

Long-term variability of growth and recruitment of cod (*Gadus morhua*) off Greenland

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Growth variation was estimated from mean lengths-at-ages 4 and 5 for Atlantic cod off Greenland based on 52 973 fish taken from commercial and scientific catches from 1955 to 2002. Mean length-at-age values were corrected for area and seasonal effects, and significant growth reductions occurred during the 1960s and from the mid-1970s until the mid-1980s. Annual growth rates of cod in Greenland waters during the most recent decade (1993–2002) were consistently among the highest recorded. Statistical growth models accounting for temperature, fishing mortality, and stock abundance effects were constructed. Multiple linear regressions revealed significant positive temperature effects on growth of both age groups and a significant negative stock density effect on length-at-age 4. Correlations between exploitation intensity and length-at-age were statistically insignificant. During the period 1955–2002, the number of recruits at age 3 was significantly correlated with the Greenland cod spawning-stock biomass, June water temperature on top of Fyllas Bank (West Greenland), and Iceland cod recruitment. All factors had a positive effect on the number of Greenland recruits and, combined, accounted for 60% of the observed variation. Spawning stock size was, by far, the most important factor contributing to recruitment variability, while June water temperature below 1°C and Iceland recruits below 150 million never coincided with high year-class strength in Greenland during the past 50 years. Thus, previous conclusions regarding a close relation between the Greenland and Icelandic cod stocks might need to be reconsidered in the light of a continued recruitment failure in Greenland waters over the two most recent decades, despite the improved environmental conditions and near-average recruitment of the Icelandic stock. The low precision of the recruitment model, however, prevents reliable predictions in the short or medium term, but a substantial short-term recovery of the Greenland cod stock remains unlikely.

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Introduction

Atlantic cod (*Gadus morhua*) is described as a common species in the Greenland fauna, although it is at its ecological northern boundary (Hansen, 1949; Buch *et al.*, 1994). Greenland cod have often been studied to quantify environmental effects on stock production determined from variation in natural mortality, growth, and recruitment. However, the southern demersal marine fish assemblage inhabiting shelves and the continental slope off Greenland is dominated by boreal species (Rätz, 1999), while arctic species are minor. Given suitable environmental conditions, cod in the offshore areas off Greenland are considered to be self-sustaining (ICES, 2003), but are among the least

productive North Atlantic cod stocks (Rätz and Lloret, 2003). Stock parameters, i.e. slow growth, poor condition (Lloret and Rätz, 2000), and late maturation, suggest that, to be sustainable, exploitation rates would need to be low, particularly during persistent cold periods.

Since the early 1920s, marine life on the shelves and continental slopes off Greenland has been significantly affected by fishing activities. The cod stock was considered the main commercial and biological species off Greenland, but collapsed during the early 1970s and has remained at a very low level since then (ICES, 2003). Cod abundance and spawning-stock biomass have declined by almost 100% from initial levels observed during the mid-1950s when annual catches first exceeded 300 000 t.

The main goal of the present investigation is to identify factors associated with the progressive commercial extinction of Greenland cod. Constrained by the data available, we focus our analyses on variations of cod length-at-age as a function of ambient temperature, exploitation rate, and fish density, and on recruitment variation as a function of temporal changes in water temperature and the spawning-stock biomass. We also considered the effects of Icelandic cod recruitment on Greenland recruitment (Figure 1), as these have been described as being closely related (Buch *et al.*, 1994; Schopka, 1994). The present analyses can be regarded as an extension of an earlier study (Rätz *et al.*, 1999), augmented by an additional 10 years of data and additional variables.

Material and methods

Length-at-age

Since 1955, cod length and age data were obtained from German commercial catches off East Greenland (ICES Division XIVb) and West Greenland (NAFO Division 1B–1F) and from annual scientific bottom trawl surveys in autumn since 1982. Length measurements and otolith collections were conducted directly on board the fishing or research vessels or derived from fresh fish landings at fish markets in Cuxhaven or Bremerhaven (Germany). Sampling strategy was stratified by area (East and West Greenland), year, season, and fish size to ensure wider and more balanced sample coverage over space and time. Length measurements were performed with a precision of 1 cm. One sagitta otolith was removed from each fish and stored

in paper envelopes for subsequent age determination as growth differences of right and left sagitta otoliths are exceptionally rare (May, 1964). Until the mid-1980s, the otolith was cut transversely across the central region using a thin, copper-bladed saw running in diamond dust and aged under a binocular microscope using transmitted light (Meyer, 1965). Thereafter, otoliths were embedded in polyester resin and thin slides of the central region of the otoliths were cut and used to determine the ages (Bedford, 1977).

The sampling programme from 1955 until 2002 comprised a total of 222 426 individual length measurements and age determinations covering the age range from 0 to 31 years. Length-at-age values vary interannually and are subject to area and seasonal (quarter) effects. Consequently, length and age data were aggregated by area (East and West Greenland), year, and quarter. Mean (arithmetic) length-at-age was calculated directly from the age–length keys for each area, year, and quarter. Only mean length-at-age values by area, year, and quarter based on at least 30 individual age determinations were considered sufficiently representative to be used in the present growth investigations. These conditions limited the data available to time-series of mean length-at-ages 4 and 5 based on 52 973 age determinations, as only these two age groups are found consistently covered by the sampling over the entire investigation period. Standard errors as a measure of variation of the mean length-at-ages 4 and 5 ranged around 10% without a trend over time.

To eliminate the seasonal effect, mean lengths-at-ages 4 and 5 were fit to linear regression models for East and West Greenland separately. Table 1 lists the resulting model parameters. For each year during the period 1955–2002,

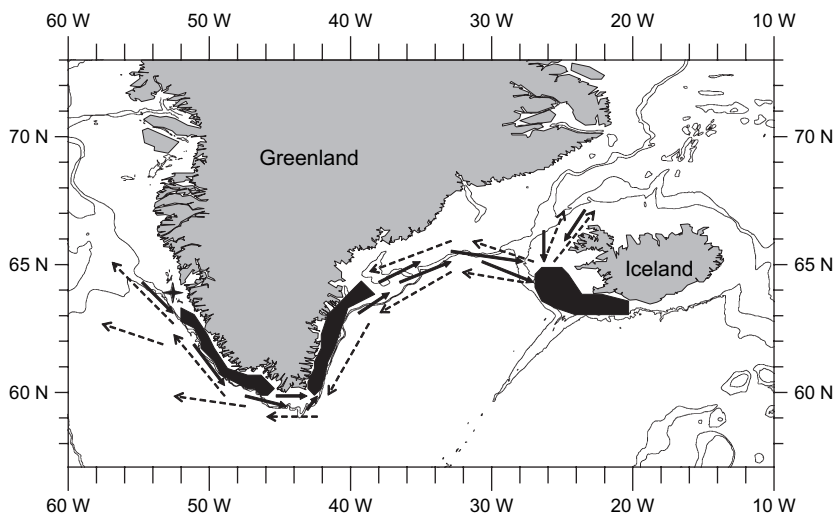


Figure 1. Continental shelves and slopes off Greenland and Iceland (500 and 1000 m isobaths) and the position of the oceanographic standard station on top of Fyllas Bank off West Greenland (+). Dark shaded areas off West and East Greenland and southwest Iceland delimit main cod spawning areas, dashed arrows indicate pelagic drift of early life stages (eggs, larvae, and 0-group), and solid arrows indicate homing migration of adult fish.

Table 1. Linear regression parameters estimating the quarter (seasonal) effect on size-at-ages 4 and 5 off East and West Greenland, respectively. *n* is the number of observations. *B*-values are the raw regression coefficients. *p*-level is the probability associated with the Student's *t*-statistic for the regression coefficients. *r*² is the squared Pearson correlation coefficient.

	Area			
	East Greenland		West Greenland	
	Age		Age	
	4	5	4	5
<i>n</i>	47	86	56	91
Intercept (cm)	49.25	55.97	44.00	53.61
<i>B</i>	6.49	10.02	7.26	6.11
<i>p</i> -level	0.02	0.00	0.00	0.00
<i>r</i> ²	0.11	0.26	0.16	0.10

the observed or estimated mean lengths by quarter were averaged to represent single annual values during the period of investigation.

Second, to account for the area effect on the cod growth off East and West Greenland (Rätz, 1994), both data sets of annual mean lengths-at-ages 4 and 5 were combined into one matrix with means calculated by weighting by landings off East and West Greenland, respectively. Historical landing shares were reviewed by Horsted (2000) and adopted from the recent report of the ICES North-western Working Group assessing cod stocks of Greenland and Iceland (ICES, 2003). This calculation of weighted mean lengths-at-ages 4 and 5 (Table 2) assumes that the fishery reflects temporal changes in the stock distribution.

Stock parameters

Commercial catch length and age and bottom trawl survey data constituted the basis for the historic Greenland cod stock assessment carried out by the North-western Working Group (ICES, 1996), which applied the VPA method including extended survivor tuning (XSA). That historic, 1996 assessment covered the offshore component of the cod stock only and used 1992 as the terminal year, in the absence of appropriate sampling, to estimate landings in numbers and other input parameters for later years. However, in order to consider more recent information (up to and including 2002) in the analysis of the growth and recruitment variations, an updated, age structured analytical assessment was formulated. It used identical model parameters compared with the earlier analysis, i.e. age range 3 to 10 years, tuning data from the more recent survey results, time taper weighting, catchability settings, and statistical shrinkage. Since 1994, officially reported landings from offshore catches varied below 500 t. Since 1993, annual landings in numbers were estimated by

applying relative age compositions for age groups 3 years and older as derived from surveys for East and West Greenland, respectively. Updates of weight and maturity-at-ages are also based on survey records, while matrices specifying natural mortality and partial fishing and natural mortality before spawning were simply extended with the standard values used previously.

Figure 2, which displays trends in spawning-stock biomass (SSB) and fishing mortality (F), demonstrates the consistency between the assessment update with the historic stock parameters except for the fishing mortality in 1992, which was significantly underestimated, being the terminal value. SSB and F do not reveal significant retrospective differences. Stock variables, including numbers of age 3 and older fish and recruitment at age 3, are listed in Table 2. The stock assessment update reveals that Greenland cod recruitment has failed for almost two decades, with 1984 being the last strong year class (recorded in 1987 as 3 year olds).

We also included recruitment estimates at age 3 of Icelandic cod to analyse the effect of Iceland cod year-class strength on the Greenland cod recruitment success. These estimates were adopted from the ICES North-western Working Group report (ICES, 2003). It can be seen from Table 2 that the Icelandic cod stock recently produced near-average recruitment with very little variation.

Water temperature

Water temperatures on top of the Fyllas Bank off West Greenland (Stein, 1988) have been measured by the Greenland Fisheries Research Institute during mid-June of each year since 1950 (Figure 1). Mean temperature of the surface layer was derived by averaging observations at six standard depth levels: 0, 10, 20, 30, 40, and 50 m. Buch (1984) showed that temperature trends in neighbouring areas were similar to those on Fyllas Bank due to advection and solar heating. Stein (2000) found that variation in subsurface temperature (0–50-m depth) over the Bank is closely related to variation in mean temperature over the slope off Fyllas Bank (0–300-m depth). Thus, the mid-June temperature regime on Fyllas Bank is considered to be a representative index of thermal conditions in the shelf region off West Greenland (Hansen and Buch, 1986). Values considered in the present analyses are the average water temperature of the upper 50 m adopted from Buch and Ribergaard (2003). The most recent decade was distinguished by near average or above average Fyllas Bank water temperatures. No measurement was taken in 1991.

Analyses of variation in growth

Stepwise multiple linear regressions were applied to analyse interannual variation in mean lengths-at-ages 4 and 5 (dependent variables). As length-at-age has a cumulative feature resulting not only from present but also from previously experienced effects, fish sizes observed at ages 4 and

Table 2. Lengths-at-ages 4 and 5 (in cm) off Greenland, mean water temperature (in °C) of the upper 50 m on top of Fyllas Bank (West Greenland), recruits at age 3 off Iceland (in numbers $\times 10^3$), stock size off Greenland (in numbers $\times 10^6$ of age 3 and older), fishing mortality (F for ages 5–8), and recruits at age 3 (in numbers $\times 10^3$) and SSB (in t) off Greenland.

Year	Length-at-age 4 (cm)	Length-at-age 5 (cm)	Temperature (°C)	Recruits aged 3 Iceland ($\times 10^3$)	Stock 3+ Greenland (millions)	F mean 5–8	Recruits aged 3 Greenland ($\times 10^3$)	SSB Greenland (t)
1955	46.5	54.1	1.2	154 700	1310.8	0.111	150 828	1 776 132
1956	47.9	55.7	0.9	182 232	1391.8	0.149	498 095	1 481 344
1957	46.9	53.9	2.3	170 017	1087.1	0.206	101 203	1 299 710
1958	47.4	55.6	2.2	218 965	967.6	0.208	128 720	1 439 424
1959	49.2	58.2	1.6	301 029	1044.2	0.194	440 175	1 012 827
1960	49.8	59.3	2.7	152 184	1274.2	0.203	507 999	1 186 883
1961	51.5	61.7	3.2	196 010	1169.5	0.270	217 996	1 035 511
1962	51.6	62.4	2.2	132 986	910.7	0.387	90 018	978 299
1963	49.1	60.3	1.6	172 384	976.8	0.365	393 287	980 748
1964	50.0	59.4	2.3	276 699	1334.8	0.398	678 161	856 437
1965	50.4	60.1	2.1	247 052	1249.6	0.400	274 392	684 099
1966	47.9	59.8	1.6	269 545	1192.0	0.406	314 670	691 768
1967	49.2	57.7	1.5	312 476	912.1	0.417	98 314	797 803
1968	47.1	56.3	2.1	170 555	611.8	0.455	34 539	743 324
1969	48.3	53.0	0.3	253 916	380.4	0.375	35 661	538 659
1970	47.4	57.1	0.3	185 905	246.3	0.239	20 133	441 435
1971	47.9	57.4	0.8	185 795	228.0	0.403	78 492	349 444
1972	47.8	56.9	0.6	139 494	144.8	0.512	3 949	227 099
1973	48.7	57.3	1.7	282 957	91.1	0.407	8 914	95 491
1974	48.7	54.8	1.4	177 179	49.2	0.610	5 527	79 949
1975	50.8	58.7	1.9	260 858	46.2	1.000	20 941	53 937
1976	50.7	63.8	1.4	391 593	130.2	0.872	107 257	26 551
1977	50.1	58.8	2.2	139 528	97.4	0.763	14 167	16 001
1978	49.9	60.4	0.9	224 158	77.4	0.328	16 139	26 244
1979	49.2	55.5	2.3	243 663	68.7	0.491	21 019	47 234
1980	47.3	56.8	1.9	146 789	107.4	0.266	59 626	49 126
1981	48.1	57.3	1.6	144 442	91.6	0.281	12 683	53 909
1982	47.9	56.7	0.8	133 815	114.5	0.817	50 098	83 197
1983	48.3	56.1	0.4	224 560	71.9	0.894	6 918	62 573
1984	49.0	57.1	1.0	140 922	49.0	0.621	12 531	68 314
1985	47.9	56.8	2.1	136 228	29.7	0.258	1 672	40 937
1986	51.9	60.0	2.2	342 946	29.4	0.175	9 325	31 908
1987	52.0	59.9	2.1	301 229	226.8	0.101	206 413	37 951
1988	50.3	58.1	2.0	181 450	240.4	0.947	60 666	71 994
1989	44.7	56.7	0.9	86 342	165.6	0.851	992	183 298
1990	47.5	51.8	0.8	128 886	79.5	1.243	1 270	105 432
1991	51.1	60.7		107 725	18.8	0.957	468	23 731
1992	54.4	61.0	1.0	165 646	5.4	2.401	265	13 394
1993	52.5	62.5	1.5	144 582	1.3	1.290	762	1 375
1994	52.5	61.0	1.4	74 331	0.6	0.596	181	756
1995	52.5	61.9	1.3	148 206	0.6	0.915	288	595
1996	52.5	61.0	2.2	181 142	0.7	0.721	284	572
1997	52.8	62.5	1.2	81 738	0.6	0.367	132	1 101
1998	52.5	61.9	3.4	155 886	0.5	0.760	177	978
1999	52.5	61.0	2.6	58 125	0.7	0.164	429	698
2000	50.1	61.0	2.5	184 586	1.1	0.121	514	904
2001	53.3	60.6	1.7	166 110	1.4	0.171	638	2 031
2002	52.5	60.7	1.8	167 018	3.3	0.273	2 271	3 519

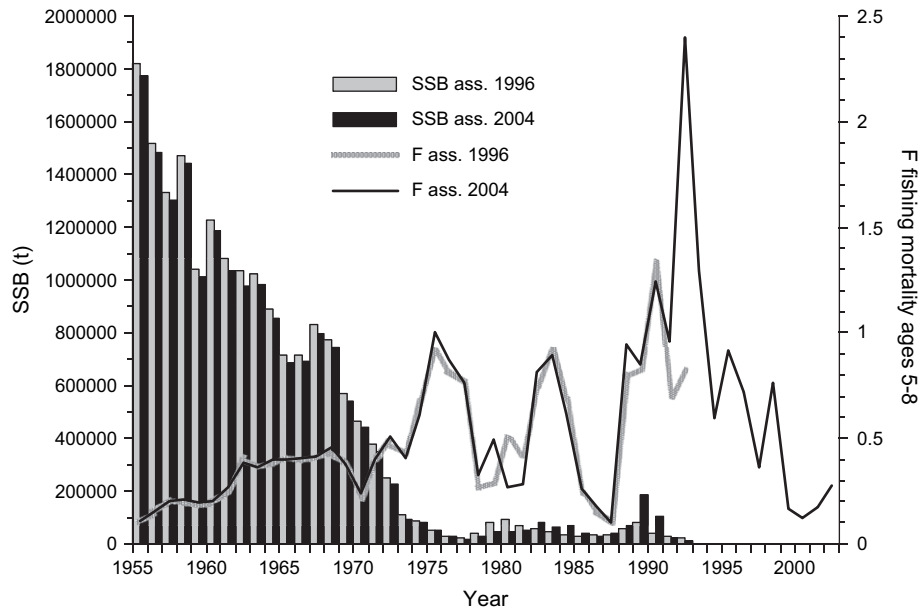


Figure 2. Spawning-stock biomass (SSB) and fishing mortality (mean over age groups 5 to 8) since 1955 as estimated in 1996 (historic assessment) and 2004 (updated assessment).

5 were regressed against the independent variables of mean water temperature, mean reference F over ages 5 to 8, and mean stock size (age 3 and older) since age 3. All statistical analyses were performed using the software STATISTICA (www.statsoft.com).

Analyses of variation in recruitment

Greenland cod recruitment at age 3 was taken as the dependent variable in a stepwise, multiple linear regression analysis with water temperature, Greenland cod SSB, and Icelandic cod recruitment as the independent variables. In order to account for the time-lag between recruitment at age 3 and SSB and temperature in a given year, respective SSB and temperature values were lagged by three years to match the birth year. Because no temperature measurement was taken in 1991, the time-series consisted of 44 years of data.

Results

Analyses of variation in length-at-age

Effects on fish lengths-at-ages 4 and 5 were analysed, first for average temperatures since age 3. A significant positive effect was found, although only 12 and 16% of the variation in length-at-ages 4 and 5 is explained by the temperature models, respectively (Tables 3 and 4; Figures 3A and 4A). The temperature effect was greater than fishing mortality or stock size effects. The effect of average fishing mortality since age 3 on size-at-ages 4 and 5 was insignificant (Tables 3 and 4; Figures 3B and 4B). There was a significant negative stock size effect on length-at-age 4 explaining

about 9% of the observed variation (Table 3; Figure 3C), but no significant correlation with the size-at-age 5 (Table 4; Figure 4C) was observed.

The multiple linear regression model used to fit lengths-at-age 4 based on temperature, fishing mortality, and stock size explained 39% of the observed variation. The temperature effect had the largest regression coefficient. The coefficient is larger than that for temperature alone. The positive correlation with fishing mortality also becomes significant when combining all three effects (Table 3). The time-series of the observed lengths-at-age 4 and the model values are illustrated in Figure 3D. In general, the model captures the observed variation with only a few points outside or close to the 95% prediction levels, the only outlier being the 1989 value (corresponding to the 1985 year class).

Results derived from the multiple regression model for age 5 are similar to that for age 4. Temperature since age 3 has the largest regression coefficient. The fishing mortality effect increased significantly compared with the single linear model. However, the stock size effect is insignificant in both the linear and multiple regression model formulations for age 5. The multiple regression model explains 38% of the variation (Table 4; Figure 4D), with the 1985 year class (5 year olds in 1990) being the only major deviation.

Analyses of variation in recruitment

Figure 5 shows the relationship between age 3 Greenland cod recruits vs. the Fyllas Bank water temperature (Figure 5A), Greenland spawning-stock biomass (Figure 5B), and the

Table 3. Parameters of single and multiple linear regression models describing variation in lengths-at-age 4, 1956–2002. Values and functions are shown in Figure 3. n is the number of observations. Beta and B values are the standardized and raw regression coefficients, respectively. s.e. is the standard error of beta values. p-level is the probability associated with the Student’s t-statistic for the regression coefficients. The magnitude of the beta coefficients allows comparison of the relative contribution of each independent variable in the prediction of the dependent variable. r² is the squared Pearson correlation coefficient.

Dependent variable	Independent variable	n	Beta	s.e.	Intercept	B	p-level	r ²
Single effects								
Length-at-age 4	Temperature since age 3	47	0.34	0.14	47.846	1.184	0.02	0.12
Length-at-age 4	F since age 3	47	0.27	0.14	48.966	1.597	0.06	0.08
Length-at-age 4	Stock size age 3+ since age 3	47	−0.30	0.14	50.328	−0.001	0.04	0.09
Multiple effects					45.810		0.00	0.39
Length-at-age 4	Temperature since age 3		0.57	0.13		1.992	0.00	
	F since age 3		0.38	0.14		2.200	0.01	
	Stock size age 3+ since age 3		−0.29	0.13		−0.001	0.03	

Icelandic cod recruitment measured at age 3 (Figure 5C). All three variables were significantly and positively correlated with the Greenland stock recruitment (Table 5). Spawning-stock biomass was the most influential variable, explaining 48% of the observed variation, followed by temperature and the Icelandic cod stock year-class strength sharing almost equal and much lower regression coefficients. No strong recruitment was observed when the water temperature fell below 1°C or if Icelandic cod recruitment fell below 150 million individuals.

We also formulated a multiple linear regression model for the number of Greenland cod stock recruits at age 3 (dependent variable) as a function of the significant and positive effects of temperature, spawning-stock biomass, and Icelandic recruitment strength (independent variables). This model explained 60% of the variation in year-class strength (Table 5). The model generally followed the negative trend to almost zero until the mid-1980s, with the strong 1984 year class being the only exceptional deviation (Figure

5D). Given the high recruitment variation during the period 1955–1975, the prediction limits at 95% confidence amount to about 200 million recruits despite the very low level of recent recruitment.

Discussion

The present assessment update for Greenland cod extends the previously available time-series of spawning-stock biomass, fishing mortality, and recruitment by 10 years until 2002 without significant retrospective changes (ICES, 1996). During 1955–2002, the Greenland cod stock underwent dramatic demographic changes. Both spawner biomass and recruitment declined by nearly 100% when initial and final estimates were compared. The spawning-stock biomass of the offshore component collapsed from 1.8 million t to 50 000 t in 1975. Since then, the estimates varied at this low level and continued

Table 4. Parameters of single and multiple linear regression models describing variation in lengths-at-age 5, 1957–2002. Values and functions are shown in Figure 4. n is the number of observations. Beta and B values are the standardized and raw regression coefficients, respectively. s.e. is the standard error of beta values. p-level is the probability associated with the Student’s t-statistic for the regression coefficients. The magnitude of the beta coefficients allows comparison of the relative contribution of each independent variable in the prediction of the dependent variable. r² is the squared Pearson correlation coefficient.

Dependent variable	Independent variable	n	Beta	s.e.	Intercept	B	p-level	r ²
Single effects								
Length-at-age 5	Temperature since age 3	46	0.40	0.14	55.475	1.974	0.01	0.16
Length-at-age 5	F since age 3	46	0.22	0.15	57.750	1.800	0.13	0.05
Length-at-age 5	Stock size age 3+ since age 3	46	−0.13	0.15	59.010	−0.001	0.37	0.02
Multiple effects					51.781		0.00	0.38
Length-at-age 5	Temperature since age 3		0.65	0.14		3.190	0.00	
	F since age 3		0.46	0.15		3.617	0.00	
	Stock size age 3+ since age 3		−0.13	0.14		−0.001	0.36	

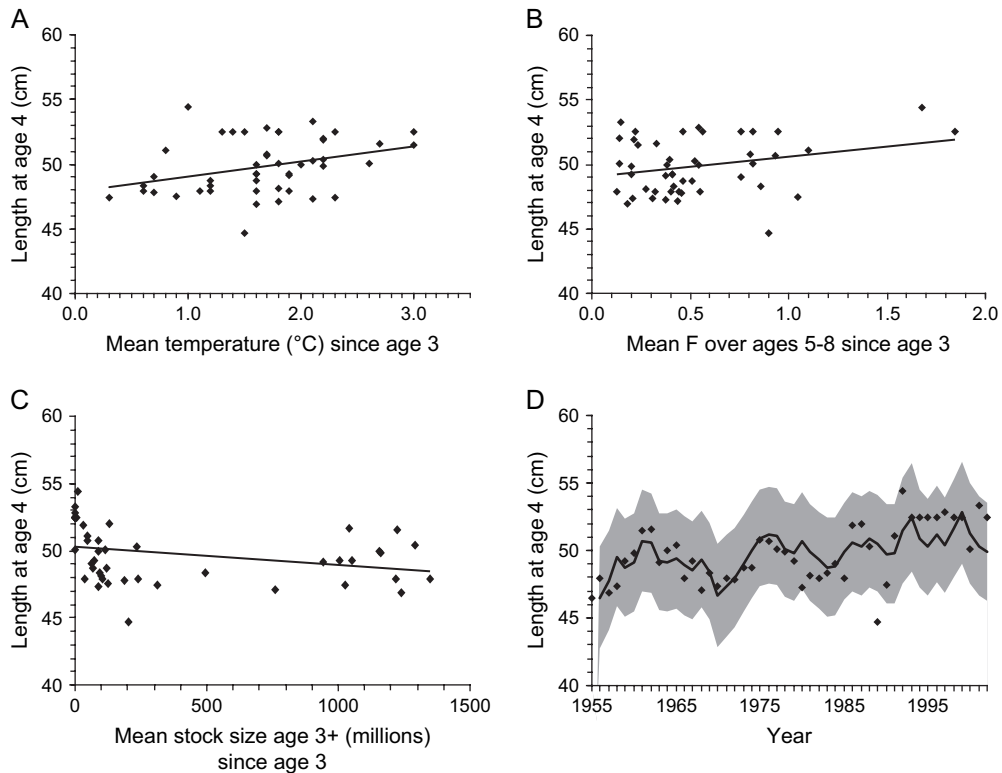


Figure 3. Single and multiple linear regression models describing variation in lengths-at-age 4, 1956–2002. A: As a function of mean temperature since age 3; B: as a function of mean F reference since age 3; C: as a function of mean stock size (density) since age 3, D: as a function of all three independent variables, prediction limits at 95% confidence are shaded grey. Regression parameters are given in Table 3.

to decline, with the exception of the strong 1973 and 1984 year-classes' recruitment to the spawning stock. However, since both year classes were subject to high fishing mortality rates, they contributed only a small increase to the spawning-stock biomass during the early and late 1980s, respectively. After that, the offshore stock component remained depleted without any significant signal of recovery. Obviously, the stock did not sustain fishing mortalities of about 0.3 to 0.4 during the 1960s and, already 30 years ago, the stock collapsed as fishing mortality increased and periodically exceeded 0.6. Since the mid-1970s, the spawning stock has remained very low and decreased to commercial extinction during the early 1990s. The stock assessment update results indicate a general decline in fishing mortality below 0.2 since the mid-1990s, as implied by the very low annual landings below 500 t reported since 1993.

Analyses of variation in length-at-age

Ambient temperature, fishing selection, and stock size (density) through food limitation are considered primary factors affecting variation in growth (ICES, 2002). Our growth analyses are limited to estimates of mean lengths-at-ages

4 and 5 as indicators of cod growth, owing to irregular data availability for other age groups throughout the period of investigation. The annual mean length-at-age values from 1955 to 2002 obtained from both commercial and scientific catches are corrected for significant quarter and area effects (West and East Greenland), applying linear models. Temperature, fishing mortality, and stock abundance were averaged over the lifespan since age 3 in order to reflect their cumulative effects on growth. Mean size-at-age over longer periods resulted in less significant correlations, probably because of some compensatory growth related to other effects.

Interannual variation in size-at-ages 4 and 5 was estimated to be about 10 cm. The analyses revealed significant reductions in mean lengths of Greenland Atlantic cod at ages 4 and 5 during the 1960s by 5 and 10 cm, respectively. A second major growth reduction occurred from the mid-1970s until the mid-1980s. During the most recent decade (1993–2002), growth rates of cod in Greenland waters were among the highest recorded. Similar size variation has been documented for the cod stocks around the Faroe Islands (Jákupsstovu and Reinert, 1994) and Labrador (Shelton and Morgan, 1994), while stocks inhabiting temperate habitats show less size variation, e.g. the North Sea (Cook *et al.*, 1999).

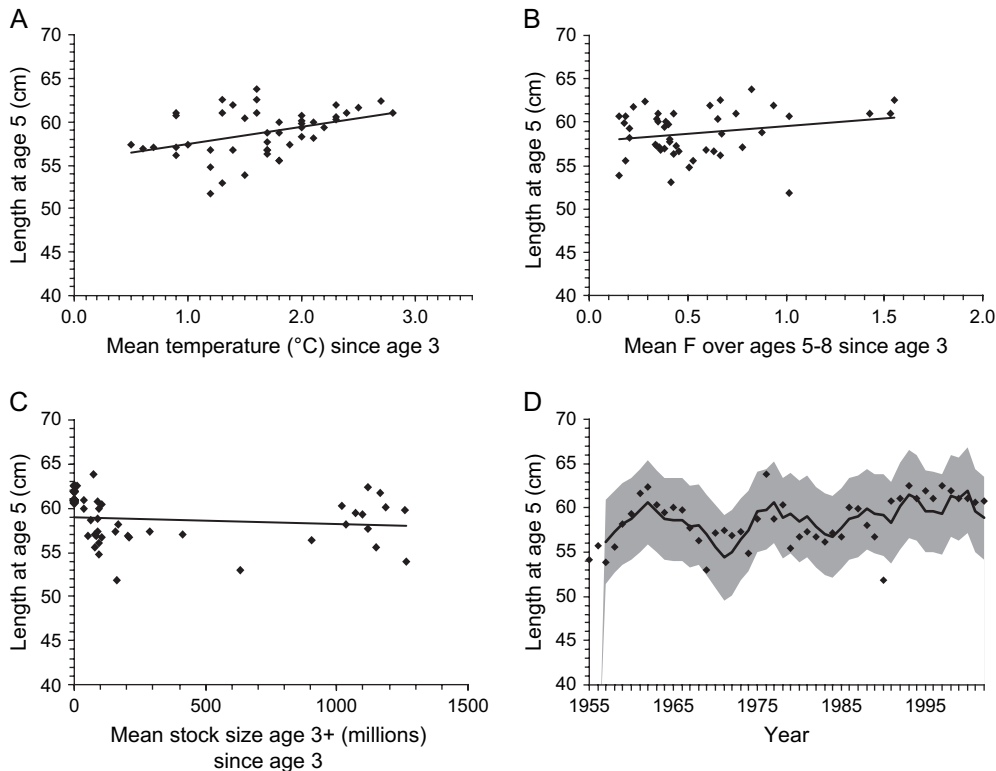


Figure 4. Single and multiple linear regression models describing variation in lengths-at-age 5, 1957–2002. A: As a function of mean temperature since age 3; B: as a function of mean F reference since age 3; C: as a function of mean stock size (density) since age 3; D: as a function of all three independent variables, prediction limits at 95% confidence are shaded grey. Regression parameters are given in Table 4.

Single and multiple linear regressions suggested that size-at-ages 4 and 5 are affected positively by temperature. Our analyses are based on arithmetic means of the water temperature of the upper 50 m recorded at a fixed station over the Fyllas Bank in June. This is the only available long-term indicator of the regional sea temperatures, and is considered to be representative of the temperature variability experienced by cod. The linear regressions were significant but explained only 12 and 16% of the observed variation in length-at-ages 4 and 5, respectively. Temperature, however, had the largest regression coefficients in the multiple models when fishing mortality and stock size effects were included. The models would gain more explanatory power by exclusion of the anomalous 1985 year-class mean lengths. For decades, the influence of environmental conditions on cod growth has been a central question in fisheries biology and has attracted considerable scientific interest (Taylor, 1958). Many authors (e.g. Hansen, 1949; Dementyeva and Mankevich, 1965; Jónsson, 1965; Jørgensen, 1992; Nakken, 1994; Brander, 1995) found positive correlations between temperature and fish size-at-age, which are consistent with the analyses presented here. Brander (1995) concluded that year-to-year variation in weight-at-age of cod within and between stocks might be

largely controlled by water temperature and highlighted the importance with respect to stock and catch assessments and resulting predictions used for management purposes.

In addition to the direct effect of temperature on the physiology of poikilothermic animals (assimilation, metabolism, transformation, and excretion; Brett, 1979), there could also be indirect effects such as changes in food quality or availability. Jørgensen (1992), Nilssen *et al.* (1994), and Steinarsson and Steffansson (1991) demonstrated positive effects of capelin (*Mallotus villosus*) abundance on Arcto-Norwegian and Icelandic cod growth rates, the main food item of these stocks. Recently developed bioenergetic models combined temperature, food quality, and quantity and condition effects to explain growth variation (Krohn *et al.*, 1997; Lambert and Dutil, 1997).

The present analyses do not confirm earlier findings suggesting low fish sizes during periods of intensive exploitation as indicated by high fishing mortalities (Rätz *et al.*, 1999). Correlations between length-at-ages 4 and 5 and mean fishing mortality since age 3 are insignificant but become significantly positive in the multiple linear regressions including temperature and density effects. The inconsistency with the previous results is due to incorporation of the new data with exceptionally high fishing

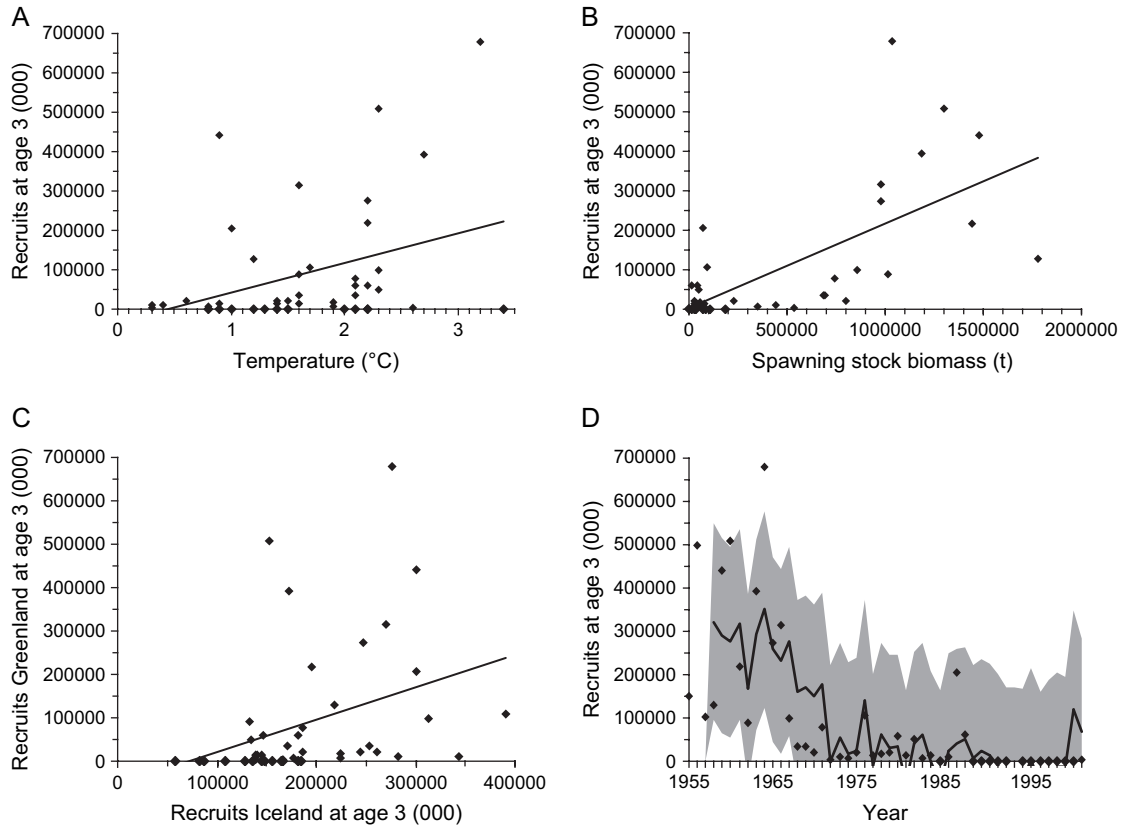


Figure 5. Single and multiple linear regression models describing variation in recruitment at age 3 of the Greenland cod stock, 1958–2002. A: As a function of mean temperature during year of birth; B: as a function of SSB during year of birth; C: as a function of recruitment at age 3 of the Icelandic cod stock; D: as a function of all three independent variables, prediction limits at 95% confidence are grey shaded. Respective regression parameters are given in Table 5.

mortalities assessed in the years 1992–1994. Consequently, the hypothesis of higher survival probability of slow-growing cod can no longer be supported. Reverse size-selective fishing owing to disproportionately high removals of slow-growing cod was also found in the southern Gulf of St. Lawrence (Hanson and Chouinard, 1992).

Fish density has been considered an important factor in determining growth rates because of intra-specific competition. Theoretically, growth rates should decrease with increasing abundance (Hempel, 1957). Results of the present study support this hypothesis for lengths-at-age 4, but not for age 5. This suggests that stock density may only

Table 5. Parameters of single and multiple linear regression models describing variation in recruitment of Greenland cod at age 3, 1958–2002. Values and functions are shown in Figure 5. n is the number of observations. Beta and B values are the standardized and raw regression coefficients, respectively. s.e. is the standard error of beta values. p-level is the probability associated with the Student's t -statistic for the regression coefficients. The magnitude of the beta coefficients allows comparison of the relative contribution of each independent variable in the prediction of the dependent variable. r^2 is the squared Pearson correlation coefficient.

Dependent variable	Independent variable	n	Beta	s.e.	Intercept	B	p-level	r^2
Single effects								
Recruits Greenland	Temperature –3 years	44	0.36	0.14	–33 679	75 604	0.02	0.13
Recruits Greenland	SSB –3 years	44	0.70	0.11	3 656	0.214	0.00	0.48
Recruits Greenland	Recruits Iceland	44	0.35	0.14	–54 060	0.746	0.02	0.12
Multiple effects								
Recruits Greenland	Temperature –3 years	44	0.31	0.10	–187 291	66 066	0.00	0.60
	SSB –3 years		0.59	0.11		0.181	0.00	
	Recruits Iceland		0.23	0.11		0.502	0.03	

affect growth of the younger age groups, and that this effect diminishes as fish grow. The multiple linear regressions, with temperature and fishing mortality included, indicate a significant negative stock size effect, although the coefficients were small. In the case of the North Sea cod there was no evidence of density effects on the growth variation (Daan *et al.*, 1994). For the Northeast Arctic stock, density-dependent growth is equivocal since some studies reported an inverse relationship (Nilssen *et al.*, 1994), while others found no evidence to support it (Jørgensen, 1992). Inverse abundance effects were reported for the Icelandic (Schopka, 1994) and the Gulf of St. Lawrence (Swain, 1999) cod stocks. Obviously, cod at ages 4 and 5 off Greenland have benefited from continued warm conditions and low stock sizes over the past decade based on the evidence of high growth rates.

Analyses of variation in recruitment

Our analyses identified spawning-stock biomass, water temperature, and Icelandic stock recruitment as significant factors affecting Greenland cod reproductive success, particularly when they are jointly considered. The multiple linear regression model based on these three independent variables explained 60% of the observed variation in 3 year olds during 1958–2002, with the dominant explanatory factor being spawning-stock biomass. Earlier analyses, based on data from 1958 to 1992, revealed a model with less explanatory power, accounting for 51% variance in recruitment variation (Rätz *et al.*, 1999). Temperature and Icelandic stock year-class strength have only half of the explanatory power of spawning stock size. Thus, our results provide strong evidence that the collapse of the Greenland cod stock in the early 1970s was caused mainly by the progressive extinction of spawners by fishing activities. Wieland and Hovgård (2002) emphasize the importance of the spawning areas off southwest and southeast Greenland in their review of historic data on cod eggs and larvae drift. The sudden decline of the spawning stock was an important factor during the collapse of northern cod of Newfoundland and Labrador in the early 1990s (Hutchings and Myers, 1994). The Northeast Arctic cod stock is the only large cod stock lacking a significant parent stock size effect on recruitment (Pope *et al.*, 2001).

Environmental parameters contribute significantly to cod recruitment success (Fogarty *et al.*, 2001), both at the minimum temperature tolerance (deYoung and Rose, 1993; Lear and Parsons, 1993) in the Northwest Atlantic and the maximum tolerance level in the North Sea (O'Brien *et al.*, 2000). However, the long time-series of upper 50 m average Fyllas Bank June water temperature, adopted from Buch and Ribergaard (2003), explains only 13% of the recruitment variation. In Greenland waters, the temperature effect hardly seems to be linear but rather constrains Greenland cod recruitment to completely collapse when the temperature falls below 1°C. Survival rates of early

cod pelagic life stages seem to be very sensitive to the June temperature of upper water layers off West Greenland. This temperature constraint on pelagic eggs, larvae, and the 0-group might explain the northern distribution limit of Atlantic cod in Greenland waters, while later ontogenetic stages inhabit deeper and generally warmer habitats. Continued adverse temperature effects have certainly impeded recruitment during periods when the parent stock size has been sufficiently high. Stein and Borovkov (2004) found closer coincidence between recruitment and annual mean surface temperature measured between Greenland and Iceland, but there is no obvious biological explanation for the close correlation between high recruitment variation and low surface temperature variation (8.5 and 9.5°C) in this area. The authors, however, did not include the most recent 10 years of data considered here. These data show average or above average water temperatures off Greenland and continued recruitment failure.

It must be noted that the statistical significance of the recruitment and growth models reported herein is weakened by the temporal autocorrelation of some variables (e.g. SSB and recruitment) and colinearity (e.g. relationship between fishing mortality and stock size) as revealed from residual analyses.

Marine fish stock intermixing is a mechanism to safeguard their genetic diversity and productivity. Thus, the qualitative and quantitative analyses of long-term cod migration patterns across the North Atlantic have been undertaken ambitiously for 100 years (Schmidt, 1931; Tåning, 1937; Cushing, 1985). Schopka (1994) describes historic knowledge about the larval drift from Iceland spawning grounds to Greenland and the homing migration of adult fish to Iceland as being very strong before 1955, but only occasionally thereafter. Based on distribution patterns derived from 0-group surveys off East Greenland, the strong 1973 and 1984 Greenland year classes are indicated to be of Icelandic origin (Vilhjálmsón and Friðgeirsson, 1976; Vilhjálmsón and Magnússon, 1984). However, a comparison of Iceland and Greenland recruitment estimates since 1955 reveals a rare and weak relationship between both stocks, explaining only 12% of the variation of the latter. It is noticeable that recruitment levels below 150 million in the Icelandic cod stock never coincide with strong Greenland year classes. Our updated VPA assessment of the offshore Greenland cod stock confirms that recruitment overfishing was an important cause of its collapse in the early 1970s, supported by adverse environmental conditions for the early recruitment processes and sparse recruitment impulses from Iceland. Thus, previous conclusions regarding a close relation between the Greenland and Icelandic cod stocks (Buch *et al.*, 1994; Schopka, 1994) might need to be reconsidered in the light of a continued recruitment failure in Greenland waters over the two most recent decades, despite the improved environmental conditions and about-average recruitment of the Icelandic stock. Genetic studies might provide insight into the relationship

between both stocks. In general, the explanatory power of the low parent cod stock off Greenland increases further with the persistent recruitment failure. The low precision of the recruitment model, however, prevents reliable predictions in the short or medium term, but a substantial short-term recovery of the cod stock off Greenland remains unlikely.

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