ICES Annual Science Conference CM 2005/AA:07
Theme session: Cod in a Changing Climate

Changes in essential life history traits of Atlantic cod (*Gadus morhua* L.) off Greenland over the past two decades

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Abstract

The present investigation deals with the ecological relationships between the observed variability in essential population parameters of the cod stock off Greenland including environmental conditions, i.e. the near bottom water temperature. The data were derived from an annual autumn survey series commenced in 1982. The survey estimates confirmed that the spawning stock biomass remained very low after the major stock collapse in the early 1970s. The estimated total stock abundance has undergone dramatic changes due to very high recruitment variability, fishing and emigration to Iceland. However, the year class 2003 is assessed as the second strongest year class since 1982 and is estimated to amount to 71 % of the strongest year class 1984 at age 1, which yielded about 170 000 t throughout its life. The variation of the mortality estimates indicates that the progressive depletion of the strong year classes 1984 and 1985 was mainly due to over-fishing. The very low mortality rates recently observed are possibly supported by increased availability due to increased stock size and/or improved environmental year effects.

Interannual fluctuations in condition are positively correlated with water temperature and negatively with stock size. The recently improved condition of the cod off Greenland is indicated as enhanced from the continued warming and the low size of the stock. Furthermore, fish condition appears to affect the growth rates positively, with well conditioned fish growing faster than poorly conditioned fish. The observed changes to earlier maturation at age are correlated with water temperature, but they may have been caused by changes in growth too.

Recent good recruitment, high condition and high growth rates as well as early maturation coincide with continued warm water temperatures. The significantly increased productivity potential implied by these changes in essential population parameters urgently requires a definite multi-annual management plan consistent with the precautionary approach in fisheries management.

Keywords: Atlantic cod, Greenland, abundance, mortality, condition, growth, maturity, water temperature

Introduction

Essential population parameters such as abundance, biomass, growth, condition and reproductive potential change under environmental and fishing pressure. Age and size at sexual maturity, fecundity, growth and condition of Atlantic cod stocks vary over time due to a number of environmental and fishery characteristics (Brander, 1995; Rochet, 1998; Marteinsdottir and Begg, 2002; Heino et al., 2002). Fishing impacts are especially remarkable since important changes to life history traits are often concomitant with prolonged periods of exploitation (Hutchings, 2005). Among the environmental parameters, water temperature is a principal factor controlling productivity (growth, maturity, recruitment and condition) of Greenlandic cod (Rätz et al., 1999; Lloret and Rätz, 2000; Rätz and Lloret 2003 and 2004).

Atlantic cod (*Gadus morhua*) is described as a common species in the Greenland marine fauna, although it is at its northern ecological boundary (Hansen, 1949; Buch et al., 1994). During the last century and the recent past, Greenland cod has 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 2004) but are among the North Atlantic cod stocks with the lowest productivity (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.

Condition is a measure of the energy reserves of Atlantic cod, cod with a low condition presumably resulting from adverse environmental and feeding conditions or parasitic infections (Rätz and Lloret, 2003; Lloret and Rätz, 2000; Yaragina and Marshall, 2000; Lambert and Dutil, 1997a,b). Physiological condition is a particular important attribute of fishes and future population success because it has a large influence on growth, reproduction and survival (Shulman and Love, 1999). Poor condition (i.e. few available energy reserves) can have several consequences for cod. Reproductive success can be reduced through lower probability of maturing at a given size, lower fecundity and reduction in egg quality (Kjesbu et al., 1992; Marshall et al., 1999; Lambert & Dutil, 2000; Marteinsdottir and Begg, 2002). Because of the cumulative impact on reproduction, condition can finally affect the recruitment potential of stocks (Rätz and Lloret, 2003). Poor condition may also lower the chances of survival of big cod, leading to an increase of natural mortality (Krivobok & Tokareva, 1972), and reducing growth (Rätz and Lloret, 2003). Condition of cod follows interannual variations and seasonal cycles, with lower energy reserves occurring during spawning (Lambert and Dutil, 1997a; Lilly, 1996; Shelton and Lilly, 1995; Taggart et al., 1994; Eliassen and Vahl, 1982).

Since the early 1920s, the 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 2004). Cod abundance and spawning stock biomass have declined by almost 100% from the initial levels observed during the mid-1950s when annual catches first exceeded 300 000 tons. Over the last 3 decades, the stock's development and its exploitation was dependent on the rare occurrence of few strong year classes of 1973, 1984 and 1985, presumably originated from the Icelandic spawning grounds as eggs and larvae (Storr-Paulsen et al., 2004).

It is recognised, that the environmental conditions off Greenland have recently undergone a continued warming (Stein 2004 a and b). Thus, this paper presents a number of essential stock parameters like cod stock abundance, fish condition (relative condition index), size at age and maturity at age derived from annual groundfish surveys commenced in 1982, the only regular source of quantitative information regarding demersal fish stocks from the traditional fishing grounds off West and East Greenland south of 67° northern latitude. As such, the survey is regarded to represent the offshore cod stock component, which is assessed separately from the smaller inshore populations (ICES 2004). Abundance at age, cohort abundance and mortality estimates as well as maturity ogives used to separate the stock into its juvenile and adult portions are given. The trend in fish condition is shown since 1989 and analysed for stock size (density) and temperature effects. The annual variations in size at ages 3-6 in terms of length are explained by the variable fish condition. The proportion mature at ages 1-5 are illustrated and the trend in age at 50 % maturity is compared with variations in temperature, fish condition and stock size.

Material and Methods

Abundance, biomass estimates and length structures were derived from annual groundfish surveys covering shelf areas and the continental slope off West and East Greenland. Surveys commenced in 1982 and were primarily designed for the assessment of cod. Because of favourable weather and ice conditions and to avoid spawning concentrations, autumn was chosen for the time of the surveys. These were carried out by the research vessel (R/V) WALTHER HERWIG (II) throughout most of the time period. In 1984, R/V ANTON DOHRN was used and she was replaced by the new R/V WALTHER HERWIG III since 1994, respectively.

The fishing gear used was a standardized 140-feet bottom trawl, its net frame rigged with heavy ground gear because of the rough nature of the fishing grounds. A small mesh liner (10mm) was used inside the cod end. The horizontal distance between wing-ends was 25 m at 300 m depth, the vertical net opening being 4 m. In 1994, smaller polyvalent doors (4.5 m^2, 1 500 kg) were used for the first time to reduce net damages due to overspread caused by bigger doors (6 m^2, 1 700 kg), which have been used earlier. All calculations of abundance and biomass indices were based on the 'swept area' method using 22 m horizontal net opening as trawl parameter, i. e. the constructional width specified by the manufacturer. The towing time was normally 30 min at a speed of 4.5 knots. Trawl parameters are listed in Table 1. Hauls which received net damage or became hang-up after less than 15 minutes, were rejected. Some hauls of the 1987 and 1988 surveys were also included although their towing time had been intentionally reduced to 10 minutes because of the expected large cod catches as observed from echo sounder traces.

The surveys were primarily designed for the assessment of cod. In order to reduce the error of abundance estimates, the subdivision of shelf areas and the continental slope into different geographic and depth strata was required due to a pronounced heterogeneity of cod distribution. The survey area was thus split into seven geographic strata. Each stratum was itself subdivided into two depth strata covering the 0-200 m and 201-400 m zones. Figure 1 and Table 2 indicate the names of the 14 strata, their geographic boundaries, depth ranges and areas in nautical square miles (nm^2). All strata were limited at the 3 mile offshore line.

The applied strategy was to distribute the sampling effort according both to the stratum areas and to cod abundance. Consequently, fifty percent of the hauls were allocated proportionally to strata by stratum area while the other fifty percent were apportioned on the basis of a review of the historical mean cod abundance/nm^2, all hauls being randomly distributed within trawlable areas of the various strata. Non-trawlable areas were mainly located inshore. During 1982-2004, 3 114 successful sets were carried out, the numbers of valid sets by year and stratum being listed in Table 3. East Greenland strata were not covered adequately in 1984, 1992 and 1994 due to technical problems. Stratum 7.1 (Dohrn Bank) has a very low area and therefore never been covered. In 1995 and 2002, the survey area off West Greenland was incompletely covered due to technical problems. In these years, less than 50 % of the strata of West Greenland were covered with at least five hauls. Since 1996, the entire survey area was considered to be almost completely covered. Figure 1 shows the positions of hauls conducted during the most recent survey.

Stratified abundance estimates were calculated from catch-per-tow data using the stratum areas as weighting factor (Cochran, 1953; Saville, 1977). Strata with less than five valid sets were rejected from the calculation. The coefficient of catchability was set arbitrarily at 1.0, implying that estimates are merely indices of abundance and biomass. Respective confidence intervals (CI) were set at the 95% level of significance of the stratified mean.

Fish were identified to species or lowest taxonomic level and the catch in number and weight was recorded. Total fish lengths were measured to cm below and individual weight was measured with a precision of 50 g since 1989 and a precision of 5 g since 1994.

Age determinations were based on length-stratified otolith (sagitta) collections and conducted using transmitted light. Until 1992, otoliths were cut into 2 halves and annuli were counted under a binocular microscope (Meyer, 1965). Since 1993, thin sections were cut from the central region of the otolith after embedding in polyester resin (Bedford, 1977). Comparative age readings revealed no significant differences between both methods. Calculations of age structures, compositions and growth were based on data pooled to 3 cm length groups. Numbers of age determinations by survey year vary on average among 1,600. Mean length at ages 3 to 6 years for the stock are weighted means by stratum abundance.

As a standard procedure, near bottom temperatures were measured directly before or after trawling in the vicinity of the swept area by a CTD-sonde with a precision of a hundredth °C. Mean stratified temperature in the near bottom layer was calculated using the stratum areas as weighting factor. The values are given in Table 3.

Maturity at age was determined from visual inspections of the gonads. However, the results should be interpreted carefully since the surveys were conducted in autumn when the majority of the gonads of mature fish were in resting stages. During this season, it was often difficult to distinguish immature from mature cod, especially regarding first time spawners. Furthermore, the age at which 50% of individuals are mature (A_{50}) was computed. The A_{50} describes the maturation process only indirectly because it also depends on survival and growth before and after maturation. Theoretical models show that maturation should depend both on age and size (Roff, 1992; Stearns, 1992). Empirical data support these findings (Stearns 1992; Heino et al., 2002).

To analyse condition of each individual cod, we used the relative condition index K_n, which is one of the various morphometric indices utilised to evaluate fish condition (Le Cren, 1951; Cone, 1989; Bolger and Connolly, 1989). It was selected because it does not assume isometric growth like other condition indices do. This condition index compares the actual weight to a standard predicted by the weight-length relationship based on the populations from which the fish was sampled. The relative condition index K_n is calculated as:

$$K_n = W/W'*100$$

where W is the observed individual fish weight and W' is the predicted length-specific weight (estimated from the weight-length relationship).

Because of the weighing precision of the scale (5g), we only computed condition of cod weighing more than 50 g. Extreme individual outliers were omitted since they probably resulted from weighting errors on board. Condition indices were log-transformed in order to obtain approximate normal distribution of model residuals and homogenous variance. Finally, we computed the arithmetic means by year.

Results

Abundance and biomass

Table 4 lists total abundance, spawning stock in numbers (SSN), recruits at age 1, total biomass and spawning stock biomass indices in 1982-2004. Indices varied significantly between years, mainly driven by the occurrence of the strong year classes 1984, 1985 and the most recent year class 2003. The recent distribution pattern of the cod off Greenland is illustrated in Figure 1. The historic trends of the abundance and biomass estimates are shown in Figures 2 and 3, respectively. These Figures illustrate the pronounced increase in stock abundance and biomass from 23 million individuals and 45 000 tons in 1984 to 828 million individuals and 690 000 tons in 1987. This trend was caused by the recruitment of the predominating year classes 1984 and 1985, which were mainly distributed in the northern and shallow strata 1.1, 2.1 and 3.1 off West Greenland during 1987-89. Such high indices were never observed off East Greenland, although their abundance and biomass estimates increased during the period 1989-91 pointing to eastbound migration. During the period 1987-89, the high abundance estimates were accompanied with high confidence intervals (CI values in Table 4). The low precisions were due to enormous variation in catch per tow data. Since 1988, stock abundance and biomass decreased dramatically by 99 % to 5 million individuals and 6 000 tons in 1993. However, the 2004 estimates confirmed the severely depleted status of the spawning stock with regard to the historic high level, although they represent the highest stock size in abundance since 14 years. The most recent total abundance and biomass indices in 2004 amounted to 50 million individuals and 39 000 tons, respectively.

Age disaggregated abundance indices are listed in Table 5. The very strong year classes 1984 and 1985 dominated the stock during 1985-1991. In 2004, the stock structure was found to be composed mainly of the strong recruiting year classes 2003 at age 1 (58 %). The recent slight increase in SSB is mainly due to the weak year class 1999. Log-transformed abundance estimates of the cohorts 1972 to 2003 at ages 1 to 10 and resulting mortality rates are illustrated in Figure 4 as linear regressions over log-transformed abundances over ages 5 to 10 years (fully recruited life span). The strong year classes 1984 and 1985 are clearly identifiable from their peaks in Figure 4 while the year classes during the 1990s and until 2002 were all very weak. With the occurrence of these strong year classes and high catches, the mortality rates increased drastically as indicated from the steep negative slopes during the late 1980s and the early 1990s. Since the early 1990s, annual landings from the offshore stock component remained below 500 t and implied mortality rates decreased again. The recent low negative slopes indicate high survival rates of the cohorts since 2000 (ICES 2004).

The year class 2003 at age one in 2004 is assessed as the second strongest year class since 1982 and is estimated to amount to 71 % of the strongest year class 1984 at age 1 (Tab. 4 and 5), which yielded about 170 000 t throughout its life. The O-group indices do no represent predictive weight as the O-group abundance is unrepresentative of year class strength at age 3 due to gear properties, while the age group 1 seems to be quantitatively estimated and to represent a reasonable recruitment index (Tab. 8, Fig. 5). With a projected relative survey abundance index of about 400-500 million individuals at age 3 in 2006, the recruiting year class 2003 implies a quick and substantial stock increase in the near future even considering the uncertainty of the survey assessment amounting usually to ±30 %. The other recruiting year classes 2000-2002 are considered weak as compared to the strong 1984 and 1985 year classes. However, the 2002 year class constitutes the third strongest age group 2 of the time series since 1982. Age groups 5 and 6 (year classes 1999 and 1998) are well represented in 2004 as compared with the mid 1990s.

Condition

The mean annual condition values of the cod stock off Greenland are listed in Table 6. Condition follows interannual fluctuations, with relatively low values recorded in the period 1989-1993 coinciding with lower than average sea temperatures (Table 3) and higher than average stock abundances (Tab. 4). In contrast, condition values were relatively high from 1994 to 2003 (Tab. 6) coinciding with relatively warm sea temperatures (Tab. 3) and low stock abundances (Tab. 4). Overall, condition was positively correlated with water temperature and negatively with stock size, with the multiple linear model explaining 48% of the variability in condition (Tab. 8; Figs. 6 a-c). The negative effect of stock size on condition is almost exclusively due to the appearance of the strong year classes 1984 and 1985 (Fig. 6a).

Length at age

The weighted mean length of the age groups 3-6 years are listed in Table 6. Overall, the mean sizes of these age groups showed marked interannual variability and were generally low in the period 1989-1991 coinciding with low condition values (Tab. 6). After 1991, the mean length at ages started to increase coinciding with the enhancement of fish condition. Thus for example, the mean length at age 4 in 1989 was 45.2 cm compared to 53.1 cm in 2004. Mean annual length at ages 4 to 6 were positively correlated with mean annual condition, with condition explaining up to 50% of the observed variability in these lengths at ages (Tab. 8, Fig. 7).

Sexual maturation

The number of mature cod at ages 0-10 sampled and resulting estimates of age at 50% maturity (A_{50}) are given in Table 7. The proportion mature at ages 1-5 and the A_{50} showed marked interannual fluctuations in the period 1982-1996 (Figs. 8 and 9 respectively). After 1996, the proportion mature at ages 1-5 increased steadily (Fig. 8). Thus for example, less than 5% of age 3 cod were mature in 1996 compared to more than 90% in 2004 (Fig. 8). Even the youngest age groups 1 and 2 showed a sharp increase in their sexual maturity over all the period, with ca 0% at age 2 cod identified as mature in 1982-1990 compared to 60% mature in 2004. The increase in the proportion mature at ages 1-5 after 1996 resulted in a progressive decline of the estimated A_{50} (Fig. 9). Age at 50% maturity declined approximately 3 years after 1996, from 5.03 in 1996 to 1.77 years in 2004 (Fig. 9). A_{50} is negatively related to increasing water temperature, but no significant relationship was found with stock size or condition (Tab. 8; Figs. 10 a-d).

Discussion

The main goal of the present investigation is to understand the ecological relationships between the observed variability in essential population parameters of the cod stock off Greenland including environmental conditions, i.e. the near bottom water temperature. The data were derived from an annual autumn survey series commenced in 1982. The survey estimates confirmed that the spawning stock biomass remained very low after the major stock collapse in the early 1970s (ICES 2004). However, the estimated total stock abundance has undergone dramatic changes due to very high recruitment variability, fishing and emigration to Iceland. Since 1982, only three exceptionally strong year classes have been recorded which were born in 1984, 1985 and recently in 2003.

All the other year classes were very poor. The general recruitment failure and the exceptional recruitment success in 1984, 1985 and 2003 can be explained by the very low SSB as compared with historic stock sizes, and with lower explanatory weights also by improved environmental conditions through continued warming and as well as larval drift from Iceland (Rätz et al., 1999; Rätz and Lloret, 2004). Also the strong year class 2003 is believed to be of Icelandic origin and implies a quick and substantial recovery potential of the cod stock off Greenland. The year class 2003 at age 1 in 2004 is assessed as the second strongest year class since 1982 and is estimated to amount to 71 % of the strongest year class 1984 at age 1, which yielded about 170 000 t throughout its life. Such recovery and exploitation potential urgently requires a definite multi-annual management plan consistent with the precautionary approach in fisheries management, considering also the technical and ecological relations to the shrimp fisheries and stocks, respectively. The homing phenomenon of cod to Iceland needs to be taken into consideration (Schopka, 1994; Storr-Paulsen, 2004), which may be affected by the continued warming since 10 years.

The variation of the mortality estimates derived from the survey indices support the results of the last age based production model conducted by ICES (2004), i.e. that the progressive depletion of the strong year classes was mainly due to over-fishing and only relatively low emigration rates to Iceland. During 1988-1990, the sensitive recruitment period of the 1984 and 1985 year classes, annual offshore cod landings exceeded 49 000 t, peaked at 86 000 t and caused very high mortality rates. In the following 2 years, the offshore fishery collapsed completely and the survival rates increased again. The recently very low mortality rates are possibly supported by increased availability due to increased stock size and/or improved environmental year effects (Stein, 2004 a and b; Buch and Ribergaard, 2003).

The significant positive effect of temperature on condition of cod inhabiting the sub-arctic shelves around Greenland has been demonstrated earlier (Lloret and Rätz, 2000) and also observed in other regions (Rätz and Lloret, 2003). The detected negative stock size effect (density) on fish condition is mainly dependent on the few strong cohorts since 1982 (year classes 1984 and 1985). The productivity at high stock sizes may suffer from intra-specific competition and depend on the status of the food resources, which are mainly shrimp and capelin (Tiedtke, 1988; Schnack et al., 1993). However, Bishop and Baird (1994) and Krohn et al. (1997) have shown a positive relationship between abundance and condition of the cod stock off southern Labrador and Newfoundland, which experienced a decrease in body condition during the period of collapse. We suggest that, under average stock sizes, there is a positive relationship between condition and stock size indicating that good ecosystem conditions can favour both condition and abundance of cod. However, under extremely high stock sizes, there is a negative effect of stock numbers on condition due to the severe competence for the food supply. Similar to this, Shulman et al. (2005) found that, despite the general positive relationship between sprat condition and stock biomass in the Black Sea, the extremely high sprat biomass in two years affected its condition negatively. In conclusion, the recently improved condition of the cod in Greenland is indicated as enhanced from the continued warming and low size of the stock. However, it is important to notice the condition of cod off Greenland is among the lowest observed in natural populations of this species (Rätz and Lloret, 2003).

Furthermore, recently observed well conditioned fish appears to be linked to the high growth rates recently recorded. The size at ages 3 to 6 were found significantly and positively correlated with the condition index. Well conditioned fish have higher growth rates than poorly conditioned fish, with the indirect coupling of temperature and stock size effects. The positive effect of condition (especially the lipid content) on growth of fishes has been demonstrated before (Hoar ,1963; Shulman, 1974; Kooijman, 1993; Hallam, (2000).

Age at maturation is an important life history trait of fishes that influences population dynamics (Rochet, 1998). The observed reduction in sexual maturation at age (A_{50}) by about 3 years in the cod stock off Greenland over the last two decades has been significant. The decline in A_{50} is stronger than the decline seen in other stocks, e.g. Scotian Shelf cod, which experienced a decline of about 1 year since the early 1980s (Hutchings, 2005). The observed ratio of mature Greenlandic cod at age 2 of 65 % in 2004 even exceeds those seen in the warm water cod stocks in the North Sea, West of Scotland and in the Irish Sea. However, the significant changes to earlier maturation at age are based on the results from visual inspections of gonads during the resting phase, when sexual stages (especially first time spawners) are difficult to identify. Therefore, some of the observed variations are considered to be caused by misclassification. Furthermore, the observed decline in maturation could be either a direct phenotypic response to some environmental variation, or the evolutionary consequence of some selective pressure. It is well known that traditionally used maturation indices, such as the one used in this study (A_{50}), are not appropriate to evaluate the causes of changes in maturation because they are influenced, in addition to maturation *per se*, by growth and survival (Heino et al., 2002). Thus, the observed early maturation of Greenlandic cod could reflect the recently increased growth rates instead of the increase in water temperature. However, we exclude a potential fishing effect since there is no relationship between stock size and maturity.

The decline in age at maturity of Greenlandic cod over the last decades was not exactly concomitant with the population decline, since the collapse of the stock occurred in the late 1980s and early 1990s whilst the decline in maturity was observed in the mid 1990s. This is in contrast to other North Atlantic cod stocks which have experienced declines in size and age at maturity during the past few decades, associated with severe declines in abundance and selective removal of older spawners as a result of increased exploitation (Marteinsdottir and Begg, 2002, Olsen et al., 2005; Hutchings, 2005). The most common response to exploitation is a reduction in population density, releasing stocks from some pressure of intraspecific competition which can thus mature earlier (Hutchings, 2005). Although sexual maturation was not found to be related to the condition, a recent study has shown an effect of the condition in the Icelandic cod stock on its sexual maturity. Cod in good condition appear to have a higher probability of maturing than a similarly sized and aged cod in poor condition (Marteinsdottir and Begg, 2002). The positive effect of condition on the probability of being mature was also found to be significant for female American plaice (Morgan, 2004).

Overall, recent good recruitment, high condition and high growth rates as well as early maturation coincide with continued warm water temperatures. The significantly increased productivity potential implied by these changes in essential population parameters urgently requires a definite multi-annual management plan consistent with the precautionary approach in fisheries management

Acknowledgements

We would like to thank all persons that were involved in the collection of the samples and data on the annual groundfish survey off Greenland. Josep Lloret benefited from a Marie Curie European Reintegration Grant.

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Table 1 Trawl parameters of the survey.

Gear	140-feet bottom trawl
Horizontal net opening	22 m
Standard trawling speed	4.5 kn
Towing time	30 minutes
Coefficient of catchability	1.0

Table 2 Specification of strata.

Stratum	geographic boundaries south	north	east	west	depth (m)	area (nm^2)
1.1	64°15'N	67°00'N	50°00'W	57°00'W	1-200	6805
1.2	64°15'N	67°00'N	50°00'W	57°00'W	201-400	1881
2.1	62°30'N	64°15'N	50°00'W	55°00'W	1-200	2350
2.2	62°30'N	64°15'N	50°00'W	55°00'W	201-400	1018
3.1	60°45'N	62°30'N	48°00'W	53°00'W	1-200	1938
3.2	60°45'N	62°30'N	48°00'W	53°00'W	201-400	742
4.1	59°00'N	60°45'N	44°00'W	50°00'W	1-200	2568
4.2	59°00'N	60°45'N	44°00'W	50°00'W	201-400	971
5.1	59°00'N	63°00'N	40°00'W	44°00'W	1-200	2468
5.2	59°00'N	63°00'N	40°00'W	44°00'W	201-400	3126
6.1	63°00'N	66°00'N	35°00'W	41°00'W	1-200	1120
6.2	63°00'N	66°00'N	35°00'W	41°00'W	201-400	7795
7.1	64°45'N	67°00'N	29°00'W	35°00'W	1-200	92
7.2	64°45'N	67°00'N	29°00'W	35°00'W	201-400	4589
Sum						37463

Table 3 Numbers of valid hauls by stratum and total and weighted (by stratum area) mean near bottom temperature, 1982-2004.

YEAR	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	Sum	Temp. (°C)
1982	20	11	16	7	9	6	13	2	1	10	3	12	1	25	136	3.139
1983	26	11	25	11	17	5	18	4	3	19	10	36	0	18	203	3.012
1984	25	13	26	8	18	6	21	4	5	4	2	8	0	5	145	2.698
1985	10	8	26	10	17	5	21	4	5	21	14	50	0	28	219	4.181
1986	27	9	21	9	16	7	18	3	3	15	14	37	1	34	214	4.136
1987	25	11	21	4	18	3	21	3	19	16	13	40	0	18	212	3.783
1988	34	21	28	5	18	5	18	2	21	8	13	39	0	26	238	3.959
1989	26	14	30	9	8	3	25	3	17	18	12	29	0	11	205	3.295
1990	19	7	23	8	16	3	21	6	18	19	6	15	0	13	174	3.461
1991	19	11	23	7	12	6	14	5	8	11	10	28	0	16	170	3.558
1992	6	6	6	5	6	6	7	5	0	0	0	0	0	6	53	3.489
1993	9	6	9	6	10	8	7	0	9	6	6	18	0	14	108	3.597
1994	16	13	13	8	10	6	7	5	0	0	0	0	0	6	84	3.620
1995	0	0	3	0	10	7	10	5	8	6	6	17	0	12	84	3.862
1996	5	5	8	5	12	5	10	5	7	9	5	13	0	9	98	4.709
1997	5	6	5	5	6	5	8	5	5	5	4	8	0	8	75	4.189
1998	9	5	10	7	11	6	10	5	5	8	6	12	0	9	103	5.181
1999	8	6	14	8	13	6	9	3	5	6	6	13	0	5	102	4.435
2000	13	6	14	7	14	5	9	5	6	5	8	16	0	11	119	3.860
2001	0	0	15	7	15	5	11	6	5	6	9	18	0	15	112	5.128
2002	0	0	7	2	5	6	8	4	6	6	5	10	0	10	69	4.904
2003	0	0	7	6	7	7	6	5	6	5	5	7	0	16	77	5.500
2004	9	7	11	9	9	6	9	5	7	7	8	12	0	15	114	5.152

Table 4 Cod off Greenland. Selected stock parameters 1982-2004: Stratified mean abundance and biomass indices, CI (95 % confidence interval in per cent of the stratified means), spawning stock size in number (SSN) and Biomass (SSB) and recruitment index at age 1. Years given in brackets indicate incomplete survey coverage.

Year	Abundance (000)	CI	SSN (000)	Recruits at age 1 (000)	Total biomass (t)	CI	SSB (t)
1982	100366	28	33793	176	152103	25	79511
1983	58195	25	23889	0	116526	25	57223
(1984)	23286	32	17653	23	45305	34	36162
1985	71747	33	17349	39948	69245	39	45630
1986	160915	32	14350	15545	127902	26	48976
1987	828026	59	25467	330	690182	63	65584
1988	650080	48	128578	282	660935	46	155556
1989	450459	59	332589	211	573393	45	514773
1990	59777	43	46355	85	100397	34	77064
1991	15213	29	6404	399	37899	36	17756
(1992)	2700	50	560	307	1826	69	1091
1993	4738	36	2327	27	5959	41	4024
(1994)	1375	36	457	370	2926	68	1732
1995	7463	93	2340	7	15579	155	10445
1996	2257	38	592	147	3974	56	2017
1997	4469	75	3411	12	14007	90	10416
1998	3394	54	1133	1882	4479	91	3820
1999	3681	34	809	1033	4157	62	3004
2000	6742	36	3556	973	5349	40	4176
2001	15764	39	8252	929	18873	42	13381
2002	13812	41	11689	21	21836	51	21299
2003	25537	45	19520	3810	53131	73	50967
2004	49147	58	20976	28342	38676	38	34429

Table 5 Cod off Greenland. Age disaggregated abundance indices (1000), 1982-2004. *) based on age compositions reported by the ICES Working Group on Cod Stocks off East Greenland (ICES, 1984). Years given in brackets indicate incomplete survey coverage.

YEAR	0	1	2	3	4	5	6	7	8	9	10	11+	TOTAL
1982	0	176	1123	34311	13132	34503	10755	3001	708	2331	164	162	100366
*1983	0	0	1880	3420	27627	6147	13094	3169	1294	582	871	1140	58198
(1984)	159	23	112	3412	2188	11245	1697	3490	494	289	63	95	23267
1985	1061	39948	2037	1066	8897	4867	9534	1252	2646	322	91	36	71757
1986	0	15545	115883	5782	1454	9240	3215	6462	699	2243	150	178	160851
1987	0	330	59258	710355	28120	6956	13583	2094	5577	187	1459	66	827985
1988	11	282	3495	109749	522074	7441	1093	2557	806	1948	130	504	650090
1989	12	211	2640	4054	111083	317218	6955	294	5405	520	2023	42	450457
1990	159	85	1087	3556	1706	26852	25233	312	72	251	0	368	59681
1991	0	399	601	870	2082	311	5406	5352	87	37	11	9	15165
(1992)	15	307	1504	294	105	131	47	171	52	0	0	6	2632
1993	0	27	876	2401	390	307	284	88	272	95	0	0	4740
(1994)	0	370	45	228	299	148	87	150	0	29	0	0	1356
1995	0	7	2764	1141	392	1730	450	141	460	36	217	125	7463
1996	0	147	11	1140	268	295	265	60	77	0	0	0	2263
1997	0	12	64	43	1771	1611	566	236	140	0	0	19	4462
1998	111	1882	192	21	50	487	435	156	43	0	0	0	3377
1999	220	1033	1057	504	145	302	185	200	0	35	24	0	3705
2000	0	973	2089	1956	903	157	291	75	141	115	31	0	6731
2001	0	929	7146	2568	2403	1400	705	211	191	73	36	9	15671
2002	108	21	1476	4796	2090	2080	1952	889	235	83	36	30	13796
2003	1170	3810	533	2157	5273	4378	4511	2374	1074	188	0	25	25493
2004	221	28342	7324	1515	1607	4559	2701	1942	738	130	44	0	49123

Table 6 Cod off Greenland. No. of observations of condition (K_n), mean log-transformed condition, standard deviation of mean condition and mean length at ages 3-6 by year, 1989-2004.

Year	N ln (Kn)	Mean ln (Kn)	St.dev. ln (Kn)	Mean length at age 3 (cm)	Mean length at age 4 (cm)	Mean length at age 5 (cm)	Mean length at age 6 (cm)
1989	2437	-0.0531	0.1442	36.3	45.2	55.7	62.6
1990	1312	-0.0677	0.1991	34.0	42.9	48.2	62.3
1991	1055	0.0271	0.1187	34.5	44.4	52.4	59.6
1992	144	-0.0447	0.1005	36.9	50.9	56.4	69.1
1993	400	-0.0144	0.1126	41.3	51.9	61.7	67.2
1994	62	0.0354	0.1374	38.4	60.0	68.6	80.5
1995	451	0.038	0.1163	36.0	53.8	68.5	76.9
1996	156	0.0515	0.1094	40.2	58.8	64.5	73.1
1997	325	0.0425	0.1284	47.8	57.7	72.2	76.2
1998	113	0.0125	0.1234	48.5	57.7	68.3	72.8
1999	260	0.0276	0.0961	40.2	50.4	68.5	73.9
2000	700	-0.0173	0.0909	36.4	45.5	55.9	61.2
2001	1191	0.0327	0.1185	43.5	57.9	62.8	67.4
2002	566	0.058	0.0963	41.6	55.2	63.0	68.4
2003	1025	0.0339	0.1306	44.5	53.5	63.0	72.2
2004	1486	0.0273	0.1072	39.4	53.1	60.8	67.4

Table 7 Cod off Greenland. Maturity stages (M=mature, I=immature) by ages 0-10 in numbers, A_{50}=age at 50 % mature and SE=standard error of A_{50} by year, 1982-2004.

Year	State	Age 0	1	2	3	4	5	6	7	8	9	10	A50	SE
1982	M	0	0	0	8	24	265	181	94	39	199	1	5.06	0.05
	I	1	7	37	240	194	213	61	11	1	1	0		
1984	M	0	0	2	53	142	1128	166	467	42	52	9	3.97	0.04
	I	39	2	11	407	126	139	2	1	0	0	0		
1985	M	0	0	1	2	165	379	866	173	417	47	14	4.82	0.03
	I	127	906	129	88	768	180	140	6	10	4	0		
1986	M	0	0	1	0	8	104	139	416	48	168	12	5.51	0.05
	I	1	477	999	141	55	318	26	28	5	5	0		
1988	M	0	1	0	23	398	102	43	177	41	152	12	4.86	0.05
	I	2	44	294	1097	1449	53	7	15	0	2	1		
1989	M	0	0	0	2	501	1533	69	5	131	13	65	4.05	0.04
	I	10	17	269	114	415	340	7	0	2	0	1		
1991	M	0	0	1	10	4	209	129	6	6	4	1	5.27	0.05
	I	46	54	83	228	27	316	43	0	0	0	0		
1992	M	0	0	5	6	11	15	7	23	12	1	1	4.07	0.19
	I	2	15	116	16	5	6	0	2	0	0	0		
1993	M	0	0	3	123	24	14	19	6	24	8	1	3.51	0.19
	I	1	3	63	107	14	15	6	2	2	1	0		
1994	M	0	0	0	1	5	3	3	5	1	1	1	4.57	0.26
	I	1	29	5	27	9	3	0	0	0	0	0		
1995	M	0	0	0	0	8	54	21	8	25	2	13	4.97	0.09
	I	1	1	171	74	20	51	5	0	0	0	0		
1996	M	0	0	0	0	5	9	14	4	5	0	0	5.03	0.19
	I	1	7	1	99	10	7	3	0	1	0	0		
1997	M	0	0	0	2	123	70	26	11	7	0	0	3.15	0.29
	I	2	1	5	5	51	20	3	1	0	0	0		
1998	M	0	0	0	2	3	32	26	11	4	0	0	3.64	0.23
	I	8	90	20	1	2	1	1	0	0	0	0		
1999	M	0	0	2	4	5	24	20	16	1	2	0	4.19	0.14
	I	16	82	101	51	9	3	0	1	0	0	0		
2000	M	0	2	61	186	116	19	31	5	8	8	1	2.54	0.06
	I	1	35	155	79	12	1	1	1	0	0	0		
2001	M	0	2	84	187	239	142	69	20	19	4	4	2.62	0.05
	I	1	33	293	70	23	5	2	0	0	0	0		
2002	M	0	0	38	317	119	117	130	67	18	6	2	1.87	0.14
	I	1	1	83	42	10	5	6	3	0	0	0		
2003	M	0	10	20	117	236	162	170	90	41	7	0	2.37	0.07
	I	41	219	21	24	13	9	1	0	0	0	0		
2004	M	0	35	100	106	115	264	163	158	69	14	4	1.77	0.05
	I	14	406	31	4	2	2	0	0	0	0	0		

Table 8 Cod off Greenland. Linear single and multiple regression analyses for condition, length at ages 3-6 and maturity. Models are illustrated in Figures 5, 6, 7 and 10, respectively. N is the number of observations. Beta and B values are the standardised and raw regression coefficients, respectively. SE is the standard error of Beta values. P-level is the probability associated with the Student-t statistic for the regression coefficients. The magnitude of the Beta coefficients allows comparing 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	SE	Intercept	B	p-level	r^2
Single effects								
Age 3 (000)	Age 0 (000)	20	0.2168	0.23	30101.15	144.2637	0.36	0.05
Age 3 (000)	Age 1 (000)	21	0.9746	0.05	-8780.88	16.6171	0.00	0.95
Single effects								
Condition ln (Kn)	Stock size (000)	16	-0.48690	0.23	0.019004	-0.0000001720	0.05	0.24
Condition ln (Kn)	Temperature (°C)	16	0.61800	0.21	-0.124791	0.0321761840	0.01	0.38
Multiple effects		16			-0.097344			0.48
Condition ln (Kn)	Stock size (000)		-0.32342	0.21		-0.0000001143	0.15	
	Temperature (°C)		0.51538	0.21		0.0268334076	0.03	
Single effects								
Length at age 3 (cm)	Condition ln (Kn)	16	0.4770	0.2349	39.3304	53.9261	0.06	0.23
Length at age 4 (cm)	Condition ln (Kn)	16	0.7074	0.1889	51.2458	100.1411	0.00	0.50
Length at age 5 (cm)	Condition ln (Kn)	16	0.7078	0.1888	60.4666	121.6175	0.00	0.50
Length at age 6 (cm)	Condition ln (Kn)	16	0.5632	0.2208	68.3867	87.7116	0.02	0.32
Single effects								
Maturity (A50)	Temperature (ºC)	15	-0.5347	0.1992	7.2397	-0.8109	0.02	0.28
Maturity (A50)	Stock size (000)	15	0.2610	0.2275	3.7454	0.0000	0.27	0.07
Maturity (A50)	Condition ln (kn)	15	-0.0728	0.2766	3.6156	-2.4752	0.80	0.01
Multiple effects		15			8.6895			0.44
Maturity (A50)	Temperature (ºC)		-0.8058	0.2772		-1.2463	0.01	
	Stock size (000)		0.0164	0.2713		0.0000	0.95	
	Condition ln (kn)		0.4022	0.3153		13.6678	0.23	

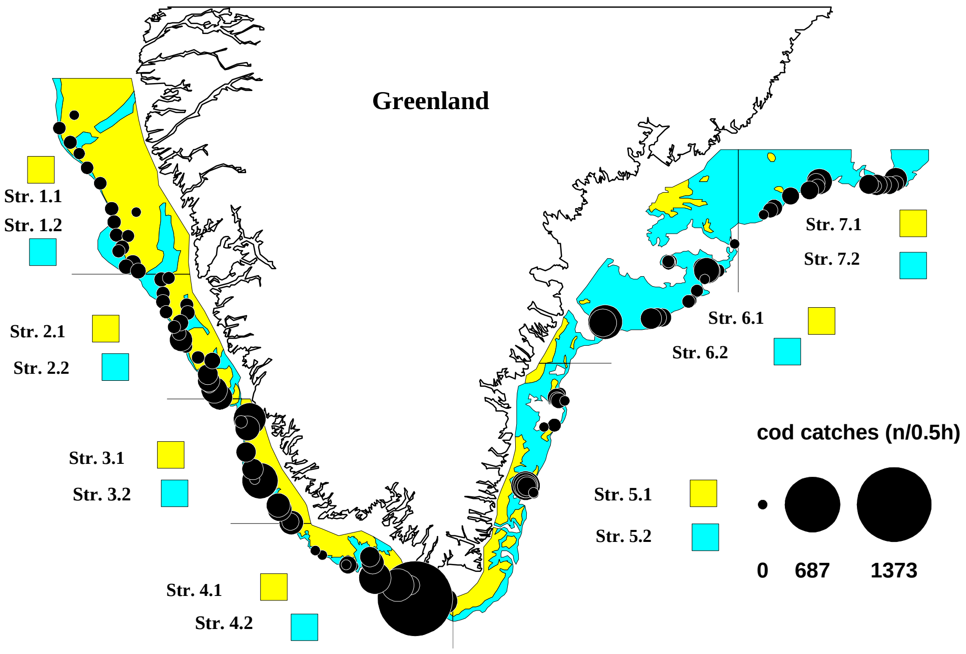


Fig. 1 Stratification of the survey area as specified in Table 2, positions of hauls carried out in 2004 and catches of cod.

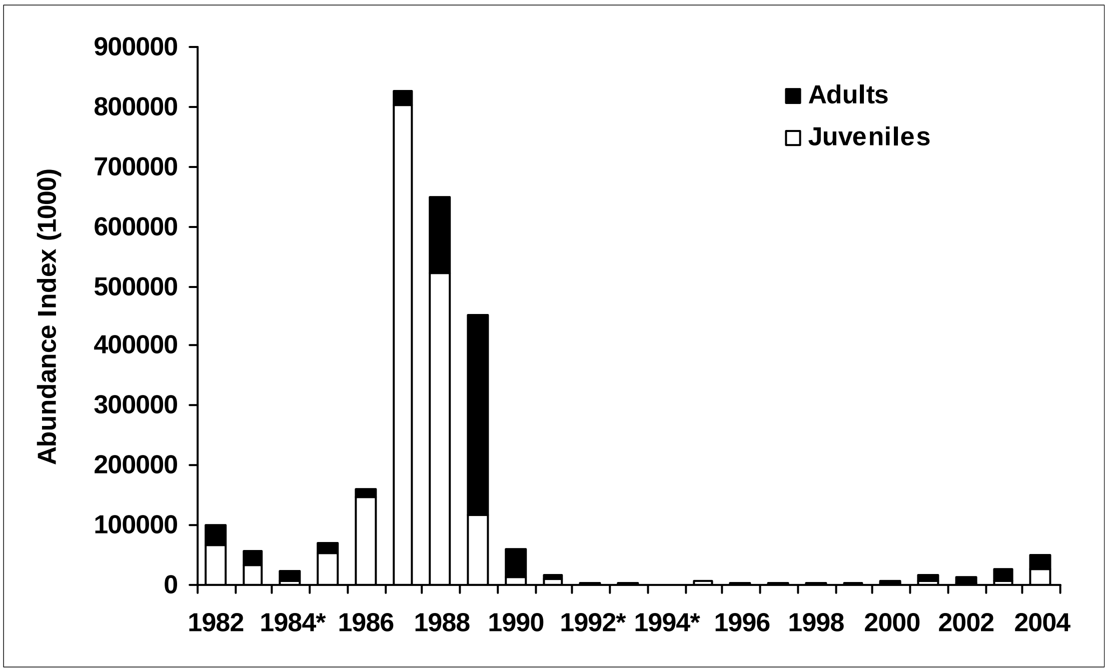


Fig. 2 Cod off Greenland. Aggregated survey abundance indices for juvenile and adult parts as listed in Table 4, 1982-2004. *) incomplete survey coverage.

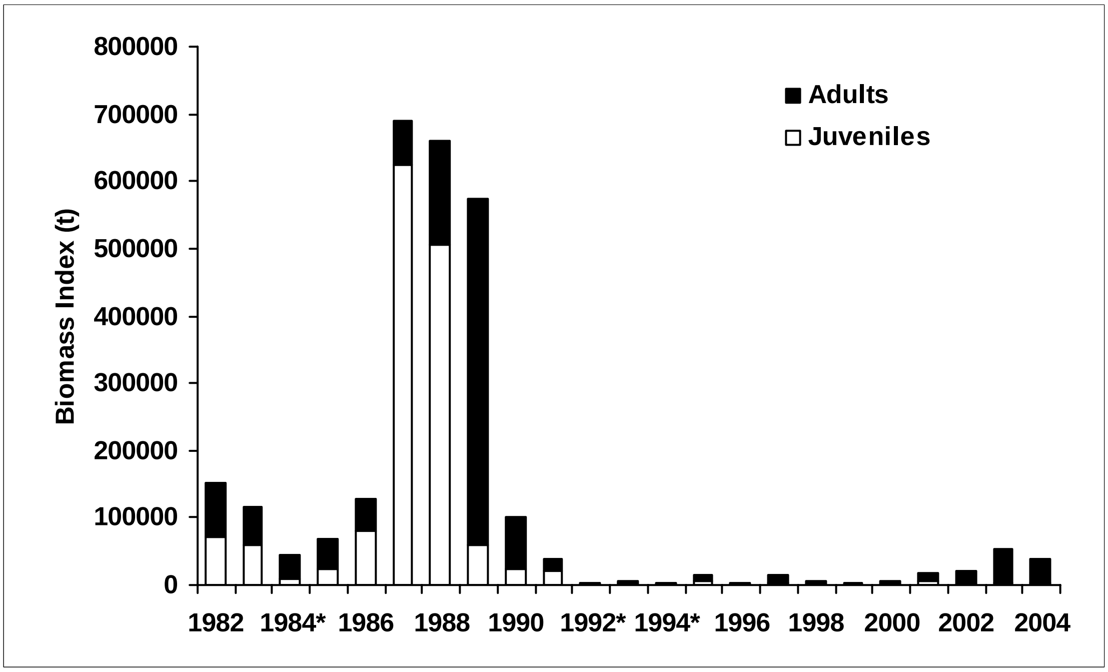


Fig. 3 Cod off Greenland. Aggregated survey biomass indices for juvenile and adult parts as listed in Table 4, 1982-2004. *) incomplete survey coverage.

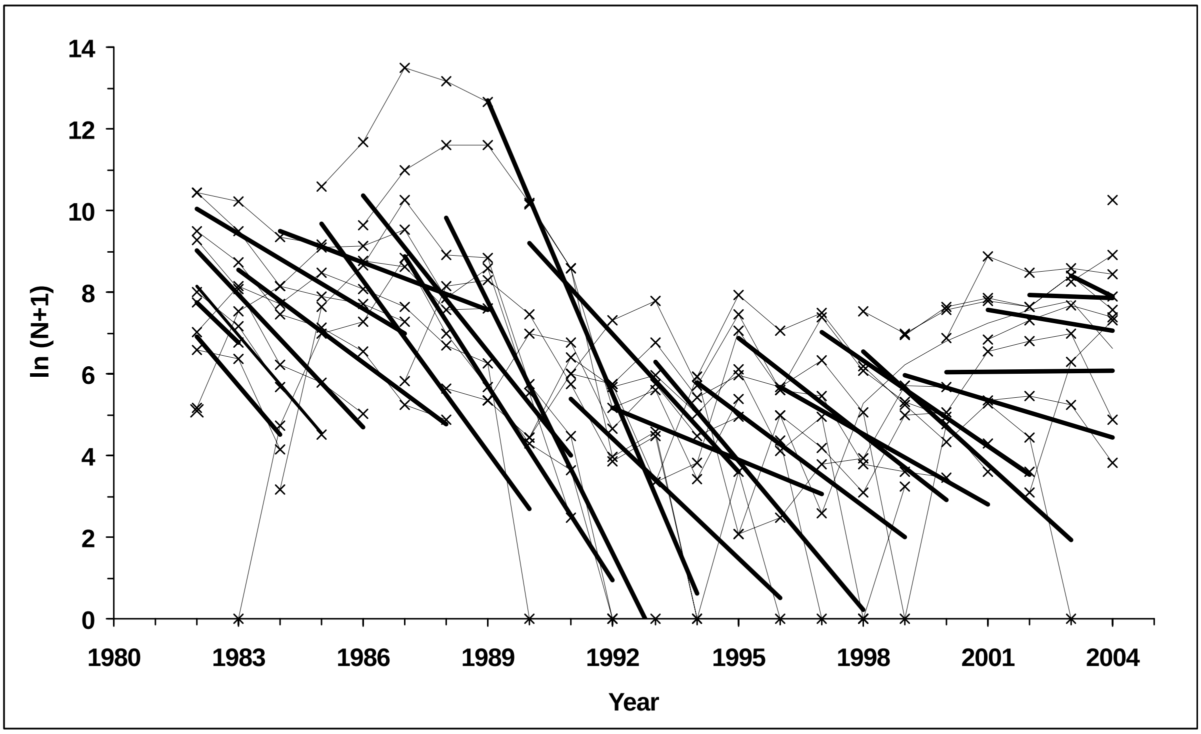
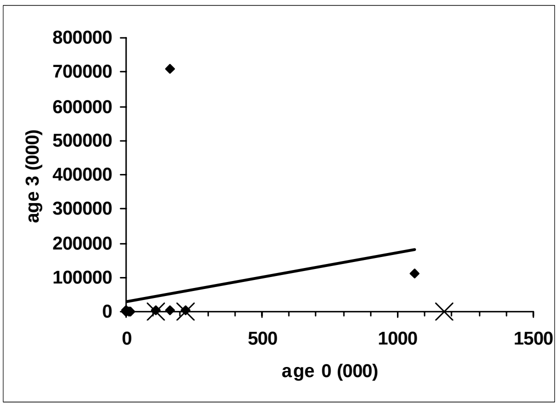
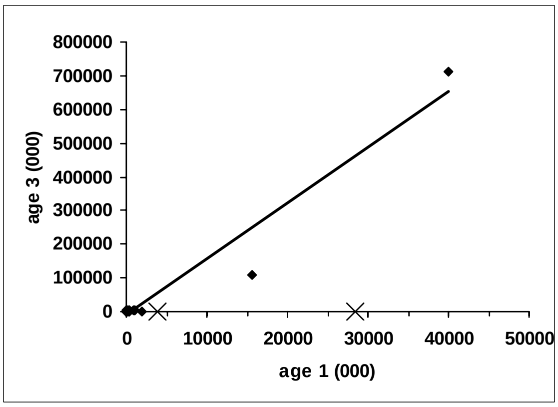


Fig. 4 Cod off Greenland. Catch curves as derived from log-transformed survey abundance values of the various cohorts 1972-2003 at ages 1 to 10 during 1982-2004 as given in Table 5. The fitted linear slopes of the bold lines indicate total cohort mortality at ages 5 to 10, after full recruitment to the survey.



a



b

Fig. 5 Cod off Greenland. Single linear regression model results for year class abundance at age 3 versus age 0 (a) and at age 3 versus age 1 (b), respectively. The x symbols indicate the 2002, 2003 and 2004 year classes at age 0 and the 2002 and 2003 at age 1, respectively. Values are listed in Table 5, and regression parameters are given in Table 8.

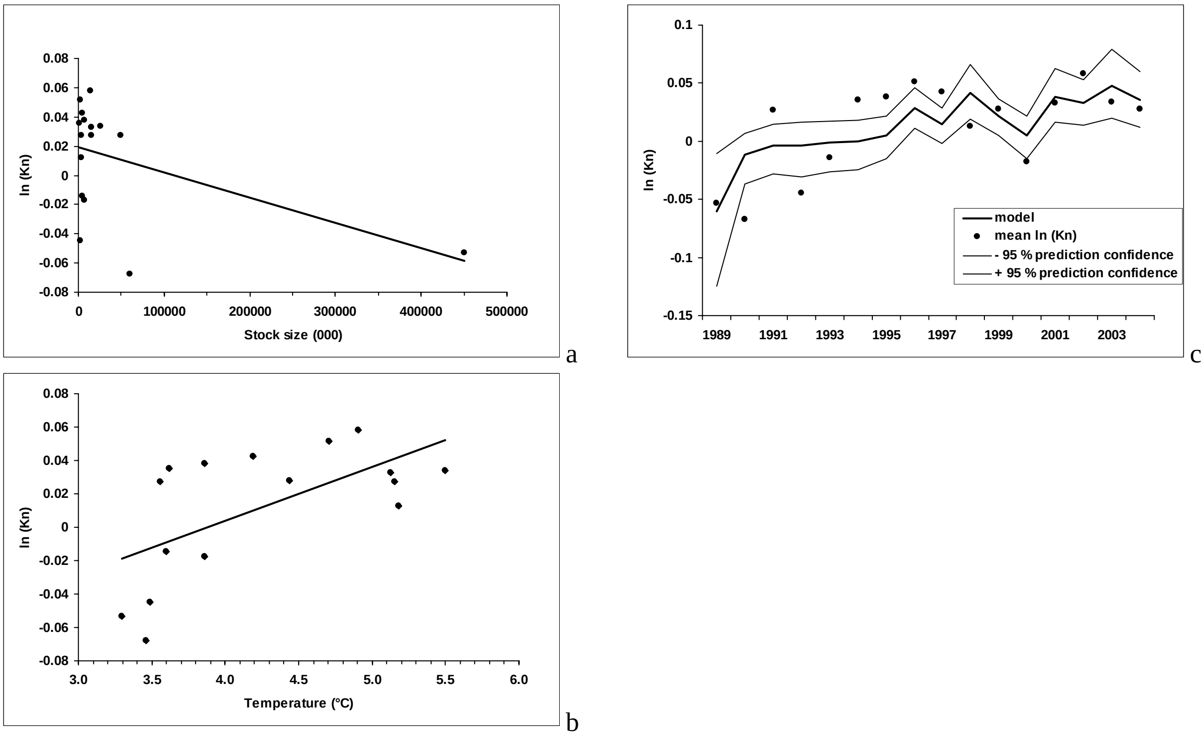


Fig. 6 Cod off Greenland. Single and multiple linear regression model results for condition ln(Kn) based on stock size (a), temperature (b) and both significant effects (c), respectively. Values are listed in Tables 3, 4 and 6, and regression parameters are given in Table 8.

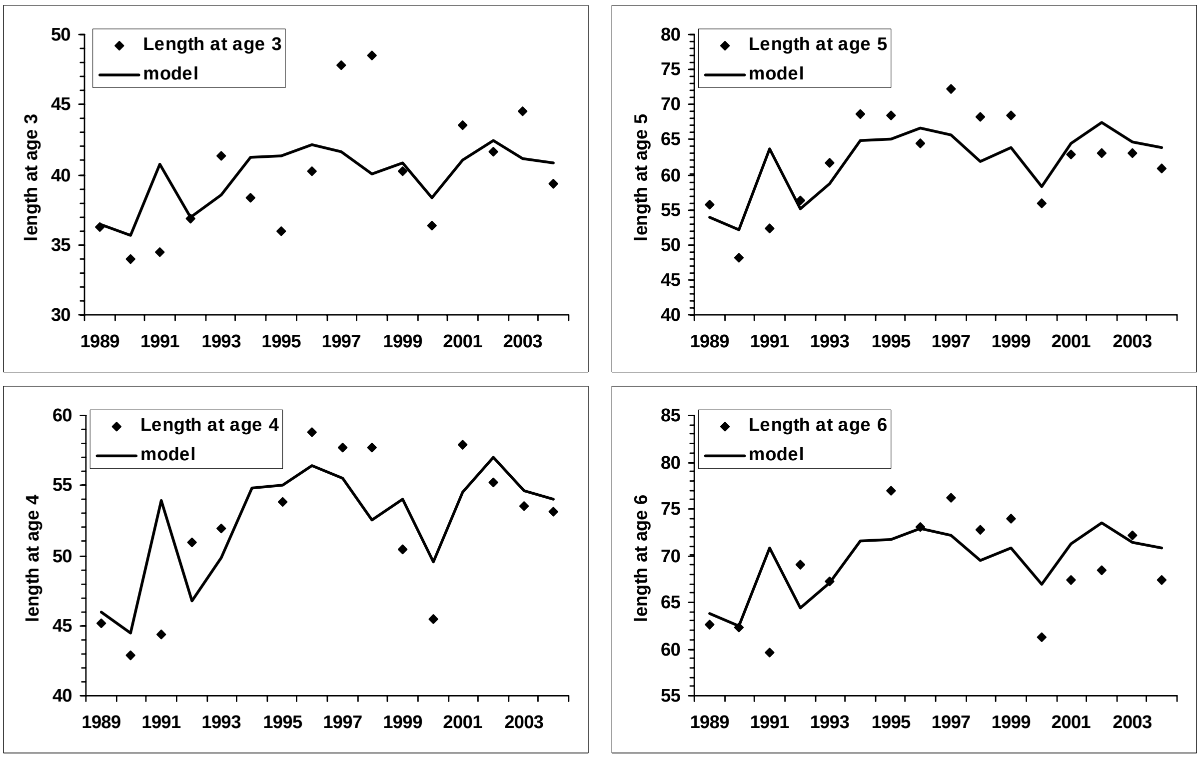


Fig. 7 Cod off Greenland. Observed weighted lengths and linear regression models at ages 3 to 6 based on mean condition, 1989-2004. Values are listed in Table 6, regression parameters are given in Table 8.

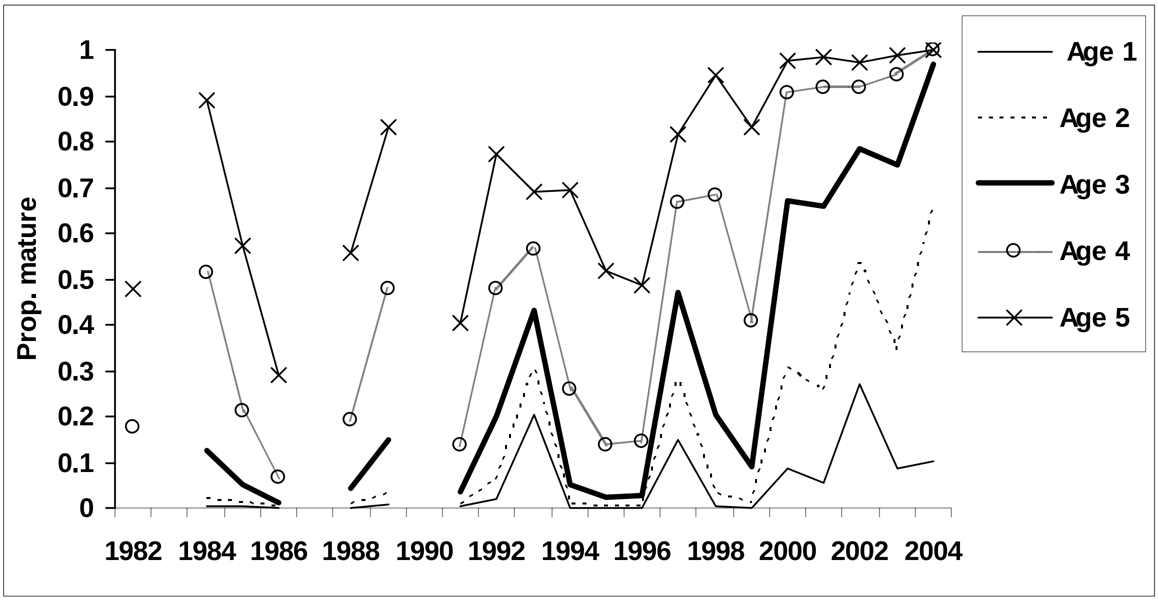


Fig. 8 Cod off Greenland. Trends in proportion mature at ages 1-5, 1982-2004. Values are listed in Table 7.

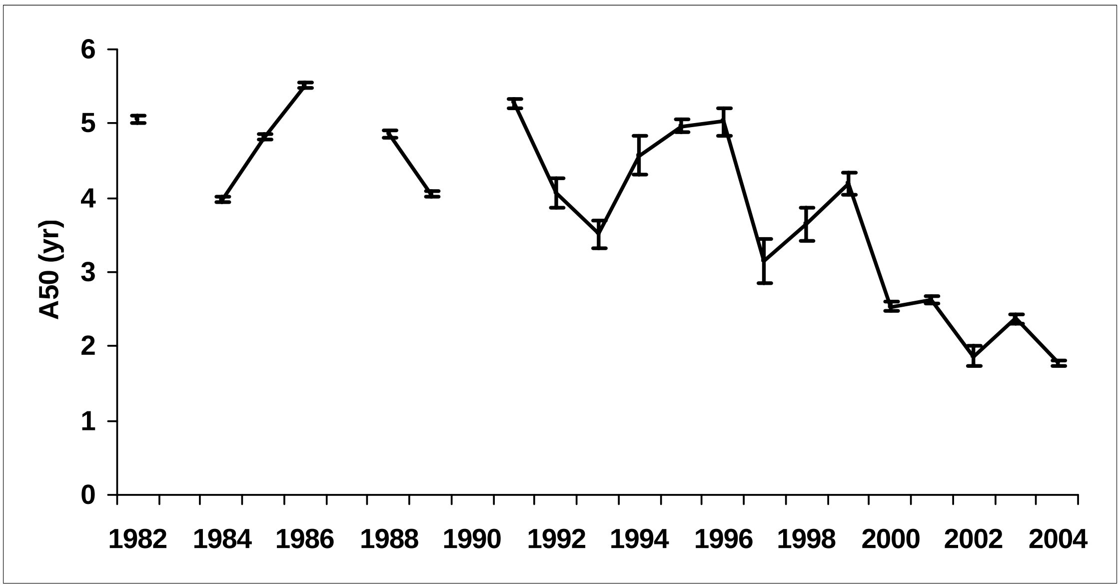


Fig. 9 Cod off Greenland. Trend in age at 50 % maturity, 1982-2004. Values are listed in Table 7.

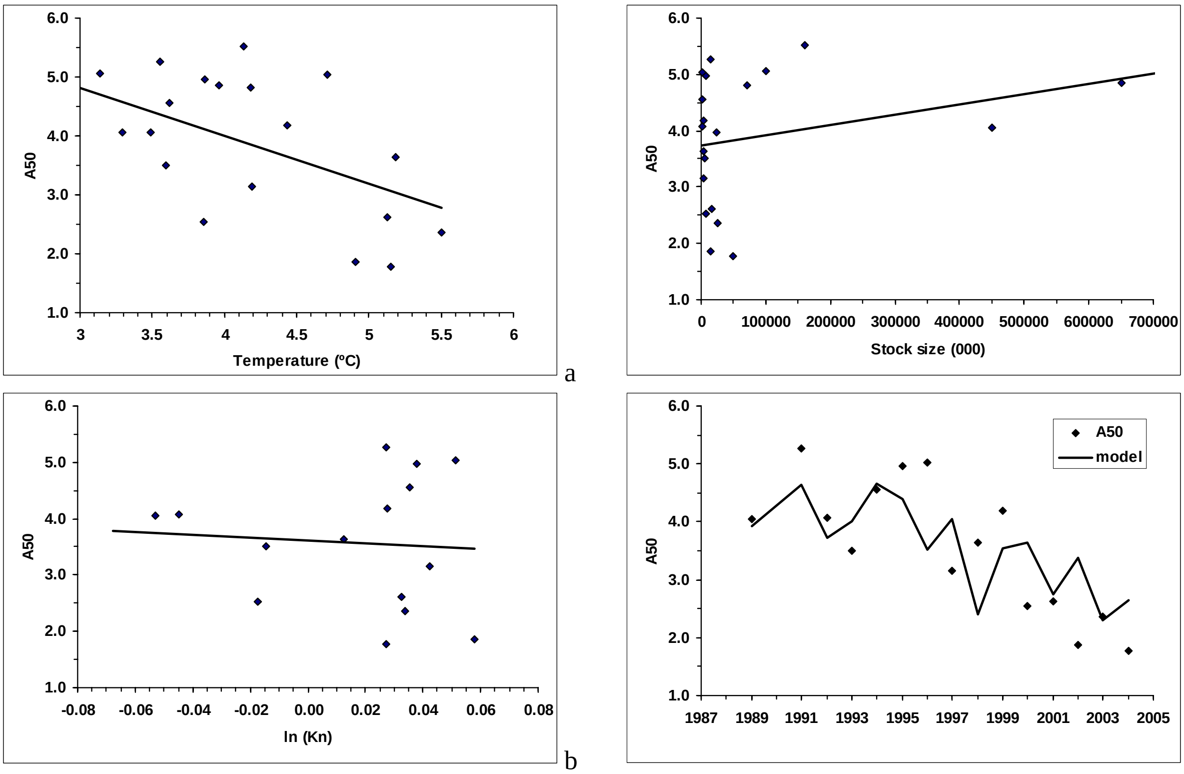


Fig. 10 Cod off Greenland. Single linear regression models between age at 50 % mature (A_{50}) and temperature (a), relative condition K_n (b), stock size (c) and as trend over 1982-2004 (d). Values are listed in Tables 3, 4, 6 and 7 and regression parameters are given in Table 8.