

Fol. 41 EE

Fisheridirektoratets
Bibliotek

International Council for
the Exploration of the Sea

CM 1997/EE:06
Environmental Factors

23 DES. 1998

Recent variations in recruitment of Northeast Atlantic Greenland
Halibut (*Reinhardtius hippoglossoides*) in relation to physical factors.

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ABSTRACT

Based on annual bottom trawl surveys in the Barents Sea and Svalbard area in 1983-96, the paper describes variations in abundance and composition of I-group Greenland halibut (*Reinhardtius hippoglossoides*). The main pattern of variation in abundance during the period was a change from high abundance in the first half of the period, to low abundance in the second half. The reduced abundance was associated with a northerly shift in distribution. In the last two years the recruits reappeared, first in northern parts of the study area and then also further south. These periodical changes in juvenile distribution, may be driven by physical oceanographical processes. Distribution changes probably extend beyond the area covered by the annual surveys. Thus, the results add uncertainty to the recent assessments of the state of the stock.

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1. INTRODUCTION

Greenland halibut (*Reinhardtius hippoglossoides*) is distributed in arctic and boreal waters on both sides of the North Atlantic (Fedorov, 1971). The stocks support important fisheries in comparatively deep waters outside Canada, Greenland, Iceland, Faeroe Islands, and Norway (Godø and Haug, 1989; Bowering and Brodie, 1995). On the eastern side the distribution is more or less continuous along the continental slope from Faeroe Islands and Shetland to Svalbard (Whitehead *et al.*, 1986; Godø and Haug, 1989). The stock separation of Atlantic Greenland halibut is not known and for management purposes a pragmatic definition is used based on statistical areas. The Northeast Atlantic stock is thus found along the slope outside Norway, including Svalbard, and in the Barents Sea.

The stock is fished with gill-nets and longlines at the spawning grounds and by trawls in the Barents Sea and along the Norwegian slope northwards to Spitsbergen. Based on reductions in estimated stock size and indications of recruitment failure the fishery has been heavily regulated since 1992 (Hysten and Nedreaas, 1995). All scientific surveys in the young fish areas showed similar tendencies of a dramatic decline in abundance of younger age-groups in the late 1980's.

Northeast Atlantic Greenland halibut spawns along the slope between Lofoten and Bear Island, and to some extent also south of this area (Godø and Haug, 1989). Eggs and larvae drift north and eastwards and the juveniles are found in the Barents Sea and in Svalbard waters (Godø and Haug, *op cit.*). The more precise location and timing of spawning is not well understood. The drift migration of the spawning products are only known indirectly by means of juvenile distribution. It is not known to what extent the annual research surveys sample the total nursery area. In fact, age composition in catches from the spawning ground have not shown the expected decline for those year-classes that were classified as weak at the juvenile stage (Anon, 1996a). This has led fishermen and their organisations to claim that the juveniles have just moved to other areas, and that the management actions are weakly based.

Both the timing of spawning and the subsequent bathymetric distribution of eggs and larvae must, together with variations in ocean currents, have a major impact on the supply of recruits to different parts of the nursery area. Understanding the drift phase may therefore be a key to understanding the recruitment process. Direct analyses of the drift phase are at present not feasible, since there is no data available on the egg and larvae stage. Therefore, in this paper a series of 14 annual surveys was analysed in order to reveal the dynamics of the decline in juvenile abundance. The objective was to describe how the distribution and composition of recruits varied between years. In particular the paper evaluates if the general decline in juvenile abundance in the study area was associated with changes in distribution in such a way that trends in abundance may not be reflected in the surveys. Possible causes to distribution changes are also briefly discussed.

2. MATERIAL AND METHODS

2.1 The survey series

Data were sampled on annual bottom trawl surveys designed for estimating shrimp biomass in the Barents Sea and Svalbard area. Available time series was from 1983 to 1996. Each year two surveys were conducted, one in the central and western Barents Sea and another from south of Bear Island and northwards along the western shelf and inside fjords of Svalbard. Each year the Barents Sea surveys were conducted during three weeks within the period 20.April - 25.May. From 1983-91, the Svalbard surveys were run within the period 15.July - 30.August, and in 1992 it was extended until mid-September. From 1993 onwards, the Svalbard surveys were made between 20.May and 20.June, as an extension of the Barents Sea surveys.

For both surveys a strata system was defined and trawls were allocated according to a stratified random design. The strata definitions were detailed and partly based on prior knowledge of shrimp biology (Aschan and Sunnanå, 1997). In order to simplify presentation and focus on main patterns, a new strata system was defined a posteriori for the whole area covered by the two surveys. Figure 2.1 shows the areas that are used in the paper. When combining data within areas, each area was subdivided into consecutive 100 m depth intervals. The Barents Sea surveys mainly sampled area 1 and 2. The Svalbard surveys mainly covered area 4 and to some extent area 3, while area 5 was only occasionally sampled. There is no comparable time series of Greenland halibut from the slope and basins east and north-east of Svalbard. Gundersen *et al.* (1997) reviewed the significans of these areas.

2.2 Sampling at sea

Campellen 1800 shrimp trawl was used on all cruises. A ground gear with rubber bobbins was used up to and including 1988. From 1989 onwards the Rockhopper ground gear (Engås and Godø, 1989) was used. Research vessel and standard duration of hauls have also varied. Trawl, equipment and procedures used in different periods are summarised in Table 2.1. More detailed information on gear and design were given by Aschan and Sunnanå (1997). No corrections were applied for the changes in trawl equipment and procedures throughout the time series.

From each trawl catch the catch of individual species in terms of weight and numbers was recorded. Length-frequency distributions of Greenland halibut were obtained, either by measuring the entire catch or a random subsample. Total length was measured to nearest 1 cm below. On some surveys individual length, weight, sex and maturity stage were recorded from selected specimens.

2.3 Abundance estimation

Prior to further analyses, all catches were converted to catch rates, given as number and weight per 1 nautical mile (nm) trawling distance. Total number of fish of length i at trawl station j was estimated as:

$$n_{ij} = m_{ij} \cdot \frac{C_j}{M_j} \cdot K \quad (1)$$

where m_{ij} is number of fish of length i in length sample from station j , M_j is total number of fish in length sample from station j , C_j is catch rate at station j in total number per 1 nm, and K is a factor that reduces the influence of small length samples from large catches. Sometimes, only a small, but random, fraction of the catch was sorted. This small fraction would normally contain a small length sample of Greenland halibut. If this small sample should be multiplied e.g. by 20 to represent the whole catch, the length distribution would become erratic and unrealistic. In order to reduce the influence of such "outliers" on accumulated distributions, factor K was defined as follows:

$$\begin{aligned} \text{If } M_j < 30 \text{ and } \frac{C_j}{M_j} > 3 \text{ then} & \quad K = 3 \cdot \frac{M_j}{C_j} \\ \text{If } 30 \leq M_j < 100 \text{ and } \frac{C_j}{M_j} > 10 \text{ then} & \quad K = 10 \cdot \frac{M_j}{C_j} \\ \text{Otherwise:} & \quad K = 1 \end{aligned}$$

Total number of Greenland halibut of length i within a stratum is given by:

$$N_i = \frac{1}{s} \cdot \sum_{j=1}^s n_{ij} \cdot \frac{A}{a} \cdot f \quad (2)$$

where s is number of trawl stations in the stratum, A is the area of the stratum measured in square nm, a is the area sampled by a 1 nm haul, and f is the catch efficiency of the trawl. Stations where Greenland halibut were caught but no length distributions recorded were excluded. The width sampled by the trawl was set constant to 25m, i.e. less than the door spread and more than the wing spread. Efficiency was set to unity inside this sampling width and zero outside.

For each area and year, the youngest age (I-group) was generally easily distinguished as a more or less completely separated mode in the length-frequency distribution. The total number of I-group Greenland halibut in a stratum was calculated as:

$$N^I = \sum_{i=\min}^{\max} N_i \quad (3)$$

where \min is the smallest length observed in a given year and stratum, and \max is the one with lowest observed frequency between 14 and 19 cm.

For abundance estimation of I-group Greenland halibut, each area in Figure 2.1 were divided in 3 depth strata delimited by the 200, 300, 400, and 500 m isobaths. Values of abundance in each area are the sums across these depth strata.

3. RESULTS

3.1 General population structure

The length of Greenland halibut caught in all surveys combined ranged from 5 to 100 cm. The smaller individuals (<30 cm) were mostly found down to 500 m, whereas larger fish were found down to more than 1000 m (Figure 3.1). The smaller fish were strongly associated with Svalbard waters and were nearly absent from the "Southern Barents Sea". Larger fish were caught in all areas. At greater depths Greenland halibut was slightly larger in southern Barents Sea than along the western slope of Spitsbergen and Bear Island. The fraction of large fish increased therefor with depth and from north to south in the survey area.

The overall length composition of males and females were similar, with two distinct modes attributable to age-groups I and II (Figure 3.2). Sex composition was approximately 50/50 for intermediate fish lengths, and above 50 cm the proportion of females increased sharply. Fish less than 25 cm were apparently dominated by males. However, for these small fishes determination of sex was only made in 1996. The male dominance of recruits may therefor not be representative of the whole time series (see chap. 3.3).

3.2 Spatial and temporal variation in recruitment

I-group Greenland halibut were recorded from 100 to 600 m depth with highest catch rates between 250 and 400 m (Figure 3.3). Within this main range, highest catch rates were an order of magnitude higher than in shallower or deeper regions. The distribution was a bit deeper and more concentrated in the "Hopen Deep" than west and north of Spitsbergen. Highest catch rates were found approximately 50 m deeper in the "Hopen Deep".

There were large interannual variation in I-group abundance within each area (Figure 3.4). Although catch rates were high in "Spitsbergen North", this area contributed very little to total abundance, due to the small size of the area. The main nursery areas distinguished in this survey series were the "Hopen Deep" and the "Spitsbergen West". Considering these two areas together, a marked reduction in I-group abundance appeared in 1990, and abundance has remained low in the rest of the time period. A slight though significant increase in I-group abundance was recorded in "Spitsbergen West" in 1996. Apparently a major recruitment failure has occurred that involves each of the yearclasses 1989-95.

Preceding this apparent recruitment failure there were significant interannual variability both with respect to total I-group abundance and to the distribution of recruits (Figure 3.4.a). In these years, estimated abundance varied by a factor of 10 in "Spitsbergen West" and by 30 in the "Hopen Deep". In each of the years 1983-1989, abundance in "Spitsbergen West" was significantly higher than in any of the subsequent years. Only in three of the years 1983-1989 were I-group abundance in "the Hopen Deep" significantly higher than in 1990-1996. Still, in both areas I-group Greenland halibut occurred more frequently in the trawls throughout the first seven years (Figure 3.4.c).

The year-effect on I-group abundance differed between the areas. While peak abundance was recorded in 1984 in "Spitsbergen West", only small numbers were found in the "Hopen Deep". In 1988 peak abundance was recorded in both areas, but the peak was much higher in the "Hopen Deep". Figure 3.4.b shows logarithmic values of abundance for each area, giving better resolution of the dynamics at low population sizes. The recruits disappeared first from

the “Southern Barents Sea” in 1990, then from the “Hopen Deep” in 1992, and finally from “Spitsbergen West” in 1994. In the latest two years they reappeared, first in “Spitsbergen West” and then in the “Hopen Deep”. It appears that after the major reduction in 1990, the distribution of I-group was gradually shifted northwards. Distribution of I-group Greenland halibut are shown for selected years in Figure 3.5.a-d.

Observations from the northernmost area were too few to fully evaluate whether the disappearance from the southern areas was associated with an increased abundance north of Svalbard. I-group catches in “Spitsbergen North” were largely concentrated in the 250-500 m deep Hinlopen Trench, which extends from the continental slope of the Arctic Ocean and south-eastwards into the strait separating the two largest islands of the Svalbard archipelago (Figure 2.1). This trench was sampled with 28 trawls in total during the years 1984, 86, 87, 92, 94, and 96. I-group Greenland halibut was caught in 48% of the trawls. There were no significant difference in either occurrence or mean catch rate between the three first and the three last years. However, in the first three years catch rates were much higher in “Spitsbergen West” than in “Spitsbergen North” ($p < 0.01$). In 92 and 94 it was the other way around, with significantly higher catch rates in the northern area. This was also true when comparing II-group in 1996. Thus, the 91, 93 and 94 year-classes may have been more north-easterly distributed than the 83, 85 and 86 year-classes. In 1996 catch rates of I-group were again higher in the western area.

3.3 Length and sex of recruits

Length measurements of I-group Greenland halibut were made at 299 trawl stations, resulting in 2298 observations. At individual stations with 10 or more, mean length varied from 10.1 to 16.8 cm. There were also substantial and significant changes in mean length during the time period (Figure 3.6.a). In the 80's, mean length decreased until a minimum in 1986, and increased afterwards to a maximum in 1989-90. The difference between these min and max is 3.3 cm ($p < 0.01$), all areas combined. In the period 1991-96, mean length was 1 cm less than in the period 1983-90 ($p < 0.01$). In the latest period weighed average of the time of capture (week number of the year) was one week earlier than in the first period.

To compensate for differences in date of capture, a generalised linear model (McCullagh and Nelder, 1989) was fitted to mean lengths from each trawl. Only trawls with at least four I-group length-measurements were used. In addition to the intercept the model included week number as a covariate and factors for year, area and depth interval. There were initially 14 levels for the year factor, two for area (only “the Hopen Deep” and “Spitsbergen West” included), and four for depth intervals 200-299, 300-399, 400-499, and 500-599 m. Without interaction terms the model accounted for 50% of the variance in the data. Main effects of areas and depth intervals were not significant (F-tests), and years could be combined in four groups with no significant within group difference. The model described the same general trend as above, with increasing size from 1986 to 1990, and comparatively small size thereafter (Figure 3.6.b).

As stated above (Chap. 3.1), there was a clear male dominance among the I-group recruits in 1996, but there was no time series available to see how this relates to year class size. Therefore larger fish had to be used in order to find out whether sex distribution varies between areas and years. Length range 30-50cm corresponds primarily to age 3-5 (Haug and Gulliksen, 1982). Within this range, sex distribution was approximately 50-50 (Figure 3.2). However, in

all areas, the percentage of females within this length range was lower in 1996 than in any preceding years (Figure 3.7). Also in 1995 males were clearly dominating among 3-5 years old Greenland halibut in some areas. Age 3-5 in 1995-96 correspond with year-classes 90-93, i.e. after the apparent recruitment failure. The proportion of females in 1996, all areas combined, was significantly lower than in any preceding years ($p < 0.001$). The high proportion of females in 1992 may be an artefact due to non-trained personnel on that cruise.

4. DISCUSSION

4.1 Recruitment variations

The main pattern of variation in I-group abundance during the period 1983-96 was a change from high abundance in the first half of the period, to low abundance in the second half. Following the reduced abundance, a northerly shift in distribution was observed. From 1990 onwards, the I-group disappeared from successively more areas, starting with the "Southern Barents Sea", continuing with the "Hopen Deep", and ending with the "Spitsbergen West" in 1994. In the last to years the recruits reappeared, first in "Spitsbergen West" and then also in the "Hopen Deep".

The distribution and abundance of I-group were comparatively similar in the first and last year of the period. Both of these years seemed to be within a period of increase, and abundance in the different areas were similar. It is tempting to consider the variation within the time period as cyclical. The available time series covers only one period of this cycle, thus obstructing inferences on the mechanisms involved. However, it may seem as if the southern end of the distribution area pulses southwards and northwards, making the occurrence of recruits in some areas to a periodic event. The study period may thus be divided into a southerly distribution period in 1984-89 and a northerly period in 1992-95. Comparing results from previous expeditions, Haug and Gulliksen (1982) also found that Greenland halibut may only be present in West-Spitsbergen waters for some periods, while in other periods they may be absent.

In the International 0-group surveys, pelagic stages of Greenland halibut are recorded both in the Barents Sea and along the West-Spitsbergen slope (Annual ICES reports, e.g. ANON, 1996b). Within the period treated in this paper, the 0-group distribution was in accordance with the subsequent distribution as I-group. Since 1970, 0-group was recorded outside north-western Spitsbergen in every year. In the Barents Sea (east of 25°E), occurrences of 0-group were more variable. In this area they were only recorded in some periods, especially in the 80's and in 1995-96. This is in accordance with our results both with respect to periods of northerly and southerly distribution and with respect to the much higher variability of I-group abundance in "the Hopen Deep" than in "Spitsbergen West".

The north-south dynamics of I-group abundance appeared only in the log-transformed abundance plot and apply to the period of low abundance that followed after the major reductions in 1989-90. It is not clear if the major reductions were caused by the same factors as those that caused the subsequent "final" reductions from few to no observations of recruits in southern and western areas. However, throughout the period studied the distribution of recruits varied considerably within the survey area. Such variations should also be expected to occur in other areas as well.

4.2 Some possible causes

The North-East Atlantic Current with which spawning products of Greenland halibut are transported makes three major branches on its way northward. The overall pattern in this current system were described by Blindheim (1989) and Loeng (1989), and a review was also given by Dragesund and Gjørseter (1988). One branch of Atlantic water enters into the Barents Sea south of Bear Island, while the other continues northwards as the Spitsbergen Current. The waters on the west side of the Spitsbergen Current leaves off into the Norwegian Sea directing towards Greenland. The remaining current follow the continental slope north of Spitsbergen. The relative volume transport in each branch depends on the weather conditions and is highly variable (Ådlandsvik and Loeng, 1991). Modelling of the drift of cod larvae showed considerable interannual variability in distribution of larvae between the Barents Sea and West-Spitsbergen (Ådlandsvik and Sundby, 1994). Such variability should also be expected for Greenland halibut, although uncertainties regarding behaviour of eggs and larvae complicates the modelling approach.

Along western Spitsbergen the distribution of 0-group was some years close to the coast (e.g. 88-92 and 95-96), other years extending west of 5°E (e.g. 78-87 and 93-94). Such westerly distributions probably result in some of the 3-8 cm long 0-groups being carried further away from the coast with the Northern Norwegian Sea circulation. The extent of this "leakage" and the fate of the individuals thus transported is unknown, but should also be expected to vary between years.

Some recruits will end their drift migration and settle in the slope and on coastal banks along the west coast of Spitsbergen (Haug et al., 1989). Others may continue eastwards, north of the Svalbard archipelago. These may in turn spread out along the deep trenches of the northern Barents Sea and along the slope of the Arctic Ocean. Only sporadic sampling has been made in these areas and no time series is available that may be compared with the one in this paper. However, Gundersen *et al.* (1997) shows that areas east of Svalbard and around Franz Josefs Land may be important nursery areas for Greenland halibut, at least in periods.

Mean length of recruits varied extensively throughout the time series, closely resembling that of young cod (Anon., 1997) and similar to the temperature variation in the Barents Sea with a minimum in 1986 and a maximum in 1990 (Sætre, 1996). After 1990 mean length decreased although temperature was still above average. However, it is difficult to separate effects of temperature and currents in these areas. If post-larvae were distributed through and out of the survey area, the mean length may not be adequately sampled. The oldest individuals would then have been underrepresented and only those hatched late in the season would still have been in the area. This may explain the relatively small size of I-group after 1990.

Greenland halibut may thus be transported along three main routes corresponding to the three branches of the North Atlantic Current. The relative importance of each route, and where on the routes most of the juveniles will settle, may vary between years. Variation in the current transport is just one reason for that. Other reasons include variations in where spawning is most intense, and in differences between areas of survival of the young fish. Kovtsova *et al.* (1987) showed that the latitudinal distribution of spawners varied between years, and Godø and Haug (1987) noted the possible impact of predation from cod and of bycatch in the fishery for shrimp. During the period 1984-1995, estimated consumption of Greenland halibut increased from near zero in 1984-1990 to a few thousand tonnes in each of the years 1991-1995 (Anon, 1997). However, the data on predation of Greenland halibut by cod are very limited.

Of 80 000 cod stomachs examined, 1-3 years old Greenland halibut were found in just 27 of them (Mehl, Institute of Marine Research, pers.com.).

The question of interest for the management of Northeast Atlantic Greenland halibut is if low juvenile abundance within the survey area indicates poor recruitment, or just that they are distributed outside the area to a greater extent than before. It is not possible to give a definitive answer to this question based on the time series of data that is available at present. However, it seems clear that currents, temperature gradients and other physical factors that may determine the drift migration, are important for understanding the recruitment variations of Greenland halibut.

4.3 Conclusions

The distribution of juvenile Greenland halibut varied interannually and apparently with a periodical component. The variations probably extends beyond the study area and may well be caused by variations in ocean currents. The main reduction in 0 and I-group abundance that appeared in the surveys in the late 80's may be caused by the recruits being distributed outside the survey area. If so, the supposition of poor recruitment may not be true. However, at present there is no direct evidence for this hypothesis. Further research should be directed towards mapping the populations total distribution by further genetical comparisons and by extending the survey area. Emphasis should also be put on establishing more knowledge of time and place of spawning, behaviour of eggs and larvae and subsequent modelling of the drift phase.

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Table 2.1. Ship, trawl equipment and procedures used in each time period and survey area.

Survey area/period	Barents Sea 1983-1991 Svalbard 1983-1990	Svalbard 1991	Barents Sea and Svalbard 1992	Barents Sea and Svalbard 1993-1996
Ship	M/S Michael Sars	M/T Anny Kræmer	M/T Gargia	R/V Jan Mayen
Length (Loa)	48m	51m	47m	64m
Trawl	Campelen 1800	Campelen 1800	Campelen 1800	Campelen 1800
Ground gear	Rubber bobbins (1983-1988) Rockhopper ¹ (1989-1996)	Rockhopper ¹	Rockhopper ¹	Rockhopper ¹
Mesh size				
Wings	80 mm	80 mm	80 mm	80 mm
Belly and bag	60 and 40 mm	60 and 40 mm	60 and 40 mm	60 and 40 mm
Cod-end lining	10 mm (4 m length)	10 mm (4 m length)	10 mm (4 m length)	20 mm (8 m length)
Doors	Vaco combination doors, 1500 kg	Steinshamn doors, 2050 kg	Steinshamn doors, 2050 kg	Steinshamn doors, 2050 kg
Sweep length	40 m	40 m	40 m	40 m
Vertical opening ²	Approx. 5 m	Approx. 5 m	Approx. 5 m	Approx. 5 m
Duration of hauls ³	60 min. (1983-1989) 30 min. (1990-1991)	30 min.	30 min.	20 min.
Towing speed	3,0 knots (1,5 m s ⁻¹)	3,0 knots (1,5 m s ⁻¹)	3,0 knots (1,5 m s ⁻¹)	3,0 knots (1,5 m s ⁻¹)

¹ Engås and Godø, 1989

² Measured with SCANMAR wireless gear control system.

³ Standard duration was adjusted according to the size of the bottom area suitable for trawling.

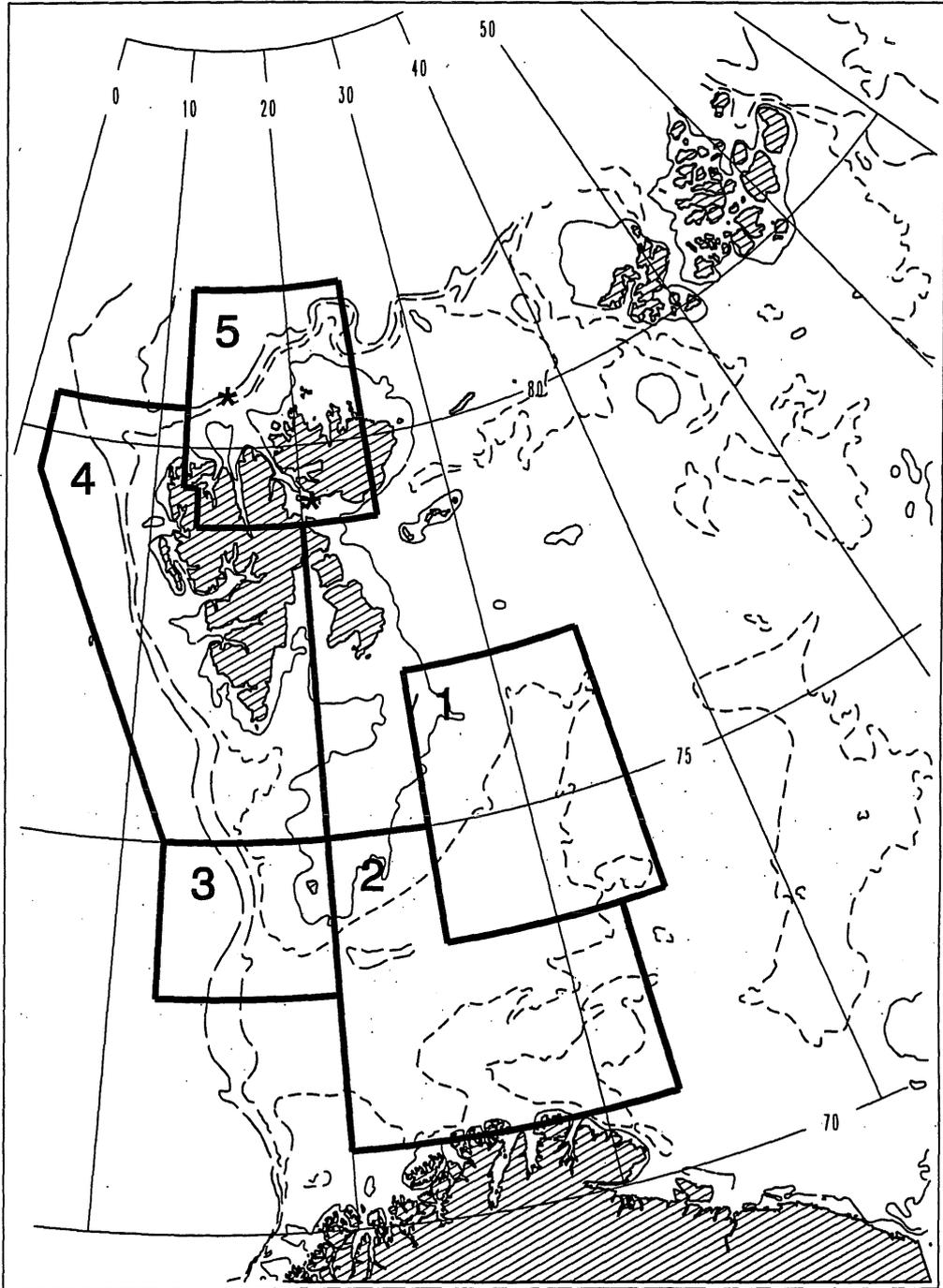


Figure 2.1. Bathymetric map of the Barents Sea and Svalbard area with the 100, 300, 500, and 1000 m isobaths. Areas referred to in the text are: 1: The Hopen Deep; 2: Southern Barents Sea; 3: Bear Island slope; 4: Spitsbergen west; 5: Spitsbergen north. The Hinlopen Trench is marked with asterixes.

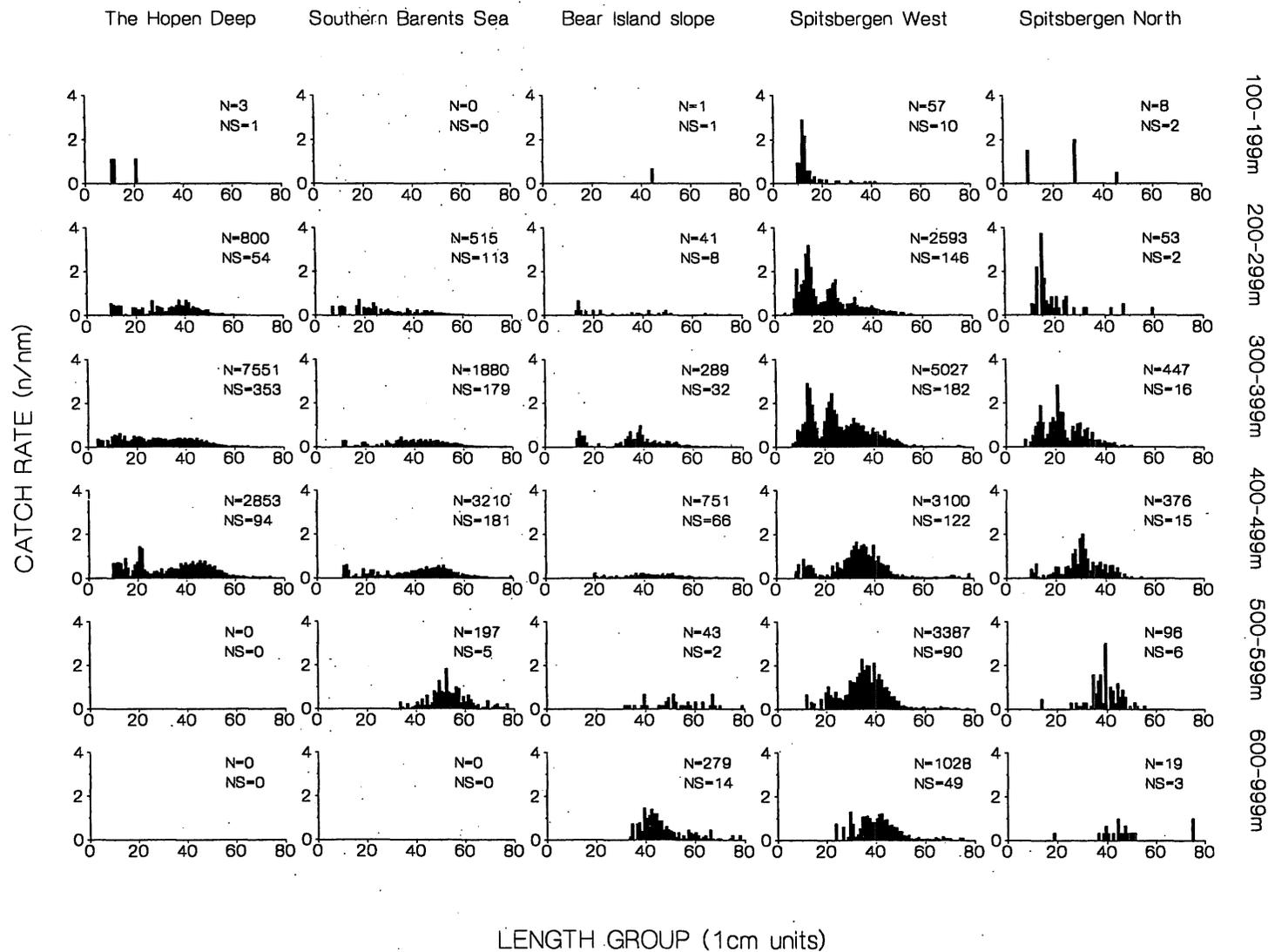


Figure 3.1. Length frequency composition of Greenland halibut from each area and consecutive 100 m depth zones. Data from all years combined. N: Number of fish measured; NS: Number of stations where length frequency distributions of Greenland halibut were recorded.

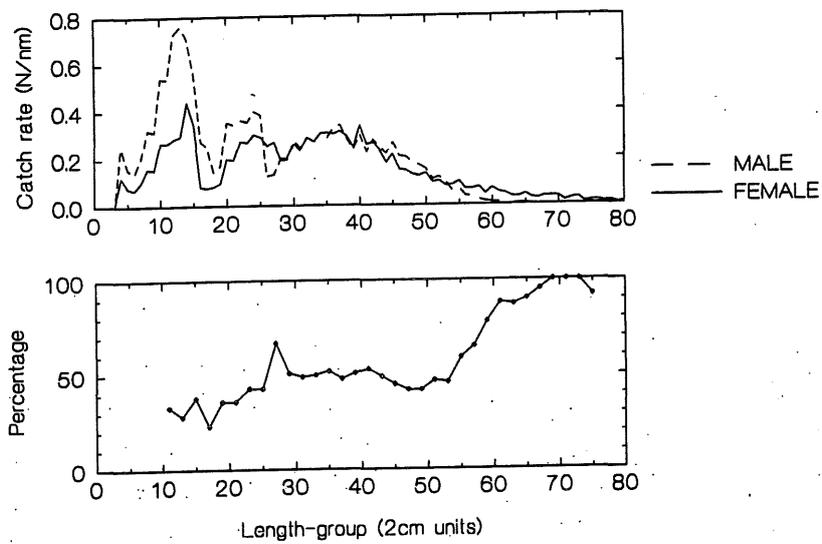


Figure 3.2. Length frequency composition of male and female Greenland halibut (upper), and percentage of females in each length group (lower). Data from all samples where sex were determined. Each percentage values are based on 30 or more observations.

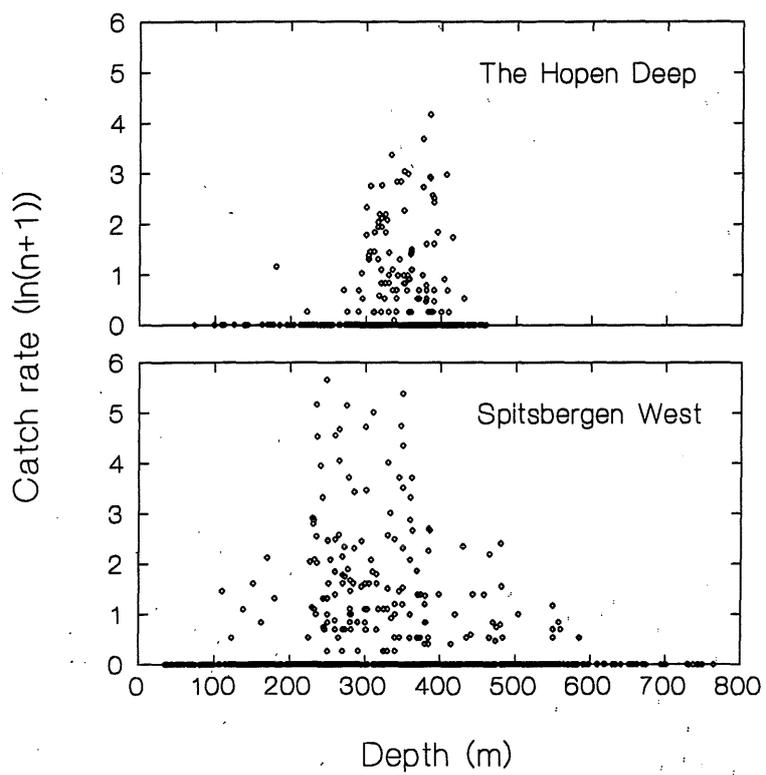


Figure 3.3. Logarithmic catch rates of I-group Greenland halibut versus trawling depth. Each symbol represents a bottom trawl. Data from all years combined.

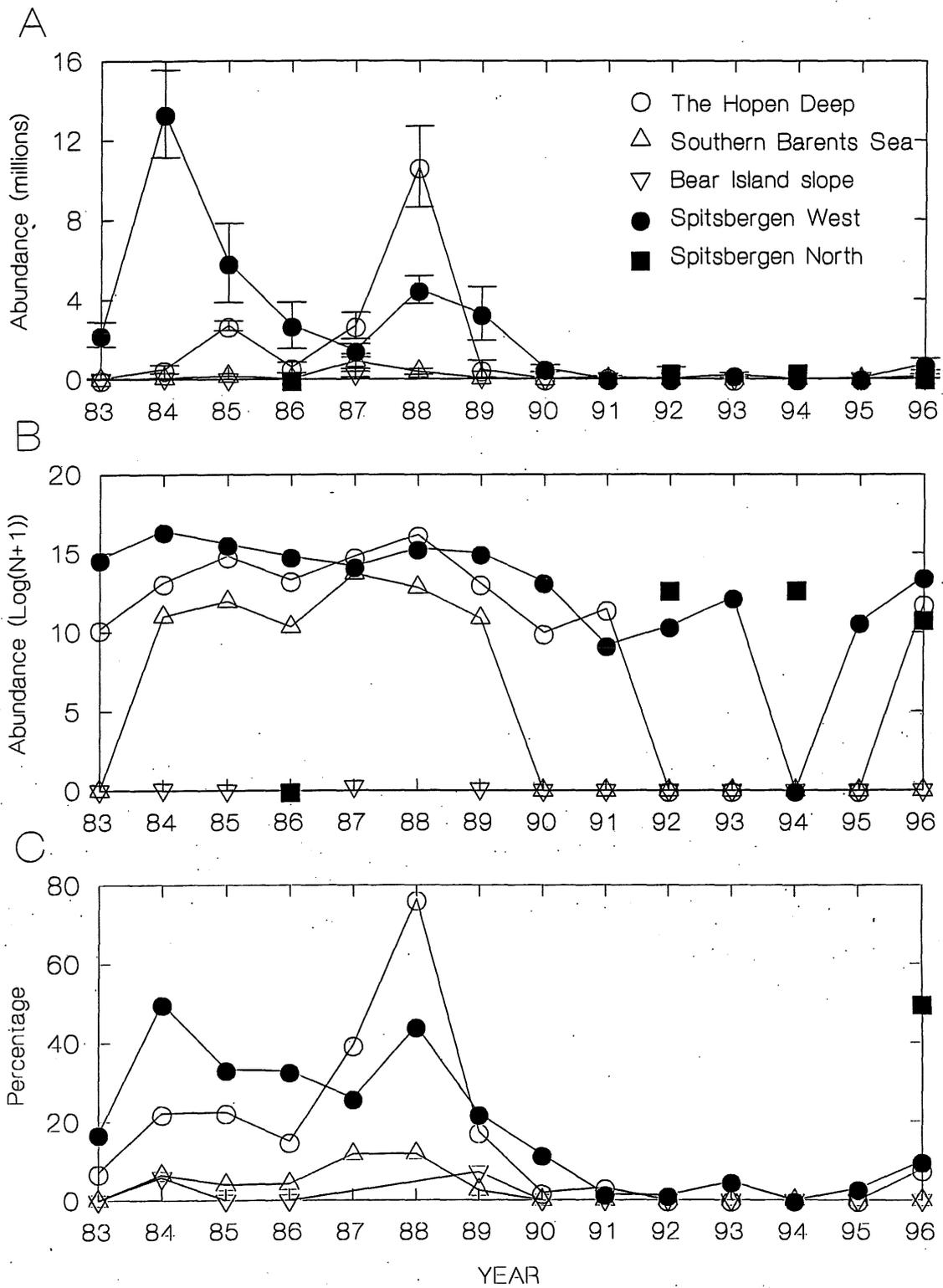


Figure 3.4. A: Annual I-group abundance indices of Greenland halibut in each area. Mean values and +/- two standard errors of the mean. Only area-year combinations with five or more bottom trawls. B: Log-transformed values from A. C: Percentage of hauls in each combination of area and year that contained I-group Greenland halibut. Only percentage values based on 10 or more observations included.

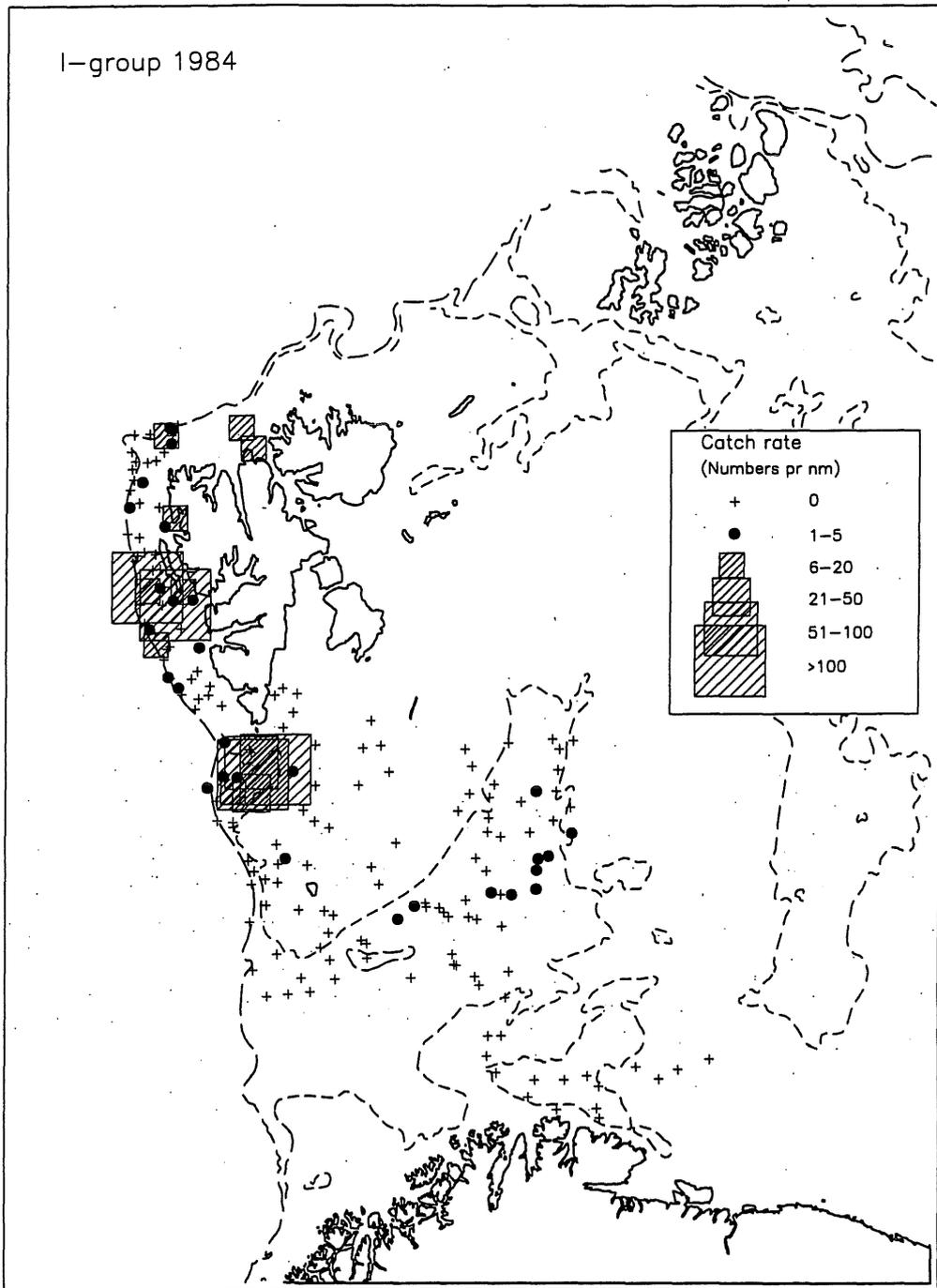
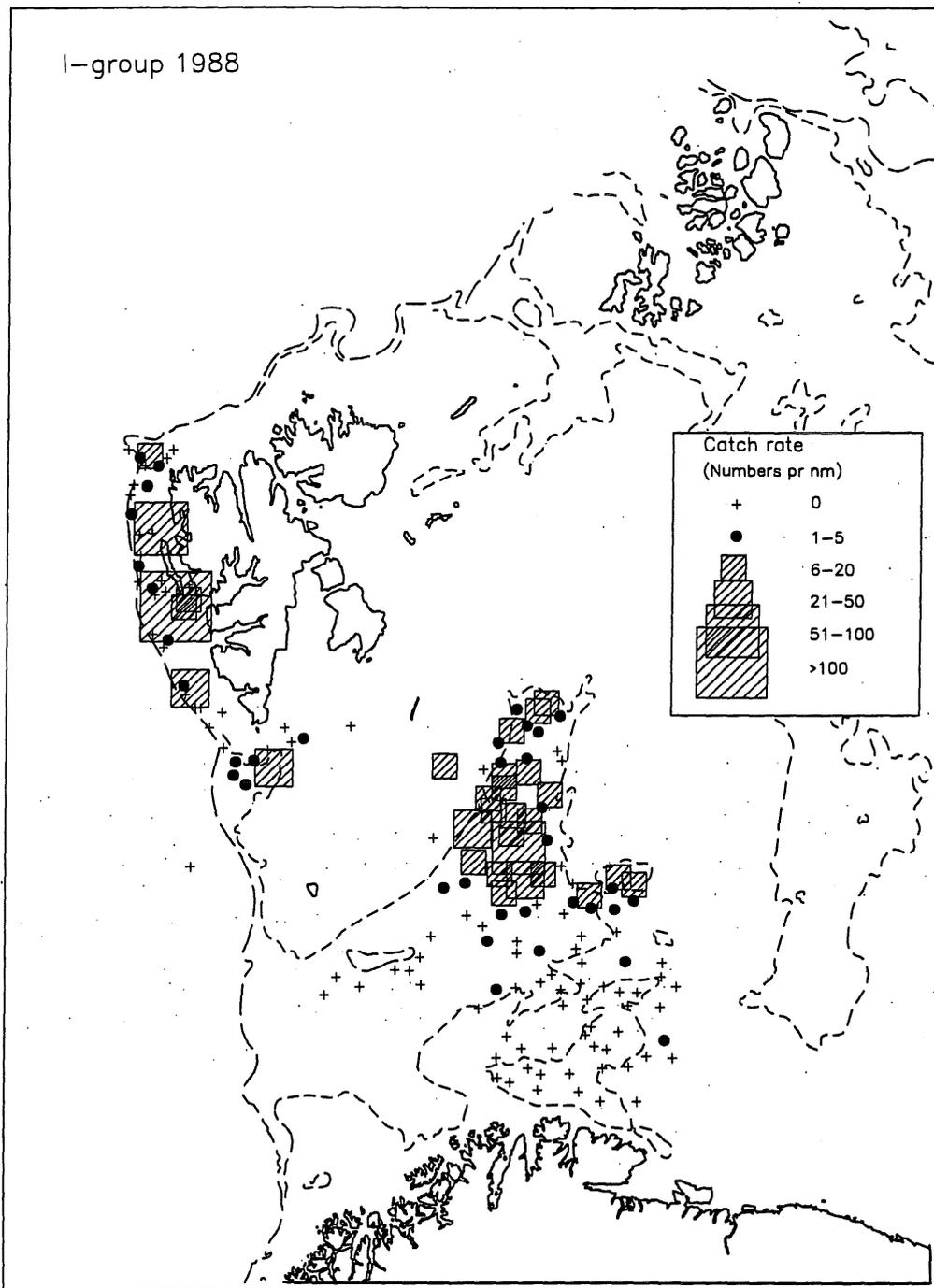


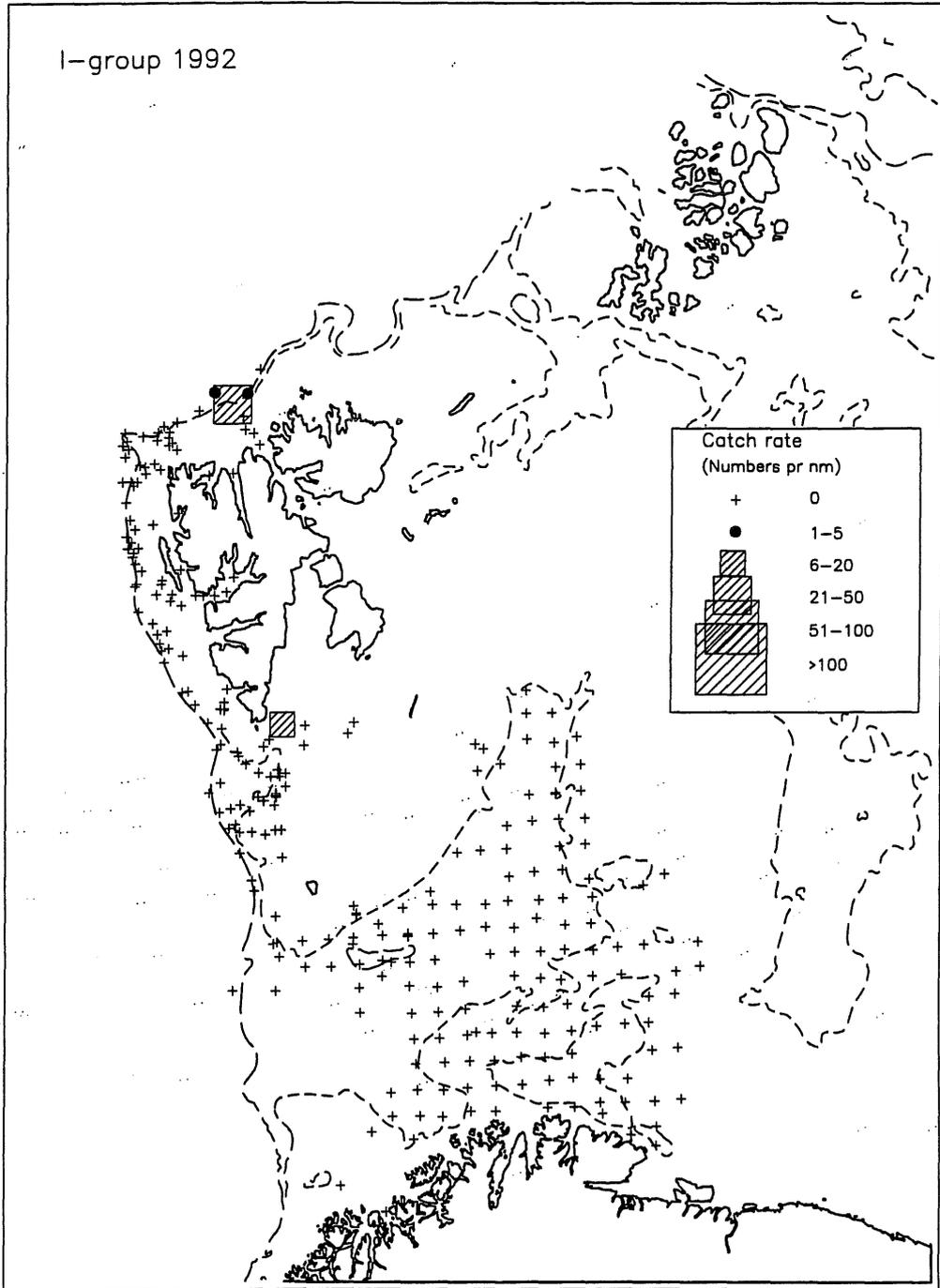
Figure 3.5.a-d. Distribution of I-group Greenland halibut in selected years. Each symbol represents one bottom trawl. The 300 and 500 m isobaths are given.

I-group 1988

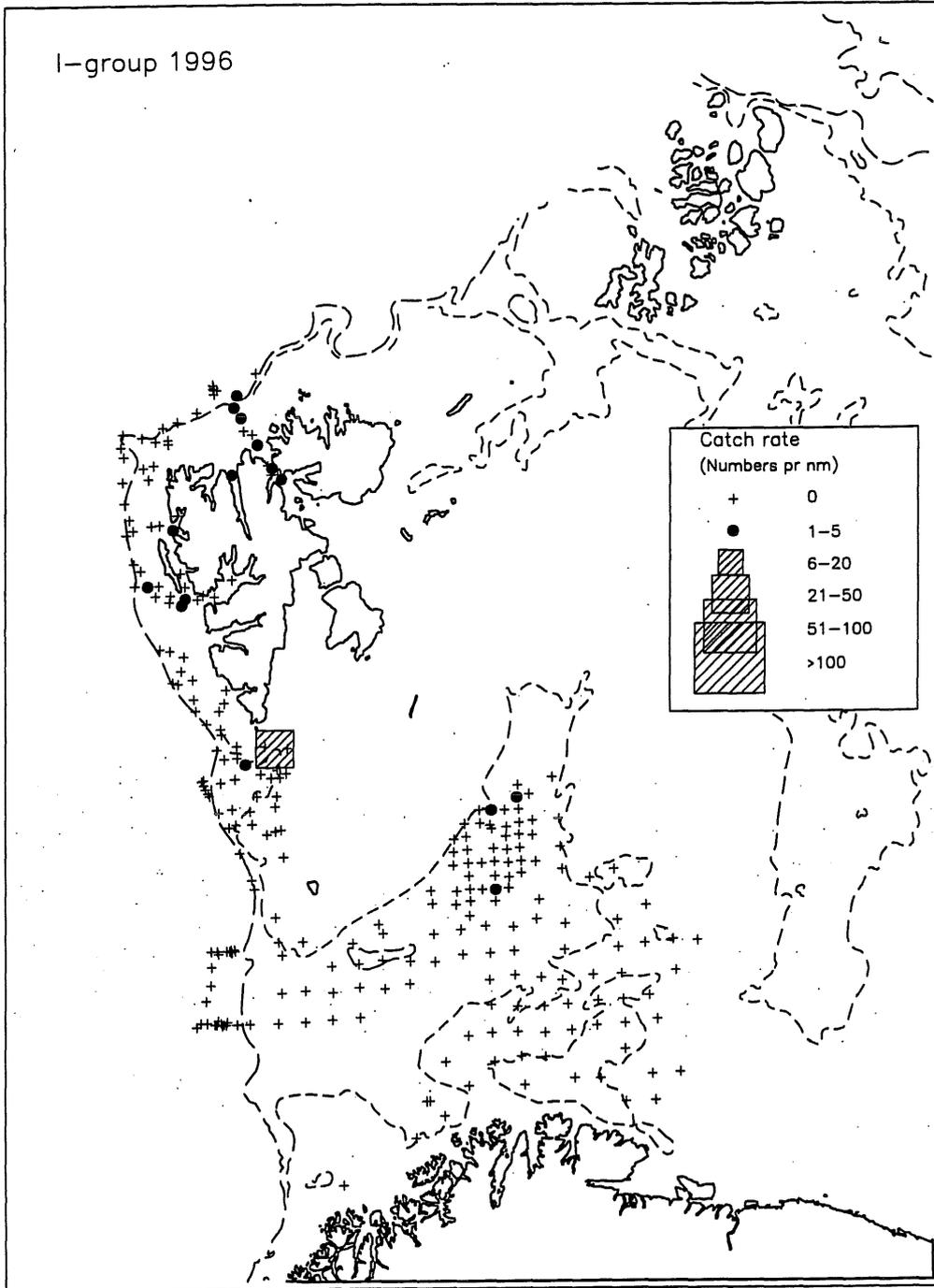


3.56

I-group 1992

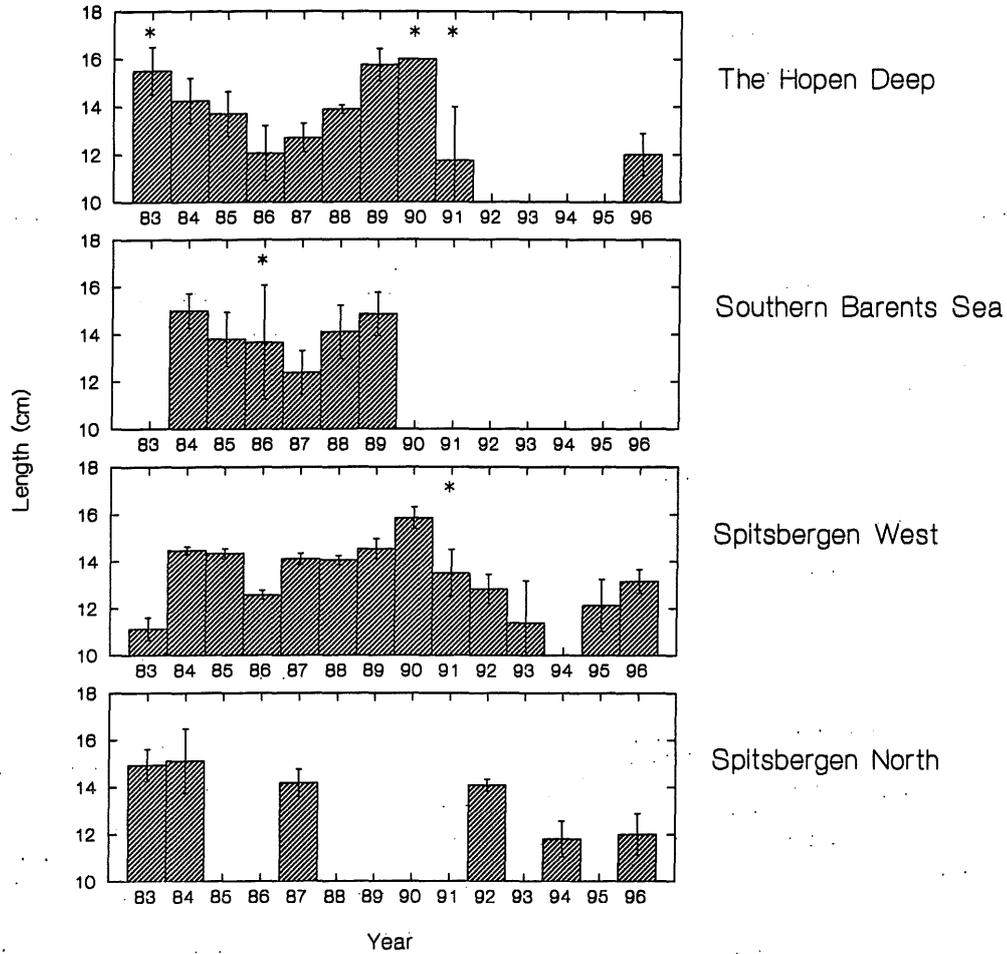


3.5.c



3.5.d

A



B

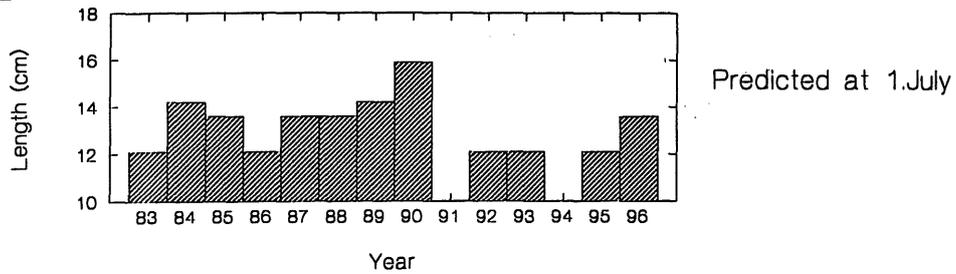


Figure 3.6. a: Mean length of I-group Greenland halibut in different areas and years. Vertical lines on top of each bar indicate \pm two standard errors of the mean. Means based on less than 6 observations are marked with an asterisk. b: Estimated length at 1. July each year for "the Hopen Deep" and "Spitsbergen West" combined. Trawls with less than four observed lengths were excluded from the model.

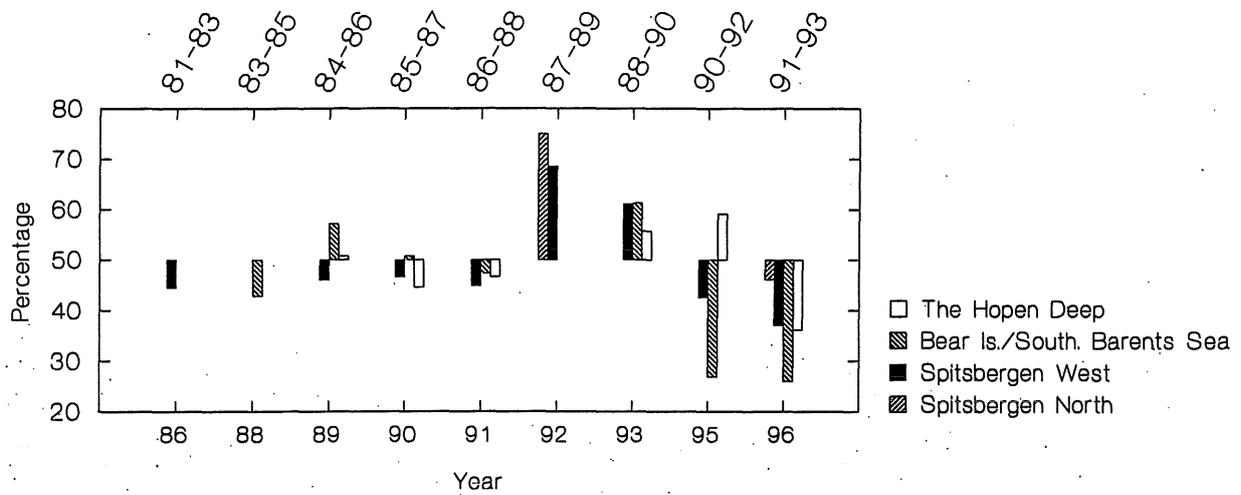


Figure 3.7. Percentage of females within length range 30-50 cm in each area and year. Figures above the bars indicate the yearclasses involved. Each percentage value based on 30 or more observations.