hyperiids (*Parathemisto* sp.) have occurred in cod stomachs in great numbers (Popova, 1962; Lilly, 1982, MS 1984, 1987; Lilly and Fleming, 1981; Lilly and Rice, MS 1983; Minet and Perodou, 1978, Turuk, 1978).

During recent years researchers have focused on two new problems. The first is to understand the quantitative relationships between abundance and growth rate of cod, and the distribution of their prey in relation to oceanographic features (Akenhead *et al.*, 1982; Miller and Myers, MS 1990; Myers, MS 1988). One approach to this problem has been to develop a multispecies model on the cod trophic relationships. However, a recent problem for researchers has been the sharp reduction in fish stocks, particularly in cod stocks on the Newfoundland Shelf. These reductions have been observed during several recent years and have been described as "ecosystem stress" (Atkinson, MS 1993). A series of investigations have been aimed at finding the causes of this phenomenon (Colbourne *et al.*, 1994; Lilly, MS 1993, 1994; Lilly and Davis, MS 1993).

The cornerstone of the analysis and modelling of a sophisticated system is the investigation of its structure. Excellent examples of such work are the investigations of biogeography of bottom communities on the Newfoundland Shelf (Gomes, 1993; Gomes *et al.*, 1992; Villagarcia, MS 1994), which have resulted in the identification of "broad geographic areas that are characterized by a relatively homogeneous and persistent biological composition" (Gomes *et al.*, 1992). Such areas can be considered as structural units when modelling dynamics of fish stocks and fishery management. In the present paper we analyze the dynamics of cod distribution and trophic links in relation to the biogeographic structure of the Newfoundland Shelf described by the authors above.

Material and Methods

Study Area

The area studied in NAFO Div. 3K, 3L, 3N, 3O is a broad continental shelf near the Newfoundland island and adjacent continental slope with a maximum depth of 1 000 m (Fig. 1). The shelf is dissected by channels which restrict access to shallower inshore areas, the Funk Island Bank with depth of 150–300 m and the Grand Bank with depth less than 100 m.

The Labrador Current determines the hydrographic structure of the study area. Its western (Inshore) Branch, cold and of low salinity, includes Arctic waters of Hudson Strait and freshwater runoff. A component from the West Greenland current, relatively warm and saline, dominates the eastern (Offshore) Branch of the Labrador current. The Inshore Branch runs through the Avalon Channel; the Offshore Branch streams along the eastern edge of the Grand Bank and meets the Gulf Stream in the south of the study area (Travin and Pechenik, 1962).

The Labrador current and winter cooling of the upper water layers promote the appearance of a cold intermediate layer in the study area. A 200 m thick layer of cold water develops in the inshore half of the shelf in February. A minimum core temperature of about -1.5°C at 75 m is reached in April. Over the offshore part of the shelf, the cold intermediate layer is about one half as thick, with a minimum core temperature of -0.7°C in June (Petrie *et al.*, 1988).

Data Collections

Data on cod abundance and stomach contents were obtained during the PINRO spring bottom–trawl surveys over the Newfoundland Shelf from 1978 to 1991 (Table 1). In the beginning of the study (1978–82) surveys were conducted using a standard grid of stations, and from 1983 onward by the stratified-random method adopted in NAFO (Doubleday, 1981) (Fig. 2). Tows were conducted by the bottom trawl with a small-mesh (12 mm) insertion in the codend.

In the first years of the study period, tows were made at 3.5 knots for one hour and from 1984 onward for 30 minutes at the same speed.

Oceanographic observations made on the trawl stations, included salinity and temperature measurements at standard hydrographic depths and 3–10 m above bottom. The water temperatures were taken with deepwater reversing thermometers. Unprotected reversing thermometers were used to confirm the depth of measurements (Borovkov and Tevs, MS 1988). In 1991, Div. 3K was not surveyed because of ice.

Data on feeding cod were obtained from stomach contents analyzed at sea. Twenty-five cod of representative sizes from the same catch were examined for length, sex, stage of gonad maturity, and

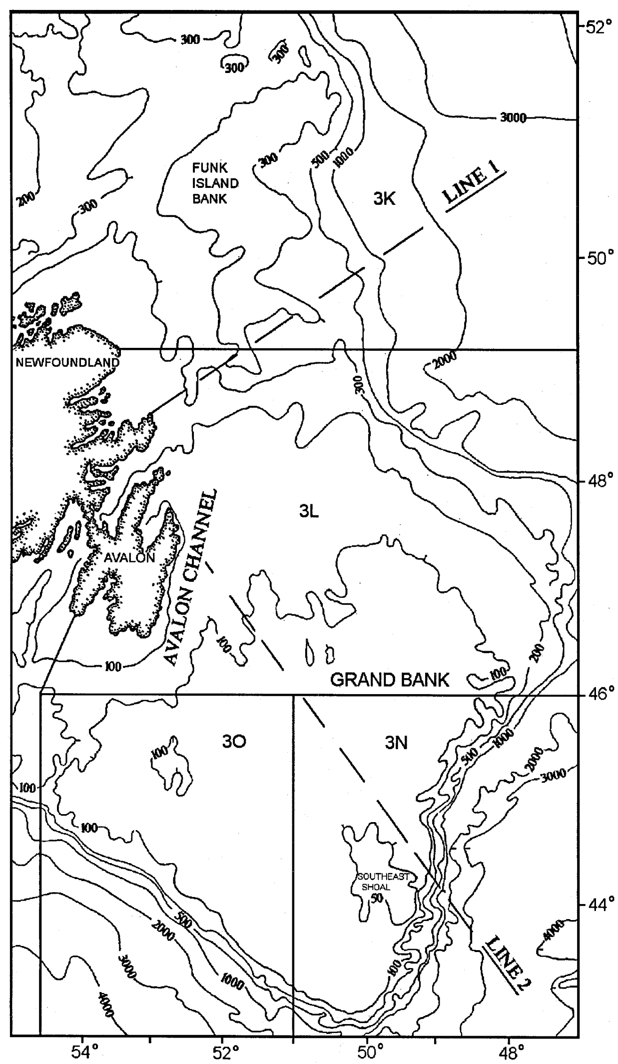


Fig. 1. Map of the study area showing physical features, NAFO Divisions and place names mentioned in the text.

Line 1 and Line 2 – hydrographic transects, mentioned in Fig. 13.

TABLE 1. Dates of Research Bottom Trawl Surveys in NAFO Div. 3KLNO in 1978–91.

	Division		
Year	3NO	3L	3K
1978	10–25 June	3 May–10 June	2–14 July
1979	8–29 April	30 April–13 May	14–25 May
1980	8 May–1 August	5–8 May	13–21 June
		2–13 June	
1981	11–27 June	8–10 June	12–22 July
		27 June–11 July	
1982	3–25 May	25May–11 June	21 June–1 July
1983	25 May–20 June	26 May–1 June	12 July–2 August
		1–12 July	
1984	30 April–30 May	6–22 June	23 June–12 July
1985	3–15 May	6–22 June	17 June–25 July
		17–19 May	
		4–17 June	
1986	19 April–10 May	16–19 April	22 May–15 June
		10–22 May	
1987	11 March–13 April	26 April–11 May	11 May–6 June
1988	17 March–6 April	7–23 April	24 April–8 May
1989	5 March–21 May	27 April–21 May	5–19 June
1990	5–26 April	25 April–23 May	1–18 June
1991	9–27 April	8 May–6 June	

main prey items in the stomach. Fish in the cod stomachs were identified to species, if possible, and invertebrates were identified to higher taxa. The degree of stomach fullness was ranked using a five-point scale: 0 – empty, 1 – low fullness, 2 – mean fullness, 3 – full stomach, 4 – full stomach with walls stretched by food. The relative importance of individual prey items in each catch was assessed as percent occurrence, calculated as the number of stomachs containing a given prey divided by the total number of stomachs analyzed in this catch, including empty ones, times 100.

Information on capelin, sand lance, crab and shrimp by-catches taken by bottom trawl were also included in the analysis. Sizes of by-catches were visually assessed during surveys (single individuals, tens, hundreds, thousands, etc.).

Data Analysis

It is well known that the food spectrum of cod changes with their growth. Age composition of cod on the Newfoundland Shelf varied in the different years of the study. To obtain comparable results on cod feeding dynamics, data on distribution and feeding of cod of ages 3–6 only were included. This age group was most numerous in catches and well represented in feeding samples (Table 2).

The number of cod of ages 3–6 in each catch was estimated using data on their mean length. According to data of PINRO surveys, the mean length of fish at ages 3–6 in Div. 3K was 30–52 cm, in Div. 3L – 30–56 cm, in Div. 3NO – 30–62 cm.

The total number of cod of ages 3–6 also varied in different years of the study. To analyze cod distribution from year to year, "normalized" abundance was used from each catch calculated as the ratio of the estimated number of cod at ages 3–6 in this catch to the total estimated number of cod at ages 3–6 in this year in Div. 3KLNO.

Oceanographic and biological data obtained from bottom surveys in each year were plotted geographically to give the following:

– geographic variation in bottom temperature,

– geographic variation in relative abundance of cod at ages 3–6 (using "normalized" values of abundance),

– geographic variation in intensity of cod feeding (using degree of stomach fullness),

– geographic variation in abundance of shrimp, capelin, sand lance and crabs (using by-catches),

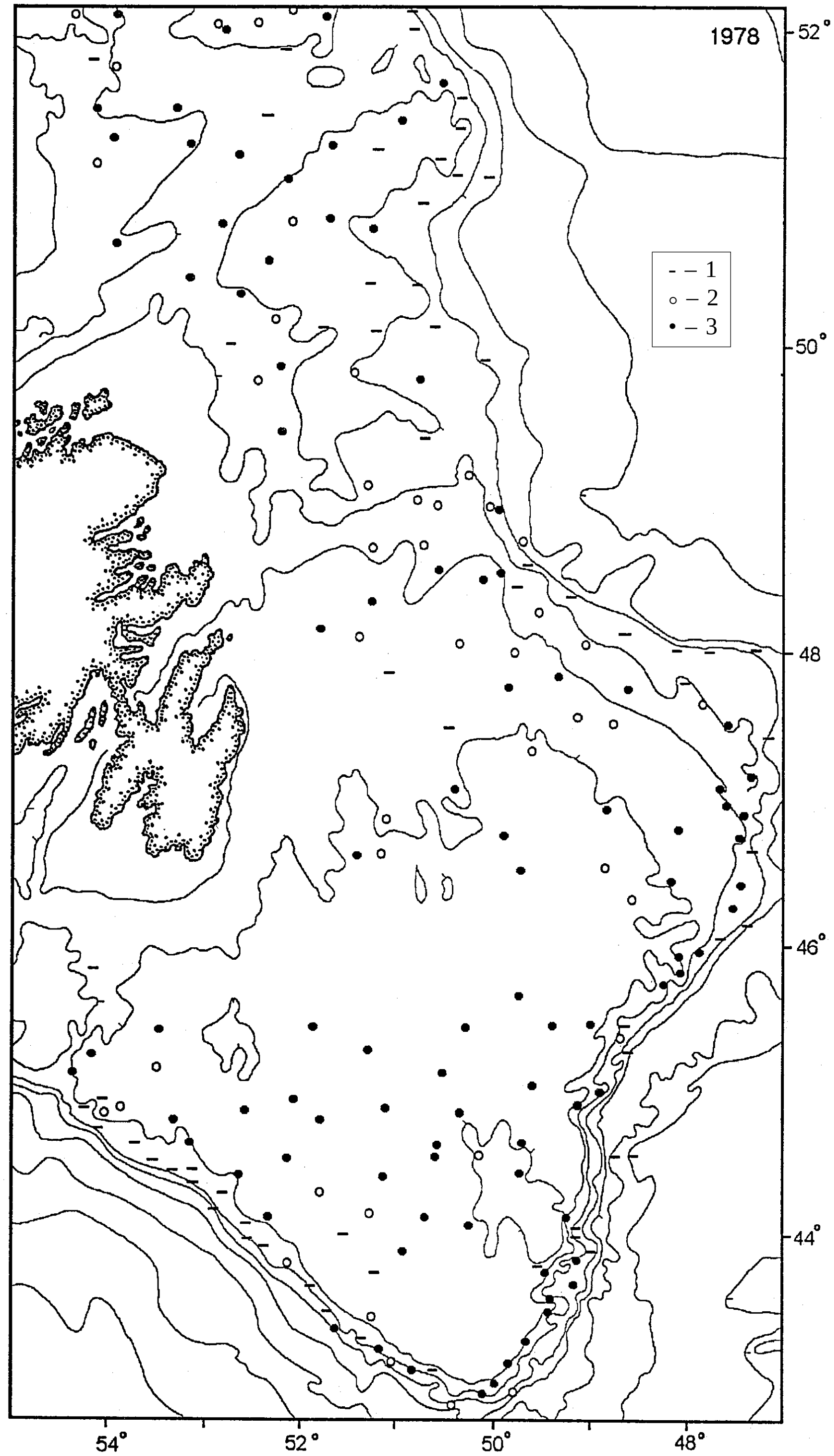
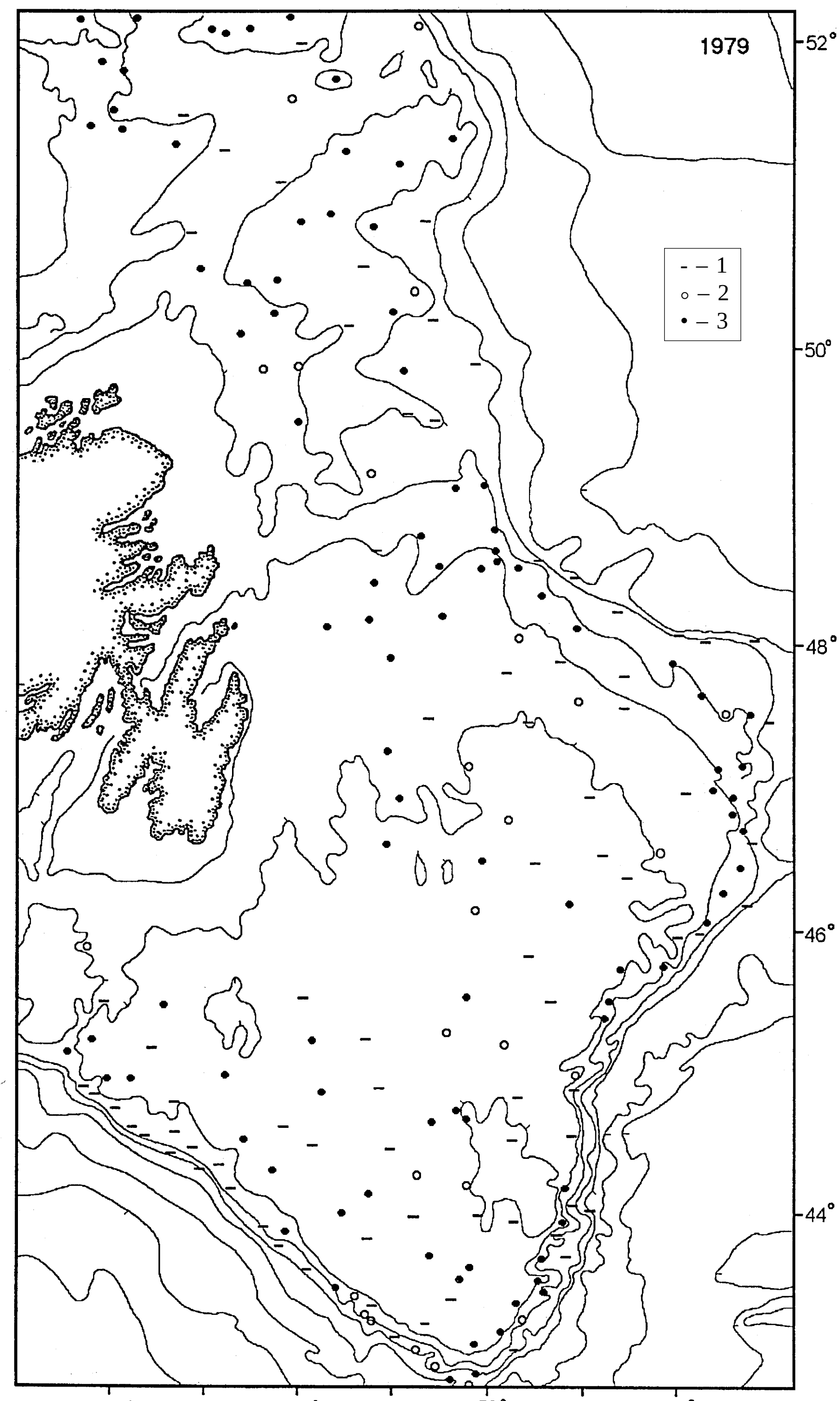


Fig. 2. Catch of cod of ages 3–6 and collection of cod stomach samples during bottom trawl surveys in the spring of 1978–91.
1 – cod ages 3–6 absent in the catch
2 – cod ages 3–6 present in the catch
3 – cod ages 3–6 present stomach sample collected



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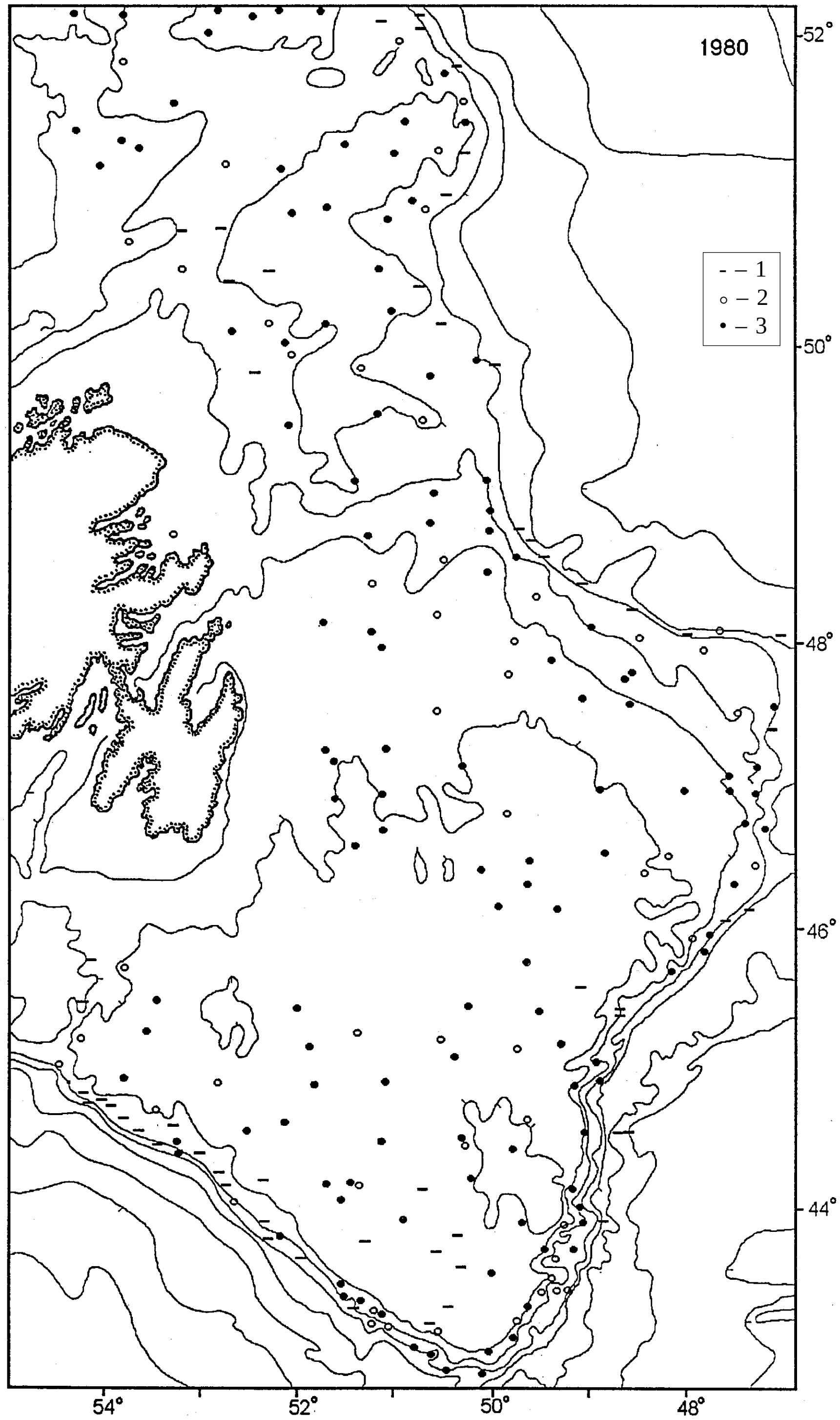

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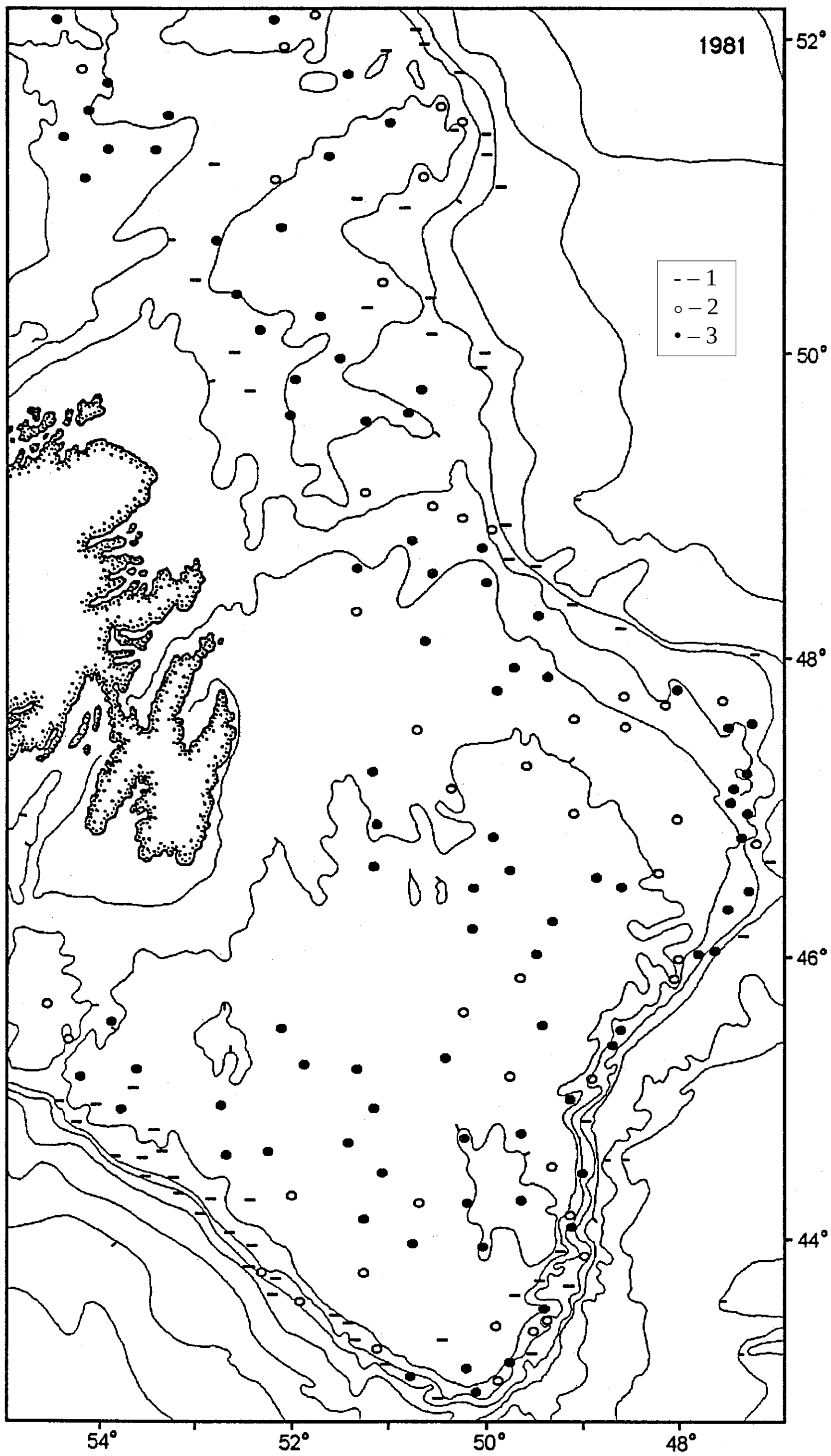

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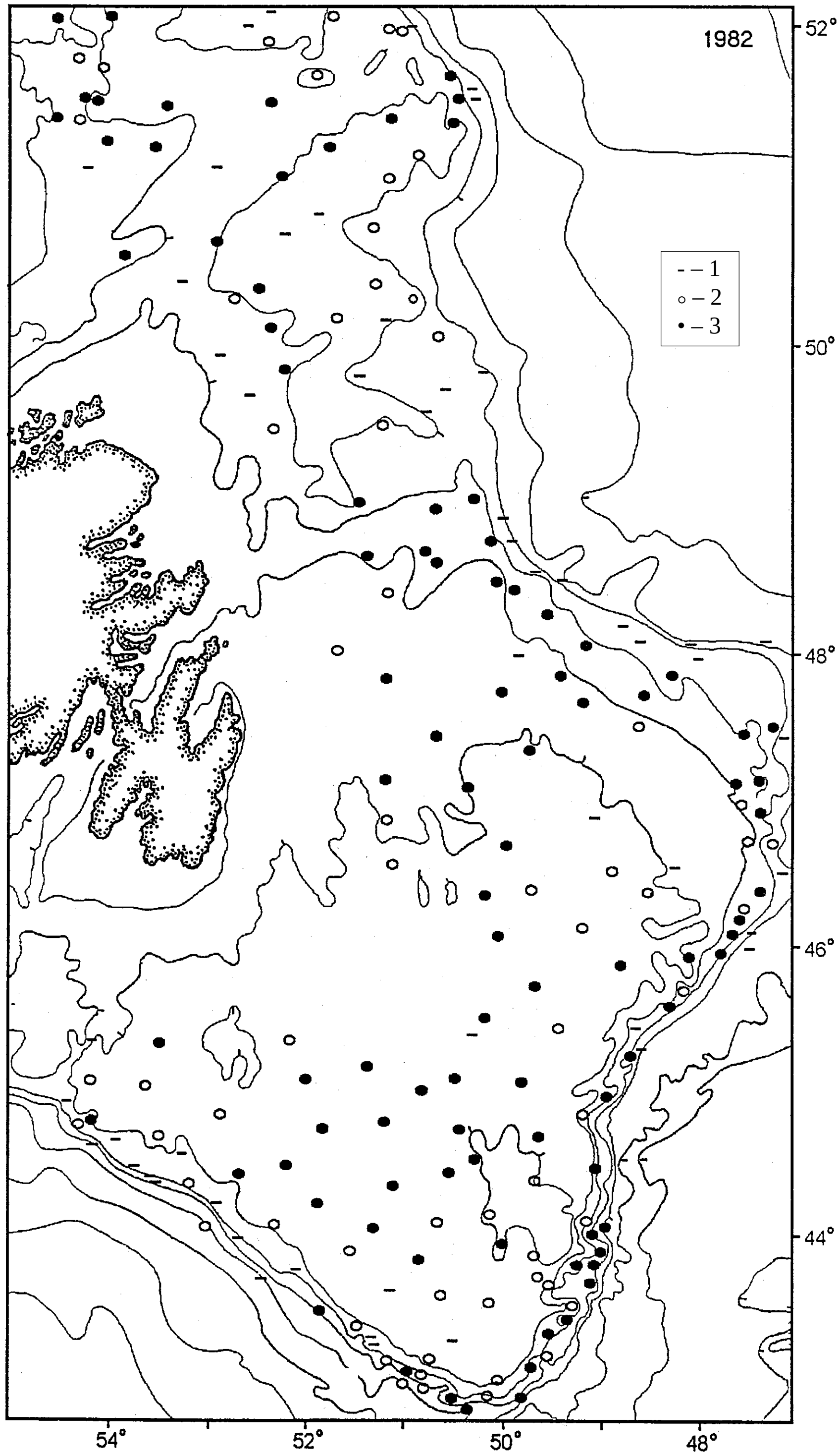

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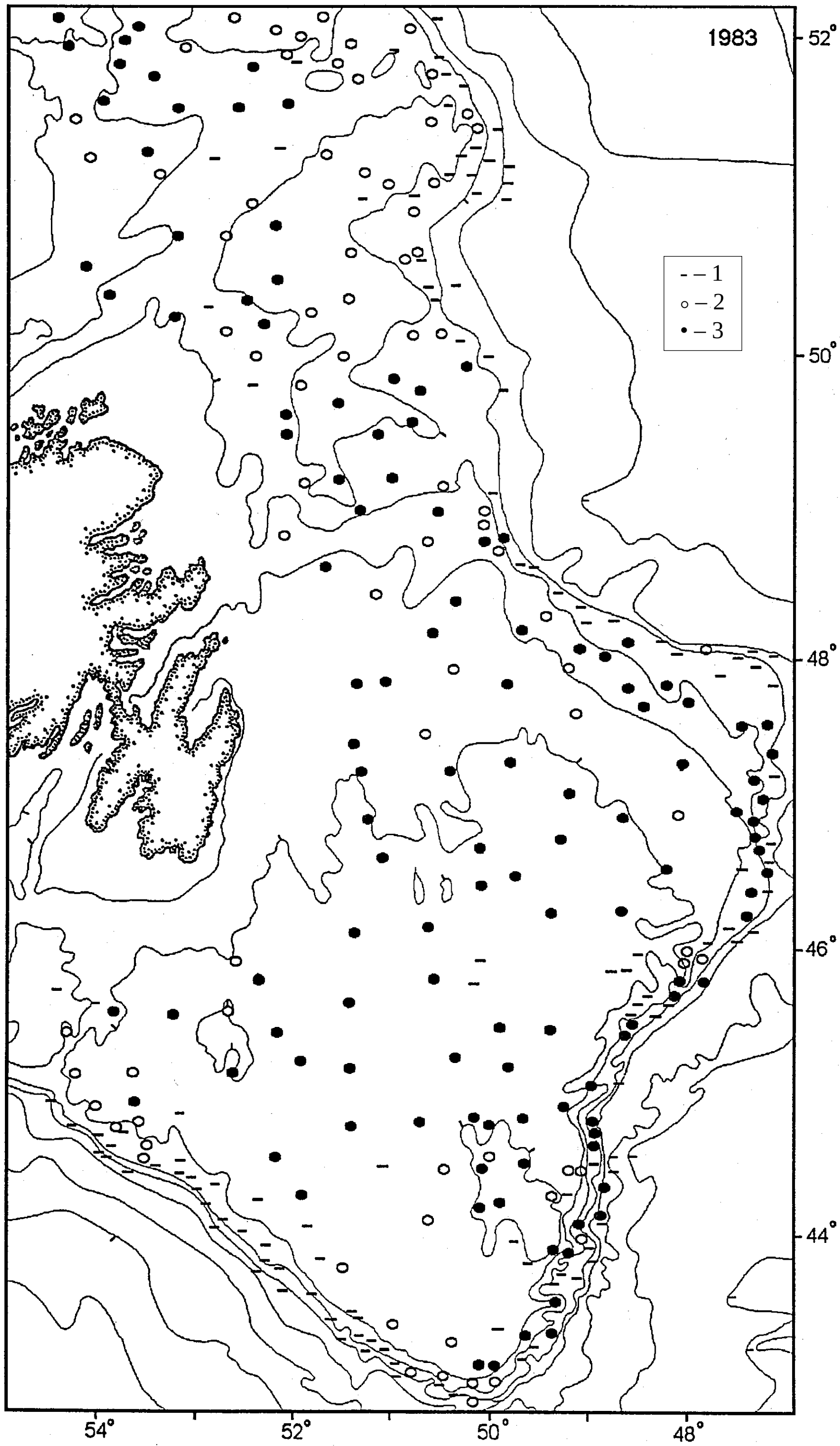

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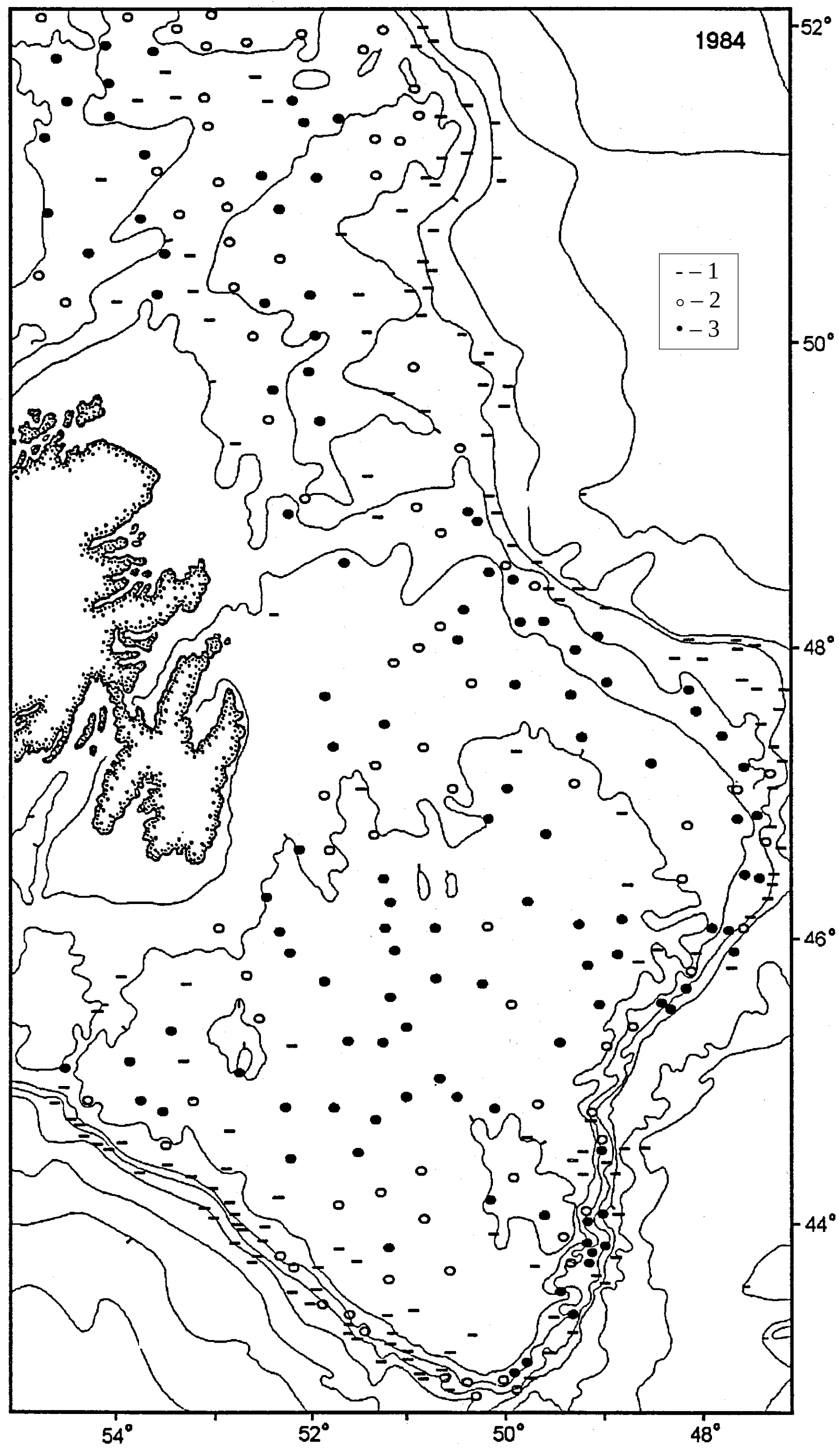

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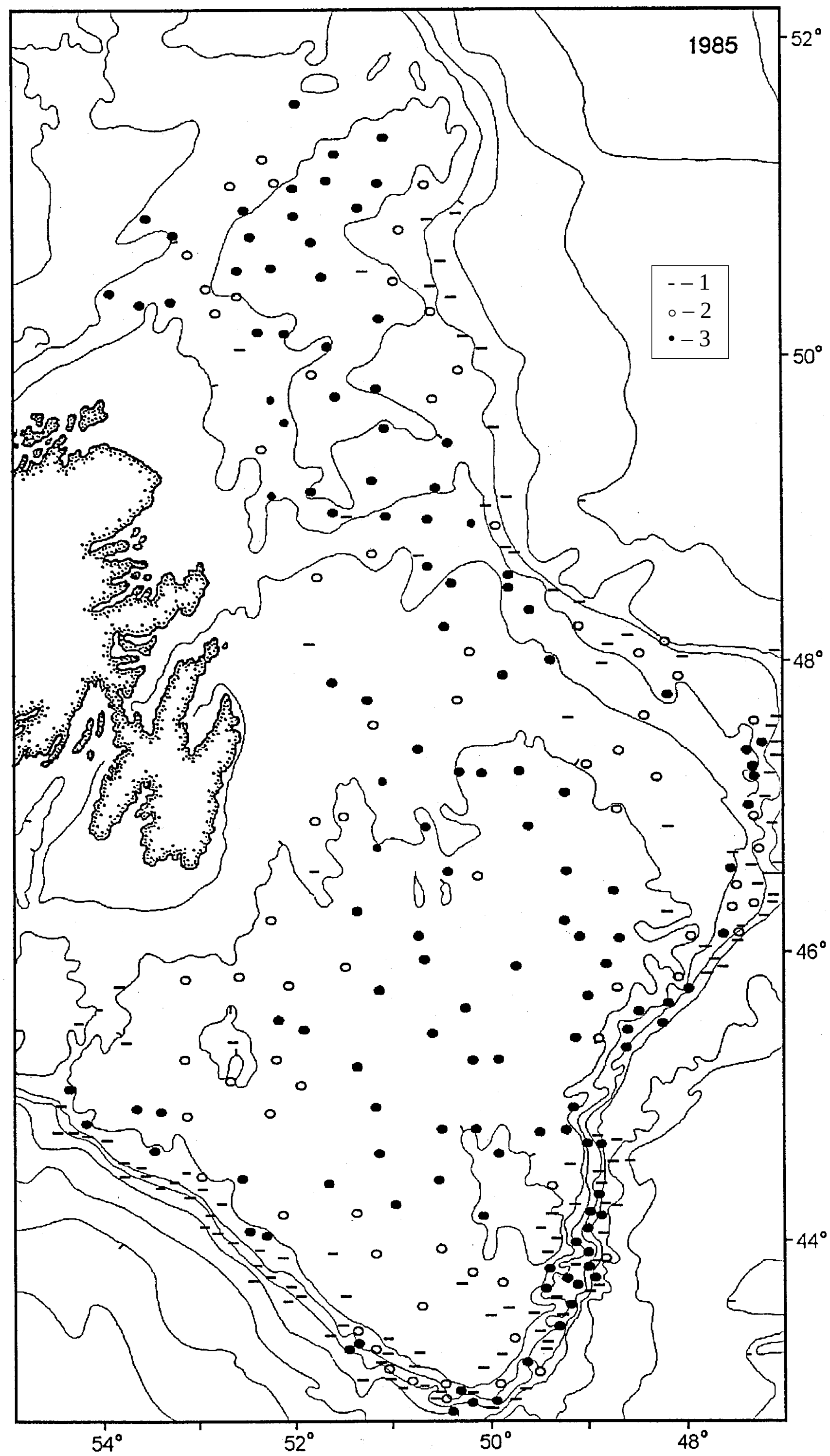

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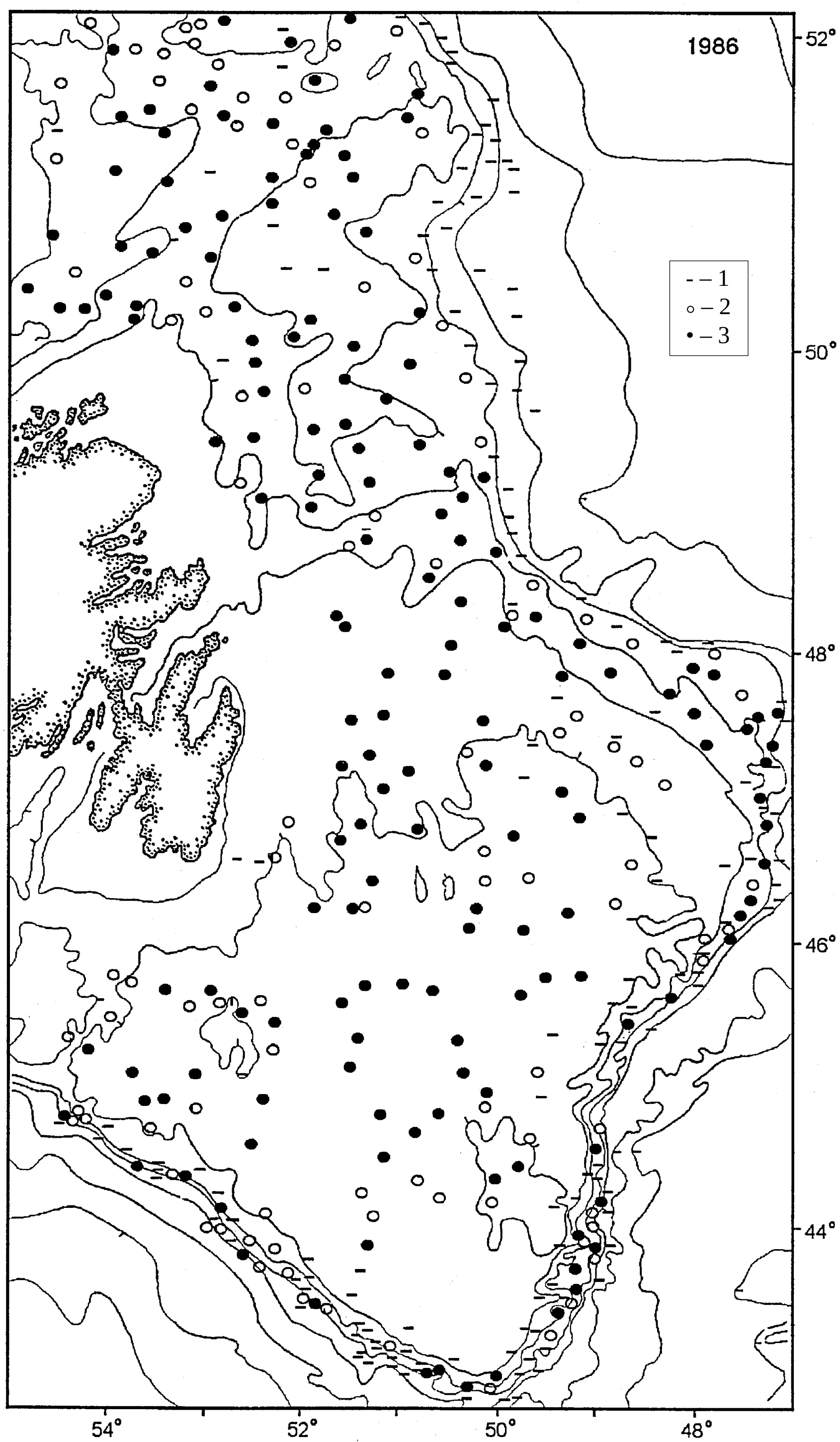

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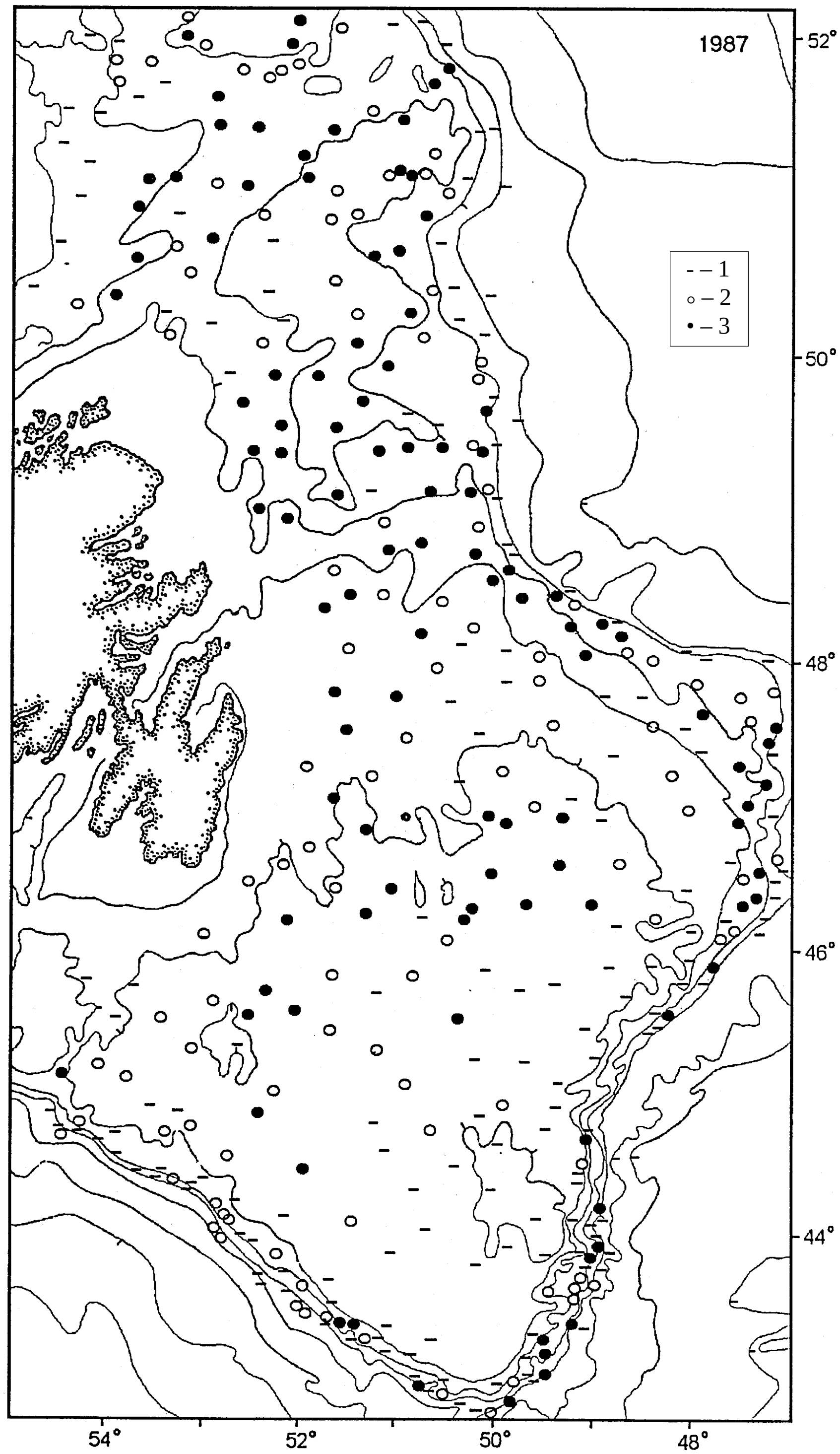

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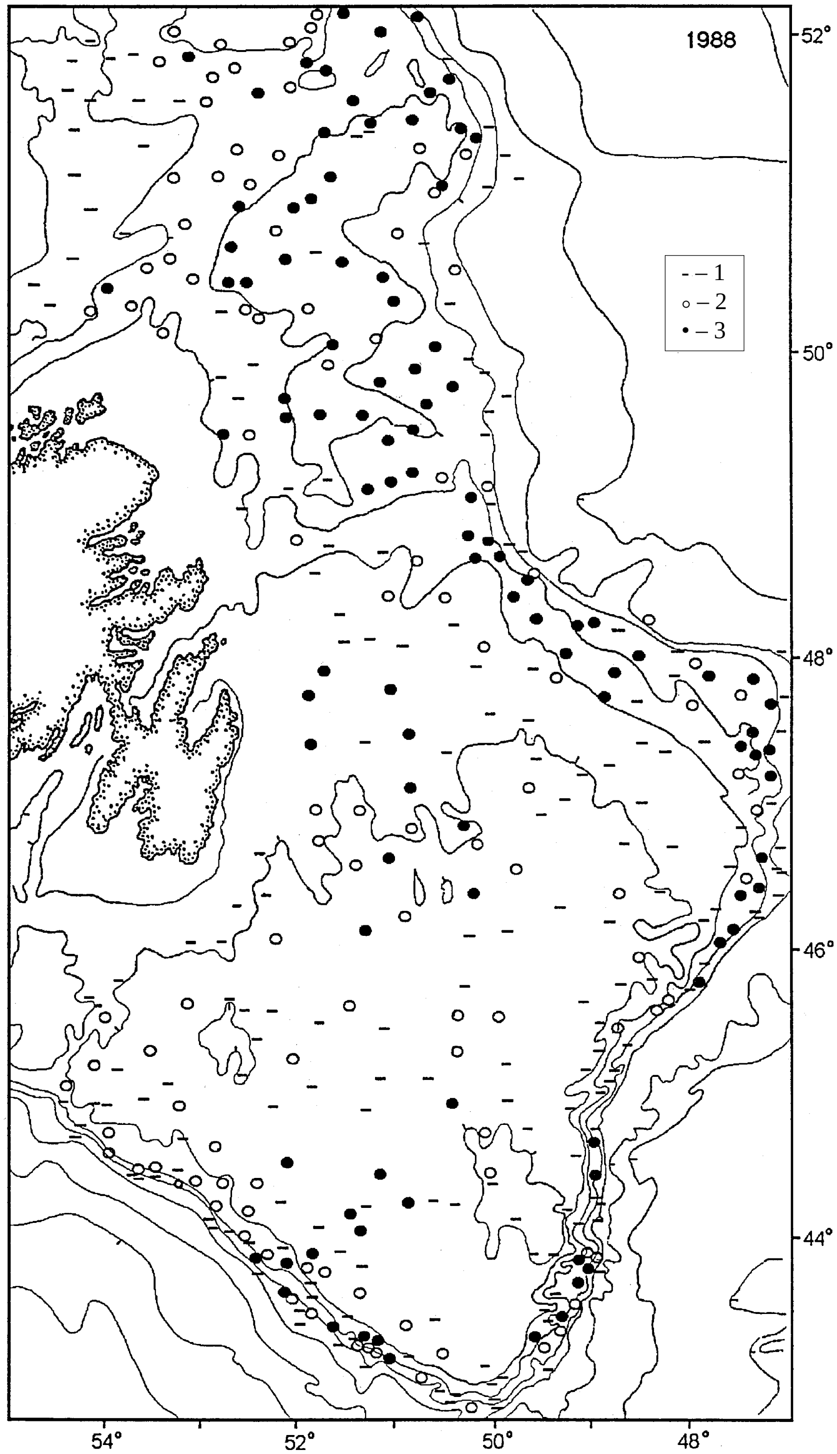

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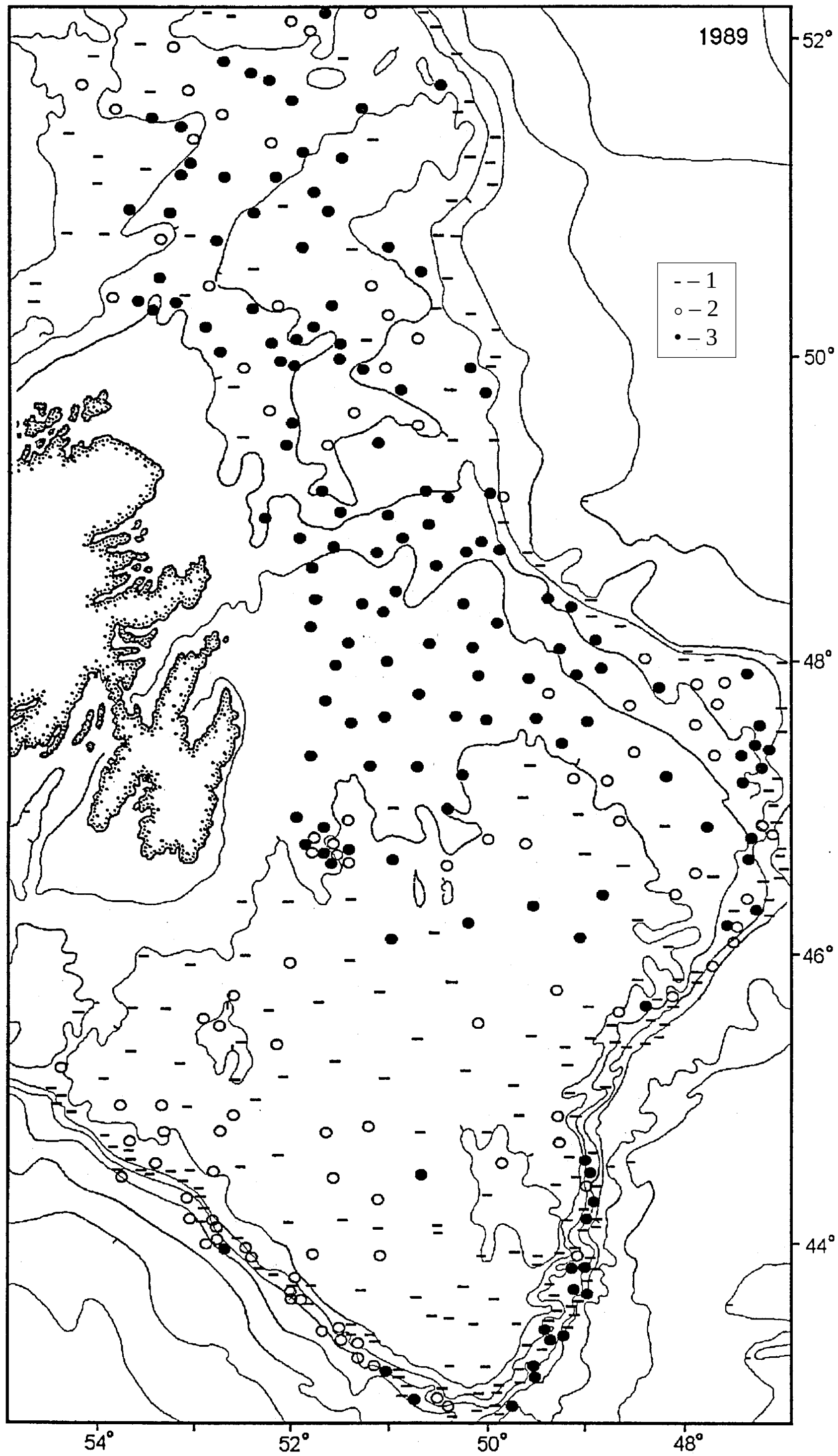

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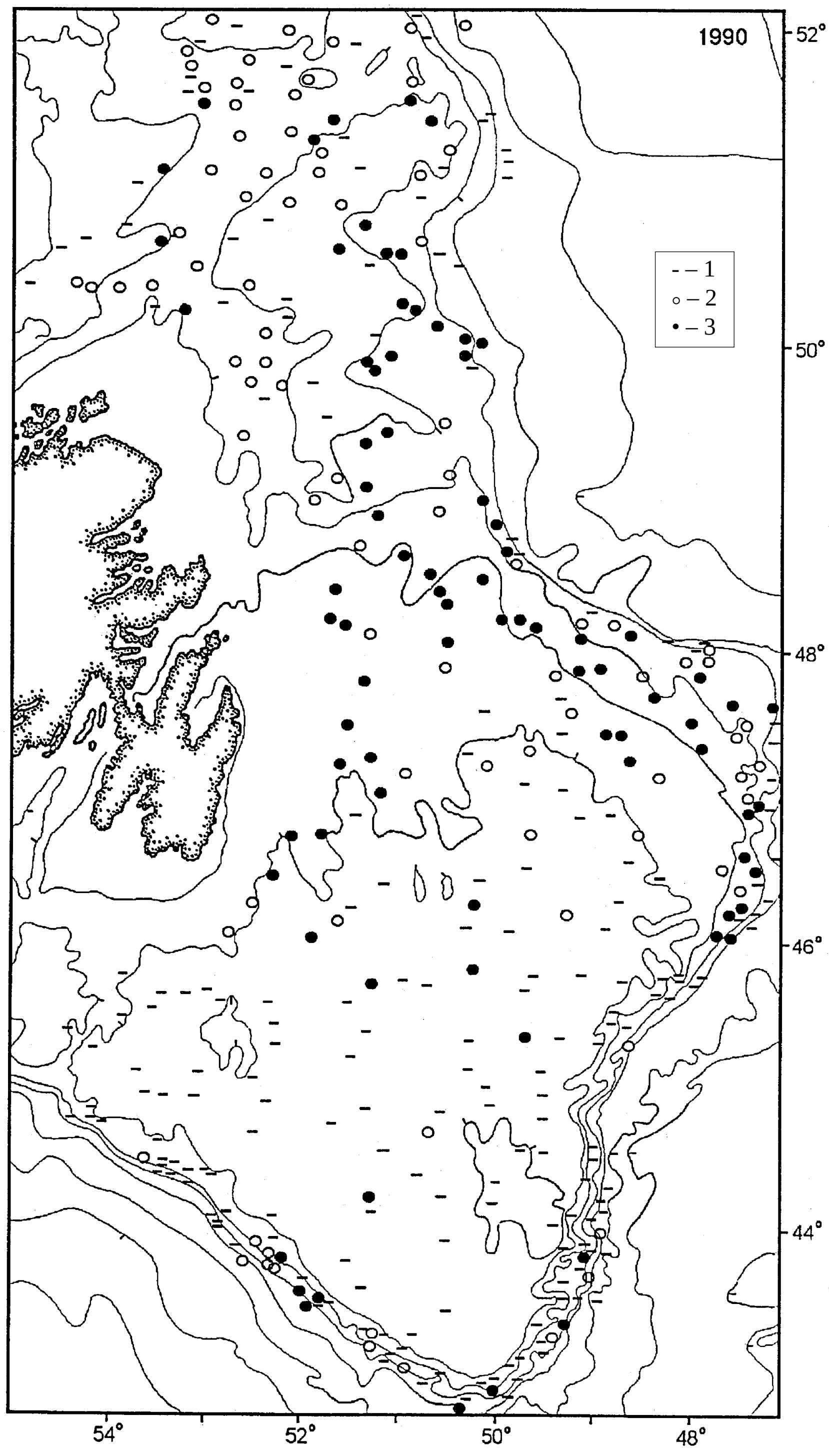

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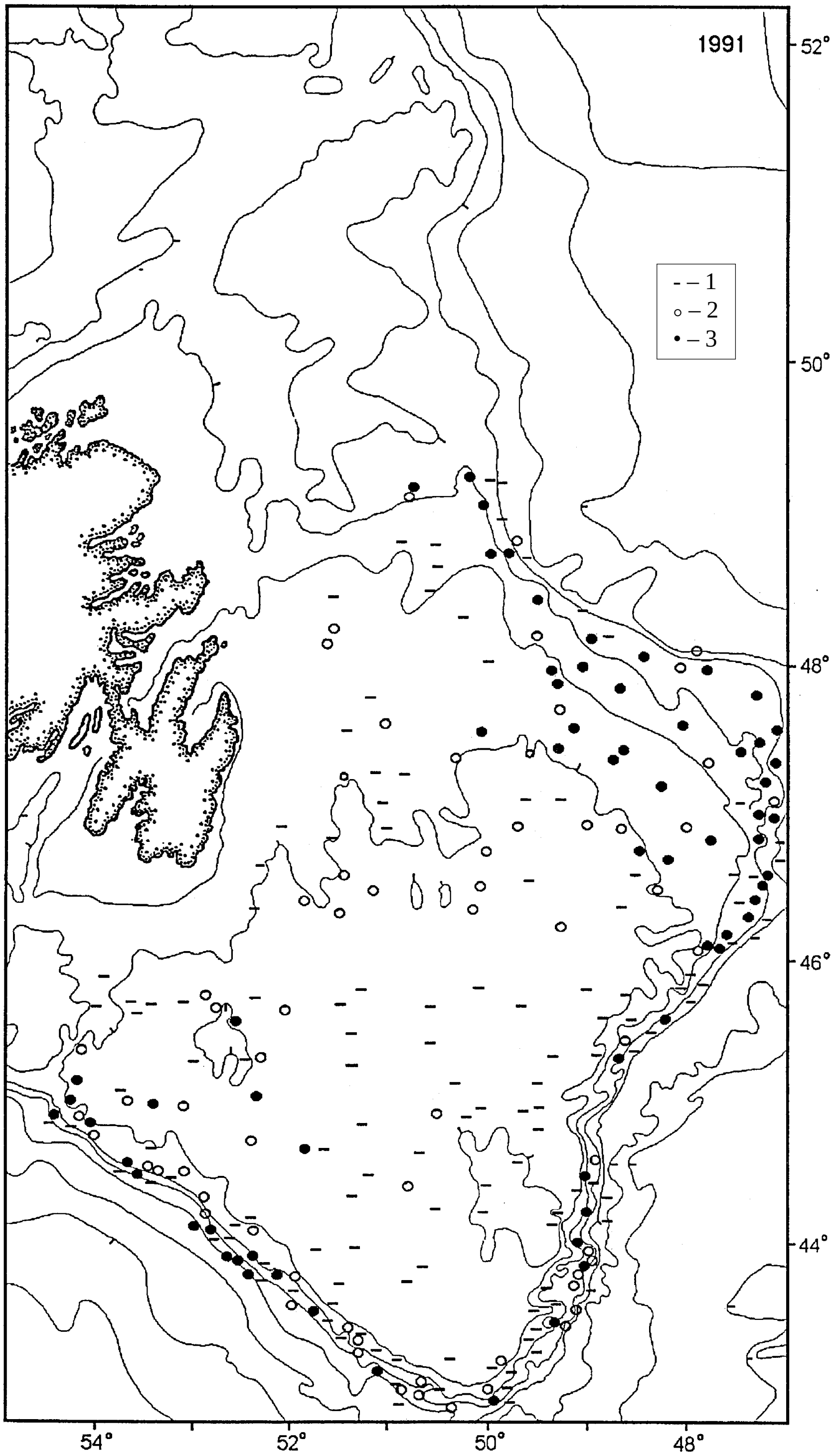

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TABLE 2. Data for samples collection in bottom trawl surveys of Newfoundland Shelf in 1978–91.

Year	No. of Stations Occupied	Stations with cod at Ages 3–6	No. of Samples Cod Feeding	No. of Stomachs Examined
1978	212	139	96	1 733
1979	262	126	89	1 605
1980	340	182	128	1 504
1981	291	131	88	1 217
1982	350	157	96	1 188
1983	555	216	131	1 551
1984	665	214	116	1 633
1985	518	205	137	2 454
1986	418	204	144	2 641
1987	448	198	109	1 572
1988	440	179	106	1 330
1989	533	220	142	1 568
1990	430	135	89	1 198
1991	378	105	70	929

– geographic variations in cod feeding on shrimp, capelin, sand lance, crabs, hyperiids and euphausiids (using frequency of their occurrence in cod stomachs).

Finally, all parameters (bottom temperature, abundance of cod and prey, degree of cod stomach fullness, frequency of prey occurrence) for each year were interpolated into points of regular grid covering the Newfoundland Shelf and adjacent continental slope. For bottom temperature, the regular grid consisted of points at 00°30' intervals of latitude and longitude (Borovkov and Tevs, MS 1988). For biological data, the grid consisted of points at intervals of 00°15'W × 00°10'N.

All subsequent analyses were made using interpolated values only, and were conducted as follows. First generalized plots were prepared of geographic variations of all the above parameters for the entire study period. Each plot was made using arithmetic means of interpolated values from 1978–91 for each grid point. Second, long–term variations were analyzed of the above parameters within some specified areas. The arithmetic mean was calculated of each parameter from all grid points inside each area for each year. The temporal rows of the means for each specified area were smoothed using simple three–year moving average (Plohinsky, 1970).

Results

Distribution of Cod and Prey

Analysis of the distribution of the relative abundance of cod revealed two main areas of concentration: one over the Funk Island Bank extending along the eastern parts of the shelf together with the adjacent slope, and the second over the central shallow of the Grand Bank (Fig. 3a). This result corresponds well with the commonly accepted current separation of the Newfoundland Shelf cod into two large stocks – northern (cod of Div. 2J and 3KL) and southern (cod of Div. 3NO) (Templeman, 1981).

Areas of the most intensive cod feeding in spring and summer did not coincide with areas of highest concentration (Fig. 3b). Feeding occurred more heavily in the western areas of distribution of cod, i.e. in deeper water (300–400 m) to the west of Funk Island Bank, and over the northwest part of Grand Bank extending into deeper water (100–200 m) to the north of the Bank, and finally in some isolated areas on the eastern edge of the Bank. The lack of coincidence of high cod concentrations with areas of their intensive feeding occurred not only in spring but also in autumn (Lilly and Rice, MS 1983; Lilly, MS 1993).

The distribution of important prey organisms of cod, capelin and shrimp, was restricted to cold

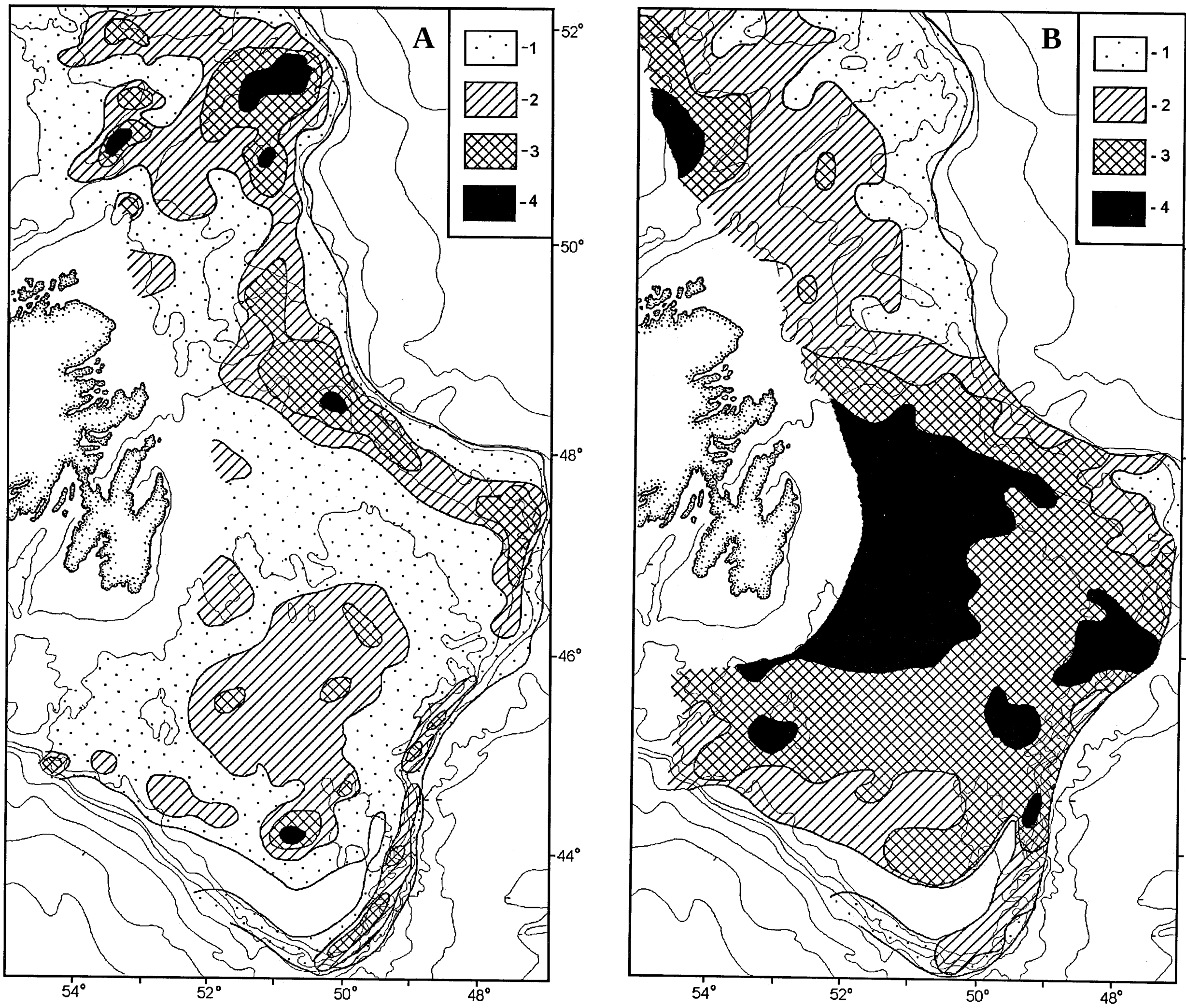

Fig. 3. **A**) Mean relative abundance of cod ages 3–6 from tows in 1978–91.
1 – less than 10°/ₒₒₒ (parts per ten thousand) in each crossing point
2 – 11–25°/ₒₒₒ
3 – 26–50°/ₒₒₒ
4 – more than 50°/ₒₒₒ

B) Distribution of mean fullness (see text for index) of cod stomach in 1978–91.
1 – less than 1.5
2 – 1.5–2.0
3 – 2.1–2.5
4 – more than 2.5

waters of the Labrador Current. Shrimp formed the densest concentrations in the coastal area, in the north of the study region, but capelin was distributed along the inshore and offshore branches of the Labrador Current on the Grand Bank (Fig. 4).

Sand lance also preferred cold waters but obviously their distribution on the Grand Bank shallows was largely related to the proper type of bottom ground (Winters, 1983) (Fig. 5a). In addition to sand lance, sizeable by-catches of crabs were

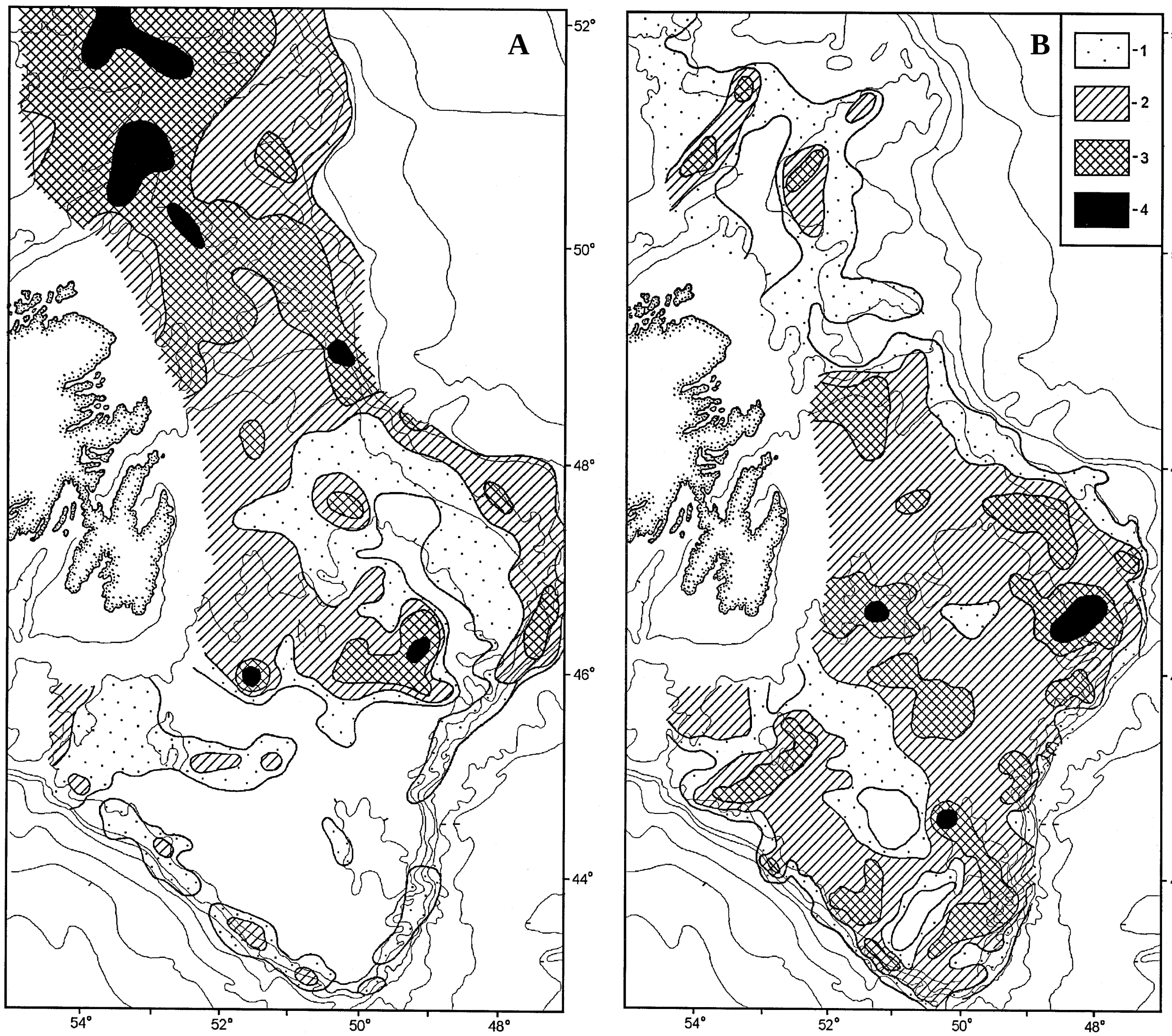

Fig. 4. **A**) Mean shrimp by-catches and **B**) mean capelin by-catches in 1978–91.
1 – single individuals
2 – tens
3 – hundreds
4 – thousands and more individuals

recorded during the study period over the extensive area of shallows adjacent to Newfoundland. The distribution of cod feeding on each of these prey species roughly coincided with the distribution of those prey (Fig. 6, 7).

Annual Changes in Water Temperatures and Distributions of Cod and Feeding

Biogeographic analysis of fish bottom communities on the Newfoundland Shelf showed several broad areas characterized by relatively constant composition of bottom fish both in time and space (Gomes, 1993; Gomes *et al.*, 1992; Villagarcia, MS 1994). The uniformity of composition was reported to be caused by the fact that each of those areas is occupied with water of a certain origin with homogeneous hydrographic characteristics – water mass. The uniformity of composition was also reported to be caused by the fact that each of those areas is occupied with the corresponding water mass. The term "water mass" means large volume of water of common origin, which shows nearly constant and continuous distribution of physical, chemical and

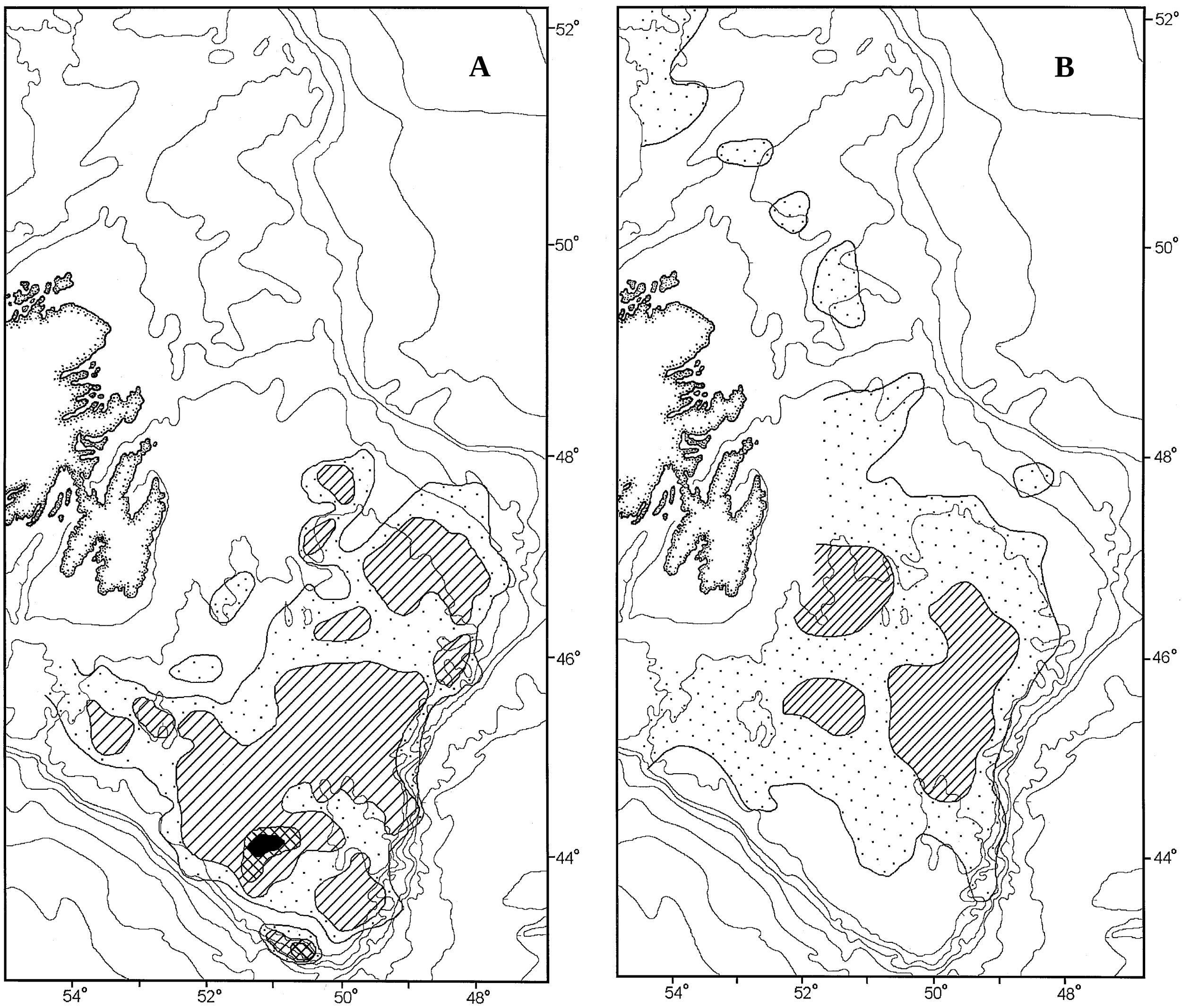

Fig. 5. **A**) Mean sand lance by-catches and **B**) mean crab by-catches in 1978–91.
1 – single individuals
2 – tens
3 – hundreds
4 – thousands and more individuals

biological characteristics constituting a unified complex (Dobrovolsky, 1961). The borders of water masses agreed well with the distribution of bottom temperature (Fig. 8a), and it was possible to distinguish four bottom water masses which are likely to be important to cod (Fig. 8b).

The main water mass (as referred to by Villagarcia, MS 1994) covered areas of the shelf and upper part of the slope and included the eastern margin of the Labrador Current (Fig. 8). This can be labelled as Mass 1. The mean bottom temperature during the study period varied here between 2.1–2.6°C, with a small downward trend during recent years. The proportion of the cod stock concentrated in that water mass sharply increased from 40% in 1978–84 to 70% in 1987 (Fig. 9). Stomach fullness was originally at a level of 2, but in recent years it decreased to 1.5. Frequency of any of the main prey species in cod stomachs did not exceed 30% (which in our opinion indicated a paucity of preferred prey in the area). Cod fed primarily on shrimp and capelin. In the first years of observations, sand lance and hyperiids were also recorded in cod stomach, but in recent years crabs occurred more often (Fig. 9).

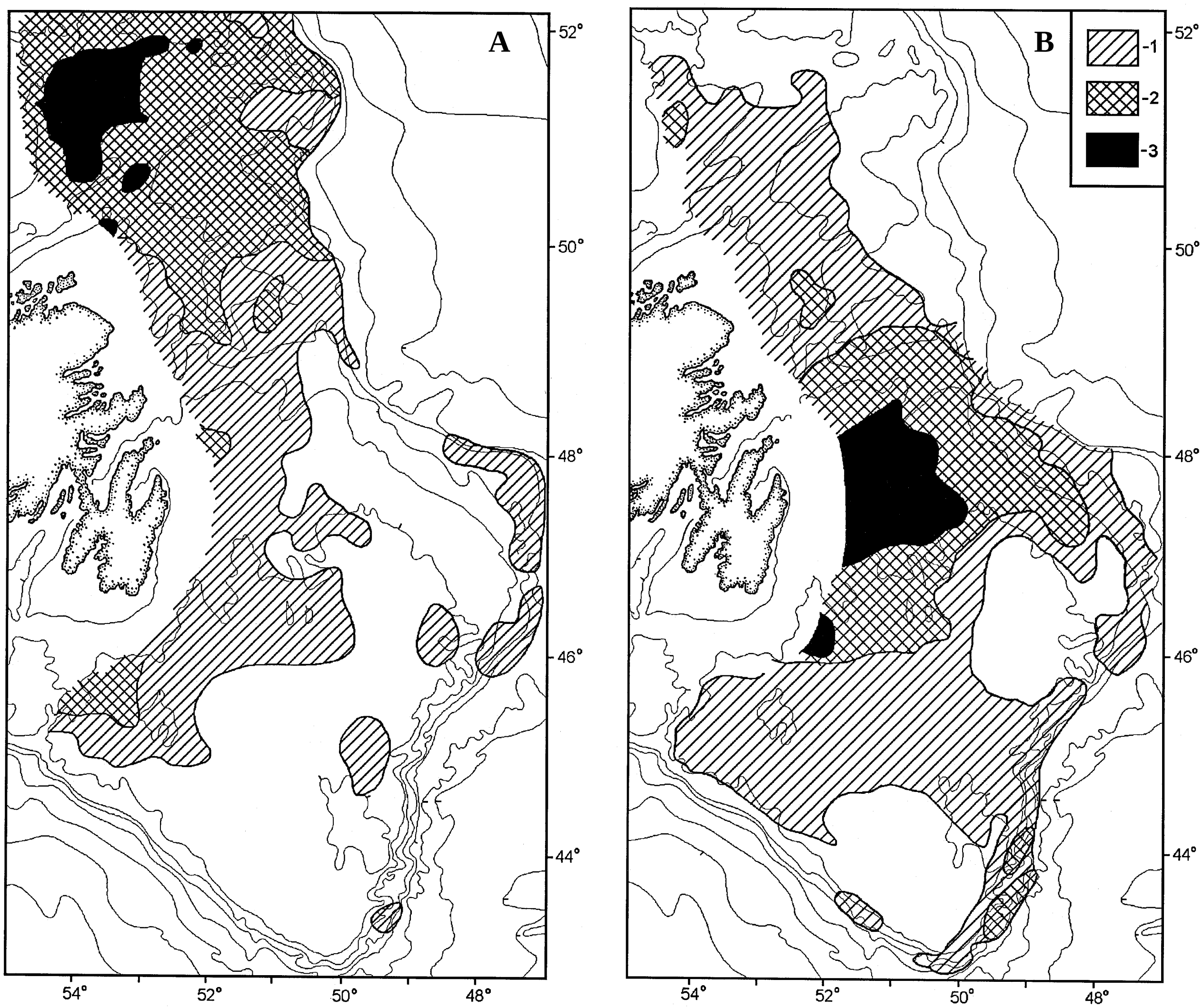

Fig. 6. Geographic variation in cod feeding on **A**) shrimp and **B**) capelin in 1978–91 given as frequency of occurrence.
1 – 10–25%
2 – 26–50%
3 – more than 50%

Inshore water mass (as referred to by Villagarcia, MS 1994) formed under the influence of continental freshwater runoff and the Inshore Branch of the Labrador Current (Fig. 8). This can be labelled as Mass 2. Variation in the mean bottom temperature of this water mass was high, ranging from 0.7 to 2.2°C (Fig. 10). The percentage of cod stock in this mass was relatively constant and did not exceed 15%. Stomach fullness varied within the range of 2.0–2.5. The preferred prey species at the beginning of the study was shrimp, while in later years it was capelin. A change in cod feeding from shrimp to capelin was followed by some increase in their stomach fullness. Frequency of crab occurrence was low. Sand lance and euphausiids were often missing from the diet. Frequency of hyperiids was relatively high in the first years of observations (Fig. 10).

An intermediate water mass (as referred to by Gomes, 1993) forms under the influence of the Inshore Branch of the Labrador Current and occupies shallower sites than the first two water masses (Fig. 8). This can be labelled as Mass 3. The intermedi-

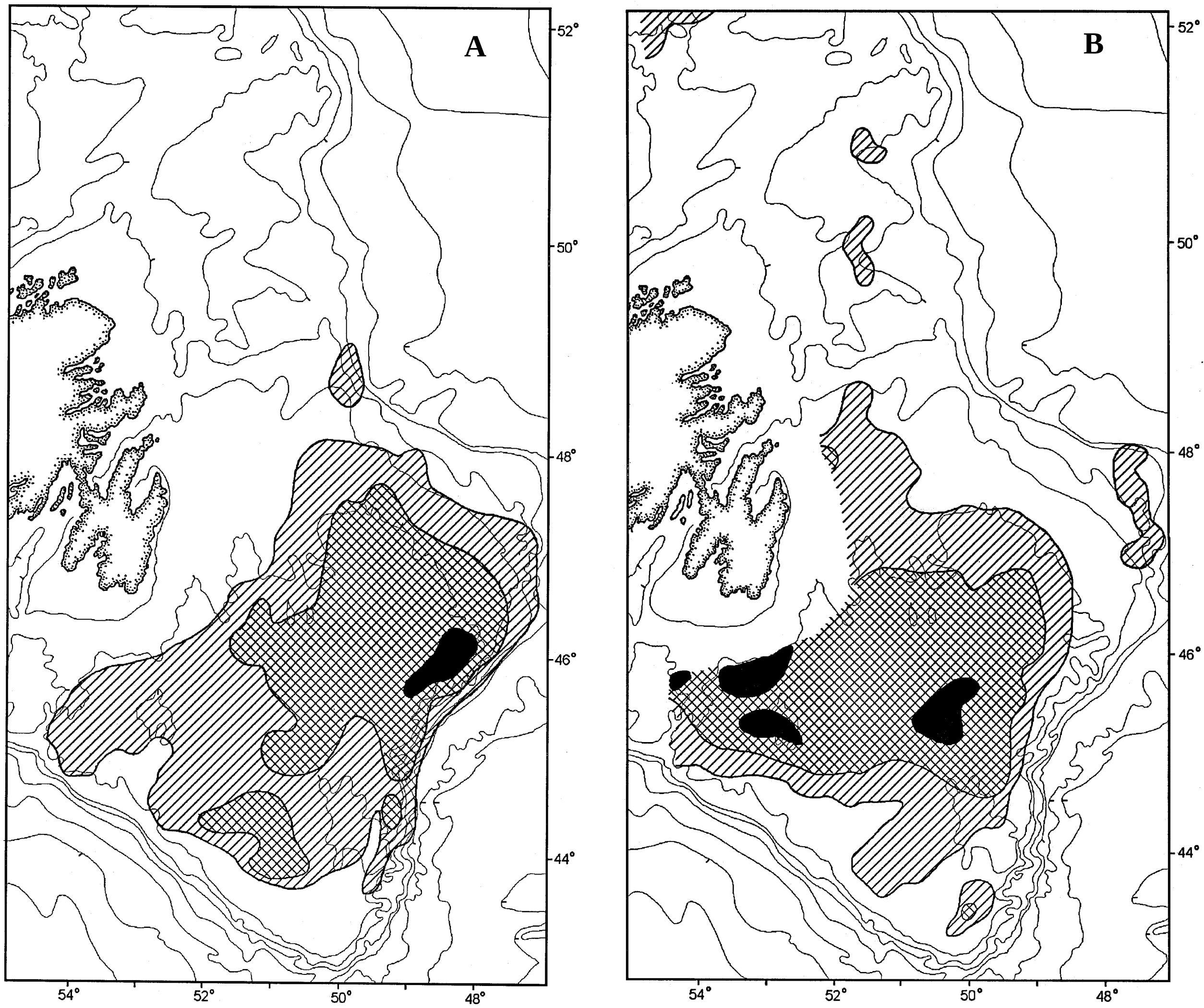

Fig. 7. Geographic variation in cod feeding on **A**) sand lance and **B**) crabs in 1978–91.
1 – 10–25%
2 – 26–50%
3 – more than 50%

ate water mass was characterized by a negative mean bottom temperature which markedly decreased during the study period (Fig. 11). The percentage of cod stock was relatively constant and did not exceed 20%. Stomach fullness in comparison to that in the other water masses was the highest, ranging from 2.5 to 3.0. The preferred prey species was capelin for which the frequency of occurrence after 1984 exceeded 50%. In the first years of observations, sand lance often occurred in the cod diet while in recent years they were replaced by crabs (Fig. 11).

A shallow water mass (as referred to by Gomes, 1993) is defined as mixed water of the Labrador Current and slope which are exposed to local seasonal heating (Fig. 8). This can be labelled as Mass 4. Processes here were markedly different from those in the three other water masses. Since 1983, a sharp reduction in mean bottom temperature occurred, reaching negative values at the end of the study period (Fig. 12). In two years, a pronounced decrease was observed in the percentage of cod stock in this water mass (from 42 to 5%) and stomach fullness dropped from 2.5 to 0.8. The frequency

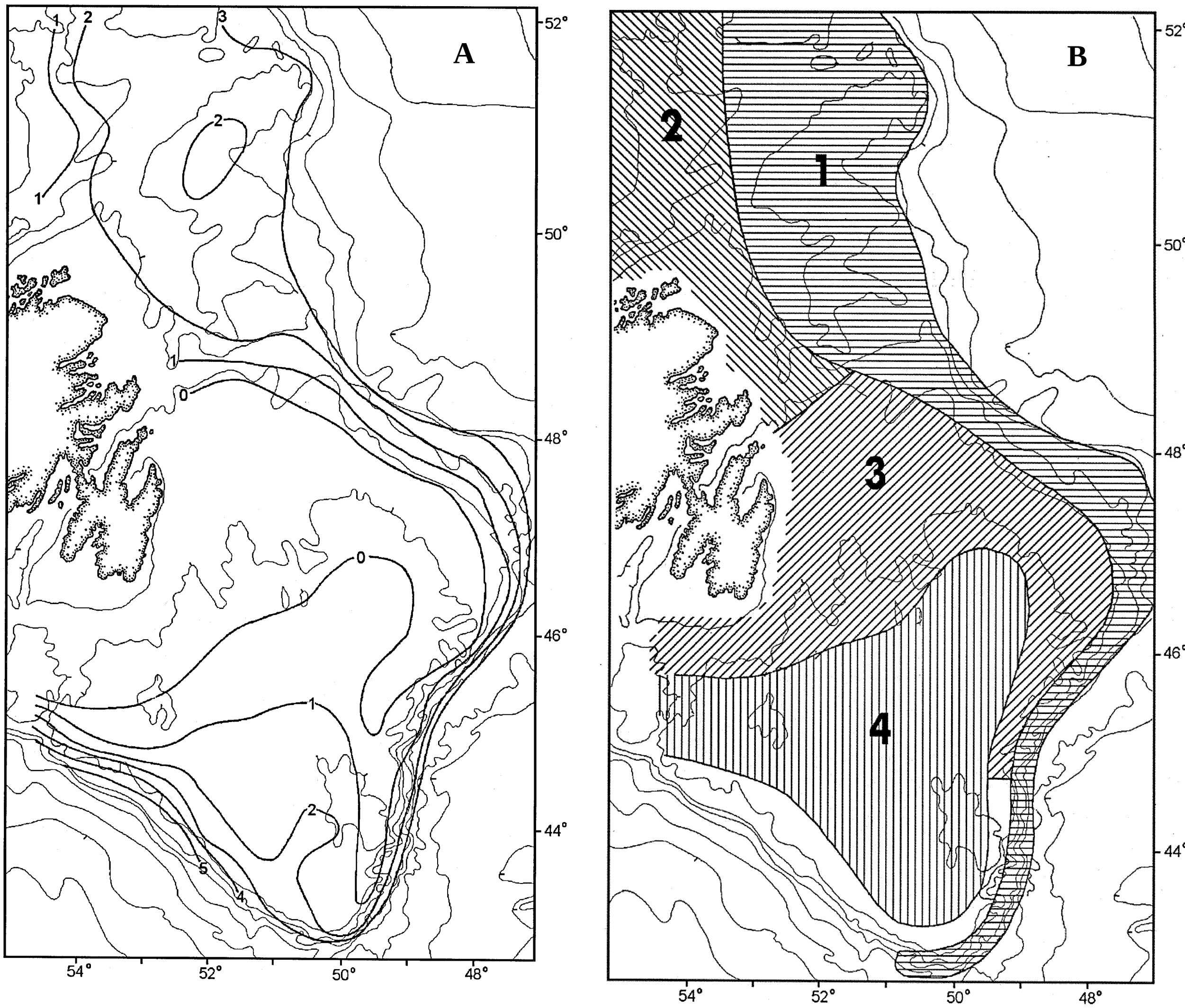

Fig. 8. **A**) Geographic variation in bottom temperature in 1978–91 (from data of Tevs, 1991; **B**) area occupied by different water masses:
1 – main water mass (Mass 1)
2 – inshore water mass (Mass 2)
3 – intermediate water mass (Mass 3)
4 – shallow water mass (Mass 4)

of capelin and shrimp in cod diet drastically decreased in the recent years, while the frequency of crab and sand lance remained around 20–30% (Fig. 12).

Discussion

The analysis showed that in the areas occupied by various water masses, the reaction of cod to changes in bottom temperature differed. In the area occupied by the intermediate water mass where the mean bottom temperature fell below 0°C (Mass 3, Fig. 8), cod fed actively and the proportion of the cod stock present remained relatively constant during the temperature decline. However, the temperature decline in the area occupied by the shallow water mass (Mass 4, Fig. 8) was accompanied by reduction of cod stomach fullness and decrease in the portion of the cod stock there, although the mean bottom temperature was below 0°C only at the end of the study period.

Cod usually avoid sub–zero temperatures (Goddard *et al.*, 1992) but according to some

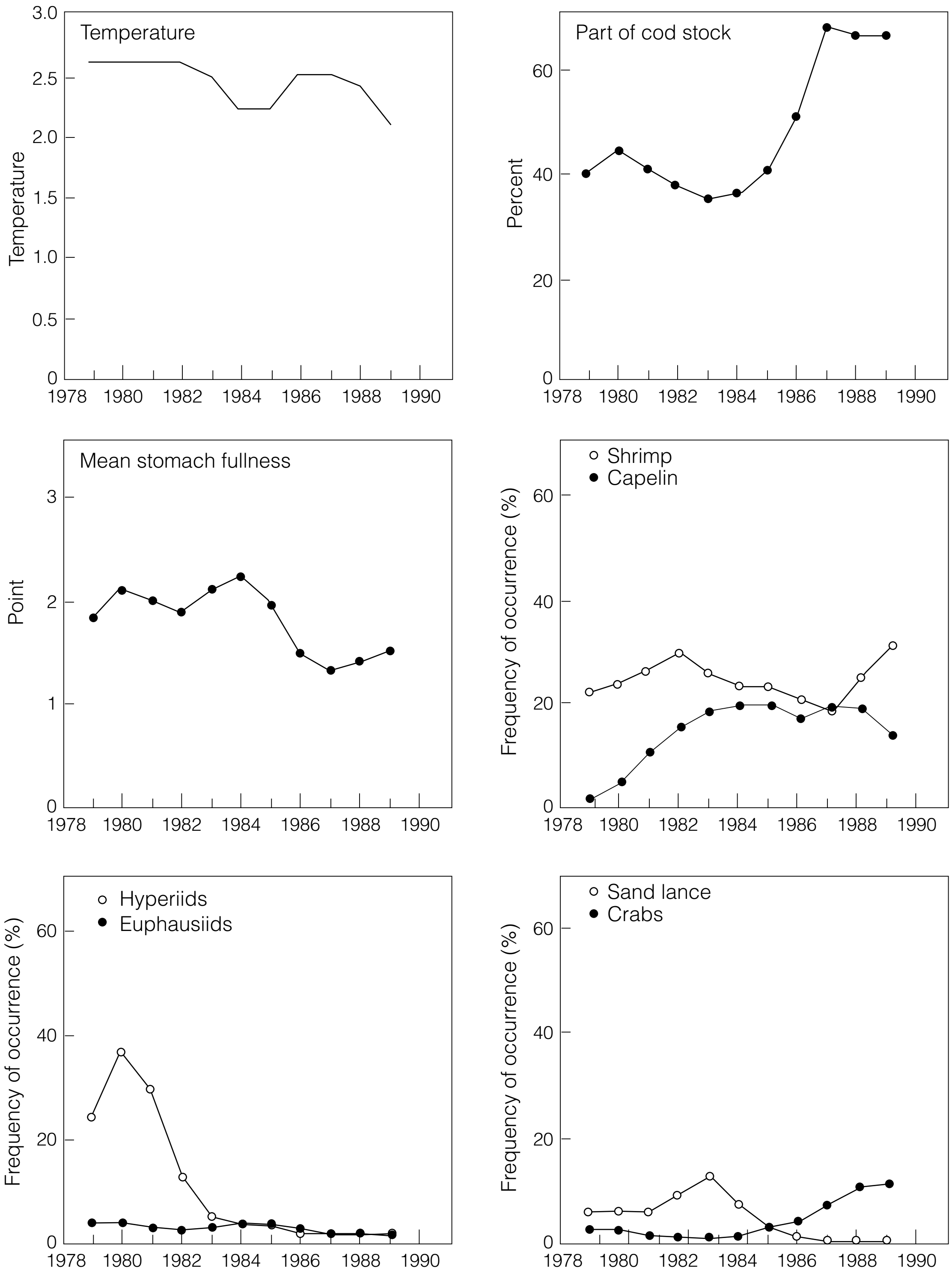

Fig. 9. Main water mass. Mean area bottom temperature, proportion of cod stock present, mean stomach fullness, and occurrence of shrimp, capelin, hyperiids, euphausiids, sand lance and crabs in cod stomachs.

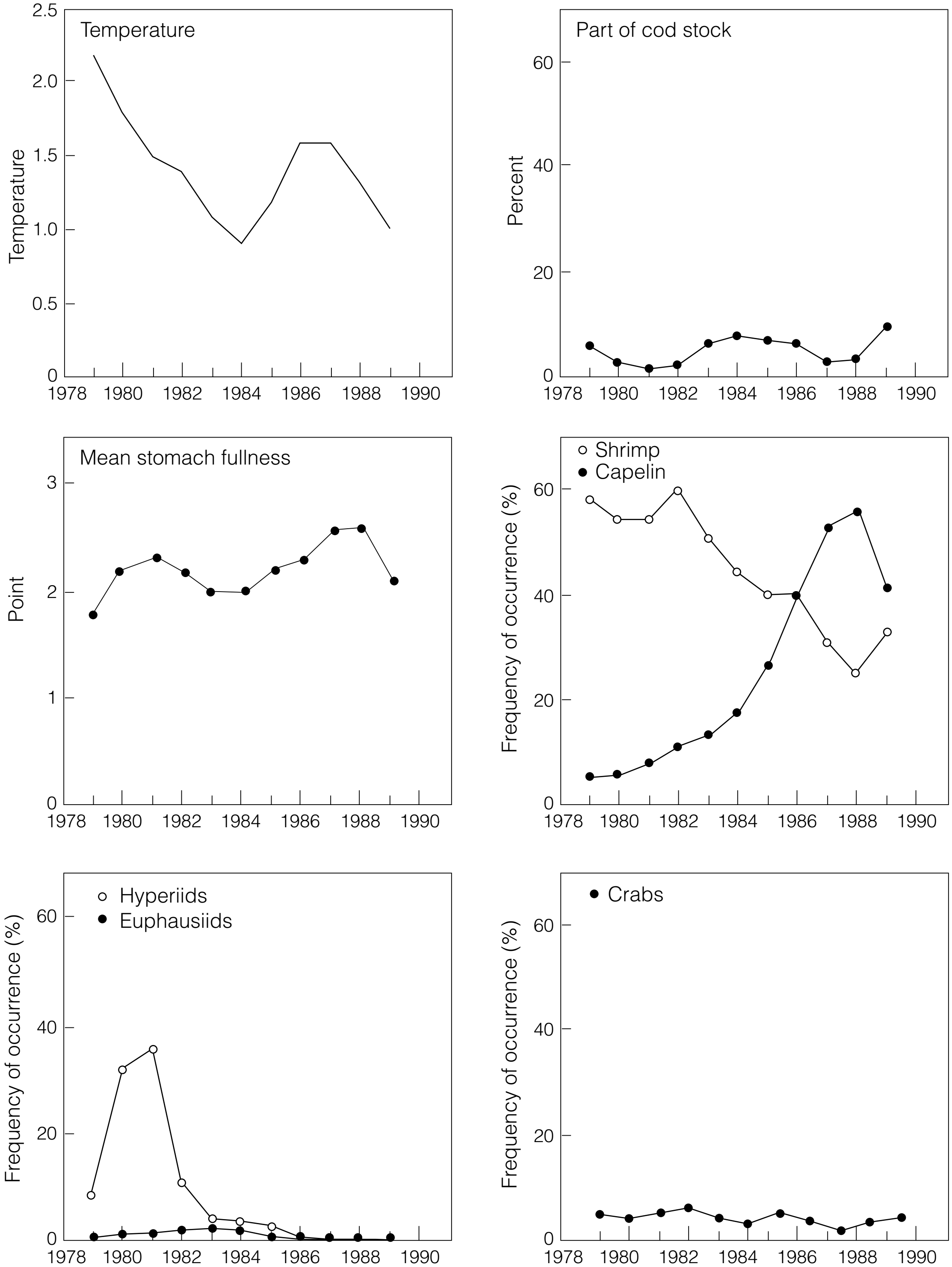

Fig. 10. Inshore water mass. Mean area bottom temperature, proportion of cod stock present, mean stomach fullness, and occurrence of shrimp, capelin, hyperiids, euphausiids, sand lance and crabs in cod stomachs.

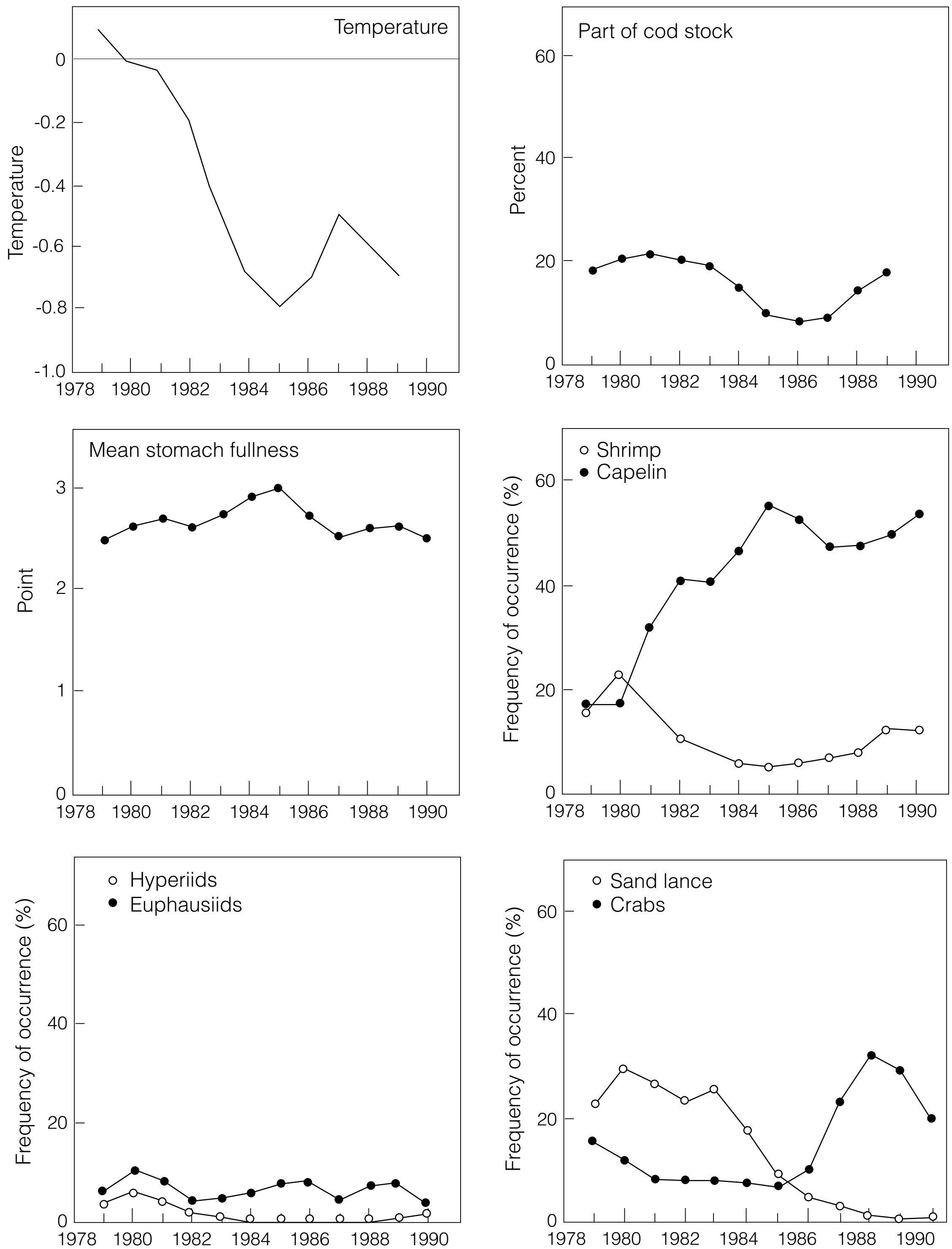

Fig. 11. Intermediate water mass. Mean area bottom temperature, proportion of cod stock present, mean stomach fullness, and occurrence of shrimp, capelin, hyperiids, euphausiids, sand lance and crabs in cod stomachs.

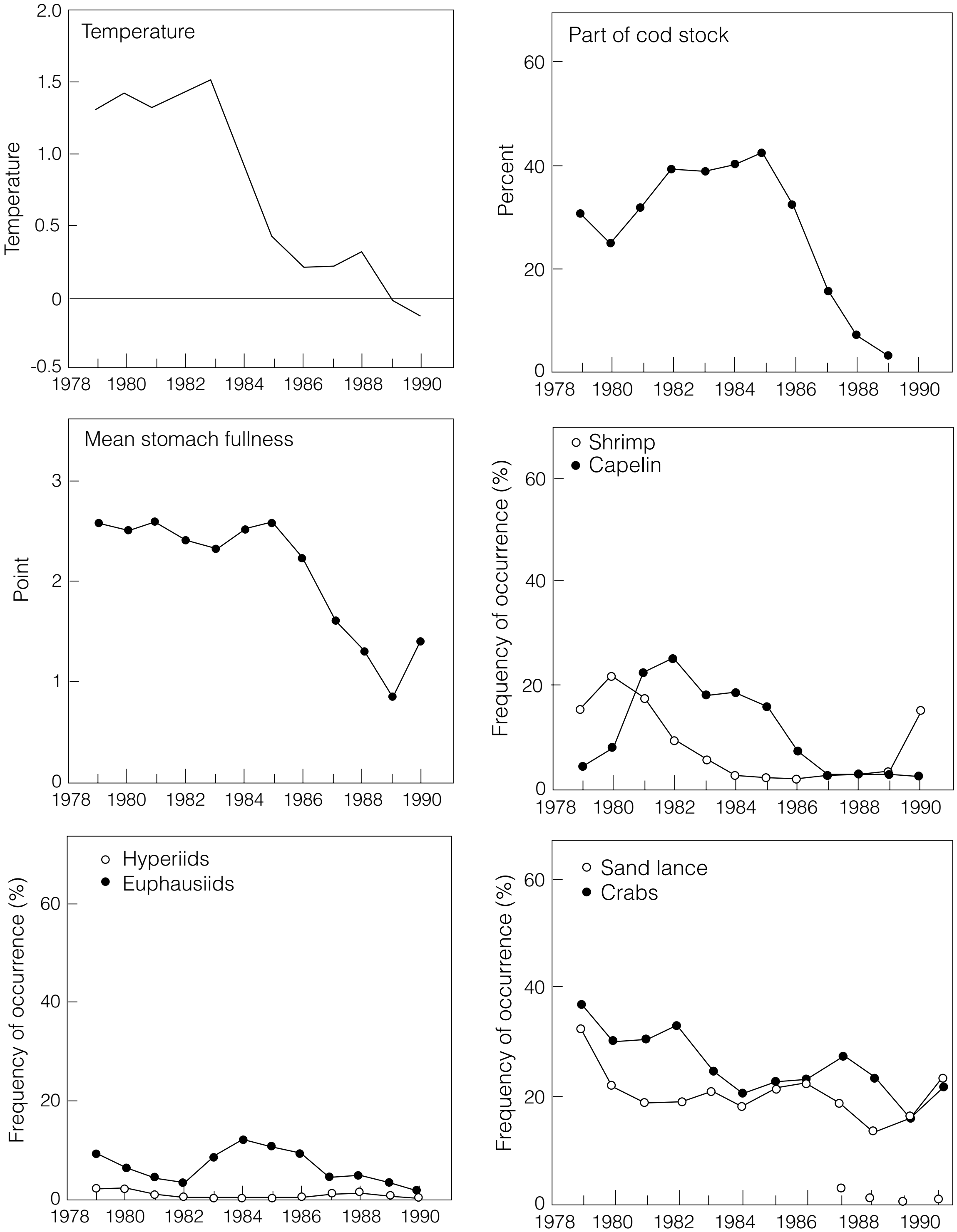

Fig. 12. Shallow water mass. Mean area bottom temperature, proportion of cod stock present, mean stomach fullness, and occurrence of shrimp, capelin, hyperiids, euphausiids, sand lance and crabs in cod stomachs.

observations, cod are often found in temperatures well below 0°C, particularly in areas where they find good food (Lilly, 1994). Templeman (1965) mentioned that when feeding pelagically, cod probably fill up to catch prey in the cold intermediate layer, and then sink near bottom, into warm water, to digest it. We propose that such behaviour occurs not only during pelagic but also during bottom feeding: cod move into cold water to catch prey and return into warm water to digest it.

As observed in this study, cod are concentrated mainly in two of the four water masses on the Newfoundland Shelf in spring and in the other two they mainly feed on. For the whole study period, the most significant changes in cod distribution and feeding occurred in the shallow water mass. To understand, if only partially, the reason for the changes observed, it is valuable to compare conditions for cod in the main water mass and shallow water mass in warm and cold years.

In the main water mass, cod were distributed in relatively warm water beneath an intermediate cold layer (Fig. 13a, b). In cold years, this layer became thicker but changes in temperature near the bottom were negligible. Cod could feed both near the bottom and pelagically, migrating to the cold layer to prey on capelin or shrimp (Lilly, 1982).

On the Grand Bank shallows, the cold water layer was no longer intermediate because it reached the bottom over an extensive area. Cod were concentrated on the area free of cold water where they could feed on sand lance and crabs or make horizontal migrations to an adjacent, intermediate water mass to feed on capelin (Fig. 13c). In cold years, the area with negative bottom temperatures became more extensive while the area with temperatures favourable for cod decreased (Fig. 13d). The opportunity to migrate to the intermediate water mass (Mass 3, Fig. 8) also decreased because over the extensive area occupied by this water mass, bottom temperatures became lower than the physiological limit for cod (–1.2°C) (Goddard *et al*., 1992). This extremely cold bottom water probably also formed a serious obstacle for cod moving to spawning grounds near the Newfoundland coast (Hutchings *et al*., 1993; Gerasimova and Kiseleva, MS 1995).

Templeman and Fleming (1962) discussed the possibility of cod migrating through the cold intermediate layer and feeding in warm surface waters. Our observations showed that cod fed on planktonic crustaceans (hyperiids) more actively in the first, warmer half of the study, while bottom crustaceans (crabs) were consumed more actively in the second colder half of the study. Bottom feeding may indicate that in cold years cod are hampered from moving to pelagic waters. For example, there are observations that cod can move to surface waters when the intermediate cold layer is thin or absent. If the cold water layer is thick, cod can only pass through the lower border of this layer (Templeman, 1965). However, high frequency of hyperiids in cod stomachs may simply be a consequence of low abundance of capelin early in our study. Capelin also prey on hyperiids (Lilly, 1991).

Cold periods, therefore, have the most negative effect on cod dwelling in the shallow water mass, which we identify with southern cod stock. Reduction of cod abundance in this area can occur either by way of their moving to other areas or as a result of the absence of recruitment because of unfavourable spawning conditions over a number of years.

Conclusions

1. The spatial distribution of cod and where they feed agrees well with the hydrographic and biogeographic structure of the Newfoundland Shelf.

2. In spring, cod concentrated in the main water mass and shallow water mass but fed in the inshore and intermediate water masses.

3. Conditions differ for cod in the main water mass and shallow water mass. In the cold periods, cod in the shallow water mass experiences the most unfavourable conditions.

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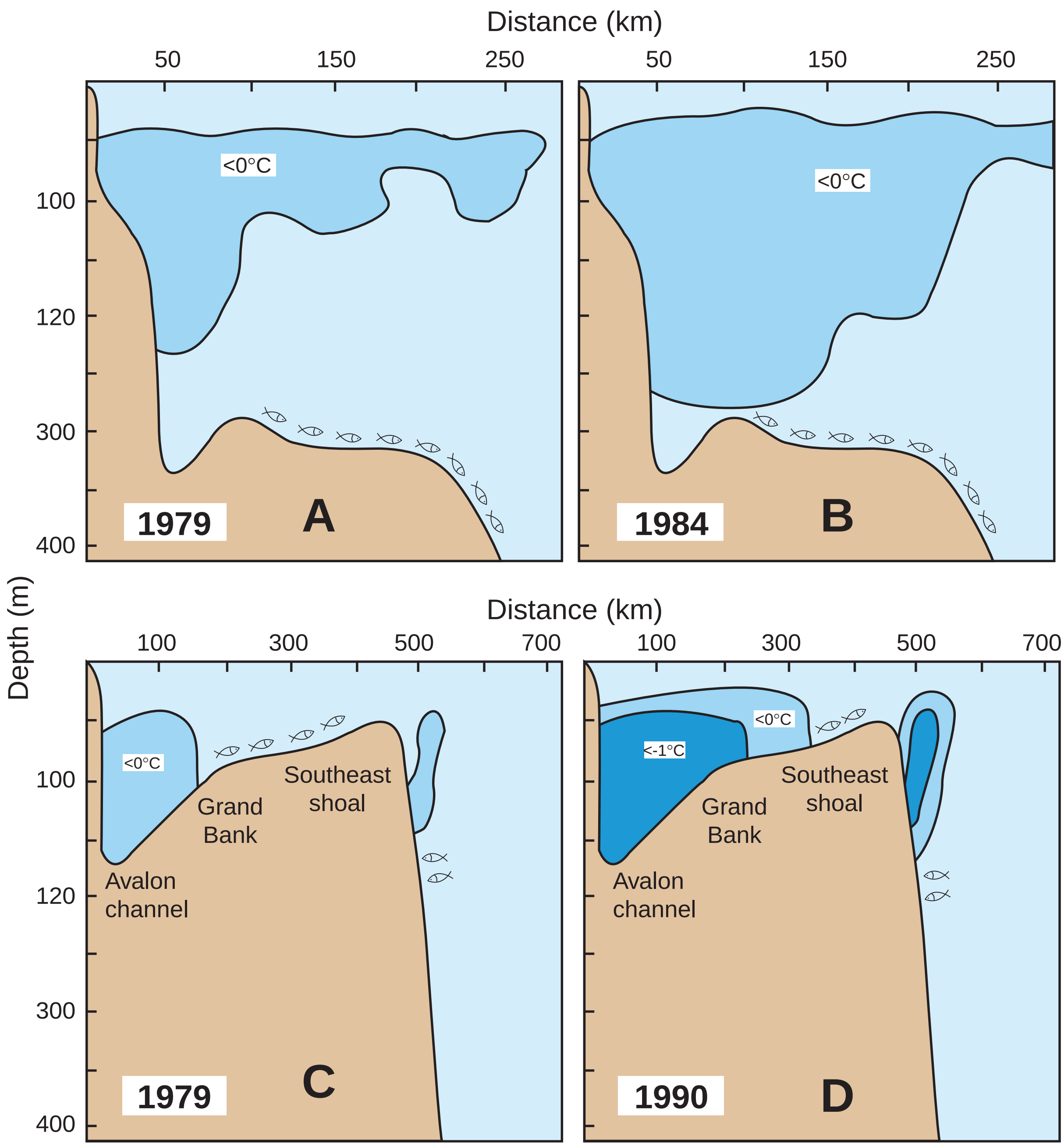

Fig. 13. Localization of cold intermediate layer (CIL) and cod concentrations in main (**A**, **B**) and shallow (**C**, **D**) water masses in the warm and cold years.

A and **B**) transect on line 1, Fig. 1 in warm 1979 and cold 1984 years. Contours of CIL, by Petrie *et al*., 1988. **C** and **D**) transects on line 2, Fig. 1 in warm 1979 and cold 1990 years. Contours of CIL, by the data of Tevs, 1991. Localization of transects and contours of bottom, by May *et al*., 1965.

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