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Variation in Population Structure of Northeast Arctic Greenland Halibut (*Reinhardtius hippoglossoides*) Based on Data from Norwegian Surveys in the Period 1992-2000

by

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Abstract

The variation in population structure of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) is analysed using data from a three different surveys, trawl, longline and gillnet, in the slope area of the western Barents Sea in the period 1992 - 2000. The design of the longline and gillnet survey had limitations in that they were set to simulate the commercial fisheries, but the vessels were forced to cover the most important part of the slope area. Greenland halibut was the dominant species both in numbers and weight and was usually caught in the range of 5–15 years old, but the catch was dominated by ages 6–12 and fish older than age 8 consisted primarily of females. The data showed differences in sex composition and age composition both by area and by depth, and catches from trawl showed the most evident pattern.

Introduction

Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) is distributed in the Arctic and boreal waters in the North Atlantic and in the North Pacific (Fedorov, 1971; Godø and Haug, 1989; Bowering and Brodie, 1995; Bowering and Nedreaas, 2000). In the northeastern Atlantic the distribution is more or less continuous along the continental slope from the Faeroe Islands and Shetland to north of Spitsbergen (Whitehead *et al.*, 1986; Godø and Haug, 1989), with the highest concentrations from 500 to 800 m depth between Norway and Bear Island, which is also regarded as the main spawning area (Godø and Haug, 1987; Albert *et al.*, 2001b). Peak spawning occurs in December in the main spawning area, but also in nearby localities during summer (Albert *et al.*, 2001b). Eggs and larvae drift northwards and the juveniles are distributed in the deeper parts of the Barents Sea and to the north and east of Spitsbergen, to the waters around Franz Josef Land (Godø and Haug, 1987; 1989; Albert *et al.*, 2001a).

Before the mid 1960's the fishery for Northeast Arctic Greenland halibut was mainly a coastal longline fishery off the coasts of eastern Finnmark and Vesterålen in Norway. Following the introduction of international trawlers in the fishery in the mid 1960's, the total landings increased from a level of about 3,000 t to about 80,000 t in the early 1970's. The total landings decreased steadily to a level of about 20,000 t during the early 1980,s (ICES, 2001). The commercial trawl fishery was concentrated in the main distribution area for the adult stock. Based on the regular 0-group survey in the Barents Sea a drop in the year-class indices were observed during the late 1980's and beginning of the 1990's, and also a historic low spawning stock biomass was detected in the same period (Hysten and Nedreaas, 1995; Smirnov, 1995). There was also a reduction in the commercial catch per unit of effort (CPUE) and this lead to strong regulations from 1992, including a total fishing ban for Greenland halibut north of 71°30N. South of this limit the regulation rules allowed only a limited longline and gillnet fishery, by vessels smaller than 28 m, to be directed for Greenland halibut. Trawl catches were limited to by-catch only.

When the catches from the commercial fishery became reduced after 1992 it turned out to be very important to increase the research effort in order to confirm or invalidate the reduction in recruitment and the decrease in spawning stock. In order to continue the already established time series of commercial trawl CPUE data, and to improve biological sampling as a basis for stock assessment, commercial fishing vessels were contracted. The vessels should perform commercial-scale fishing, but restricted to certain time periods and areas. The gears used were trawl, longlines and gillnets. In 1994 a scientific bottom trawl survey also was started in the slope area from 68°N to 80°N.

Based on a stratified trawl survey in the Svalbard area (Godø and Haug, 1987) documented that depth distribution of Greenland halibut was size dependent, i.e. higher proportions of large fish were found in deeper strata. The same investigation concluded also that north of 76°N the stock consisted of a relatively higher proportion of small fish. The structure of the catch, i.e. length, age and sex composition changes with different gear. Longline and gillnet catch larger fish than trawl (Nedreaas *et al.*, 1996). The present study therefore used data from these gear types and the objective was to describe how the population structure of the Greenland halibut stock varied between years, areas and between gears along the slope area between Norway and Svalbard in the period 1992-2000.

Material and Methods

Surveys and sampling

Data were collected during several cruises between Norway and Svalbard in autumn in the period 1992-2000 (Table 1, Fig. 1). Some of the trawl surveys were designed as a stratified bottom trawl survey with Greenland halibut as target species, but all the longline and gillnet surveys were set up in a way attempting to mimic the commercial Greenland halibut fishery. Commercial fishing vessels were contracted to conduct regular fishing operations, but there were set some restrictions in the area where they were able to operate, i.e. between 70°N and 76°N. The scientific bottom trawl survey operated in a wider area, 68°N - 80°N, with fixed positions of the hauls with a depth range of 400 to 1500 m. Due to the expectation of low catches deeper than 1000 m very few hauls were carried out at these depths.

The trawlers used standard cod bottom trawls (Alfredo 5) with 135 mm mesh width (inside stretched mesh), and a 60 mm inner lining in the codend. The vertical opening of the trawl was about 4 m and the distance between the doors averaged to 170-175 m. The trawls were equipped with rock-hopper gear. The length of the ground gear was approx. 110 m and the lengths of the sweeps were 130-140 m. The warp length under towing was 2.5-2.8 times the bottom depth depending on current and bottom conditions. Towing speed was 4 knots and the towing duration in the "commercial" experiments were normally 4-5 hours. Towing duration in the bottom trawl survey was usually one hour.

The longliners used in most cases Mustad EZ-baiter hooks no. 12 with hook spacing of 1.4 m. During the time period each setting varied between 3000 and 6000 hooks. The hooks were baited mechanically (Mustad Autoline System) mostly with sequences of squid and mackerel, but also other bait types were used occasionally. The soak time varied between 6 and 24 hours. Each setting was treated as one separate station.

The gillnets were made of monofilament with a varying mesh size from 70 to 110 mm (bar-length, i.e. 140-220 mm stretched mesh), but most of the settings were made with 110 mm bar-length, which is most often used in the commercial fishery. The proportion of different mesh sizes was constant between years. Each setting consisted of 30 nets each 30 m long, tied end to end in a fleet. The height of the nets was 20 meshes, and the hanging ratio 60%. The fleets were bottom-set, anchored to the bottom at one end only, letting the other end drift freely with the current. The soak time varied from 50 to 140 hours and each fleet was treated as one separate station.

The procedure for collecting individual samples was unfortunately not consistent throughout the time-series, but individual samples, when collected, was stratified both geographically and by depth. The inconsistency in sampling caused problems getting enough samples from different gears in some of the years, but most of the years weight and numbers of Greenland halibut for each separate station were recorded. Total length-frequency distributions (to the nearest cm below) were obtained, either by measuring the entire catch or from a random subsample. In some stations individual length, weight, sex, age and maturity stage were recorded, stratified to 5 individuals of each sex in 5 cm length groups.

Analyses

Different population characteristics and structures were studied using three different models. The first model used age as the dependent variable and related age in catch to year, sex, area and depth using a traditional analysis of variance (ANOVA).

$$Age = I + Year_i + Sex_j + Area_k + Depth_l + \mathbf{e} \quad (1)$$

This model is predicting the mean age in a catch by sex given year area and depth interval. In addition to the intercept up to nine-year effect parameters was estimated (1992-2000). Due to the lack of unique solutions the last year parameter was not really estimated, but set to zero. The sex and area effect had two levels each while the depth effect had two or three levels. This because age was sampled in three different depth intervals (400-500, 500-600 and 600-700 meters) in the longline survey, but only in two intervals (400-500 and 500-600 meters) in the gill-net survey and (500-600 and 600-700 meters) in the trawl survey.

The second model had length as the dependent variable explained by age, cohort, sex and maturity (both interacting with age) and depth.

$$Length = I + Age_a + Cohort_b + Sex_a + Maturity_a + Depth_c + \mathbf{e} \quad (2)$$

The sex effect is really the interaction between age and sex so a separate sex effect was estimated for each age group. The maturity effect is also the interaction with age while the depth effect is used as in model (1).

The importance of sex in the two first models led us to look at a third model which used age, depth and area as explanatory variables for the proportion females. The proportion females $P_{females}$ was modelled using a logistic regression:

$$\text{Log} \left(\frac{P_{females}}{1 - P_{females}} \right) = I + Age_a + Area_b + Depth_c + \mathbf{e} \quad (3)$$

One age parameter for each age group (ages 5-12), two areas and two or three depth intervals. The model was checked for over-dispersion and if the model showed a significant lack of fit the covariance matrix was rescaled. Note that the parameter estimates are not changed by this method. However, their standard errors are adjusted affecting their significance tests.

Results

Comparison of mean age in the catches revealed a relatively clear pattern, i.e. the mean age of Greenland halibut caught in different gears were not the same. Gillnet caught the oldest fish and trawl the youngest. Fish caught with longline had a mean age between gillnet and trawl (Fig. 2). The model predicting fish age exposed some differences between gears, but only catches from trawl revealed significant differences by all effects investigated (i.e. year, sex, area and depth; Table 2). Longline and gillnet showed a significant difference in mean age only by sex and area, and sex and year, respectively.

The standardized length distributions of Greenland halibut in the catches from the different gear types showed some variability throughout the period, but they were relatively stable within gillnet and longline surveys. In the trawl catches the length increased during the period, exemplified with the years 1995 and 1999 (Fig. 3). The modal lengths of fish caught in gillnet and longline was generally 15-20 cm larger than fish caught in trawl. The estimated age parameters in the length model (length at age) showed that the different gears caught fish of the same size at age (Fig. 4). Fish caught in gillnet showed slightly lower R^2 , with no clear reason. No difference in the mean length by depth was found in catches from gillnet and longline, but in trawl catches the depth effect was significant (Table 3).

The length of Greenland halibut showed an increasing trend from the 1980 year-class to the year-classes in the beginning of 1990's, i.e. fish from the earliest cohorts in the years investigated was generally smaller than fish from later ones (Fig. 5). Even if there were few observations for the first and the latest years the cohort effect was significant in all gears (Table 3).

In most age groups males were significantly smaller than females (Fig. 6, Table 3). The trend was increasing with age (i.e. the difference between the sexes became larger with older ages), but in the oldest age groups the numbers of observations were few and this could be the cause for an unexpected change in this pattern. For these age groups the size of males and females were not different or the males were larger, but in these observations females were highly dominant. The general trend was shown for all gears.

Immature Greenland halibut was smaller than mature with exception of the youngest age group (Fig. 7), and the difference was significant in catches from all gears (Table 3).

Generally males dominated the younger age groups in all gears and Greenland halibut older than 10 years were virtually all females (Fig. 8, Table 4). The youngest age group from gillnet (5 year old) was different from the others, showing higher proportion of females in the different strata. In catches from longline the area and depth difference was not significant, i.e. corresponding proportion females were found both north and south of 74°30N and in all depth strata. Trawl caught larger proportion females in the north, and catches from the depth stratum between 500 and 600 m had higher proportion females both in the north and south.

Discussion

The analyses of the three survey series from the slope area between Norway and Spitsbergen expressed a more homogenous pattern in the investigated population parameters than expected, but still there were some differences. Earlier work in the same area has demonstrated that there are patterns in size-, and thus age distribution along the slope. Polish investigations stated in 1973 that Greenland halibut west of Spitsbergen were smaller than individuals further south (Kosior, 1975). This was also observed on Norwegian groundfish surveys early in the 1980's (Randa and Smestad, 1982; 1983; Godø *et al.*, 1984), but all these surveys compared fish from a wider survey area than our investigation. In the beginning of the 1990's the limited fishery for Greenland halibut was only allowed south of 71°30N and from the commercial fisheries organizations it was expressed concern about the stock status in the whole distribution area. The only information on the Greenland halibut stock further north was from the scientific surveys conducted in that area. It was claimed that this was not enough and in addition to these scientific surveys it was set a proposal for an experimental fishery with conventional gears in the area. In the beginning this experimental fishery was highly motivated from the fishermen themselves and these surveys, longline and gillnet, have been driven mainly by research quotas and carried out like a "fisherman's choice" on where to put their effort. Hence, there have been changes in area and depth coverage throughout the time series causing problems with the consistency and the sampling regime of these data series. Most effort have been carried out on clusters north and south of a natural boundary around 74°30N, covering an area which is known as the main area for the adult (mature) stock (Godø and Haug, 1987; 1989; Albert *et al.*, 2001b). The trawl survey has been a scientific fixed station survey covering a wider area and also a wider depth gradient, i.e. a more homogenous coverage along the whole slope area in the whole time period investigated. The result of this has probably been a better coverage of the adult Greenland halibut stock in the area. The result also reflects this since the analyses showed the highest variability in the population parameters investigated in the catches from this data series.

The selection properties of the different gear types used is highly different from each other, especially trawl differs from the other two. Trawl catches had a wider size specter than catches from gillnet and longline and caught also fish of small sizes. The differences between gillnet and trawl is explained by the mesh selection properties of gillnet (Nedreaas *et al.*, 1996) and trawl is an active gear catching more or less all in its path, thus better reflecting the true size composition in the stock. But the catch composition of the trawl is also affected by avoidance reactions to the approaching gear, which may bias the length composition in these catches (Ona and Godø, 1990). This factor is probably most important for the largest individuals causing the trawl catches to be dominated by relatively smaller fish. The selection properties of longline are dependent of several factors including feeding behavior or feeding motivation, and the hooks ability to catch different groups of fish. Another important factor in longline is the competition between species and size groups of species and their different swimming range and speed. It is probable

that the largest and fastest fish are approaching the baited hooks first, i.e. hooking the larger ones in the area that again increases the mean size of fish caught on longline.

Some differences were found in all gears used, and as mentioned trawl data showed that there were significant area, depth, length, age and sex effects. Greenland halibut caught in trawl showed that there were significant difference in length and age by depth, i.e. suggesting size segregation of the individuals by depth. The largest fish was found in intermediate depths below 550 m depth, but smaller fish again appeared on larger depths. This pattern was not confirmed by gillnet and the reason for this is that gillnets were set in a more narrow depth interval, which did not reveal the difference in size by depth. Even if the difference was not significant for longline the data showed that the mean length changed in the time period, and these changes could be due to changes in mean depth of the settings (Høines and Korsbrette, 2001). Bowering and Nedreaas (2000) stated that mean individual size in trawl catches increased below 500 m, peaked and then declined, which our findings confirms. The largest fish were found in the southern part and in the corresponding age groups the proportion females were high. This is in accordance with earlier work in this area because the most important area for mature fish is found to be the area between Norway and Bear Island (Albert *et al.*, 2001b), i.e. the southern part of our survey area. Therefore we would expect the largest fish to congregate in this area. In the younger age groups males dominated, but in these age groups the highest proportion females were found in the northern area. The catches from gillnet showed the same pattern, but not so evident as trawl. Dominance of females in the largest and oldest part of the stock is explained to be due to higher natural mortality for males (Kovtsova and Nizovtsev, 1985; de Cardenas, 1996).

The analyses also showed that immature fish were smaller than mature fish in all gears and age groups. One probable explanation for the fact that immature Greenland halibut is smaller than mature individuals is that only those that grow fast and reach a given size are maturing causing always the largest fish in each age group to be mature. These individuals may generally have higher growth rate than fish that do not ripe, thus the mature part in each age group is always the larger ones. The survey area only covers the larger individuals from the immature part of the Greenland halibut population, since the juvenile part of the population are distributed further north and east (Smirnov, 1995; Albert and Høines, (in subm.); Albert *et al.*, 2001a). When growing to the adult stock the larger individuals migrate to the slope area between Norway and Spitsbergen (Godø and Haug, 1987; Albert *et al.*, 2001a), and this migration to the spawning area may be a continual process starting long before the fish is actually maturing. Consequently individuals that are immature reach the spawning area and are joined together with the mature part of the stock. Another probable cause is that Greenland halibut not necessarily ripe and spawn every year (Fedorov, 1971), which is causing problems in the determination on maturity stage, i.e. misclassifying mature fish to immature. Generally the largest number of misclassification of juveniles using macroscopic determination of maturity is between early maturing and resting stages (Morgan *et al.*, 2001). Our data were too sparse to go further into these questions.

References

- ALBERT O. T. and Å. S. HØINES. (in subm.). Comparing survey and assessment data: Consequences for stock evaluation of Northeast Arctic Greenland halibut. Submitted to Proceedings from SAP-Symposium, 4-6 December, Bergen, Norway, to be published in *Scientia Marina*
- ALBERT O. T., E. M. NILSSEN, K. H. NEDREAAS and A. C. GUNDERSEN. 2001a. Distribution and abundance of juvenile Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*) in relation to survey coverage and physical environment. *ICES J. mar. Sci.* **58**: 000-000.
- ALBERT O. T., E. M. NILSSEN, A. STENE, A. C. GUNDERSEN and K. H. NEDREAAS. 2001b. Maturity classes and spawning behaviour of Greenland halibut (*Reinhardtius hippoglossoides*). *Fish. Res.* **51**: 217-228.
- BOWERING W. R. and W. B. BRODIE. 1995. Greenland halibut (*Reinhardtius hippoglossoides*). A review of the dynamics of its distribution and fisheries off eastern Canada and Greenland. In: Deep-Water Fisheries of the North Atlantic Oceanic Slope, HOPPER, A. G.(ed.). Northwest Atlantic Treaty Organization Advanced Science Institutes Series. Boston, USA. Kluwer Academic Publishers, pp. 113-160
- BOWERING W. R. and K. H. NEDREAAS. 2000. A comparison of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) fisheries and distribution in the Northwest and Northeast Atlantic. *Sarsia* **85**: 61-76.

- DE CARDENAS E. 1996. The females ratio by length as an indicator of sexual differences in mortality of Greenland halibut (*Reinhardtius hippoglossoides*) at ages 8+. *NAFO SCR. Doc.* **96/35**, Serial no. N2710, 10 pp.
- FEDOROV K. Y. 1971. Zoogeographic characteristics of the Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum). *J. Ichthyol.* **11**: 971-976.
- GODØ O. R. and T. HAUG. 1987. Migration and recruitment to the commercial stock of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Svalbard area. *FiskDir. Skr. Ser. HavUnders.* **18**: 311-328.
- GODØ O. R. and T. HAUG. 1989. A review of the natural history, fisheries and management of Greenland halibut (*Reinhardtius hippoglossoides*) in the eastern Norwegian and Barents Seas. *J. Cons. int. Explor. Mer* **46**: 62-75.
- GODØ O. R., K. RANDA and O. M. SMESTAD. 1984. Preliminary report of the Norwegian groundfish survey at Bear Island and West Spitsbergen in the autumn 1983. *ICES C.M.* **1984 / G:46**, 1-18.
- HØINES Å. S. and K. KORSBREKKE. 2001. Some aspects of a time series of longline catch per unit of effort data for Greenland halibut (*Reinhardtius hippoglossoides*). *NAFO SCR. Doc.* **xx/xx**, Serial no. Nxxxx, 12 pp.
- HYLEN A. and K. H. NEDREAAS. 1995. Pre-recruit studies of the North-East Arctic Greenland halibut stock. *In*: Precision and relevance of pre-recruit studies for fishery management related to fish stocks in the Barents Sea and adjacent waters, HYLEN, A.(ed.). Proceedings of the sixth IMR-PINRO symposium, Bergen 14-17 June 1994. Bergen, Norway. Institute of Marine Research, pp. 229-237
- ICES 2001. Report of the Arctic Fisheries Working Group. *ICES CM 2001/ACFM:19*, 390 p.
- KOSIOR A. 1975. Polish investigations on Greenland halibut in the northeast Arctic in 1973. *Annls. biol., Copenh.* **30**: 172-173.
- KOVTSOVA M. V. and G. P. NIZOVITSEV. 1985. Peculiarities of growth and maturation of Greenland halibut of the Norwegian-Barents Sea stock in 1974 - 1984. *ICES C.M.* **1985 / G:7**, 16 pp.
- MORGAN M. J., W. R. BOWERING, A. C. GUNDERSEN, Å. S. HØINES, B. MORIN, O. V. SMIRNOV and E. HJØRLEIFSSON. 2001. Comparative analyses of Greenland halibut (*Reinhardtius hippoglossoides*) maturation for populations throughout the North Atlantic. *NAFO SCR. Doc.* **xx/xx**, Serial no. Nxxxx, pp.
- NEDREAAS K. H., A. V. SOLDAL and Å. BJORDAL. 1996. Performance and biological implications of a multi-gear fishery for Greenland halibut (*Reinhardtius hippoglossoides*). *J. Northw. Atl. Fish. Sci.* **19**: 59-72.
- ONA E. and O. R. GODØ. 1990. Fish reactions to trawling noise: the significance for trawl sampling. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* **189**: 159-166.
- RANDA K. and O. M. SMESTAD. 1982. The Norwegian groundfish survey at Bear Island and west Spitsbergen in the autumn 1981. *ICES C.M.* **1982 / G:42**, 1-17.
- RANDA K. and O. M. SMESTAD. 1983. Preliminary report of the Norwegian groundfish survey at Bear Island and West Spitsbergen in the autumn 1982. *ICES C.M.* **1983 / G:34**, 1-19.
- SMIRNOV O. V. 1995. Dynamics of Greenland halibut recruitment to the Norwegian - Barents Sea stock from 1983-1993 trawl survey data. *In*: Precision and relevance of pre-recruit studies for fishery management related to fish stocks in the Barents Sea and adjacent waters, HYLEN, A.(ed.). Proceedings of the sixth IMR-PINRO symposium, Bergen 14-17 June 1994. Bergen, Norway. Institute of Marine Research, pp. 239-242
- WHITEHEAD P. J. P., M.-L. BAUCHOT, J.-C. HUREAU, J. NIELSEN and E. TORTONESE 1986. Fishes of the North-eastern Atlantic and the Mediterranean. (Eds.), Paris, France: UNESCO. 1473 p.

TABLE 1. List of cruises from which data for this paper were collected. Number of samples by gear, N denotes number of stations, N_L is number of stations with length sample and N_A is number of stations with age sampling.

<i>Year</i>	<i>Gear type</i>	<i>Time period</i>	<i>N</i>	<i>N_L</i>	<i>N_A</i>
1992	Trawl	6.10 – 21.10	108	107	41
	Longline	5.10 – 21.10	85	84	28
	Gillnet	9.10 – 21.10	120	120	30
1993	Trawl	10.10 – 23.10	56	53	19
	Longline	7.10 – 16.10	41	40	15
	Gillnet	7.10 – 20.10	235	234	52
1994	Trawl	13.9 – 30.9	34	34	16
	Longline	27.9 – 8.10	71	49	8
	Gillnet	27.9 – 11.10	130	126	13
1995	Trawl	16.8 – 7.9	38	38	11
	Longline	22.9 – 3.10	58	41	4
	Gillnet	22.9 – 5.10	88	69	8
1996	Trawl	2.8 – 23.8	38	38	7
	Longline	17.9 – 27.9	43	26	3
	Gillnet	19.9 – 26.9	46	43	9
1997	Trawl	2.8 – 21.8	47	47	7
	Longline	17.9 – 29.9	67	34	0
	Gillnet	21.9 – 30.9	42	29	0
1998	Trawl	2.8 – 25.8	55	55	6
	Longline	21.9 – 1.10	58	27	3
	Gillnet	19.9 – 29.9	26	25	2
1999	Trawl	2.8 – 21.8	46	46	4
	Longline	21.9 – 5.10	64	27	8
	Gillnet	23.9 – 1.10	32	28	11
2000	Trawl	31.7 – 20.8	53	53	5
	Longline	21.9 – 3.10	42	19	6
	Gillnet	19.9 – 28.9	33	31	16 ¹

¹ Data not available for analysis; age samples to be punched at later stage.

Table 2. Type III analyses of effects for the models predicting fish age.

<i>Model</i>	<i>R²</i>	<i>Effect</i>	<i>df</i>	<i>Type III SS</i>	<i>MS</i>	<i>F Value</i>	<i>P</i>
Longline	0.5143	Year	7	6.4098	0.916	3.39	0.0013
		Sex	1	608.90	608.9	2256.6	<.0001
		Area	1	9.0322	9.032	33.47	<.0001
		Depth	2	0.7079	0.354	1.31	0.2695
Gillnet	0.3953	Year	6	59.831	9.972	17.07	<.0001
		Sex	1	660.08	660.1	1130.1	<.0001
		Area	1	0.0345	0.035	0.06	0.8081
		Depth	1	0.6120	0.612	1.05	0.3062
Trawl	0.2076	Year	8	1668.8	208.6	11.63	<.0001
		Sex	1	8467.0	8467	471.85	<.0001
		Area	1	718.25	718.2	40.03	<.0001
		Depth	1	2506.8	2506	139.70	<.0001

Table 3. Type III analyses of effects for the models predicting fish length.

<i>Model</i>	<i>R²</i>	<i>Effect</i>	<i>df</i>	<i>Type III SS</i>	<i>MS</i>	<i>F Value</i>	<i>P</i>
Longline	0.9246	Cohort	15	66.836	4.456	6.05	<.0001
		Age	7	2339.9	334.2	453.85	<.0001
		Age*Sex	8	61.735	7.717	10.48	<.0001
		Age*M	8	57.644	7.206	9.78	<.0001
		Depth	2	2.8472	1.424	1.93	0.1449
		Area					
Gillnet	0.8767	Cohort	14	261.78	18.70	8.77	<.0001
		Age	7	2187.2	312.5	146.55	<.0001
		Age*Sex	8	59.993	7.499	3.52	0.0005
		Age*M	8	135.21	16.90	7.93	<.0001
		Depth	1	0.5074	0.507	0.24	0.6257
		Area					
Trawl	0.9299	Cohort	15	4135.6	275.7	9.44	<.0001
		Age	7	288092	41156	1409.68	<.0001
		Age*Sex	7	1433.2	204.7	7.01	<.0001
		Age*M	8	3205.9	400.7	13.73	<.0001
		Depth	1	977.84	977.8	33.49	<.0001
		Area					

Table 4. Type III analysis of effects for the models predicting proportions female.

<i>Model</i>	<i>R²</i>	<i>Effect</i>	<i>df</i>	<i>Wald c²</i>	<i>P</i>
Longline ¹	0.2335	Age	7	234.89	<.0001
		Depth	2	2.88	0.2375
		Area	1	0.34	0.5581
Gillnet	0.3617	Age	7	389.48	<.0001
		Depth	1	5.64	0.0175
		Area	1	10.17	0.0014
Trawl	0.3502	Age	7	439.86	<.0001
		Depth	1	10.05	0.0015
		Area	1	46.62	<.0001

¹ Due to significant over-dispersion the covariance matrix was rescaled (multiplied with 2.02616).

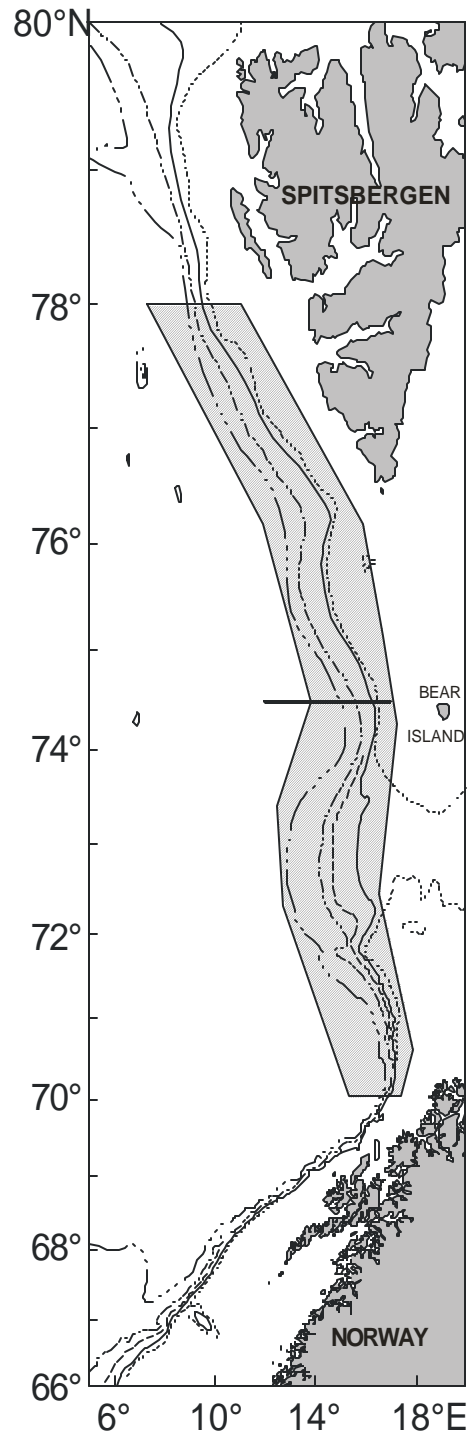


Figure 1. Experimental area (shaded), with depth contours 400, 500, 700, 1000 and 1500 m drawn. The horizontal line is the division used in the paper.

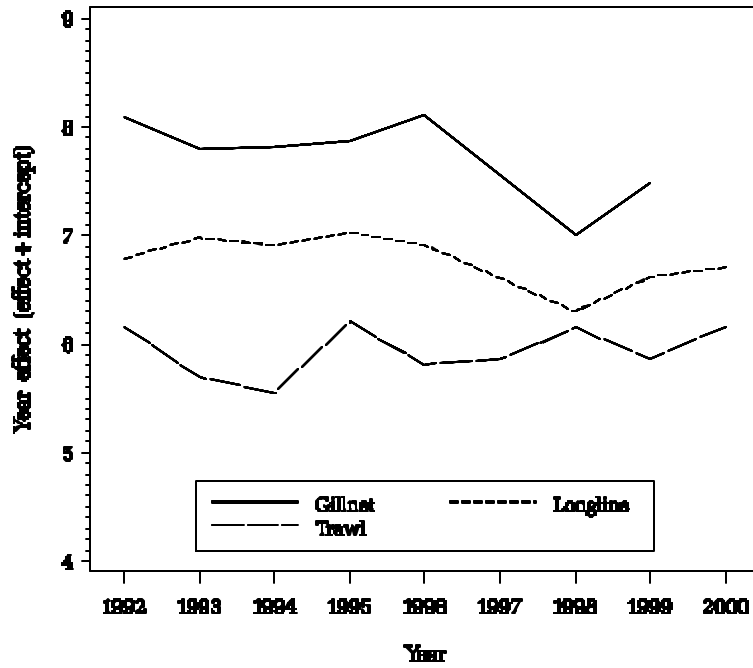


Figure 2. Trends in mean age in catches of Greenland halibut in the period 1992-2000.

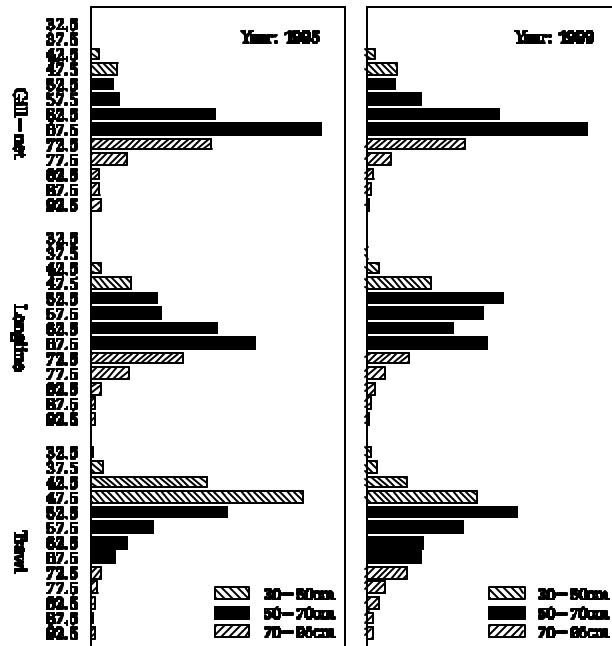


Figure 3. Length distributions from catches of Greenland halibut in gillnet, longline and trawl in 1995 and 1999.

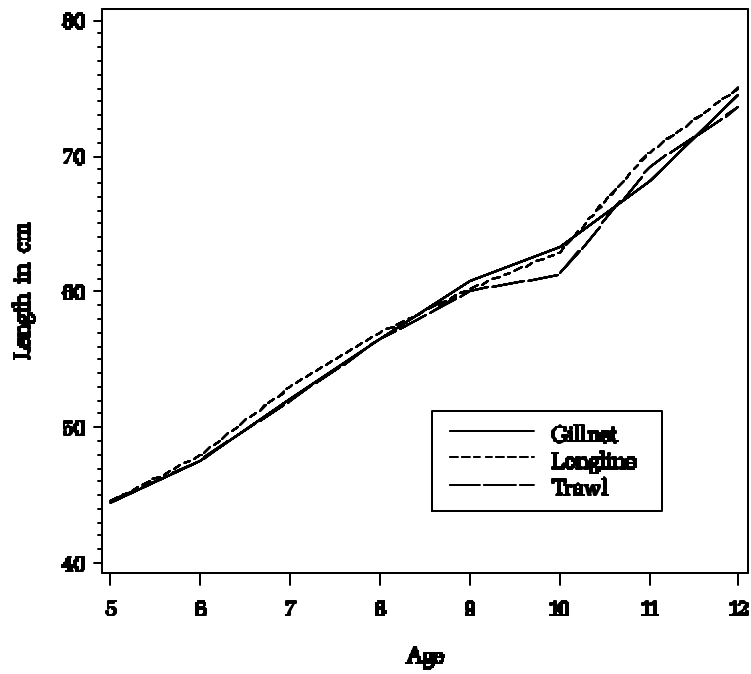


Figure 4. Estimated age parameters (age effect) in catches of Greenland halibut from gillnet, longline and trawl.

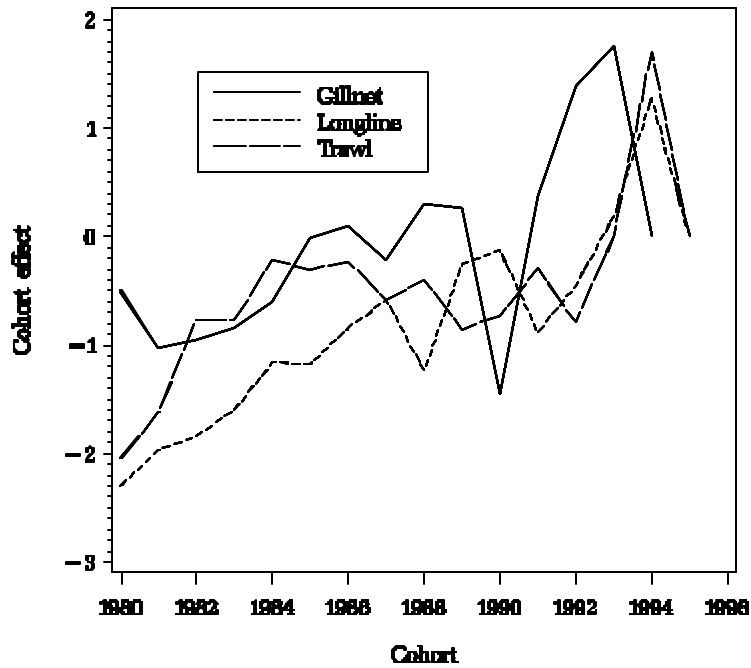


Figure 5. Estimated cohort parameters (cohort effect) in the length models.

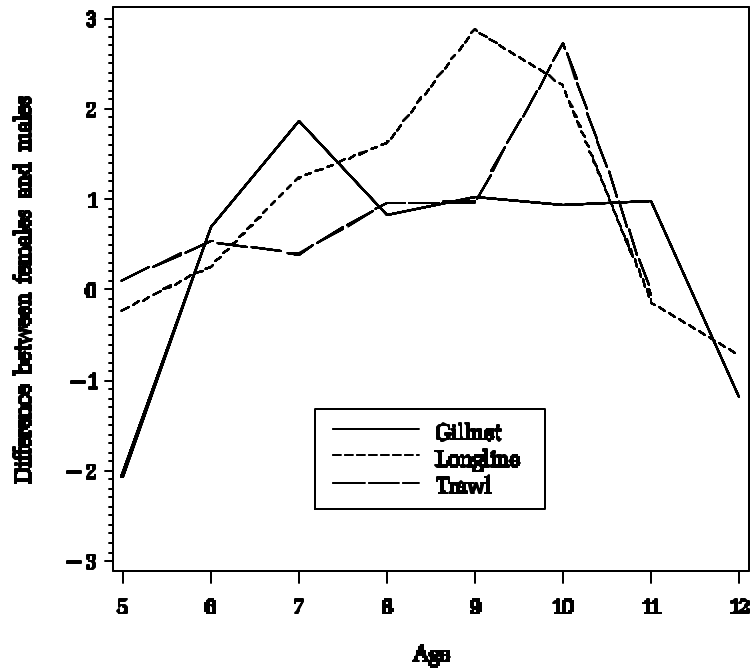


Figure 6. Estimated interaction between sex and age. The lines represent the difference in length between females and males at different age groups.

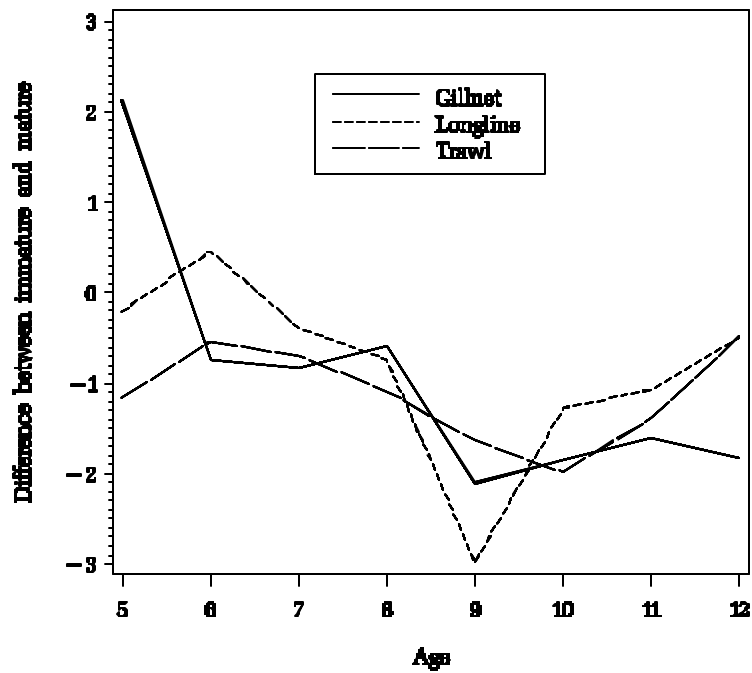


Figure 7. Estimated interaction between maturity and age. The lines represent the difference in length between immature and mature fish at different age groups.

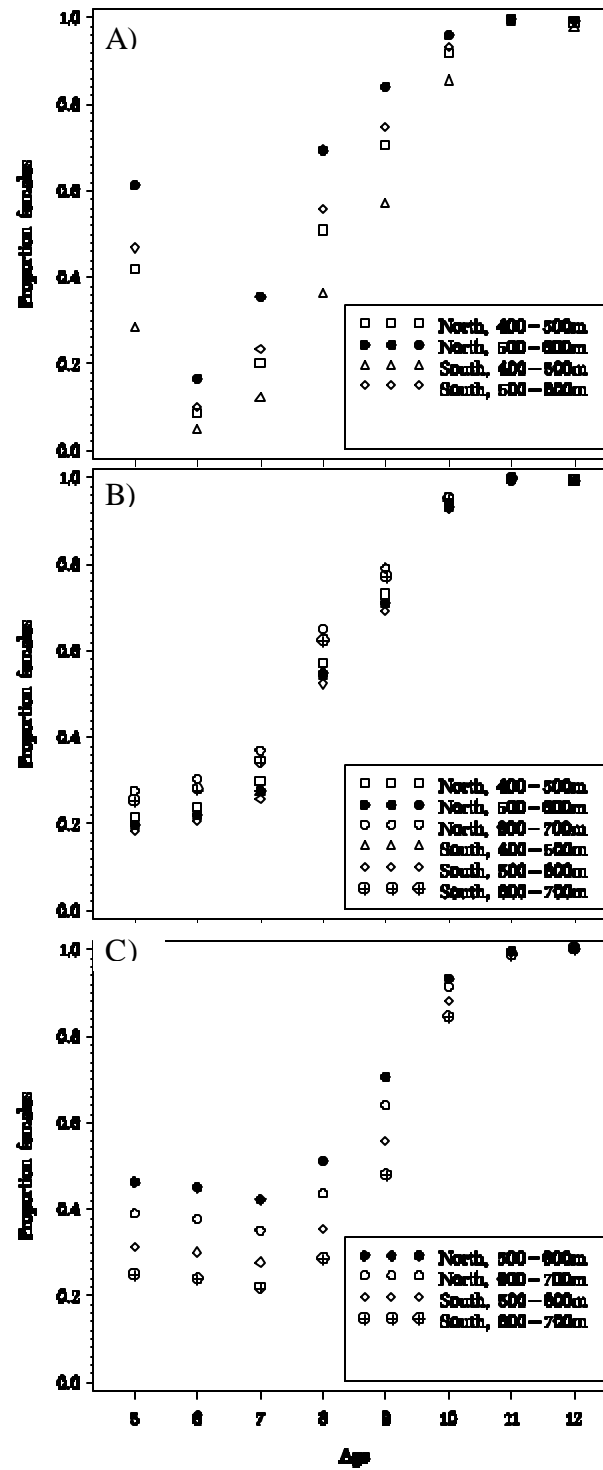


Figure 8. Modelled proportion females at age in catches of Greenland halibut from A) gillnet, B) longline and C) trawl.