

Energy content and fecundity of capelin (*Mallotus villosus*) along a 1,500-km latitudinal gradient

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Abstract Capelin is a planktivorous key fish species in many subarctic ecosystems representing the link between lower trophic levels and apex predators. Little is known, however, of capelin in Greenland waters, but it has been suggested that size and growth increases due to difference in food availability and temperature conditions along a 1,500 km south–north gradient on the west coast. It is presently unknown how the qualitative state of capelin energy content is affected along this gradient. Based on 2007 and 2008 samples, we show that energy content increases with capelin length in both spawning and non-spawning fish and that it varies with latitude in spawning fish along West Greenland (60–71°N). Combining our results on energy content with information on capelin growth along the same latitudinal climate gradient demonstrates that less and lower-quality food is available to capelin predators in the south than in the north.

Introduction

Capelin (*Mallotus villosus*, Osmeridae) is a planktivorous fish with a northern circumpolar distribution. Similar to other planktivorous species in the “wasp-waist species” guild (i.e., sardines, anchovy, sprat, Cury et al. 2000; Bakun 2006) capelin have a life cycle characterized by a short lifespan, high mobility, high energetic need (as a result of their numbers and high growth rates), and variable cohort strength (Frank and Carscadden 1989; Gjørseter et al. 2002; Vilhjalmsen 2002). These characteristics can result in a fluctuating population biomass on a short time scale as demonstrated for both capelin (Gjørseter 1998; Vilhjalmsen 2002) and sardine–anchovy systems across world oceans (Schwartzlose et al. 1999).

In Greenland, capelin is found on both the east and the west coast extending north to 73°N and 66°N, respectively (Friis-Rødel and Kannevorff 2002). On the west coast, this covers a 1,500 km unbroken latitudinal gradient making capelin in this region a perfect candidate for studying the effects of changes in environmental and climatic conditions. Capelin sensitivity to environmental changes is evident both historically and presently. In the relatively warm 1930 s, capelin distribution extended as far north as 76°N and at the same time showed reduced abundance in southern Greenland (Jensen 1939). Currently, sustained spawning is limited to the area south of 72°N. More recently, changes in life history characteristics such as growth and feeding behavior along the distributional range of capelin have been shown (Hedeholm et al. 2010, Hedeholm et al., submitted manuscript), underlining the applicability of capelin in this region as a model species for studying the effect of (future) environmental changes (Anonymous 2005) and latitudinal differences in vital life history characteristics such as fecundity, energy allocation, condition, and productivity.

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Ecosystem-wide impacts of capelin, and wasp-waist species in general, have been shown theoretically (Rice 1995; Jordan et al. 2005), and the effect of a capelin-deprived diet has been shown for Canadian cod (Rose and O’Driscoll 2002) and in relation to the junk-food hypothesis in sea birds (Romano et al. 2006). In Greenland waters, the importance of capelin as prey has been demonstrated in marine mammals (Angantyr and Kapel 1990; Neve 2000), cod (*Gadus morhua*, Nielsen and Andersen 2001), Greenland halibut (*Reinhardtius hippoglossoides*, Woll and Gundersen 2004), and sea birds (Falk and Durinck 1993; Phillips et al. 1999). In all cases, capelin constituted a substantial part of the diet. Due to its lipid content, capelin has a high-energy density compared to other species (Montevecchi and Piatt 1984; Lawson et al. 1998), and thus the importance of capelin is related not only to abundance but also to tissue composition, which determines the nutritional value of this important prey species. However, the energy density and possible latitudinal trends for Greenland capelin are unknown, and satisfactory energy flow calculations including this key species cannot be developed.

In this study, we provide the first area-specific data on energetic densities, fecundity, and reproductive investment for West Greenland capelin. As stomach content and growth rates have been shown to increase with latitude in this area (Hedeholm et al. 2010, Hedeholm et al., submitted manuscript) two scenarios are possible: (1) either the observed increase in food intake is all used for growth; or (2) there is an increase in the energetic storage as well. Hence, as a null hypothesis for non-spawning capelin, we suggest that there is no increase in energy density with increasing latitude and thus no relationship between latitude and tissue energy density. In spawning fish, all accessible tissue energy will be converted to gonads as Greenland capelin are most likely semelparous (Friis-Rødel and Kannevorff 2002). Consequently, tissue energy density should not vary with latitude but be markedly reduced relative to non-spawning individuals; a non-trivial point in constructing biomass-based energetic models. Knowledge of Greenland capelin is scarce, and the present analysis will be useful in modeling (Fiksen et al. 1995). Additionally, if capelin displays a latitudinal gradient in nutritional value similar to those shown for growth, the impact of future climate changes may be more pronounced than previously thought.

Materials and methods

Sampling

Capelin were collected during 2007 and 2008 along the west coast of Greenland (Fig. 1, Tables 1 and 2). Non-

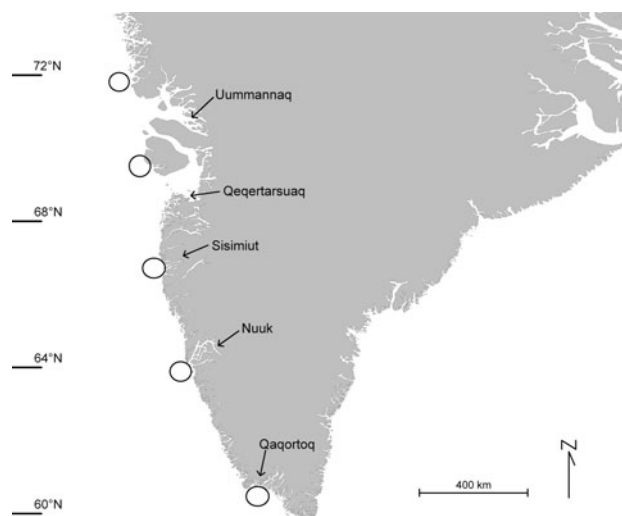


Fig. 1 The southern part of Greenland with the study areas marked. The arrows mark areas where spawning capelin were sampled in 2007. From south to north, these are Qaqortoq, Nuuk, Sisimiut, Qeqertarsuaq, and Uummannaq. The circles mark the offshore areas where non-spawning capelin were sampled in 2007 and 2008

spawning capelin were collected in both years by RV “Paamiut” during yearly shrimp and fish surveys conducted by the Greenland Institute of Natural Resources. This stratified random bottom-trawl survey covered the continental shelf from the southern tip of Greenland to 72°N on the west coast. The survey was done using a bottom trawl with a vertical opening of 14 m and a towing speed of 2.5 knots. The trawl was not aimed at capelin, but these were occasionally caught, most likely during trawl haul in. All capelin caught were frozen immediately after capture. At stations where the catch exceeded 150 individuals, a random subsample of 50 individuals were taken. Spawning capelin were only sampled in 2007. The samples were collected during beach spawning events in five general areas spanning 1,300 km along the Greenland West coast: Qaqortoq (61°N), Nuuk (64°N), Sisimiut (66°N), Qeqertarsuaq (69°N), and Uummannaq (71°N, Fig. 1). Females were, however, only caught in the Nuuk area and unless specifically mentioned, all comparisons are based on male capelin. Samples of both spawning and non-spawning capelin were frozen at -20°C immediately after capture.

Physical measurements and fecundity

Capelin were measured to the nearest mm below (fork length) and weighed to the nearest 0.1 g. No correction was made for shrinkage due to freezing. All spawning fish were sexed based on morphological characteristics. This was not done for non-spawning fish as sexes appear similar prior to spawning. Ovaries were removed from spawning females, blotted dry, and weighed to the nearest 0.1 g. Fish that had

Table 1 Sampling data on capelin caught along the Greenlandic west coast in 2007–2008

Position	No. of stations	Location	Date		State		Depth (m)	N	Female/male ratio
			2007	2008	Non-spawning	Spawning			
60.17–61.04°N 46.10–49.53°W	7	Qaqortoq	16–19/8	4/8	X		96–264	41	–
62.74–63.95°N 51.06–52.74°W	6	Nuuk	9–11/8	27–29/7	X		135–374	39	–
66.47°N 54.69°W	1	Sisimiut		21/6	X		348	5	–
68.80–70.06°N 51.60–57.39°W	5	Qeqertarsuaq	29–30/7	30/6–7/7	X		66–237	26	–
71.66–72.04°N 56.77–57.13°W	4	Uummannaq		7/7–10/7	X		185–287	24	–
60.82°N 45.77°W	1	Qaqortoq	9/7			X	Beach	6	0
64.44°N/64.22°N 50.21°W/50.96°W	2	Nuuk	11/5–13/6			X	Beach	31	0.97
66.92°N 53.21°W	1	Sisimiut	24/6			X	Beach	22	0
69.25°N 53.51°W	1	Qeqertarsuaq	10/6–19/7			X	Beach	14	0
70.75°N 51.28°W	1	Uummannaq	30/6			X	Beach	21	0

The non-spawning fish were caught offshore and not sexed. The spawning fish were sampled during beach spawning events using hand nets

Table 2 Location, number, physical data, water content (%), and energy density (kJ g dw⁻¹) for all sampled capelin (mean ± SD)

Area	Latitude (°N)	N	Fork length (mm)	Wet mass (g)	Water content (%)	Energy density (kJ g dw ⁻¹)
Spawning (2007)						
Qaqortoq	60–61	6	120 ± 4	10.1 ± 1.4	82.1 ± 1.1	20.86 ± 0.29
Nuuk	63–64	61	124 ± 13	13.0 ± 4.5	82.5 ± 0.9	21.28 ± 0.69
Sisimiut	66–67	22	144 ± 6	21.8 ± 3.3	82.8 ± 1.1	21.16 ± 0.27
Qeqertarsuaq	68.5–70	14	149 ± 5	29.9 ± 4.0	81.8 ± 1.0	21.86 ± 0.60
Uummannaq	71–72	21	145 ± 7	24.5 ± 4.3	84.0 ± 0.8	21.42 ± 0.34
Non-spawning (2007–2008)						
Qaqortoq	60–61	41	113 ± 2	7.7 ± 3.9	79.7 ± 1.0	20.87 ± 0.75
Nuuk	63–64	42	122 ± 1	10.1 ± 3.1	79.7 ± 1.3	21.12 ± 0.69
Sisimiut	66–67	5	124 ± 0	10.7 ± 2.0	80.0 ± 0.6	20.98 ± 0.38
Qeqertarsuaq	68.5–70	26	142 ± 2	16.0 ± 5.2	79.3 ± 0.6	21.28 ± 0.55
Uummannaq	71–72	24	126 ± 2	8.9 ± 1.7	78.7 ± 0.6	20.95 ± 0.61
Gonads (2007)						
Nuuk		18	111 ± 9	9.5 ± 2.3	71.3 ± 1.6	24.80 ± 0.25

Length and mass data in the “gonads” section refers to the fish, while the remainder refers to the gonads

released eggs into the body cavity were excluded from analysis as some eggs may already have been spawned.

About 20–60 eggs from the posterior part of the right ovary were weighed and counted, as the left ovary is known to be underdeveloped (Winters 1971). Based on this and

total ovary wet weight, absolute fecundity was calculated assuming that no difference existed between various parts of the ovary (Huse and Gjøsæter 1997). The gonadosomatic index (GSI) was calculated as the proportional wet mass of ovaries in relation to total fish wet weight.

Energy measurements

Muscle tissue (mean \pm SE = 1.09 ± 0.03 g) was removed dorsally from both sides of the fish posterior to the dorsal fin to ensure that no bones were present. All skin was subsequently removed. Muscle tissue from all fish and ovaries from spawning females were freeze dried for 24 h after which no further weight loss took place. The tissue samples were weighed (dry mass, dw), and the water content was calculated (% of wet mass, ww). Prior to any further analysis, the samples were kept in an exsiccator over a dry silica gel. The tissue samples were homogenized to a fine powder using a glass mortar and compressed into pellets of at least 25 mg. The energy density of the pellets was determined using an 1109a semimicro bomb and Parr 6725 bomb calorimeter (Parr Instruments, Moline, USA). The bomb was calibrated with benzoic acid (energy density: 26.454 kJ g^{-1}) with regular intervals, and triplicates of randomly chosen samples demonstrated low variation between samples (<2%). Energy densities differing to a large extent from other values were reanalyzed. Energy density is reported for both wet (kJ g ww^{-1}) and dry samples (kJ g dw^{-1}) with the latter used in most analyses. From an ecological perspective, the wet-mass values may be more relevant (Anthony et al. 2000) but do not form the main focus of this study as energy density expressed on a dry weight basis is more appropriate for comparative purposes, as the variation caused by desiccation is minimized (Hislop et al. 1991). Additionally, wet-mass values are easily calculated by multiplying dry-mass-energy density (kJ g dw^{-1}) by the proportion of dry mass to wet mass. Freeze-dried muscle tissue from five fish was incinerated for 24 h at 550°C to determine the ash content of the samples, and energy density was calculated based on these values ($\text{kJ g ash free dw}^{-1}$). Samples from ovaries were analyzed using the same procedure.

Lastly, data on water content, energy density, and fecundity enabled calculation of individual egg energy content and, consequently, calculation of total energetic investment of the individual female. The relative reproductive investment of each female was calculated as the amount of energy in the ovaries relative to total fish energy content (ovaries excluded), under the assumption that the muscle energy density was representative of the entire fish.

Analysis

Spawning and non-spawning fish were analyzed separately. All fish were assigned to the nearest 0.5 latitudinal degree and to one of five locations: Qaqortoq ($60\text{--}61^\circ\text{N}$), Nuuk ($63\text{--}64^\circ\text{N}$), Sisimiut ($66\text{--}67^\circ\text{N}$), Qeqertarsuaq ($68.5\text{--}70^\circ\text{N}$), and Uummannaq ($71\text{--}72^\circ\text{N}$, see Fig. 1) for ANOVA-based tests. However, Sisimiut was excluded from most statistical analyses concerning non-spawning fish, as few fish were caught in

this area. Analyses on spawning fish only include males unless stated otherwise, as spawning females were sampled only in Nuuk. All analyses were carried out using SPSS 18.0. 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

Energy densities of 259 fish (124 spawning and 135 non-spawning) and 18 female ovaries were determined (Table 2). As no difference in energy density (kJ g dw^{-1}) was found between 2007 and 2008 for spawning fish (ANCOVA, $F_{(1,128)} = 0.01$, $P = 0.94$), irrespective of both size and capture location, the 2 years were pooled.

Latitudinal and length effect

In non-spawning capelin, there was a significant effect of both area (ANCOVA, $F_{(3,122)} = 3.57$, $P = 0.016$) and length (ANCOVA, $F_{(1,122)} = 26.90$, $P < 0.0005$) on energy density but also a significant interaction between the two (ANCOVA, $F_{(3,122)} = 4.08$, $P = 0.008$, Fig. 2). The interaction was caused by Qeqertarsuaq and removing this area from the analysis yielded non-significant interaction and area terms (ANCOVA, $F_{(2,98)} = 2.11$, $P = 0.127$ and $F_{(1,98)} = 34.77$, $P = 0.172$, respectively). Using the parameter estimates (following model reduction), the overall length effect and difference between the three similar areas (Qaqortoq, Nuuk, and Uummannaq) and Qeqertarsuaq can be depicted as shown in Fig. 3. A clear positive relationship between length and energy density was seen for the pooled areas, while size effects in the Qeqertarsuaq area were positive but insignificant.

No length effect was seen in the individual areas in spawning capelin (linear regression, $P \geq 0.08$). However, combining areas and thereby increasing the length span gave a significant effect of length (linear regression, $r^2 = 0.58$, $F_{1,16} = 8.24$, $P = 0.028$) under the assumption that the single outlier in the [110–115] category can be disregarded. This was done as this point was based on a single fish from Nuuk. The data did not allow parametric statistics in area comparisons. Disregarding length, all but one of ten (Nuuk and Uummannaq, $P = 0.89$) intergroup comparisons were significant (Mann–Whitney, $P \leq 0.034$), but the most noticeable distinction was between high values at Qeqertarsuaq and low values at Qaqortoq (medians = 21.89 and $20.83 \text{ kJ g dw}^{-1}$, respectively, Fig. 4).

Spawners vs. non-spawners

Irrespective of size and location, a mean difference of $0.286 \text{ kJ g dw}^{-1}$ was found in energy density (based on dry weight, kJ g dw^{-1}) between spawners and non-spawners

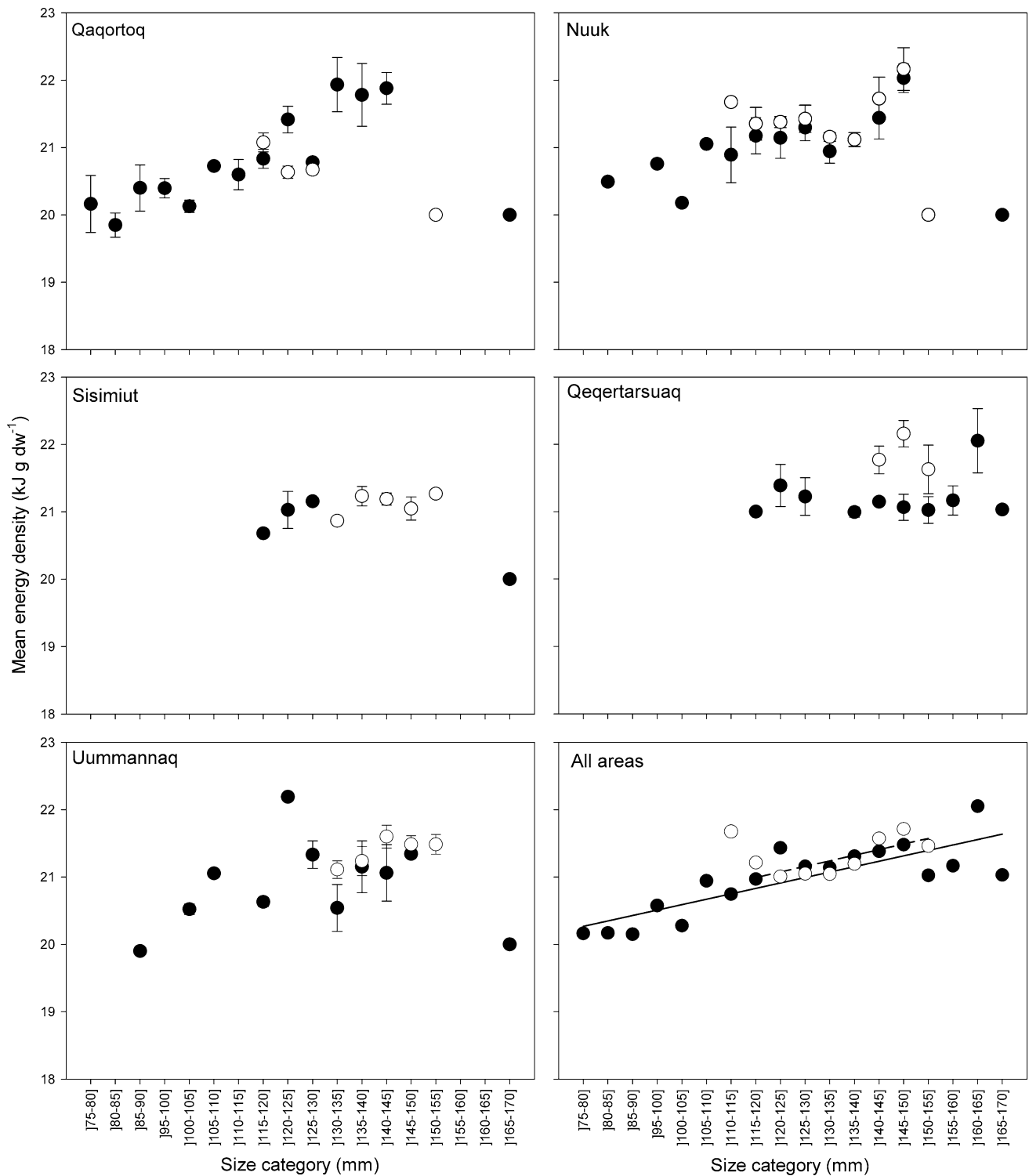


Fig. 2 Mean energy density (kJ g dw⁻¹) of spawning (*open circles*) and non-spawning (*filled circles*) capelin caught in 2007 and 2008 along the Greenland west coast at five locations (N_{spawners} , $N_{\text{non-spawners}}$): Qaqortoq (6, 41), Nuuk (31, 39), Sisimiut (22, 5), Qeqertarsuaq (14, 26), and Uummannaq (21, 24). All areas are shown separately and

(ANCOVA, $F_{(1,248)} = 248.36$, $P < 0.0005$, Fig. 2). However, when comparisons were based on wet mass (kJ g ww⁻¹), the non-spawning fish had energy densities ranging

combined. The combined values are unweighted averages. The lines in the combined graph represent linear regression of energy density on length for both spawning (*dashed*, $r^2 = 0.58$, $P = 0.03$, disregarding the [110–115] category (see text)) and non-spawning (*solid*, $r^2 = 0.67$, $P < 0.0005$). Bars represent standard error

from 4 to 4.5 kJ g ww⁻¹ (mean ± SD = 4.32 ± 0.29 kJ g ww⁻¹), whereas spawning fish had much lower densities (mean ± SD = 3.68 ± 0.28 kJ g ww⁻¹, Fig. 5). The pattern

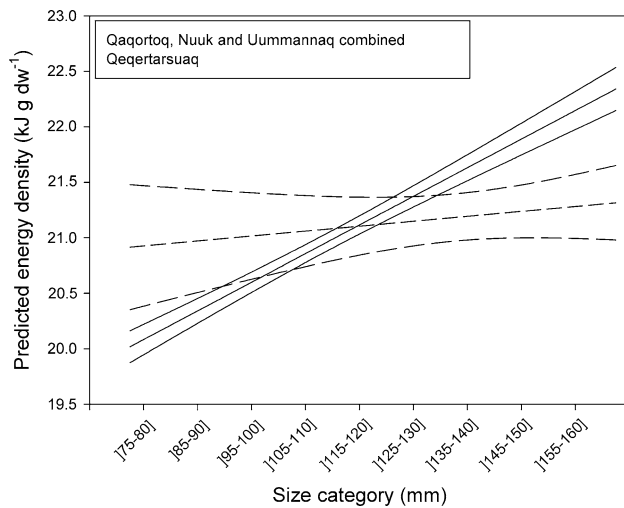


Fig. 3 The predicted relationship and 95% confidence intervals between energy density (kJ g dw^{-1}) and size in non-spawning capelin from Greenland based on model parameter estimates (see text). The areas that did not differ statistically are combined (Qaqortoq, Nuuk, and Uummannaq, solid lines), while Qeqertarsuaq is depicted alone (dashed lines). Parameter estimates are ($y = a * x + b$): $a = 0.025$; $b = 18.015$ and $a = 0.004$; $b = 20.571$ for combined areas and Qeqertarsuaq, respectively

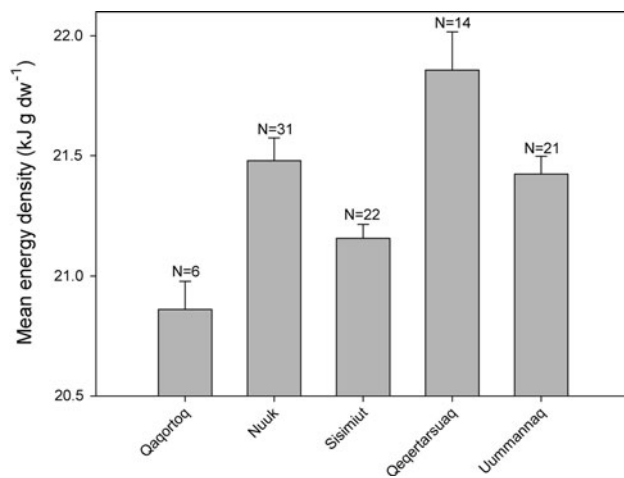


Fig. 4 Mean energy density (kJ g dw^{-1}) in male spawning capelin from five locations on the Greenland west coast: Qaqortoq ($60\text{--}61^\circ\text{N}$), Nuuk ($63\text{--}64^\circ\text{N}$), Sisimiut ($66\text{--}67^\circ\text{N}$), Qeqertarsuaq ($68.5\text{--}70^\circ\text{N}$), and Uummannaq ($71\text{--}72^\circ\text{N}$). N is noted for each area. Bars represent standard error

was seen for all individual areas but most clearly in Uummannaq with a difference of more than 1 kJ g ww^{-1} in comparable weight groups. This discrepancy between dry- and wet-mass-based comparison was caused by a significant difference in water content between spawners and non-spawners, irrespective of length (mean \pm SD = 82.7 ± 1.1 and $79.4 \pm 1.0\%$, respectively, ANCOVA, $F_{(1,199)} = 452.71$, $P < 0.0005$).

Temporal effect

Because samples were taken in the summer feeding period, time-of-capture could possibly affect the results, as energetic reserves can be expected to build during summer months, thus increasing energy density. In general, for all non-spawning fish, there was no effect of time-of-capture on energy density over a period of 59 days (Spearman's correlation, $r_s = -0.09$, $N = 135$, $P = 0.285$). In the individual areas, the sampling time span enabled such analyses in three cases (Nuuk, Qaqortoq, and Qeqertarsuaq). In the latter two no effect of time-of-capture was seen ($P \geq 0.40$), while a weak positive correlation was seen in Nuuk (Spearman's correlation, $r_s = 0.900$, $N = 39$, $P = 0.037$). Here, sampling took place over 14 days starting from 29 July and showed an average increase from 20.6 to 21.6 kJ g dw^{-1} .

In spawning capelin, a temporal development in energy density was seen in the Nuuk area, which was the only area where such an analysis was possible as sampling took place over a period of 33 days. The energy density decreased from 22.37 to 21.24 kJ g dw^{-1} (ANCOVA, $F_{(4,25)} = 5.04$, $P = 0.004$), while no change in size was seen during the same period (ANCOVA, $F_{(1,25)} = 1.28$, $P = 0.27$).

Sex effect

A test of differences in energy density between sexes in spawning capelin was restricted to Nuuk, as spawning females were absent in samples from other areas. In general, energy density increased with size (kJ g dw^{-1} , ANCOVA, $F_{(1,57)} = 19.39$, $P < 0.0005$, Fig. 6). A difference was also found between the sexes (ANCOVA, $F_{(1,57)} = 4.89$, $P = 0.031$), but a significant interaction (ANCOVA, $F_{(1,57)} = 5.37$, $P = 0.024$) made comparisons across the sampled length range ambiguous. Within the overlapping size range (115–132 mm), no difference was found between sexes when pooling all individuals based on both dry (kJ g dw^{-1} , Student's t -test, $t_{20,25} = -0.21$, $P = 0.83$) and wet mass (kJ g ww^{-1} , Student's t -test, $t_{30} = 0.11$, $P = 0.91$).

Fecundity and reproductive investment

Absolute fecundity increased with gutted mass (range: 3,745–11,317 eggs, regression, $r^2 = 0.69$, $F_{1,16} = 35.955$, $P < 0.0001$), and the relationship was best described as: Fecundity = $356.63 * \text{gutted mass}^{1.4414}$ (Fig. 7). The female GSI was $21.56 \pm 5.98\%$, and on average the female ovaries contained (mean \pm SD) $37.8 \pm 3.3\%$ of total female capelin energy with the mean (mean \pm SD) egg energy density being $24.80 \pm 0.25 \text{ kJ g dw}^{-1}$. The reproductive investment was positively related to gutted mass (linear regression, $r^2 = 0.36$, $F_{1,16} = 8.91$, $P = 0.009$, Fig. 7) as was GSI (linear regression, $r^2 = 0.35$, $F_{1,16} = 19.18$, $P < 0.0005$, data not shown). The

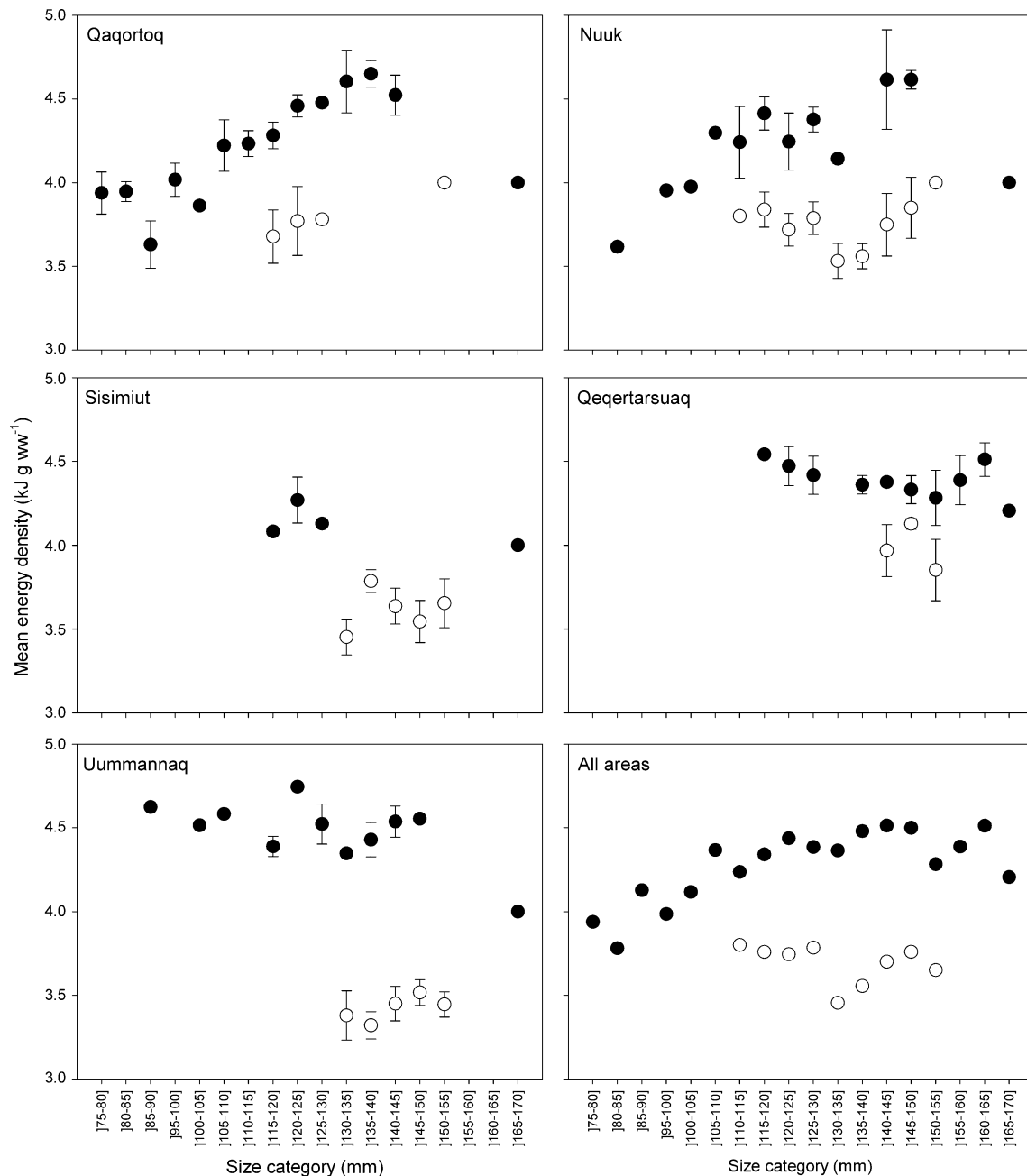


Fig. 5 Mean energy density (kJ g ww⁻¹) of spawning (open circles) and non-spawning (closed circles) capelin caught in 2007 and 2008 along the Greenland west coast at five locations (N_{spawners} , $N_{\text{non-spawners}}$): Qaqortoq (6, 41), Nuuk (61, 42), Sisimiut (22, 5), Qeqertarsuaq

(14, 26), and Uummannaq (21, 24). All areas are shown separately and combined. The combined values are unweighted averages. Bars represent standard error

individual egg energy content was (mean \pm SD) 2.67 ± 0.36 J, but was not related to fish gutted mass (Spearman’s correlation, $r_s = 0.18$, $N = 18$, $P = 0.486$).

Discussion

To our knowledge, this study represents the first data on energy density for Greenland capelin. The densities (based

on dry matter, kJ g dw⁻¹) are lower than seen in other studies (e.g., Jangaard 1974; Lawson et al. 1998; Anthony et al. 2000). As these studies demonstrate higher energy densities than shown here, spatial differences may exist. However, most other studies convert proximate composition to energy density, thus relying on energetic conversion factors, and often use low conversion factors for protein including only assimilable energy (17.8–20.0 kJ g dw⁻¹). Converting values given by Anthony et al. (2000) on

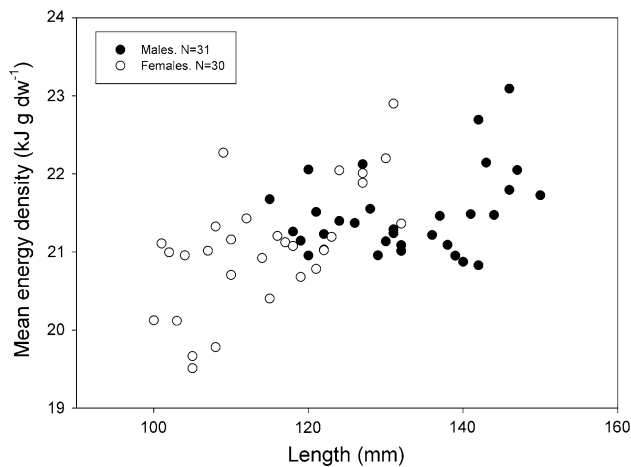


Fig. 6 Mean energy density (kJ g dw^{-1}) of spawning male (filled circles) and female (open circles) capelin caught from 11 May to 13 June 2007, in the Nuuk fjord system, Greenland

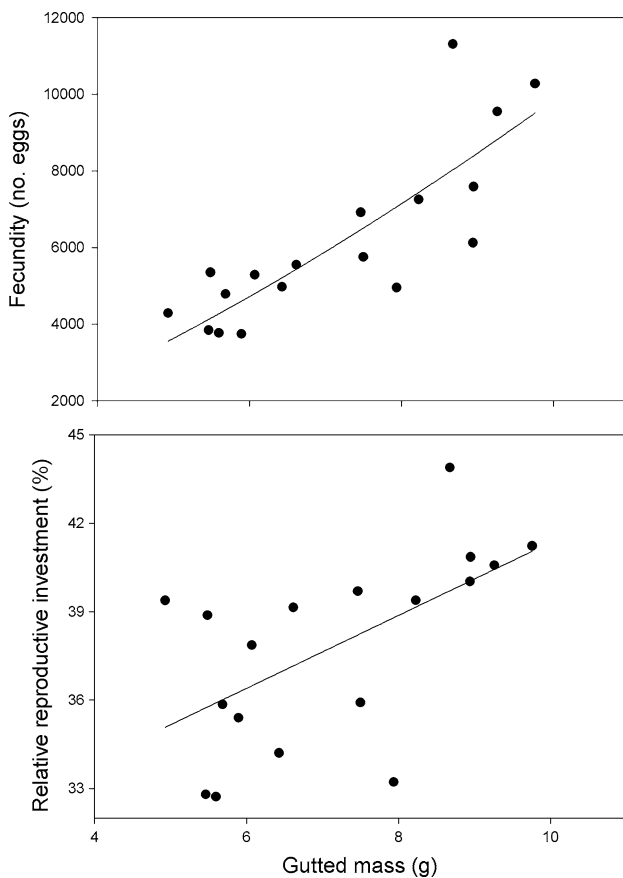


Fig. 7 Top fecundity of female capelin from Nuuk fjord (64°N) as a function of gutted mass ($N = 18$). The line represents power regression (Fecundity = $356.63 * \text{gutted mass}^{1.4414}$, $r^2 = 0.69$, $P < 0.0001$). Bottom the relative reproductive investment (%) measured as total ovary energy relative to total fish energy content (ovaries excluded). The line represents linear regression (Reproductive investment = $28.98 + 1.24 * \text{gutted mass}$, $r^2 = 0.35$, $P = 0.01$)

Alaska capelin to energetic densities using an energy equivalent of $23.2 \text{ kJ g dw}^{-1}$ for protein (as determined in this study using reference material), we find an energy density of $26.6 \text{ kJ g ash-free dw}^{-1}$ in non-spawning capelin compared to $22.3 \text{ kJ g ash-free dw}^{-1}$ in this study (the ash content of capelin was 5.72%). Similarly, Montevecchi and Piatt (1984) present results from Newfoundland, Canada, with non-spawning capelin having re-calculated energy densities of $24\text{--}29 \text{ kJ g dw}^{-1}$, similar to those presented by Jangaard (1974) and Lawson et al. (1998). As calculations in the mentioned studies, and other energetic studies on fish (e.g., Van Pelt et al. 1997; Ball et al. 2007), are made from proximate fish composition, the difference may be a result of differences in methodology (i.e., lipid extraction) causing overestimation (Jeziarska 1974; Craig et al. 1978). Other studies using bomb calorimetry on pelagic fishes obtain values much like those shown here (e.g., Smith et al. 1990; Kitts et al. 2004), and we believe that the values are accurate, but if they are to be used in energetic budgets of capelin predators, correction to efficiency of the metabolic pathway is needed (Ball et al. 2007). The timing of the samples collected in this study may partly explain the difference between studies, as a seasonal change in proximal composition, and thus energy density, of capelin has been reported from other waters (Jangaard 1974; Eaton et al. 1975; Montevecchi and Piatt 1984; Lawson et al. 1998 and references; Anthony et al. 2000) as well as in other fishes (e.g., Hislop et al. 1991; Schwarz and Hammer 1996; Kitts et al. 2004) with a minimum in the mid-summer months because of a bimodal production cycle in temperate regions. Hence, Jangaard (1974) observed an increase from $21.2 \text{ kJ g dw}^{-1}$ in June/July to $26.7 \text{ kJ g dw}^{-1}$ in August in Canadian capelin (determined from proximate fish composition). The “energy density/water” ratio changes due to reciprocal substitution of tissue and water as the tissue is metabolized. Anthony et al. (2000) used water content in capelin as a proxy for energy content explaining 97% of the variation (based on energy density in wet mass), and Jangaard (1974) found a peak in water content of 82%, to be coincident with the lowest energy density. As the mean water content in this study was 80%, a matching low-energy density may be expected. In general, we saw no effect of time-of-capture on energy density, but in Nuuk there was a 1-kJ g dw^{-1} increase over time in non-spawning fish, suggesting that sampling throughout the season is necessary to allow detailed comparison with other studies.

There are differences in energy density between tissues, as demonstrated here between ovaries and muscle tissue, so conclusions regarding the nutritional value of capelin to predators should ideally be based on whole fish and not assuming that muscle is representative as done here. However, non-spawning capelin do not have developed gonads, and the remaining tissues make up a small amount of total

fish weight, making it unlikely that the exclusion of these tissues will influence the overall energy density significantly or change the conclusions of the present study.

The non-spawning capelin were caught as bycatch in a bottom-trawl survey and not as a part of a sampling survey directed toward capelin. This could suggest an opportunistic sampling design complicating direct hypotheses testing. However, the capelin were caught using the same standard procedure at all stations, and we have no reason to expect that the sampled capelin should be biased in a way that would alter conclusions. Furthermore, the number of capelin caught was sufficiently large to allow for a good spatial coverage and five well-defined and separate sampling areas. The data provide significant new knowledge on capelin biology in this area, sets a baseline with regard to spatial differences in capelin energy density and allocation, and will allow more specific future hypothesis to be generated along with specific and more structured sampling designs. Therefore, we consider the use of this imperfect sampling design justified.

Fecundity and reproductive investment

Fecundity estimates (mean \pm SD = 6,185 \pm 2,249 eggs) were much lower than estimates from the Barents Sea (approx. 11,000, e.g., Gjøsæter and Monstad 1973; Huse and Gjøsæter 1997), Pacific (approx. 20,000, Velikanov 2002), and Canada (>20,000, Nakashima 1987). However, as all studies (the present one included) show positive fecundity–size relationships (Fig. 7), the size-specific fecundity in this study is as high or higher than in other studies (converting fork length to total length using a conversion factor of 1.08).

The reproductive investment was high (38%), which was as expected for a—to a varying degree—semelparous species (Karamushko and Christiansen 2002) that undertakes at least some migration associated with spawning (Behrens et al. 2006) and corresponds well with the semelparous/iteroparous limit of 60% (migration and spawning) suggested by Glebe and Leggett (1981). Hence, values of 10–30% have been demonstrated for iteroparous species such as Arctic char (Jonsson and Jonsson 1997; Finstad et al. 2002) and Atlantic cod in Greenland (Hedeholm et al., unpublished manuscript).

Reproductive investment increased with mass, but individual egg energy content (mean \pm SD = 2.67 \pm 0.36 J) did not. This has several possible explanations. The increase in investment could simply be a result of body cavity volume increasing more with a given mass increase (i.e., higher fecundity) than somatic energy content, or that smaller fish have a higher proportion of essential tissue that is not convertible to ovaries. However, it could also reflect a need to conserve more energy in smaller capelin as a

response to an iteroparous life history strategy, which has been suggested for female capelin (Sørensen 1985; Vilhjálmsson 1994; Huse 1998; Friis-Rødel and Kannevorff 2002). In iteroparous species, it might be expected that first-time spawners produce lower-quality eggs and/or invest less in reproduction than more experienced individuals (Trippel 1998; Carr and Kaufman 2009). This study supports the latter of these notions and encourages further research on both male and female capelin.

Latitudinal and length effects

There was no evidence of a clear latitude-related trend in energetic density in non-spawning capelin. As growth increases along the same latitudinal gradient (Hedeholm et al. 2010), this indicates that the increase in energy intake with latitude is all converted to growth and not stored as energy. However, there was a significant difference between Qaqortoq and Qeqertarsuaq in spawning fish (20.86 and 21.87 kJ g dw⁻¹, respectively), which are also the two areas showing the largest growth differences, indicating that these areas represent the southern distributional limit where environmental constraints limit capelin growth (Qaqortoq) and the optimal living conditions (Qeqertarsuaq), respectively. Hence, the decline in energy density in Uummannaq north of Qeqertarsuaq may represent the early signs of a northern distributional limit, and the decrease is again similar to that observed in capelin growth. Indeed, the latitudinal gradient in growth may be viewed as energy storage in terms of increased somatic mass, which serves as a positive fitness parameter in that the reproductive investment was found to be positively related to length (Fig. 7). However, the possibility of a temporal artifact needs to be considered, as energy density in Nuuk was shown to decline with almost 1 kJ g dw⁻¹ over a 1-month period. This needs to be confirmed with sampling on a finer temporal scale along the latitudinal gradient.

There was a clear general increase in energy density (kJ g dw⁻¹) with size in non-spawning capelin in three (Qaqortoq, Nuuk, and Uummannaq) of the four analyzed areas (Sisimiut excluded, Fig. 2). The reason for the inconsistency in the Qeqertarsuaq area, where only a slight increase in energy density with length was seen, is unknown. However, the analyzed size spectrum is smaller in this area, and the inclusion of smaller individuals may have resulted in an increase similar to that seen in other areas.

The positive relationship between size and energy density is similar to that shown in Alaska capelin (Anthony et al. 2000) as well as other pelagic species (Hislop et al. 1991). This length-related difference in nutritional value in interaction with similar latitudinal growth variation may have an important impact on higher trophic levels depending

on capelin (Lavigne et al. 1985; Falk and Durinck 1993; Nielsen and Andersen 2001). As the average length-at-age increases by more than 50% across the latitudinal gradient, changes in capelin growth conditions may have a large effect on the ecosystem (Carscadden et al. 2001) as energetic densities can be expected to change accordingly—further emphasized by the fact that a reduction in size reduces not only energy density but also energy intake, as capelin weight can be expected to decrease by 87% with a 50% length reduction (Hedeholm et al. 2010). Faced with climate change (Holland and Bitz 2003) and a partly temperature-controlled growth pattern (Gjøsæter and Loeng 1987; Hedeholm et al. 2010), such changes are likely to occur in Greenland waters (Huse and Ellingsen 2008) and they will affect energy flow (Carscadden et al. 2001) and probably species distribution (Drinkwater 2005).

Although less clear, there was also a length effect on energy density in male spawning capelin. Capelin spawning takes place in shallow waters (Friis-Rødel and Kannevorff 2002) forcing capelin into large easily accessible shoals during this period, and it is during this period that they are preyed heavily upon by cod, seabirds, whales, and seals. Hence, the latitudinal growth (Hedeholm et al. 2010) and energy density (this study) gradients present along the Greenland west coast indicate that increasing temperatures will increase both capelin size and energy density, providing better feeding conditions for many predators. This is, however, dependent on temperatures staying within the optimal range and food being sufficient to meet metabolic demand.

The energy density was similar to that of non-spawning capelin based on dry mass (mean \pm SD = 21.4 \pm 0.5 kJ g dw⁻¹), but differed significantly based on wet mass (mean \pm SD = 3.44 \pm 0.97 kJ g ww⁻¹) because of a significant difference in water content (Figs. 2 and 5). This leads to the conclusion that as spawning approaches, feeding is reduced (O'Driscoll et al. 2001) and tissue is broken down and progressively replaced by water, while remaining tissue maintains the same composition until metabolized. The decline in energy content with time in male spawning capelin is consistent with knowledge on capelin spawning behavior. Males stay on the spawning grounds for longer periods awaiting small schools of females (Vilhjálmsson 1994) and to support metabolism in this period of limited food intake (Templeman 1948; R. Hedeholm, pers. obs.), tissue must be metabolized.

In addition to the latitudinal and length-related patterns demonstrated here, a possible genetic component to variations in capelin life history traits may also be relevant. Genetic differences along the latitudinal gradient examined here have been suggested (Sørensen and Simonsen 1988) and clearly demonstrated throughout capelin-inhabited waters (Præbel et al. 2008). Such differences can affect capelin life history traits (Christiansen et al. 2008) as also

shown for similar species such as Atlantic silverside (*Menidia menidia*), and a genetic component to the patterns demonstrated here cannot be ruled out. However, present knowledge does not allow for an evaluation of such an effect, and further research into not only this aspect but also the overall genetic structure of Greenland capelin is encouraged as it would benefit this and other studies (Hedeholm et al. 2010).

In response to expected temperature changes in Greenland waters (Holland and Bitz 2003), the future distribution of capelin might well change (Huse and Ellingsen 2008) causing this key species to inhabit new areas. Capelin is found further north in other waters (i.e., The Barents Sea, Præbel et al. 2008) suggesting that it is not the potential length of the growing season that prevents capelin from extending its Greenland distribution further north. More likely, capelin distribution is limited by extensive sea ice cover. A late sea ice break up can prevent capelin from reaching spawning grounds in a given year, which could prove detrimental to a species with a large degree of semelparity (Friis-Rødel and Kannevorff 2002). Furthermore, as primary production in ice-covered regions is initiated by the increasing spring irradiance as well as the disappearance of sea ice (Madsen et al. 2008), a sea ice cover extending for much of the year reduces the growing season beyond that caused solely by a lack of sunlight. This could limit capelin distribution, as physiological limits of capelin feeding and assimilation may restrict them from obtaining sufficient energy in the short time period available. Feeding migrations as in other capelin populations (e.g., Vilhjálmsson 2002) could compensate for this, but Greenland capelin tends to be fairly non-migratory (Friis-Rødel and Kannevorff 2002). Hence, if increasing ocean temperatures limits the extent (spatial and temporal) of sea ice, the distribution of capelin will most likely be extended further north, which is also supported by the fact that capelin in Greenland show positive latitudinal responses in both growth (Hedeholm et al. 2010) and prey availability (Hedeholm et al., submitted manuscript).

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