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Growth variability of Greenlandic cod (*Gadus morhua* L.)
estimated by means of otolith annual increments

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Contents:

Abstract:	III
Sumário:	IV
Résumé:	V
Acknowledgements:	VI
Introduction:.....	1
Material and Methods:	5
Otolith collection and preparation:	5
Otolith interpretation and variables measured:	7
Data analysis:	8
<i>Backcalculation of Growth:</i>	8
<i>Fulton's K Condition Factor:</i>	8
Biological and climate data:	9
Results:	11
Increment analysis:.....	11
<i>Annual Increment Growth:</i>	11
<i>Back-calculated Growth:</i>	14
Otolith weight:	16
Fulton's K Condition Factor:.....	17
Fish length:	18
Discussion:	20
Increment Analysis:	20
Fulton's K Condition Factor:.....	22
Climate change and growth:	22
Zooplankton abundance and growth:.....	24
Conclusion:.....	26
Bibliography:.....	27
Appendices:.....	32

Tables:

Table 1. Selected otoliths:6
Table 2. Annual Increment and Back-calculated Growth:.....16
Table 3. Correlation between Growth and Environmental parameters:19

Figures:

Figure 1. Southern part of Greenland:.....5
Figure 2. Sectioned otolith:.....7
Figure 3. Annual Increment Growth:.....12
Figure 4. Water temperature:12
Figure 5. Annual Increment Growth vs Water Temperature:13
Figure 6. Fish length vs Otolith radius:14
Figure 7. Back-calculated Growth:15
Figure 8. Otolith weight:17
Figure 9. Fulton's *K* and Fish length:.....18

Appendices:

Appendix 1. Climate time series:32
Appendix 2. Biological time series:.....33

Abstract:

World-wide Atlantic cod (*Gadus morhua*) productivity has suffered a severe decline primarily due to fisheries exploitation, but environmental changes might also be at play. Otoliths of Atlantic cod collected during the period 1940-1985 in the Nuuk fjord, Greenland, have been read and analysed to provide a 45 year growth chronology. Constructed growth chronologies of cod growth during the period from age 4 to 5 based on otolith annual increment analysis, length-at-age and fish condition were correlated with available climate (temperature, NAO, salinity) and biological data (abundance of zooplankton). The growth chronologies showed large interannual variations with the highest growth found in 1961 and 1977, and the lowest in 1955 and 1981. In terms of annual increment widths and back-calculated growth, age 5 cod was around 60µm and 30mm longer, respectively, in strong than in poor growth years. Differences in 6 years old cod were slightly less pronounced with 50µm for annual increment width and 25mm for back-calculated growth. Otolith growth, length-at-age and cod condition demonstrated a moderate positive correlation with temperature which corresponded with previous studies. It was difficult to assign relationships with other climate and biological time series mainly because of the spatial mismatch between adult cod and climatic/zooplankton sampling areas. Results suggest that responses of cod to future climate changes are highly uncertain and difficult to predict as they seem to depend on several environmental variables besides temperature, such as plankton production and prey-predator interactions.

Keywords: Atlantic cod; Greenland; growth; chronology; otolith; climate change.

Sumário:

A produtividade do bacalhau do Atlântico (*Gadus morhua*) têm vindo a sofrer quebras acentuadas e para além do impacto negativo de uma exploração insustentável, alterações ambientais poderão também ter a sua contribuição. Otólitos de bacalhau do Atlântico capturado durante o período de 1940-1985 no fiorde de Nuuk, Gronelândia, foram analisados para construir uma cronologia de crescimento de 45 anos. As cronologias obtidas com base na análise dos incrementos anuais dos otólitos, comprimento total e condição corporal foram posteriormente correlacionadas com séries temporais de dados climáticos (temperatura, NAO, salinidade) e biológicos (abundância de zooplâncton) disponíveis. Todas as cronologias de crescimento obtidas demonstraram grande variabilidade interanual, com elevado crescimento nos anos 1961 e 1977, e fraco crescimento em 1955 e 1981. Em termos de espessura dos incrementos anuais e crescimento retro-calculado, indivíduos com 5 anos de idade demonstraram ser cerca de 60um e 30mm maiores, respectivamente, nos anos de forte comparativamente com anos de fraco crescimento. Estas diferenças foram menos acentuadas em indivíduos com 6 anos, com 50um e 25mm na espessura dos incrementos anuais e crescimento retro-calculado, respectivamente. Crescimento dos otólitos, comprimento total e condição corporal demonstraram uma moderada correlação com a temperatura da água, concordante com observações em estudos anteriores. Foi difícil detectar correlações entre as cronologias de crescimento obtidas e as restantes séries temporais de dados climáticos e biológicos, principalmente devido à falta de correspondência entre a área de amostragem das variáveis ambientais (climáticas e biológicas) e do local de captura do bacalhau adulto. Os resultados sugerem que a resposta do bacalhau a futuras alterações climáticas é incerta e difícil de prever uma vez que parece depender de vários factores ambientais para além da temperatura, nomeadamente da produção planctónica e de interacções predador-presa.

Palavras-chave: Bacalhau do Atlântico; Gronelândia; crescimento; cronologia; otólito; alterações climáticas.

Résumé:

La productivité de morue atlantique (*Gadus morhua*) a souffert un important déclin et hormis la surexploitation halieutique, les changements environnementaux paraissent comme à l'origine de cette variabilité. Les Otolithes de morue atlantique du large de Groenland, récoltés pendant la période 1940-1985 au fjord de Nuuk, Groenland, ont été lus et analysés pour constituer une chronologie de croissance de 45 années. Des chronologies de croissance construites à base de l'analyse d'incrément d'otolithe, la relation taille-âge et la condition des poissons ont été croisées avec des indicateurs de climat disponible (la température, NAO, salinité) et des données biologiques (abondance de zooplancton). Toutes les chronologies de croissance ont suivi un modèle assez semblable, montrant une grande variabilité interannuelles avec la croissance la plus élevée trouvée en 1961 et 1977, et la plus faible en 1955 et 1981. En termes d'incrément annuel et croissance retro-calculée, l'âge 5 de la morue était autour de 60 μ m et 30mm en longueur, respectivement, plutôt en hautes qu'en faibles années de croissance. Des différences à l'âge de 6 ans de morue ont été légèrement moins prononcées avec 50 μ m pour l'incrément annuel et 25mm pour la croissance retro-calculée. La croissance de l'otolithe, la taille-âge et la condition des morues ont présenté une faible corrélation positive avec la température ce qui corrobore de précédentes études. Il était difficile d'assigner des correspondances avec d'autres séries temporelles climatiques et biologiques principalement en raison de la disparité spatiale entre l'échantillonnage de la morue adulte avec celles du climat et du zooplancton. Les résultats suggèrent que la réponse de la morue à de futurs changements climatiques soit fortement incertaine et difficile à prévoir car elles semblent dépendre de plusieurs variables environnementales sans compter que la température, ainsi que la production planctonique et les interactions prédateurs-proies.

Mots clé: Morue atlantique; Groenland; croissance; chronologie; otolithe; changements climatiques.

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Introduction:

The Atlantic cod (*Gadus morhua*) is a cold temperate, demersal gadoid distributed in the North Atlantic from Greenland to North Carolina (Pentilla and Dery, 1988). It is an eurithermic and eurihaline species which enable its survival both in brackish and salt waters and in a wide range of temperatures from near freezing to 20° (Drinkwater, 2005). These characteristics allow the species to be spread across a broad variety of habitats, from fjords and coastal areas to the continental shelf (Cohen et al., 1990). On average they reach maturity around 4 years old but maturity age may vary greatly among populations and in responses to fisheries exploitation (Fahay et al., 1999). It is among the most productive teleost species, with an average production of one million eggs per female per year (Cohen et al., 1990). Atlantic cod has a varied diet. Reported food items vary by life stage and habitat area. Larvae feed essentially on plankton, juveniles on invertebrates and adults on invertebrates and fish (Rose et al., 2000; Drinkwater, 2005).

The Atlantic cod supported one of the largest and economically most important fisheries throughout the North Atlantic for almost 500 years. However, beginning in the early 1960s, cod productivity has suffered a severe decline and extremely low recovery rates have been reported since then (Hutchings, 2000). It is presently listed as 'vulnerable' by the International Union for Conservation of Nature (IUCN) and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Hutchings and Reynolds, 2004). Greenland is no exception to the general situation observed in the North Atlantic. Also there the Atlantic cod has been the most important resource for commercial fisheries since 1920 (Pedersen and Rice, 2002; Hamilton et al., 2003). Although, after 1970 cod productivity started to drop and at present abundance levels are so low that only small inshore fishery takes place (Horsted, 2000; Wieland and Hovgard, 2002; Buch et al., 2003). While many studies have concluded that over fishing was the main factor causing the decline of Atlantic cod (Hutchings and Myers, 1993; Rose et al., 2000; Smedbol et al., 2002; Brander, 2007) there is also evidence that environmental factors, such as climate change, have impact on stock productivity (Buch et al., 1994; Ratz et al., 1999; Horsted, 2000; Pörtner et al., 2001; Cook and Heath, 2005; Hannesson, 2007). Currently, is generally accepted that both fishing and climate interact and that both have contributed to recent declines (Clark et al., 2003; Hamilton et al., 2003; Perry et al., 2005).

Climate Models predict significant warming around the globe under higher levels of greenhouse gases (IPCC, 2001). The physical dynamic characteristics of the Northern Atlantic are critical for the global circulation pattern, and this area is implicated in rapid

pre-historic and possible future climatic shifts (Blunier and Brook, 2001). Hence dramatic changes in its marine ecosystem may be expected. Indeed, over the next 50 years, temperatures in the North Atlantic are likely to rise by 1-3° and this is expected to lead changes in several fish stocks (Hannesson, 2007). Moreover because it is located on margins of an ice sheet (Hamilton et al., 2003) and in the subarctic and arctic regions, where some of the greatest climatic variations are expected (Drinkwater, 2005), Greenland is an exceptionally vulnerable area to global warming effects.

The surface circulation off West Greenland is dominated by the north going West Greenland current. It is a mixture of cold low-saline Polar Water of the Arctic and the temperate saline Irminger Water of the Atlantic Ocean. Labrador Sea Water is found at intermediate depths and overflow from the Nordic Seas at the bottom. The water mass in the Nuuk fjord is believed to be a mixture of fresh water river runoffs, the temperate water of Irminger current and the cold Polar Water of the Arctic (Ribergaard et al., 2004). Studies on climatic and oceanographic conditions around Greenland point to variations in this hydrographic regime (Ratz et al., 1999). Although not in a simple consistent way, air pressures variation (e.g. NAO) have been shown to affect wind and sea conditions around Greenland, and hence sea and air temperatures (Buch et al., 2003; Hamilton et al., 2003). There is also evidence that the growing discharge from the Greenland Ice Sheet due to global warming contributed to salinity anomalies and altered water temperatures (Belkin et al., 1998; Hamilton et al., 2003). Thus, even with temperature being the climate factor most directly acting on cod populations (Pörtner et al., 2001), fluctuation on several other climate related variables, such as NAO and salinity, might also induce changes on the fish growth and productivity in this area.

Temperature is known to directly affect the biology of fish (Brander, 1995; Folkvord et al., 2004; Cook and Heath, 2005), especially in the case of thermal conformer species, such as Atlantic cod, with their internal temperature primarily controlled by that of the surrounding water. In these species, even small changes in temperature will greatly impact on metabolic rates (Clark et al., 2003). At extremely low or high temperatures the progressively insufficient capacity of mitochondria to supply oxygen to the tissues will lead to an increased mitochondrial proliferation. As a tradeoff, energy available for growth and reproduction may be reduced owing increased fractions of energy allocated to the maintenance of elevated mitochondrial densities (Pörtner et al., 2001). In the Northern Hemisphere, increasing temperatures seem favourable for stocks at the highest latitudes but detrimental for those at the southern limit (O'Brien et al., 2000). This is probably because while north stocks live closer to their lower thermal limits, in the south they come

near the upper temperature boundaries (Pörtner et al., 2001; Hannesson, 2007). Considering its high latitudinal environment, a positive effect from increasing water temperature may be expected on the Greenlandic cod stock. Indeed, there is already evidence that the occurrence of strong year-classes at West Greenland is linked to warm periods (Buch et al., 1994; Brander, 1995).

Temperature effects on growth rates are a result of an integration of multiple processes including feeding, assimilation and metabolism (Wootton, 1998). Consequently, in addition to its direct influence on the growth physiology, temperature can have indirect effects by altering the distribution and composition of prey, as well as the timing and duration of the feeding periods (Ratz et al., 1999; Clark et al., 2003). In fact, primary and secondary production may change substantially owing to temperature changes, as well as in the strength of the mixing and stratification (Pedersen and Smidt, 2000; Drinkwater, 2005). As such, bearing in mind the importance of zooplankton (e.g. copepods), invertebrates (e.g. shrimp, crabs) and fish (e.g. capelin) in the food base for larval, juvenile and adult cod, respectively (Fahay et al., 1999; Pedersen and Smidt, 2000), changes in their abundance and quality are likely to impose visible variation in cod growth (Brander and Mohn, 2004).

Growth variability has several consequences for population dynamics. Reduced growth may lead to decreased fecundity, egg size and offspring survival. In addition, with slower growth rates, the age of maturity is likely to increase, meaning that less of the population will live to become sexually mature, all of which would be expected to have a negative effect on population productivity (Hutchings and Reynolds, 2004; Drinkwater, 2005). This is particularly important in threatened fish stocks, as it is the case of Greenlandic cod, since faster potential recovery is associated with species or populations with rapid individual growth (Denney et al., 2002).

Otoliths are structures located in the inner ear acting as equilibrium organs. They are composed of a combination of calcium carbonate, generally in the form of aragonite, and a protein matrix consisting of otoline, accreted in cyclic layers which results in the appearance of distinct growth increments (Mugiya, 1987). They have been widely used for age estimation and studies of previous growth history, and are fundamental in the fisheries assessment of commercial fish species (Panfili et al., 2002). Most studies analysing the effect of temperature on fish growth focus on size-at-age or fish condition (Brander, 1995; Ratz et al., 1999; Pörtner et al., 2001; Clark et al., 2003; Brander, 2007). However, otolith characteristics are a powerful tool that may provide significant information about previous growth history of Greenlandic cod, which is ideally suited to be cross-

matched with available climate and biological data. Firstly, the growth of an otolith continues throughout the entire fish lifetime holding permanent information about age and growth history. Once they formed they do not degenerate even when fish experience poor environmental conditions (Fowler, 1995). Secondly, their growth is influenced by numerous abiotic and biotic factors including temperature, habitat and diet and their analysis may provide relevant information of past environmental events (Campana and Thorrold, 2001). Finally, fish size fluctuates considerably through the year (Cardinale et al., 2000) and therefore, otoliths may provide a more reliable growth assessment compared to size-at-age or condition indices. However, some authors report that difficulties may arise when using back-calculated growth results, since it is believed that otolith growth is a reflection of metabolism rather than somatic growth (Panfili and Tomas, 2001). Others argue that metabolism and somatic growth are interconnected processes regulated by temperature and energy intake (Sinclair et al., 2002; Pilling et al., 2007) and therefore, back-calculated growth information from otoliths might still provide reliable estimates of somatic growth.

For decades, the influence of environmental conditions on growth of cod has been a central question in fisheries biology, but recent crisis in the European fishing industry has intensified the public and scientific interest into the problem (Cook and Heath, 2005). Several authors have found positive correlations between temperature and fish size. For example, Brander (2007) concluded that year-to-year variation in weight of cod might be largely controlled by water temperature; similar findings were reported by Ratz and Lloret (2003), the authors found a significant positive linear relationship between temperature and cod growth. Others defend that establishing a convincing link between the environment and population change is often difficult. Myers et al. (1997), for example, found that most published correlations between fish performance and environmental parameters were not robust and tended to break down when data from additional years in the time series were added. The present study investigates the annual otolith growth variability of the Greenlandic cod population from Nuuk fjord. The results are discussed and compared with corresponding abiotic and biotic data from the Fyllas Bank station. Understanding the causes of past growth variability may provide a useful basis for future discussions about stock structure and management strategies for sustainable resources exploitation. Furthermore, we believe that such knowledge applied to the Nuuk fjord West Greenland population has an increased relevance as 90% of the cod landing in Greenland come from such fjord systems (Storr-Paulsen et al., 2004).

Material and Methods:

Otolith collection and preparation:

Otoliths used were collected in the Nuuk fjord system, located on the West coast of Greenland (from 64° to 65°N and 51° to 52°W), between 1940 and 1985 (figure 1). Otoliths were obtained from both commercial fishery and research survey catches. Left and right *sagittae* were removed from the fish and stored in paper envelopes.

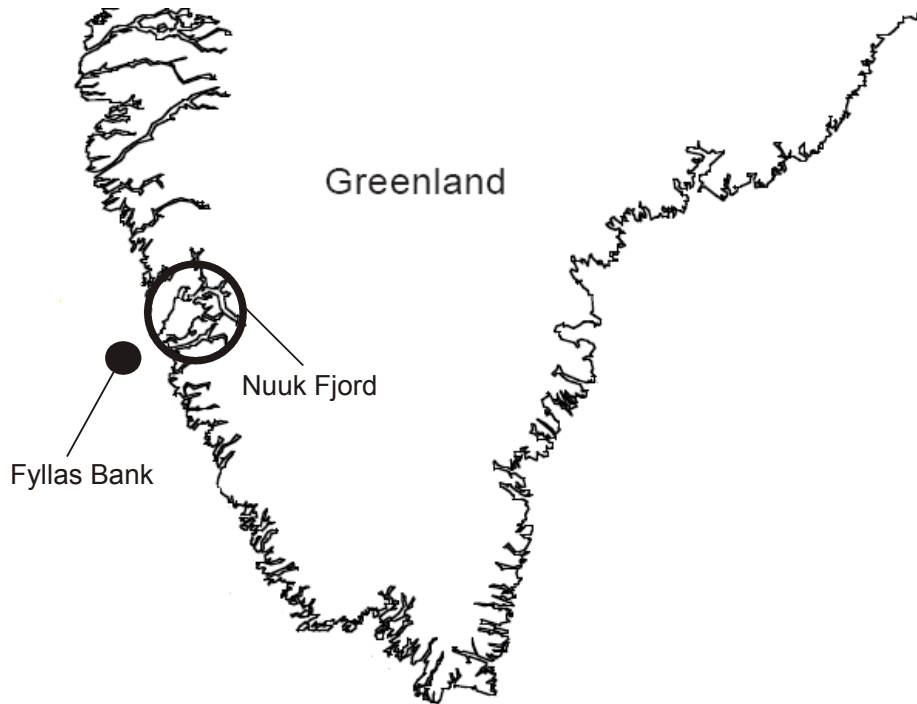


Figure 1. Southern part of Greenland. The position of the oceanographic station of Fyllas Bank where the climate and biological measures were taken is indicated by a black dot. The circle indicates the Nuuk Fjord where the adult cod was captured.

The collection was maintained by The Greenland Institute of Natural Resources and a total of 1,693 samples were selected for this study (table 1). For most of them total length, total weight, gender, age and capture date were available. To reduce the age effect on increment width the samples were limited to two age groups. Five and six years old otoliths were selected since at age 5 cod is expected to be mature and rather stationary except for the spawning related migration (Joensen et al., 2005). In order to account for the time lag between formation of the growth estimate (growth between fourth and fifth year) and capture date, the respective capture year was lagged by one year for age 5 and two for age 6. We attempted to get as many otoliths as possible per year class. Although, for some classes sample size was too small or even null due to variation in the number of fish caught and age composition among years (table 1).

Capture year	Capture month	Age		Gender			Total
		Five	Six	Unknown	Male	Female	
1940	6	5	28	2	15	16	33
1941	10	4	2		3	3	6
1942	8,9		36	10	17	9	36
1943	9	2	21	13	7	3	23
1944	4	6	20	9	10	7	26
1945	10		7			7	7
1946	7	13	13	4	11	11	26
1947	5,7	6	6		6	6	12
1948	10	9	14		8	15	23
1949	10	5			1	4	5
1950	5,7	1	11		10	2	12
1951	6		14		6	8	14
1952	6		6		3	3	6
1953	5,6	4	26		13	17	30
1954	5,7	15	26		19	22	41
1955	2	6	3		5	4	9
1956	12,6	14	33		26	21	47
1957	5	41	8		25	24	49
1958	5,7	48	2		29	21	50
1959	8,10,11	2	45		25	22	47
1960	2,4	27	20		18	29	47
1961	2,4	20	30		22	28	50
1962	4	29	16		22	23	45
1963	6	24	23		19	28	47
1964	5,9	36	2		16	22	38
1965	2,7	35	9		20	24	44
1966	9	24	26	13	15	22	50
1967	4,7	26	12	17	12	9	38
1968	6	15	28	10	19	14	43
1969	3,5,6	42	5	39	4	4	47
1970	6	16	24	11	18	11	40
1971	6	26	24	19	13	18	50
1972	7	32	13		19	26	45
1973	8	4	46	23	12	15	50
1974	9	46	3	4	31	14	49
1975	6	25	25	45	1	4	50
1976	7	34	15	48		1	49
1977	6	44	3	43	1	3	47
1978	5,7,8,12	3	37	3	13	24	40
1979	9,10	36	13	27	8	14	49
1980	1,2,5,10	31	15	7	17	22	46
1981	3,8,9	32	11	30	5	8	43
1982	6	10	38	47	1		48
1983	8	39		31	8		39
1984	8	6	44	50			50
1985	7,8	47		37	4	6	47
Total		890	803	542	557	594	1693

Table 1. Selected otoliths. Number of selected otoliths by capture year, month (jan=1, feb=2,..., dec=12), age and gender.

All otoliths selected were weighed on a Sartorius BP210P scale with a precision of 0.0001g before preparation. The preparation of transversal sections followed the procedures described by Pentilla (1988). Only one of each pair of otoliths was analysed because differences have rarely been recorded between the right and the left *sagitta* (Ratz, 1994). The random chosen otolith was broken and one of the two sections was polished using a polisher (Struers LaboPol-5 speed range 100 – 500 rpm, sandpaper grain size 800) through the centre until exposing the nucleus and the annual ring structure. Using a Bunsen burner the polished section was baked until it turned a caramel brown color. The flame was kept as low as possible to avoid shattering the otolith. The prepared section was mounted on black plasticine and wetted with oil in order to enhance the visibility of the rings. Otolith images were captured using a Stereomicroscope (Leica MZ12.5) equipped with a fixed digital camera (Olympus DP50) at a magnification of 16X.

Otolith interpretation and variables measured:

Rings formed during periods of slow winter-type growth appear as dark/hyaline zones while growth increments formed during periods of rapid summer-type growth appear as white/opaque zones with reflected light. According to Pentilla (1988) an annulus was defined as a dark/hyaline zone marking the end of a year of growth. For all otoliths the width of each annual increment and main radius (maximum distance from the core to the outermost edge) were measured using ImageJ 1.37v software (Rasband, 1997-2007).

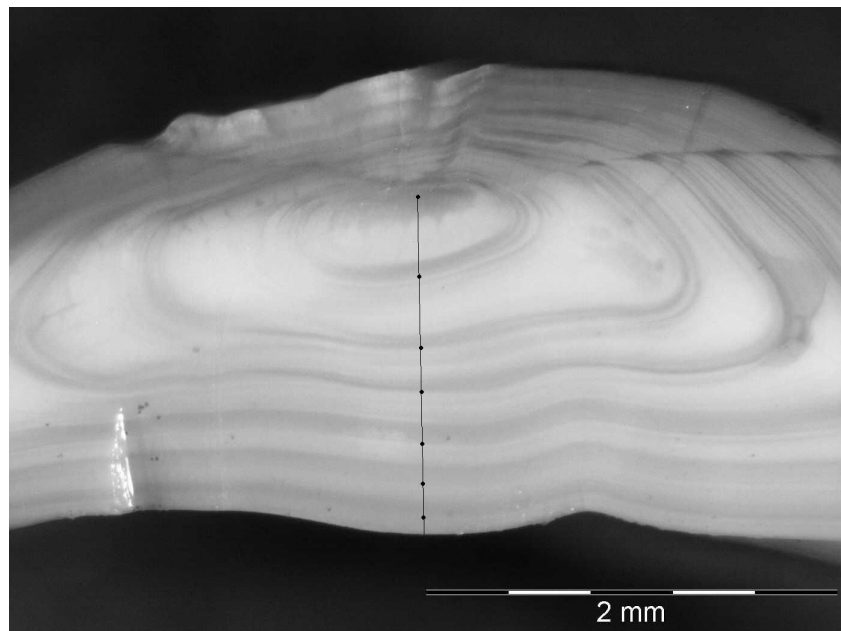


Figure 2. Sectioned otolith. Sectioned otolith from Greendic cod (age 6) caught in September 1942. Otolith viewed under reflected light at 16X magnification. Line shows axis (L-axis) of measurement and points show the position of annual rings (complete opaque and hyaline bands).

Three measurements of each individual annual increment and radius were taken near the “Longer axis”, i.e. L-axis on the ventral lobe (figure 2) and the mean of the three measures was used for subsequent data analysis. An arbitrary scale from 1 (unambiguous measure) to 3 (little confidence) was used to score all otoliths measured. Samples scored with 3 were discarded. This approach was followed in an attempt to reduce the influence of single, aberrant measurements since otolith interpretation is not equally reliable between a group of samples (Campana and Jones, 1992).

Data analysis:

Backcalculation of Growth:

The increase in fish length from fourth to fifth year was estimated by means of the Biological Intercept back-calculation method. Like traditional growth back-calculations, the biological intercept method assumes proportionality between fish and otolith growth within an individual. However, the value of the biological intercept is determined by the mean size of the fish and otolith at the initiation of proportionality, and thus variation between samples does not affect regression parameters (Campana and Jones, 1992). A biological intercept value of 26mm body length with an otolith length of 316um was used. These values were estimated from a previous study by Poulsen (2005), who validated a strong linear relationship between *sagitta* otolith radius and body length of Atlantic cod juveniles on the Faroe Plateau. Applying back-calculation with the biological intercept equation (Campana and Jones, 1992) and considering estimated values from Poulsen (2005), the following formula was used:

$$\Delta L_{4-5} = [(L_c - 26) / O_c - 316] * (O_5 - O_4)$$

Where ΔL_{4-5} = fish length increase from fourth to fifth year (mm);

L_c = fish length at capture (mm);

O_c = otolith radius at capture (um);

$O_5 - O_4$ = measured growth increment from fourth to fifth year (um).

Fulton's K Condition Factor:

In an attempt to compare as many growth related variables as possible, interannual variations in the cod condition were assessed by calculating the Fulton's *K* condition factor from all age 5 samples for each year with available data on fish length and weight. The *K* condition factor was expressed as:

$$K = 100 * (W / L^3)$$

Where W = total body weight (g);

L = total body length (cm).

The constant = 3 assumes an isometric growth in fish ([Lloret and Ratz, 2000](#)).

Biological and climate data:

Abundance indices of zooplankton in West Greenland were obtained from [Pedersen and Smidt \(2000\)](#). Annual oceanographic surveys were made during late-June-mid-July from 1950 to 1984 along a sampling section at Fyllas Bank (figure 1). Seven indices were selected for comparison with our estimated growth parameters based on their potential as indicators of changes and variability in the Greenlandic ecosystem. The selected indices were: zooplankton displacement volume (PLVOL); copepods (COP); euphausiid (EUPH); shrimp larvae (SHR); crab larvae (CRAB); atlantic cod larvae (COD) and sandeel larvae (SAND). For a detailed description of these data see [Pedersen and Smidt \(2000\)](#). In order to investigate their effect on cod growth, the growth parameters were lagged by one year compared to these data. The hypothesis of high cod larvae abundance as a result of high adult cod growth was also tested lagging cod larvae abundance indices by one year.

Two different data sets of temperature were used to assess possible correlations with growth parameters. The first one (TEMP1) was sampled during mid-June of each year since 1950 by the (Greenland Fisheries Research Institute, GFRI). The mean temperature was derived by averaging the observations at the standard levels, 0, 10, 20, 30 and 40m ([Ratz et al., 1999](#)). The second set (TEMP2) consisted of measurements taken simultaneously with zooplankton sampling at five standard depths: 10, 20, 30, 40 and 50m. Salinity (SAL) was calculated as means of measurements taken at same time and depth levels as TEMP2 ([Pedersen and Smidt, 2000](#)).

Mean annual NAO Index based on the difference of normalized sea level pressures between Ponta Delgada, Azores and Stykkisholmur/Reykjavik, Iceland was obtained from Climate & Global Dynamics (CGD's), Climate Analysis Section (<http://www.cgd.ucar.edu/cas/jhurrell/indices.data.htm>).

Statistical analyses:

The focus of the analyses was the growth of cod otoliths from the fourth to the fifth year. Data analyses were carried out using SPSS (Version 15.0 for windows). One-way Anova pre-tests were performed to investigate effect of gender and age on Annual Increment (AIG) and Back-calculated growth (BCG) for selected years with more than 7 samples per group (male/female or age5/age6). After pre-tests, AIG and BCG were tested for year factor, separately for each age class (5 and 6), using one-way Anova, followed by Ryan-Einot-Gabriel-Welsch-Range-Q post hoc test. In all analysis, normality and homogeneity of variance was tested. When assumption of equal variances was not verified, year classes with extremely high or low variance were excluded. Also years with sample size smaller or equal to 4 were not statistically tested. For Fulton's K (FK), fish length (FL) and otolith weight (OW) the gender effect was investigated following the same procedure as for AIG and BCG. Age effect was not tested since only 5 years old samples were analysed for these three parameters. Year effect was tested with non-parametric (Kruskal-Wallis) because normality and homogeneity of variance assumptions were not verified. Ultimately, the degree of association between analysed growth parameters and climate/biological variables were investigated using Pearson correlations.

Results:

Increment measurements were taken from a total of 1,693 cod otoliths (ages 5 and 6) spread across 45 years (table 1). However, due to poorly visible increments some samples were excluded (grade 3 otoliths). After selection a total of 1,352 otoliths remained for further analysis.

Increment analysis:

Annual Increment Growth:

No gender effect was found with regards to mean Annual Increment Growth (AIG) between fourth and fifth year (One-Way Anova, $P > 0.05$ between 4 out of 4 years tested) but age 6 otoliths showed a significantly higher AIG compared to age 5 (One-Way Anova, $P < 0.05$ between 5 out of 6 years tested). Thus, males and females were pooled together and five and six years old samples were analysed separately.

Annual increment growth chronology for age 5 and 6 is shown in figure 3. Both revealed that AIG fluctuated significantly among the years (One-Way Anova, $F_{26,571} = 6.0$, $P < 0.0005$ (age 5); $F_{29,568} = 4.0$, $P < 0.0005$ (age 6)) and a similar pattern between the two age classes was identified within the covered time series (figure 3). For age 5 almost no variation was observed from 1938 to 1952. After 1952 a general increase trend was noticed until 1961 remaining fairly stable till 1968. From 1969 to 1973 growth decreased followed by a recovery period in the next 4 years, reaching the maximum statistically recorded in 1977. After 1977 and till the end of the covered time series a general decreased trend was verified (figure 3). Age 6 class showed a general decreased trend in the first years (1938 – 1944) followed by a long increased growth period until the year of 1961. After this the trend became less stable but still a growth declined was observed in the last years (1977-1984) as for age 5 (figure 3).

The highest growth for age 5 was recorded in 1977 with 196.1 μm followed by 1961 with 194.6 μm . On the opposite, 1955 (135.8 μm) and 1981 (147.0 μm) were the years with the poorest growth. Similar peaks were observed for age 6 class with a maximum growth in 1961 (220.6 μm) and a minimum in 1981 (170.5 μm). These evidences are also apparent from the post hoc test (Einot-Gabriel-Welsch-Range-Q) where 1981 and 1961 were assigned to the minimum (C) and maximum (A) range, respectively, for both age classes (table 2).

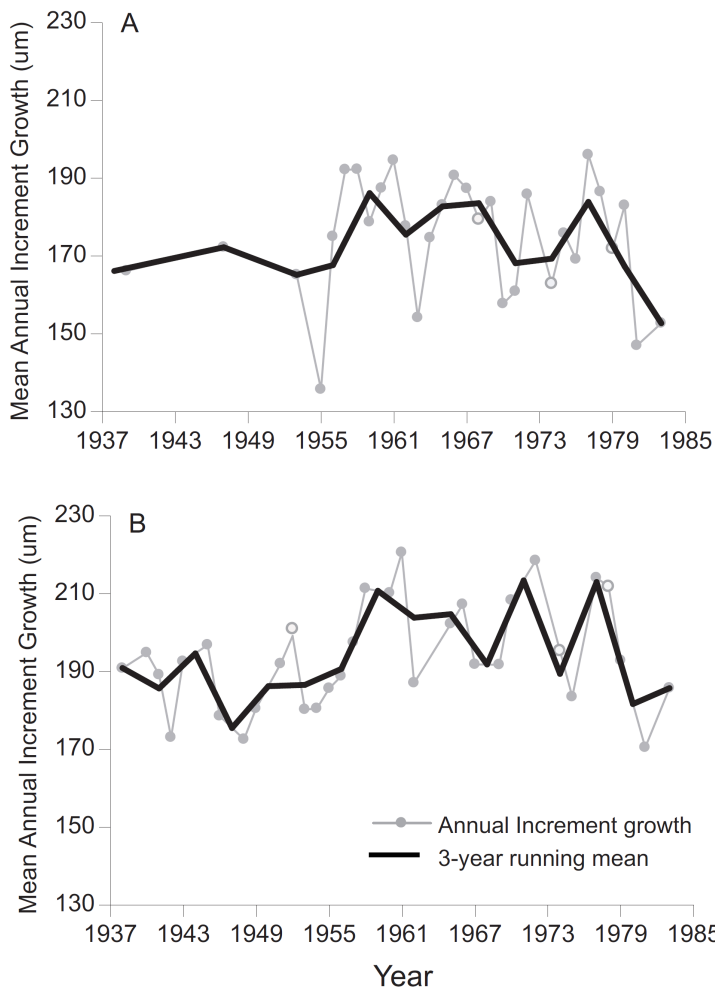


Figure 3. Annual Increment Growth. Mean Annual Increment Growth (AIG) from fourth to fifth year for age 5 (A) and age 6 (B). Open dots (o) refer to years excluded from statistical analysis due to extremely high or low variance. Trends were smoothed by taking a 3-year running means (heavy black line).

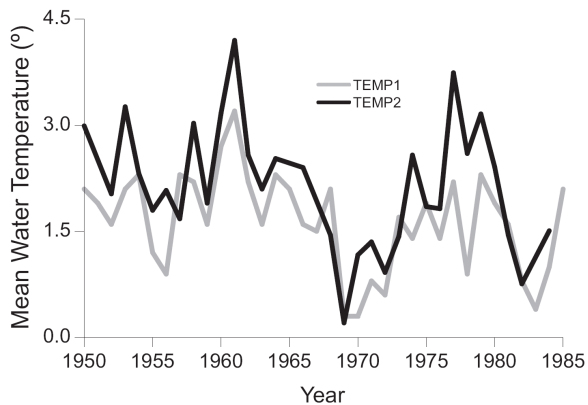


Figure 4. Water temperature. The two different sets of interannual variations in water temperature at Fyllas Bank.

AIG for age 5 class was found to be positive correlated with both water temperature data sets but only for the group of samples scored with CL=1 in both data sets and for CL=1,2 in TEMP 1 (table 3 and figure 5). Temperature data sets showed the same trend, although generally with higher values for TEMP2 (figure 4).

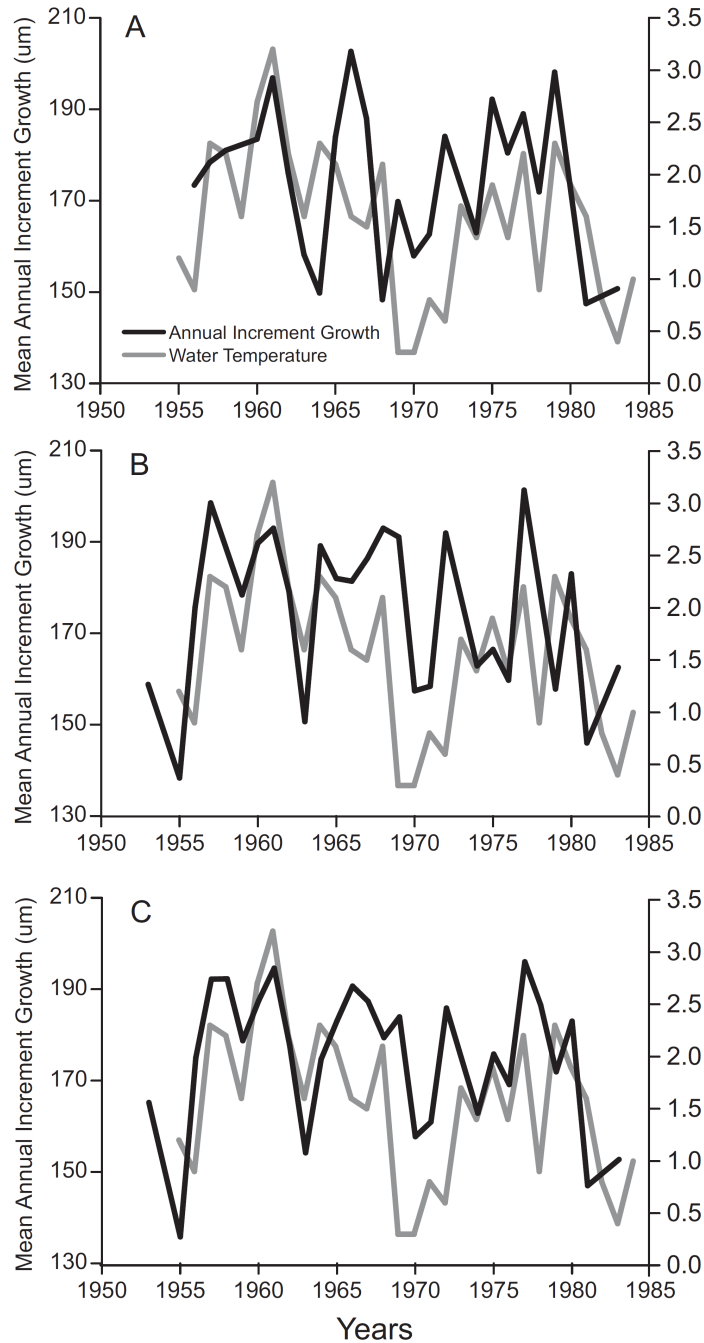


Figure 5. Annual Increment Growth vs Water Temperature. Mean Annual Increment Growth (AIG) from fourth to fifth year for 5 year old cod and Water Temperature from the first data set (Ratz *et al.*, 1999). (A) average measurements scored with a confidence level of 1 (CL=1). For (B) CL=2. (C) average both CL=1 and CL=2.

A negative correlation with cod larvae (COD t-1) abundance was also verified for AIG age 5, but only in group samples scored with 1. CL=2 and CL=1,2 samples were negatively correlated with shrimp larvae (SHR) abundance (table 3). For age 6 class no correlations

with climatic variables and AIG were found. Measurements scored with CL=2 and CL=1,2 showed a significant negative correlation with cod larvae (COD t-1) abundance (table 3).

Back-calculated Growth:

A linear relationship was observed between fish length and otolith radius when mean annual values from both variables were plotted against each other (figure 6). This linear relationship was also confirmed statistically (Linear regression: $F_{1,37} = 30.8$; $P < 0.0005$).

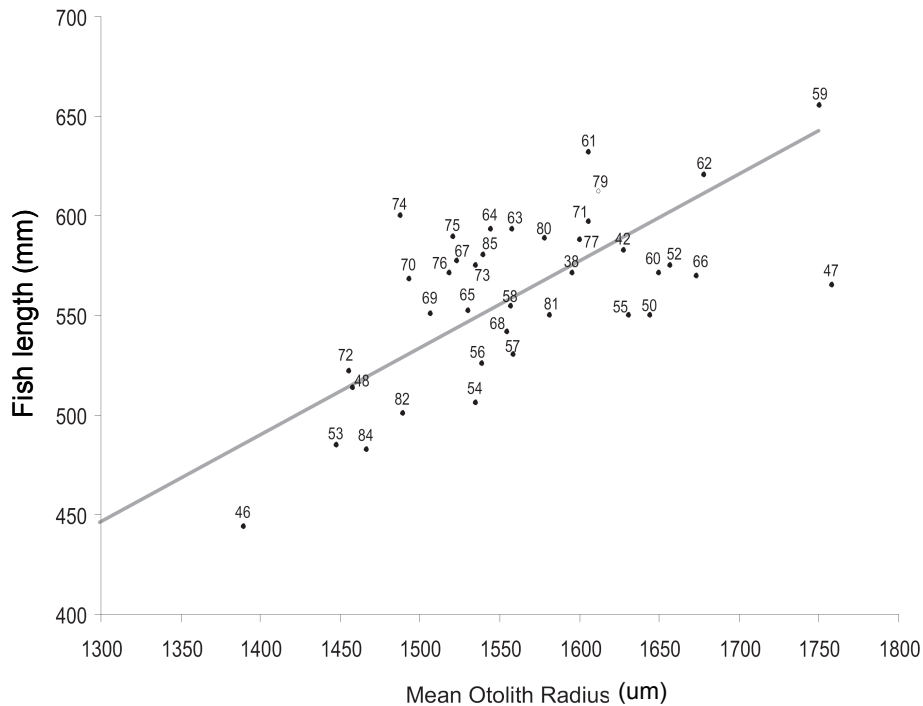


Figure 6. Fish length vs Otolith radius. Correlation between fish length and otolith radius for five years old cod. Regression line (heavy grey) forced through the biological intercept point of 316, 26 (x, y respectively according to Poulsen, 2005).

As for AIG, no statistical evidences were found for gender effect on BCG (One-Way Anova, $P > 0.05$ between 4 out of 4 years tested) and a significantly higher back-calculated growth on age 6 class was observed (One-Way Anova, $P < 0.05$ between 5 out of 6 years tested). Again, age classes were analysed separately and males and females pooled together. In both age classes the BCG length followed a trend similar to AIG, although with a less pronounced difference between years (figure 3 and 7) but still significantly different (One-Way Anova, $F_{26,562} = 14.6$, $P < 0.0005$ (age 5); $F_{28,536} = 11.2$, $P < 0.0005$ (age 6)). For age 5, the highest (1977, 88.5mm) and lowest (1955, 56.3mm) BCG growth years were coincident with the observations for AIG. For age 6 class a different maximum (1972; 102.2mm) and minimum (1948; 67.8mm) were found, nevertheless, highest and lowest

years for BCG still corresponded to good and poor AIG years, respectively, and vice-versa (table 2).

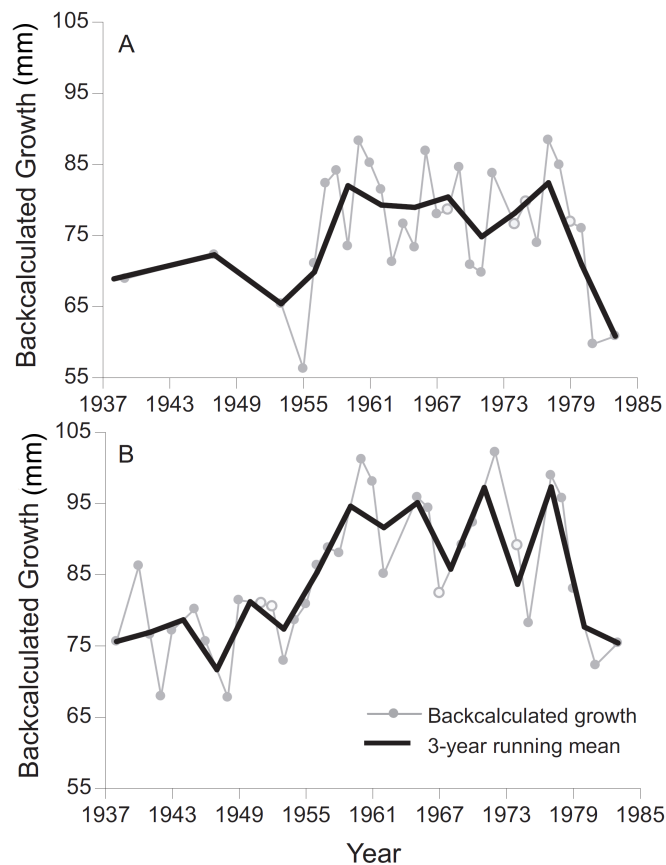


Figure 7. Back-calculated Growth. Mean Back-calculated Growth (BCG) from fourth to fifth year for age 5 (A) and age 6 (B). Open dots (o) refer to year classes excluded from statistical analysis due to extremely high or low variance. Trends were smoothed by taking a 3-year running means (heavy black line).

Age 5 samples scored with CL=1 were positively correlated with TEMP2 but age 6 showed no correlation with any of the climatic variables. One of the biological indices (COD t-1) found to be negatively correlated with BCG for group samples scored with CL=1 in age 5 class (table 3).

Year Class	AIG (uM)				BCG (mm)							
	Age 5		Age 6		Age 5				Age 6			
	Mean ± SE	N	Stat	Mean ± SE	N	Stat	Mean ± SE	N	Stat	Mean ± SE	N	Stat
1938				190.9 ± 7.1	25	ABC				75.66 ± 2.39	25	EFG
1939	166.2 ± 7.7	9	ABC				68.93 ± 2.42	9	DEFG			
1940				194.9 ± 5.1	42	ABC				86.25 ± 2.25	42	CDEF
1941	199.8 ± 6.6	4	**	189.2 ± 8.7	13	ABC	85.38 ± 4.22	4	**	75.81 ± 3.89	13	DEFG
1942				173.1 ± 12.3	12	BC				67.93 ± 4.78	12	G
1943				192.6 ± 16.0	5	ABC				81.95 ± 5.25	5	CDEFG
1944				146.2 ± 17.6	3	**				53.35 ± 7.33	3	**
1945				196.9 ± 10.4	6	ABC				80.19 ± 4.58	6	CDEFG
1946	194.2 ± 9.2	4	**	178.6 ± 5.2	12	BC	73.99 ± 7.87	4	**	75.64 ± 3.63	12	EFG
1947	172.3 ± 14.6	5	ABC	192.0 ± 6.3	4	**	72.31 ± 2.78	5	CDEF	88.55 ± 4.24	4	**
1948				172.6 ± 7.1	9	BC				67.77 ± 2.54	9	G
1949				180.5 ± 7.4	12	BC				81.43 ± 4.28	12	CDEFG
1950				215.8 ± 17.7	4	**				90.88 ± 6.51	4	**
1951	205.7 ± 17.7	2	**	192.0 ± 8.7	19	ABC	84.22 ± 7.27	2	**	81.00 ± 4.09	19	*
1952	152.7 ± 19.6	4	**	199.2 ± 10.9	20	*	61.77 ± 7.26	4	**	80.58 ± 4.02	20	*
1953	165.2 ± 8.4	15	ABC	180.3 ± 17.5	5	BC	65.42 ± 3.77	15	EFG	77.53 ± 5.24	5	FG
1954	133.7 ± 12.0	2	**	180.5 ± 7.4	12	BC	53.59 ± 7.83	2	**	78.65 ± 3.34	12	CDEFG
1955	135.8 ± 7.4	10	C	185.7 ± 12.6	7	BC	56.30 ± 3.28	10	G	80.91 ± 4.17	7	CDEFG
1956	175.0 ± 6.5	27	ABC	188.9 ± 10.3	7	ABC	71.09 ± 2.57	27	DEF	86.34 ± 3.41	7	BCDEF
1957	192.2 ± 5.1	35	A	197.5 ± 5.9	34	ABC	82.34 ± 2.40	35	ABC	88.80 ± 2.23	34	BCDE
1958	192.3 ± 10.9	8	AB	211.4 ± 6.9	6	AB	84.15 ± 2.50	8	AB	88.26 ± 1.68	6	BCDEF
1959	178.8 ± 8.0	20	ABC	177.8 ± 23.8	4	**	73.54 ± 3.86	20	BCDE	88.42 ± 13.21	4	**
1960	187.5 ± 4.5	33	AB	210.2 ± 5.7	25	AB	88.33 ± 2.07	33	A	101.24 ± 2.52	25	AB
1961	194.6 ± 7.6	19	A	220.6 ± 7.5	23	A	85.22 ± 3.11	19	AB	98.10 ± 3.05	23	ABC
1962	177.7 ± 5.0	24	ABC	187.1 ± 13.5	8	ABC	81.48 ± 2.31	24	ABCD	85.15 ± 5.55	8	CDEFG
1963	154.2 ± 5.0	17	BC				71.30 ± 2.36	17	CDEF			
1964	174.7 ± 6.8	19	ABC				76.63 ± 4.11	19	ABCDE			
1965	183.1 ± 4.4	44	AB	202.3 ± 6.0	27	ABC	73.36 ± 1.75	44	CDE	95.91 ± 2.96	27	ABCD
1966	190.7 ± 7.8	16	AB	207.3 ± 7.5	21	ABC	86.90 ± 2.92	16	AB	94.38 ± 3.17	21	ABCD
1967	187.3 ± 6.7	21	AB	191.9 ± 11.8	15	ABC	78.04 ± 2.58	21	ABCDE	82.44 ± 5.49	15	*
1968	179.4 ± 10.5	23	*				78.66 ± 4.26	23	*			
1969	184.0 ± 7.4	15	AB	191.8 ± 4.9	31	ABC	84.62 ± 3.93	15	AB	89.21 ± 2.46	31	BCDE
1970	157.8 ± 7.2	15	ABC	208.4 ± 7.1	26	AB	70.91 ± 4.32	15	DEFG	92.34 ± 3.37	26	ABCD
1971	161.0 ± 8.9	17	ABC				69.82 ± 3.68	17	DEFG			
1972	185.9 ± 4.8	48	AB	218.5 ± 5.0	46	A	83.79 ± 1.94	48	AB	102.24 ± 2.51	46	A
1973	148.4 ± 14.7	3	**				73.11 ± 7.79	3	**			
1974	162.9 ± 8.1	39	*	195.4 ± 14.0	15	*	76.59 ± 3.93	39	*	89.15 ± 6.38	15	*
1975	175.9 ± 10.0	22	ABC	183.5 ± 11.7	8	BC	79.79 ± 4.82	22	*	78.21 ± 4.77	8	CDEFG
1976	169.2 ± 6.4	22	ABC				73.97 ± 2.53	22	BCDE			
1977	196.1 ± 5.9	28	A	214.1 ± 5.8	36	AB	88.45 ± 2.62	28	A	98.98 ± 2.66	36	AB
1978	186.6 ± 7.7	8	AB	211.9 ± 14.1	12	*	84.94 ± 4.31	8	AB	95.75 ± 4.87	12	ABCD
1979	172.0 ± 10.5	20	*	192.9 ± 12.6	5	ABC	76.95 ± 5.27	20	*	83.05 ± 6.55	5	CDEFG
1980	183.0 ± 9.6	15	ABC				76.02 ± 3.51	15	ABCDE			
1981	147.0 ± 3.7	43	C	170.5 ± 2.9	47	C	59.75 ± 1.63	43	G	72.32 ± 1.42	47	G
1982												
1983	152.8 ± 4.4	47	C	185.8 ± 6.1	39	BC	60.89 ± 2.01	47	FG	75.43 ± 2.36	39	FG
1984	169.7 ± 8.8	4	**				68.39 ± 1.05	4	**			

Table 2. Annual Increment and Back-calculated Growth. Mean Annual Increment (AIG) and Back-calculated Growth (BCG) between fourth and fifth year with standard error (SE) and sample size (N) by age and year class. Stat column relate to the groups formed in the post hoc test (Einot-Gabriel-Welsch-Range-Q). ** indicates year classes with $N \leq 4$ and * refers to years excluded from statistical analysis due to extremely high or low variance.

Otolith weight:

The otolith weight (OW) was analysed for samples of five years old cod. No statistical evidence of gender effect was found (One-Way Anova, $P > 0.05$ between 8 out of 9 years tested) allowing to pool males and females in the same group. Annual mean otolith weight showed clear interannual variations (Kruskall Wallis, $\chi^2_{30} = 260.4$, $P < 0.0005$) with high weight during 1978 (399.6mg) and 1959 (372.4g), and the lowest in 1946 (216.5mg). Between 1940 and 1954 data was not consistent enough showing a strong variation due

to years with small ($N \leq 4$) or null sample size. The period between 1955 and 1961 was characterized by an accented increase in otolith weight. From 1961 to 1975 a decreased was observed followed by a recovery until 1978. From this point and until 1985 OW dropped quite sharply (figure 8). Annual mean OW values were positively correlated with water temperature (TEMP2, table 3).

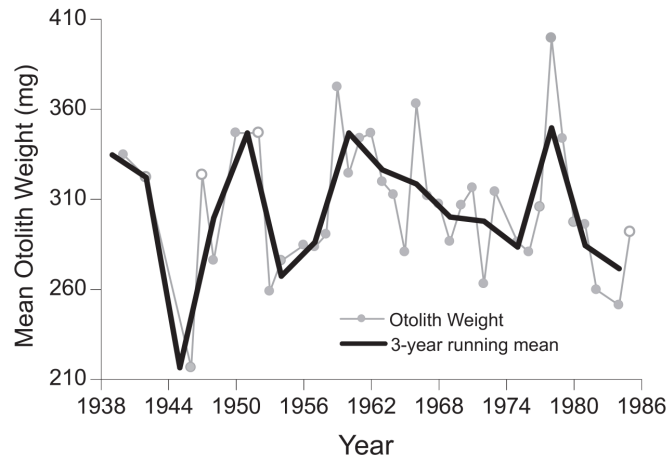


Figure 8. Otolith weight. Mean otolith weight for 5 year old cod. Open dots (o) represent mean per year class with $N \leq 4$. Trends were smoothed by taking 3-year running means (heavy black line).

Fulton's K Condition Factor:

Fulton's K was calculated for five years old cod when fish length and weight was available. No effect of gender was found (One-Way Anova, $P > 0.05$ between 4 out of 4 years tested) and hence male and female were pooled together. Fulton's K condition factor demonstrated a significant interannual variation (Kruskall Wallis, $\chi^2_{19} = 236.1$, $P < 0.0005$). Excluding the first 16 years (1940 – 1956) where sample size was too small ($N \leq 4$) or even null (exception for the first year, 1940), a fairly similar trend was observed when comparing 3-year running means between Fulton's K (FK) and otolith weight (OW) (figure 8,9). Specially when looking at the end of the time series, the observed increased condition between 1973 and 1978 followed by a drop from 1978 to 1985 is in well agreement for the two growth parameters. Among the years with $N > 4$, the highest condition was verified in 1960 and 1970 (1.11) and the lowest in 1984 (0.73). FK showed to be positively correlated with TEMP2 and negatively with shrimp larvae (SHR) (table 3).

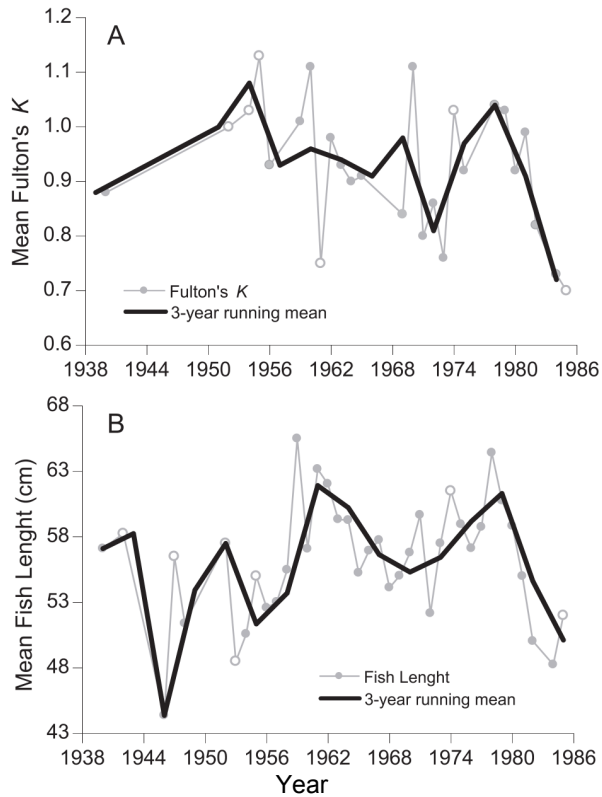


Figure 9. Fulton's K and Fish length. Mean (A) Fulton's K and (B) fish length for 5 year old cod. Open dots (o) represent mean per year class with $N \leq 4$. Trends were smoothed by taking 3-year running means (heavy black line).

Fish length:

Fish length (FL) was also analysed only for age 5 class. Length was independent of gender (One-Way Anova, $P > 0.05$ in 5 out of 5 years tested). A significant variation among the years was observed (Kruskall Wallis, $\chi^2_{30} = 334.0$, $P < 0.0005$) showing a maximum in 1959 (65.5cm) and a minimum in 1946 (44.4cm). Time series for fish length followed very close the trend for otolith weight and Fulton's K. Maximum and minimum peaks for FL were in accordance to the observations taken for OW (figure 8,9). A positive correlation was found between fish length and sea temperature (TEMP2). Crab larvae abundance (CRAB) was found to be negatively correlated with fish length (table 3).

	AIG			BCG						FK			FL			OW		
	Age 5			Age 6			Age 5			Age 6			Age 5			Age 6		
	CL=1	CL=2	CL=1,2	CL=1	CL=2	CL=1,2	CL=1	CL=2	CL=1,2	CL=1	CL=2	CL=1,2	CL=1	CL=2	CL=1,2	CL=1	CL=2	CL=1,2
TEMP1	r	0.398*	0.326	0.134	0.142	0.102	0.367	0.279	0.352	0.235	0.016	0.089	0.295	0.281	0.218			
	P	0.036	0.090	0.574	0.507	0.636	0.057	0.151	0.066	0.318	0.942	0.681	0.219	0.148	0.266			
	N	28	28	20	24	24	28	28	28	20	24	24	19	28	28			
TEMP2	r	0.457*	0.231	0.274	0.403	0.289	0.456*	0.163	0.285	0.294	0.212	0.196	0.553*	0.492*	0.467*			
	P	0.022	0.266	0.305	0.078	0.216	0.022	0.436	0.167	0.268	0.370	0.408	0.017	0.011	0.016			
	N	25	25	16	20	20	25	25	25	16	20	20	18	26	26			
SAL	r	0.181	-0.004	0.041	0.177	0.195	0.181	0.176	-0.059	0.014	-0.073	0.012	-0.102	0.163	0.040			
	P	0.396	0.986	0.848	0.513	0.424	0.459	0.410	0.783	0.949	0.768	0.961	0.696	0.436	0.849			
	N	24	24	16	19	19	24	24	24	16	19	19	17	25	25			
NAO	r	0.209	-0.203	-0.086	-0.267	-0.242	-0.274	0.027	-0.208	-0.174	-0.259	-0.258	-0.318	-0.321	-0.314			
	P	0.276	0.292	0.653	0.188	0.182	0.123	0.889	0.280	0.358	0.192	0.148	0.172	0.078	0.086			
	N	29	29	30	26	32	33	29	29	30	27	33	20	31	31			
PLVOL	r	0.011	0.006	-0.092	-0.085	-0.103	-0.169	-0.076	-0.110	-0.046	0.036	-0.002	-0.038	-0.274	-0.160			
	P	0.959	0.976	0.707	0.700	0.641	0.418	0.718	0.601	0.853	0.872	0.993	0.888	0.206	0.466			
	N	25	25	19	23	23	25	25	25	19	23	23	16	23	23			
COP	r	0.302	0.183	0.241	0.102	0.055	0.060	0.113	0.141	0.131	0.133	0.090	0.276	-0.025	0.220			
	P	0.208	0.454	0.321	0.741	0.845	0.831	0.646	0.565	0.594	0.636	0.750	0.319	0.922	0.381			
	N	19	19	13	15	15	19	19	19	13	15	15	15	18	18			
EUPH	r	0.277	0.295	0.320	0.119	0.245	0.185	0.221	0.284	0.283	0.310	0.288	0.302	-0.169	0.118			
	P	0.251	0.220	0.182	0.699	0.379	0.508	0.364	0.238	0.241	0.260	0.298	0.274	0.503	0.640			
	N	19	19	19	13	15	15	19	19	19	13	15	15	18	18			
SHR	r	-0.147	-0.540*	-0.469*	-0.402	-0.221	-0.269	-0.065	-0.418	-0.323	-0.345	-0.306	-0.515*	0.040	-0.144			
	P	0.549	0.017	0.043	0.173	0.429	0.333	0.792	0.075	0.178	0.208	0.268	0.049	0.875	0.568			
	N	19	19	19	13	15	15	19	19	19	13	15	15	18	18			
CRAB	r	-0.215	0.022	-0.081	0.090	0.104	0.194	-0.239	-0.010	-0.095	0.165	0.203	-0.344	-0.585*	-0.432			
	P	0.377	0.928	0.743	0.770	0.712	0.488	0.324	0.967	0.698	0.557	0.469	0.210	0.011	0.073			
	N	19	19	19	13	15	15	19	19	19	13	15	15	18	18			
SAND	r	-0.271	-0.136	-0.208	0.001	0.148	0.133	-0.198	-0.002	-0.074	0.163	0.166	0.280	-0.355	-0.213			
	P	0.181	0.506	0.308	0.996	0.489	0.536	0.332	0.993	0.721	0.447	0.438	0.293	0.089	0.318			
	N	26	26	26	20	24	24	26	26	26	24	24	16	24	24			
COD	r	-0.404*	-0.178	-0.304	-0.427	-0.436*	-0.455*	-0.413*	-0.291	-0.348	-0.361	-0.379	0.280	-0.355	-0.213			
	P	0.041	0.384	0.131	0.060	0.033	0.026	0.036	0.149	0.081	0.083	0.068	0.293	0.089	0.318			
	N	26	26	26	20	24	24	26	26	26	20	24	16	24	24			
COD	r	-0.040	0.193	0.053	0.010	0.108	0.016	-0.165	-0.026	-0.119	-0.128	-0.142	0.315	0.122	0.180			
	P	0.847	0.346	0.796	0.969	0.633	0.945	0.421	0.901	0.564	0.571	0.528	0.202	0.560	0.388			
	N	26	26	26	18	22	22	26	26	26	18	22	18	25	25			

Table 3. Correlation between growth and environmental parameters. Pearson correlation coefficients (r) between growth and climatic/biological variables. t-1 indicates that biological variables were lagged by -1 year in relation to growth parameters and t+1 refers to +1 year lag between COD and growth values. P indicates the associated probability and N the number of observations. * refers to significant correlation at the 0.05 level (2-tailed).

Discussion:

Increment Analysis:

Our results revealed a large interannual variation in annual increment growth from fourth to fifth year of Greenlandic cod from the Nuuk fjord. Observations confirmed that large fluctuations in growth are detectable on a short timescale, as reported in previous investigations conducted on the Faroe Plateau cod stock ([Jákupsstovu and Reinert, 1994](#)) and other cod populations ([Brander, 2007](#)). Five main intervals were detected in the constructed chronologies: A) decreasing from 1938-1944; B) increasing from 1945-1958; C) decreasing from 1959-1976; D) increasing from 1977-1978; E) decreasing from 1979-1984. Age 6 chronology was more robust within the first two intervals (A,B) while age 5 chronology presented the most clear signal in the last three (C,D,E). This was associated with the lack of age 5 samples in the first and age 6 in the last years. Looking at fish length time series from 1955-1985, a fairly similar pattern was identified with a slightly longer recovery interval from 1974 to 1978. A significant correlation was found between fish length and otolith radius (figure 6), confirming that although not always in a simple linear relationship, otolith size - fish size are correlated ([Campana and Jones, 1992](#)). Current back-calculation techniques should be used with caution provided that incorrect assumptions about the model may cause errors in prediction of fish growth rates ([Suthers and Sundby, 1996](#)). As expected, given that back-calculated growth was calculated based on annual increment growth, AIG and BCG chronologies corresponded well (figure 3 and 7). Unfortunately, due to the lack of data, it was not possible to investigate if they correlate with actual growth, but in a similar study, [Petersen \(2008\)](#) found a strong correlation between back-calculated growth rates obtained using the same method as the present and population growth rates calculated from size-at-age data from the Faroe shelf cod.

In spite of a similar trend, age 5 samples grew significantly less than age 6 during their fourth to fifth year. This was quite surprisingly since approximately equal results within the two age groups were observed before in similar studies ([Petersen, 2008](#); [Rasmussen, 2008](#)). Considering that the otolith structures cannot be reabsorbed ([Fowler, 1995](#)) the difference detected in increment width between age classes is difficult to explain. One possible explanation for the observed differences could be related with the fact that growth estimation for age 5 was based in the marginal increment width while the preceding growth zone was considered for age 6. In fact, otolith growth is not a linear process and slows down as accretion continues ([Van Neer et al., 2004](#)) but that's valid only for increments in the same otolith. In this study, despite a different position in relation to the otolith edge, we always considered the same increment (fourth to fifth), and thus the

expected width of age 5 marginal increments should equal the width of the age 6 preceding ring. A reasonable explanation for the observed growth differences could be that the growth increment in 5 year old cod was not completed at the time of capture. This will have to be investigated through marginal increment analysis of cod caught at different times during the year. Based on these results we recommend that the fish age should be considered in the sampling design and the measurement of marginal increments should be avoided unless there is clear evidence that the annual growth increment has been completed.

All samples were scored accordingly to otolith image quality, which ultimately impacted on the reliability of all measurements taken. Trends of high (CL=1), median (CL=2) and pooled high-median (CL=1,2) confidence scored data sets for age 5 are shown on figure 5 and differences are evident. Ideally, only CL=1 should be used for the chronology construction since high confidence level scored (CL=1) samples theoretically provide more reliable measurements, and thus, potentially reflect with high accuracy the real growth. Nevertheless, a compromise between quality and quantity of data had to be established. There is consensus that low quality otoliths may guide to incorrect estimation of growth rate (Campana and Thorrold, 2001), but it's also clear that small sample size can lead to decreased precision in estimates of various properties of the population, as well as contribute to less sensitive hypothesis tests with lower statistical power (Sokal and Rohlf, 1995). Accounting for the relatively limited available data we decided to exclude only the low confidence scored level (CL=3) samples from analysis. Furthermore, the otoliths scored with CL=2 were generally in a reasonable condition allowing for definable growth rings making the points of measurements determined with an acceptable degree of certainty. As such, we assumed that observed differences among CL=1 and CL=2 time series had more to do with sample size than with measurements quality and thus, the incorporation of median score measurements in the chronology is not believed to significantly affect the results.

We also found significant differences between years in terms of otolith weight from 5 years old individuals. Several authors have used otolith weight as a growth indicator to investigate environmental effect on fish growth (Wright et al., 2001; Otterlei et al., 2002; Høie et al., 2003). Looking at the period 1955-1985, OW showed a decreased trend since late 1950's, only interrupted by a brief recovery episode during late 1970's, which is in agreement with AIG and BCG chronologies. Still, the purpose of this research work was to compare growth and environmental variables on an annual timescale, therefore, information provided from annual increment analysis was considered more relevant

because it refers exclusively to the growth observed in one year, while total otolith weight is an integration of five years growth.

Fulton's K Condition Factor:

Fulton's K can provide an estimation of energy reserves, and high condition factor is thought to be associated with superior growth conditions as the surplus energy might be used for somatic growth. At the other hand, poor condition may lead to increased mortality and slower growth through a reduced capacity of cod to escape predation or mobile fishing gears and to catch mobile prey (Dutil et al., 2006). Though our results didn't show a clear pattern particularly during the first 16 years (1940-1956), a trend similar to the others growth parameters was observed from 1956 onwards. Nevertheless, we found some limitations regards to the use of Fulton's K as a growth estimator. Firstly, FK is estimated based on weight and length at the time of sampling. In this study we were limited to samples of adult cod randomly captured during the entire year, and moreover, weight and length were not available for many of them. Considering the high seasonal fluctuation in condition (Lambert and Dutil, 1997) and the large number of years lacking of information it is unlikely that a robust time series for this parameter can be attained. Secondly, as FK is based on the assumption of isometric growth, problems with condition and length can arise if this is violated (Lloret and Ratz, 2000). Finally, good feeding conditions might not necessarily translate into a high Fulton's condition considering that increased food intake may be turned into increased length and hence tend to reduce the condition factor.

Climate change and growth:

There is evidence that cod growth is influenced by variations in temperature, with lower temperatures leading to decreased growth and vice-versa in populations dwelling in cold waters (Pörtner et al., 2001). A positive and significant correlation was observed between temperature and otolith growth parameters (AIG, BCG, OW) for age 5 cod. This corresponded well with results reported in previous studies conducted on larvae-juvenile cod. For example, Høie et al. (2003) carried out a controlled laboratory experiment where they reared cod larvae and juveniles at different temperatures generating different otolith growth rates. Similarly, Otterlei et al. (2002) found evidences that temperature significantly affected lapillus growth in cod larvae and juveniles, with increased otolith growth at higher temperatures. Although, adults may behave differently with regard to temperature, for example, Brander (1995) did find a good correlation between growth rate in terms of weight-at-age and temperature but only significant for younger cod. To our knowledge there are few published studies investigating the effect of temperature on the growth rate

of adult cod otoliths. [Petersen \(2008\)](#) and [Rasmussen \(2008\)](#) did not observe significant correlations between annual increment growth and water temperature using a similar technique as present. We found that both TEMP1 and TEMP2 were positively correlated with AIG CL=1 scored samples, and TEMP1 also showed a positive correlation with AIG CL=1,2 (table 3). BCG correlations with temperature were weaker, only CL=1 samples showed a positive correlation with TEMP2. This was probably a consequence of the 'noise' added to data after back-calculation. Even minimizing errors due to the disassociated otolith and somatic growth applying the biological intercept method ([Suthers and Sundby, 1996](#)), it is likely that BCG data were more susceptible to decoupling from real growth compared to AIG direct measurements taken from otoliths. The lack of correlation in age 6 class was probably caused by the low robustness of constructed chronology for the period 1955-1985 coincident with existing temperature time series, as a consequence of the limited available data. Fulton's *K* condition factor was also positively related to water temperature (TEMP2) as suggested by [Lloret and Ratz \(2000\)](#). The variation in fish length to 5 years cod was also positively affected by temperature (TEMP2). In a very similar field study, [Ratz et al. \(1999\)](#) revealed that positive temperature effects were found to dominate the variation in length-at-age of Atlantic cod off Greenland during the second half of the 20th century.

It is worth noting the differences between temperature data sets. They were both provided by the same institution (Greenland Fisheries Research Institute, GFRI) and measurements were taken at the same sample station (Fyllas Bank). However, the mean temperature was derived by averaging observations at different standard depth levels (TEMP1: 0-40m; TEMP2: 10-50m) and the second set was systematically measured few weeks later in the year. Despite a very similar trend, the differences indicate how variable and sensitive can be water temperature in terms of space and time ([Buch et al., 2003](#)). This fact supports the weak ability of the sampling design to detect and describe relationships between temperature and growth parameters. Firstly, it should be taken into account the spatial distance among climatic (Fyllas Bank) and fish (Nuuk fjord) sample stations. Secondly, there is a mismatch between depths of temperature measurements and typical adult cod habitat. Despite the lack of knowledge on cod vertical migration in the Nuuk fjord ([Brander, 1995](#)), it is likely that they behave similar to what was observed in other populations, i.e., a benthic species with occasionally pelagic behaviour during spawning and feeding periods ([Cohen et al., 1990](#)). Finally, the temporal difference between sample periods: climatic variables were measured every year in the same season, while cod captures were spread across the whole year (table 1). As such, it might be speculated if available temperature datasets reflect the ambient temperature

experienced by the captured cod in the Nuuk fjord, even considering the hypothesis that Greenland water temperature trends in neighbouring areas and periods are similar to those on Fyllas Bank due to the process of advection and solar heating (Buch, 1984).

The same reasons might be pointed to explain the lack of correlation between cod growth and salinity. Additionally, salinity can be an indicator of altered ocean currents and freshwater discharge from ice sheet melting (Belkin et al., 1998) but it doesn't seem to exert as direct an effect as temperature on fish growth. Besides, no correlation was found with regards to NAO. Buch et al. (2003) showed that this climatic index affect wind and sea conditions around Greenland, and hence sea and air temperatures. Concordant findings were reported by Stein (2004) suggesting that NAO explained 50% of winter air temperature variance in Nuuk. But as salinity, this variable doesn't have a direct mode of action on growth parameters (Ottersen et al., 2001) which might have contributed to the lack of correlation.

Zooplankton abundance and growth:

A long time series of zooplankton samples was used in an attempt to identify its correlation with adult cod growth. Quantity and quality of zooplankton is known to directly influence the growth of fish larvae (Beaugrand et al., 2003) but its effect on adult cod is more complex than the result of a simple prey-predator interaction. Greenlandic adult cod mainly feed on other smaller fish species, capelin being the most important item in their diet, constituting on average almost 50% by weight of the total food consumption by cod (Vilhjálmsson, 2002). The same author demonstrated that the mean weight-at-age of cod aged 5-8 years dropped by up to 25-30% when capelin abundance was low. At the other hand, it is also known that capelin depend on zooplankton. Actually, it was suggested by Malmberg and Blindheim (1994) that low zooplankton production was associated with reduced capelin growth and recruitment. Relying on these facts it was conjectured that longer term variability on zooplankton abundance might affect adult cod growth. The null hypothesis was that strong years in zooplankton abundance could lead to increased capelin growth and recruitment which in turn would reflect a positive effect on adult cod growth after one year. To our knowledge, there are no reported observations of the effect of zooplankton abundance on adult cod growth, and our results are not conclusive of any relationship. In terms of otolith growth a significant negative correlation between AIG age 5 and shrimp larvae lagged by -1 year (SHR t-1); AIG and BCG age 5 and cod larvae also -1 year lagged (COD t-1); AIG age 6 and COD t-1 was observed. Fulton's condition was also negatively related with shrimp larvae and fish length seemed to decrease with increasing crab larvae lagged by -1 year (CRAB t-1) abundance (table 3). Observed

correlations between otolith increment growth and shrimp larvae were believed to be meaningless considering the lack of correlation with samples with high score which supposedly are more reliable (CL=1, $p=0.549$, table 3). Correlations found for FK and FL were also attributed to chance since they seem to be isolated cases. The negative correlation between growth parameters and cod larvae abundance seemed more robust and meaningful as both age classes and both AIG and BCG showed a significant correlation. Moreover, AIG age 6 CL=1 although not significant, was very close ($p=0.060$, table 3). Our results suggest that strong years in cod larvae abundance negatively impacted on adult cod growth. Indeed, the growth of adult cod appears to be related with good feeding conditions (Ratz et al., 1999), but it could also happen that during the preceding year cod larvae were eaten by capelin. It would be interesting to confirm the speculated relationships but no data exists on capelin abundance in the study area. Additional sampling on this prey species is needed to address its effect on cod growth. As with climatic data, the lack of correlation with other biological variables could be caused by the mismatch between zooplankton and adult cod sample stations.

In order to investigate the impact of adult cod growth on the stock recruitment success, growth parameters and cod larvae abundance lagged by one year were correlated. It has been demonstrated before that the intensity and period of spawning vary greatly with the size of the individual spawning cod (Kjesbu et al., 1998; Jónsdóttir et al., 2002). This is probably related with decreased fecundity, egg size and offspring survival in consequence of reduced growth (Hutchings and Reynolds, 2004). However, our results showed no correlation between growth and cod larvae (COD t+1). Also here, the mismatch between larvae and adult cod sampling areas can be pointed as the main cause for the lack of correlation. It has been documented that some of the coastal cod might migrate inside the fjord (Buch et al., 1994) but the cod in the Nuuk fjord is not believed to migrate outside to coastal areas. Thus, it is unlikely that cod larvae sampled in Fyllas bank station had been spawned by adult cod from the Nuuk fjord.

Conclusion:

The main purpose of this study was to create a growth chronology based on the analysis of otolith annual increments. Both AIG and BCG chronologies corresponded well with somatic (FL) and condition (FK) time series and hence confirmed that otolith increment measurements are a useful method for investigating growth in the past. It must be noted that this study is based upon a relatively limited data spanning the period 1938-1984. The examination of additional years of data is required to determine the generality of the influence of environmental variables on growth. Apparently interannual changes in temperature and cod larvae abundance correlate with adult cod growth in the Nuuk fjord but it is difficult to assign causes with confidence because of the poor quality of field information available. Moreover, despite environmental factors considered, selective effects of fishing may also cause changes in growth. Effects can be direct or indirect and they can interact with each other complicating the understanding of their mode of action. Results suggest that expected changes in temperature might benefit adult cod growth from Nuuk fjord and thus the recovery of the stock. However, it is unlikely that improved environmental conditions will be enough for the recovery process, and sustainable resource exploitation strategies are urgent. With the existence of historical otolith collections and given the potential impacts of environmental change on growth identified here, the ability of otolith chronologies to act as an easily referenced library could provide a key input into the implementation of future cod fishery management plans.

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Appendices:

Year class	TEMP1 (°C)	TEMP2 (°C)	SAL (ppm)	NAO
1938	-	-	-	1.33
1939	-	-	-	-0.32
1940	-	-	-	-0.21
1941	-	-	-	-0.47
1942	-	-	-	-0.03
1943	-	-	-	1.03
1944	-	-	-	0.20
1945	-	-	-	-0.48
1946	-	-	-	0.68
1947	-	-	-	-0.48
1948	-	-	-	0.13
1949	-	-	-	0.23
1950	2.1	2.99	33.61	0.39
1951	1.9	-	-	0.00
1952	1.6	2.03	33.24	-0.46
1953	2.1	3.26	33.37	0.65
1954	2.3	2.32	33.18	1.12
1955	1.2	1.80	33.18	-0.42
1956	0.9	2.08	32.87	0.29
1957	2.3	1.68	33.36	-0.29
1958	2.2	3.03	33.30	-0.68
1959	1.6	1.90	33.07	0.69
1960	2.7	3.17	33.09	-0.37
1961	3.2	4.20	33.55	0.33
1962	2.2	2.58	33.26	-0.43
1963	1.6	2.10	33.64	-0.38
1964	2.3	2.53	33.16	-0.20
1965	2.1	-	-	-0.33
1966	1.6	2.40	33.11	-0.64
1967	1.5	-	-	0.54
1968	2.1	1.45	33.16	-1.15
1969	0.3	0.21	32.69	-0.44
1970	0.3	1.17	33.00	-0.21
1971	0.8	1.35	32.87	-0.11
1972	0.6	0.92	33.33	0.58
1973	1.7	1.43	33.51	0.02
1974	1.4	2.58	33.32	0.54
1975	1.9	1.85	33.20	-0.08
1976	1.4	1.82	33.18	-0.18
1977	2.2	3.74	33.10	-0.58
1978	0.9	2.60	32.99	-0.22
1979	2.3	3.16	-	0.03
1980	1.9	2.41	33.52	-0.57
1981	1.6	1.45	33.07	-0.18
1982	0.8	0.76	32.64	0.70
1983	0.4	-	-	0.02
1984	1	1.51	33.37	0.53
1985	2.1	-	-	-0.87

Appendix 1. Climate time series. Mean temperature, salinity and NAO. TEMP1 adapted from Ratz et al. (1999); TEMP2 and SAL from Pedersen and Smidt (2000), NAO index from Climate & Global Dynamics (CGD's), Climate Analysis Section (<http://www.cgd.ucar.edu/cas/jhurrell/indices.data.htm>)

Year class	PLVOL	COP	EUPH	SHR	CRAB	COD	SAND
1938	-	-	-	-	-	-	-
1939	-	-	-	-	-	-	-
1940	-	-	-	-	-	-	-
1941	-	-	-	-	-	-	-
1942	-	-	-	-	-	-	-
1943	-	-	-	-	-	-	-
1944	-	-	-	-	-	-	-
1945	-	-	-	-	-	-	-
1946	-	-	-	-	-	-	-
1947	-	-	-	-	-	-	-
1948	-	-	-	-	-	-	-
1949	-	-	-	-	-	-	-
1950	2.79	-	-	-	-	1.20	0
1951	-	-	-	-	-	-	-
1952	2.59	-	-	-	-	0.38	0
1953	2.90	-	-	-	-	0.18	0
1954	2.44	-	-	-	-	0.10	0.05
1955	3.06	-	-	-	-	0.30	0
1956	2.58	0	0	1.12	0	0.31	0.05
1957	2.29	3.24	1.76	0.78	0.78	0.38	0
1958	2.47	1.18	1.18	0.85	1.46	0.62	0.16
1959	1.95	-	-	-	-	0.38	0.16
1960	2.40	-	-	-	-	0.30	0
1961	3.30	2.46	2.08	0.43	0.58	0.10	0
1962	-	-	-	-	-	0	0.26
1963	2.10	0.3	0.38	1.51	0.13	0.31	0.29
1964	1.88	1.42	0.96	1.66	1.23	0.18	0.36
1965	-	-	-	-	-	-	-
1966	2.23	0.67	0.34	0.85	0.55	0.06	0.19
1967	-	-	-	-	-	-	-
1968	2.02	-	-	-	-	0.07	0.11
1969	2.33	-	-	-	-	0.12	0.66
1970	1.77	0.6	0.21	0.8	0.59	0.11	0.54
1971	1.68	0.18	0.15	1.15	1.33	0.33	0.89
1972	1.35	1.09	0.54	1.3	1.51	0	1.04
1973	2.15	1.01	0.45	1.45	1.76	0.22	1.38
1974	2.33	0.71	0.52	1.97	1.04	0.10	0.8
1975	2.59	0.84	0.68	1.60	0.97	0.19	0.34
1976	2.43	0	0	1.14	0.22	0.10	0.61
1977	3.13	0.17	0.10	1.28	0	0.22	0.06
1978	2.55	1.33	0.51	0.46	0.47	0.06	0.06
1979	2.50	1.6	0.50	0.32	0	0.15	0
1980	3.06	3.05	1.08	1.34	0	0.06	0
1981	2.37	2.18	0.85	1.09	0.57	0.12	0.12
1982	2.97	1.68	0.33	0.85	1.27	0.92	0.87
1983	-	-	-	-	-	-	-
1984	3.00	-	-	-	-	0.21	0.27

Appendix 2. Biological time series. Mean abundance indices [$\log_{10}(x+1)$] of different zooplankton taxa adapted from Pedersen and Smidt (2000).