Variation in size and growth of West Greenland capelin (*Mallotus villosus*) along latitudinal gradients

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Hedeholm, R., Grønkjær, P., Rosing-Asvid, A., and Rysgaard, S. 2010. Variation in size and growth of West Greenland capelin (*Mallotus villosus*) along latitudinal gradients. – ICES Journal of Marine Science, 67: 1128–1137.

Capelin (*Mallotus villosus*) is the dominant pelagic species in the West Greenland ecosystem. Historical data are re-examined and new data are presented on the size distribution and the growth pattern of capelin along latitudinal gradients of temperature and other growth factors extending over a distance of 1300 km. The average size of capelin increases with latitude. Fish 3 years old were 48 mm larger (54%) at the secondmost northern station compared with the most southern one. Otolith analysis revealed a significant effect of age as well as area on back-calculated growth. Hence, at all ages, fish grew faster in the north than in the south. Average somatic growth across areas in the first and fourth years was 56 and 15 mm, respectively. Temperature data suggest a 2°C difference in temperature between areas, temperatures being warmest in the north. Hence, the increase in temperature with latitude explains much of the latitudinal growth gradient and suggests a growth difference in West Greenland capelin of 0.4–0.6 cm $^{\circ}C^{-1}$ year^{-1}. However, the difference in growth and size distribution between northern and southernmost stations, where temperatures are similar, suggests that other factors, such as differences in available prey and diet composition, also contribute to the differences.

Keywords: capelin, *Mallotus villosus*, North Atlantic, temperature-regulated growth.

Received 21 September 2009; accepted 4 March 2010; advance access publication 27 March 2010.

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Introduction

Capelin (*Mallotus villosus*) are small osmerid fish with a circumpolar distribution. They are considered the dominant pelagic species in Subarctic waters and important predators of zooplankton, as well as prey of many species of fish (e.g. cod, haddock), birds (e.g. guillemot), and marine mammals (e.g. harp seal, minke whale; Lawson *et al.*, 1998; Vilhjálmsson, 2002). Some capelin stocks are commercially exploited, and annual catches amounted to 746 534 t in 2005, with the main catches by Iceland and Norway. In some years, Icelandic catches alone have been close to 2 million tonnes (Carscadden and Vilhjálmsson, 2002). Capelin are found along the east and west coasts of Greenland from Kap Farvel in the south to Tassiilaq (66°N) and Upernavik (73°N), respectively. The East Greenland capelin stock is often considered to be part of the Icelandic stock (Vilhjálmsson, 2002), but the West Greenland stock is commercially unexploited and little is known about capelin biology there (though see the review of Friis-Rødel and Kanneworff, 2002). It is the latter stock that is the focus of the present study.

A latitudinal gradient in the size of West Greenland capelin was first reported by Hansen (1943), based on historical data from 1906 on. These historical data, combined with new data, were analysed by Kanneworff (1967), Sørensen (1985), and Kleist (1988). According to those studies, the maximum size of capelin increases northwards along the coast. Kanneworff (1967) estimated the growth of capelin in the Nuuk fjord system as well as at other West Greenland localities, although focus was on the fjord system. However, he failed to find a major difference in the growth pattern between areas and did not address this aspect further because of his small sample size. Sørensen (1985) suggested that the different maximum size observed along the coast could be caused by differences in growth rates, although she did not present any data or references. Hence, very little is known about the age-specific growth pattern of Greenland capelin and how this is expressed in the size distribution along the latitudinal gradient. The notion of a latitudinal gradient has been based on historical data that often are associated with uncertainties (i.e. the length measure applied, time and place of capture, age determination, etc.). Furthermore, in Greenland as well as elsewhere, capelin size varies on an interannual basis (Gjøsæter, 1999; Carscadden and Frank, 2002), likely obscuring patterns based on a compilation of historical data.

Temperature increase has a positive influence on growth in fish, where prey availability is non-limiting and temperatures are below the optimum temperature for growth, which most often is the case in temperate and boreal fish species (Gjøsæter and Loeng, 1987; Wootton, 1990; Brander, 1995; Garvey and Marschall, 2003). The direct effect of temperature on capelin has been studied in the Barents Sea. Gjøsæter and Loeng (1987) showed that annual temperature influences the capelin growth there, with growth increasing by 0.3 cm $^{\circ}C^{-1}$.

In addition to temperature, food availability influences capelin growth in the Barents Sea (Gjøsæter *et al.*, 2002). The importance of feeding behaviour has been demonstrated in the Atlantic silverside (*Menidia menidia*), another pelagic species, for which latitude-related growth differences were analysed by Conover and Present (1990). Using laboratory-reared fish, they showed that fish caught farthest north had the fastest growth rate, allowing them to compensate for the shorter growth season and to match the absolute growth of fish at lower latitudes. Present and Conover (1992) demonstrated that this interpopulation variation in growth rate was the result of increased consumption of food and a greater growth efficiency. Therefore, in that case, the constraints on growth imposed by low temperatures were counterbalanced by adaptations in feeding biology.

Temperature and length of the growing season differ considerably along the 1300-km north–south distance evaluated here, so West Greenland capelin provide an opportunity to consider the possible effects of climate change, which are thought to be most apparent in the Arctic region (Holland and Bitz, 2003). The temperature differences observed along the latitudinal temperature gradient are comparable with the changes expected in each of the areas investigated during the coming century (Levitus *et al*., 2000; Flato and Boer, 2001), so the present data provide insights into possible future changes in growth and size of Greenland capelin.

Here, we re-examine the historical data on capelin in Greenland to demonstrate a historical difference in the size distribution in different areas. We use contemporary data for which otoliths are available to elucidate whether these differences result from differences in growth rate along the observed latitudinal gradients of temperature and other factors.

Material and methods

Study site and 2007 sampling

All 2007 samples were collected on the west coast of Greenland. Four areas spanning 1300 km were selected for further study: Qaqortoq (60–61°N), Nuuk (64.00–64.75°N), Disko (68.50–69.50°N), and Uummannaq (70.30–71.30°N; Figure 1). The latitudinal borders were selected according to hydrographic and topographic features and their comparability with the historical data. Within each area, capelin were collected during beach-spawning events using handnets. In all, 461 fish were sampled with 88, 219, 79, and 75 individuals, respectively, being collected from south to north at the different locations. Samples were collected from as many spawning sites within each area as possible between 11 May and 19 July, with no relation between latitude and sampling time. All samples were deep-frozen and brought to the laboratory, then upon thawing, all fish were measured to the nearest millimetre below (fork length), sexed, dried, and weighed to the nearest 0.1 g. No correction for length changes caused by freezing was applied, which might have introduced an error of up to 3% (Sørensen, 1985). When comparisons with historical samples were made, fork length was converted to standard length using the relationship for Greenland capelin documented by Kanneworff (1967), i.e. standard length = 0.92 × fork length + 0.042. The relationship was confirmed using a random subsample of fish sampled in 2007 across all areas.

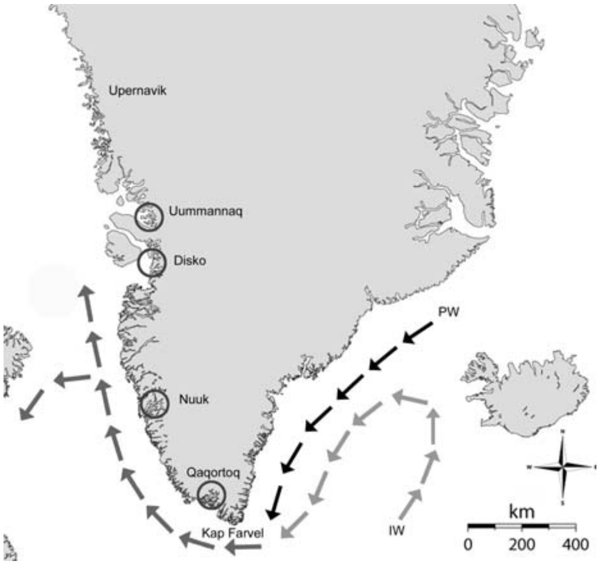

Figure 1. The southern part of West Greenland with the four study areas encircled, from south to north Qaqortoq (60–61°N), Nuuk (64.00–64.75°N), Disko (68.50–69.50°N), and Uummannaq (70.30–71.30°N). Arrows indicate the dominating currents; from the north flows the cold low-saline water of polar origin (Polar Water, PW), and from the south, highly saline warmer water (Irminger Sea Water, IW), the two water bodies mixing along the west coast of Greenland.

Latitudinal gradients in capelin size

The historical samples were from 1908 to 2005, although several years are not represented. Most samples (>90%) were from spawning events taken using dipnets and hand-seines, though pelagic trawls were used at greater depth and outside the spawning season on a few occasions. A few samples were caught in poundnets and gillnets aimed at cod (*Gadus morhua*). Only fish caught in the areas sampled in 2007 were used. All sampled fish were measured, weighed, and in some cases aged and sexed. All measurements before 1967 were made to the nearest 0.5 cm below. To allow comparisons with new material, 0.25 cm (0.5 unit) was added to these measurements. From 1967 to 2005, all measurements were to the nearest millimetre below. Samples that differed greatly from what should be expected (e.g. mean length or weight, time of sampling, place of sampling, or duplicates) were investigated and excluded from further analysis if errors were found. Moreover, as the sexes differ in size and males dominated the 2007 sample, all females and unsexed individuals were excluded. These criteria reduced the initial historical sample size from 45 810 to 13 990 capelin, but the reduction was justified by a large increase in data quality (Table 1). The size distribution of the historical data was plotted for the four areas to determine whether any latitudinal differences in size have been evident historically.

All fish caught in 2007 were assigned to length intervals of 2 mm, and the length frequency distributions were calculated for the four areas. To ensure that any pattern found was not due to different age groups being more or less represented in different areas, the average length of all 3-year-old males from 2007 was plotted as a function of the latitude at which they were caught. Fish 3 years old were used because that was the age group that dominated samples ($n = 176$) when all areas were considered. The other age groups produced patterns identical to those shown by 3-year olds (data not shown). When fish were caught at several latitudes within each of the four areas, the average latitude and length was used, and no weighting in terms of sample size was applied.

Otolith-based growth analysis

Only males were used in growth studies because of the scarcity of females ($n = 45$) and the belief that some females survive

Table 1. The number of West Greenland capelin and the years used for the historical and 2007 length frequency distributions (Figure 3) at Qaqortoq, Nuuk, Disko, and Uummannaq.

	Historical data			
Location	**Original number**	**Number used**	**Years**	***n* in 2007**
Qaqortoq	8 097	2 264	1937, 1968, 1972, 1987	87
Nuuk	23 179	9 807	1909, 1966–1978, 1982, 1985, 1987	175
Disko	1 646	930	1967, 1968, 1985	79
Uummannaq	1 499	989	1966–1968, 1978	75
Total	34 421	13 990		416

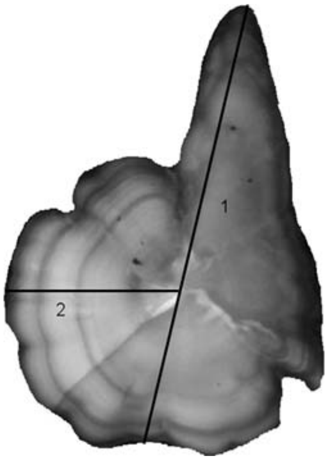

Figure 2. A saggital otolith from a 4-year-old male capelin caught at Disko in 2007. Line 1 runs from the end of the rostrum through the centre of the otolith, and Line 2 from the centre of the otolith to intersect growth increments at an angle of 90°. The growth increments used in the analyses were measured along the latter line.

spawning, which might produce otolith structures that would make the interpretation and subsequent analysis difficult (Sørensen, 1985; Kleist, 1988; Friis-Rødel and Kanneworff, 2002). The saggital otoliths were removed, rinsed in water, and dried. As growth increments in capelin are prominent, it was sufficient to submerge the otoliths in alcohol and place them on a black background. Age determinations were carried out independently by two readers. When discrepancies were found ($<10\%$ overall), the otoliths were re-analysed and discarded if the age could not be determined with certainty. There was no age bias in the discarded otoliths. Using a stereoscope and an Olympus DP50 camera, all otoliths were photographed at different magnification ($\times 16-40$) under reflected light. The pictures with the clearest growth increments were selected for further analysis. Using "Image-J" image analysis software (Rasband, 1997–2007), a line was drawn from the rostrum through the otolith centre (Line 1 in Figure 2). A line was also drawn from the centre of the otolith to the edge of the otolith, along which the growth increments (μm) were determined (Line 2 in Figure 2). The latter line was drawn so that it was perpendicular to the growth rings. The total otolith radius was defined as the sum of all measured growth increments along that line. All growth increments were measured to the end of the translucent zone. The process was repeated twice for each otolith, and if the measurements differed by $>10\%$, they were discarded; if not, the mean of the two measurements was used in further analysis. Owing to the small sample size ($n = 19$), growth between 4 and 5 years of age was not used in the analysis. To compare somatic growth between areas independent of differences in the relationship between otolith size and fish length between areas, length-at-age was back-calculated using the biological intercept method (Campana, 1990):

$$L_a = L_c + (O_a - O_c) \times (L_c - L_i) \times (O_c - O_i)^{-1},$$

where L_a is the length at a given age, L_c the length at capture, O_a the otolith radius at a given age, O_c the total otolith radius at capture, L_i the length of fish at the biological intercept, and O_i the otolith radius at biological intercept. The biological intercept was set at a fish length of 35 mm and an otolith size of 0.08 mm (Gjøsæter, 1999). Growth was then calculated by subtracting length-at-age$_t$ from length-at-age$_{t+1}$, and plotted for each age and area.

To validate the timing of the first growth increment, sagittae from young of the year (YOY) caught on 12 September in the Nuuk area were analysed ($n = 6$). Because of the late sampling date, it was assumed that the growth season was complete but that the translucent (winter) increment had not yet formed. Hence, the test was to determine whether the radius of YOY otoliths was similar to the radius of the first opaque (summer) increment in adult fish caught in the Nuuk area. To ensure that the innermost growth increment was measured correctly, a random sample of 10 saggital pairs was selected from all areas. One otolith from each pair was polished on grain size 800 sandpaper until the innermost increment was at its clearest, then the growth increment was re-measured and compared with the measurement of the unpolished otolith. The first-growth increment sizes of the re-measured polished otoliths were similar to those of the unpolished ones (Student's t-test, $t_{10} = 0.11$, $p = 0.917$), so polishing was not deemed necessary.

Owing to the time of sampling, adult fish were assumed to have experienced almost a full growth season, and the marginal growth increment was considered to constitute a full growth season. To validate this assumption, the marginal growth increment of the most abundant year class within an area was compared with the growth increment in older fish in their corresponding growth year within the same area. For instance, at Qaqortoq, the marginal growth increment in 3-year-old capelin was compared with the third-year growth in 4- and 5-year-old fish. This was done for all areas. Had the fish not completed the growth season, older fish would have had wider increments than younger fish.

Temperature and salinity

To evaluate temperature differences along the latitudinal gradient, all available temperature data for West Greenland (60–73°N 44–57°W) were extracted from the ICES database (www.ices.dk; $n = 114\,072$). As all literature indicates that Greenland capelin are restricted to fjords and near-coastal waters (see review by

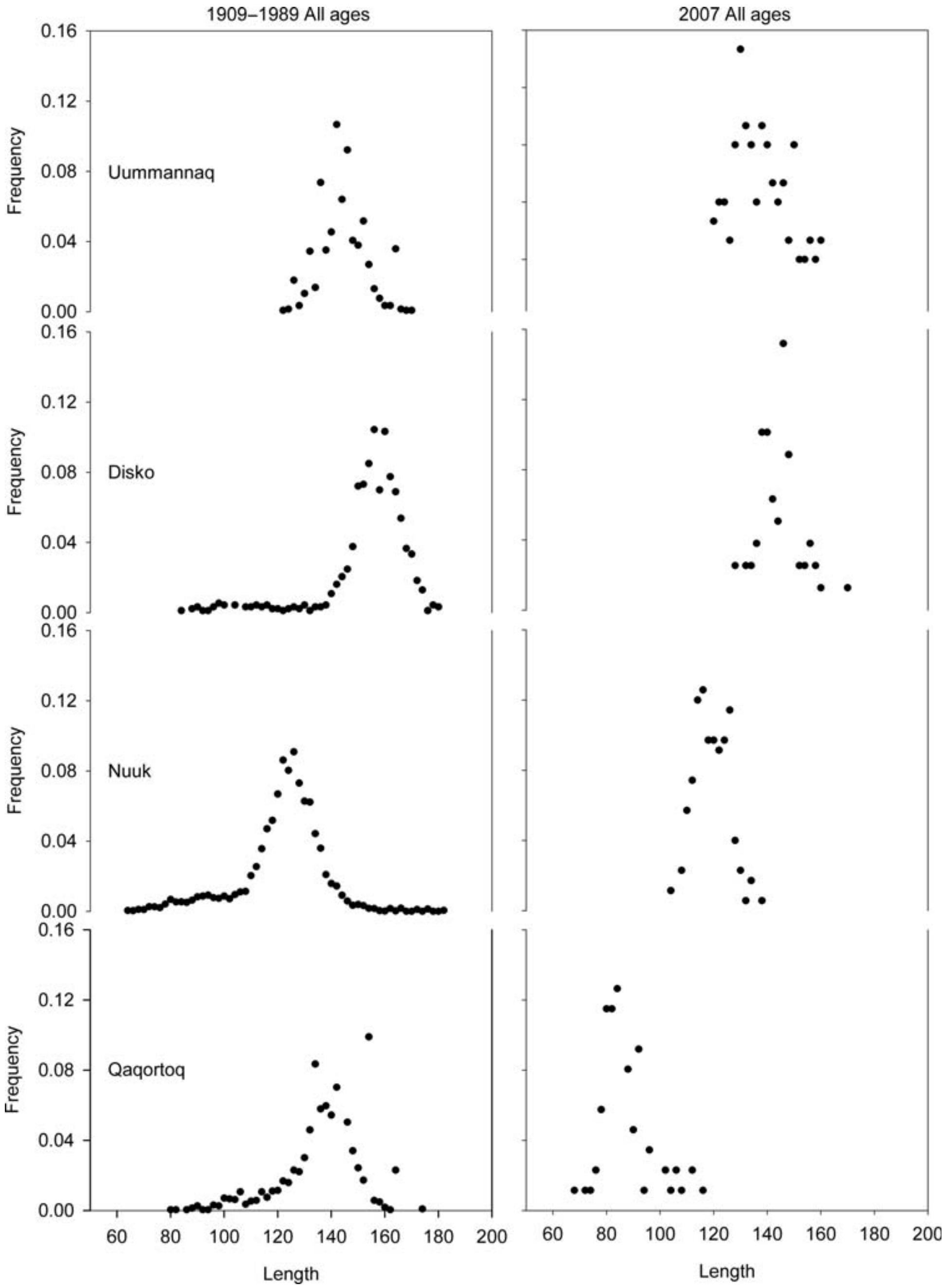

Figure 3. Historical length distributions for male West Greenland capelin in 1909–1989 (left, $n = 13\,990$) and in 2007 (right, $n = 416$). All fish lengths are assigned to 2 mm intervals. Table 1 lists the years included in the historical data.

Friis-Rødel and Kanneworff, 2002), all measurements taken at locations where the bottom depth exceeded 500 m were excluded. This ensured that no data west of the shelf break were used. Moreover, all measurements from 0 to 20 m were discarded because these may be influenced by episodic disturbances such as freshwater inflow. As capelin in the feeding period primarily reside in the upper water layers, and more so at younger life stages (Gjøsæter, 1998), measurements from 20 to 50 m were used. Data deeper than 50 m could well have been included because adult capelin make diurnal vertical migrations (Sørensen, 1985; Gjøsæter, 1998), but the same general pattern in latitudinal temperature trends was observed when data from 10 to 100 m were used. However, those data showed more variability because progressively fewer years were available for analysis (the data are therefore not shown).

Temperature data were averaged for all stations. As capelin growth is most rapid in summer, data for July ($n = 1137$), August ($n = 478$), and September ($n = 282$) were considered separately. The plots were constructed by assigning each temperature to the nearest latitudinal degree, then taking the unweighted average of all years at all latitudes, so avoiding overrepresentation of an unusually warm or cold year. In all, data from 78 years were used, spanning almost a century (1908–2007). Usually, salinity was determined along with temperature measurements

($n = 17\,489$), also extracted from the ICES database, and used to determine possible differences in the origin of water masses at the different locations. To avoid overrepresentation of certain (cold or warm) months, only data from August are presented here ($n = 1362$).

Statistical analysis

All analyses were carried out using SPSS (Statistical Package of Social Sciences). Standard parametric tests were preceded by tests for assumptions. When these were violated, the data were either transformed or non-parametric statistics were applied.

Results

Latitudinal size gradient

Length frequencies for historical data and for 2007 samples are shown in Figure 3. The historical data show that capelin are largest at Disko, with an average male size of 155 ± 14.3 mm (s.d.). Average size then declines northwards to Uummannaq (144 ± 7.3 mm) and southwards to Nuuk (122 ± 14.6 mm). At the southernmost point of sampling, Qaqortoq, average size increased to 139 ± 12.9 mm. Hence, although capelin appeared to be bigger in the northern area, there was no obvious latitudinal gradient, because fish from Qaqortoq were as big as capelin caught farther north. Focusing instead on the 2007 data, the size distribution at Qaqortoq shifted towards smaller sizes than the historical data, an effect that was most evident in the decrease in average size, to 88 mm in the 2007 samples. Therefore, the average sizes from south to north in the 2007 samples were 88 ± 11.5, 120 ± 10.3, 146 ± 20.5, and 137 ± 8.8 mm, respectively. The lengths of 3-year-old males in 2007 ($n = 176$) also revealed that mean length was related to latitude (one-way ANOVA, $F_{3,172} = 398.040$, $p < 0.0005$), with all areas except the two northern areas (Tukey's *post hoc* test, $p = 0.054$) being significantly different (Tukey's *post hoc* test, $p < 0.0005$; Figure 4).

Growth analysis

There was a clear positive relationship between otolith radius (Figure 2) and length (Figure 5), justifying the assumption of a relationship between otolith growth and somatic growth (linear regression, $F_{1,183} = 375.79$, $r^2 = 0.67$, $p < 0.0005$). The determination and the interpretation of the first and marginal growth increments were also supported by the analysis. Comparisons of the marginal growth increment of the most abundant age group with the corresponding growth increment in older fish showed that the older fish had similar increments. Only fish from Qaqortoq had marginal increments significantly different from the corresponding increment of older fish (one-way ANOVA, $F_{1,29} = 28.32$, $p < 0.01$; Table 2), indicating that the growth season was over at the time of sampling. The first growth increment in YOY (i.e. total otolith radius) from Nuuk had an average size of 0.103 mm, significantly smaller than the radius of the first opaque increment in adult fish caught in the same area (0.134 mm; Student's *t*-test, $t_{44} = 2.83$, $p = 0.007$). However, the absolute difference in radius (0.031 mm) is small enough to justify the assumption that the first growth increment was determined correctly.

Growth patterns for males caught in 2007 in the four areas are presented in Figure 6. An analysis of covariance (ANCOVA) was performed to determine the effect of area and age on log-transformed growth increments (linear regression, $F_{1,79-158} \geq 164.005$, $p < 0.0005$). The full factorial model showed an effect of area (ANCOVA, $F_{3,540} = 4.753$, $p = 0.003$) and age (ANCOVA, $F_{1,540} = 1082.664$, $p < 0.0005$), but also a significant interaction between area and age (ANCOVA, $F_{3,540} = 8.557$, $p < 0.0005$), demonstrating that differences in growth could not be based solely on area. However, this significant interaction was primarily caused by irregular growth in the northernmost area (Uummannaq), as seen in Figure 6. In the 0+ period, growth was the second lowest of the four areas (55 mm), but highest in the 2+ period (42.7 mm). Another anomaly was the increase in growth from 1+ to 2+ (38.0 and 42.7 mm, respectively), which was not seen in the other areas. However, removing Uummannaq from the analysis did not render the interaction

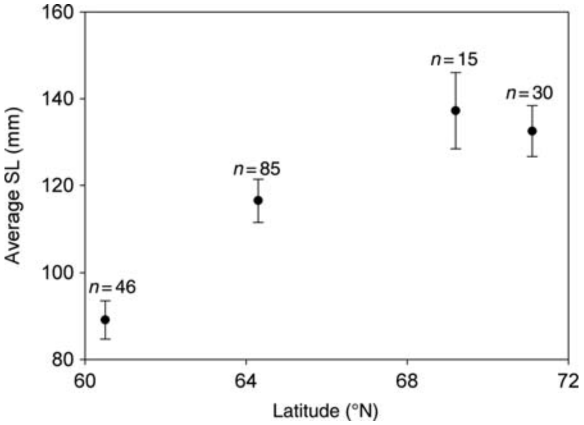

Figure 4. Mean length (SL) of 3-year-old male capelin caught at four different latitudes along the west coast of Greenland in 2007 (one-way ANOVA, $F_{3,172} = 398.040$, $p < 0.0005$). Average mean lengths and average latitude were used when fish from several locations within each area were used. The number of fish measured (n) is shown for each area.

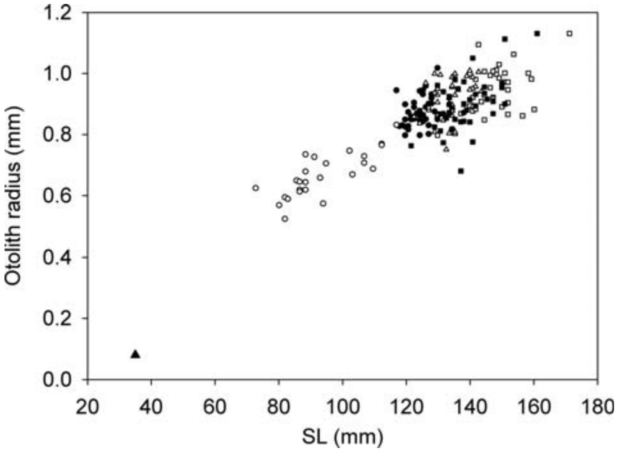

Figure 5. Otolith radius as a function of standard length (SL) for all capelin from Qaqortoq (open circles, $n = 25$, 60°N), Nuuk (dots, $n = 40$, 64°N), Disko (open squares, $n = 40$, 69°N), and Uummannaq (filled squares, $n = 40$, 71°N) used in growth analysis. An additional 39 fish from other locations along the coast were not used in the growth analysis (open triangles, $n = 39$). The solid triangle at the bottom left indicates the biological intercept used in back-calculation. The otolith radius was defined as the cumulative sum of the growth increments (see Figure 2 and text).

Table 2. Average marginal growth increment (mm) of the most abundant year class within an area, the average growth increment (mm) in older fish in their corresponding growth year within the same area, and the age increment used in each area (the number of otoliths used in the analysis is given in parenthesis).

Area	Increment compared	Average marginal growth increment (mm)	Average growth increment of older fish (mm)
Qaqortoq	3	0.245 (19)	0.184 (6)*
Nuuk	4	0.156 (38)	0.113 (2)
Disko	4	0.175 (28)	0.153 (7)
Uummannaq	4	0.140 (20)	0.178 (5)

Note that growth at Qaqortoq is faster than that in the other areas, because younger ages are used in the increment comparison.

*A significant difference (Student's *t*-test, $p < 0.05$) between the average marginal growth increment and the average growth increment of older fish.

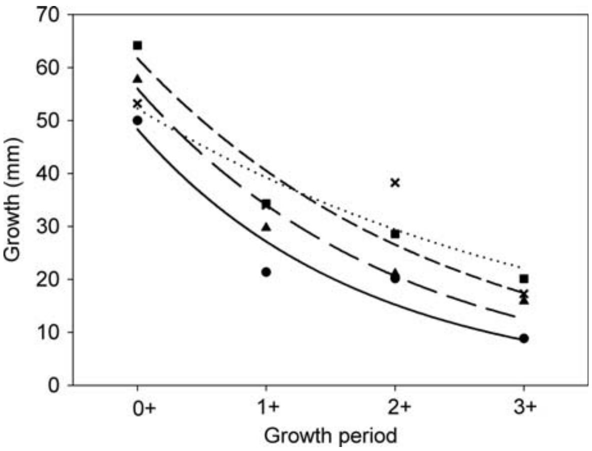

Figure 6. Somatic growth (in millimetres) of capelin from Qaqortoq (dots, $n = 25$, 60°N), Nuuk (triangles, $n = 40$, 64°N), Disko (squares, $n = 40$, 69°N), and Uummannaq (crosses, $n = 40$, 71°N). Growth was estimated from the back-calculated lengths using the biological intercept method. Lines represent the exponential trend lines for each area, with Qaqortoq the solid line, Nuuk the long-dashed line, Disko the short-dashed line, and Uummannaq the dotted line.

insignificant ($p = 0.003$). Overall, it appears that capelin of all ages grow faster at Disko than at Nuuk and Qaqortoq, whereas capelin at Nuuk grow faster than those from Qaqortoq, and that somatic growth declines significantly as the fish age in all areas. However, the growth pattern can be seen as reflecting three separate life stages and not necessarily a steady growth decline. Growth in the first year is fast, but more moderate in the second and third years. In the fourth year, the capelin approach their spawning age, and growth is at its minimum.

Temperature and salinity

According to the ICES temperature database, average temperatures increase from south to north (Figure 7). Considering all months, the temperature was close to 1°C at 60°N, increasing to 2°C at 68°N, then declining towards the north. The same pattern was evident for the three selected months, but with greater latitudinal differences. Hence, there was a 2°C difference between 60°N and 68°N in July, August, and September, with individual temperatures varying by 1°C between months. The drop in temperature of ~1°C from the Disko area to Uummannaq was also apparent in all 3 months.

Salinity also changed with latitude, increasing from 32.3 in the south to 33.4 in the Disko area, and dropping to 33 in Uummannaq (Figure 8). Salinity in the Nuuk area does not follow the overall trend, displaying values well below those of adjacent latitudes (32.5), probably because of the outflow of freshwater from the Nuuk fjord.

Discussion

Growth pattern

Both historical and new data show a latitudinal variation in the size of male West Greenland capelin. In the contemporary data, average size increases with latitude except in the area farthest north (Uummannaq), where it declines slightly. This size gradient is not a result of altering age distribution along the coast, because the pattern is the same in the average size of 3-year-old males (Figure 4), and the growth analysis showed that the gradient was expressed at all ages (Figure 6). Uummannaq differs from the other areas in that growth rates there do not decline consistently with age, being unexpectedly high in the period 2+.

In the historical data, the pattern is the same, except at Qaqortoq where the size distribution is skewed towards larger sizes than in the 2007 data. There could be several reasons for this. As a large proportion (>80%) of the samples were caught offshore, the distribution could be skewed by containing capelin that might have migrated or drifted from the east coast around the southern tip of Greenland, creating a sampling bias (Wileman *et al.*, 1996). This would skew the distribution, because capelin in East Greenland are larger (Hansen, 1943; Vilhjálmsson, 1994). However, this does not appear to be the case when comparing historical trawl catches with other sampling gear, though insufficiency of information on catching methods renders such conclusions tentative. Additionally, the spawning stock could historically have been dominated by larger East Greenland capelin, whereas the present-day spawning stock is mainly small fish. As otoliths are available for the 2007 samples, however, the present-day gradient is deemed correctly determined, and the reason for the discrepancy with historical data is unknown. Therefore, we believe that the growth gradient demonstrated using the 2007 samples represents the current situation, although this needs to be supported by more study, to allow for additional comparison with the historical information.

Only one peak in size distribution was observed always, despite there likely being multiple cohorts in the samples, because sampling was concentrated in the spawning season, which homogenizes the distribution for two reasons. First, the spawning population consists primarily of a single cohort (Bailey *et al.*, 1977; Vilhjálmsson, 1994) and, second, it is mainly the larger fish of a cohort that spawn (Friis-Rødel and Kanneworff, 2002), which further reduces the size variation.

Our study focused solely on male growth. Female growth of Greenland capelin was researched by Kanneworff (1967), who showed that females grew slower than males and achieved a smaller maximum size. However, males and females most likely differ in life strategy, being semelparous and iteroparous, respectively (Huse, 1998; Carscadden *et al.*, 2001; Friis-Rødel and Kanneworff, 2002). As a result, female growth increments may be erratic in repeat spawners, which makes growth interpretation

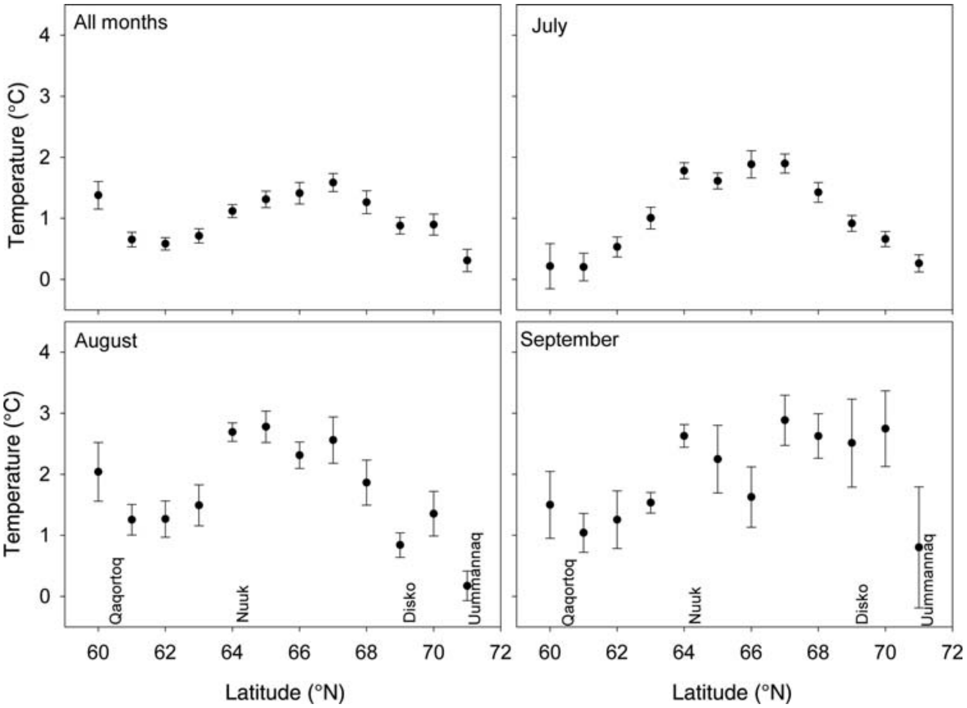

Figure 7. Average temperatures for 20–50 m averaged from 1908 to 2007 for West Greenland waters (60–73°N 44–57°W) from the ICES database (see text). Only measurements east of the shelf break on the west coast of Greenland were used (<500 m). Top left, data from all months and years ($n = 18\,753$); top right, data for July ($n = 4671$); bottom left, data for August ($n = 1632$); bottom right, data for September ($n = 808$). Error bars represent the standard error based on the mean values of all years at the latitudes evaluated ($n = 28–71$). The areas where fish were sampled for the growth analysis are noted at their respective latitude (see text).

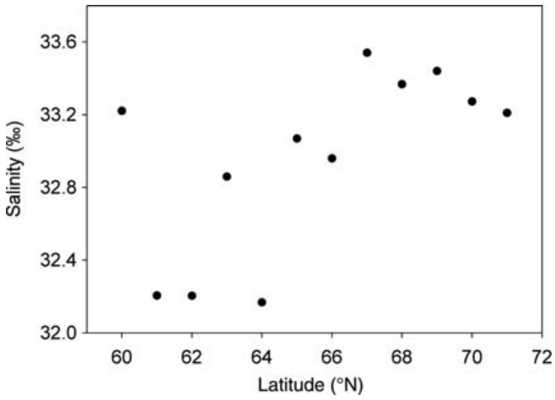

Figure 8. Average salinity in August for 20–50 m averaged over the period 1908–2007 for West Greenland waters (60–73°N 44–57°W) from the ICES database (see text). Only measurements east of the shelf break on the west coast of Greenland (<500 m) were used ($n = 1362$).

difficult and does not allow comparison between first-time and repeat spawners (Kleist, 1988).

To validate otolith interpretation, three issues were addressed: (i) whether the fish had completed a full growth season as assumed, (ii) whether the first growth increment was measured correctly, and (iii) whether the timing of laying down of the first increment was correct. Assumptions (i) and (ii) were met, but YOY from the Nuuk area had a smaller first growth increment than adult fish from the same area (0.103 and 0.134 mm, respectively). We feel confident that the small difference is not attributable to the first growth increment being wrongly determined, but rather to the growth season in YOY being incomplete, with the growth period extending beyond mid-September for that age group. In addition, size-selective mortality in later life with smaller fish of a cohort having a greater mortality rate could cause a wider first increment in surviving fish than in YOY. These growth patterns may arise from either inherent genetic differences or environmental effects. Such effects are likely to be linked to temperature and prey availability.

Greenland capelin display some degree of genetic differentiation (Sørensen and Simonsen, 1988). Genetic differences along latitudinal gradients influence growth patterns in Atlantic silverside (Conover and Present, 1990; Present and Conover, 1992) and could well explain a proportion of the growth variation demonstrated here, especially given that the selective forces (low winter temperature and a short growing season) proposed to have generated the genetically based growth differences in the silverside are the same in Greenland waters.

However, as no thorough and recent genetic studies on Greenland capelin exist and no controlled experimental work addressing the genetic influence on phenotypic variation has been performed, a genetic effect cannot yet be quantified. Hence, latitudinal growth variation is discussed based on available environmental data, although future exploration of a possible genetic component is encouraged. A further advantage at higher latitudes that should also be considered by future work is the increase in the daily feeding period for active visual predators associated with an increase in daylight hours, as demonstrated for juvenile cod by Suthers and Sundby (1996).

Temperature effect

The average growth of West Greenland capelin shown here is similar to that of other capelin populations in terms of absolute growth as well as the decline in growth with age (Templeman, 1948; Vilhjálmsson, 1994; Gjøsæter *et al.*, 2002). Latitudinal growth differences have been shown in Barents Sea capelin by Gjøsæter and Loeng (1987), who calculated growth from six areas in the period 1974–1985. They found a 15.5-mm reduction in growth with increasing latitude (71–77°N) in the last growth season of 2-year-old fish, similar to the 12.9 mm we found over a greater distance (61–69°N). However, the growth pattern was reversed, with growth being least in the north in their study. The growth difference is most likely caused by a large temperature difference between the subareas in the Barents Sea, because Gjøsæter and Loeng (1987) demonstrated a growth increase of 0.3 cm $^{\circ}C^{-1}$ $year^{-1}$ in both 2- and 3-year-old fish, using sea surface (10–200 m) temperatures. Obviously, the relationship between growth and temperature is not necessarily linear and may differ between ages, but assuming that the same relationship applies to West Greenland capelin and calculating the growth difference in 2- and 3-year-old fish for comparison, the expected experienced temperature difference between Qaqortoq (60°N) and Disko (69°N) should be between 2.8°C for 2-year olds and 4.3°C for 3-year olds. The temperature data analysed (Figure 7) showed an increase from Qaqortoq to Disko and a decline at Uummannaq, a trend similar to that of fish growth (Figures 4 and 6), growth being lowest at Qaqortoq, highest at Disko, and dropping slightly at Uummannaq. The large temperature drop at Uummannaq could be expected to cause a more pronounced growth decrease than observed, however. As the temperature drop is over a relatively short distance, the capelin may escape the unfavourable growth environment through annual migrations, as elsewhere (Vilhjálmsson, 2002). However, capelin migration patterns have not been investigated in West Greenland waters.

The inverse relationship between temperature and latitude along the west coast of Greenland is caused by mixing of the dominant currents in the area. East of Greenland, cold saline Polar Water (PW; Figure 1) that lies inshore along the Greenland coast meets offshore warmer, highly saline Irminger Sea Water (IW; Figure 1). The two currents progressively mix as they flow clockwise around the coast of Greenland, causing gradual warming of the inshore surface waters towards the north (see review by Buch, 2000; Ribergaard, 2007). This was also evident from the salinity measurements made simultaneously with the temperature recordings (Figure 8), which show an increase in salinity with latitude in accordance with the gradual mixing shorewards of the more saline, warmer Irminger Water. In comparison, the salinity of pure Irminger Water and Polar Water is ca. 35 and 32, respectively (Ribergaard *et al.*, 2008), confirming the presence of Polar Water in the surface layers in the south. Salinity in the Nuuk area did not follow the overall trend (Figure 8). This may be due to many (ca. 20%) of the measurements being made at the opening of the fjord, where there is a high degree of mixing and a substantial input of freshwater run-off from glaciers in summer (Mikkelsen *et al.*, 2008).

Additional data on Greenland west coast temperature are found in Ribergaard (2007), who made CTD measurements along the Greenland west coast in March, May, and July 2006. He showed that temperature near the coast was similar across latitudes. However, there was a tendency towards the upper layers (<200 m) being 1–2°C warmer at higher latitudes and for the temperature to drop again north of Disko. Ribergaard (2007) also measured temperatures in three fjords along the coast and in Disko Bay, yielding the same result, i.e. a small temperature increase from south to north. Munk *et al.* (2003) presented data from a northern subset of the area covered by Ribergaard (2007), measured in late June and early July 1996, and documented small differences between areas of 1–2°C, but no clear latitudinal gradient. Finally, a capelin trial fishery in September and October 2005 made CTD measurements from 59 to 73°N (Bergstrøm and Vilhjálmsson, 2006). The measurements were made east and west of the banks. From 0 to 20 m, the temperature was at least 2–3°C higher in the north, but deeper than 50 m, the pattern was reversed.

Therefore, the available temperature data are not conclusive, but the ICES data used here suggest a latitudinal temperature gradient in the upper water layers, with temperatures ca. 2°C higher in the capelin growth season at Disko than at Qaqortoq. This suggests that the effect of temperature on growth is greater in West Greenland capelin than in Barents Sea capelin (0.4–0.6 and 0.3 cm $^{\circ}C^{-1}$ $year^{-1}$, respectively).

The decline in average size and the unique age-specific growth pattern in the Uummannaq area may be a result of pronounced year-to-year temperature variation in this area. Capelin live close to their northern boundary at Uummannaq, where the yearly average temperature is ~0.8°C, and in warm years, they have been found farther north and in colder years farther south (Hansen and Hermann, 1953; Friis-Rødel and Kanneworff, 2002). The growth of capelin there may therefore be more variable, and the increased growth seen in 2+ fish in Uummannaq does coincide with the majority of the sampled fish (50%) experiencing a warm 2006 in the 2+ growth season (Ribergaard, 2007).

Prey effects

Although the temperature regime appears to be a likely explanation for the latitudinal size variation, the fact that Qaqortoq and Uummannaq capelin show very different growth rates despite similar average annual temperatures, whereas Uummannaq and Disko capelin show similar growth despite different temperatures suggests that other factors may be playing a role too.

Capelin growth rates have been correlated with zooplankton abundance (Gjøsæter *et al.*, 2002), and because we analysed a large latitudinal gradient, prey availability and quality may have differed between areas. Studies on zooplankton abundance along the Greenland west coast suggest a similar abundance of prey species between areas (Pedersen and Smidt, 2000; Levinsen and Nielsen, 2002; Jensen and Rasch, 2008). However, there appears to be a shift in dominant species. Towards the north, the copepod community is increasingly dominated by the large *Calanus hyperboreus*, replacing the smaller *Calanus finmarchicus*. This is also evident in the results of a recent unpublished feeding study on Greenland capelin, in which the former (larger) species gradually replaced the latter (smaller) one in capelin stomach contents towards the north. This may give the northern species an increased energy intake, especially in the youngest stages where copepods dominate the diet (O'Driscoll *et al.*, 2001). In larger capelin, krill became increasingly more important as prey with latitude. As krill are larger and with similarly high energy content (Falk-Petersen *et al.*, 2000), this may infer some feeding advantage for large capelin in the north. Hence, latitudinal feeding differences at all life stages may contribute to maintaining the growth gradient in West Greenland capelin seen in other waters (Gjøsæter *et al*., 2002). Moreover, a shift in energy consumption of capelin, and therefore in its own growth potential and energy content, can affect higher trophic levels, as seen in sprat (*Sprattus sprattus*) in the Baltic (Cardinale *et al*., 2002; MacKenzie and Köster, 2004; Österblom *et al*., 2006) and in North Sea herring (*Clupea harengus*; Alheit *et al*., 2005).

In addition to prey abundance, capelin abundance may also affect feeding possibilities. Hence, if capelin abundance is low in the north, the food intake *per capita* may be higher than elsewhere, although evidence of density-dependent processes is equivocal (Millner and Whiting, 1996; Melvin and Stephenson, 2007). Abundance estimates of Greenland capelin are scarce. In 2005, an attempt was made to quantify capelin abundance along the Greenland west coast (Bergstrøm and Vilhjálmsson, 2006), and it suggested that density was highest in the Disko area (233.8 t nautical mile^{-1}) and the Nuuk fjord system (170.2 t nautical mile^{-1}), and lowest in the south (42.0 t nautical mile^{-1}). Based on these findings, capelin density should, if anything, limit growth in the northern part of the study area, and density-dependence is not likely to play a role in the growth regulation we have documented.

Conclusions

In summary, growth differences in West Greenland capelin are related to the 2°C difference between the areas studied. Hence, predictions of increased future temperatures along Greenland (Stendel *et al*., 2008) will most likely affect the growth of Greenland capelin, and consequently the entire West Greenland ecosystem. Such changes are attributable to the direct effect of temperature on growth and metabolism, but the effect is likely to be modified by concurrent changes in prey availability and energy changes in prey composition. Therefore, the effects might be many and non-linear, making an overall response of both capelin and the ecosystem likely, but not easily predictable.

Acknowledgements

We thank the staff at the Greenland Institute of Natural Resources for help with sampling and processing of the temperature data, as well as in interpreting the otoliths. Holger Hovgård, Kaj Sünksen, Arne Geisler, and Aili Lage Labansen in particular provided appreciated assistance. Additionally we thank two anonymous reviewers for helpful comments on an earlier version of the manuscript.

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doi:10.1093/icesjms/fsq024