The suitability of vertebral counts in stock delineation studies of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in West Greenland

E. B. Rasmussen, M.-B. Salhauge, and J. Boje

Vertebral counts of Greenland halibut collected from West Greenland in 1995 were compared to samples from the same areas for the period 1987–1989. The 1995 samples, obtained in Davis Strait, Baffin Bay, and two North-west Greenland fjords, showed no significant differences in mean vertebral numbers. Previous studies in 1987–1989, however, showed significant differences in mean vertebral counts between some of the same areas. Inter-annual variation in vertebral numbers is therefore suggested to be greater than the variation between sample areas. Despite the protracted egg and larval stage of Greenland halibut, the currents along the West Coast of Greenland are unlikely to transport juveniles in any significant amount from the Davis Strait spawning grounds to the North-west Greenland fjords. The origin of the northernmost populations therefore remains unknown. As single cohorts in the material seem to affect the total average counts per area significantly it is suggested that a change in the distribution of Greenland halibut might have occurred during the period studied. The results also emphasize the importance of relying on data based on more than one year and question the suitability of vertebral counts in stock delineation studies of Greenland halibut.

E. B. Rasmussen, M.-B. Salhauge, and J. Boje: Greenland Institute of Natural Resources, Pilestræde 52, PO Box 2151, 1016 Copenhagen K, Denmark. Correspondence to Rasmussen: tel: +45 33 96 3400; fax: +45 33 96 3406; email: msebr@email.dk

Introduction

Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), are widely distributed in the North-west Atlantic, from Smith Sound between Greenland and Canada, southward throughout Baffin Bay and Davis Strait to North-east USA and eastward along East Greenland to Iceland (Smidt, 1969; Bowering and Brodie, 1995).

Greenland halibut reach maturity after 6–11 years for males and 8–12 years for females (Smidt, 1969; Bowering, 1982; Serebryakov *et al.*, 1992; Junquera and Zamarro, 1994; Nielsen and Boje, 1995; Anon., 1996). Greenland halibut are known to be bathypelagic spawners and spawning occurs at depths of more than 600 m. Eggs and larvae less than about 18 mm are believed to drift bathypelagic, while larger larvae live pelagically near the surface (Jensen, 1935).

Spawning appears to take place in spring in deeper waters (approximately 800–2000 m depths) extending from Davis Strait, south of 67°N (Jensen, 1935; Smidt, 1969) to Flemish Pass, off Newfoundland (Junquera and Zamarro, 1994). The assumption that there is a spawning area located in Davis Strait is mainly based on observations of eggs and larvae, as very few adults have been caught in ripe condition (Smidt, 1969). From observations in Davis Strait and along West Greenland during spring and summer (May to August), the highest densities of pelagic eggs and larvae have been found from about 62°N to about 66°N. No records of eggs and larvae have been made north of 68°N. Furthermore, no eggs or larvae have been caught during surveys in the fjords of West Greenland where adult populations are usually abundant (Smidt, 1969). Eggs and larvae from the spawning area in Davis Strait are dispersed northward by the West Greenland Current, to the western

shore of Greenland, and southward by the East Canadian Polar Current, to the eastern shore of Canada (Templeman, 1973). Larval settlement occurs in September/October when larvae approach a length of about 7 cm (Smidt, 1969). In the East Greenland/Iceland area, spawning occurs on the continental slopes west of Iceland (Sigurdsson, 1979). From there, eggs and larvae are carried either towards East Greenland by the Irminger Current, or north-eastward along the northern Icelandic coast (Sigurdsson, 1979).

Greenland halibut on the inner continental slopes off West Greenland probably migrate as they grow to the deeper parts of the fjords (Smidt, 1969), while those on the outer slopes are believed to migrate to deeper parts of Davis Strait (Riget and Boje, 1989). Bowering (1978, 1984) suggested that a prespawning migration of maturing Greenland halibut occurs along the Canadian coast towards the deeper part of the continental slopes in Davis Strait and off Labrador. Similarly, a prespawning migration of Greenland halibut from North-west, north, and east Iceland towards the spawning area west of Iceland in late summer has been described by Chumakov (1969) and Sigurdsson (1979). Furthermore migrations from South-west Greenland fjords to Iceland have been observed (Boje, 1994).

Several studies on stock identification of Greenland halibut in the North-west Atlantic have been carried out using meristic characters (Templeman, 1970; Misra and Bowering, 1984; Riget et al., 1992), morphometric characters (Bowering, 1988), genetic differentiation (Fairbairn, 1981; Riget et al., 1992; Vis et al., 1997), parasite infestation as biological tags (Khan et al., 1982; Reimer and Ernst, 1989; Arthur and Albert, 1993; Boje et al., 1997), and external tagging (Bowering, 1984; Boje, 1994). These studies indicate that Greenland halibut throughout the East Canadian–West Greenland area form a single homogeneous stock, with the exception of some East Canadian components (Templeman, 1970; Fairbairn, 1981; Misra and Bowering, 1984; Arthur and Albert, 1993) and some components in fjords of West Greenland (Riget et al., 1992; Boje, 1994; Boje et al., 1997). Tagging experiments indicate that the spawning stock west of Iceland and the fjord components in South-west Greenland are related (Smidt, 1969; Riget et al., 1992; Boje, 1994). To date there have not been any studies to investigate Baffin Bay and the adjacent fjords in North-west Greenland simultaneously.

Previously, meristic characters have been widely used in stock delineation studies. The presence of various vertebral counts within the same species was ascribed to the presence of different spawning populations as early as 1898, when Heincke (1898) used meristic characters to describe different races of herring. Since then a more comprehensive understanding of the formation of vertebrae has been developed. For other species of fish, the number of vertebrae is determined during the embryonic development, before the eyed egg stage (Tåning, 1946; Fahy, 1976). Vertebral number is inherited (Christiansen et al., 1988), however most differences in vertebral number observed between fish stocks are probably determined by environmental factors, among which temperature is especially well-documented (Tåning, 1946; Fahy, 1972; Brander, 1978; Hulme, 1995).

For Greenland halibut, determination of vertebral number is assumed to occur during the bathypelagic life-stage (Templeman, 1970), which occurs mainly in May in West Greenland (Jensen, 1935). The water masses at depths of more than 1000 m are conveyed from other parts of the North Atlantic, i.e. the North-east Atlantic Deep Water and North-west Atlantic Bottom Water. Temperature and salinity conditions in the deep water-masses in the Davis Strait are relatively stable at about 3°C and 34.9 all year round (Buch, 1990). Furthermore, currents in these deep water-masses presumably exhibit the same patterns as surface currents, but at lower velocities (Buch, 1990). Independent of precise location, Greenland halibut originating from the Davis Strait spawning complex are therefore expected to spend the bathypelagic egg and larval stage in a stable environment. As the development of vertebrae is assumed to correspond to environmental conditions, especially temperature, these fish are not expected to deviate from each other in terms of number of vertebrae.

Two previous studies using vertebral counts from 1950 to 1968 (Templeman, 1970) and from 1987 to 1988 (Riget et al., 1992) cover parts of the areas sampled in this study. Templeman found no significant difference between vertebral counts of Greenland halibut throughout the area from Baffin Bay to Southern Grand Bank, except for one sample in the Gulf of St Lawrence. Riget et al. (1992) sampled inshore as well as offshore areas from Newfoundland, in the south, to Umanak Fjord in West Greenland, in the north. They found significant differences in vertebral counts among three West Greenland Fjords, between offshore and inshore samples, and also between eastern Newfoundland and Davis Strait.

The present study was carried out to illustrate the suitability of vertebral counts in stock delineation and to clarify stock relations of Greenland halibut especially in the North-west Greenland area. The study focused on the northern components of the Greenland halibut stock in Baffin Bay and the North-west Greenland fjords.

Materials and methods

Greenland halibut ranging from 29 to 87 cm were collected in Upernavik in August to September 1989, and in Upernavik, Umanak, Baffin Bay, and Davis Strait from July to August 1995 (Table 1, Fig. 1). The samples from Upernavik and Umanak were collected during annual scientific longline surveys by RV ''Adolf Jensen''. The

Table 1. Data on Greenland halibut samples included in this analysis: mean length, mean weight, mean age of specimens and standard deviations of the mean values.

Site no.	Locality	NAFO Div.	Sampling month and year	Depth interval (m)	Number of fish	Length (cm) Mean	s.d.	Weight (g) Mean	s.d.	Age (years) Mean	s.d.
1	Upernavik	1A	Jul 1995	240–820	99	62	8.43	2645	325	9.95	2.04
2	Umanak	1A	Aug 1995	200–960	170	60	10.67	2130	1225	9.56	2.60
3	Baffin Bay	1A	Aug 1995	450–745	61	53	8.71	1400	715	7.69	1.68
4	Davis Strait	1D	Aug 1995	1103–1410	97	58	5.54	1680	557	8.77	1.42
1	Upernavik	1A	Aug–Sep 1989	100–1300	96	56	5.76	*		9.17	1.10
2	Umanak	1A	Aug 1987	210–1080	88	59	6.08	*		9.62	1.31
4	Davis Strait	1D	Sep 1988	603–869	100	56	4.62	*		9.31	0.89

*The fish were not weighed.
Data from Umanak 1987 and Davis Strait 1988 are from Riget *et al.*, 1992.
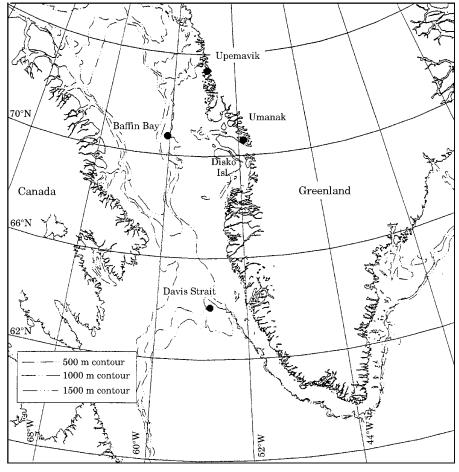Abbreviations (summary statistics): s.d., standard deviation of the mean.

Figure 1. Map of the area investigated and sample localities.

Baffin Bay samples were collected by the use of both longline and gillnets from RV "Adolf Jensen". The Davis Strait samples were collected from the Japanese research trawler, "Shinkai Maru". Sampling was restricted to the length interval 50–70 cm, but small catches necessitated including a broader length range. All fish were weighed to the nearest 5 g, total lengths were measured to the cm below, and the age and sex of

Table 2. Frequency distribution of vertebral counts in different areas in 1995 and 1987–1989. Areas ranked by decreasing mean count.

Sample	Vertebral counts									
	58	59	60	61	62	63	64	n	Mean	s.d.
Davis Strait 1995	0	0	2	28	51	14	0	95	61.81	0.704
Umanak 1995	0	0	4	57	78	26	0	165	61.76	0.740
Baffin Bay 1995	0	0	1	18	37	3	0	59	61.71	0.59
Upernavik 1995	0	0	2	41	44	10	1	98	61.66	0.731
Davis Strait 1988*	0	0	6	48	40	6	0	100	61.46	0.702
Umanak 1987*	1	3	28	37	18	3	0	88	60.83	0.913
Upernavik 1989	2	17	33	41	2	1	0	96	60.28	0.89

*Data from Riget *et al.* (1992), re-analysed.
Abbreviations (summary statistics): n, number of fish sampled; s.d., standard deviation.

each specimen was determined (Table 1). The vertebral columns were exposed by filleting the fish. All vertebrae, including the urostylar half, were counted. Fish with fused vertebrae were excluded. A total of 523 fish were examined. Data from the study by Riget *et al.* (1992) are included in present analyses (Table 2). Hence, the total data set consist of four samples from 1995, one sample from 1989 and a sample from 1987 and 1988, respectively, Riget *et al.* (1992). A total of 701 fish were used in the analyses.

Vertebral counts are discrete values with only a limited number of categories so a logistic model for polytomous data – the *proportional-odds model* Equation (1) has been used to fit the data (Hosmer and Lemeshow, 1989; McCullagh and Nelder, 1989). The statistical modelling and calculations has been performed by use of the SAS statistic software (SAS, 1990) using the following basic formula:

$$\text{logit Pr}(Y \leq i|\mathbf{x}) = \alpha_i + \beta^T x \tag{1}$$

Y is the number of vertebrae of one individual, $i = 1, \ldots, k$ is the response categories $(k+1)$ minus one (categories of vertebral counts minus one) and $\mathbf{x}$ is a vector of the values of the explanatory variables included in the analysis, i.e. sampling area, sex, length, and cohort. α_i is the intercept parameter for response category i. β is the vector of slope parameters $(\beta_1, \ldots, \beta_s)$ where s is the number of explanatory variables. β denotes the magnitude of each value of the explanatory variables in the model.

For each statistical test the validity of the model was tested. A regression line is calculated for each category of vertebral count (k regression lines for each explanatory variable). If the k regression lines are parallel for each explanatory variable the model is supposed to perform an acceptable fit to the data. A score test for the proportionality of the regression lines has been applied (this is also called a score test for the proportional odds assumption, SAS, 1990). In none of the final models was

there any significant deviations from the proportional odds assumption, but the univariate analysis of the length effect of the Upernavik sample from 1989 used in the selection of variables did deviate significantly from the proportional odds assumption (p<0.05). However, the importance of this variable on the distribution of vertebral counts in the sample could be judged through simple data plots, and length as an explanatory variable was excluded for this sample.

In addition to sampling area and year the variables fish length, cohort, and sex have been included as possible explanatory variables. For each analysis a model was designed with the relevant explanatory variables included. In order to identify the explanatory variables of importance, univariate analysis of each explanatory variable for each sample area, and sample year were performed. Some of the variables included in the subsequent multivariate models could then be excluded through the following stepwise selection procedure. Each explanatory variable included in a model was evaluated by calculating the Wald chi-square statistic as the square of the slope parameter β_i divided by its standard error and finding the associated p-value. Further the log likelihood values were calculated for the model with and without the explanatory variable in question. A likelihood ratio test was obtained by multiplying the difference between the two log likelihood values with −2, and finding the associated p-value for the chi-square distribution (Hosmer and Lemeshow, 1989). If the p-value for the Wald chi-square statistics and the comparisons of the model with and without the variable in question was larger than about 0.25 the variable was excluded. The final models were then confined to include the variables listed in Table 3.

The three areas sampled in 1987–1989 were compared among each other and the four areas sampled in 1995 were compared among each other. Also, pairwise comparison between the same areas sampled in different years were obtained, i.e. Umanak, 1987 vs. Umanak, 1995; Upernavik, 1989 vs. Upernavik, 1995; Davis

Table 3. Explanatory variables included in each comparison analysis.

Comparison analysis	Explanatory variables included in the logistic model
All samples 1987–1989	Sampling area and cohort
All samples 1995	Sampling area
Umanak 1987 vs. Umanak 1995	Sampling area and cohort
Davis Strait 1988 vs. Davis Strait 1995	Sampling area and cohort
Upernavik 1989 vs. Upernavik 1995	Sampling area
Cohorts within Umanak 1987	Cohort
Cohorts within Davis Strait 1995	Cohort

Table 4. Comparisons of vertebral counts among sampling areas, samples from 1987 to 1989. Umanak and Davis Strait samples compared to Upernavik, with cohort included as an explanatory variable.

	Proportional Odds Assumption (Pr>chi-square)	Joint effect of explanatory variables (Pr>chi-square)	Parameter estimate	Standard error	Wald chi-square	Pr>chi-square	Standardized estimate
Model	0.11	<0.0001					
Explanatory variables							
X1 (Davis Strait 1988)			− 2.32	0.34	47.40	<0.0001	− 0.610
X2 (Umanak 1987)			− 0.38	0.38	1.00	0.32	− 0.099
X3 (Upernavik 1989)			0				0
Cohort			0.28	0.11	7.09	0.008	0.230

X1, X2 and X3 are the design variables applied to compare the sampling areas. The Proportional Odds Assumption has been tested by the score test and the joint effect of explanatory variables by comparing the log likelihood values for the model with and without the variables.

Strait, 1988 vs. Davis Strait, 1995. The latter tests were performed to validate the method of vertebral counting on Greenland halibut. In order to describe the effect of single cohorts on the vertebral counts within each of the areas where univariate analysis indicated that cohort could be an important explanatory variable, a comparison of the vertebral counts between cohorts was also included in the analysis. To perform the comparisons between areas and between cohorts, m design variables were defined for each sample. The design variables were labeled X_1–X_m, where β_m were set to zero and X_m was the design variable that X_1–$X_{(m-1)}$ were compared to. X_m was always chosen so all of the β_{m-1} turned out to have the same sign, negative or positive. Through this procedure the two most extreme design variables would always be compared to evaluate the maximal difference in the data set. Further the design values, $X_{(m-1)}$, could be ordered by the distance to X_m and any gradients in vertebral distributions would be exposed. The number of design values (m) was equal to the number of levels for the explanatory variable in question, minus one (Hosmer and Lemeshow, 1989; McCullagh and Nelder, 1989).

Results

The comparison of Davis Strait, Umanak, and Upernavik sampled in 1987–1989 is given in Table 4.

The model includes cohort and the area design variables, X_1–X_3, in the analysis. There is an overall effect of area and cohort (joint effect of the explanatory variables, p<0.0001). There is a pronounced area effect as Davis Strait differs significantly from Upernavik (Wald chi-square, p<0.0001) and also from Umanak. These two northernmost areas do not show any significant difference in the distribution of vertebral counts. In this model there is also a pronounced effect of cohort (Wald chi-square, p=0.008). There is an estimated difference of 1.18 between the mean vertebral numbers from Upernavik and Davis Strait (Table 2).

Comparison of Davis Strait, Baffin Bay, Umanak, and Upernavik sampled in 1995 is given in Table 5. The model includes only the area design variables, X_1–X_4, in the analysis. There is no overall effect of sampling area (joint effect of the explanatory variables, p=0.40), but there is a numerically larger difference between the standardized estimate for the two geographically most distantly diverged areas, Davis Strait and Upernavik, than between all other areas, although, this difference is not significant (Wald chi-square, p=0.11). There is a numeric value of 0.15 between mean vertebral number from Upernavik and Davis Strait (Table 2).

The effect of sampling year on the vertebral counts is given in Table 6. Overall there is a significant difference between the two periods for each of the two areas, Umanak and Upernavik, while there is no significant

Table 5. Comparison of vertebral counts among sampling areas, samples from 1995. Upernavik, Baffin Bay and Umanak samples compared to Davis Strait.

	Proportional Odds Assumption (Pr>chi-square)	Joint effect of explanatory variables (Pr>chi-square)	Parameter estimate	Standard error	Wald chi-square	Pr>chi-square	Standardized estimate
Model	0.31	0.40					
Explanatory variables							
X1 (Upernavik 1995)			0.44	0.28	2.49	0.11	0.102
X2 (Umanak 1995)			0.15	0.25	0.35	0.55	0.039
X3 (Baffin 1995)			0.23	0.32	0.54	0.46	0.045
X4 (Davis Strait 1995)			0				0

X1, X2, X3, and X4 are the design variables applied to compare the sampling areas. The Proportional Odds Assumption has been tested by the score test and the joint effect of explanatory variables by comparing the log likelihood values for the model with and without the variables.

Table 6. Pairwise comparisons of vertebral counts between sampling years, within the same areas. Cohort is included as an explanatory variable in the comparison with Umanak and Davis Strait samples.

	Score test for Proportional Odds Assumption (Pr>chi-square)	Score test for joint effect of explanatory variables (Pr>chi-square)	Parameter estimate	Standard error	Wald chi-square	Pr>chi-square	Standardized estimate
Umanak							
Model	0.29	<0.0001					
Explanatory variables							
X1 (Umanak 1987)			2.99	0.53	31.61	<0.0001	0.78
X2 (Umanak 1995)			0				0
Cohort			0.091	0.053	2.93	0.09	0.22
Davis Strait							
Model	0.97	0.0013					
Explanatory variables							
X1 (Davis Strait 1988)			−0.24	0.93	0.068	0.79	−0.067
X2 (Davis Strait 1995)			0				0
Cohort			−0.16	0.12	1.79	0.18	−0.35
Upernavik							
Model	0.82	<0.0001					
Explanatory variables							
X1 (Upernavik 1989)			3.68	0.46	63.2	<0.0001	−1.02
X2 (Upernavik 1995)			0				0

X1 and X2 are the design variables applied to compare the sampling periods. The Proportional Odds Assumption has been tested by the score test and the joint effect of explanatory variables by comparing the log likelihood values for the model with and without the variables.

difference between the Davis Strait samples. The effect of sampling year on the results from Umanak is analysed by a comparison of the 1987 sample vs. the 1995 sample. The model includes cohort and the two design variables for each sampling year in the analysis. There is a clear overall effect of sampling year and cohort (joint effect of the explanatory variables, p<0.0001), and also of sampling year itself (Wald chi-square, p<0.0001). There might be a small but not significant effect of cohort in this model (Wald chi-square, p=0.09). The effect of sampling year on the results from Davis Strait is analysed by a comparison of the 1988 sample vs. the 1995 sample. The model includes cohort and the two design variables for each sampling year in the analysis. There is a clear overall effect of sampling year and cohort (joint effect of the explanatory variables, p<0.0013), but not sampling year itself (Wald chi-square, p=0.79), or cohort itself (Wald chi-square, p=0.18). The effect of sampling year on the results from Upernavik is analysed by a comparison of the 1989 sample vs. the 1995 sample. The model includes only the two design variables for each sampling year in the

Table 7. Comparisons of vertebral counts among cohorts, by sampling area and year. Samples from Umanak 1987, Baffin Bay 1995 and Davis Strait 1995.

	Proportional Odds Assumption (Pr>chi-square)	Joint effect of explanatory variables (Pr>chi-square)	Parameter estimate	Standard error	Wald chi-square	Pr>chi-square	Standardized estimate
Umanak 1987							
Model	0.95	0.013					
Explanatory variables							
X1 1974 (17)			−4.69	1.57	8.87	0.003	−0.81
X2 1975 (29)			−2.36	0.79	8.83	0.003	−0.78
X3 1976 (20)			−0.80	0.72	1.24	0.27	−0.28
X4 1977 (9)			−0.46	0.55	0.70	0.40	−0.22
X5 1979 (8)			−0.24	0.57	0.18	0.68	−0.11
X6 1978 (2)			0				0
Davis Strait 1995							
Model	0.85	0.17					
Explanatory variables							
X1 1983 (21)			3.24	1.59	4.17	0.04	0.61
X2 1984 (24)			0.70	0.68	1.07	0.30	0.32
X3 1985 (23)			1.20	0.73	2.69	0.10	0.50
X4 1986 (11)			1.07	0.60	3.18	0.07	0.60
X5 1987 (14)			0.95	0.59	2.57	0.11	0.54
X6 1988 (2)			0				0

X1, X2, X3, X4, X5, and X6 are the design variables applied to compare the sampling cohorts. Number of fish in each cohort in parentheses. The Proportional Odds Assumption has been tested by the score test and the joint effect of explanatory variables by comparing the log likelihood values for the model with and without the variables.

analysis. There is a clear effect of sampling year (joint effect of the explanatory variables, $p < 0.0001$ and Wald chi-square, $p < 0.0001$).

The analysis of the effect of different cohorts is given in Table 7 for Umanak, 1987 and Davis Strait, 1995. The analysis for Umanak, 1987 shows that there is a clear overall effect of cohort on the vertebral distribution (joint effect of the explanatory variables, $p = 0.013$). Further the model points out the 1974 and 1975 cohorts as especially different from the 1978 cohort (Wald chi-square, $p = 0.003$). A comparison of the numeric values of the standardized estimates indicates a division of the cohorts into two groups, 1974–1975 with a deviation of 0.03 between each other, and 1976–1979 with a maximum deviation of 0.28 between the two most distant cohorts. Between the two groups there is a minimum distance of 0.50. Similar analysis of the cohorts from Davis Strait, 1995 does not show any significant overall cohort effect (joint effect of the explanatory variables, $p = 0.17$), but indicates that the 1988 cohort could be deviating from at least some of the other cohorts. When the two most extreme cohorts are compared the Wald chi-square value is significant ($p = 0.04$).

Discussion

There were no significant differences in vertebral numbers between areas in 1995 while significant differences in vertebral numbers between areas were detected in 1987–1989. Also counts from fish sampled from the same areas were significantly different between 1987–1989 and 1995. The reason for the small variability in samples from 1995 could either be due to homogenous temperature regimes during egg and larval development for cohorts sampled in 1995 or the fish sampled could have originated from the same spawning area. For fish sampled in 1987–1989, on the other hand, temperature regimes within the area where eggs and larvae were distributed must have been variable or the fish sampled could have originated from more than one spawning stock.

The observed inconsistency between the two sampling periods (1987–1989 and 1995) indicates that sampling year can have a pronounced effect on vertebral number. A comparison of mean vertebral counts from Davis Strait in 1995 with the results from Davis Strait obtained by Templeman (1970) also supports this finding. It was found that among four samples collected by Templeman (1970) in Davis Strait and Baffin Bay, three differed significantly from those sampled at the same locations in 1995 (z-test, $p < 0.05$). Therefore, the effect of sampling year can be larger than any effect of sampling location. Even though the number of fish in each year class are quite small our analysis on cohorts from Umanak, 1987 and Davis Strait, 1995 indicates a year-class effect on the number of vertebrae for at least these two samples. This result indicates that some of the observed effects of

sampling year can be explained by annual changes in the hydrographic conditions in the spawning areas or in annual fluctuations in the recruitment pattern. Further explanations could be that each sample comprised a mixture of populations, the proportions of which may change in time, i.e. changed spawning success or larval drift, or sampled populations may have been spatial separated because of separated spawning and/or feeding areas. Another explanation could be that the observed differences between the same areas sampled in different sampling years could be due to a shift in distribution pattern during the 1990s. This has been found for Greenland halibut and other fish in the western Atlantic (i.e. witch flounder and American plaice) and may be associated with major shifts in ocean climate (Bowering *et al.*, 1995; Bowering *et al.*, 1997; Vis *et al.*, 1997).

Recruitment processes north of 70°N remain unknown. The northernmost area where settled larvae have been observed is about 70°N latitude (Riget and Boje, 1989). Catch compositions off West Greenland do not imply any northward migration of young fish (Jørgensen, 1997). A simple calculation assuming passive drift at speeds of 3–5 cm s^{-1} in the upper layer of the West Greenland Current over 6 months will result in drifted distances of about 600 km; enough to carry eggs and larvae to their northernmost distribution, Disko, about 70°N latitude. Adult populations of Greenland halibut in the North-west Greenland fjords must therefore have their origin in a spawning area other than the one in the Davis Strait. The Baffin Bay basin population, however, could possibly be recruited from Davis Strait by a northwestward migration of young fish from the banks west of Disko Island into the deep Baffin Bay. The water masses in Baffin Bay at 500–2000 m are characterized by low temperatures (0–1°C above 1000 m and negative temperatures below 1000 m) (Buch, 1990). The adjacent fjords in North-west Greenland also have low bottom temperatures of about 1–2°C (Nielsen and Boje, 1995). As Greenland halibut seem to require temperatures of 3–4°C for gonad development (Jensen, 1935; Smidt, 1969; Templeman, 1973), spawning is unlikely to occur in the Baffin Bay basin or the adjacent North-west Greenland fjords. Further the results of tagging experiments along the Greenland West Coast do not indicate any northward migration of adult fish, although the recaptures obtained so far are very sparse in the offshore areas. The origin of Greenland halibut in the fjords north of 70°N latitude therefore remains a mystery.

Conclusions

The significant differences between the sampled populations found by Riget *et al.* (1989) are not confirmed by present analysis included in this study. However the largest difference in vertebral counts was found between the northernmost and southernmost samples which could indicate a gradient from south to north. The effect of different cohorts indicates that a change in the distribution of Greenland halibut could have occurred during the period studied. This can explain some of the observed difference between samples from 1987 to 1989 and 1995, but other factors like changes in hydrographic patterns might contribute. The very large deviations in vertebral counts between identical areas from 1987–1989 to 1995 suggests that number of vertebrae may not be a conclusive method of determining stock affinities when used alone. The results presented here emphasize the importance of relying on data based on more than one year.

Acknowledgements

References

Anon. 1996. Report of the North-western Working Group. ICES CM 1996/Assess: 15.

Arthur, J. R., and Albert, E. 1993. Use of parasites for separating stocks of Greenland halibut (*Reinhardtius hippoglossoides*) in the Canadian Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Science, 50: 2175–2181.

Boje, J. 1994. Migrations of Greenland halibut in the Northeast Atlantic based on tagging experiments in Greenland waters, 1986–1992. NAFO SCR. Doc. 94/18 (mimeo).

Boje, J., Riget, F., and Køie, M. 1997. Helminth parasites as biological tags in population studies of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Northwest Atlantic. ICES Journal of Marine Science, 54: 886–895.

Bowering, W. R. 1978. Age and growth of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in ICNAF Subareas 2–4. International Commission of Northwest Atlantic Fisheries Research Bulletin. 13: 5–10.

Bowering, W. R. 1983. Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) in the Canadian Northwest Atlantic. Fishery Bulletin, 81: 599–611.

Bowering, W. R. 1984. Migrations of Greenland halibut, *Reinhardtius hippoglossoides*, in the Northwest Atlantic from tagging in the Labrador-Newfoundland region. Journal of Northwest Atlantic Fishery Science, 5: 85–91.

Bowering, W. R. 1988. An analysis of morphometric characters of Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic using a multivariate analysis of covariance. Canadian Journal of Fisheries and Aquatic Science, 45: 580–585.

Bowering, W. R., and Brodie, W. B. 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 slope. Ed. by A. G. Hopper. Kluwer Academic Publishers.

Bowering, W. R., Power, D., and Morgan, M. J. 1995. Distribution and abundance of five major groundfish species at the continental slope of Divisions 3KLMN based upon Canadian deepwater surveys in 1991, 1994 and 1995. NAFO SCR. Doc. 95/51 (mimeo).

Bowering, W. R., Morgan, M. J., and Brodie, W. B. 1997. Changes in population of American plaice (*Hippoglossoides platessoides*) off Labrador and northeastern Newfoundland: A collapsing stock with low exploitation. Fisheries Research, 30: 199–216.

Buch, E. 1990. A monograph on the physical oceanography of the Greenland waters. Greenland Fisheries Research Institute. Copenhagen 1990 (mimeo).

Brander, K. 1978. The relationship between vertebral number and water temperature in cod. Journal du Counseil International pour l'Exploration de la Mer, 38: 286–292.

Christiansen, F. B., Nielsen, V. H., and Simonsen, V. 1988. Genetics of Zoarces populations XV. Genetic and morphological variation in Mariager Fjord. Hereditas, 109: 99–112.

Chumakov, A. K. 1969. The Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Iceland area – The halibut fishery and tagging. Journal of Ichthyology, 9: 901–902.

Fahy, W. E. 1972. Influence of temperature change on number of vertebrae and caudal fin rays in *Fundulus majalis* (Walbaum). Journal du Counseil International pour l'Exploration de la Mer, 34: 217–231.

Fahy, W. E. 1976. The morphological time of fixation of the total number of vertebrae in *Fundulus majalis* (Walbaum). Journal du Counseil International pour l'Exploration de la Mer, 36: 243–250.

Fairbairn, D. J. 1981. Biochemical genetic analysis of population differentiation in Greenland halibut (*Reinhardtius hippoglossoides*) from the Northwest Atlantic, Gulf of St Lawrence and Bering Sea. Canadian Journal of Fisheries and Aquatic Science, 38: 669–677.

Heincke, F. 1898. Naturgeschichte des Herings. Teil I. Die lokalformen und die wanderungen des Herings in den Europäischen Meeren. Deutschen Seefischerei-Verein. II. Band. Heft 2.

Hosmer, D. W., and Lemeshow, S. 1989. Applied logistic regression. John Wiley & Sons, Inc. 307 pp.

Hulme, T. J. 1995. The use of vertebral counts to discriminate between North Sea herring stocks. ICES Journal of Marine Science, 52: 775–779.

Jensen, A. S. 1935. The Greenland halibut (*Reinhardtius hippoglossoides* (Walb.)) its development and migrations. K. Danske Vidensk. Selsk. Skr., 9RK., 6: 1–32.

Junquera, S., and Zamarro, J. 1994. Sexual maturity and spawning of Greenland halibut (*Reinhardtius hippoglossoides*) from Flemish Pass area. NAFO Scientific Council Studies, 20: 47–52.

Jørgensen, O. A. 1997. Movement patterns of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), at West Greenland, as inferred from trawl survey distribution and size data. Journal of Northwest Atlantic Fishery Science, 21: 23–37.

Khan, R. A., Dawe, M., Bowering, R., and Misra, R. K. 1982. Blood Protozoa as an aid for separating stocks of Greenland halibut, *Reinhardtius hippoglossoides*, in the North-western Atlantic. Canadian Journal of Fisheries and Aquatic Science, 39: 1317–1322.

McCullagh, P., and Nelder, J. A. 1989. Generalized linear models. Second Edition. Chapman and Hall. London. 551 pp.

Misra, R. K., and Bowering, W. R. 1984. Stock delineation of Greenland halibut in the Northwest Atlantic using a recently developed multivariate statistical analysis based on meristic characters. North American Journal of Fisheries Management, 4: 390–398.

Nielsen, J. G., and Boje, J. 1995. Sexual maturity of Greenland halibut at West Greenland based on visual and histological observations. NAFO SCR. Doc. 95/18, Ser. No. N2525 (mimeo).

Reimer, L. W., and Ernst, P. 1989. Results of parasitological investigations as an index of stock delimitations concerning occurrence of Greenland halibut (*Reinhardtius hippoglossoides* Walb) in the Northwest Atlantic. NAFO SCR. Doc. 89/73 Ser. No. N1654 (mimeo).

Riget, F., and Boje, J. 1989. Fishery and some biological aspects of Greenland halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. NAFO Scientific Council Studies, 13: 41–52.

Riget, F., Boje, J., and Simonsen, V. 1992. Analysis of meristic characters and genetic differentiation in Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic. Journal of Northwest Atlantic Fishery Science, 12: 7–14.

SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6. Fourth edition. Vol. 2. Cary, NC: SAS Institute Inc. pp. 1086–1090.

Serebryakov, V. P., Chumakov, A. K., and Tevs, I. I. 1992. Spawning stock, population fecundity and year-class strength of Greenland halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic, 1969–88. Journal of Northwest Atlantic Fishery Science, 14: 107–113.

Sigurdsson, A. 1979. The Greenland halibut *Reinhardtius hippoglossoides* (Walb.) from Iceland to Norway. Rit. Fiskideildar, 6: 3–6.

Smidt, E. L. B. 1969. The Greenland halibut, *Reinhardtius hippoglossoides* (Walb.), biology and exploitation in Greenland waters. Medd. Danm. Fisk.-og Havunders, 6: 79–148.

Templeman, W. 1970. Vertebral and other meristic characters of Greenland halibut, *Reinhardtius hippoglossoides*, from the Northwest Atlantic. Journal of the Fisheries Board of Canada, 27: 1549–1562.

Templeman, W. 1973. Distribution and abundance of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Northwest Atlantic. ICNAF Research Bulletin, 10: 83–98.

Tåning, Å. V. 1946. Stage of determination of vertebrae in teleostean fishes. Nature, 157 (3992): 594–595.

Vis, L. M., Carr, S. M., Bowering, W. R., and Davidson, W. S. 1997. Greenland halibut (*Reinhardtius hippoglossoides*) in the North Atlantic are genetically homogeneous. Canadian Journal of Fisheries and Aquatic Science, 54: 1813–1821.