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The importance of small pelagic fishes to the energy flow in marine ecosystems: the Greenlandic capelin

Ph.D. dissertation

by

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Preface and Acknowledgements

The present thesis “The importance of small pelagic fishes to the energy flow in marine ecosystems: the Greenlandic capelin” has been funded by the Aarhus Graduate School of Science (AGSoS) and made in collaboration with The Greenland Institute of Natural Resources, who have provided logistical support and funded sampling programs. Individual projects were financially supported by the COWI foundation, the OTICON foundation, 15. Juni foundation, Aalborg Zoo and the Augustinus fondation.
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Rasmus Berg Hedeholm
Århus, August 2010

Thesis structure

In this thesis, I will present my work on the importance of small pelagic fishes in marine eocsystems. The work has centred on the Greenlandic ecosystem and its primary pelagic species; capelin (*Mallotus villosus*). Capelin was chosen as it is a key species in the ecosystem and changes in its life history can propagate to other trophic levels. Furthermore, capelin in Greenlandic waters are relatively unstudied, inhabits a latitudinal gradient of 17 degrees and is commercially unexploited in this area making the results unbiased by the effects of fishery. Hence, conditions for studying the effects of temperature and spatial differences across the species distributional range are excellent.

First, I will introduce some direct and indirect effects of climate change, especially temperature, on marine ecosystems, the wasp-waist ecosystem concept and describe the importance pelagic organisms' play in structuring the energy flow in such ecosystems. This is followed by an introduction to capelin in general and its role in Greenland. The introductory text is concluded by summarizing the rationale of the study. Second, I will present the specific scientific issues to be addressed and the methods applied. This is followed by a summary of the major findings of the individual studies, a discussion of these and how they have added to the current knowledge of climate effects on wasp-waist ecosystems. The specific papers will be cited by number in accordance with the list given below and for further elaboration on methodological and statistical procedures as well as in depth discussion of the individual studies, I refer to the articles included at the back of the thesis. These are included in order corresponding to the introductory text and do not reflect their chronological order.

List of papers

Paper I: Feeding ecology of capelin (*Mallotus villous Müller) in West Greenlandic waters.*

R. Hedeholm, P. Grønkjær and S. Rysgaard

Submitted to Polar Biology

Paper II: Variation in size and growth of West Greenland capelin (Mallotus villosus) along latitudinal gradients.

R. Hedeholm, P. Grønkjær, A. Rosing-Asvid and S. Rysgaard

ICES Journal of Marine Science. doi:10.1093/icesjms/fsq024.

Paper III: Energetic content and fecundity of capelin (Mallotus villosus) along a 1500 km latitudinal gradient.

R. Hedeholm, P. Grønkjær and S. Rysgaard

Submitted to Marine Biology

Paper IV: Summer diet of inshore cod in West Greenland: importance of capelin.

R. Hedeholm, K.N. Mouritsen, J. Carl and P. Grønkjær

Prepared for submission to Journal of Marine Biology

Paper V: Intra-fjord variation in reproductive output in Atlantic cod (Gadus morhua).

R. Hedeholm, A. Retzel, S. Thomsen, K. Haidarz and K.T. Jensen

Prepared for submission to ICES journal of Marine Science

Paper VI: An Ecopath model for the Nuuk fjord, Greenland.

R. Hedeholm

Unfinished manuscript

Dansk resumé

I de fleste marine økosystemer ses et jævnt faldende antal af arter og individer med stigende trofisk niveau. Visse økosystemer er dog anderledes, idet et mellemliggende trofisk niveau domineres af en enkelt meget talrig art. Dette er typisk en planktivor fiskeart, som således er det primære forbindelsesled mellem de lavere trofiske niveauer og top-predatorerene. Grundet denne indsnævring i energiflowet kaldes sådanne arter for ”wasp-waist” (hvepsetalje) arter, og på grund af deres centrale placering har de afgørende betydning for energiflowet i deres respektive økosystemer. Således kan de gennem fødeindtag begrænse byttedyrsudbredelsen (top-down kontrol) og ligeledes begrænse fourageringsmulighederne for prædatorerne (bottom-up kontrol). På denne baggrund er wasp-waist arternes biologi og respons på miljøvariation yderst relevant når variation i produktion og energi omsætning skal forklares i sådanne økosystemer.

Klimatiske ændringer vil påvirke arter og marine økosystemer på mange direkte såvel som indirekte måder, hvilket gør det vanskeligt at kvantificere og forudsige effekten af ændringerne. På grund af deres centrale position og strukturerende rolle, er wasp-waist arterne oplagte udgangspunkter for at adressere potentielle biologiske konsekvenser af klimaændringer. Tilgangen til sådanne studier spænder fra kontrollerede laboratorieforsøg til *in situ* indsamlede prøver. Begge er forbundet med fordele og ulemper, men sidstnævnte tilgang har dog som forudsætning, at studieområdet er forbundet med naturligt forekommende klimatiske gradienter. Sådan en 1500 km gradient er til stede langs den Grønlandske kyst, hvor lodden langs hele gradienten er den dominerende wasp-waist art. Da lodden endvidere er uudnyttet i Grønland er fiskeriinducerede økologiske effekter minimale, og området er særligt velegnet til studier af det generelle energiflow i wasp-waist økosystemer, samt til at opnå en øget forståelse af hvilke effekter klimatiske ændringer vil have på energiflowet i lignende systemer.

I dette studie beskrives rummelig variation i udvalgte træk af loddens livshistorie, og de relateres til de potentielle klimatiske ændringer. Således beskrives loddens vækst ved otolith analyse, og der vises en klar vækstforøgelse med stigende breddegrad. Dette er sammenfaldende med stigende temperaturer, og tilsyneladende øges væksten årligt med 0,5 cm pr 1˚C temperaturstigning. En lignende breddegrads-relateret gradient vises for loddens fødebiologi, hvor det totale relative fødeindtag stiger med breddegrad og loddens diæt domineres i stigende grad af større og mere energetisk favorabelt bytte. Fælles for gradienterne i vækst og fødeindtag er dog, at der længst mod nord ses et fald, hvilket er sammenfaldende med et temperaturfald. Endvidere demonstreres det, at loddens energidensitet stiger med loddens størrelse, og desuden varierer med geografisk position og livsstadie (gydende/ikke-gydende). Sammenholdt

viser disse studier, at loddens biologi ændres kraftigt langs breddegradsgradienten, og man kan da forvente en stor respons på forestående klimatiske forandringer.

Ud over disse studier af loddens biologi, præsenteres to studier, som illustrerer loddens betydning som byttedyr. Hos torsk udgør lodden 70% af føden i sommerperioden i to Grønlandske fjorde, og det reproduktive output (kJ) er tilsyneladende større, når torsken har øget adgang til lodde som byttedyr. Da loddens størrelse, energiindhold og udbredelse kan forventes at ændres med temperaturforandringer, så indikerer dette, at sådanne ændringer kan have stor betydning for såvel lavere som højere trofiske niveauer. Loddens dominerende rolle underbygges endvidere af en samlende Ecopath model, som implementerer den nye viden præsenteret her i en model over Nuuk fjorden, hvor allerede eksisterende data ligeledes er indeholdt.

Dette arbejde understreger den dominerende rolle, som lodden har i det Grønlandske økosystem, hvilket kan tages som en proxy for den generelle betydning af wasp-waist arter. Endvidere påvises det, at klimatiske ændringer vil have en effekt på klassiske livshistorie træk såsom vækst og fødebiologi, men også på kvalitative aspekter i form af energiindhold, Disse resultater forudsiger store ændringer i energi flow wasp-waist økosystemer som følge af temperatur ændringer, og er et skridt imod den svære opgave det er, at kvantificere sådanne effekter.

English summary

In most marine ecosystems, there is a decline in number of species and individuals with increasing trophic level. Some ecosystems, however, differ and are dominated by very high abundance of a single species of intermediate trophic level. This is typically a planktivorous fish species that functions as the primary connection between lower trophic levels and top predators. Such species are called “wasp-waist species” due to the constriction of energy flow through their central position in the ecosystems. They are of vital importance to the energy flow in their respective ecosystems, restricting prey distribution through their consumption (top-down control) and also limiting predator foraging possibilities (bottom-up control). Based on this, wasp-waist species biology and response to environmental variation is integral to explaining variability in production and energy cycling in such ecosystems.

Climate change will affect species and ecosystems in multiple direct and indirect ways, making quantification and prediction of effects difficult. With their central position and structuring role in the ecosystem, the wasp-waist species present an obvious starting point to begin addressing the potential biological consequences of climate change. As such, there have been a number of studies implemented to address climate-related questions on such keystone species with approaches varying from controlled laboratory studies to *in situ* collected samples. All approaches have various advantages and disadvantages but a prerequisite to the latter is a study area associated with naturally occurring climatic gradients. Such a 1500 km gradient is present along the Greenlandic coast with capelin being the dominant wasp-waist species along the entire gradient. Furthermore, as capelin is unexploited in Greenland, the area is unencumbered by fisheries-induced ecological effects and particularly well-suited to studies concerning the natural energy flow in wasp-waist systems, as well as increasing knowledge on the possible effects of climate change on similar systems.

In this study, spatial variability of capelin life history parameters are described in relation to potential climate change. Capelin growth is estimated from analysis of otoliths and shown to increase with increasing latitude. This is coincident with increasing temperatures with a 0.5 cm increase in total length for a 1˚C temperature increase. Similarly, a latitudinal gradient was found for capelin feeding with increases in relative prey intake and a diet increasingly dominated by more energetically favourable prey moving north. An exception to this trend occurs in the most northerly part of the study area where there is a decline in temperature and corresponding declines in growth and prey intake gradients. Furthermore, capelin energy density is shown to increase with capelin size and also vary with geographical position and life stage (spawning/non-spawning). Jointly, these studies demonstrate that capelin biology changes drastically along the latitudinal gradient and a large response to eminent climatic change can be expected.

In addition to these studies on capelin biology, two studies that illustrate capelin importance as prey are presented. For cod, capelin constitutes 70% of the prey during the summer period in two Greenlandic fjords and there is an apparent increase in cod reproductive output with increased access to capelin prey. Thus, capelin size, energy content and distribution can be expected to change with expected climate change with dramatic implications to both low and high trophic levels. The dominant role of capelin is further supported a unifying Ecopath model for the Nuuk fjord, which implements the new knowledge presented here along with existing data.

The present work emphasizes the dominant role of capelin in the Greenlandic ecosystem and can be seen as a proxy for the general importance of wasp-waist species. Further, the work demonstrates the likely influence of climatic changes on classical life history traits such as growth and feeding ecology as well as qualitative aspects such as energy density. These results predicts large changes in energy flow of wasp-waist ecosystems following temperature changes and provide a step towards the difficult task of quantifying such effects.

Introduction

Climate changes are presently the focus of much of the scientific community and have seen an accelerating representation in the literature over the past decades since the first in Nature in 1910 (Lockyer, 1910). A simple search in the primary literature reveals an exponential increase in the number of publications addressing climate change (Fig. 1). This increase in scientific interest reflects the expected changes in both global air and ocean temperatures projected in climate models and the effect it will have on biological and oceanographic systems. The projected changes from climate models vary with modelling approach and the area in question (Fig. 2, Meehl *et al.*, 2007), but the majority of models project global air and ocean temperature rises in the order of 2-4˚C and 0.5-1˚C within a millennium, respectively (Meehl *et al.*, 2007) with differences caused by the greater heat capacity of water compared to air. These increases would be a further development of recent documented trends. Hence, ocean temperatures has increased by 0.31˚C in the top 300 meters of the water column since the 1950's (Levitus *et al.*, 2000) but changes have been documented as deep as 3000 meters (Barnett *et al.*, 2005). However, climatic changes will not be uniformly distributed. Hence, in the last 50 years a large part of the North Atlantic has warmed whereas waters in southern Greenland have cooled as a result of NAO fluctuations superimposed on large scale patterns (Fig. 3, Bindoff *et al.*, 2007). This serves to underline the complexity associated with predicting future changes, but that changes are eminent seems beyond doubt.

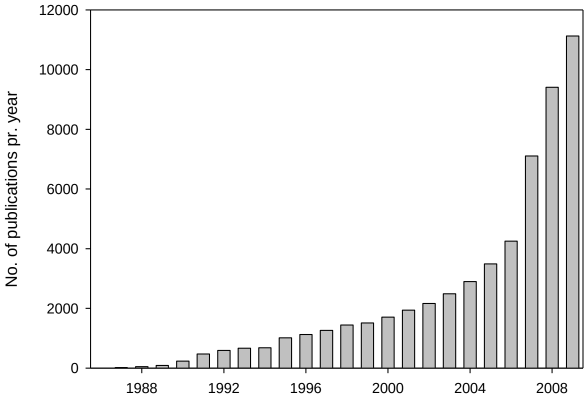

Figure 1: The number of publications found in a Web of Science search using a "Climate change" search term. The search was done on May 2nd 2010.

In marine systems, the expected temperature changes will have both direct and indirect effects on living organisms. Such effects include changes in productivity, distribution and feeding ecology of individual species and in turn, such changes can alter the overall energy flow of the ecosystem. In order to understand and predict these ecosystem changes the response of individual species to temperature changes must be understood, and subsequently integrated in a larger context.

Focusing on fish species, the production and energetic demands are linked to the direct temperature effect through it influence on key physiological rates such as metabolism (Sylvestre *et al.*, 2007), assimilation, gastric evacuation (Andersen, 2001) and gonad maturation (Hutchings and Myers, 1994),

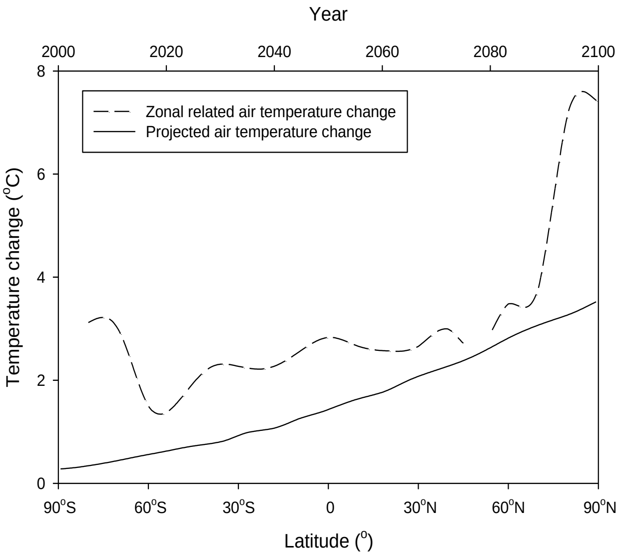

Figure 2: The solid line refers to the top axis and shows the projected changes in air temperature under the A2 IPCC model scenario (see reference) in the 21st century. The line represents the mean of the model ensemble.
The dashed line refers to the bottom axis and is the spatial resolution of the solid line at the end of the 21st century. Hence, it shows the projected change in temperature at all latitudes under the A2 IPCC model scenario. Based on data in Meehl et al. (2007).

which result in a positive temperature-growth relationship (Michalsen *et al.*, 1998). However, the increased metabolic demands imposed by temperature increases means that such positive effects are dependent on sufficient prey availability and furthermore, the temperature tolerance of individual species can entail worsening conditions in their southern distributional limit if the changes are not restricted to the positive phase of the temperature optimum curve (Fig. 4, Wootton, 1990). This was the case in Greenland cod (*Gadus ogac*) along the Greenlandic West coast in the relatively warm 1920's and 1930's, where a northerly distributional shift resulted in cod disappearance from South Greenland coincident with an increased abundance in the north (Nielsen, 1992 and references therein). The positive effects of temperature are apparent when comparing growth of Atlantic cod (*Gadus morhua*) throughout its North Atlantic distribution. There is a highly elevated growth in warmer (e.g. the Irish Sea) compared to the colder areas (e.g. Greenlandic waters) where a four year cod is five times heavier in the former and overall, temperature explains 90% of cod growth variation (Brander, 1995). Similar temperature effects are also evident within populations subject to yearly temperature fluctuations which has been shown both in larvae (Otterlei *et al.*, 1999) and adults (de Cárdenas, 1996).

Reproduction is naturally a highly fitness related trait and is subject to temperature dependent variation. Hence, gonad development is directly linked to temperature, with higher temperatures leading to earlier maturation on both large spatial scale (Drinkwater, 1999) and on a local scale with inter-annual temperature variation giving rise to delayed spawning in certain years. This is seen in Newfoundland capelin where peak spawning was delayed by two weeks over a period of 5-6 years following a colder period (Nakashima, 1996).

In addition to these very direct effects of temperature on both growth and reproduction as well as other metabolically dependent processes, the indirect effects are equally important although often less

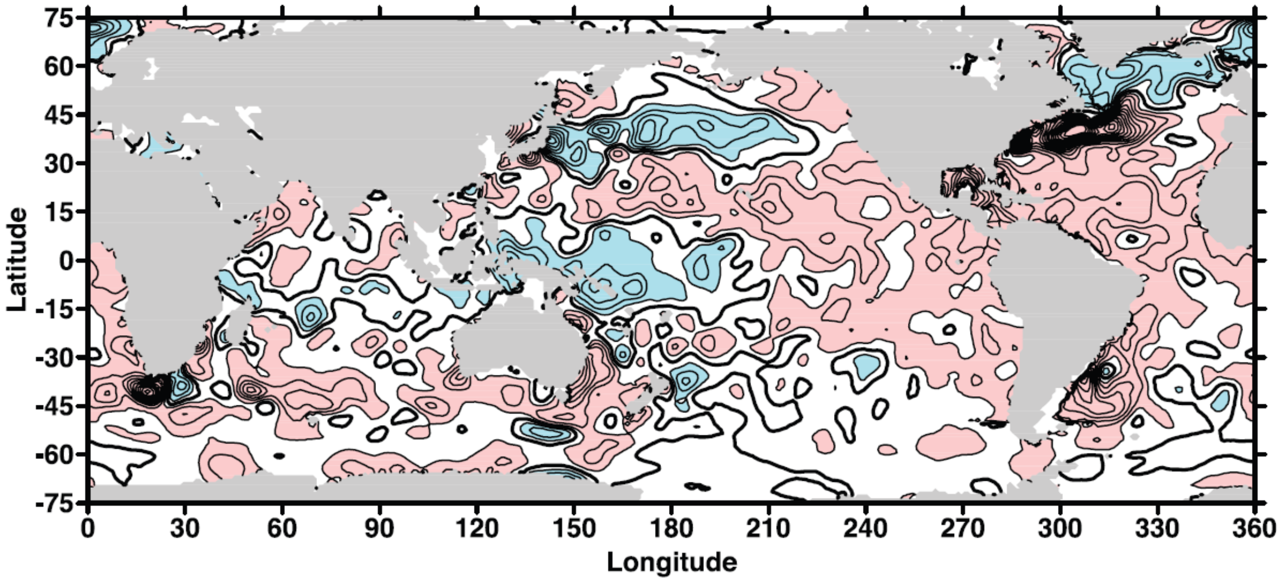

Figure 3: Linear trends of change in ocean heat content from 1955 to 2003. Red shading indicates heating equal to or greater than 0.25 W m^{-2} and blue shading indicates cooling equal to or less than -0.25 W m^{-2}. From "IPCC Fourth Assessment Report: Climate Change 2007, The Physical Science Basis" (Bindoff et al., 2007) and data from Levitus et al. (2005).

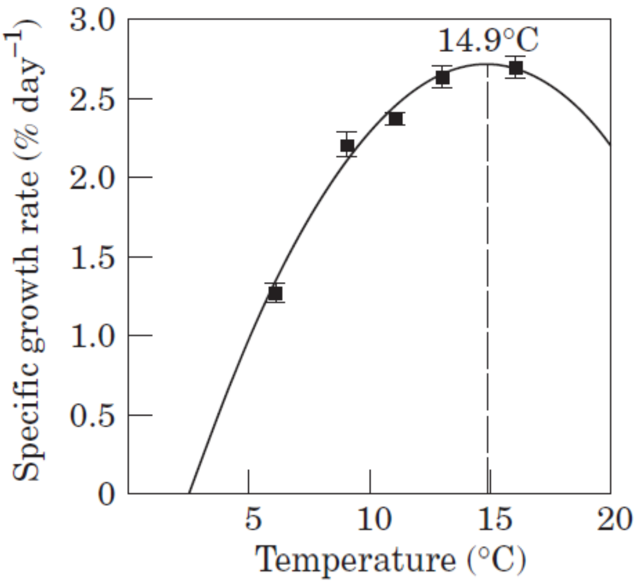

Figure 4: Changes in the specific growth rate of juvenile Atlantic halibut (Hippoglossus hippoglossus) with temperature. The line represents the best second order polynomial fit. The vertical dashed line marks the curve optimum. Modified from Jonassen et al. (1999).

predictable and quantifiable as they originate in many and complex interrelationships. For instance, in the arctic area around Disko Island, Greenland, at 69˚N the spring bloom is dependent on nutrients, sunlight and a stratified water column. The latter two become available when the winter ice breaks, causing sunlight to enter the water column, water heating and freshwater runoff. This in turn creates favourable growth conditions for phytoplankton causing an exponential growth in the following weeks (Heide-Jørgensen *et al.*, 2007). This bloom feeds the largely calanoid dominated zooplankton community (Nielsen and Hansen, 1995) ensuring transfer of converted solar energy to higher tropic levels. Warm (or windy) years may result in an early-ice break anomaly (Anonymous, 2005) and subsequently an early zooplankton bloom. If the

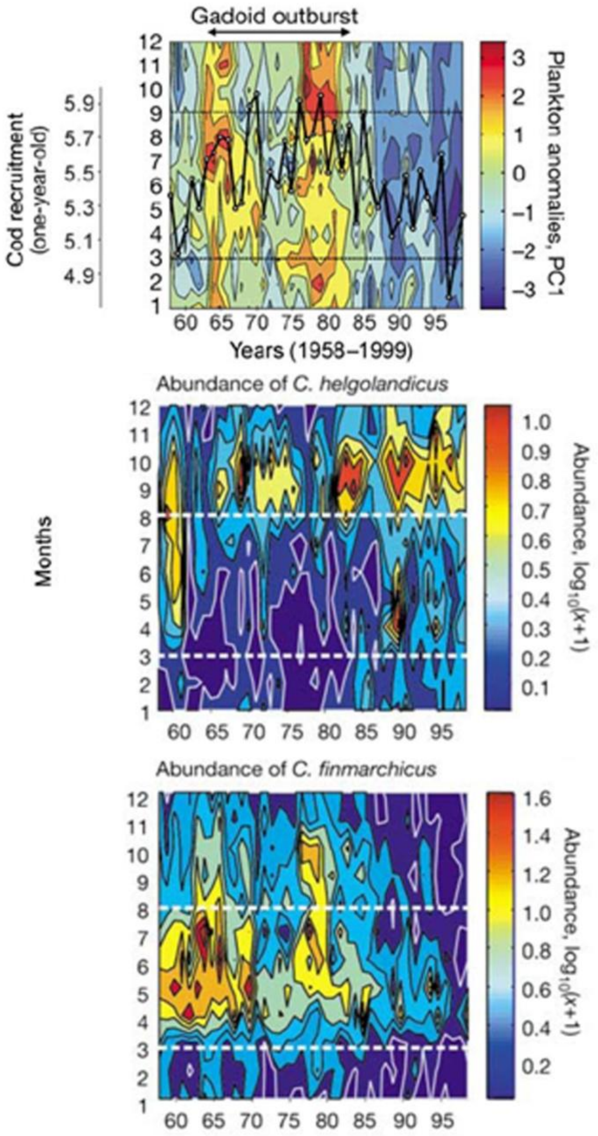

Figure 5: All graphs reefer to the North Sea in the period 1958 to 1999. Left: Shows the temporal development in cod recruitment (solid line) and the plankton anomalies (colored legend) as determined from principal component analysis with mean Calanus finmarchicus abundance, calanoid size and copepod abundance as the primary explanatory parameters. The dashed lines indicate the period of cod larvae occurrence in the North Sea and the gadiod outburst period is indicated over the graph.
Right: Mean abundance in each year of Calanus finmarchicus and Calanus helgolandicus (data from Continuous Plankton Recorder, CPR). The dashed lines indicate the period where cod larvae feed on calanoid prey. From Beaugrand et al. (2003).

shift is large enough this could result in a classical mismatch situation between fish larvae and their prey (Cushing, 1975) hampering recruitment in spite of otherwise optimal temperature conditions. Such a mismatch situation has been speculated to have caused a decline in Atlantic cod recruitment in the North Sea where alterations in inflow of water masses increased water temperatures in the 1980’s, and caused a shift in copepod dominance from *Calanus finmarchicus* to *Calanus helgolandicus* (Fig. 5, Beaugrand *et al.*, 2003). The latter is temporally displaced from peak cod larvae abundance, which causes starvation mortality in early larval stages thus hampering recruitment. Additionally, the increased metabolic demand of the larvae associated with warmer temperatures may prove a further disadvantage, as feeding possibilities must support the increase in demand. Hence, indirect negative effects annul the seemingly positive effect of a temperature increase.

One possible result of the integrated effect of these direct and indirect effects is a shift in the benthic-pelagic coupling. This entails that the supply of carbon to the benthic community is altered in either composition (i.e. fecal pellets or phytoplankton) or quantity. Hence, if temperature effects results in an increased pelagic biomass a larger proportion of the biomass is unavailable to the benthic community and the biomass and/or production is reduced. In the 1960’s, changes in the North Atlantic plankton community caused the counter clockwise migration pattern of Norwegian spring-spawning herring (*Clupea harengus*) to change (Alheit and Hagen, 1997; Loeng *et al.*, 2005). The feeding migration was in subsequent years restricted to more easterly waters around Svalbard and Northern Norway. Such a drastic change in behaviour of the dominating pelagic planktivorous species can have immense impact on the structure of an ecosystem. An abundant planktivorous species can potentially top-down control the zooplankton community (Hassel *et al.*, 1991; Paper VI) and the reduced grazing pressure associated with declining herring abundance could result in a decrease in benthic production, as an increase in zooplankton abundance would lower the supply of organic carbon to the benthic community through increased grazing intensity. Alternatively, the increased sedimentation rate of fecal pellets compared to phytoplankton (Taguchi, 1982; Riebesell, 1989) could increase benthic carbon supply if the slower sinking phytoplanktons are re-mineralised during sedimentation. Hence, knowledge on water depth, water column stability, the detritus food chain and temperature is needed to predict ecosystem response.

The possible impact of similar changes in the pelagic community has been documented in the North Bering Sea, where conditions is conducive for a tightly coupled benthic-pelagic system (e.g. cold and shallow) that supported a large benthic community as a result of limited grazing impact on the primary production around the ice edge (Lovvorn *et al.*, 2005). Climatic changes in the region, probably forced by the Arctic oscillation, caused a shift in the community with pelagic fishes becoming more abundant as a result of a warming trend (http://www.afsc.noaa.gov, Grebmeier *et al.*, 2006). The higher pelagic consumption resulted in a reduced oxygen uptake in the sediment, indicating reduced benthic metabolic activity and coincidently the benthic macro faunal biomass halved (Fig. 6). At the same time, on higher trophic levels, a spatial shift in primary feeding grounds was observed in walrus (*Odobenus rosmarus*) and grey whales (*Eschrichtius robustus*). Hence, in a warming scenario, the benthic-pelagic coupling was apparently weakened.

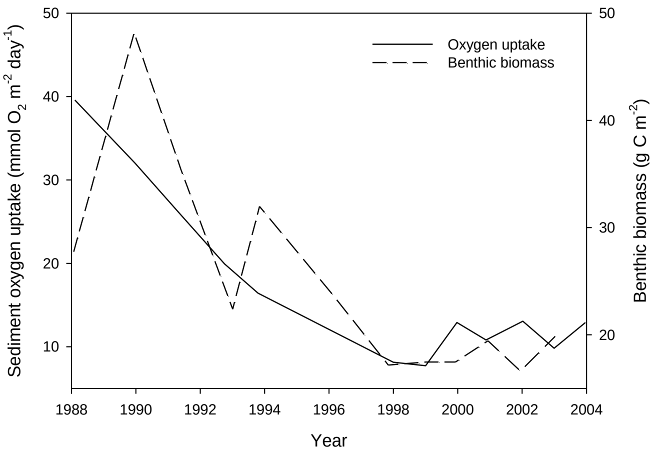

Figure 6: Based on data from 1988 to 2004 the solid line shows the average yearly oxygen uptake in the sediment (mmol O_2 m^{-2} day^{-1}, left axis) and the dashed line shows the benthic macrofaunal biomass (g C m^{-2}, right axis). Redone from data in Grebmeier et al. (2006).

A further example of the complexity of the response of an ecosystem undergoing climatic changes is seen in the Baltic Sea, which due to its semi-enclosed nature is a good place to study how interconnected the various species in a “small world” are, and how perturbations propagate in the system. In the last decades the Baltic has undergone changes in the physical environment due to a low frequency of major inflows from the North Sea, which has reduced salinity and oxygen content in the deeper waters, but under stable temperature conditions (Matthaus and Franck, 1992; Møller and Hansen, 1994; Möllmann *et al.*, 2000). This has favoured small pelagic species herring and sprat (*Sprattus sprattus*), which have increased in abundance reaching very high numbers in the mid 1990’s (Fig. 7, Casini *et al.*, 2006). Casini *et al*. (2006) suggest that this apparent clupeid success prompted increased interspecific competition which lead to a decrease in condition of both species (Fig 7.). In addition to the effect this may have on either species’ reproductive potential (Rideout *et al.*, 2000) such energetic deterioration can have effects on higher trophic levels through reduced energy intake *per capita* of apex predators (i.e. "The Junk Food Hypothesis", Anderson and Piatt, 1999). Such changes have been shown to be well correlated to reduced breeding success of common guillemots (*Uria aalge*) in different areas (Wanless *et al.*, 2005; Österblom *et al.*, 2006) and pigeon guillemot (*Cepphus columba*, Litzow *et al.*, 2002). These ecological observations have also been supported by experimental feeding trials in for instance steller sea lions (*Eumetopias jubatus*, Rosen and Trites, 2000), black-legged kittiwakes (*Rissa tridactyla*) and tufted puffins (*Fratercula cirrhata*, Romano *et al.*, 2006). This underlines the complexity of ecosystem response to changes not only in terms of presence and abundance, but also points to the need for qualitative considerations in describing and predicting the effect of climatic changes. Hence, climatic changes are to be expected in most world oceans and not least so in the North Atlantic. The effects on fishes and ecosystems will be direct as well as indirect. How these changes will alter species distributions, abundance, interactions and ecosystem energy flow is not easily predictable but already noticeable distributional shifts in marine fishes have been seen across species, areas and assemblages with an estimated migration rate of several kilometres pr. year in the current warming period (Perry *et al.*, 2005). Drinkwater (2005) attempted to predict the response of a single species by reviewing current knowledge, which is extensive, of temperature effects on Atlantic cod throughout the North Atlantic. This knowledge was used to

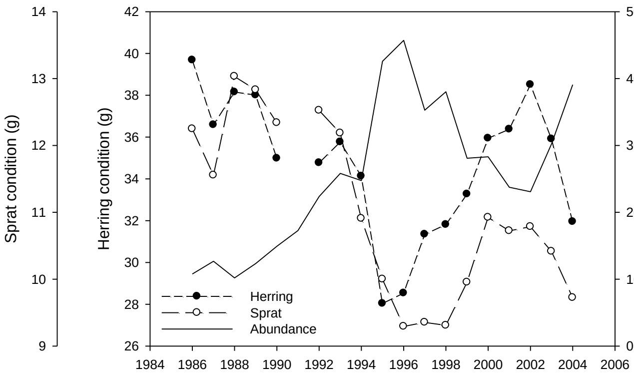

Figure 7: The individual points and associated broken curves reefer to herring (solid) and sprat (open) condition (left axes) from 1986 to 2004 in the Baltic Sea. The solid line reefers to joint clupeid abundance (right axis) in the same period. Redone from data in Casini et al. (2006).

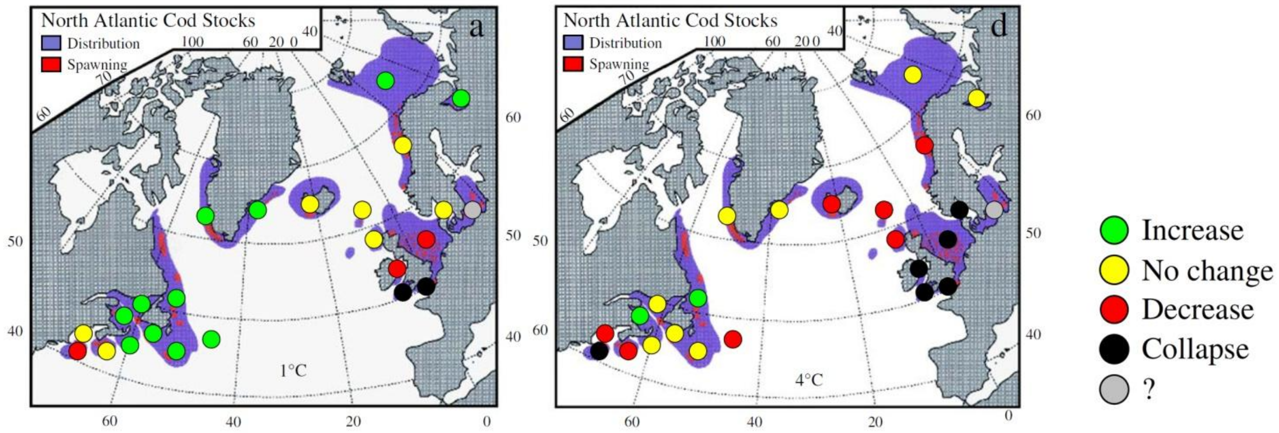

Figure 8: Shows the projected changes in cod abundance following a 1˚C and a 4˚C temperature increase, respectively. The colored dots indicate whether the changes following the temperature increase are positive or negative. Purple and red areas show current distribution and spawning locations, respectively. Modified from Drinkwater 2005.

project changes in abundance and distribution of cod under different climate scenarios (Fig. 8). It is clear that cod can be expected to extend its distribution northwards and supposedly at the same time disappearing from southern areas such as the British Isles because of ocean warming. However, even as cod is one of the most studied species, Drinkwater (2005) still makes these predictions without including the effect of fishing and also emphasizes: "*that future changes to cod will also depend on the changes to other parts of the ecosystem*" especially with regards to the important parameter of larval feeding possibilities, being crucial to ensure successful recruitment (Sundby, 2000). Adding to this statement, is the presence of cod in Danish waters during a warm period between 7000-3900 BC (Enghoff *et al.*, 2007) were cod should not have been present given their present day phenotypic response to high temperatures. Enghoff *et al*. (2007) point to genetic adaptation, migration and/or phenotypic plasticity as possible explanations, but also mention the effect present day fishery may have on these factors. Add to this some of the indirect effects mentioned here, it is clear that to be able to predict and understand the effects of climatic changes to fishes and ecosystems, extensive knowledge on not only fishes, but on all aspects of the ecosystem and the way in which they are related, is needed.

In the following, I will introduce wasp-waist systems in general, the study area and the approach applied in the present study.

Wasp-waist species and systems

Most marine ecosystems consist of a multitude of species from primary producers to top predators. This also includes from one to several pelagic fish species that often possess some shared characteristics that include schooling behaviour, planktivorous diet, great abundance, high mobility and short life cycles. Examples of such planktivorous pelagic fish can be found in all major water bodies and include anchovies, sardines, herring, sprat, menhaden, atlantic silverside, capelin and sandeels. Their distinct characteristics make these species very dynamic with a high production and capable of having a large impact on other trophic levels. Their mobility and high energetic need (because of their numbers and high growth rates) force them to find and subsequently exert a high predation pressure on the zooplankton community in order to sustain the population. This makes the pelagic fish the primary converters of planktonic energy resources to fish biomass. This also entails, that ecosystem stability and energy flow are very much affected by these species and any environmental changes that might influence their abundance, production, distribution and feeding ecology.

The most common structure of marine systems is one with great species diversity at the lowest trophic levels (primary producers) and a subsequent decrease in both species and abundance with increasing trophic level. This loss in diversity and biomass is often explained by an energy transfer efficiency of only 10% between trophic levels caused by respiratory losses, unassimilated consumed food and unconsumed food (Pauly and Christensen, 1995). However, in many highly productive marine ecosystems across all latitudes such as upwelling zones (e.g. South American coast) and shelf areas (e.g. West Greenland) across all latitudes the pattern differs. Here, an intermediate trophic level is dominated by one (or a few) pelagic species (Rice, 1995); usually small planktivorous fishes (Cury *et al.*, 2000). As these fish are the sole species on their trophic level, all available energy generated by the primary producers has to pass through them to become available to predators. Hence, the planktivorous fish become important both as predator (top-down control) and prey (bottom-up control) in the system and are often considered key stone species with a high number of linkages within the system. Such systems containing an intermediate, energy mediating, abundant species capable of having an influence on both lower and higher trophic levels (top-down and bottom-up from the middle) are referred to as wasp-waist systems, inspired by the crucial connecting link that both the pelagic species and the petiole in wasps constitute in their respective systems (Rice, 1995). Wasp-waist system can by systematically depicted as in Fig. 9 (right), where the waist species by virtue of their abundance and dominance of their intermediate trophic level ensures all transfer of energy from lower to higher trophic levels. This is of course an extreme case. Many of the higher predators will feed on levels below the waist species, at the very least in the juvenile stages as an ontogentic shift in diet is the general rule in predatory fishes (Wootton, 1990). Furthermore, larval stages of top predators are themselves subject to predation from many species (e.g. Köster and Möllmann, 2000).

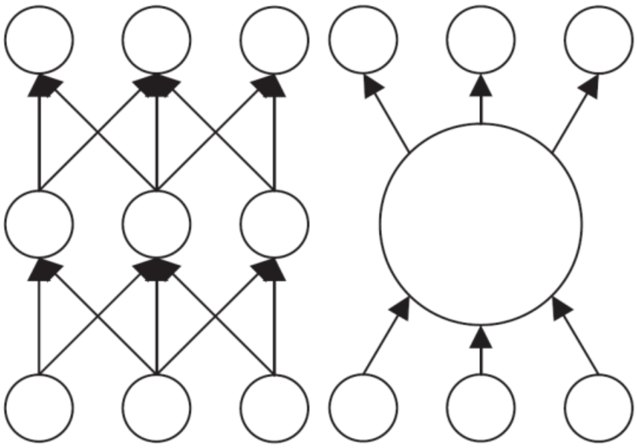

Figure 9: Two simplified food webs. Left: a food web with no dominating wasp-waist species connecting lower and higher trophic levels. Right: a food web with a single abundant wasp-waist species that transfer all energy from low to high trophic levels. Based on Jórdan (2005).

Due to their key position in the system, wasp-waist species expectedly have a large influence on other components of the system. This importance has been demonstrated theoretically by Jordán *et al.* (2005), who created ten hypothetical systems with varying degree of waistedness (i.e. more or less connections circumventing the waist species) and calculated the importance of each species to the rest of the system in all cases. They found that a higher waistedness was associated with higher system dependency on changes in the wasp-waist species. This seemingly introduces potential yearly cascadal effects into the system caused by the highly variable year-class strength of wasp-waist species. However, the stability of the system is ensured by a built in system redundancy, owing to the massive abundance of the wasp-waist species, which dampen external influences on the system (Jordán *et al.*, 2005). Naturally, decreasing abundances will over longer time periods have large effects as seen in Canadian waters, were the disappearance of capelin has been speculated to be the proximate cause of the continued depressed state of the cod population (Rose and O'Driscoll, 2002). The contrast to such an extremely waisted system is a system where the number of connecting nodes between species creates the same stability (Fig. 9, left). Here, the interdependency between species is low making no single species crucial and changes are diluted in the system by diet switching. The North Sea could serve as an example, with its multiple planktivorous species (i.e. sprat, herring, sandeel, Norway pout etc.) creating many energy flow pathways from bottom to top.

Reviewing wasp-waist systems across all oceans Bakun (2006) suggests that wasp-waist species possess four characteristics that together make them the hub of their respective ecosystems and explain the theoretical importance, which goes further than simply being a mediator of changes across trophic levels. In summary, these are

1. Complex life histories (e.g. short-lived, pelagic larvae). This makes the waist populations vulnerable to environmental fluctuations giving large inter-year variation.

2. The species dominate their trophic level which will make changes propagate to other trophic levels because no antagonistic change is seen in similar species on the same trophic level. Hence, bottom-up and top-down controls are realistic scenarios.
3. They are the lowest mobile trophic level. This enables wasp-waist species to follow prey items thus forcing changes in the spatial distribution of predators and trophic interactions of the system.
4. They can predate heavily on egg and larval stages of top predators forming a negative feedback loop in some systems that keep them abundant while suppressing that of piscivorous predators (i.e. the “predator pit”).

Wasp-waist species and their impact

To address possible effects of climate change mediated through the wasp-waist species on other trophic levels, the issue can be simplified by focusing on the one-to-one interactions between wasp-waist species predators (bottom-up) and prey (top-down).

Bottom-up effects

A species or trophic guild must have a controlling influence in higher trophic levels for bottom-up effects to be present. Such an importance of small pelagic fish as prey is well documented. For example, in Icelandic waters capelin is the main single prey item for Atlantic cod making up 50% of the prey, and in the capelin spawning season this number reaches 80-90% (Vilhjalmsson, 2002) similar to numbers also seen in Greenland (Paper IV). Similarly, in the Baltic Sea the main prey of cod is sprat and herring which together make up approximately 70% of yearly averaged cod diet (Harvey *et al.*, 2003; Österblom *et al.*, 2006). In seabirds, the importance of pilchard (*Sardinops ocellata*) and anchovy has been shown for cape cormorant (*Phalacrocorax capensis)* and jackass penguin (*Spheniscus demersus*) in South African waters (Crawford and Shelton, 1978) and marine mammals such as seals and whales also feed heavily on pelagic fish (Wathne *et al.*, 2000; Witteveen *et al.*, 2006).

Wasp waist species are short lived (generation time from 1-4 years) and hence, they respond quickly to biotic and abiotic changes giving large yearly variations in abundance. This was seen in Barents Sea capelin where a 12 fold increase in 1990 (0.23 to 3.18 mio. tonnes) was followed in 1993 by a severe reduction of 80% (3.93 to 0.84 mio. tonnes, Gjøsæter *et al.*, 1998). This large inter-year abundance variability in connection with the predator’s dependency of one or a few prey species seemingly renders predators highly vulnerable to such fluctuations**.** However, these changes do not necessarily propagate to higher trophic levels. The system redundancy caused by waist species abundance mentioned above is one aspect of this, but a predator lag-phase is also present due to the longer generation times generally seen at the higher predatory trophic levels. This allows for a buffer effect of wasp-waist communities where the effect of oscillations of waist species abundance are dampened (Bakun, 2006). Cury *et al.* (2000) mention two examples of such delayed effects where predatory fish populations suffer severe declines a few years after the collapse of their main pelagic fish prey, illustrating both the bottom-up effect and the inherent lag-phase of the predator populations. Hence, the snoek (*Thyrsites atun*) and chub mackerel (*Scomber australasicus*) collapsed two and four years after their prey, chilean anchoveta (*Engraulis ringens*) and round sardinella (*Sardinella aurita*), respectively, suffered severe population declines (see Cury 2000 for other examples). However, had the pelagic wasp-waist species rebounded within a couple of years the predator population would probably have avoided the collapse. Supporting this is the simple fact that predator population continue to survive without extreme population fluctuations in spite of ongoing prey availability variation.

Top-down effects

That planktivorous fish prey on zooplankton does not automatically entail top-down control. In order for top-down control to become an issue, the planktivorous fish must exert a predation pressure that limits the abundance of zooplankton, creating an - for now disregarding the many other variables that have a considerable influence on zooplankton abundance – inverse relationship between planktivorous fish and zooplankton abundance. If the zooplankton is present in abundance, the planktivorous fish become satiated and no such relationship exists.

That planktivorous fish do indeed consume a lot of energy and thus prey heavily on zooplankton has been shown among others by Jarre-Teichmann and Christensen (1998) who estimated that in four major upwelling systems 15-30% of the primary production is required (mediated by zooplankton) to support the pelagic fish production. Similarly, Arrhenius (1997) estimated that herring consumed 30-60% of all zooplankton in the Baltic and Arrhenius and Hanson (1993) showed through bioenergetic modelling of the same system that together herring and sprat were capable of consuming as much as 80% of the zooplankton. However, they also showed that the model was sensitive to small perturbations (i.e. 5%) in for instance larval fish survival, which is common. For the Baltic, it has also been suggested that intense predation can cause behavioural changes in the zooplankton community such as intensified vertical migrations (Arrhenius, 1997) suggesting another aspect of the top-down control mechanism.

Clear top-down causal relationships are not common in the literature. This can be due to rarity of the phenomenon, but can also be explained by the extensive sampling needed to test hypotheses and the many other variables influencing species abundance. These include oceanographic variation, fisheries, density dependent processes, spatial and temporal overlap (Möllmann and Köster, 2002) explaining why clear cascadal-like relationships are not the general rule. However, there are some studies showing very

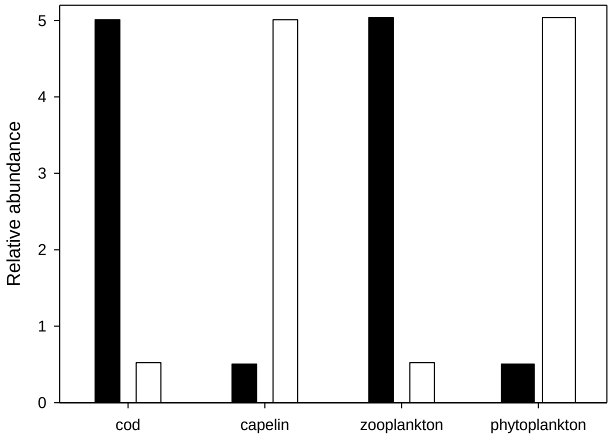

Figure 10: Relative changes in abundance of cod, capelin, zooplankton and phytoplankton. White bars represents the period prior to the 1990's and black bars during the 1990's. Redone from Carscadden (2001).

convincing data. In the Canadian West Atlantic, environmental changes induced a southwards shift in capelin distribution and at the same time, cod (and other capelin predators) collapsed in the area releasing capelin from its main predators. This resulted in an increase in capelin abundance which supposedly brought with it a top-down control on zooplankton and subsequently phytoplankton abundance in reciprocal relationships consistent with a trophic cascade (Fig. 10, Pace *et al.*, 1999; Carscadden *et al.*, 2001). Similarly, Shiomoto *et al*. (1997) demonstrated that the primary productivity in the Northern Pacific fluctuated on a yearly basis in spite of environmental conditions being similar between years. The phytoplankton fluctuations were mirrored in zooplankton but with one year temporal displacement suggesting a causal relationship (Fig. 11). This apparent top-down regulation was supposedly caused by pink salmon (*Oncorhynchus gorbuscha*) which accordingly displayed a pattern of inverse abundance with macrozooplankton. This was most clear towards the end of the study period (1990-1994) where salmon catch-per-unit-effort (CPUE) indicated a sufficiently large population capable of predating heavily upon the macrozooplankton community. Both these studies underline, that top-down regulation is only a valid notion when prey abundances are indeed limited by predation, and not only if a prey is important to one/more predators. Thus, it appears that a top-down effect of zooplanktivorous fishes is present across oceans although subject to inter-year and strength variability (Cury *et al.*, 2000).

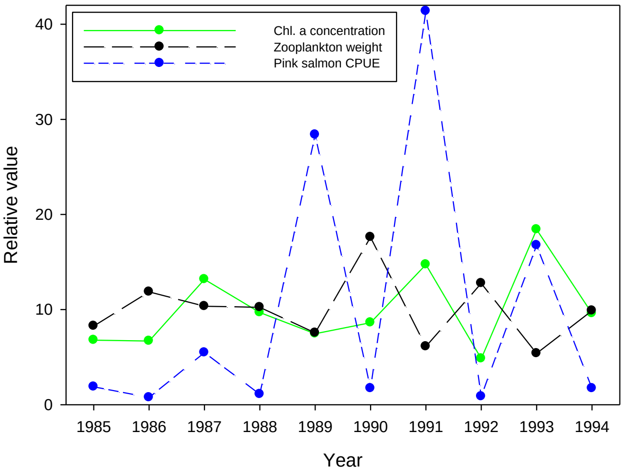

Figure 11: The relative changes in surface chlorophyll a concentration (green line), macro zooplankton mean weight (black line) and Pink salmon catch per unit effort (CPUE, blue line) from 1985 to 1994 in the North Pacific (approximately 50˚N). Based on data in Shiomoto et al. (1997).

The study area

Greenland has an unbroken north-south oriented coastline extending 2300 km from 60˚N to 78˚N, which is naturally associated with gradients of ecological relevance in a climate related study. Due to the latitude and extent of the gradient, there is a large difference in solar irradiance from south to north as the period with sunlight and ice-free conditions becomes progressively shorter moving north thereby limiting the growing season (Sejr *et al.*, 2009). Because the spring phytoplankton bloom is dependent on the sunlight and the stratification it initiates (Hansen *et al.*, 2003) this gradient creates similar temporal differences in the start of spring production and causes a temporal displacement of processes dependent on the bloom. Such timely displacement is, however, not restricted to the lowest trophic levels. For instance, in North America the result of a shorter growing season is reflected in the spawning behaviour of Atlantic silverside (*Menidia menidia*) which is delayed by two months covering a 14˚ latitudinal gradient and also shortened significantly (Fig. 12). Similarly, capelin in Greenland shows the same progressing spawning pattern over a similar distance although less well described (Friis-Rødel and Kanneworff, 2002). Another parameter that also varies with latitude, and often covaries with length of the growth season, is temperature. Indeed, this covariance is one of the main problems when studying certain latitudinal related patterns, as it is difficult to separate their joint effects on for instance growth patterns or onset of spawning. The usual pattern is that

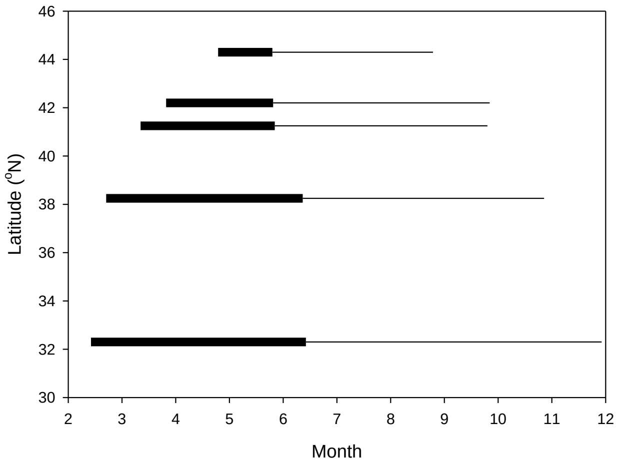

Figure 12: The entire lengths of the lines represent the length of the growth season at various latitudes along the east coast of North America. The growth season is defined as the period from the onset of Atlantic silverside spawning to the start of winter migration or when temperatures dropped below 12˚C. The thick segment of the lines is the length of the spawning season as determined from reports of ripe adults. Based on Conover and Present (1990).

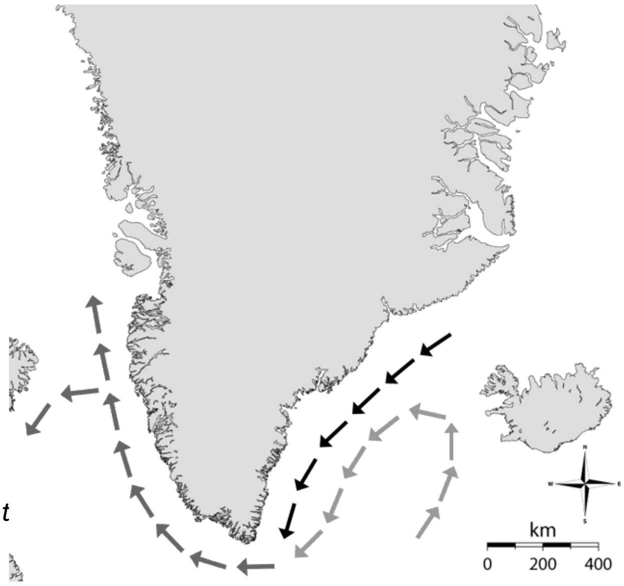

Figure 13: The southern part of Greenland with arrows indicating dominating currents. The darkest arrows flowing from the north is the cold low-saline water of polar origin and the light grey arrows indicate high saline warmer water from the south. These mix along the West coast of Greenland (dark grey arrows).

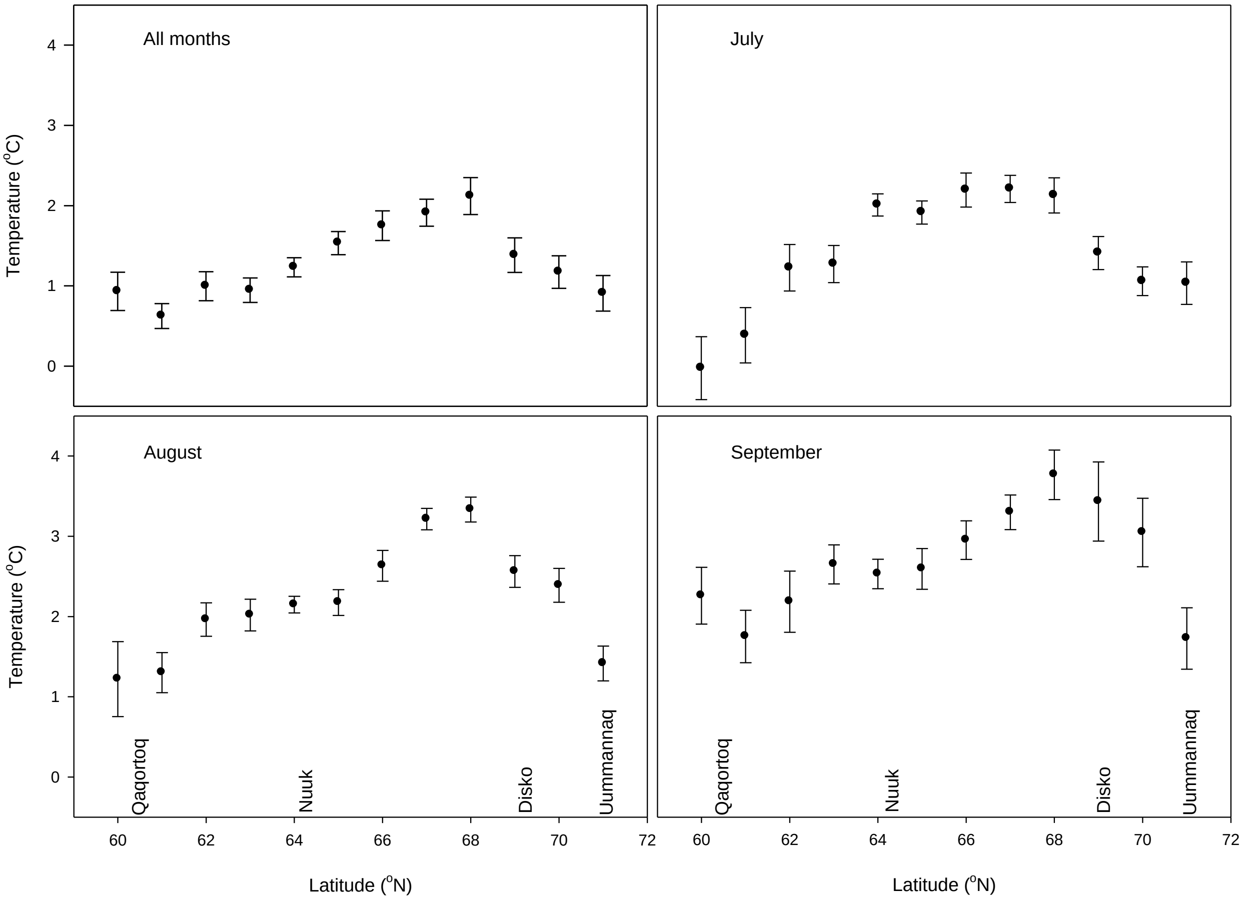

Figure 14: Average temperatures from 20-50 m averaged from 1908-2007 for West Greenland shelf waters (60˚N-73˚N and 44˚W-57˚W). Top left: data from all months and years. Top right: data for July. Bottom left: data for August. Bottom right: data for September. Error bars represent standard error based on the mean values of all years at given latitudes. The areas where capelin were sampled for several of the included studies are noted at their respective latitude. Based on data from the ICES database.

of lower temperatures at higher latitudes. This may be true for air temperatures, but the pattern on the West Greenland shelf and near-coastal waters is more complex. The water masses in this area are a mix of two bodies of water (Fig. 13). From the north, flowing along the East coast of Greenland is a cold, low salinity current. From the south a small part of the Gulf Stream, the Irminger current, flows south of Iceland. This water is warmer and has a higher salinity (Ribergaard *et al.*, 2008). Hence, when the two water masses flow up the West coast of Greenland, the warm water is situated below the cold water. The water masses gradually mix causing a heating of the surface water moving north. Around Disko Island at 69˚N, the current has weakened and it breaks off into the Davis Strait causing a gradual cooling of the surface water further north. This is the case both when considering the yearly average, but even more pronounced in the summer months, which is the primary growth season (Fig. 14). The growth pattern of various species in Greenlandic waters reflects these spatial differences in temperature regime. Hence, benthic organisms such as Greenland halibut (*Reinhardtius hippoglossoides*, Sünksen, 2009) and sea urchin (*Strongylocentrotus droebachiensis*, Blicher *et al.*, 2007) show a decreased growth rate with latitude in accordance with Bergmann's rule (Lindsey, 1966) as ambient bottom temperatures in both cases display the expected pattern of a negative latitudinal relationship. Contrastingly, capelin, a pelagic species, displays the opposite pattern of increased growth with latitude consistent with the warming surface waters (Paper II).

Due to the extensive unbroken north-south gradient, the expected impact of climate change in the arctic and sub-arctic region and the many processes at all trophic levels that will be greatly affected by an altered climate, Greenland offers a perfect platform to study the possible effects of climate change. This is both in terms of local change where basic life history parameters such as spawning, growth rate, metabolism and maturity can be expected to change for a number of organisms, but also on a larger scale where the distributional pattern, spawning areas, community composition, spring bloom initiation, freshwater inflow and benthic-pelagic coupling can be expected to change affecting the ecosystem energy flow. Many aspects of the Greenlandic ecosystem have not been studied, although recent years have seen initiatives on especially lower trophic levels including monthly monitoring programs (Jensen and Rasch, 2008). However, much research on all ecosystem levels is still needed to understand interrelationships and predict upcoming changes. Recognizing logistic, economical and timely limitations this leaves the question of which part of the ecosystem to study to progress ecosystem understanding the furthest.

In highly connected food webs (Dunne *et al.*, 2002) the obvious point of interest is the central part of this food web as changes here would most directly affect the highest number of other species through top-down and bottom-up processes. As for the arctic region in general the Greenlandic ecosystem is dominated by relatively few species (Roy *et al.*, 1998; Allen *et al.*, 2002). Additionally, the Greenlandic ecosystem displays typical wasp-waist system characteristics, with capelin functioning as the key species (Rice, 1995). Hence, to increase knowledge on sub-arctic ecosystems under climatic influence and wasp-waist systems in general, this study has focused on the Greenlandic capelin as it serves as the natural point of interest and any climatic changes imposed on this key species could have cascading effects on the ecosystem through top-down and/or bottom up processes.

Capelin biology

Many good reviews have been written on capelin biology, especially Icelandic, Barents Sea and Canadian stocks (Gjøsæter, 1998; Carscadden *et al.*, 2001; Vilhjalmsson, 2002), and only a brief summary is given here.

Capelin is a small silvery member of the Osmeridae family with circumpolar distribution (Fig. 15). It reaches different sizes at different locations but has a maximum size of 25 cm (TL, Fishbase 2008) with the males growing the fastest but not reaching the same age as the females. Capelin has been fished in Icelandic, Canadian and Norwegian waters with yearly catches occasionally exceeding 2 mio. tonnes (FAO - Fisheries and Aquaculture Information and Statistics Service) making the species commercially important in some fisheries. However, the largest fishery, the Icelandic, has in the last decade been reduced to one tenth of previous catches and current total allowable catch is recommended at 0 tonnes due failing recruitment (Anonymous, 2010).

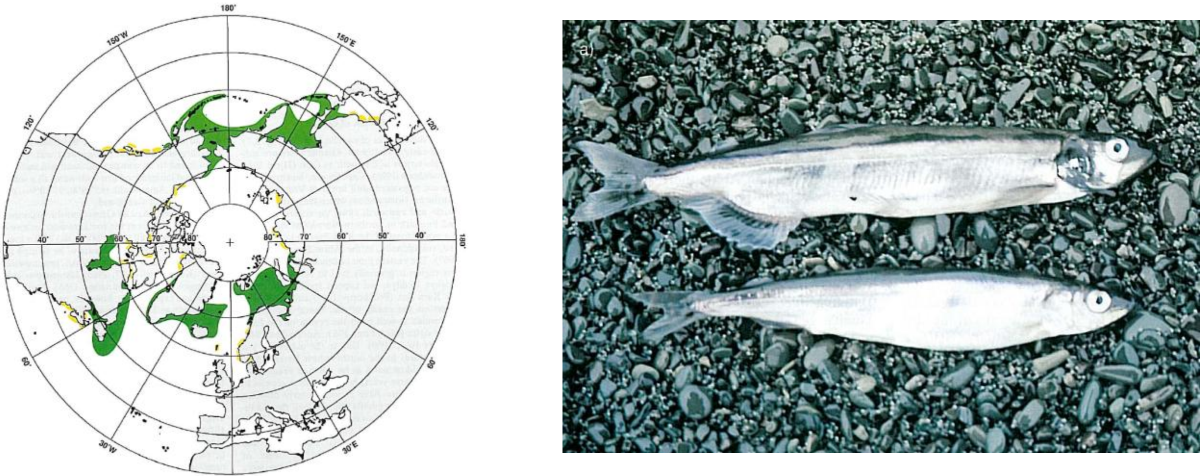

Figure 15: Left: The distributional range of capelin. Green indicates common presence while yellow is rare occurrences (Vilhjálmsson, 1994). Right: male (top) and female (below) capelin with clear sexual differences in the spawning season.

Spawning

Capelin spawning occurs during the summer months and usually takes place at a few meters depth (sometimes on the beach) but demersal spawning at more than 50 meters is also seen (Kanneworff, 1967; Vilhjálmsson, 1994; Nakashima and Wheeler, 2002). Spawning events are triggered by a multitude of environmental factors (grain size, beach orientation, tide, waves, lunar cycle etc.) but their relative importance is poorly understood although temperatures from 2-10˚C seems to be preferred (Vilhjálmsson, 1994; Therriault *et al.*, 1996). Prior to spawning a sexual dimorphism develops (Fig. 15), with male pelvic, anal and pectoral fins becoming enlarged and two ridges of enlarged scales form just above the lateral line and ventrally. These function as “holders” of the female during spawning events as the male(s) lie on either side of the female fertilizing the eggs. Fecundity is 6000-12000 and the eggs are 0.5mm (Huse and Gjøsæter, 1997; Tereshchenko, 2002, Paper III) with an incubation time of approximately 120 degree days (Gjøsæter, 1998). Spawning capelin are usually 3-5 year old with the biggest fish in each cohort spawning first (Kanneworff, 1967; Vandeperre and Methven, 2007). There has been some debate over the fate of spent individuals. That males experience very high post-spawning mortality seems to be accepted (Vilhjálmsson, 1994; Friis-Rødel and Kanneworff, 2002; Christiansen *et al.*, 2008) although Nakashima (1992) found through tagging that some spawning males returned the next year. Females are supposedly iteroparous and may survive spawning but it is not known to what extent (Kleist, 1988; Vilhjálmsson, 1994; Flynn *et al.*, 2001). Estimates range from survival rates of 5-50% and in some cases functionally 0% as predation on spent females is high. Theoretically, the most profitable strategy (semelparity vs. iteroparity) is dependent on mortality pattern in the environment. Hence, high adult mortality favours semelparity while high/variable juvenile mortality is an incentive for iteroparity (Orzack and Tuljapurkar, 1989; Christiansen *et al.*, 2008). Based on these assumptions and on knowledge on capelin life history, Huse (1998) showed through modelling that such a sex-specific life strategy theoretically maximizes reproductive output in capelin which is also consistent with laboratory studies (Christiansen *et al.*, 2008).

Feeding

Capelin are planktivorous with 0-group capelin feeding mainly on copepodites, copepod eggs, phytoplankton, small euphausiids and other small prey items (Pedersen and Fossheim, 2008) that are probably chosen based on size appropriateness (Gjøsæter, 1998). The diet of older capelin is dominated by three main food groups: copepods (mainly *Calanus*), euphausiids (krill) and amphipods in order of importance and it appears that copepods are dominant at the smaller sizes while an increase in capelin size is followed by an increase in krill consumption (Huse and Toresen, 1996; O'Driscoll *et al.*, 2001; Orlova *et al.*, 2002; Paper I). Occasionally, eggs and fish larvae (including cannibalism) are consumed (Gerasimova, 1994).

In some areas the entire population undertake feeding migrations, for instance in Iceland where feeding takes place north of Iceland and is followed by a spawning migration to the south (Vilhjalmsson, 2002). The same is seen in Canadian (Nakashima, 1992; O'Driscoll *et al.*, 2001) and Barents sea populations (Gjøsæter, 1998). In Greenland the populations in separate fjords are believed to stay in or very close to the fjords for feeding as well as spawning (Friis-Rødel and Kanneworff, 2002) but capelin are caught in surveys on the near coastal banks (K. Sünksen, Greenland Institute of Natural Resources, Pers. comm.) suggesting at least some migration and feeding outside the fjord.

Predation

Capelin is an important prey to many species and must be considered good quality prey due to its high energy content of approximately 21 kJ g^{-1} dry weight compared to for instance pollock and cod which are much leaner (approximately 16 kJ g^{-1} dry weight; Van Pelt *et al.*, 1997; Paper III). It is the main prey of many commercially important fish (e.g. cod, salmon), marine mammals (e.g. seals, whales) and seabirds (e.g. common murre). Especially the cod-capelin interaction has received much attention, as capelin is the main prey item of commercially important cod in many waters (Vilhjálmsson, 1994; Bogstad and Gjøsaeter, 2001; Carscadden *et al.*, 2001; Paper IV). Hence, Vilhjálmsson (2002) estimated the total annual consumption of all capelin predators (13 species in total of fish, whales and birds) in Icelandic waters to be 2-3.8 mio. tonnes (Vilhjálmsson 2002 and references therein) roughly equivalent to one third of the population.

Capelin in Greenland

Even though capelin has been studied for many years from different perspectives not many studies focus on the Greenlandic capelin. Friis-Rødel and Kanneworff (2002) reviewed the available literature and since then, besides the work presented here, only one article including Greenlandic capelin has been published concerning the evolutionary origin of capelin populations (Dodson *et al.*, 2007). The conclusions made by Friis-Rødel and Kanneworff (2002) are however often based on assumptions and circumstantial evidence. The best-documented conclusions concern distribution, size-at-age and spawning behaviour along the Greenlandic coast. Capelin are distributed from Cape Farewell in the south (60˚N) to Umanak (73˚N) and Illorqqortoormiut (70˚N) in the north on the west and east coast respectively with the northern limit shifting with altering temperatures (Hansen, 1943; Friis-Rødel and Kanneworff, 2002). Maximum age and length increase towards the north and the females are the larger sex at a given age although very little is known about the actual growth pattern (Friis-Rødel and Kanneworff, 2002, Paper II)

Known differences between areas such as maximum length, progressive spawning and well separated fjord systems suggests that individual fjord systems may contain separate stocks. This hypothesis is supported by Sørensen and Simonsen (1988) who used proteins and gel electrophoresis to demonstrate differences among three areas on the Greenlandic west coast. However, the number of stocks, their distribution and total stock size is unknown although a few local biomass estimates exists (Jákupsstovu and Røttingen, 1975; Bergstrøm and Vilhjálmsson, 2006). The feeding behaviour of capelin in Greenlandic waters has only been briefly and superficially addressed in two master theses (Kanneworff, 1967; Kleist, 1988). Sampling has been sporadic since 1906, no new research on the ecological role of Greenlandic capelin has been done since 1988 and since then sampling has been non-existent apart from capelin sampled on the first day of spawning in the Nuuk fjord system.

Research approach and study focus

In the present study, the overall aim is to provide knowledge on the role of small pelagic fishes in wasp-waist ecosystems, with special focus on the role they play in energy transfer and expected changes following a temperature change. Recognizing that an entire ecosystem is not explainable from a single study or species, the challenge is to select the approach most likely to reveal most information about the system and any species of particular interest. The present work has been conducted from a "changing climate" perspective and possible approaches span from controlled experimental designs with a minimum of realism (Conover and Present, 1990) to the inverse situation of realistic but uncontrolled *in situ* sampling (Sünksen, 2009) and theoretical (speculative) modelling of possible changes (Drinkwater, 2005). The *in situ* sampling offers data that represent the actual situation in space or time, but also offers the challenge of suggesting a clear causal relationship when faced with many influential parameters, which may not even have been recorded. Ideally, the laboratory approach should be used to validate or test specific hypotheses generated by the more holistic ecosystem approach (Conover and Present, 1990) but the appropriate approach is naturally dependent on the study area and issues addressed.

I have chosen to focus on capelin in the Greenlandic ecosystem as a model species using a field-based and ecosystem approach, as vital capelin parameters are lacking in this area. Capelin distribution along an unbroken latitudinal gradient in West Greenlandic waters offers a unique chance to study a wasp-waist system with little impact from fishing and with a natural climate gradient covering the entire distributional range of capelin. In order to describe and to some extent quantify the importance of capelin, knowledge on consumption rates, production, biomass, predator-prey relationships, spawning behaviour and how these parameters are related to temperature is needed. Although many of these temperature dependent processes are also well suited for laboratory testing, the lack of basic knowledge and logistical challenges associated with obtaining live specimens (eggs, larvae and adults) resulted in an ecosystem based approach and subsequently *in situ* sampling procedures. In some cases, logistical limitations further dictated sampling procedures and consequently the studies focused mainly on capelin older than two years-of-age.

Substantial knowledge is needed to fully understand the role of capelin within the ecosystem, and the present work only allows for certain aspects of capelin ecology to be addressed. First, I have chosen to explore the naturally occurring latitudinal gradient concerning fundamental capelin traits, namely feeding (Paper I) and growth (Paper II) as these are essential in quantifying capelin importance and are often temperature dependent. Second, I explore the effect of latitude on capelin energy density and fecundity, which will affect capelin quality as prey and its reproductive potential (Paper III). In addition to exploring the latitudinal gradient, possible bottom-up effects are addressed based on samples restricted to the Nuuk fjord system as it is both historically and presently the best-studied and most logistically accessible area. This includes a cod feeding study (Paper IV) and a study on the reproductive output of cod (Paper V). Lastly, all generated data is put into an ecosystem perspective through their implementation in an Ecopath model of the Nuuk fjord. This summarizes current knowledge from both this study and elsewhere, sheds light on the role of capelin (the overall study focus) and importantly identifies areas of future research.

In the following, I will present the individual studies. This includes a short rationale behind each study and a summarization of the methodological procedures applied. The papers referring to the individual studies are mentioned initially at each paragraph and for further elaboration, they should be consulted. The main findings of each study are presented and discussed in later paragraphs.

Individual studies and methods

Capelin feeding

R. Hedeholm, P. Grønkjær and S. Rysgaard: Feeding ecology of capelin (*Mallotus villous* Müller) in West Greenlandic waters. Submitted to Polar Biology.

As capelin function as the prime converter of planktivorous energy to higher trophic levels, knowledge on capelin feeding behaviour is essential in quantifying its role in the ecosystem. Capelin in other waters are dependent on various zooplankton groups such as copepods and krill (e.g. Huse and Toresen, 1996; O'Driscoll *et al.*, 2001) and since these groups have been known to react quickly and noticeably to climatic changes (e.g. Richardson, 2008) effects may propagate to higher trophic levels. Such effects may arise from temporal mismatch between fish larvae and their preferred prey (Cushing, 1975) caused by changed zooplankton community, which was seen for North Sea cod larvae as mentioned earlier (Fig. 5, Beaugrand *et al.*, 2003). In addition to such direct effects of missing prey, zooplankton changes may indirectly alter conditions for capelin through a reduced energy intake. Hence, if ocean warming continues along the Greenlandic coast colder water adapted copepod species such as *Calanus hyperboreus* and *Calanus glacialis* will expectedly move northwards and be replaced by smaller warmer adapted species such as *Calanus finmarchicus*. These are not only smaller, but also contain relatively less energy (R. Hedeholm, unpublished data, Swalethorp *et al.*, unpublished manuscript). This can lead to leaner capelin which will affect the many predators depending on capelin through a reduced energy intake (Vilhjalmsson, 2002; Romano *et al.*, 2006) or capelin growth will decline as a result of reduced energy intake (Gjøsæter *et al.*, 2002). In addition to being the first quantification of Greenlandic capelin feeding, a feeding study will also serve as an initial step in quantifying the importance of capelin feeding in this area , and the possible top-down controlling potential of the species; especially so when viewed in a larger context (Paper VI).

Capelin were sampled during the main summer feeding period throughout as much of the distributional range as possible extending from 60˚N to 72˚N. Only fish from the West coast were used as samples from the East coast might be confounded with Icelandic capelin (Vilhjalmsson, 2002). Although classical stomach analyses provide great detail on prey composition they are temporally limited, providing only a snapshot of feeding behaviour. To ensure a more integrated picture of feeding behaviour stable isotope analysis was also done on capelin muscle tissue (Post, 2002). This allowed for a general description of feeding including geographical and length related differences, and the isotopic analyses additionally led to speculation regarding progressive changes in the biologically available nitrogen along the latitudinal gradient. To further explore this notion, isotopic analyses were also preformed on krill (*Thysanoessa raschii*) sampled coincidentally with capelin along the coast.

Capelin growth

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

In addition to the effects of feeding conditions, temperature has a well documented effect on growth of not only fishes (e.g. Hay *et al.*, 2008) but poikilotherms in general (Lindsey, 1966). In the Barents Sea Gjøsæter and Loeng (1987) demonstrated a significant temperature dependent growth variation in capelin with yearly growth increasing by 0.3 cm for every 1˚C temperature increase. Such production increases, or decreases in areas where temperatures increase beyond the optimal temperature, will have an impact on capelin grazing pressure, stock biomass and overall energy flow. Gjøsæter and Loeng (1987) estimated that a 1˚C temperature increase would increase stock size by one million tonnes. This would lead to better feeding conditions for top pelagic predators, but also an increased zooplankton consumption by capelin. This will subsequently affect the benthic-pelagic coupling through changes in the sedimentation rate and composition. If the energetic turnover mediated by capelin is to be quantified, growth, together with consumption, is an essential variable. Growth of Greenlandic capelin has been briefly addressed in two master theses and later reviewed (Kanneworff, 1967; Kleist, 1988; Friis-Rødel and Kanneworff, 2002) and geographical size variation is well documented. However, detailed knowledge on capelin growth patterns and its relation to temperature are not available for Greenlandic waters. Analyzing capelin growth pattern along its latitudinal distribution and relating it to temperature data will provide a first detailed estimate of capelin growth and of the effect a temperature change may have from a single species perspective.

Beach spawning capelin were selected for this study due to easy accessibility and a specific affiliation with individual fjords. These were sampled in four general areas along the Greenlandic West coast spanning 1300 km. Growth patterns were described using saggital otoliths and back calculation procedures (Campana, 1990). Only males were analyzed to avoid possible growth confounding effects of multiple stressful spawning events in iteroparous females (Huse, 1998). Growth is affected by various biotic and abiotic parameters (Wootton, 1990) but temperature through its metabolic and behavioural effects is the most prominent. The best available temperature data were obtained from the ICES database (www.ICES.dk) covering the entire latitudinal gradient through the last century. These data were compared to capelin growth patterns and the possible temperature effect on growth was estimated.

Capelin energy density

R. Hedeholm, P. Grønkjær and S. Rysgaard: Energetic content and fecundity of capelin (*Mallotus villosus*) along a latitudinal gradient in West Greenland. Submitted to Marine Biology.

Capelin is a lipid rich fish with high energy density (Lawson *et al.*, 1998). Therefore, in addition to its importance through abundance, capelin is also a high quality prey to predators. However, in order to address this importance beyond descriptive analyses, knowledge on the energy content of not only capelin, but all prey items, is needed to make accurate energetic budgets (Lavigne *et al.*, 1985; Romano *et al.*, 2006). Because the latitudinal gradient is associated with environmental variability and coincident changes in metabolic demands, feeding and other life history traits, the qualitative state of capelin must be determined on a small scale. Such resolution will allow for prediction of possible changes in energy density with increasing temperatures, and subsequent possible reductions in predator energy intake. Furthermore, capelin are to a large extent semelparous (Friis-Rødel and Kanneworff, 2002) and spawning is a costly behaviour in terms of energy. Feeding is limited during spawning (Templeman, 1948), which entails that a large proportion of tissue is metabolized leaving the fish leaner in this period. During spawning capelin aggregate in shallower waters making them most easily accessible to predators in this period and consequently a need for distinguishing between spawning and non-spawning capelin in the diet arises (Montevecchi and Piatt, 1984) and data are presented on both. Additionally, data on capelin fecundity and reproductive investment are presented. This is useful both in future management through spawner-recruit relationships but also adds to the distinction between an itero- or semelparous life style in capelin females. Hence, some propose a high female survival rate (Friis-Rødel and Kanneworff, 2002) while others state that most females share the fate of single spawning males (Vilhjálmsson, 2002). By calculating the reproductive investment of females in terms of energy the survival probability of the females may become clearer as large differences in reproductive investment is seen between itero- and semelparous species, with a suggested limit of 60% including both spawning and associated behaviour (Glebe and Leggett, 1981; Finstad *et al.*, 2002, Paper III).

The energy density of all sample types (kJ g^{-1}) was determined using bomb calorimetry. The data were compared both with regard to length, spawning state and catch location. Capelin fecundity was determined by counting and weighing a gonad sub-sample and, similar to the study on cod reproductive investment, the reproductive potential and individual egg energy content was calculated.

Capelin and Cod

R. Hedeholm, K.N. Mouritsen, J. Carl and P. Grønkjær: Summer diet of inshore cod in West Greenland: importance of capelin. Prepared for submission for Journal of Marine Biology.

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R. Hedeholm, A. Retzel, S. Thomsen, K. Haidarz and K.T. Jensen: Intra-fjord variation in reproductive output in Atlantic cod (*Gadus morhua*). Prepared for submission to ICES journal of Marine Science.

Capelin constitutes a significant part of many predator diets (Friis-Rødel and Kanneworff, 2002; Vilhjalmsson, 2002). Of these interactions, the cod-capelin relationship has received much attention due to the commercial importance of both species. In Greenland, there are presumably different cod stocks with the offshore component being separate from multiple inshore components (Storr-Paulsen *et al.*, 2004). Cod elsewhere rely heavily on capelin during summer feeding (Methven and Piatt, 1989; Vilhjalmsson, 2002), and capelin abundance has been shown to affect cod condition and recruitment (Marshall *et al.*, 1999). Hence, we wanted to address the importance of capelin to cod in the Greenlandic fjords during summer through a classical feeding study and cod were sampled in Nuuk (64˚N) and Sisimiut (66˚N) fjord systems in June-July and all prey species were determined. This was followed by analyses of length and area related differences in feeding behavior.

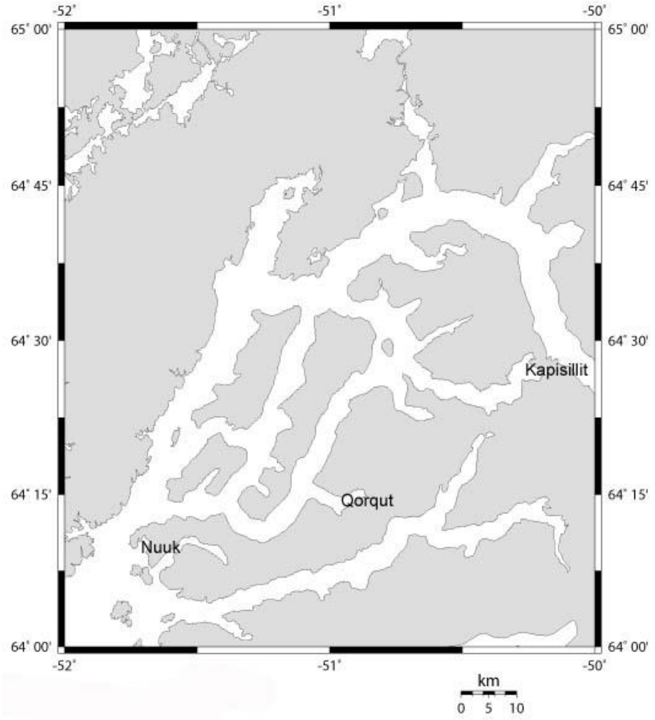

Figure 16: The Nuuk fjord system. Nuuk city and the inshore cod spawning site of Kapisillit and Qorqut are indicated.

In addition to this general study of regional capelin importance we addressed the issue on a more local scale. The Greenlandic inshore cod are to a large extent non-migratory completing their life cycle within fjords. In the Nuuk fjord, the inner area (Kapisillit) has historically been known as a key spawning site (Smidt, 1979; Storr-Paulsen *et al.*, 2004) but spawning is also taking place on other more near-coastal sites such as Qorqut (Fig. 16). We wanted to address the apparent superiority of Kapisillit as a spawning site under the hypothesis that capelin are more abundant and/or easily accessible at Kapisillit. This would facilitate a more favorable environment being conducive for higher cod fitness in Kapisillit, which could manifest itself in a number of ways. This includes improved cod condition, which can in turn result in increased reproductive output (Marshall *et al.*, 1999; Rose and O'Driscoll, 2002). As increased reproductive success is the ultimate Darwinian fitness parameter we chose to focus on fecundity and egg energy content as these are correlated with parameters such as growth rate, larval survival and overall recruitment (Marteinsdottir and Steinarsson, 1998; MacKenzie *et al.*, 2003). Hence, an increase in egg number naturally increases the probability that some individuals will survive, whereas eggs with higher energy content will sustain yolk-sac larvae for longer periods before first-feeding and/or larvae will be larger upon hatching (Marteinsdottir and Steinarsson, 1998). Even small advantages in terms of energy and yolk composition may prove essential to larval survival (Chambers *et al.*, 1989; Riveiro *et al.*, 2000) as there is extremely high egg and larval mortality in marine environments (Houde, 1987).

Females close to spawning were sampled at both Kapisillit and Qorqut. This was done by assigning a maturity state to each fish according to Tomkiewicz *et al*. (2003) and selecting stages four and five for further analyses. Fecundity was determined following the standardized procedure described in detail in Thorsen and Kjesbu (2001) and the energy density (kJ g^{-1}) of the individual egg was determined using bomb calorimetry. This allowed for calculations of the total reproductive investment as a function of total cod energy content (Finstad *et al.*, 2002).

Ecopath model

R. Hedeholm: An Ecopath model for the Nuuk fjord, Greenland. Unfinished manuscript.

Ecopath is a well established ecological tool that from relatively basic knowledge on ecosystem characteristics estimates a snapshot of the system in a mass balanced state using a series of algorithms (Christensen and Walters, 2004). The theory is based on Polovina (1984) but has since undergone changes and improvements. Basically, the system is considered as boxes such that each species/guild is a box, as is the entire ecosystem (or the part of it defined in the model). Each box has to balance, which for the individual box means that what is consumed must cover respiration, catch, biomass accumulation (if any), predation mortality, net migration and other mortality. Overall system balance entails that what is removed (consumption, predation and exported) of a species/guild box cannot exceed the available biomass. If there are system discrepancies the model is un-balanced and modifications (balancing) must be made.

In order to run the Ecopath model, information on at least three of the following parameters must be entered for all groups: biomass, production, consumption and/or ecotrophic efficiency, with the latter most often the one left out and estimated by the model. Additionally, the diet composition of each species/guild represented in the system must be entered. To accommodate migrating species, different fisheries and ontogenetic changes (i.e. feeding) several options are available within the program and for further theory behind the program see Christensen and Walters (2004).

Due to the scarcity of ecological studies on the Greenlandic ecosystem (Pedersen, 1994), we chose to implement the Ecopath model only in the Nuuk fjord. It is the area of Greenland most intensely studied both historically and presently and most likely also so in the future as monitoring programs are set up in the region (Jensen and Rasch, 2008). Additionally, The Nuuk fjord is a semi-closed fjord system ensuring a minimum of migration and area heterogeneity although recent studies have documented within fjord community variation (Arendt *et al.*, 2010). In addition to data generated in the studies included in this dissertation, data from other studies from Nuuk were used whenever possible and otherwise data from other Greenlandic areas were used. However, in some cases estimates from the literature on other sub-arctic systems had to be used. Hence, the model is not perfect but gives an overview of current knowledge, identifies areas of future research and provides an estimate of capelin impact on the system as both prey and predator - the overall focus of this study.

Capelin, cod and other groups where the estimates could be made from local data (including catch data) were defined as “ecological anchors”. These anchors also included primary production, detritus and zooplankton data which were available through the monitoring program MarineBasis (Jensen and Rasch, 2008). In general, higher trophic levels estimates were less certain, and in addition to cod, only whale biomass could be determined with some accuracy (Boye *et al.*, 2010). The ecological anchors served as starting points in the model balancing procedure. These were kept fixed whenever possible, and estimates on more uncertain groups were changed to accommodate this when trying to obtain a mass balanced model. Especially diet compositions were varied to balance the model as it undergoes large yearly variation, and the procedure is in accordance with that suggested by program developers (Christensen *et al.*, 2005). See Appendix A in Paper VI for details on model inputs and the balancing procedure.

In addition to the mass balanced Ecopath model, the Ecosim component of the software allows for temporal simulation runs, where changes following a system disturbance such as a commercial fishery can be explored. Hence, the prospect of a commercial capelin fishery in Greenlandic waters have been explored over the last decade, and by estimating fishing mortality the perturbations this would have on the system could be simulated over a given period under these circumstances. To produce realistic estimates of a fishery three scenarios were set up spanning from low to high fishing intensity based on knowledge from the Icelandic fishery. Each scenario was set to run for ten years and I report on the effect on cod and capelin groups and other groups that show a more than 50% change in biomass.

The Ecopath with Ecosim model included in this thesis has not been prepared for submission to any particular journal, as data on certain parts of the model are insufficient to allow for peer reviewed publication. However, all data and mass balancing procedures have been done, and the model is included as certain patterns and conclusions can be made.

Summary of results

The following section only includes main findings of the different studies and for further elaboration, I refer to the individual papers. The discussion of the results is included in a more coherent state in a later section. Figure references correspond with the numbering in the relevant paper.

Paper I: Feeding ecology of capelin (Mallotus villous Müller) in West Greenlandic waters.

The feeding study revealed a capelin diet consisting of few species. The overall diet was dominated by euphausiids (by weight) followed by amphipods and copepods (Fig. 1 and 2). Across the latitudinal gradient (59-72˚N) only the copepod group showed significant changes in species composition as the smaller species (*C. finmarchicus*, *C. glacialis* and *Metridia* sp.) were gradually replaced by the largest calanus species, *C. hyperboreus*, which dominated from 64˚N and northwards (Fig. 4). Additionally, the latitudinal gradient saw changes in the relative importance of the three dominant prey groups with euphausiids increasing in importance while amphipods and copepods decreased. In the southern area euphausiids were completely absent from the diet whereas they constituted nearly 100% of the diet at more northern locations where fish in general were larger indicating that the changes could be a size artefact (Fig. 2 and 5). However, the trend was also observed in similar sized fish across the latitudinal gradient indicating changes beyond that of simple ontogenetic effects. Lastly, increasing latitude was generally associated with an increase in relative prey amount and prey size coincident with the progressively larger euphausiid importance in the diet (Fig. 3 and 6). A notable exception was the relative prey amount in the northern part of the study area (70-72˚N), where a decrease was seen (Fig. 3).

The stable isotope analyses supported the findings of the stomach analyses in that there was an increase in δ^{15}N values with latitude (Fig. 7). However, feeding differences cannot be the sole explanation for this increase, as there was a difference of 3.23‰ in δ^{15}N values, equivalent to a full trophic level (Post, 2002), between the southern and northern part of the study area. In addition to the effect of increased euphausiid consumption on δ^{15}N values, such changes must in part be caused by changes in the biologically available nitrogen. To address this hypothesis, euphausiids (*Thysanoessa raschii*), from the same latitudinal gradient were examined. These were found to display a similar latitudinal δ^{15}N value change to that of capelin, although less drastic and the difference in mean values was only 1.38‰ (Fig. 8). Thus, the differences seen in capelin isotopic values are most likely the result of a changes in both feeding and nitrogen baseline values. In support of this, capelin from Disko (69-70.5˚N) showed a significant positive relationship between length and δ^{15}N values consistent with a clear ontogentic prey shift including euphausiids in larger fish. Additionally, there was no length effect in δ^{15}N values in Qaqortoq (59.5-61˚N). This was coincident with diet containing no euphausiids and thus no clear ontogenetic feeding shift was observed. The ultimate cause of the difference in the biological available nitrogen is unknown, but the mixing of different water masses along the Greenlandic west coast is the likely proximate explanation (Fig 1 in Paper II).

Paper II: Variation in size and growth of West Greenland capelin (Mallotus villosus) along latitudinal gradients.

Growth increased progressively with latitude at all ages moving north except at in the most northern area where growth decreased slightly (Fig. 6). This pattern was reflected in the mean size-at-age of three year-old fish which increased from 90 to 140 mm from Qaqortoq (60°N) to Disko (68°N) only to decrease to 135 mm in Uummannaq (72˚N, Fig. 4). With small discrepancies in the southern part of the study area, this pattern was also observed historically based on capelin size frequency data from the last century (Fig. 3). The reason for the southern discrepancy is unknown but it is suspected that the larger East-Greenland/Icelandic capelin have influenced the samples (Vilhjálmsson, 1994), but see later discussion.

The growth pattern correlated well with temperatures along the latitudinal gradient as determined from the ICES online database. Hence, temperatures increased from southern Greenland towards the northern part (Fig. 7) and similar to growth, there was a small decline in the most northern area (Uummannaq) supporting the notion of a temperature regulated growth. This difference was apparent based both on yearly averages with an approximate difference of 1°C between south and north, but especially so in the main growth months (July-September) with differences of up to 2°C. This suggests that temperature plays a major role in determining growth and that all else being equal a 1˚C temperature increase corresponds to a 0.4-0.6 cm increase in capelin growth over a year. This would in turn increase the length of a three-year-old fish by 1.2-1.8 cm roughly equivalent to an 80% weight increase.

Paper III: Energetic content and fecundity of capelin (Mallotus villosus) along a 1500 km latitudinal gradient.

A positive effect of length on energy density (based on dry weight) was found in both spawning and non-spawning capelin (Fig. 2). Regarding latitudinal differences, there were clear differences in spawning capelin, where all area-based comparisons were significant (except one out of ten, Fig. 4) whereas only one area (Disko, Fig. 1) was significantly different from other areas in non-spawning fish (Fig. 3). Hence, in spawning fish the mean energy density ranged from 20.86 kJ g dw^{-1} in the south (Qaqortoq) to 21.87 kJ g dw^{-1} in the north (Disko, Fig. 1 and 4) while the overall mean in non-spawning fish was 21.04 kJ g dw^{-1}.

The comparison of spawning and non-spawning capelin revealed large energetic differences between the two. The former contained relatively more water (means of 82.7% and 79.4%, respectively), which was reflected in non-spawning fish having significantly higher energy density based on wet weight (kJ g ww^{-1}) in spite of dry weight based estimates being similar. Hence, the mean difference was only 0.286 kJ g dw^{-1} (Fig. 2) based on dry weight, compared to 0.64 kJ g ww^{-1} based on wet weight. The largest difference was 1 kJ g ww^{-1} (Uummannaq) and overall mean values were 4.32 kJ g ww^{-1} and 3.68 kJ g ww^{-1} in non-spawning and spawning fish, respectively. No temporal effect on energy density was found in non-spawning fish, but values for Nuuk spawning fish declined by more than 1 kJ g ww^{-1} during one month of the spawning season.

Lastly, the fecundity of Nuuk capelin was determined and was best described as Fecundity = 356.63 * gutted weight$^{1.4414}$ (Fig. 7). Each individual egg contained on average 2.67 J which is equivalent to each female on average producing gonads containing 38% of total capelin energy (Fig. 7). For comparison, cod gonads from the Nuuk fjord contained on average 10% of total fish energy (Paper V), clearly visualizing the fundamental difference in life history strategy between the two species.

Paper IV: Summer diet of inshore cod in West Greenland: importance of capelin.

Cod diet was mainly piscivorous with capelin as the clearly dominating prey constituting 70% of prey wet weight (Table 1). This became increasingly evident in larger fish, as smaller prey items such as crustaceans and capelin eggs were an important diet component in smaller fish (below 30 cm., Fig. 2 and 3). Hence the hypothesis of high overall capelin importance was confirmed in this study, although based on a temporally limited sampling period and non-random sampling. There was no significant difference in prey composition or amount between the two main study areas, Nuuk (64˚N) and Sisimiut (66.5˚N) fjord systems. However, the mean condition factor of Sisimiut fish was significantly higher (Sisimiut = 0.886; Nuuk = 0.836, Fig. 4) across all size groups, indicating an integrated environmental difference. The temperature gradient previously mentioned (Fig. 7 in Paper II) could explain this as could prey differences. Hence, historical data on condition factor demonstrated that in fish older than four years a decline in condition has been seen in the last three decades, whereas no change has been documented in younger fish (Fig. 5). Since younger fish rely less on fish prey, the decrease in condition factor over time could be attributed to declining fish prey availability and may also explain the difference between Nuuk and Sisimiut.

Paper V: Intra-fjord variation in reproductive output in Atlantic cod (Gadus morhua).

Cod potential fecundity (PF) was identical in the outer and inner region of the Nuuk fjord (Fig. 1) and was best described by a relationship similar to that of other cod stocks: $\ln PF = 4.811 + 1.171 \times \ln weight$ (Fig.

4). The other reproductive related parameters differed between fjord regions, with the inner regions having larger eggs (Fig. 2) containing more energy (Fig. 5) across all sampled size groups. Hence, the mean individual egg energy content was 1.81 kJ and 0.86 kJ in the inner and outer regions respectively (mean energy densities were 22.947 kJ g dw^{-1} and 22.124 kJ g dw^{-1} respectively). Time of capture was also found to have an effect on egg energy content caused by a rise in mean energy content in the outer region with time. However, fish caught coincidently in both regions had similar egg energy densities suggesting that the difference in energy content was not caused by sampling of different maturity stages. Due to the higher egg energy content in the inner region, the reproductive investment was accordingly higher with reproductive output being twice as high compared to the outer region (approximately 20% and 10% of total cod energy content respectively, Fig. 6). This higher output did however not come at the expense of reduced somatic growth, as the growth was identical between regions.

The differences in reproductive output can be attributable to other factors than capelin accessibility, such as genetic differences, temperature, density dependence etc. Studies attempting to increase knowledge on the subject have been initiated, with year-round temperature profiles being sampled and genetic studies being preformed. However, these are not yet available, and the notion of higher capelin abundance seems a likely contributing factor based on local knowledge as well as the previously mentioned cod feeding study. Here, the cod sampled in the Nuuk fjord displayed some degree of spatial variation; with cod stomachs from the inner regions (Kapisillit) having a higher proportion of capelin than outer region (Qorqut) cod, but the material was insufficient to elaborate on this or make conclusions.

Paper VI: An Ecopath model for the Nuuk fjord, Greenland.

The Ecopath model is only one possible representation of the available data, but with only minor modifications, the Ecopath model was balanced (Tables II and III) indicating a high degree of realism. The major adjustment made to the original model was to the proportion of capelin consumption that was imported from outside the Nuuk fjord. This was increased from 50% to 90%, as the production within the system was otherwise insufficient to fuel capelin predatory demands (EE to high for lower trophic level groups). In the balanced model, sustaining capelin production required 56% of primary production, but in combination with the demand of other groups (i.e. zooplankton), the consumption can easily exceed the available production if the capelin imported diet fraction is not kept very high. Only the zooplankton groups (meso- and protozooplankton combined) had higher energetic demands than capelin, and these groups where comprised of multiple species underlining the energy mediating role of capelin within the system. Supporting the apparent intermediate key position of capelin (trophic level of 2.96, Table III) was the mixed trophic impact (Fig. 3) and keystoneness analyses (Fig. 2). The former showed that many groups on especially lower trophic levels would be negatively affected by a capelin biomass increase while the latter combines this with the actual biomass of capelin in calculating a high overall keystoneness. Another group that had a noticeable impact throughout the system was phytoplankton, where an increased production would positively affect most other groups, demonstrating the basic bottom-up rule of grazer food chains (Sherman *et al.*, 2009). The same pattern was evident in the keystoneness where phytoplankton and large capelin where the two most important groups.

On a community level, model estimates indicated a mature ecosystem evidenced by a lower than 1 (0.94) “total primary production/total respiration” ratio (Table IV) and a connectance index of 0.27 (Odum, 1971). The later indicates the realized number of links out of the possible number and with ecosystem age this becomes higher as species interactions and ecosystem “webness” increases. These estimates are similar to other studies using Ecopath (e.g. Tudela *et al.*, 2005; Chen *et al.*, 2008) further supporting the notion that the model fairly well represents the actual situation and does not produce unrealistic results. The system transfer efficiency, defined as the fraction of total food intake by a trophic level that is transferred to the next higher level, was 9.3 % overall (Table V) which is close to the often used estimate of 10 % for aquatic system (Pauly and Christensen, 1995). The efficiency was a mean value and values were higher at lower trophic levels which was also reflected in very high ecotrophic efficiencies (EE) at these levels. Hence, 93% of the phytoplankton was transferred to consumers indicating a very effective system, which is mainly a result of high capelin predation on effectively grazing zooplankton groups. Of the transferred primary production, 17.5% is needed to support current catches within the system. This is high compared to the low catches in absolute terms (0.06 g C m^{-2} yr^{-1}), but this is solely a result of catches being restricted to the highest trophic levels (mean of 3.8 – seals and cod). In comparison, the mean value of primary production required to sustain fisheries has been reported as high as 35.3% on non-tropical shelves (Pauly and Christensen, 1995) demonstrating that currently, the Nuuk fjord is very lightly exploited (Tudela *et al.*, 2005).

The Ecosim scenarios estimating the effect of a possible capelin fishery in the Nuuk fjord gave some clear indications. Low fishing intensity (1.32 g C m^{-2} yr^{-1}) resulted in small biomass variation in most species at the end of the ten-year scenario (Fig. 4). Only small capelin declined severely as it did in all fishing scenarios, including a not shown “no fishing” scenario. Therefore, the decline is most likely a result of initial parameterization (using the “multiple stanza” option in Ecopath) and does not reflect fishing intensity but rather the actual biomass of the group. With medium (4.37 g C m^{-2} yr^{-1}) and high fishing intensity (5.29 g C m^{-2} yr^{-1}) all capelin and cod groups declined to less than half of the initial biomass – capelin as a result of fishing mortality and cod as a result a both fishing and declining prey resources. In spite of capelin importance in the system, the redundancy maintained by its high biomass ensures that effects from declining capelin biomass are dampened in the system such that other species do not immediately respond with large biomass changes. Hence, a scenario running for 100 years with high fishing intensity caused near extinction of capelin benefitting those species that relies less on capelin while causing severe declines in capelin dependent groups such as seals, cod, whales (and probably birds had they been included).

Discussion and conclusions

The study presented here supports the notion of capelin as key species in the West Greenland ecosystem. It further adds support to the classification of the ecosystem as a typical wasp-waist ecosystem. This is similar to the role of capelin in other sub-arctic systems (e.g. Vilhjalmsson, 2002) and wasp-waist species in general (Cury *et al.*, 2000), which suggest that the Greenlandic ecosystem is susceptible to alterations in capelin ecology through bottom-up and top-down processes with possible cascading effects.

The unbroken latitudinal gradient that formed the basis of this work offered ideal conditions to study *in situ* patterns in capelin life traits, and proved associated with large difference in capelin life history traits such as growth, feeding and capelin quality. From a changing climate perspective, this indicates that capelin, and subsequently the ecosystem, is highly susceptible to climatic changes, both directly through temperature effects on key metabolic processes and indirectly through an altered environment such as prey availability. Hence, if wasp-waist ecosystem response to climatic changes are to be predicted knowledge on its key species is essential, and the present work offers first insight into the possible response of Greenlandic key species, capelin, and suggests possible ecosystem alterations.

Climate change, growth and feeding

The individual studies presented here provide novel knowledge on Greenlandic capelin life history traits growth, feeding and energy density and these are all subject to clear latitudinal variability. Hence, growth and food intake increased with latitude until both dropped slightly near the northern distributional limit. Prey composition and energy density varied between regions and both showed a clear relationship with capelin length, thus being indirectly related to temperature through its dependence on temperature. If climate changes in the sub-arctic follow suggested trends (Holland and Bitz, 2003; Loeng *et al.*, 2005), growth seems the most easily predictable capelin trait addressed here. Being directly related to temperature, growth is expected to increase with temperature within the tolerated temperature range of capelin (Gjøsæter and Loeng, 1987, Paper II). Furthermore, a northwards expansion in the distributional range of capelin is likely as conditions seem to be less than optimal in the northern part of the area studied, where a decline was observed in both temperature, capelin growth and relative prey weight (Fig. 6 and 7 in Paper II; Fig. 3 in Paper I). Such an expansion has also been the case historically, were a northward shift in both spawning activity and presence has been seen during warmer periods (Hansen, 1943; Hansen and Hermann, 1953). Counter intuitively, a similar northward shift and absent spawning is seen in the south during warm periods, which is in contradiction with the generally colder temperatures in this area (Fig. 7 in Paper II). However, in the most southern Greenland (59-60˚N) temperatures tend to increase, suggesting that capelin from this region may be located on the upper-end downward slope of the temperature optimum curve (Fig. 4, Wootton, 1990) thus suffering during ocean warming. Alternatively, a different temperature dependent mechanism such as prey responses may be detrimental to capelin but whatever the explanation; ocean warming will most likely see the disappearance of capelin from the most southern part of Greenland.

The direct quantification of a temperature effect on growth is of course dependent on other temperature related processes and their indirect effect on growth (see below), but as Gjøsæter and Loeng (1987) point out, a 1 cm. average length increase in the Barents Sea capelin stock would increase capelin biomass by 1 mio. tonnes. Similar calculations based on abundance estimates in Bergstrøm and Vilhjálmsson (2006) for the Nuuk fjord, the predicted yearly temperature effect (0.5 cm pr. 1˚C, Paper II) and length-weight relationship for the area (own data) suggest an increase from 160000 to 220000 tonnes (38%) in the Nuuk fjord alone. Total abundance estimates from Greenland are non-existent and it is not possible to extend the calculations to cover the entire area. It can, however, be concluded that a growth increase would have an effect through increased capelin grazing pressure needed to support the increased production. This increase must be supported by secondary production, as the growth rate increase seems to be associated with an increase in prey consumption (Paper I). Regarding the higher prey consumption, this consideration is especially important because current evidence suggests that the secondary production is heavily predated upon by capelin at least in the Nuuk fjord and possibly top-down controlled in the ecosystem (Paper VI). Furthermore, there is an apparent shifting source of the secondary production with latitude (Paper I) making the prediction of zooplankton response to climatic changes equally important to the direct effect of temperature on growth of capelin. Hence, much of the ecosystem response ultimately rests upon the primary producers, and their potential to increase production proportional to demands. Model studies suggests a slight decline in global primary production, but an increase of 20-30% in high latitude regions (Bopp *et al.*, 2005; Richardson, 2008) which could be sufficient to fuel the increased demand.

Evidence strongly suggests, that in a warming Greenlandic ocean, the coldwater adapted largest calanoid species, *Calanus hyperboreus* and C*alanus glacialis*, will shift its distribution north being replaced by smaller calanoids such as *Calanus finmarchicus* and Metridia sp. (Nielsen and Hansen, 1995; Pedersen and Smidt, 2000; Beaugrand *et al.*, 2002; Jensen and Rasch, 2008) which can be considered lower quality prey both in terms of size and relative energy density (R. Hedeholm, unpublished data). This is consistent with the capelin feeding study (Paper I) where there was an increase in both amount and average size of prey with increasing latitude caused by a shift from small to larger copepods and the inclusion of krill in the diet. This may be counterintuitive; due to the “inverse” latitude-temperature gradient, but this does not reverse the distributional limits of the involved zooplankton species but more likely shifts them slightly. Hence, capelin at increasing latitudes may benefit double, experiencing both warmer temperatures and extending their distribution well into *C. hyperboreus* waters as well as apparently having access to krill. Such a “double advantage” may also explain the extremely large growth gradient in spite of northern capelin experiencing a shorter growth season. In comparison, a similar elevated growth gradient is present in Atlantic silverside (*Menidia menidia*) where high latitude fish outgrew their southern counterparts such that they obtained the same size following a 2.5 times shorter growth season (Conover and Present, 1990). The latitudinal gradient examined here is similar (twelve degrees) but shifted northwards, and as a result, the difference in growth season length is less pronounced. Nevertheless, the growth season is approximately 35% shorter in Disko than in Nuuk (Sejr *et al.*, 2009) but capelin from the north (69˚N) are 28% longer than capelin from the south (60˚N) after the first growing season indicating a vastly superior growth rate (Paper I).

The expected changes in the copepod community will most likely have the largest effect on larvae and juveniles, who rely heavily on these prey groups (Folkvord *et al.*, 1994; Turner, 2004). In adult capelin, which have received the most attention here, krill presence seems to be the key feeding difference between the southern and northern part of the Greenlandic West coast (Paper I). Hence, in the Disko area where the largest and fastest growing capelin were found, krill was the main diet constituent. Krill was absent from the diet in the southern part but was included further north in fish of similar size suggesting krill absence in the south and not only an ontogenetic diet shift. Another possibility is active prey selection, but as krill is a larger and energetically favourable prey, a decision to exclude them seems unlikely. However, historically krill presence has been documented in the southern part (Pedersen and Smidt, 2000) and they were also observed during capelin sampling for this study. However, the one-year study presented here may represent a negative krill abundance anomaly. Such anomalies, negative and positive, are common in arctic krill populations (Fig. 17) but they do not appear to be related to temperature variation, but are probably more influenced by frontal zones, water intrusions and system productivity (Dalpadado and Skjoldal, 1991; Nishikawa *et al.*, 1995; Siegel, 2000). Thus, current knowledge on krill distribution is inconclusive and not predictable in a warming ocean scenario, but an abundance decline could negatively affect adult capelin fitness.

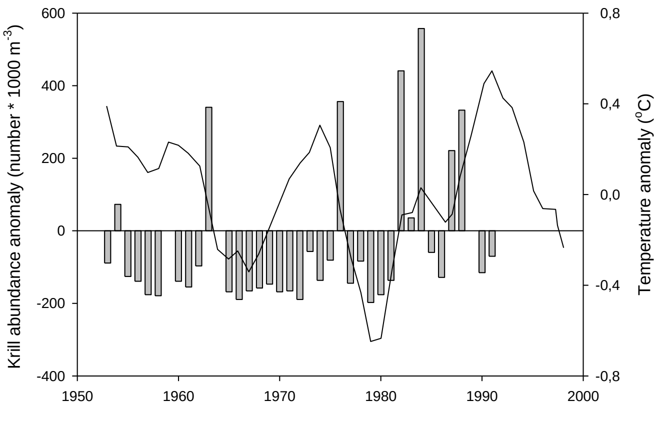

Figure 17: Anomalies in krill (Thysanoessa inermis) abundance in the Barents Sea and coincident anomalies in sea surface temperature. Based on Siegel et al. (2000) and data from Drobysheva (1987; 1994).

In conclusion, increasing temperatures will positively and consistently affect capelin growth. It is possible that capelin can top-down control prey abundance (Arrhenius, 1997; Cury *et al.*, 2000) and such an intense predation could leave capelin vulnerable to bottom-up growth limitation, as could a possible decline in krill abundance. However, in the current situation, moderate temperature increases will most likely result in a net capelin production increase and the occasional prey limitation will not become a sustained growth limiting factor but rather cause inter-year variation.

Temperature and feeding seemingly play a large role in maintaining a latitudinal growth gradient, but rather than attributing this difference solely to these factors other aspects have to be considered. One obvious variable is genetics. Conover and Present (1990) demonstrated a clear genetic component in the atlantic silverside growth gradient with northern populations outgrowing southern populations at identical temperatures. They suggest size selective winter mortality as the evolutionary explanation, with larger individuals better adapted to survive the longer winters in the north thus selecting for faster growth rate. Unfortunately, no data allows for such analysis on Greenlandic capelin, but there are indications that genetics do play a role. Hence, Sørensen and Simonsen (1988) demonstrate differences in local capelin populations based on gel electrophoresis sampling from Nuuk (64˚N) to Aasiaat (68˚N) but no recent and more thorough studies exists. Other circumstantial evidence includes the differences in growth rate, progressive spawning and the geographically well-separated fjord systems producing possible isolating barriers. Addressing the population structure using microsatellite techniques seems an obvious approach and similar studies has been done on other capelin populations (Gordos *et al.*, 2005) where it is concluded that the examined loci are well suited in addressing questions related to fine-scale population structure and spawning fidelity. Hence, not only the overall Greenlandic population structure can be examined, but also the possible finer scale structure within large fjord systems such as the Nuuk fjord.To elaborate on the relative importance of genetics, controlled experiments must be preformed, keeping confounding effects of temperature and length of growth season constant.

The benthic-pelagic coupling

Shelf areas in the Arctic are in general large and there is a strong benthic-pelagic coupling (Wassmann *et al.*, 2006) supporting a high benthic biomass (Nilsen *et al.*, 2006; Sejr *et al.*, 2010). The likely increase in capelin production (but not necessarily primary production in general, Sherman *et al.*, 2009) as a result of increasing temperature will affect the energy flow of the ecosystem in various ways. For instance, intensified capelin predation can cause a higher sedimentation of primary producers through reduced zooplankton grazing pressure (Wassmann, 1998) thereby enriching the benthic community and strengthening the benthic-pelagic coupling. However, as suggested for instance in the Bering Sea, environmental changes such as warming oceans can also weaken the coupling, shifting the ecosystem towards one more dominated by pelagic species (Grebmeier *et al.*, 2006). In support of this, increases in zooplankton abundance and fisheries yield in the warming North Atlantic have been seen (Sherman *et al*. 2009). A weakened coupling is the likely scenario in Greenland waters (and the Arctic in general) both because of increased production by individual pelagic species, but also through increasing abundance of new species. Hence, several novel species have recently been found in Greenland waters and their presence is suggested to be caused by steadily increasing temperatures (Møller *et al.*, 2010). Furthermore, other pelagics such as herring are found in increasing numbers and further north in warm periods (Hansen and Hermann, 1953). Thus, if Greenland waters follow a general ocean warming trend, pelagic zooplanktivorous fish biomass will increase, intensifying grazing on zooplankton, which in turn reduces the grazing on primary producers. These primary producers sediment slowly and will be re-mineralized by the pelagic microbial food web, and re-enter the grazer food chain. Furthermore, expected hydrographical changes will increase zooplankton abundance, which is also conducive for maintaining an enriched pelagic community. Hence, the likely result is that a larger fraction of energy will be kept in the pelagic weakening the benthic-pelagic coupling and reducing current benthic production.

Qualitatively changes in capelin

If variability or shifts in prey composition and availability are the result of future climatic changes, this may become apparent in the qualitative state of marine organisms, changing their energy density which can have subsequent influences on higher trophic levels. As an example, the energy content of sprat and sandeel (*Ammodytes marinus*) declined by approximately 75% in the North Sea in the early 2000's (Wanless *et al.*, 2005). In this area, common guillemots (*Uria aalge*) rely solely on these prey species for their chicks and as a result of reduced *per capita* energy intake, chick fledging success declined by 26% (Wanless *et al.*, 2005) and similar examples are present from different species and areas (Paiva *et al.*, 2006; Wolf *et al.*, 2006). Indeed, this so-called "junk food hypotheses" (Alverson, 1992) is currently recognized as general feature of many marine related organisms (Österblom *et al.*, 2008) underlining the need to consider prey composition and its relation to environmental variation as well as mere abundance. In the North Sea, the conditional decline of sprat and sandeel was supposedly the result of changes in zooplankton availability (Beaugrand *et al.*, 2002). Such a causal relationship also potentially links the difference in capelin feeding found here (Paper I) with the latitudinal changes in energy density (Sherwood *et al.*, 2007, Paper III). Hence, there was a clear positive length effect on energy density, suggesting that as capelin grow larger they consume more favourable prey which is in accordance with a shift from smaller copepod prey (*C. finmarchicus* and metridia sp.) towards larger copepods (*C. hyperboreus*) and krill (Paper I; Paper III). However, due to the confounding latitudinal growth gradient (Paper II) any strict causal relationship cannot be suggested but the clear variation in energy density strongly encourages further study. This should also cover the temporal development of capelin energy density, as it is sure to develop over the growth season (Jangaard, 1974). Additionally, with the current study functioning as a baseline, future capelin monitoring should include the qualitative state of capelin; especially if future climatic changes cause changes at lower trophic levels as seen in the North Sea and other locations (Österblom *et al.*, 2008). Furthermore, zooplankton are recognized as climatic beacon indicators (Richardson, 2008), and changes to the zooplankton community will quickly propagate to capelin via feeding, and thus to higher trophic levels. Rather than monitoring the complexity of the zooplankton community, which is expensive and time consuming, the energetic state of capelin is easily determined and might well be a good proxy for environmental changes.

The joint effect of temperature on growth (Paper II), the length effect on energy density and the influence of temperature on capelin prey (Paper I) suggests that capelin will increase in energy density following ocean warming, assuming that prey availability does not limit capelin foraging and that temperature and prey effects do not cancel out. Such an increase will benefit capelin predators and combined the *per capita* energy intake, when consuming capelin, will increase by approximately 65% if conditions cause a length increase of 2 cm in capelin. This large change is, however, predominantly caused by the length increase and only 5% is attributable to qualitative changes in energy density. Hence, the future combination of temperature effects, density dependent processes (Casini *et al.*, 2006) and planktivorous community changes (Beaugrand, 2004; Wanless *et al.*, 2005) may well result in even larger changes in the Greenlandic capelin pending future ecosystem responses as the qualitative changes may become even more pronounced. However, in addition to local importance to predators, the relevance of capelin's high energy content compared to other prey (Van Pelt *et al.*, 1997) may be more a question of presence rather than energy density variation as changes in energy density may to some extent be compensated for by predators through behavioral changes. This means that the greatest impact will be in the north, where capelin will likely replace the ecologically similar Arctic cod (*Boreogadus saida*) in a warming ocean as they have limited overlapping distribution (based on survey data, unpublished). This will benefit regional predators as capelin have higher energy density than the lean cod fish (Van Pelt *et al.*, 1997). This is again indicative of a future weakened benthic-pelagic coupling, as this improved pelagic predation scenario will help to maintain energy in the pelagic.

The positive effect of such capelin presence to predators is suggested in the study of cod spawning and feeding in the Nuuk fjord (Papers IV and V). Unfortunately, present data does not allow a causal relationship to be determined, but cod from the inner fjord region have a significantly higher reproductive output than outer region cod (Fig. 5 in Paper V) and this can be linked to higher capelin presence in the inner region. The more general importance of capelin as prey and thus its importance as a bottom-up regulating species, was evident in the high keystoneness estimated by the Ecopath model (Paper VI) taking all predators into account and placing capelin as the second most important group. If recent trial fisheries for capelin result in an actual fishery in West Greenlandic waters this bottom-up regulation will become relevant, as the Ecosim simulation demonstrates a large capelin abundance decrease if the fishing effort is not kept at a low level (Fig. 5 in Paper VI). The joint effect of fishing, temperature and a shift in capelin prey distribution could be large, due to the dynamic nature of wasp-waist species in general, capelin will respond quickly, and in this case fishing can cause a population collapse.

Perspectives and future research

This work has demonstrated that capelin is a key species in the Greenlandic wasp-waist ecosystem, and that capelin life traits vary along the latitudinal gradient examined. This includes a highly temperature dependent growth, a latitudinal feeding pattern and differences in energy allocation, which demonstrate that capelin will be highly affected by climatic variability. The sensitivity of this key-species to climate change will likely propagate to other trophic levels as capelin importance has been demonstrated from both a top-down and bottom-up perspective. Hence, further research into the importance of wasp-waist species in general, and their response to climate change is essential as these can cascade through the ecosystem.

The Greenlandic system offers ideal conditions to continue such studies but in addition to future detailed studies some basic parameters should be regularly monitored if the importance of capelin is to be further clarified. This includes biomass estimates on both capelin and zooplankton and community composition of the latter. Recognizing that covering the entire Greenlandic coast is logistically difficult, such high-resolution sampling could initially be restricted to 2-4 locations. This will allow for additional studies on growth variability and the relative effect of temperature and feeding, as well as addressing their joint effect on capelin energy density. One study, however, that needs to cover all of Greenland is a much needed genetic analyses of capelin population structure. This is vital from a management perspective but would also support studies exploring the system using a laboratory approach, which is a natural and highly profitable extension of the *in situ* approach applied here. Hence, hypotheses regarding the quantitative effect of temperature and feeding on growth can be examined, and the possible impact of any genetic component can be quantified.

Studies on the interrelationships of capelin with higher trophic levels should also be elaborated upon to evaluate the bottom-up regulatory control capelin exerts on the system. This should initially include estimates of capelin consumption by its main predators such as cod, seals and humpback whales, which should be supported by more ecosystem based studies such as an isotopic food web analysis. Additionally, I strongly suggest that studies elaborating on the variability in energy density of capelin and the possible impact on predator condition should be undertaken. This is based on the apparent importance of capelin seen in the study on cod reproductive output but also as a response to recent documented breeding failures in sea birds in the North Sea. Apparently, no decline has been seen in Greenlandic birds breeding success, and this offers an opportunity to monitor the energetic development of capelin under changing environmental conditions. Such energetic studies can with similar relevance be extended to include capelin prey species.

Jointly, the many research opportunities and subsequent results from studies on the Greenlandic ecosystem and its key wasp-waist species will increase understanding of similar systems and due to the ubiquitous presence of capelin in sub-arctic ecosystems, such knowledge can be extrapolated to cover much of the sub-arctic region.

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Paper I

Feeding ecology of capelin (*Mallotus villous* Müller) in West Greenlandic waters

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Feeding ecology of capelin (*Mallotus villous* Müller) in West Greenlandic waters

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Stomachs contents from 572 capelin sampled along 1500 km of the Greenlandic west coast were examined. The most dominant prey by wet mass was euphausiids (61%) followed by amphipods (18%) and copepods (10%). By count the copepods dominated (54%) with the heavier amphipods (13%) and euphausiids (9%) being less important. The most common species were *Thysanoessa raschii, Themisto libulla, Calanus finmarchicus* and *Calanus hyperboreus*. Copepods dominated in smaller capelin but were replaced by euphausiids in larger fish. A similar prey shift towards euphausiids was seen with increasing latitude and so was an increase in prey mass (relative and absolute). The spatial variation in feeding pattern was supported by stable isotope analyses. The mean δ^{15}N values for the south (60-64˚N) and north (68-72˚N) were 9.24‰±0.72 and 12.47‰±0.38 (mean±SD) respectively which is equivalent to a full trophic level. This difference is probably generated by the observed diet differences and changes in the isotopic baseline as evidenced by a 1.38‰ difference in δ^{15}N values in krill (*Thysanoessa raschii*) sampled in the southern and northern part of the study area. This study shows that the diet composition and biomass of capelin differs significantly along the Greenlandic west coast with potential implications for capelin growth and condition.

Key words: Capelin, feeding, latitudinal gradient, stable isotopes

INTRODUCTION

Capelin (*Mallotus villosus* Müller) is a small planktivorous fish of the Osmeridae family with a circumpolar distribution. It is an important part of many marine ecosystems as a mediator of energy from lower to higher trophic levels and can be influential throughout the ecosystem through bottom-up and top-down control respectively (Cury *et al.*, 2000; Carscadden *et al.*, 2001; Bakun, 2006). Hence, capelin has been shown to be able to grass down its main zooplankton prey within days (Hassel *et al.*, 1991), and its importance as prey has been demonstrated repeatedly, especially in connection with the capelin-cod (*Gadus morhua* Linnaeus) interaction, where it has been found to constitute a significant part of cod diet in various areas (Lilly, 1994; Carscadden *et al.*, 2001; Vilhjalmsson, 2002). This importance of capelin is also seen in West Greenlandic waters where capelin is a major prey item to commercially important species of fish (e.g. cod, halibut (*Reinhardtius hippoglossoides* Walbaum), marine mammals (e.g. minke whale, harp seal) and marine birds (e.g. common mure, Friis-Rødel and Kanneworff, 2002).

Unlike the intense capelin fishery in Iceland and Norway no significant fishery for the West Greenlandic capelin is present with only 138 tonnes caught in 2005 (Unpublished data, Greenland Ministry of Environment and Nature) but trial fisheries have been conducted on several occasions (e.g. 1987 and 2007) indicating the commercial potential of the population. The stock size is unknown with "tentative" estimates as high as 250.000-1.000.000 tonnes but this is at best a qualified guess (Jákupsstovu and Røttingen, 1975; Gjøsæter, 1998). On a more local basis, the population size has been evaluated within individual fjord system, and has been shown to be large and with the potential to significantly influence the fjord ecosystem (Bergstrøm and Vilhjálmsson, 2006).

In spite of the ecological importance of capelin in West Greenland, and the impact a potential commercial fishery would have on these ecological interactions little is known on capelin in Greenland in general and on capelin feeding in particular (for review see Friis-Rødel and Kanneworff 2002). Capelin feeding has been described and quantified in other populations (Huse and Toresen, 1996; O'Driscoll *et al.*, 2001; Wilson *et al.*, 2006; Pedersen and Fossheim, 2008), but only two accounts on feeding of the Greenlandic capelin are available. Kanneworff (1967) analyzed stomachs from capelin caught on one day at a single location concluding that euphausiids dominated and Kleist (1988) found that crustaceans was the dominant prey in a southern fjord but he does not go into further detail.

Classic stomach content analyses only provide a snapshot of feeding behaviour, and therefore the use of stable nitrogen and carbon isotopes ratios in feeding studies is increasing rapidly (Michner and Schnell, 1994; Hansson *et al.*, 1997; Sherwood and Rose, 2005) and data also exists for a number of marine organisms from West Greenland (Møller, 2007). The use of stable isotopes as indicators of trophic level and food web structure allows for a time integrated picture of feeding behaviour (Post, 2002), but does not give a qualitative description of the stomach analyses.

Hence, we use a combination of stable isotopes and stomach analysis and present quantitative data on capelin feeding along a 1500 km south-north gradient in West Greenlandic waters providing an integrated understanding of feeding behaviour. Furthermore, Hedeholm *et al.* (2010) demonstrated a latitudinal growth gradient in capelin along the same gradient and suggested that the latitudinal related growth differences could be related to differences in feeding behaviour as also suggested for Barents Sea capelin (Gjøsæter *et al.*, 2002). This study will allow for an evaluation of the role of feeding in generating the observed latitudinal growth gradient, improve knowledge on this ecological key species and contribute towards quantifying the role of capelin in the West Greenlandic ecosystem.

MATERIALS AND METHODS

SAMPLING

Capelin were collected during trawl surveys in 2007 and 2008 by RV "Paamiut" during a yearly shrimp and fish survey conducted by the Greenland Institute of Natural Resources. In 2007 sampling took place from 13 June to 9 September along the West coast of Greenland and in 2008 from 19 June to 8 August. This stratified-random bottom trawl survey covers the continental shelf from the southern tip of Greenland to 72˚N on the West coast and 66˚N on the East coast. Only samples collected off the west coast were used in this study as the East Greenland capelin were less well sampled and also to some extend considered part of the Icelandic capelin stock (Vilhjalmsson, 2002). In addition, capelin from two locations were caught by RV "Erika" from the East-Greenland Codfish A/S. Samples were obtained on the West coast continuously along a latitudinal gradient from 59.46˚N to 72.04˚N. At stations where the catch exceeded 150 individuals a random subsample of 50 individuals was taken. All sampled capelin were frozen immediately after capture (-20˚C).

STOMACH ANALYSIS

All fish were measured (fork length, nearest mm below), weighed (nearest 1/10 g) and aged (except nine fish) using saggital otoliths. The stomach was removed and stomach fullness was determined (0-5, with 0 being empty and 5 completely full). Stomach content was determined to the lowest possible taxonomic level and placed into categories according to this taxonomy. Due to digestion, identification was often limited to class or order (e.g. amphipods, decapods, euphausiids, and copepods). When less digested prey was found it was determined to a lower level – most often genera. The unidentified prey category only constituted 2.7% of prey wet mass. The total length was determined for all prey groups except copepods where prosome length was measured. All prey was blotted dry and weighed (nearest 1/1000 mg). All prey items were counted but in some cases the number of individuals could not be determined due to digestion. In these cases the number was estimated based on mass and count of similar prey from other stomachs from the same area. Subsamples from all prey categories were dried for 24 hours at 60˚C to determine the water content. However, mean water content (82.3% ± 0.70, mean ± SE) did not differ significantly between any of the prey groups (Mann-Whitney, P≥0.35) and all reported values and further analyses are based on wet mass.

To estimate the general prey composition the proportional mass and count contribution of the most important prey groups were calculated. To describe the spatial pattern of prey consumption along the coast, the proportional contribution of each prey group was compared between latitudes. To accommodate this all fish were assigned to the nearest latitudinal degree. The analysis was done for all fish sizes together but fish between 115-130 mm were furthermore analyzed separately (N=279) to address possible size unrelated feeding differences. Differences in the amount of prey consumed at a given latitude irrespective of fish size were determined by calculating prey mass relative to fish mass.

Using catch latitude capelin were assigned to four general areas (N=396). These were Qaqortoq (59.5˚N-61˚N), Nuuk (63.5˚N-65˚N), Disko (69˚N-70.5˚N) and Uummannaq (71.5˚N-72.5˚N). Fish sampled in between area boundaries were not included in this area based length analyses. Feeding patterns in these areas were used to describe ontogenetic changes in prey composition such that possible confounding effects of length and latitude could be separated.

STABLE ISOTOPES - SAMPLE PREPARATION

Forty-eight capelin were randomly selected for isotope analyses. These were distributed evenly among the four areas defined above (Qaqortoq, Nuuk, Disko and Uummannaq, N=12 for each area) spanning as wide a size range within each area as possible. Samples were prepared by removing muscle tissue (mean ± SD, 0.97g ww±0.40) dorsally from both sides of the fish posterior to the dorsal fin, which ensured that no bones were present in the sample. All skin was subsequently removed. The samples were freeze dried for 24 hours after which no further weight loss took place. The muscle tissue was ground to a fine powder using a glass mortar. No carbonates were removed from the samples as they did not contain skin or bones, nor were lipids extracted.

Prior to analysis the samples were kept in an exsiccator. Samples (1 mg ± 0.1 mg) were randomized and analysed at Mylnefield Research Services Ltd. Dundee, Scotland using an automated nitrogen-carbon analyser (ANCA) coupled to a 20/20 isotope ratio mass spectrometer (SerCon Ltd, Crewe, UK). Samples in crimped tin capsules were introduced via a solid autosampler. The elemental analyser (EA) reactor tubes

were comprised of two quartz glass tubes filled with chromium(III) oxide and copper oxide held at 1000°C and reduced copper, held at 620° C for combustion and reduction, respectively. A post-reactor gas chromatography (GC) column was kept at 70°C for separation of evolved N_2 and CO_2. Measured $^{13}C/^{12}C$ isotope ratios were processed using the instrument manufacturer's proprietary software Calisto (SerCon Ltd, Crewe, UK) and anchored to the VPDB scale by contemporaneous analysis of international reference materials IAEA-600 (δ^{13}CVPDB = -27.77 ‰; IAEA, Vienna, Austria) and IAEA-CH6 (δ^{13}CVPDB = 160 -10.45 ‰. IAEA, Vienna, Austria). The working standard for N analysis was 1 mg leucine prepared by freeze drying 50 µl of a 20 mg/ml stock solution into tin cups, and calibrated against 'Europa
flour' and IAEA standards N1 and N2. Data are reported as δ^{13}C relative to PDB and δ^{15}N relative to
163 air according to the formula:

$$\delta I = [(R_{sample}/R_{standard}) - 1] \cdot 1000,$$

where I is ^{13}C or ^{15}N and R is the ratio of the heavy to the light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$).

STATISTICAL ANALYSIS

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

RESULTS

572 stomachs were analyzed from 52 stations across 2007 and 2008 and 35% where empty (Table I). There was no significant relationship between the fraction of empty stomachs and catch latitude (ANCOVA, $F_{1,26}$=0.755, P=0.40) nor was there any difference between years (ANCOVA, $F_{1,26}$=2.535, P=0.12) and empty stomachs were excluded from further analysis. The analyzed fish were 78-170 mm in length and 2-5 years of age. However, mean size varied between stations increasing from 116 mm at the most southern stations to 143 mm at the more northern station while the average age varied from 2.9 to 3.8 years (Table I).

STOMACH ANALYSIS - GENERAL COMPOSITION

The stomach content consisted of relatively few species. The euphausiids were in general difficult to determine to species, but the identifiable specimens were all identified as *Thysanoessa raschii* and in one case *Meganyctiphanes norvegica*. Likewise for the amphipods, most identifiable specimens were *Themisto libulla* but a few specimens of *Themisto gaudichaudii* were also found. More variation was found in the copepod group where calanoid species dominated and *Calanus finmarchicus*, *Calanus hyperboreus*, *Calanus glacialis*, *Metridia longa, Metridia lucens* and *Pseudocalanus* spp. were found. Of the copepods, *C.*

finmarchicus and *glacialis* were not easily distinguishingable and thus pooled when quantifying prey in subsequent analyses. Thus, five major categories were used when describing and comparing prey composition: euphausiids, amphipods, copepods, other and unidentified (Fig. 1). The unidentified category is not included on the count graph as this prey was not countable.

Interyear comparison on similar sized fish (115-130 mm) showed no significant effect of year on the share of euphausiids (ANCOVA, $F_{1,196}$=0.895, P=0.35), amphipods (P=0.58) or copepods (P=0.06). Based on this and the similar proportion of empty stomachs in 2007 and 2008, the two years were pooled in further analyses. The most dominant prey by wet mass was euphausiids which made up 61% (18.5g) of the total consumed prey (30.4g). Next in order of importance were amphipods (18%) and copepods (10%). By count the copepods dominated (54%) over the heavier amphipods (13%) and euphausiids (9%, Fig. 1). The other category was the second most abundant prey by count, but this was the result of fish from one station (61˚N) that had eaten only cirripedea nauplii and due to their small size (mean±SD, 0.6 mm±0.04) they constituted 13% of the total number of prey although present at only one station. The three dominant groups (by mass) consistently dominated across all latitudes, but they were not uniformly distributed at all stations and there was a significant effect of latitude on prey group proportions (Kruskal-Wallis, Euphausiids: $\chi^2_{[11]}$=116.960; Amphipods: $\chi^2_{[11]}$=31.244; Copepods: $\chi^2_{[11]}$=141.239, P≤0.001 for all, Fig. 2). The pattern was similar for both all sized fish and for the similar sized. At the southern latitudes copepods and amphipods dominate the diet while especially copepods tend to decrease in abundance moving north although important at 70˚N especially in the 115-130 mm fish. The importance of Euphausiids increases with latitude with a peak at 66˚N and 67˚N. At the former latitude however, only six fish were caught at the same station so this is to be taken with caution. Removing these from the analyses did however not alter the result of the latitude effect on prey proportions (P≤0.002 in all cases).

In addition to the proportional composition of prey changing with latitude an increase in prey amount relative to fish mass from 60˚N to 67˚N and then a subsequent decline further north towards 72˚N was also found (Kruskall-Wallis, $\chi^2_{[8]}$=66.003, P<0.0005, Fig. 3). This change in prey amount was also evident in an increase in the average stomach fullness (mean±SD) from 1.9 ± 0.9 at 60˚N to 3.1 ± 1.1 at 67˚N followed by a drop to 1.9 ± 1.1 at 72˚N (Kruskall-Wallis, $\chi^2_{[8]}$=39.060, P<0.0005, Fig. 3).

The only taxonomic group that showed any latitudinal change with regard to species composition was the copepod group (Fig. 4 – only shown for similar sized fish). Using copepods that were identified to species (N=2417) and making the analyses for both all fish and fish of overlapping size it was clear that the large *C. hyperboreus* (mean±SD, 4.53mm±0.9) constituted a low proportion of the total copepod wet mass at southern latitudes while it was dominant in the north constituting 100% of copepod prey at most latitudes north of 63˚N. The other abundant copepod category, *C. finmarchicus/glacialis* (mean±SD, 1.59mm±0.01) showed the inverse pattern, constituting >50% at southern latitudes while being present only in minor amounts north of 63˚N. The smallest copepod present in appreciable amounts was *M. longa*, but here no significant effect of latitude was seen in neither all or the same sized fish, but it was only present at the lowest latitudes and the lack of a significant relationship was caused by the relatively small contribution to the overall diet.

STOMACH ANALYSIS – LENGTH RELATED DIFFERENCES

Length specific feeding behaviour was addressed in four areas (Qaqortoq: 59.5-61˚N, Nuuk: 63.5-65˚N, Disko: 69-70.5˚N and Uummannaq: 71.5-72.5˚N). Fish length range was largest in Qaqortoq (78-130 mm, N=242, 26% empty) and Disko (95-164 mm, N=196, 29% empty) whereas fewer fish covering a smaller range where caught in Nuuk (94-132 mm, N=61, 34% empty) and Uummannaq (94-132 mm, N=18, 22% empty). Stomach content from the smallest fish in Qaqortoq was dominated by the "other" category which was primarily a result of the one station previously mentioned, where the fish had preyed solely on cirripedea nauplii (Fig. 5). Disregarding these, the smallest fish up to 110 mm had feed mostly on copepods in both the south and north. However, the size of the copepods were slightly larger in the north than in the south both in the overlapping fish size groups (3.13 mm and 2.77 mm respectively) and in general (4.03 mm and 2.93 mm, respectively (Student's t-test, $t_{26.190}$=3.557, P=0.001). In fish larger than 110 mm amphipods constitute a large part of the diet and in Disko euphausiids appear in the diet of fish larger than 130 mm dominating the diet in larger fish whereas no euphausiids were found in Qaqortoq, where all capelin were smaller than 130 mm.

In Qaqortoq and Disko, that spanned the largest length range, the average prey size increased with fish length in both areas separately and when combined (Linear regression, F≥16.138, P<0.0005 for all cases, Fig. 6). A sharp increase in the average prey size was seen in the] 140-150] size category at Disko which was caused by the inclusion of euphausiids in the diet as these on average were 21.9 mm±4.2 (mean±SD).

ISOTOPE ANALYSIS

There were large differences in δ^{15}N values between areas (mean±SD) increasing from 9.18±0.79 and 9.89±1.14 for Qaqortoq and Nuuk respectively in the south, to 12.45±0.37 and 12.50±0.40 in Disko and Uummannaq in the north (Fig. 7). A full factorial ANCOVA using area as a fixed factor and length as a covariate showed no significant area-length interaction (ANCOVA, $F_{3,36}$=2.264, P=0.10) and the reduced model showed a significant effect of area ($F_{3,39}$=133.911, P<0.0005) but not of capelin length ($F_{1,39}$=0.504, P=0.48) on δ^{15}N values. Subsequent ANOVA's showed that the two southern areas (Qaqortoq and Nuuk) did not differ from each other (P=0.49) but both differed from the northern areas (Disko and Uummannaq, P<0.0005). Likewise, the two northern areas were not different from each other (P=0.99). Combining Qaqortoq and Nuuk (south) and Disko and Uummannaq (north) the mean δ^{15}N values were (mean±SD) 9.24±0.72 and 12.47±0.38 respectively – a difference of 3.23‰.

δ^{13}C-values did not show a clear pattern with similar mean values between areas and large variation within each area. Hence, from south to north the mean±SD were: -21.04±0.53‰, -20.43±0.54‰, -20.18±0.28‰ and -20.66±0.26‰ with no effect of length (ANCOVA, $F_{1,1}$=0.419, P=0.52) but a significant effect of area (P<0.0005) as Qaqortoq had a lower δ^{13}C value than other areas (P<0.05, Fig. 7).

DISCUSSION

STOMACH ANALYSIS - GENERAL COMPOSITION

Adult capelin feeding during summer in western Greenlandic waters was dominated by euphausiids followed by amphipods and copepods with the groups making up 61%, 18% and 10% by wet mass in non-empty stomachs, respectively. This composition of prey is similar to that found in other North Atlantic studies (Barents Sea: Huse and Toresen (1996), Labrador Sea: O'Driscoll *et al.* (2001), Iceland: Asstthorsson and Gislason (1997)). There are differences between the relative importances of the prey groups between studies. Some rate copepods as the most important prey group and others euphausiids (Astthorsson and Gislason, 1997; O'Driscoll *et al.*, 2001), but the relative importance also varies seasonally and spatially (Vesin *et al.*, 1981; Astthorsson and Gislason, 1997). Only a few studies in the Bering Sea and Barents Sea have found euphausiids to dominate the diet (Naumenko, 1984; Ajiad and Pushchaeva, 1992). The importance of hyperiid amphipods was also shown in some studies (e.g. O'Driscoll *et al.*, 2001), but was in general higher in this study than in other waters (Gerasimova, 1994; Astthorsson and Gislason, 1997). As an ontogentic shift in diet with euphausiids becoming relatively more important and copepods less important with an increase in fish size is shown in most studies of capelin diets (e.g. Astthorsson and Gislason, 1997; O'Driscoll *et al.*, 2001, this study, Fig. 5), the relatively high proportion of the diet made up by euphausiids in this study could be an artefact of sampling large capelin with no zero or one year old fish being sampled. In conclusion, no clear difference between the feeding patterns of West Greenland capelin compared to other capelin populations was found.

Differences in prey composition along the 1500 km latitudinal gradient were found. Copepods and amphipods tended to decrease in importance with latitude while euphausiids became more important. This was evident when all fish sizes were considered together, but also among similar sized fish (115-130 mm, Fig. 2).

As capelin is a planktivorous filter feeder the diet can be expected to reflect prey availability in the environment. Pedersen and Smidt (2000) reviewed zooplankton data from 1950-84 from the southern tip of Greenland to Disko in the north sampled in late June/early July. They found that all three major prey groups (euphausiids, amphipods and copepods) were present at all latitudes. Within the copepod group Pedersen and Smidt (2000) differentiated between *C. hyperboreus* and *C. finmarchicus*/*glacialis* and found both groups present along the entire coast with the proportions differing at individual stations but with no clear latitudinal pattern. If feeding capelin are passively sampling the zooplankton community, these findings do not support the inverse contribution of euphausiids and copepods to the diet shown here. However, Pedersen and Smidt (2000) also show a large interannual variability in the abundance of the different zooplankton species, and sampling only took place during a very short period of the year and, hence, the lack of spatial and temporal resolution may account for the discrepancies. Furthermore, the prey environment may have changed considerably over the past two decades (Mikkelsen *et al.*, 2009; in prep.). For instance, Nielsen and Hansen (1995) showed that *C. hyperboreus* was the dominant calanoid in June/July at Disko which is supports our findings, and Hirche (1991) also found *C. hyperboreus* to dominate at northern latitudes in Greenlandic waters in late fall.

Another possibility explaining latitudinal related feeding differences is prey selection. If prey is more abundant at northern latitudes capelin may select the more profitable prey (i.e. larger euphausiids). According to Smidt and Pedersen (2000) there appears to be higher zooplankton abundance at Disko than in the south. This is also supported by estimates on copepod biomass at Disko (Thor *et al.*, 2005) and Nuuk (Arendt *et al.*, 2010) which indicate a higher biomass in the former. Results from this study also showed that there was an increase in the amount of prey in the stomachs from low latitudes to Disko independent of fish biomass (Fig. 3). Hence, prey appears to be more abundant in the northern regions perhaps facilitating selective foraging, and euphausiids constitute a rich energy source as evidenced by an energy density of 22.65 kJ g dw^{-1} in *T. raschii* sampled coincident with this study (determined using an adiabatic bomb calorimeter – data are not presented here but they are in general agreement with published values for euphausiids elsewhere (Nicol *et al.*, 1995)). This is similar to or slightly higher than the energy density of copepods (Evjemo *et al.*, 2003; Swalethorp *et al.*, unpublished manuscript). Hence, size and composition make euphausiids a lucrative prey, but whether the feeding differences presented are a result of predator preference or prey distribution needs further investigation.

If superior feeding conditions persist permanently in the northern regions, an increase in production can be expected with increasing latitude. As it has been shown that fish growth is affected by feeding conditions, both in capelin and other pelagic species (Gjøsæter *et al.*, 2002; Ronkkonen *et al.*, 2004), the mechanism of partly food mediated growth differentiation along the Greenlandic west coast suggested by Hedeholm *et al*. (2010) is supported by this study. However, there is a general tendency for an increase in capelin size with latitude as also found in other species (Blaxter, 1985; Hay *et al.*, 2008) and in poikilotherms in general (Lindsey, 1966).

A factor that could potentially have an effect on results of feeding studies is sampling location. All fish in this study were sampled on the shelf but outside of the fjords. Arendt *et al*. (2010) have shown, that the zooplankton community changes progressively through the Nuuk fjord system and since capelin spend at least parts of the year in the fjord their feeding pattern are likely to show temporal variations not addressed in this study.

STOMACH ANALYSIS – LENGTH RELATED DIFFERENCES

In both the south (Qaqortoq) and north (Disko) ontogentetic changes in prey composition was found (Fig. 5). Copepods dominated in the smallest size groups (<110 mm) with larger prey items (amphipods and euphausiids) becoming increasingly more important in larger fish. The large "other" part of the diet in the largest fish from Disko in the north was composed mainly of malacostraca, and was most likely euphausiids based on the appearance of the stomach content such as the presence of appendages and single thoracic segments. The "other" proportion of the diet in the smaller fish from Qaqortoq was due to cirripedea nauplii found only in stomachs from this area. The shift in diet in both areas and the inclusion of euphausiids at Disko is also evident in the average prey size which increased with size in both areas. This size related feeding pattern is consistent with results from other areas (Astthorsson and Gislason, 1997; O'Driscoll *et al.*, 2001). Capelin from Nuuk had likewise to Disko fed on euphausiids but at a smaller size (100-130 mm). Assuming that euphausiids is the more profitable prey, this leaves the question of why they are not consumed in these size groups in Disko and why they are absent from Qaqortoq. There are multiple explanations. The fact that the stomach analyses are only a snapshot of feeding behaviour is one. Others include availability, and euphausiids could well be less abundant in near coastal waters off southern Greenland (Pedersen and Smidt, 2000) but no recent studies are too our knowledge available. Lastly, if prey is as plentiful in Disko, as suggested by stomach fullness, euphausiid-sized prey may be energetically inferior prey to smaller fish through decreased capture success and increased handling time compared to smaller copepods and amphipods.

ISOTOPE ANALYSES

In general the result from the stomach analysis was reflected in the δ^{15}N values. There was an effect of length in the two northern areas, Disko and Uummannaq, which is most likely a result of the inclusion of euphausiids in the diet in larger fish, something not seen in the southern areas where no length effect on δ^{15}N values was apparent. Additionally, the mean δ^{15}N values presented here are similar to other published values for Greenlandic capelin (Møller, 2007) as well as other populations (e.g. Sherwood and Rose, 2005). However, the most striking result from the isotope analyses is the clear shift in $\delta^{15}N$ values from the two southern areas compared to the northern areas (Fig. 7). This could indicate a fundamental difference in the feeding pattern, as the difference of 3.23‰ is equivalent to one trophic level (Post, 2002). Most noticeably this difference does not appear to be related to difference in average fish size and subsequent size related feeding preferences, as the same difference is seen in similar sized fish. Based on the stomach data, the latitudinal change in euphausiid contribution to the diet seems the most likely explanation. This is of course under the assumption, that euphausiids have a higher $\delta^{15}N$ value than the replaced prey items (i.e. copepods and amphipods). To evaluate this, *T. raschii* sampled from 59.2˚N to 69.1˚N in 2008 coincident with capelin sampling, was analysed with regard to $\delta^{15}N$ and $\delta^{13}C$ values using the same procedure as described for capelin. The mean $\delta^{15}N$ value was 8.27‰±0.8 (mean±SD) which is higher than the literature values for *C. finmarchicus* from other arctic waters, such as Iceland and the Fram Strait (approximately 3.5‰ and 6.4‰ respectively, Soreide *et al*., 2006a; Petursdottir *et al*., 2008) and similar to copepod values from the same area (Møller, 2007, Fig. 8). The differences in $\delta^{13}C$ between krill (this study) and calanoids (Møller, 2007) are most likely caused by lipid extraction in the latter study (Soreide *et al*., 2006b). This indicates that the difference in $\delta^{15}N$ values may to some extent be caused by latitudinal related feeding differences which are also consistent with the documented partly carnivorous diet of *T. raschii* (Båmstedt and Karlson, 1998; Falk-Petersen *et al.*, 2000). However, this does not fully explain the difference of 3.32‰ in $\delta^{15}N$ values between areas. The *T. raschii* data also showed a significant latitudinal difference in $\delta^{15}N$ with mean values increasing from south to north (7.72‰ and 9.10‰, respectively, one-way ANOVA, $F_{2,8}$=8.923, P=0.009, Fig. 8). This indicates that a significant shift in the isotopic baseline along the latitudinal gradient which could also influence capelin $\delta^{15}N$ values. The ultimate reason for this fairly large change in baseline is unknown. However, currents along the Greenlandic west coast are a mixture of Polar and Atlantic water masses (Pedersen and Smidt, 2000; Ribergaard *et al.*, 2008). These mix along the West coast homogenizing the water masses moving north. If these differ in isotope signal in the biological available nitrogen this will be reflected in phytoplankton and accordingly in higher trophic levels. Petursdottir *et al*. (2008) found $\delta^{15}N$ values for *Calanus finmarchicus* of 3.5‰ caught on the Reykjanes Ridge south of Iceland, whereas Soreide *et al*. (2006a) found values of 6.4‰ in the Fram strait supporting the notion that the two water masses do indeed differ. Data from these studies on $\delta^{13}C$ also show a slight difference in $\delta^{13}C$ values between areas (-20.3‰ and -21.6‰, respectively). However, this difference is similar to both krill and capelin $\delta^{13}C$ within area variations shown in this study (Fig. 7 and 8) and do not offer further explanation concerning different water masses.

Other sources of the unexplained latitudinal gradient in $\delta^{15}N$ values could be feeding differences not found in the present study such as fish larvae predation including cannibalism (Gerasimova, 1994) or variable terrestrial run could off enrich the water with nutrients with a different isotopic signal. However, it appears that the gradual mixing along the Greenlandic west coast causes a gradual increase in $\delta^{15}N$ values moving north in similar organisms irrespective of feeding behaviour and this must be taken into account when addressing hypotheses by means of stable isotope analysis in Greenland (Møller, 2007). To address the problem in more detail extended temporal resolution in stomach analysis should be accompanied by isotopic samples from low to high trophic levels across latitudes should and preferably the isotopic baseline should be determined in the two dominant water masses as well as in a possible terrestrial component.

IMPLICATIONS OF FEEDING BEHAVIOUR

The considerable differences in feeding pattern across the latitudinal gradient demonstrated here may well affect capelin growth in the region. The growth patterns shown by Hedeholm *et al*. (2010) show convergence with results presented here, in that growth rate increases with latitude which follows the pattern of increased euphausiids importance. Hence, growth rate is highest at Disko throughout capelin life span, as is euphausiid consumption and stomach fullness. Additionally, stomach fullness declined in Uummannaq as does growth rate. In earlier life stages, euphausiids cannot account for the growth differences as they are not consumed before the capelin attain a certain size. Rather, the latitudinal gradient also seen in copepod prey size may partly explain early life stage growth differences. However, the joint effect of temperature (as proposed by Hedeholm *et a*l., 2010) and feeding are not easily separated. Due to insufficient knowledge on capelin migration patterns and population size it is still not possible to make any reliable quantification of capelin predatory impact on the zooplankton community. However, the spatial patterns demonstrated here serve as an initial step in such quantification, but further research on the temporal feeding pattern of capelin is needed.

CONCLUSION

It has been shown that capelin feeding in West Greenland waters is dominated by euphausiids, copepods and amphipods. The diet changes with latitude and fish size with euphausiids becoming more important in the north and in larger fish while the opposite was found for copepods. Stable isotope analysis supported the findings, but also showed a large latitudinal related difference in $\delta^{15}N$ values which could be the result of the joint effect of feeding differences and changes in the isotopic baseline related to different water masses along the investigated section. The significant spatial differences in feeding may well affect growth along the Greenlandic West coast, but further knowledge is needed to allow for anything but tentative estimates.

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Table I. Summary (mean±SD) of samples used to address feeding behaviour in West Greenlandic waters. N is the number of fish caught at a given latitude. Mass is reported as wet mass (g). Length is fork length (mm). No correction for shrinkage caused by freezing was done.

Latitude (˚N)	N	Length (mm)	Mass (g)	Age
60	73	116±0.9	8.3±2.5	2.9
61	130	105±1.3	5.9±2.4	3.0
62	67	120±0.8	9.5±2.6	3.3
63	52	123±1.0	10.4±3.4	3.0
64	45	115±1.0	8.5±2.2	3.2
66	6	125±0.4	9.6±1.3	2.8
67	9	124±0.4	10.6±1.6	3.6
68	9	120±0.5	9.0±2.0	3.1
69	131	143±1.3	17.2±4.9	3.7
70	35	134±1.4	13.8±4.7	3.4
72	14	123±0.5	9.7±1.9	3.8
Total	572	122±1.74	10.6±5.3	3.3

Fig. 1

Composition of stomach content in capelin (N=572) from the Greenlandic west coast .The proportion made up by the individual prey categories are reported based on wet mass (top) and by number (bottom).

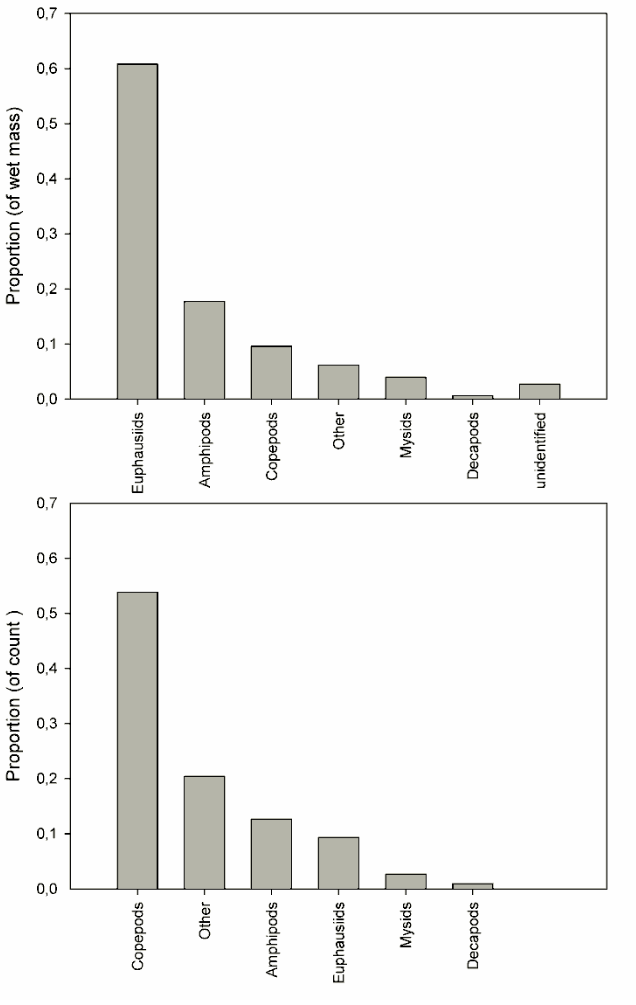


Fig. 2

The relative contribution (of wet mass) of individual prey categories to the overall prey composition in Greenlandic capelin at different latitudes along the Greenlandic west coast. The composition is reported for both all sampled fish (top) and for fish within the same size range (115-130mm, bottom). See text for a more detailed description of the individual prey categories. ■: Euphausiids, ▨: Amphipods, ■: Copepods, □: Other, ▢: Unidentified.

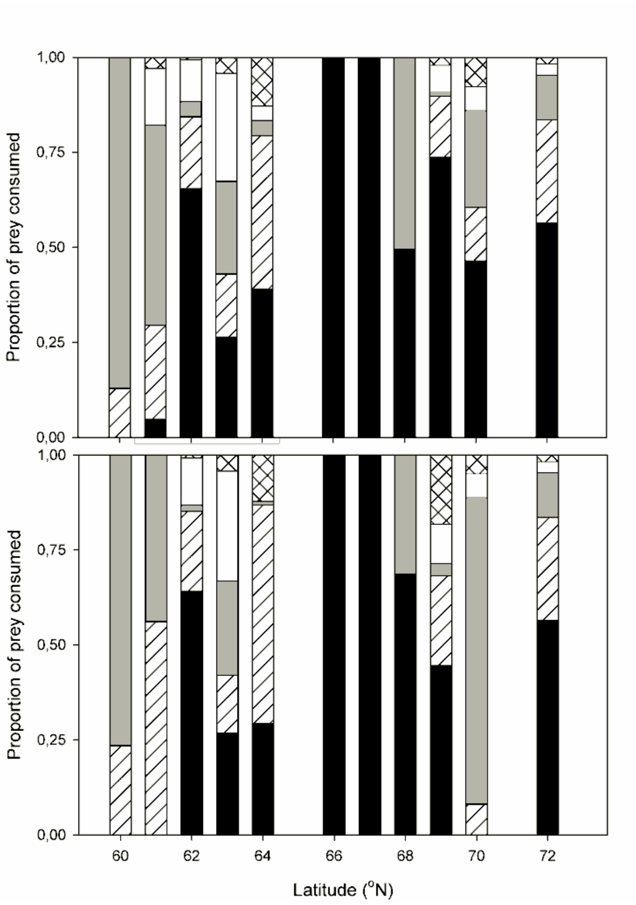


Fig. 3

The left Y-axis and filled circles represent the relative amount of prey as a function of the latitude at which the capelin were caught. The right Y-axis and open circles represent the mean stomach fullness (ranging from 0-5) as a function of latitude. The line represents a fitted line to the relative amount of prey: $Y=41.7988x-0.3173x^2-1364.759$, $R^2=0.55$, $P=0.039$. ●: relative prey wet mass, ○: stomach fullness.

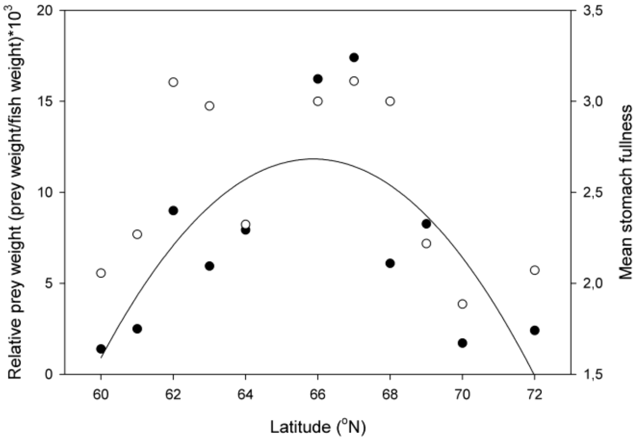


Fig. 4

The proportion (% of wet mass) of three individual calanoid species to the overall composition of the copepods (that were identified to species) in 115-130 mm Greenlandic capelin. *Calanus finmarchicus* and *Calanus glacialis* are grouped together due to difficulties in correct identification due to digestion (●: *Calanus finarchicus/glacialis*,: x: *Calanus hyperboreus*, ○: *Metridia longa*).

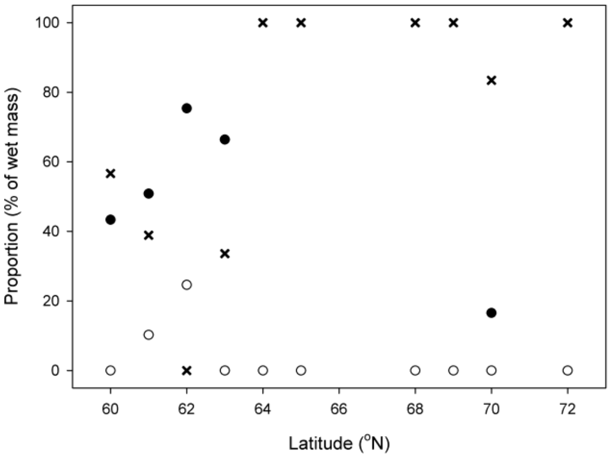


Fig. 5

The proportional (of wet mass) contribution of individual prey groups to the overall diet of capelin in different size categories (mm, fork length). Data are from four areas along the Greenlandic west coast (Qaqortoq, 59.5-61˚N, N=242; Nuuk, 63.5-65˚N, N=61; Disko, 69-70.5˚N, N=196; Uummannaq, 71.5-72.5˚N, N=18). See text for more details on prey categories. ■: Euphausiids, ◩: Amphipods, ■: Copepods, □: Other, ❏: Unidentified.

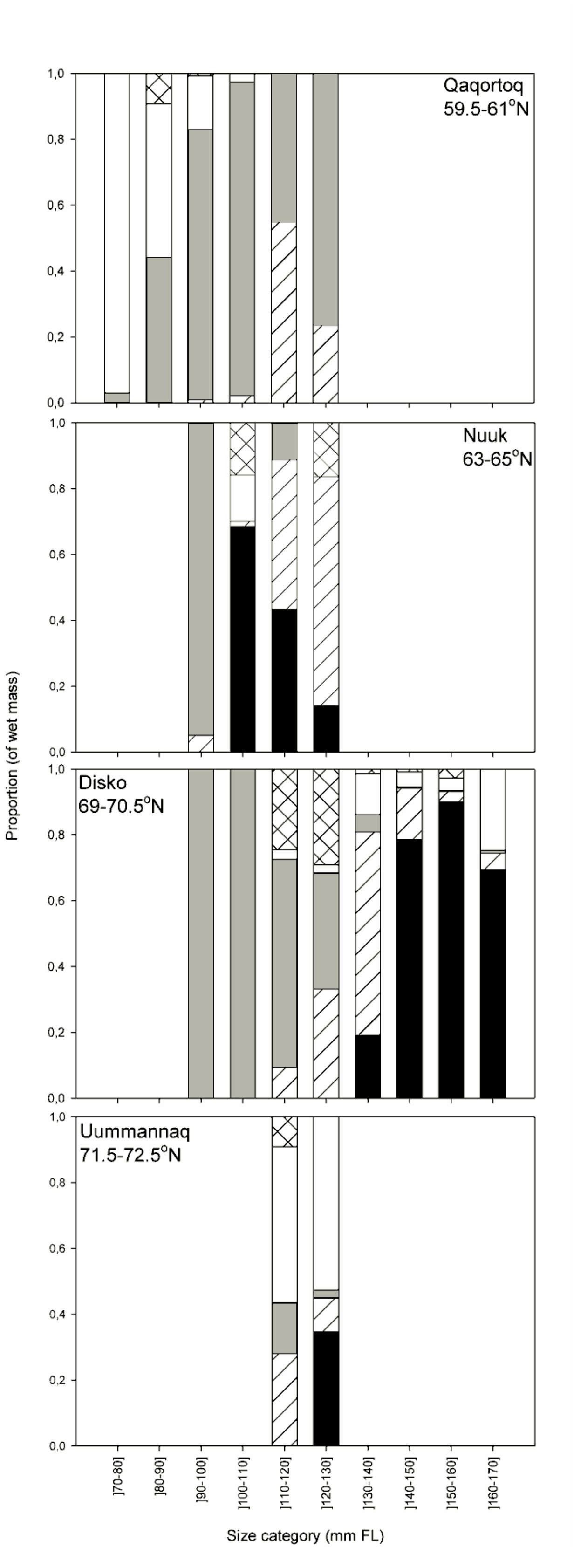

Qaqortoq
59.5-61°N
Nuuk
63-65°N
Disko
69-70.5°N
Uummannaq
71.5-72.5°N
Proportion (of wet mass)
1,0
0,8
0,6
0,4
0,2
0,0
]70-80]
]80-90]
]90-100]
]100-110]
]110-120]
]120-130]
]130-140]
]140-150]
]150-160]
]160-170]
Size category (mm FL)

Fig. 6

Mean prey size (mm) of all prey from individual capelin as a function of capelin length (mm, fork length). Data are from four areas along the Greenlandic west coast: ●: Qaqortoq (59.5-61˚N); ■: Nuuk (63.5-65˚N); ○: Disko (69-70.5˚N) and □: Uummannaq (71.5-72.5˚N).

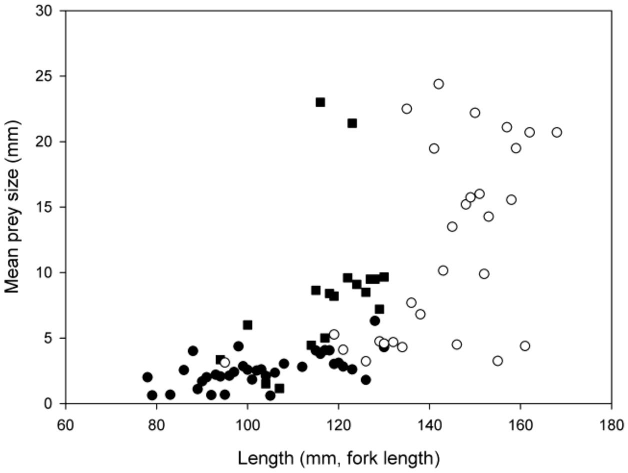


Fig. 7

$\delta^{15}N$ and $\delta^{13}C$ values in capelin from the Greenlandic west coast. ●: Qaqortoq (59.5-61˚N); ■: Nuuk (63.5-65˚N); ○: Disko (69-70.5˚N) and □: Uummannaq (71.5-72.5˚N); N=12 in all cases.

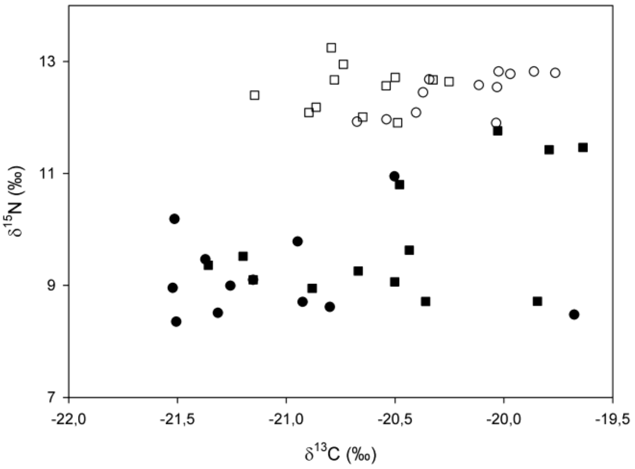
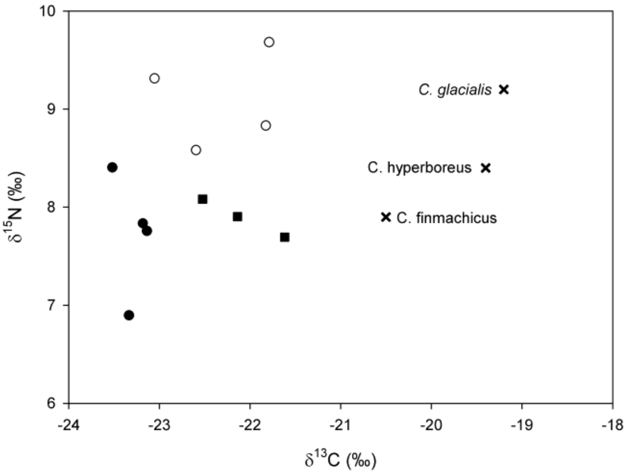


Fig. 8

δ^{15}N and δ^{13}C values in krill (*Thysanoessa raschii*) from the Greenlandic west coast. ●: Qaqortoq (59.5-61˚N, N=4); ■: Nuuk (63.5-65˚N, N=3) and ○: Disko (69-70.5˚N, N=4). Each sample was taken from a homogenized sample of 5-8 individuals and each point represents a mean value of these individuals. Data on *Calanus finmachicus, Calanus hyperboreus* and *Calanus glacialis* are based on Møller (2007).



Paper II

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

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

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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.

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 beachspawning 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.

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 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 (×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 (mm) 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 backcalculated 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 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 = 1 137), 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), and was 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 = 1 362).

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 logtransformed 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 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 18C 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 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 $˚C^{-1}$ $year^{-1}$ 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 1–28C 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.

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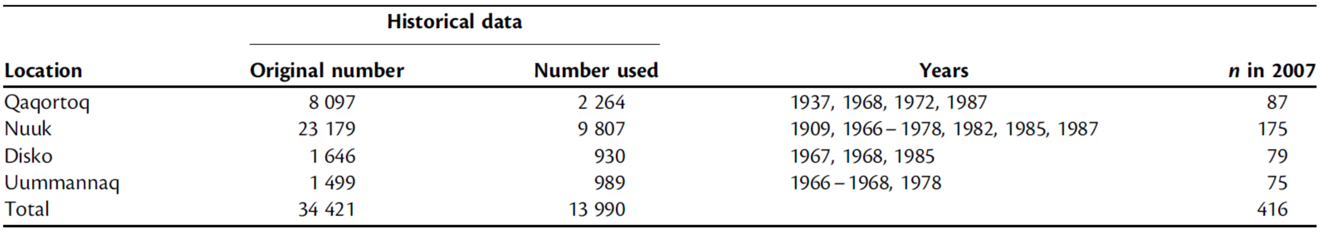
Table 1. The number of West Greenland capelin and the years used for the historical and 2007 length frequency distributions (Figure 3) at Qaqortoq, Nuuk, Disko, and Uummannaq.



	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

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). 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.

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)

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.

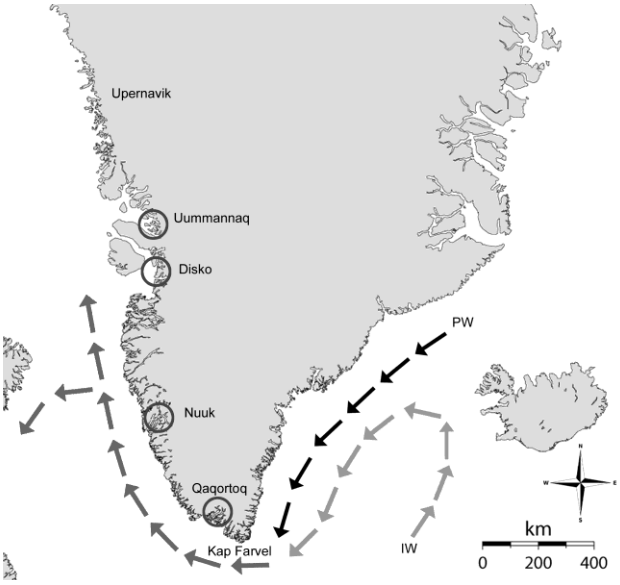


Figure 2. A saggital otolith from a 4-year-old male capelin caught at Disko in 2007. Line 1 runs from the end of the rostrum through the centre of the otolith, and Line 2 from the centre of the otolith to intersect growth increments at an angle of 90˚. The growth increments used in the analyses were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

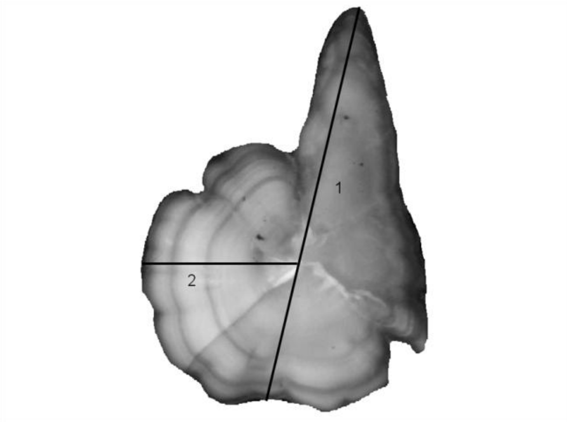


Figure 3. Historical length distributions for male West Greenland capelin in 1909–1989 (left, n = 13 990) and in 2007 (right, n = 416). All fish lengths are assigned to 2 mm intervals. Table 1 lists the years included in the historical data.

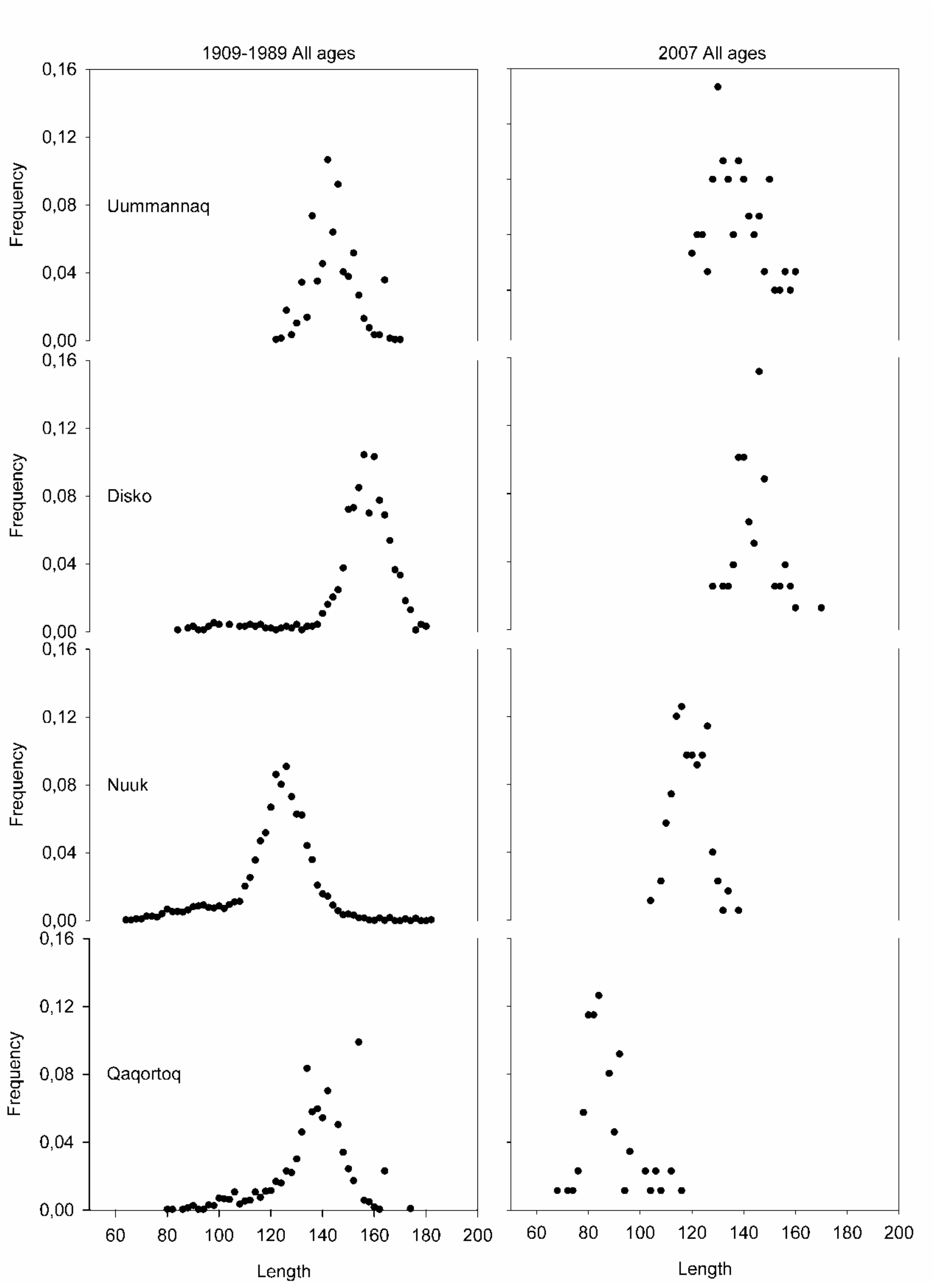


Figure 4. Mean length (SL) of 3-year-old male capelin caught at four different latitudes along the west coast of Greenland in 2007 (one-way ANOVA, $F_{3,172} = 398.040$, $p < 0.0005$). Average mean lengths and average latitude were used when fish from several locations within each area were used. The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

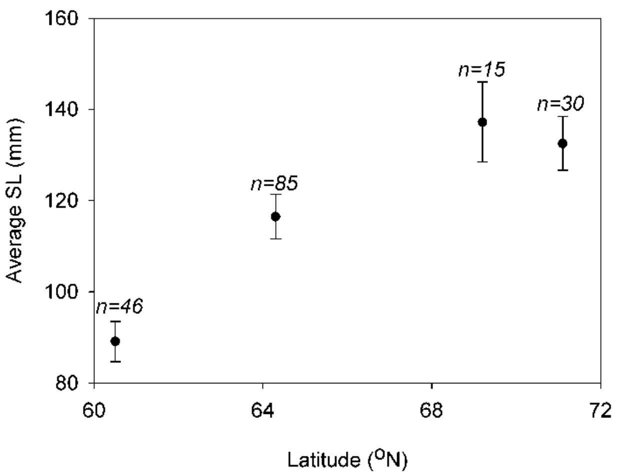


Figure 5. Otolith radius as a function of standard length (SL) for all capelin from Qaqortoq (open circles, n = 25, 60˚N), Nuuk (dots, n = 40, 64˚N), Disko (open squares, n = 40, 69˚N), and Uummannaq (filled squares, n = 40, 71˚N) used in growth analysis. An additional 39 fish from other locations along 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).

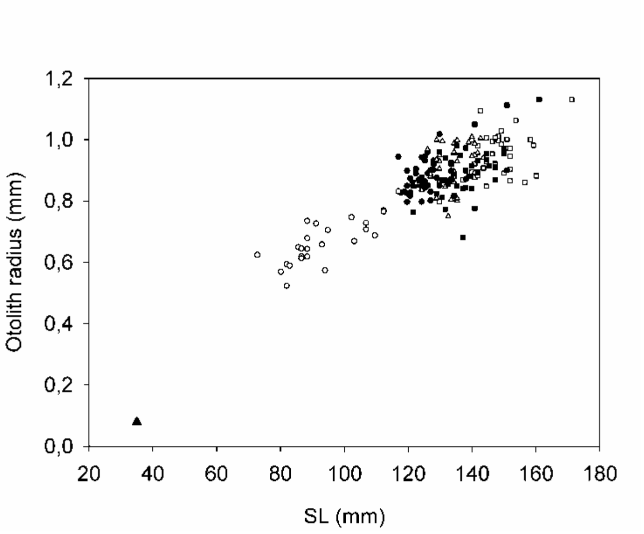


Figure 6. Somatic growth (in millimetres) of capelin from Qaqortoq (dots, n = 25, 60˚N), Nuuk (triangles, n = 40, 64˚N), Disko (squares, n = 40, 69˚N), and Uummannaq (crosses, n = 40, 71˚N). Growth was estimated from the back-calculated lengths using the biological intercept method. Lines represent the 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.

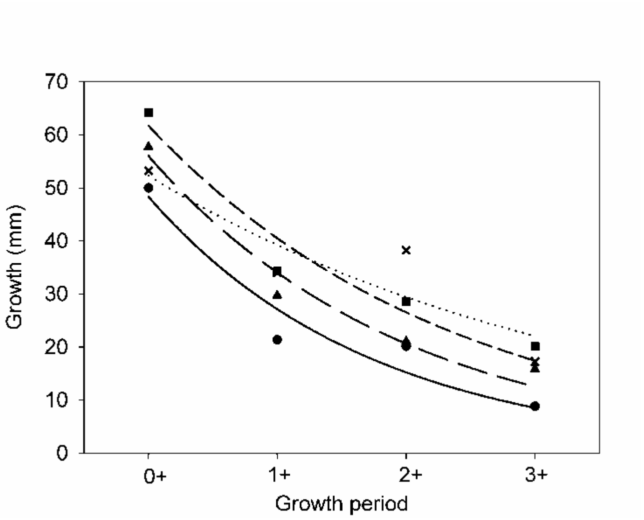


Figure 7. Average temperatures for 20–50 m averaged from 1908 to 2007 for West Greenland waters (60–73˚N 44–57˚W) from the ICES database (see text). Only measurements east of the shelf break on the west coast of Greenland were used (<500 m). Top left, data from all months and years (n = 18 753); top right, data for July (n = 4 671); bottom left, data for August (n = 1 632); 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).

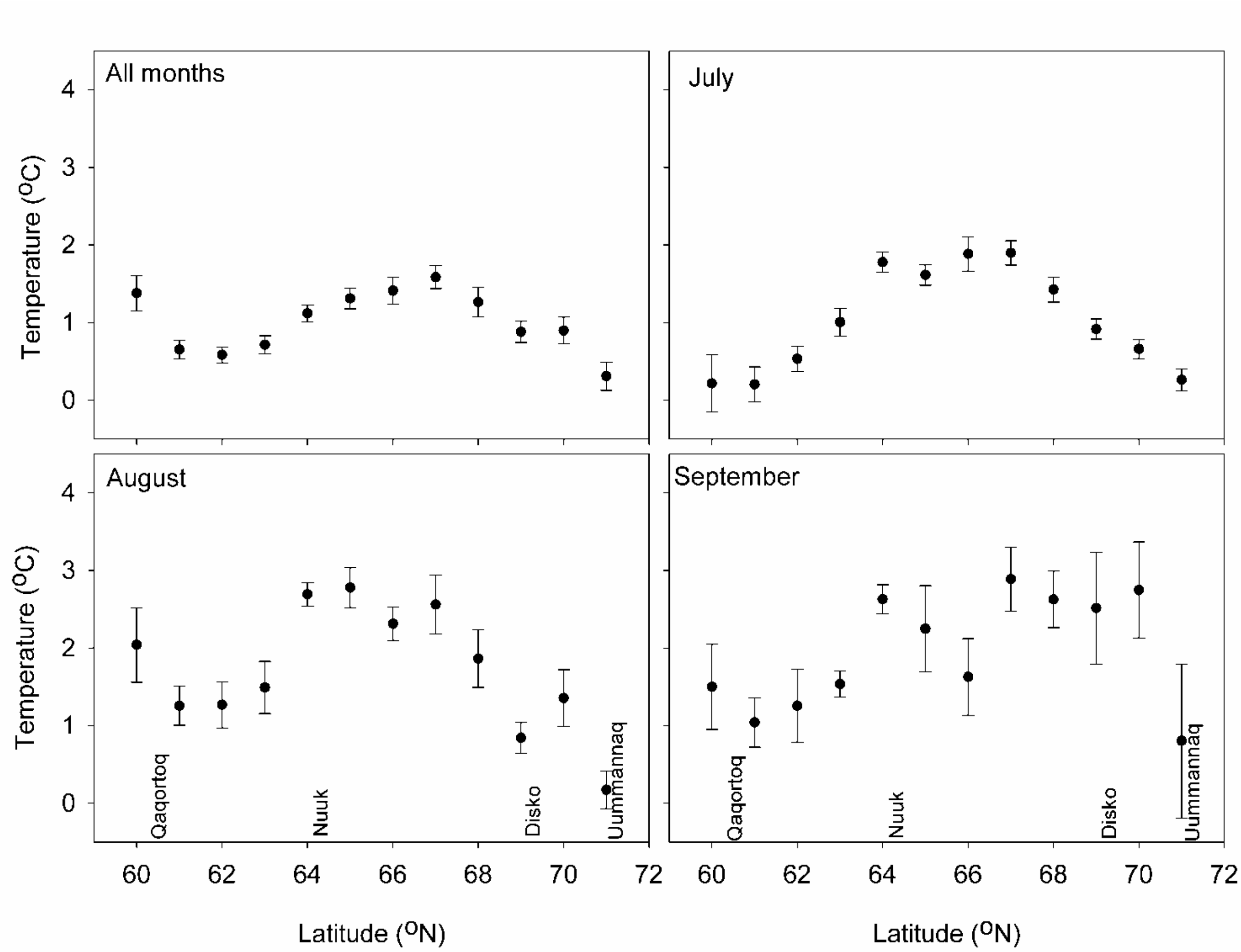
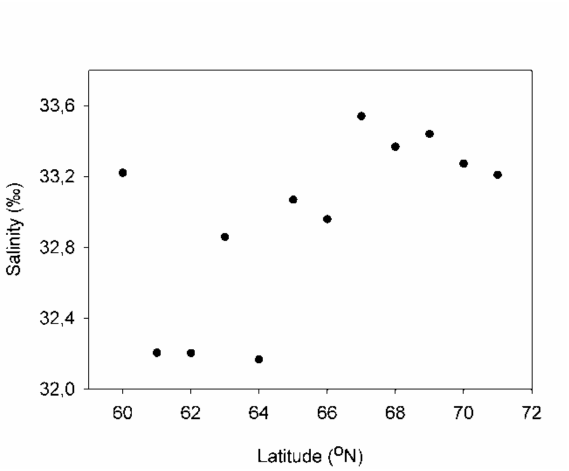


Figure 8. Average salinity in August for 20–50 m averaged over the period 1908–2007 for West Greenland waters (60–73˚N 44–57˚W) from the ICES database (see text). Only measurements east of the shelf break on the west coast of Greenland (<500 m) were used (n = 1 362).



Paper III

Energy content and fecundity of capelin (*Mallotus villosus*) along a 1500 km latitudinal gradient

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Submitted to Marine Biology

Energy content and fecundity of capelin (*Mallotus villosus*) along a 1500 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 1500 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 etc., Cury *et al.*, 2000; Bakun, 2006) capelin have a life cycle characterised by a short lifespan, high mobility, high energetic need (as a result of their numbers and high growth rates) and variable cohort strength (Gjøsæter and Loeng, 1987; Frank and Carscadden, 1989; Carscadden *et al.*, 2001; Gjøsæter *et al.*, 2002; Vilhjalmsson, 2002). These characteristics can result in a fluctuating population biomass on a short time scale as demonstrated for both capelin (Gjøsæter, 1998; Vilhjalmsson, 2002) and sardine-anchovy systems across world oceans (Schwartzlose *et al.*, 1999).

In Greenland, capelin is found on both the east and west coast extending north to 73˚N and 66˚N, respectively (Friis-Rødel and Kanneworff, 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 1930s 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*. 2010, 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 spatial differences in vital life history characteristics such as fecundity, energy allocation, condition and productivity.

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 not only related 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 Greenlandic 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 Greenlandic capelin. As stomach content and growth rates have been shown to increase with latitude in this area (Hedeholm *et al*. 2010, Hedeholm *et al*. 2010, 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 Kanneworff, 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 Greenlandic 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 (Figure 1). Non-spawning capelin were collected in both years by RV “Paamiut” during yearly shrimp and fish surveys conducted by the Greenland Institute of Natural Resources. In 2007, sampling was done from 13 June to 9 September and in 2008 from 19 June to 8 August. 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 was taken.

Spawning capelin were only sampled in 2007. The samples were collected during beach spawning events in five general areas spanning 1300 km along the Greenlandic West coast: Qaqortoq (60˚00N), Nuuk (64˚00N), Sisimiut (66˚50N) Disko (69˚00N) and Uummannaq (71˚00N, Figure 1). As spawning is temporally displaced along the coast (Kanneworff, 1967), samples were collected later in the north than in the south, and sampling took place from 11 May to 19 July. Samples of both spawning and non-spawning capelin were frozen at -20 ˚C immediately after capture (see Table 1).

Physical measurements and fecundity

Capelin were measured to the nearest mm below (fork length) and weighed to the nearest 1/10 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. Gonads were removed from spawning females, blotted dry and weighed to the nearest 1/1000 g. Fish that had released eggs into the body cavity were excluded from analysis as some eggs may already have been spawned.

20-60 eggs from the posterior part of the right gonad were weighed and counted, as the left gonad is known to be underdeveloped (Winters, 1971). Based on this and total gonad weight fecundity was calculated assuming that no difference existed between various parts of the gonad (Huse and Gjøsæter, 1997).

Energy measurements

Muscle tissue (mean ± 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 gonads from spawning females were freeze dried for 24 hours after which no further weight loss took place. The tissue samples were weighed (dry weight, dw) and the water content was calculated (% of wet weight, 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 reanalysed. Energy density in wet samples (reported as: kJ g ww^{-1}) is reported in some aspects of the study while energy density in dry samples was used in most analyses (kJ g dw^{-1}). 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 are 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 hours at 550˚C to determine the ash content of the samples, and energy density was calculated based on these values (kJ g ash free dw^{-1}). Samples from gonads 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 fish. The relative reproductive investment of each fish was calculated as the amount of energy in the gonads relative to total fish energy content (gonads 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 (60-61˚N), Nuuk (63-64˚N), Sisimiut (66-67˚N), Disko (68.5-70˚N) and Uummannaq (71-72˚N, see Figure 1) to for the purpose of 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 (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

Energy densities of 259 fish (124 spawning and 135 non-spawning) and 18 female gonads were determined (Table 1). As no difference in energy density (kJ g dw^{-1}) was found between 2007 and 2008 for spawning fish (ANCOVA, $F_{(1,128)} = 0.006$, $P = 0.94$) irrespective of both size and capture location the two years were pooled.

Latitudinal and length effect

In non-spawning capelin there was a significant effect of both area (ANCOVA, $F_{(3,122)} = 3.573$, $P = 0.016$) and length (ANCOVA, $F_{(1,122)} = 26.903$, $P < 0.0005$) on energy density, but also a significant interaction between the two (ANCOVA, $F_{(3,122)} = 4.084$, $P = 0.008$, Figure 2). The interaction was caused by Disko and removing this area from the analysis yielded non-significant interaction and area terms (ANCOVA, $F_{(2,98)} = 2.105$, $P = 0.127$ and $F_{(1,98)} = 34.768$, $P = 0.172$, respectively). Using the parameter estimates (following model reduction), the overall length effect and difference between the three similar areas (Qaqortoq, Nuuk and Uummannaq) and Disko can be depicted as shown in Figure 3. A clear positive relationship between length and energy density was seen for the pooled areas, while size effects in the Disko 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, $r^2 = 0.58$, $F_{1,16}=8.243$, $P=0.028$) under the assumption that the single outlier (]110-115]) 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 Disko and low values at Qaqortoq (mean ± SD = 21.87 ± 0.60 kJ g dw^{-1} and 20.86 ± 0.29 kJ g dw^{-1}, respectively, Figure 4).

Spawners vs. non-spawners

Irrespective of size and location, a mean difference of 0.286 kJ g dw^{-1} was found in energy density (based on dry weight, kJ g dw^{-1}) between spawners and non-spawners (ANCOVA, $F_{(1,248)} = 248.362$, $P < 0.0005$, Figure 2). However, when comparisons were based on wet weight (kJ g ww^{-1}), the non-spawning fish had energy densities ranging from 4-4.5 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}, Figure 5). The pattern 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 weight based comparison was caused by a significant difference in water content between spawners and non-spawners, irrespective of length (mean ± SD = 82.7 ± 1.11 % and 79.4 ± 1.02 %, respectively, ANCOVA, $F_{(1,199)} = 452.713$, $P < 0.0005$).

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, $r_s=-0.093$, $N = 135$, $P=0.285$). In the individual areas, the sampling time span enabled such analyses in three cases (Nuuk, Qaqortoq and Disko). 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 kJ g dw^{-1} 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 kJ g dw^{-1} to 21.24 kJ g dw^{-1} (ANCOVA, $F_{(4,25)} = 5.044$, $P = 0.004$), while no change in size was seen during the same period (ANCOVA, $F_{(1,25)} = 1.279$, $P = 0.27$).

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, $F_{(1,57)} = 19.385$, $P < 0.0005$, Figure 6). A difference was also found between the sexes (ANCOVA, $F_{(1,57)} = 4.893$, $P = 0.031$) but a significant interaction (ANCOVA, $F_{(1,57)} = 5.366$, $P = 0.024$) made comparisons across the sampled length range ambiguous. Within the overlapping size range (115-132mm), no difference was found between sexes when pooling all individuals based both on dry (kJ g dw^{-1}, Student's t-test, $t_{20.25} = -0.216$, $P = 0.83$) and wet mass (kJ g ww^{-1}, Student's t-test, $t_{30} = 0.112$, $P = 0.91$).

Fecundity and reproductive investment

Fecundity increased with gutted weight (range: 3745-11317 eggs, regression, $r^2 = 0.69$, $F_{1,16} = 35.955$, $P < 0.0001$) and the relationship was best described as: Fecundity = 356.63 * gutted weight$^{1.4414}$, Figure 7). On average the female gonads contained (mean ± SD) 37.8 ± 3.3 % of total female capelin energy, and reproductive investment was positively related to weight (Linear regression, $r^2 = 0.36$, $F_{1,16} = 8.912$, $P = 0.009$, Figure 7) as was the gonadosomatic index (Linear regression, $r^2 = 0.35$, $F_{1,16} = 19.176$, $P < 0.0005$, data not shown). The individual egg energy content was (mean ± SD) 2.67 ± 0.36 J but was not related to weight (Spearman's correlation, $r_s=0.176$, $N = 18$, $P = 0.486$).

Discussion

To our knowledge, this study represents the first data on energy density for Greenlandic 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 include only assimilable energy (17.8-20.0 kJ g dw^{-1}). Converting values given by Anthony *et al.* (2000) on Alaskan capelin to energetic densities using an energy equivalent of 23.2 kJ g dw^{-1} for protein (as determined in this study using reference material) we find an energy density of 26.6 kJ g ash free dw^{-1} in non-spawning capelin compared to 22.3 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 24-29 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 (Jezierska, 1974; Craig *et al.*, 1978). Other studies using bomb calorimetry on pelagic fishes obtain values much like those showed 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, correcting for efficiency of the metabolic pathway is needed (Ball *et al*. 2007).

Lastly, the timing of the samples collected in this study may partly explain the difference, 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. Hence, Jangaard (1974) observed an increase from 21.2 kJ g dw^{-1} in June/July to 26.7 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.

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 large difference between Qaqortoq and Disko 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 (Disko), respectively. Hence, the decline in energy density in Uummannaq north of Disko 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 one-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, Figure 2). The reason for the inconsistency in the Disko 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 Alaskan 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 not only reduces 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 Greenlandic 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 Kanneworff, 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 Greenlandic 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 ± SD = 21.4 ± 0.5 kJ g dw^{-1}), but differed significantly based on wet mass (mean ± SD = 3.44 ± 0.97 kJ g ww^{-1}) because of a significant difference in water content (Figures 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.

Fecundity and reproductive investment

Fecundity estimates (mean ± SD = 6185 ± 2249 eggs) were much lower than estimates from the Barents Sea (approx. 11000, e.g. Gjøsæter and Monstad, 1973; Huse and Gjøsæter, 1997), Pacific (approx. 20000, Velikanov, 2002) and Canada (>20000, Nakashima, 1987). However, as all studies (the present one included) show positive fecundity-size relationships (Figure 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 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 charr (Jonsson and Jonsson, 1997; Finstad *et al.*, 2002) and Atlantic cod in Greenland (Hedeholm *et al.*, unpublished manuscript).

Reproductive investment increased with weight, but individual egg energy content (mean ± SD = 2.67 ± 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 weight 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 gonads. 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 Kanneworff, 2002). In iteroparous species it might be expected that first time spawners produce lower quality eggs or/and 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.

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Table I

Location, number, physical data, water content (%) and energy density (kJ g dw^{-1}) for all sampled capelin (mean ± SD). Length and weight data in the "gonads" section refers to the fish, while the remainder refers to the gonads. Qaqortoq: 60-61˚N, Nuuk: 63-64˚N, Sisimiut: 66-67˚N, Disko: 68.5-70˚N and Uummannaq: 71-72˚N.

Area	N	Length (mm)	Weight (g)	Water content (%)	Energy density (kJ g dw^{-1})
			Spawning (2007)		
Qaqortoq	6	120 ± 4.2	10.1 ± 1.4	82.1 ± 1.1	20.861 ± 0.287
Nuuk	61	124 ± 13.3	13.0 ± 4.5	82.5 ± 0.9	21.276 ± 0.691
Sisimiut	22	144 ± 6.3	21.8 ± 3.3	82.8 ± 1.1	21.155 ± 0.273
Disko	14	149 ± 4.6	29.9 ± 4.0	81.8 ± 1.0	21.856 ± 0.597
Uummannaq	21	145 ± 6.9	24.5 ± 4.3	84.0 ± 0.8	21.423 ± 0.340
			Non-spawning (2007+2008)		
Qaqortoq	41	113 ± 1.9	7.7 ± 3.9	79.7 ± 1.0	20.869 ± 0.748
Nuuk	42	122 ± 1.2	10.1 ± 3.1	79.7 ± 1.3	21.122 ± 0.691
Sisimiut	5	124 ± 0.4	10.7 ± 2.0	80.0 ± 0.6	20.984 ± 0.381
Disko	26	142 ± 1.5	16.0 ± 5.2	79.3 ± 0.6	21.276 ± 0.545
Uummannaq	24	126 ± 1.5	8.9 ± 1.7	78.7 ± 0.6	20.950 ± 0.612
			Gonads (2007)		
Nuuk	18	111 ± 8.9	9.5 ± 2.3	71.3 ± 1.6	24.795 ± 0.251

Figure 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, Disko and Uummannaq. The circles mark the off-shore areas where non-spawning capelin were sampled in 2007 and 2008.

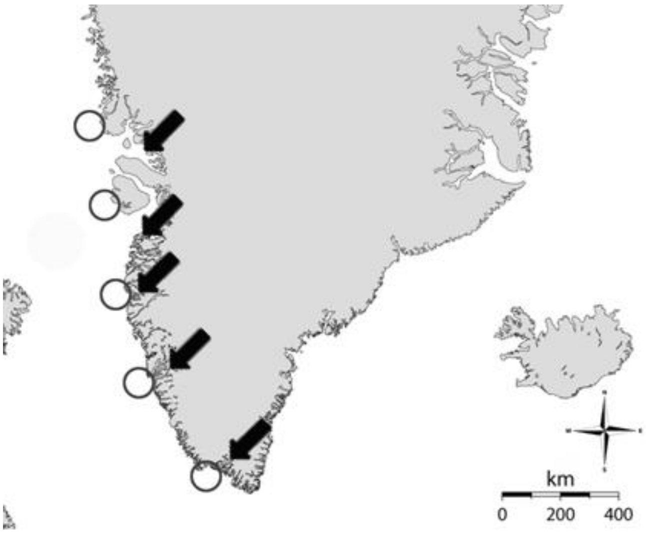


Figure 2

Mean energy density (kJ g dw^{-1}) of spawning (open circles) and non-spawning (filled circles) capelin caught in 2007 and 2008 along the Greenlandic west coast at five locations ($N_{spawners}$, $N_{non\text{-}spawners}$): Qaqortoq (6, 41), Nuuk (61, 42), Sisimiut (22, 5), Disko (14, 26), Uummannaq (21, 24). All areas are shown separately and combined. The combined values are un-weighted 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.

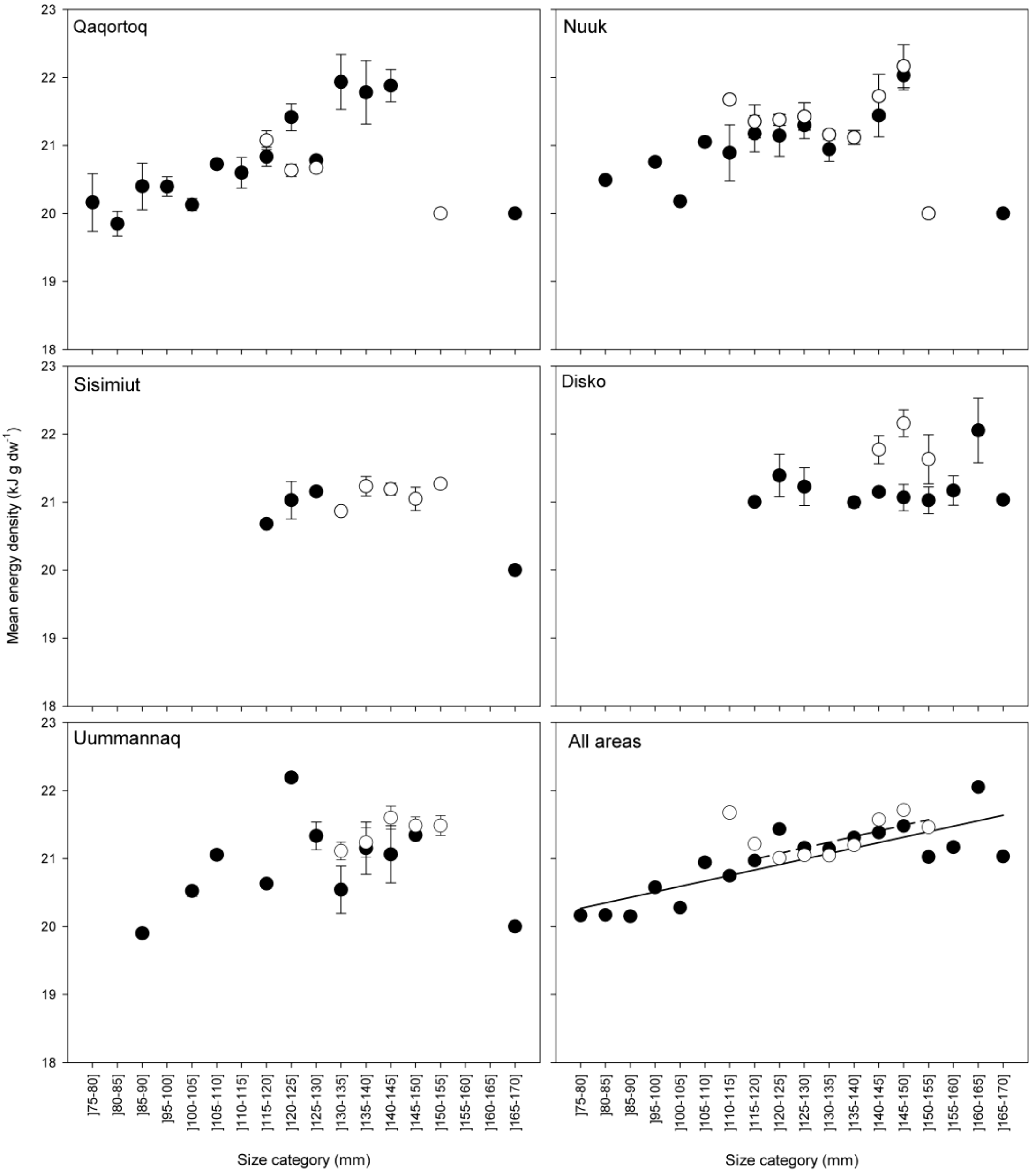


Figure 3

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 Disko 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 Disko respectively.

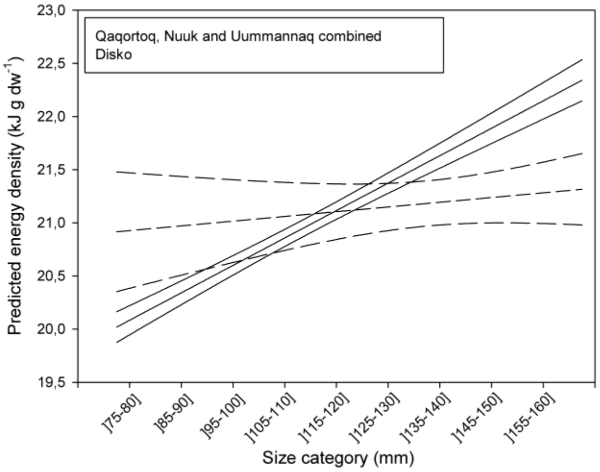


Figure 4

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

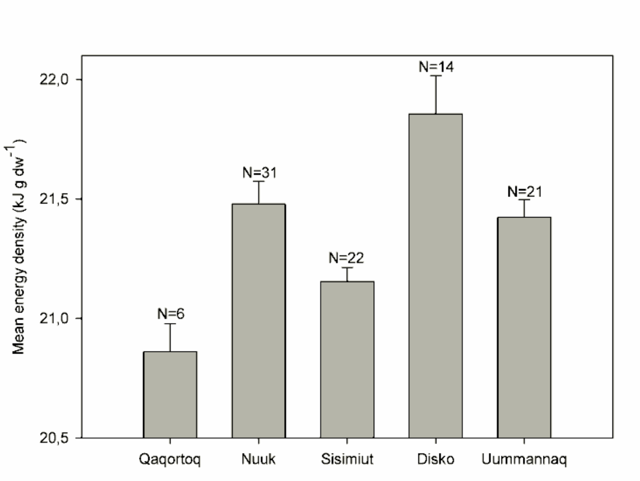


Figure 5

Mean energy density (kJ g ww^{-1}) of spawning (open circles) and non-spawning (closed circles) capelin caught in 2007 and 2008 along the Greenlandic west coast at five locations ($N_{spawners}$, $N_{non\text{-}spawners}$): Qaqortoq (6, 41), Nuuk (61, 42), Sisimiut (22, 5), Disko (14, 26), Uummannaq (21, 24). All areas are shown separately and combined. The combined values are un-weighted averages. Bars represent standard error.

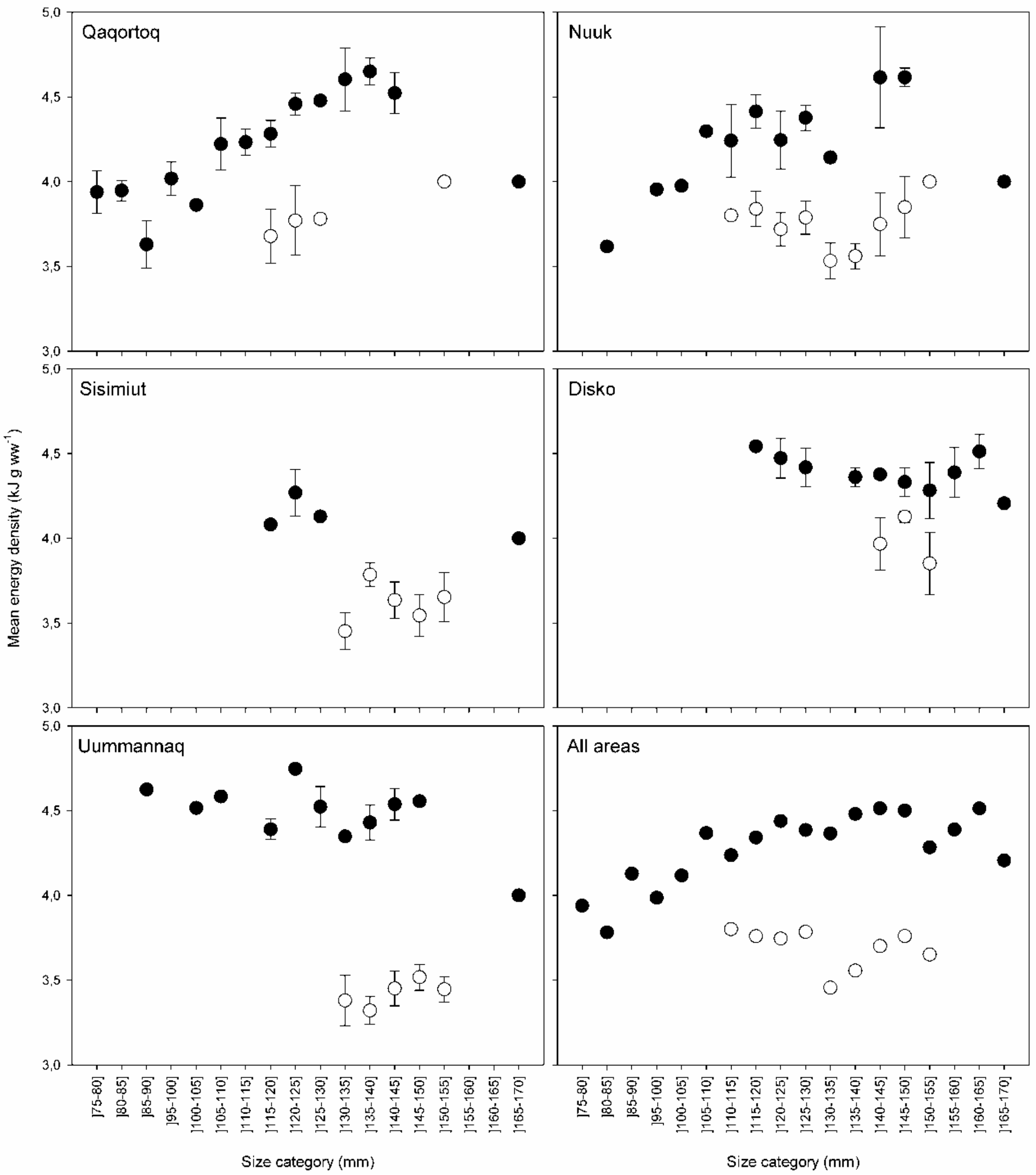


Figure 6

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.

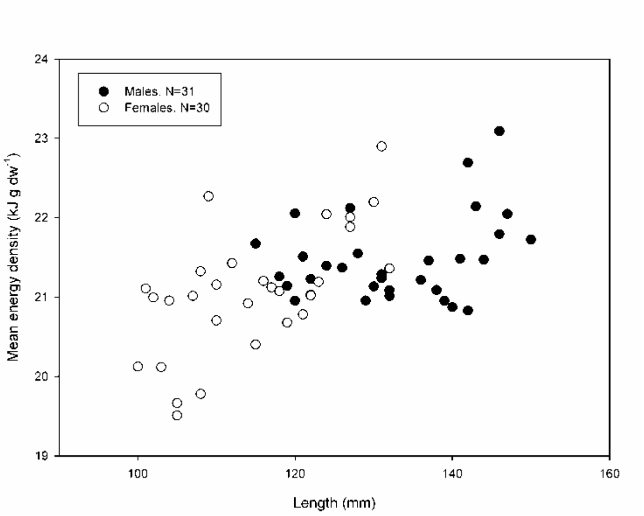
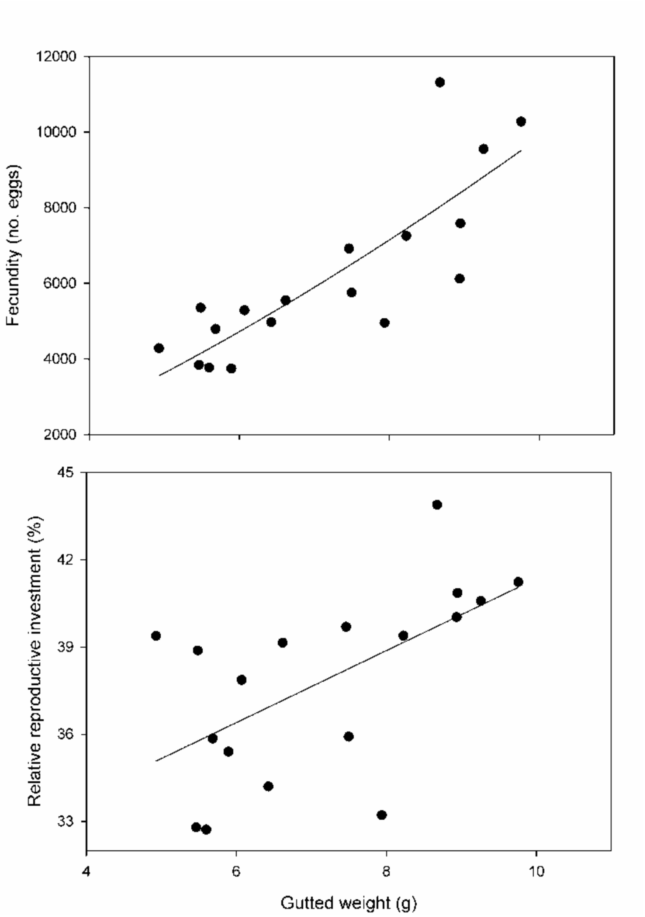


Figure 7

Top: fecundity of female capelin from Nuuk fjord (64˚N) as a function of gutted wet weight (N=18). The line represents power regression (Fecundity = 356.63 * gutted weight$^{1.4414}$, r^2=0.69, P<0.0001).

Bottom: the relative reproductive investment (%) measured as total gonad energy relative to total fish energy content (gonads excluded). The line represents linear regression.



Paper IV

Summer diet of inshore cod in West Greenland: importance of capelin

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Summer diet of inshore cod in West Greenland: importance of capelin

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Abstract

The summer feeding ecology of Atlantic cod (Gadus morhua) *was investigated in two West Greenlandic fjord systems (Nuuk and Sisimiut fjords) in order to quantify the relative importance of different prey species. The prey composition based on stomach content was similar in cod from both fjords, with capelin* (Mallotus villosus) *being the most important prey by weight (70%) followed by "other prey" (mostly other fish species, 12%) and crabs (8%). There were indications of an ontogenetic shift in diet with non-fish prey (fish eggs, crustaceans) being more dominant in smaller cod below 30 cm in length (24%) while fish prey dominated in larger cod (84%). The condition factor of cod differed between fjords being the highest in the most northerly fjord (Sisimiut) in all size classes. In both fjords, the condition factor declined in the largest fish. This could possibly be related to completed spawning activity. However, decreased capelin availability during recent years may have also influenced the condition of larger cod. The latter assumption is consistent with a demonstrated historical decline in length-at-age in larger cod.*

Key words: capelin, condition factor, crustaceans, *Gadus morhua*, inshore, length-at-age, ontogenetic shift

INTRODUCTION

Atlantic cod (*Gadus morhua* L.) is found throughout the North Atlantic. This also includes the coast of Greenland where it lives at the northern limit of its range (Drinkwater, 2005). Here Atlantic cod has been a very important species for commercial fisheries in the past with catches up to 500.000 metric tons in the late 1960's. Subsequently, the population collapsed (Buch *et al.*, 1994), and shortly thereafter, the yearly catch decreased to about 50 metric tons in the 1990's and has at present not recovered (Storr-Paulsen *et al.*, 2004).

Feeding behaviour, along with temperature, has been shown to affect cod condition (Rose & O'Driscoll, 2002; Mello & Rose, 2005; Ratz & Lloret, 2005). Because there are only a few studies on feeding habits and condition of Atlantic Cod in West Greenland (e.g. Hansen, 1949; Lloret & Ratz, 2000), more knowledge on the feeding ecology of cod in Greenlandic waters is important from two perspectives. Firstly, these studies could help elucidate the importance of different prey species as one step toward understanding why cod populations have not regained their former population strengths. For instance, it has been shown that the lipid-rich capelin (*Mallotus villosus* Müller) (Montevecchi & Piatt, 1984; Lawson *et al.*, 1998) is a key prey item for Atlantic cod in Canadian and Icelandic waters (Methven & Piatt, 1989; Magnusson & Aspelund, 1997), and cod populations are affected by fluctuations in capelin stock size (Marshall *et al.*, 1999; Vilhjalmsson, 2002). Furthermore, Hansen (1949) has shown that this has also been the case for the Atlantic cod in West Greenland in the past. Secondly, if cod once again becomes abundant in West Greenlandic waters, knowledge of its feeding behaviour and subsequent impact on the prey community through top down effects would be important, as a large abundance of cod will affect the ecology of other species, including commercially exploited species such as snow crabs (*Chionoecetes opilio*), deepwater shrimp (*Pandalus borealis*) and capelin.

Thus, to add to the knowledge of Atlantic cod's feeding ecology in West Greenland this study was undertaken to investigate their summer diets in inshore areas. In particular, it was of interest to evaluate the importance of capelin in the diet of cod and describe possible ontogenetic diet shifts. Additionally, as the inshore cod in Greenland is largely non-migratory (Storr-Paulsen *et al.*, 2004) two separate fjord systems were investigated to assess the possible existence of regional differences in prey composition. A large spatial variation in prey composition might suggest that the reason for the lack of recovery of the cod population in West Greenland would not necessarily be linked to absence of specific key prey species.

MATERIALS AND METHODS

Study site and sampling

The study was carried out from June 19th to July 9th in 2005 in West Greenland, where a total of 227 Atlantic cod were caught in two main areas: the Nuuk (Godthaab) fjord system (100 fish) and the Sisimiut (Holsteinsborg) fjord system (127 fish). These areas are in NAFO division's 1D (North of 62°30' and south of 64°15') and 1B (North of 68°00' and south of 68°50'), respectively.

Fish were caught using survey gillnets with five different mesh sizes (16.5, 18, 24, 28 and 33 mm) in sections of equal length (10 m). Ten gillnets were combined to make up a total of 100 meters of net with each of the five mesh sizes represented twice. The order of the different mesh sizes was randomized, and each net was separated from neighbouring nets by 2 m. The nets were set 2 m off the bottom.

At each location the 100 m nets were set at a maximum depth of 20 m. Depending on weather conditions, the nets were set to fish for 6½ - 12 hours which ensured at least one tidal cycle during the fishing period. Due to the latitude and time of year the light intensity varied little over the course of a day. At the end of the fishing period the nets were retrieved and all Atlantic cod were measured (total length, L_T, cm) and weighed (wet weight, W, g). With the exponent determined from length-weight regression (3.033), the condition factor (CF) was calculated as follows:

$$CF = 100 \times \frac{W}{L_T^{\ 3.033}}$$

Fish showing evidence of regurgitation (i.e. stomach content in the mouth) or having been partly eaten by scavengers were not included in this study. Remaining fish were gutted, sexed and the stomach was removed and frozen within one hour. The stomach was defined as the section of the alimentary canal from the oesophagus to the pylorus sphincter.

Stomach analysis

In the laboratory, the stomachs were slowly thawed at 10 ˚C and cut open with scissors. The entire stomach content was blotted dry and weighed and all prey was determined to the lowest possible taxonomic level and subsequently placed into taxonomic categories accordingly.

Eleven prey species were identified and these were pooled into a total of seven prey categories because of the rarity of some of the prey species. The category 'large crustaceans' contained krill (*Euphausiidae* sp.) as the most dominating prey species along with the crustaceans' deepwater shrimp and polar lebbeid (*Lebbeus polaris*). The category 'crabs' contained snow crab and sand crab (*Hyas araneus*). These two species were pooled into one category since appendages (e.g. legs) were the most commonly eaten parts and these were often indistinguishable between species due to digestion. Taxonomic groups that occurred only seldom were placed in a joint category ('other'), which included echinoderms *Asteroide* sp., bristle worms *Polychates* sp., cephalopods *Gonatus* sp., and the fish *Pholis gunnellus* L., and *Cottidae* sp. in which the fish were the dominant species. The category 'capelin' consisted of adult individuals of this species (no juveniles were found). The category 'small crustaceans' was made up of juvenile stages of several crustaceans, of which juvenile crabs (primarily *Chionoecetes opilio* and *Hyas araneus*) made up the largest fraction. 'Unknown' and 'capelin eggs' made up the two last categories (Table 1).

Prey composition was expressed as relative prey abundance (A_W),

$$A_W = (\Sigma W_i) \times (\Sigma W_{ti})^{-1}$$

where W_i is the wet mass (g) of prey in a given category and W_{ti} is the total wet mass (g) of prey in the stomachs containing prey (Nielsen & Andersen, 2001).

Statistical analysis

All analyses were carried out using SPSS (Statistical Package of Social Sciences). Standard parametric tests were preceded by test for assumptions. When these were violated, the data were either transformed or non-parametric statistics were applied. Percentage data were arcsine-transformed prior to analyses. The mean share of each prey group in each size group was compared between areas (e.g. capelin share compared between Nuuk and Sisimiut etc.) yielding a total of 42 comparisons.

RESULTS

Prey composition

The cod ranged in mass from 30 to 3840 g and in length from 13 to 69 cm. The share of empty stomachs constituted 19% of all stomachs and did not differ between the two fjords (Table 1, Fisher's exact test, P=0.87). Empty stomachs were excluded from further stomach analysis, however these cod were included in the condition analysis.

The stomach content was similar between areas (Table 1). Specific size group comparisons between areas only yielded one significant difference between areas out of 42 possible. This was within the 'large crustaceans' category, where there was a larger share in of this prey in cod from Nuuk than in cod from Sisimiut (Mann-Whitney, Z_{31}=3.552, P=0.004). However, as 'large crustaceans' constituted less than 1.5% of the total prey weight and this did not differ between study areas the overall prey compositions of Nuuk and Sisimiut cod were pooled in further analyses. Further supporting a similar spatial feeding pattern between cod in both fjords was the similarity in the relative amount of prey (standardized to fish weight) in both fjords (Student's t-test, t_{181}=0.321, P=0.75, Figure 1).

Capelin was the dominant prey group (70% of total prey weight) while only the prey category ‘other’ also constituted more than 10% (12%, Table 1) when all stomach contents was pooled. The relatively large contribution from the ‘other’ prey group was due to the inclusion of large prey fish in this category. The dominance of capelin as prey was evident in most size groups in both areas; however a decline was seen in the largest cod in both areas coinciding with an increase in the ‘other’ prey category. Because the ‘other’ prey category is dominated by fish prey, the overall importance of fish prey appears to increase with size at the expense of smaller prey. Hence, in the smaller cod size groups ‘small crustaceans’, ’large crustaceans’ and ’capelin eggs’ constituted a comparatively important part of the diet. The overall pattern of fish (mainly capelin) increasing in importance as prey with increasing cod size is further supported by the contrast in the share of fish prey and non-fish prey in small (≤30cm) and large cod (>30cm, Figure 2). However, as these comparisons are based on prey wet weight, large fish prey will contribute considerably more to the overall picture than small prey, even if large fish prey are present in only a small fraction of the investigated cod. Hence, if the size related feeding behaviour is viewed as the mean share of prey groups in individual fish it appears that smaller cod (less than 30 cm) generally do not eat fish prey, but subsist mainly on a diet of non-fish organisms (Figure 3).

Condition factor

The condition factor (CF) of inshore cod was significantly higher in Sisimiut (mean ±SD: 0.886 ± 0.123) than in Nuuk (0.836 ± 0.106, Student’s t-test, t_{225}=3.251, P=0.001, Figure 4). The uncharacteristically low CF in the 40-50 cm length group of cod from Nuuk was not caused by any outliers or lack of data points and the reason for this inconsistency is unknown. In both areas there was a tendency for CF to decline in fish above 50 cm. Due to the unexplained low CF-value in Nuuk in the 40-50 cm size category this was most clear in Sisimiut. However, assuming that the 40-50 cm size category was similar in both areas a decline similar to that in Sisimiut was seen in the two largest size groups in Nuuk, suggesting an overall pattern of decreasing CF in larger fish in both fjord systems.

DISCUSSION

The present results show that the primary food source of Atlantic cod in two West Greenland fjord systems during the early summer is capelin, without notable differences between Nuuk and Sisimiut fjord systems. This trend tends to increase as the cod grow larger. These results are in general agreement with previous studies in the region (Hansen, 1949; Nielsen & Andersen, 2001). Nielsen & Andersen (2001) found that capelin in West Greenland constituted 44% of total prey weight, which is less than what was observed in the present study where capelin made up more than 50% of prey in most size groups and 70% in total

(Table 1). This discrepancy can probably be explained by differences in the sampling season. Nielsen & Andersen (2001) sampled in November when capelin have generally migrated to deeper waters along the coastline. In contrast, capelin gather in large numbers in the shallow waters of the fjords during spawning in the Spring (May-June, this study) which makes them more easily accessible to cod (Friis-Rødel & Kanneworff, 2002). A similar pattern is seen in Iceland, where capelin comprise as much as 90% of the prey mass in Atlantic cod during the capelin spawning season and as little as 25% outside this period (Pálsson, 1997).

Hence, the importance of capelin seems almost ubiquitous at least during summer and the effect of a capelin deprived diet has been demonstrated in Canada, where an inadequate supply of capelin as prey has been suggested to have hampered the cod´s ability to recover to former population numbers prior to the collapse of the stock in the 1990's (Rose & O'Driscoll, 2000). Additionally, a drop in weight-at-age (25-30%) for cod has been shown in Icelandic waters in the 1980's and 1990's, which was shown to correlate with a decrease in capelin abundance (Vilhjalmsson, 2002). The Greenland Institute of Natural Resources has since 1977 undertaken a yearly survey of Atlantic cod in and around the Nuuk fjord system. Data from these surveys suggest that length-at-age of inshore cod ages 5-8 years has been decreasing over time (6-8%), while it has been more constant in 2-4 year-old fish (Figure 5). As younger cod rely less on fish prey, this could indicate that the decline in cod length at age is partly due to a decline in capelin accessibility. Unfortunately, few quantitative studies of capelin in Greenlandic waters exist and no reliable stock estimations are to our knowledge presently available (Friis-Rødel & Kanneworff, 2002). Furthermore, the decline in length-at-age could also be due to other factors such as the selective effect of continuous removal of the largest fish over time due to commercial fishing (e.g. Borisov, 1979; Law, 2000) or changes in ocean temperature (Brander, 1995). Although temperature effects are not necessarily uniform across ages, a similar response at all ages could have been expected had temperature been the main driver of the length-at-age decline and this is not seen.

Cod condition (CF) was higher in Sisimiut than in Nuuk (Figure 4). Because this was the case in all size groups and since the two areas generally show the same length-CF relationship the difference is most likely caused by a stabile environmental gradient. Such a gradient could be temperature related as Greenlandic inshore cod are non-migratory and temperature related growth differences along the Greenlandic West coast has been demonstrated in capelin and Greenland halibut (Sünksen *et al*, 2009; Hedeholm *et al.*, 2010,). As to a feeding effect on condition, the present study did not indicate regional feeding differences in either prey type or prey amount (Table 1, Figure 1), but data are too limited on a temporal scale to allow for an extensive integrated feeding analysis.

The decrease in condition factor (CF) with length in the largest size classes in both study areas could be a result of spawning (Lambert & Dutil, 2000). Hence, maturity for inshore cod in Nuuk show that 50% of both males and females mature at 40-50 cm and sampling was done just after spawning (Olesen, 2009). However, the pattern could also in part reflect that capelin, as the most important prey item, is in short supply in line with studies from Canada (Rose & O'Driscoll, 2002). If this is the case, this supports to the possibility that the recovery of the cod population in West Greenland may also be hampered by lower availability of its main prey; a prey choice that appear consistent across all spatial scales investigated.

The present study was carried out during one month in summer. As this is the time of capelin spawning, the pattern of capelin specialization is probably less pronounced during other times of the year (Pálsson, 1997) as capelin migrates to deeper waters after spawning has ceased. Therefore, it is suggested that future studies take into consideration potential seasonal variations in the diets of cod, and sample cod over a broader timescale. Additionally, including data on prey availability would allow for better assessment of the impact that changes in prey availability at different trophic levels would have on cod feeding behaviour and cod condition.

The diet composition for cod in this study illustrates the apparent importance of capelin as prey. Capelin has also been found to be a major prey contributor to other species (seals, fishes, whales and seabirds, Friis-Rødel & Kanneworff, 2002; Ushakov & Prozorkevich, 2002). Hence, capelin clearly holds an important position in the Greenlandic food web, and their role as a key prey species in the Arctic food web (Carscadden *et al.*, 2002; Dolgov, 2002; Friis-Rødel & Kanneworff, 2002) needs to be addressed further.

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Table 1. The mean ± SD proportion of total prey weight (wet weight) made up by the individual prey groups in Atlantic cod (*Gadus morhua*) in the Nuuk (64˚N) and Sisimiut (66.80˚N) fjord systems on the Greenlandic west coast. For each length group N_{prey} and N_{empty} denotes the number of non-empty and empty stomachs respectively. See text for further explanation on prey groups.

Location	**Length group**	**Adult capelin**	**Large crustaceans**	**Crabs**	**Small crustaceans**	**Capelin eggs**	**Other**	**Unknown**	N_{prey}	N_{empty}
Nuuk	]10-20]	0	0.15	0	0.59	0.17	0	0.09	14	1
	]20-30]	0.72	0.06	0	0.02	0.13	0.04	0.03	27	4
	]30-40]	0.87	0.03	0.02	0	0.05	0	0.04	16	7
	]40-50]	0.63	0.03	0.24	0	0.01	0.06	0.03	15	5
	]50-60]	0.55	0.02	0.36	0	0	0.02	0.05	5	2
	]60-70]	0	0.06	0	0	0	0.88	0.06	3	1
	Total	0.60	0.04	0.17	0.01	0.03	0.11	0.04	80	20
Sisimiut	]10-20]	0.53	0.02	0	0.33	0.10	0	0.02	18	1
	]20-30]	0.72	0.01	0.02	0.07	0.13	0.05	0.01	26	4
	]30-40]	0.86	0	0.10	0.01	0	0.03	0	23	7
	]40-50]	0.92	0	0.03	0	0	0.04	0.01	16	8
	]50-60]	0.84	0	0	0	0	0.12	0.03	14	3
	]60-70]	0.52	0	0	0	0	0.30	0.18	6	1
	Total	0.76	<0.01	0.02	0.01	0.01	0.13	0.06	103	24
	Combined	0.70	0.01	0.08	0.01	0.02	0.12	0.05	183	44

Fig.1.

The mean relative prey weight (g prey/kg fish) in Atlantic cod from Sisimiut (N=103, open circles) and Nuuk (N=80, filled circles) fjord systems caught in 2007. Bars represent standard error.

Figure 1

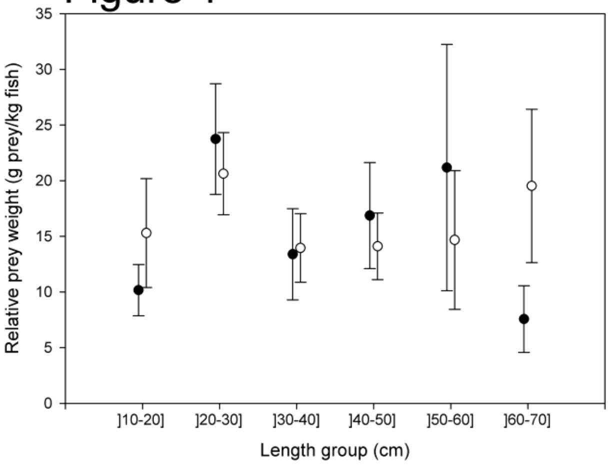


Fig. 2.

The share of total prey wet weight (g) made up by fish (categories “capelin” and “other”) and non-fish (categories “crabs”, “small crustaceans”, “large crustaceans” and “capelin eggs”) in Atlantic cod above and below 30 cm (N=98 and N=85, respectively).

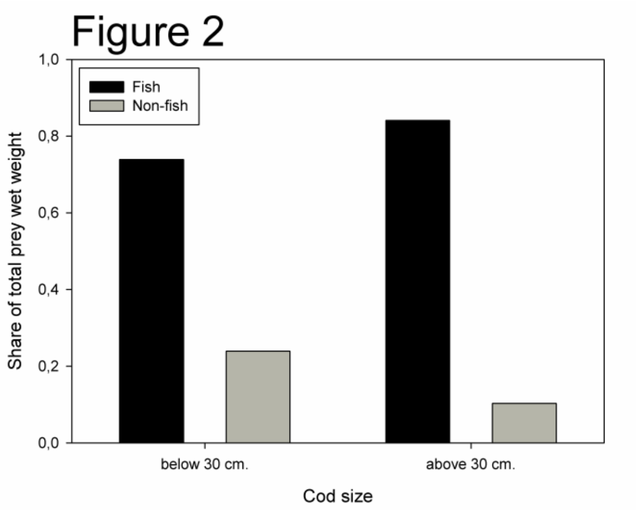


Fig. 3.

The mean share of small prey items (A, small crustaceans and capelin eggs combined) and large prey (B, adult capelin and other combined) of total prey wet weight at all lengths in Atlantic cod (*Gadus morhua*) from the Greenlandic West coast. Cod from Nuuk and Sisimiut fjord systems are combined. N=183. The inclusion of the “other” category as fish prey was based on it being mainly comprised of different fish species eaten by larger fish (see text).

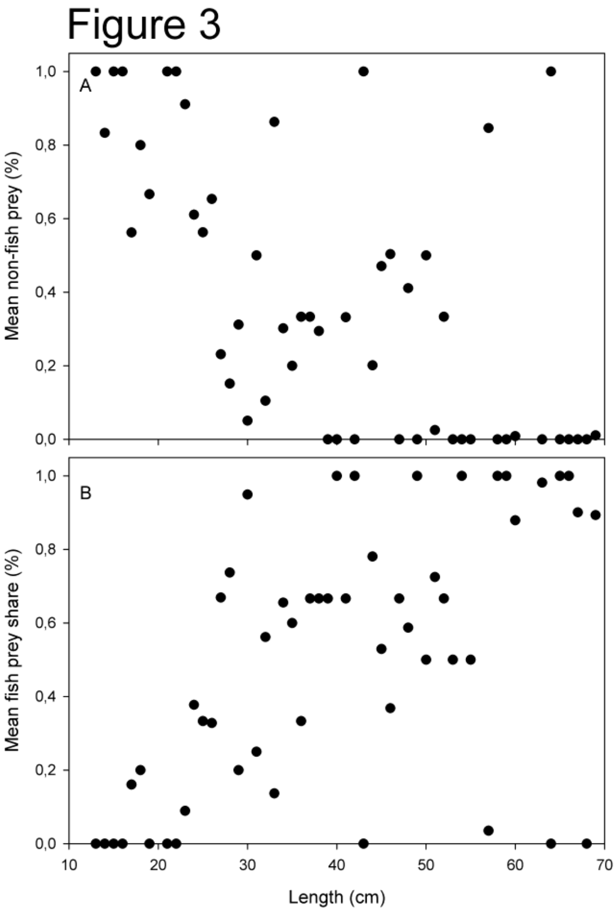


Fig. 4.

Mean condition factor (CF) of West Greenlandic Atlantic cod from the Sisimiut (N=127, open circles) and Nuuk (N=100, filled circles) fjord systems caught in 2007. For calculation of CF see materials and methods. Bars represent standard error.

Figure 4

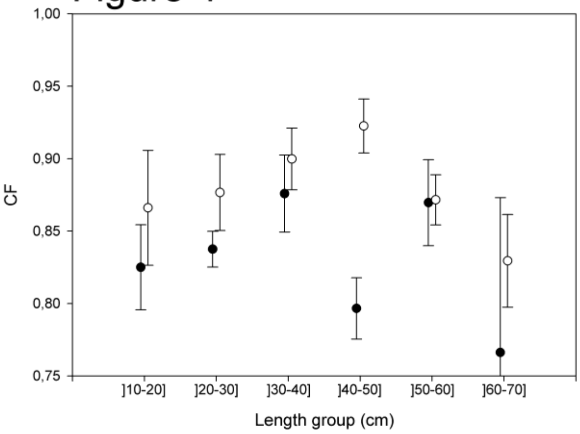
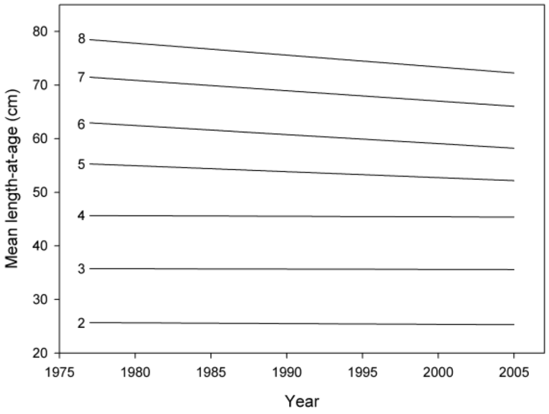


Fig. 5.

The development of length-at-age from 1977-2005 in Atlantic cod (*Gadus morhua*) (data from Greenland Institute of Natural Resources). Each line represents a specific age, which is noted next to the line. The slopes for the different ages are: α_2=-0.014, α_3=-0.006, α_4=-0.010, α_5=-0.111, α_6=-0.169, α_7=-0.194, α_8=-0.222. N=19872. P<0.0005 for all ages except age 2, where P=0.37.

Figure 5



Paper V

Intra-fjord variation in reproductive output in Atlantic cod (*Gadus morhua*)

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Intra-fjord variation in reproductive output in Atlantic cod (*Gadus morhua*)

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Abstract

To explore the effect of small scale geographic variation on reproductive output in Atlantic cod (*Gadus morhua*) the potential fecundity (PF) and reproductive output of mature female cod from a Greenlandic fjord (Nuuk fjord system, 2 013 km^2) was determined. While there was no intra-fjord variability in PF between the outer and inner area of the fjord system, cod eggs from the inner area had twice the energy content of eggs from the outer area (1.806 J egg^{-1} ± 0.457; 0.862 J egg^{-1} ± 0.461, respectively). Hence, the present study demonstrates the importance of the inner fjord area as a key site for cod reproduction and suggests that information on spawning sites is important from a management perspective. At present, the causative agent for this difference between areas has not been identified but it is suggested that stocks of lipid rich capelin in the inner fjord area could be important.

Keywords: egg energy content, fecundity, Greenland, small scale variation

Introduction

Climatic variation has historically caused noticeable latitudinal changes in cod distribution along the Greenlandic west coast (Jensen, 1939; Drinkwater, 2005) and more recently fishery has also affected population size and cod characteristics (Ratz and Lloret, 2005; Hovgård and Wieland, 2008). So far, there has been most focus on the off-shore cod stock along the Greenlandic west coast as it has contributed with a major fraction of the fishery in many years, but due to its recent decline the inshore cod population is now more important (71% in 2007, ICES, 2008). The individual fjord systems along the west Greenlandic coastline harbour what is considered fairly isolated and sedentary cod populations (Storr-Paulsen *et al*., 2004) and the present study aims to describe the quality of a West Greenlandic inshore habitat to cod by using their investment in reproduction and growth as proxy.

Maternal and environmental impacts on reproductive investment have been evidenced both from laboratory experiments and from natural populations. Hence, Ouellet *et al*. (2001) measured the energy density of laboratory reared Canadian cod eggs, and showed that the conditional state of females had an influence on egg energy density. In support of this, Lambert and Dutil (2000) concluded that low-condition females had lower fecundity and reduced egg dry weight. Furthermore, Marteinsdottir *et al*. (2000) demonstrated a clear shift in female cod spawner characteristics and egg viability in adjacent near coastal spawning sites in Icelandic waters, with egg viability decreasing with distance from the coast. Furthermore, Ouellet *et al*. (2001) showed that relatively small temperature changes can alter individual egg energy content by nearly a factor two and Yoneda and Wright (2004) demonstrated difference in potential fecundity between inshore and offshore cod populations in the North Sea.

Cod for analyses were collected from two sites in the Nuuk fjord system (spans an area of 2013 km^2) representing the amplitude of environmental variation. Historical information supports the notion of spatially differentiated reproductive conditions, as the inner fjord region has been a well-known cod spawning site for many years (Hansen, 1949; Hovgard and Wieland , 2008), whereas spawning in the outer regions is less well described and cod egg density has been shown to be lower (Storr-Paulsen *et al*., 2004). We determine cod growth and total female reproductive output in terms of gonad energy content, energy density of eggs and explore maternal size and/or condition effects on egg quality.

Materials and methods

Sampling was done from December 2007 to May 2008 in Nuuk and Paamiut fjord systems on the Greenlandic West coast (Figure 1). In the Nuuk fjord system cod were caught continuously throughout the period but only fish from February to April were used in this study. To allow for small scale comparisons between regions all cod were classified as belonging to either the inner or outer region of the fjord. The outer region was characterized by being close to deeper parts and mouth of the fjord, while the inner region was further inland and in a shallower area (see Figure 1). The Paamiut fjord system was only sampled on one occasion in March, and the four sampled fish were assigned to the outer region. Due to permanent winter ice the inner part of the Nuuk fjord was inaccessible early in the study period.

Cod were caught using hand held jig lines or on long lines that were allowed to fish for two hours. Upon capture the cod were brought to the laboratory, sexed, measured to the nearest cm (Total length, L_T), weighed to the nearest g (total, W_T and gutted, W_C) and aged using saggital otoliths. Furthermore, liver and gonad weights were recorded (W_L and W_G) allowing for calculation of hepatosomatic (HSI) and gonadosomatic (GSI) indices as follows:

$$HSI = 100 \times \left(\frac{W_L}{W_C}\right)$$

and

$$GSI = 100 \times \left(\frac{W_G}{W_C}\right)$$

In addition Fulton's condition index was calculated as follows:

$$K = 100 \times \left(\frac{W_T}{{L_T}^3}\right)$$

To allow for size based comparative analysis concerning fecundity, energy density of the eggs and total reproductive investment, females on a similar stage in the spawning process were selected. Based on Tomkiewicz *et al.* (2003) all females were assigned a stage of gonadal maturation (1-10) and all females of stage four were selected for further analyses. Stage four is defined as the ripening stage or late vitellogenesis where yolk granules fill the entire cytoplasm of the oocytes and was chosen as it represents a stage were all the energy in the oocyte has been deposited, while no oocytes have yet been spawned. The stage was initially determined macroscopically from the external appearance of the gonad. In addition to fish used in this study all gonadal stages were sampled for histological analyses (N=100) and these results are presented in detail elsewhere (Retzel *et al.*, in prep). However, as macroscopical gonadal staging can be inaccurate (Vitale *et al.*, 2006) the mean oocyte diameter in gonad stages 3-5 was measured manually on histological samples (N=8) sampled in all parts of the fjord, in order to validate the gonad staging. As both formaldehyde and histological preparation causes oocyte shrinkage, a conversion factor of 1.40 was applied to convert oocyte diameters from the histological samples to formaldehyde preserved equivalents (Wieland and Koster ,1996; Kraus *et al.*, 2008). The validity of this conversion was confirmed by comparing measurements done on a single fish from this study that was also available histologically. Hence, the corrected mean oocyte diameter from gonad stages 3-5 were compared to the frequency distribution of oocyte diameters in fish used in this study (see below). As seen in Figure 2 there was a slight overlap in the frequency distribution of oocytes diameters from the outer region and the mean diameter of stage three oocytes as determined from the histological samples. The smallest mean oocyte diameter from a single cod in the outer region was 415 µm (range: 309-519 µm measured auto-diametrically, see below) and only three additional fish had mean oocyte diameters below 500 μm. These are all above the mean stage three oocyte diameter (317 μm ± 83, mean ± SD, measured manually on histological samples), hence the overlap was not the result of a few stage three fish but was caused by a few small oocytes being present in most fish, and it is assumed that no female cod having stage three gonads were included in the study. In total 52 female cod were used for further analyses of fecundity and energetic analysis.

Oocyte diameter and potential fecundity (PF)

From stage four gonads approximately 3 g of gonad was removed from the middle part of the right lobe. This was preserved in 3.7 % buffered histoformaldehyd until further processing. PF was determined using the auto-diametric method described in detail in Thorsen and Kjesbu (2001). In short, a small gonad subsample (approximately 250 eggs) was placed in a petri dish which was prefilled with buffered histoformaldehyde and a drop of dishwasher detergent to avoid oocyte surface attachment. The petri dish was photographed at 8× magnification at standardized settings using a DP Infinity X camera. Subsequently, all pictures were analyzed using the "Analyze particles" module of the ImageJ picture software (Rasband, 1997-2007). All measured particles in the pictures were sorted to eliminate non-oocyte particles. This was done by applying a circularity factor and size threshold (10 000 μm^2-1 000 000 μm^2) estimated to be valid for oocytes (see Thorsen and Kjesbu, 2001). A circularity factor of one indicates a completely round particle (an oocyte) while decreasing values indicate less round particles (equivalent to the inverse of the "roundness factor" defined by Thorsen and Kjesbu, 2001). All particles with a circularity ≤ 0.83 were discarded as they were mostly connective tissue or eggs in close proximity. Lastly, oocytes in contact with the picture edge were disregarded. The diameter of all remaining oocytes was determined and a mean oocyte diameter for each gonad was calculated (OD, μm). 40 oocytes in four different samples were also measured manually and compared to the computed diameter, and all measurements were within 2.5 % of the computed values with equal positive and negative error. Hence, based on Thorsen and Kjesbu (2001) the oocyte density (NG) was calculated as follows:

$$NG = 2.137 \times 10^{11} \times OD^{-2.700}$$

To assess if this relationship was also valid for Atlantic cod in Greenland, five gonads were randomly chosen. The number of oocytes in a 1 g subsample were counted manually and compared to equation 4 using the computed mean diameter. This confirmed the validity of the relationship (Figure 3) although the oocyte density was slightly above the expected in all cases. However, these deviations are not larger than the variation in the original study (see fig. 4 in Thorsen and Kjesbu, 2001). Hence the potential fecundity (PF) was determined from the NG and the measured gonad weight (W_G):

$$PF = W_G \times NG$$

It is noted, that Thorsen and Kjesbu (2001) only show the relationship to be valid within an oocyte diameter range of 300-850 μm. As only 3 % of all measured oocytes in the present study were outside this range (Figure 2) no exclusions were made.

Energy density

From the same gonads used for fecundity determination a similar subsample of approximately 3 g was removed from all fish and frozen at -20 ˚C. The frozen samples were placed in a freeze drier for 24 hours after which no further weight loss took place. Prior to any further analysis the samples were kept in an exsiccator over a silica gel. The dry samples were weighed to determine water content of each gonad, homogenized in a glass mortar and a subsample of 471 mg ± 0.06 (mean ± SE) was compressed into a pellet. The energy density of the pellet was determined using a 1109a semimicro bomb and Parr 6725 bomb calorimeter using benzoic acid as standard material (energy density: 26.454 kJ g^{-1}). Triplicates of randomly chosen samples demonstrated the validity of the method as deviations were small (1.2% ± 0.8, mean ± SD). Energy densities that differed to a large extend from other values were reanalysed and discarded if the results were inconsistent. Data on energy density, fecundity, water content and gonad weight allowed for calculation of individual egg energy content and total reproductive investment at the time of sampling.

Reproductive output and somatic growth

To assess the allocation of energy to reproduction at a given size total gonad energy content was plotted as a function of cod size measured in terms of total energy content (J) assuming an average energy density of cod tissue of 4.2 kJ g ww^{-1} (Figure 6a, Lawson *et al.*, 1998). Although this approach is subject to several growth assumptions and natural variation it was deemed an appropriate estimate in this case. This was based on a highly significant relationship between mean weight-at-age and age when considering all sampled fish from three to ten years-of-age and maturity stages three to seven (mean weight-at-age = $24.991 \times \text{age}^{2.5138}$, $P<0.0001$, $r^2=0.99$) which indicates stable growth conditions having produced similar growth pattern on all cohorts considered in this study. We also assume that these stable growth conditions have prevailed in the earliest life stages. Lastly, the reproductive investment in the inner and outer regions at a given size was visualized by calculating the proportion of energy allocated to gonads at a given weight relative to fish size (Figure 6b).

Statistical analyses

To reduce unnecessary variation caused by differences in stomach content, gutted weight (W_C) was used in all further analyses including weight. All fish were grouped in accordance to length (five cm), gutted weight (200 g) and time of capture (two week) to allow for certain analyses. For statistical reasons, only the first 100 measured oocyte diameters from each fish was used. In one case only 99 correctly measured oocytes were available, but no corrective measures were applied. To determine the effect of several variables on PF, a stepwise regression was preformed. This was preceded by a series of zero-order regressions to maximize linearity between factors and PF prior to further 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 was either transformed or non-parametric statistics were applied.

Results

In total 852 Atlantic cod were sampled of which 52 ranging from 42-75 cm (L_T) and 0.72-3.62 kg (W_C) were used in this study. Thirty-nine belonged to the outer region and 13 to the inner region (see Figure 1). There was no difference in mean weight (W_C) between regions (1509 g ± 589 (inner region) and 1415 g ± 633 (outer region), Student's t-test, t_{50}=0.470, P=0.64) nor was there a difference in condition (K) (1.00 ± 0.1 (inner region) and 0.97 ± 0.1 (outer region), Student's t-test, t_{50}=0.931, P=0.36).

Potential fecundity (PF)

PF did not differ in general between the inner and outer region as evidenced by a non-significant interaction term (ANCOVA, $F_{1,48}$=0.23, P=0.63) nor in any of the comparable weight groups (Students t-test, $P \geq 0.23$) (Figure 4). PF increased significantly with weight (ANCOVA, $F_{1,48}$=87.315, P<0.0005, $\ln PF = 4.811 + 1.171 \times \ln W_C$, table 1). A stepwise regression analysis using the conditional indices (HSI, GSI, K, weight (W_C) and length (L_T)) as independent variables showed that weight was the best predictor of PF (P<0.0005, R^2=0.71) although including GSI increased the amount of explained variation (P<0.0005, R^2=0.76). The condition index (K) did not improve the model as K was positively correlated with W_C (i.e. the larger fish are in the best condition) although marginally insignificant (Spearman's correlation, r_s=0.27, P=0.06).

Egg size, energy density and total gonad energy content

The mean oocyte diameter was the single best predictor of mean egg energy content (linear regression, $F_{1,50}$=1019.62, P<0.0005, r^2=0.953). The weight specific energy density of the eggs differed between regions (Student's t-test, $t_{44.483}$=7.500, P<0.0005) being higher in the inner than in the outer region (22.947 kJ g dw^{-1} ± 0.247 and 22.124 kJ g dw^{-1} ± 0.535 (mean ± SD) respectively). Similarly, the energy content of the individual egg differed being (mean ± SD) 1.806 J egg^{-1} ± 0.457 (inner) and 0.862 J egg^{-1} ± 0.461 (outer) respectively (Student's t-test, t_{50}=6.409, P<0.0005). An ANCOVA including time and place of capture, K, HSI and W_C as explanatory variables, showed that there was a significant effect of place of capture (GLM, $F_{1,43}$=15.077, P<0.0005) with the individual egg energy content being ca. 1 J higher in the inner region of the fjord in all comparable weight groups except the]1600-1800] category (Figure 5). In addition to place of capture, W_C (GLM, $F_{1,43}$=5.084, P=0.029) and time of capture had a significant effect on egg energy content (GLM, $F_{4,43}$=6.352, P<0.0005). The significant effect of time of capture was caused by a positive relationship between egg energy content and time of capture in the outer region irrespective of fish weight (ANCOVA, $F_{4,33}$=9.701, P<0.0001). However, when comparing similar sized fish caught at the same time (Student's t-test, P≥0.23) there was a significantly higher egg energy content in the inner region (mean ± SD, 1.26 ± 0.59 (outer), 1.81 ± 0.46 (inner), Student's t-test, t_{23}=2.599, P=0.016).

As cod from both sites were similar in PF but differ in individual egg energy content, it follows that total gonad energy content also varied between regions (mean ± SD, 1286 kJ ± 817 (inner) and 557 kJ ± 524 (outer), GLM, $F_{1,49}$=23.191, P<0.0005) and increased with size (W_C, GLM, $F_{1,49}$=51.188, P<0.0005). Accordingly, the GSI was also highest in the inner region irrespective of size (mean ± SD, 11.53% ± 3.81 (inner) and 5.93% ± 2.95 (outer), ANCOVA, $F_{1,49}$=31.454, P<0.005).

Reproductive output and somatic growth

There was a significant positive relationship between cod size (measured as total calorific value, J) and total gonad energy content in both the inner and outer fjord region (linear regression, $F_{1,11}$=31.840, P<0.0001 and $F_{1,37}$=31.413, P<0.0001 respectively, Figure 6a). However, the slope was steeper for the inner region (0.285 and 0.1340, respectively), indicating a larger reproductive investment for a given size increment (growth) in this region although marginally insignificant. Based on the linear regressions the energy allocation to gonads relative to cod size increased asymptotically in both regions (Figure 6b). However, in the outer region the gonads contained at maximum 12 % of total cod energy content at any size, whereas gonads from the inner region contained 25 % of total cod energy content. The apparent higher relative reproductive output in the inner region was not the result of a compromised somatic growth as the growth pattern was similar ($W_C=20.653 \times age^{2.6432}$ and $W_C=19.710 \times age^{2,6342}$ for the inner and outer region respectively, P<0.005 in both cases).

Discussion

Potential fecundity (PF)

To our knowledge this study represents the first quantification of potential fecundity in West Greenland inshore cod. The size dependent variation in fecundity seen in all studies shows a large degree of geographical variation (Table 1). Hence, fecundity is similar for cod populations in cold regions such as the Barents Sea, Iceland and West Greenland (this study) and higher in warmer regions such as the Baltic and North Sea. This temperature-dependent variation in PF matches that of temperature-dependent variation in size-at-age (Brander, 1995; Marteinsdottir and Begg, 2002). The clear effect of temperature, as well as biotic factors such as prey availability and female condition, causes large temporal variation in fecundity within populations (Kjesbu *et al.*, 1998; Lambert and Dutil, 2000; Marteinsdottir and Begg, 2002).

The inner and outer regions of the Nuuk fjord showed similar PF-cod size relationships. However, as no studies on the frequencies of atresia and skipped spawning are available for Atlantic cod in Greenland, the realized fecundity may be lower than the estimates presented here (Rideout and Rose, 2006; Skjaeraasen *et al.*, 2009). The degree of atresia may be small (Kjesbu *et al.*, 1998) but could be substantial in years of food shortage and/or low temperatures (Kjesbu *et al.*, 1991; Rideout *et al.*, 2000) and a concomitant drop in cod condition. Similarly, skipped spawning may drastically reduce population fecundity (Jorgensen *et al.*, 2006; Skjaeraasen *et al*., 2009) and in general other studies have found a clear effect of cod condition on fecundity (e.g. Lambert and Dutil, 2000) and the same may be expected in Greenland where low temperatures are conducive for poor condition. However, we found no significant effect of condition (K) or liver index (HSI) on PF. The lack of a HSI effect could be the result of a shift in energy allocation from liver to gonads, leaving the liver equally energy depleted in all individuals, and variability in condition among individuals is more likely evident in gonad energy content at this late stage of ripening.

Egg and gonad energy content

The conclusions concerning reproductive energy allocation and small scale differences made in this study are based on the vital assumption that all reproductive energy has been allocated to the individual eggs at the time of sampling. Contesting this, is the positive relationship between time of capture and individual egg energy content irrespective of size in the outer region, which might suggest that not all energy had been allocated to the eggs in the early sampling stages. However, as regional differences are present when comparing coincident samples late in the sampling period (and late in the spawning season) we believe the difference is not merely a sampling artefact but actually reflects regional differences. We do not, however, exclude the possibility that some early caught samples in the outer region may not have been in the final energetic state.

Temperature and prey effects on reproductive output

Cod were similar in size between the inner and outer regions, but, for a given weight increase; there was a more than two-fold difference in the amount of energy allocated to reproduction (highest in the inner region). This can only be the case if cod from the inner region have a higher scope for growth (Jobling, 1988) which could be caused by beneficial temperatures and prey quality and/or quantity in the inner area (Brander, 1995; Rose and O'Driscoll, 2002).

Only one other study has determined cod egg energy content using the same method as the present (Ouellet *et al*., 2001). Here, cod were acclimated between 2 ˚C and 6 ˚C and individual egg energy was estimated at 1-3 J egg^{-1}. In one year, cod where acclimated at 2 or 6 ˚C, with egg energy content being highest at 2 ˚C. Egg energy content in cod from the present study was similar with eggs from the inner region containing more energy than those from the outer region of the fjord (ca. 2 J egg^{-1} and 1 J egg^{-1}, respectively, see Figure 5). If the temperature effect demonstrated by Ouellet *et al*. (2001) is also valid in the present study, we would expect temperatures to be lowest in the inner regions of the Nuuk fjord.

While temperatures in the fjord mouth are below 2˚C for most of the year (Mikkelsen *et al.*, *2*008), temperatures are most likely higher in the shallow inlets sampled in this study as insulating winter ice and summer solar heating will increase temperatures. However, no recently published temperature data exists for the inner and outer area of the Nuuk fjord, but CTD-profiles from May 2009 indicated small differences between the areas (P. Munk, pers. com). Additionally, Smidt (1979) reviewed temperature measurements made from 1953-66 throughout the year in the Nuuk fjord and found only small differences between the inner and outer regions. Hence, the sparse current evidence from this fjord system suggests that the temperature effect shown by Ouellet *et al*. (2001) is unlikely as an explanation for the difference of energy content of cod eggs between the two regions.

As in other cod populations (Carscadden and Vilhjalmsson, 2002; Vilhjalmsson, 2002), Greenland inshore cod prey heavily on lipid rich capelin during summer feeding (Lawson *et al*., 1998; Nielsen and Andersen, 2001) and these are known to spawn throughout the fjord, but most intensively in the inner regions (Kanneworff, 1967; first author, pers. obs.). Additionally, Nielsen and Andersen (2001) found that inshore cod had fuller stomachs compared to coastal cod indicating higher prey availability in the inner regions of the fjord.

Hence, both abiotic and biotic factors may contribute to a higher scope for growth for inner region cod. The explanation to why this manifests itself as an increased allocation of energy to reproduction and not somatic growth could be low adult mortality and no apparent size-selection as the inshore Nuuk cod has historically not been subject to intense fishing (Sinclair *et al.*, 2002; Olsen *et al.*, 2005; ICES, 2008). In addition, the inshore fishing is primarily done using pound nets which presumably are not selecting for large fish as fishing is done very near shore, thereby excluding larger fish from the catch. While such evidence indicates low fishing mortality for cod in the Nuuk fjord, more information is needed to assess fishing effects on this population including the influence of cod behaviour, fishing intensity and gear selectivity (Heino and Godo, 2002; Sinclair *et al.*, 2002).

A low adult mortality may also partly explain the lack of increased somatic growth, as retention of energy may ensure a higher degree of post-spawning survival (Lambert and Dutil, 2000) thus maximizing life time reproduction through an increased number of spawning events. Hence, Jørgensen and Fiksen (2006) states that “reproduction is low-risk instantaneous liquidation of available capital (stored energy), whereas growth is an investment in the future”. Simply stated, this investment is more likely to pay off if mortality is low, and theoretical approaches have shown that a low adult mortality will shift the allocation of surplus energy towards somatic growth in indeterminately growing species (reviewed by Heino and Kaitala, 1999).

Reproductive output and total somatic growth

The potential energetic reproductive output increased with size in both the inner and outer regions of the fjord, with the youngest fish producing the smallest gonads both in absolute and relative terms (Figure 6).

This is consistent with the literature which contains many examples of first-time-spawners producing fewer (e.g. Trippel, 1998) and smaller eggs (Carr and Kaufman, 2009) of less energy (this study) associated with less viable offspring. This age-dependent variability is dependent on the validity of the stable growth assumptions (see Materials and methods). If the assumptions are valid, the findings highlight the potential dangers of shifting the size-distribution of heavily fished populations towards a higher proportion of first-time-spawners as this will reduce the population's reproductive potential (Hutchings, 2005; Lilly *et al.*, 2008).

To our knowledge few studies on gonad energy content for cod or similar species exists, restricting comparisons to more distantly related species. For comparative reasons, the potential reproductive energy output was considered relative to the fish energy content at a given size (Figure 6). Thus, cod from the inner region produced gonads containing at maximum 25 % of total somatic energy at a given size while it is less than half (12%) in the outer region. Finstad *et al*. (2002) found that in a stunted Arctic charr population, the spent gonad tissue equaled 13% of total pre-spawning energy in spite of four orders of magnitude difference in fecundity between the two species (means of 60 and 654 077 eggs, respectively). Anadromous and resident brown trout from southern Norway had higher values of ca. 32 % (Jonsson and Jonsson, 1997) and the difference between fundamentally different reproductive strategies is most pronounced when the same calculations are done on beach-spawning capelin from the Nuuk fjord. These are believed to display a high degree of semelparity (Friis-Rødel and Kanneworff, 2002), and females on average had gonads that contained 61 % of their total somatic energy content (first author, unpublished data). Finstad *et al*. (2002) argue that the Arctic charr population serves "as an example of particular low reproductive investment among iteroparous fish", probably as a result of limited feeding possibilities in the sampled ultra-oligotrophic lake and compared to the anadromous brown trout this statement seems reasonable (Jonsson and Jonsson, 1997).

This study has demonstrated an apparent small scale variation in reproductive output of Atlantic cod. However, further research is needed to examine how these trends of energy allocation varies intra- and inter-annually. In the meantime, based on our results we suggest that the inner region of the Nuuk fjord is considered especially important regarding management due to it being a key spawning site with cod demonstrating higher egg energy density most likely associated with offspring with higher survival potential (Marteinsdottir and Steinarsson, 1998).

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Table 1

Mean potential fecundity (no. eggs × 10^6) of female Atlantic cod from various populations. When an empirical relationship was used to calculate the potential fecundity, the midpoint of each length group is used. The mean fecundity is based on an un-weighted average of the individual groups. In Canadian waters several references are listed, but only minimum and maximum fecundity are reported. F=potential fecundity, L_T=total length.

	Length groups (cm)							
	]40-45]	]45-50]	]50-55]	]55-60]	]60-65]	]65-70]	]70-75]	Mean
West Greenland (N)	0.236 (8)	0.340 (9)	0.523 (11)	0.896 (12)	0.986 (7)	0.945 (3)	1.409 (2)	0.762 (52)
Barents Sea[a]	0.221	0.318	0.442	0.599	0.791	1.024	1.304	0.671
Iceland[b]	0.155	0.253	0.391	0.582	0.838	1.17	1.604	0.714
North sea[c]	0.428	0.648	0.941	1.322	1.804	2.403	3.137	1.526
Baltic[d]	0.769	1.046	1.426	1.860	2.373	2.971	3.660	2.018
Canada[e]	0.112-0.468	0.172-0.613	0.253-0.781	0.355-0.974	0.470-1.191	0.609-1.435	0.775-1.706	0.392-1.024

[a] Kjesbu *et al*. (1998). Based on averaged empirical relationships in five years from 1986-1991: $F=8.0^{-7} L_T^{3,3279}$.

[b] Marteinsdottir and Begg (2002): $F=0.0118\ L_T^{4.372}$

[c] Yoneda and Wright (2004): The relationship for inshore North Sea cod (INS) is used: $F=0.361\ L_T^{3.73}$

[d] Kraus *et al*. (2000). The relationship covering all sampled months is used: $F=13.53\ L_T^{2.92}$

[e] Various areas considered:

Pinhorn (1984): Placentia Bay: $F=53.703\ L_T^{2.42}$

Pinhorn (1984): St. Pierre Bank: $F=0.417\ L_T^{3,37}$

Wells (1986) and Wells and Baird (1989): Flemish cap: $F=1.172\ L_T^{3,16}$

May (1967): Southern Grand Bank (NAFO area 3N): $F=0.089\ L_T^{3,81}$

May (1967): Southern Grand Bank (NAFO area 3O): $F=0.054\ L_T^{3.88}$

Buzeta and Wainwood (1982): Southern Gulf of St. Lawrence: $F=1.1\ L_T^{3.28}$

Fig. 1

The study area on the Greenlandic west coast. All sampled stations are marked. White circles indicate stations classified as being in the inner region of the fjord. Filled circles indicate stations classified as being in the outer region of the fjord. Numbers indicate the sample size at the individual stations

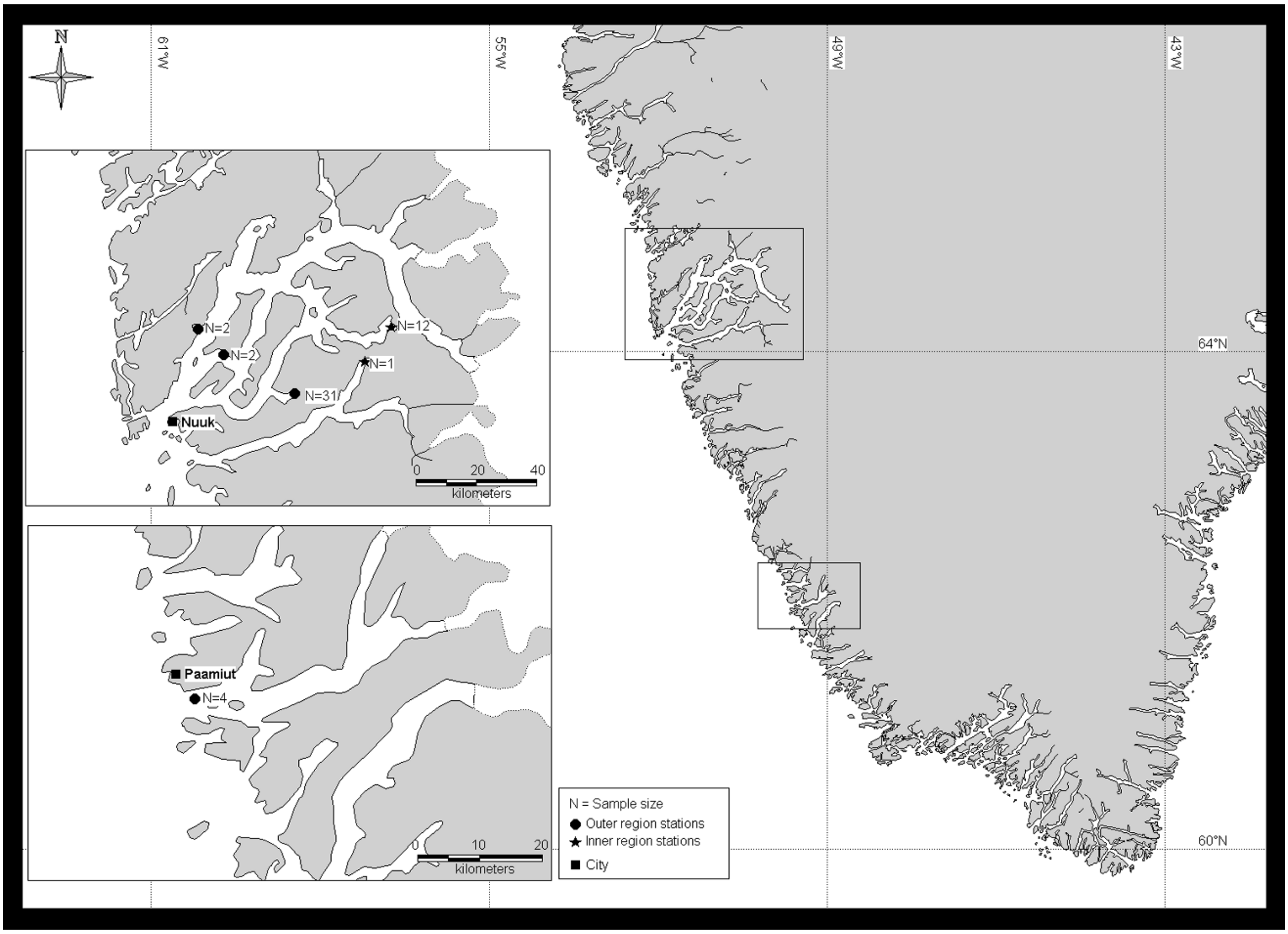


Fig. 2

Frequency distributions of oocyte diameters in stage four gonads from West Greenland female Atlantic cod (*Gadus morhua*) from the inner (N=1200) and outer (N=3999) region of the Nuuk fjord system. 100 oocytes were measured from each of the sampled 52 cod (99 in one case). The filled circles represent the mean oocyte diameter at gonad maturation stage 3-5 (N=41) determined from histological samples of Atlantic cod sampled simultaneously to those in this study. Bars represent standard deviations

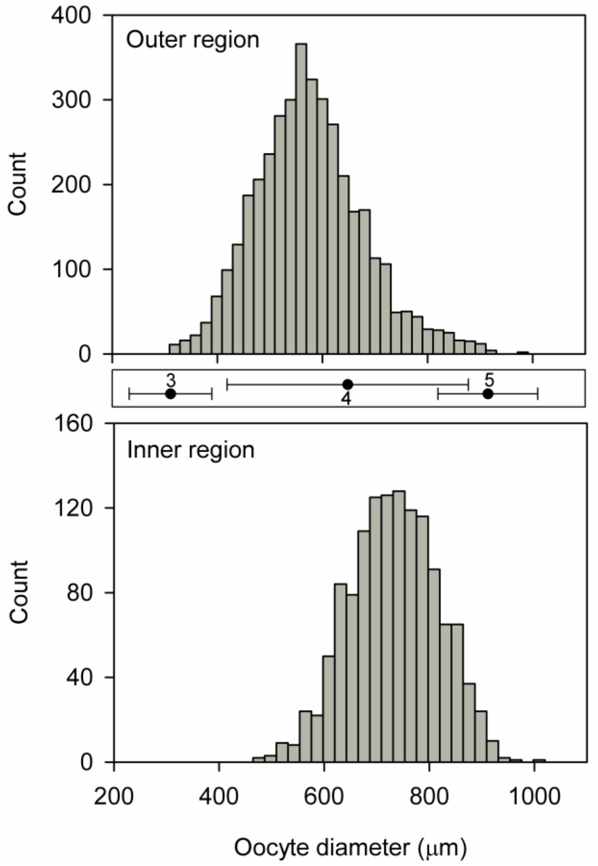


Fig. 3

Redone from Thorsen and Kjesbu (2001). The line represents the relationship between mean oocyte diameter (μm) and oocyty density (no. eggs g^{-1}) as determined for Northeast arctic cod by Thorsen and Kjesbu (2001): Oocyte density = 2.137 × 10^{11} × oocyte $\text{diameter}^{-2.700}$. The filled dots shows the results from a 1 g manually counted sub sample using fish from this study and the corresponding mean oocyte diameter as determined using the auto-diametric analysis (see materials and methods)

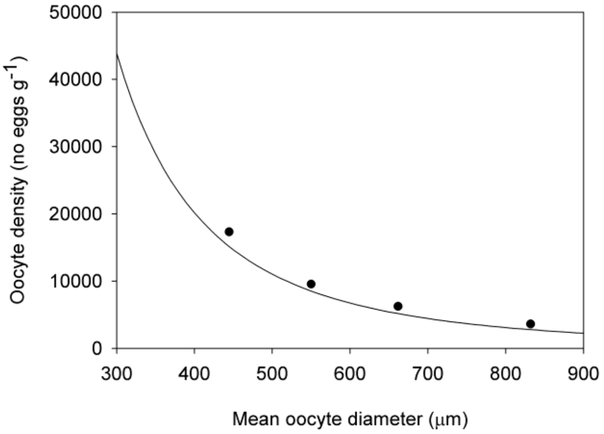


Fig. 4

The mean potential fecundity (no. eggs × 10^6) in West Greenland female Atlantic cod (*Gadus morhua*) from the Nuuk fjord system. Open circles: cod from the inner region of the fjord (N=12). Filled circles: cod from the outer region of the fjord (N=40). Lines represents linear regression done separately for each area on the full data set (lines are coincident): Inner region, Y = 0.1068 + 0.1184x, r^2 = 0.69, P=0.021. Outer region, y = 0.1079 + 0.1189 x, r^2=0.72, P<0.0001, where the length groups are numbered sequentially from 1-9. Bars represent standard error.

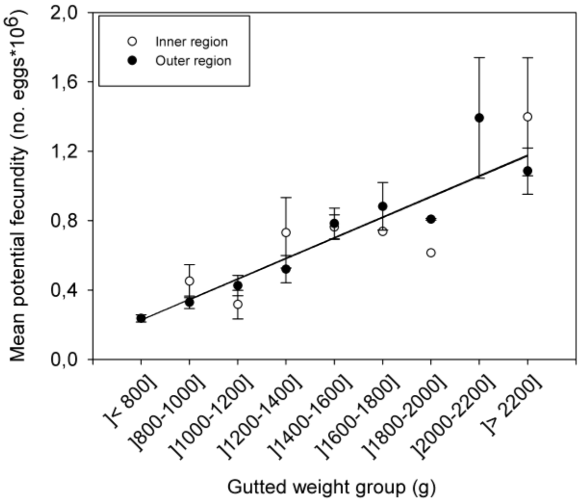


Fig. 5

The mean egg energy content (J) in female Atlantic cod (*Gadus morhua*) sampled in the inner (open circles, N=13) and outer (filled circles, N=39) region of the Nuuk fjord system as a function of gutted weight (g). Bars indicate standard error

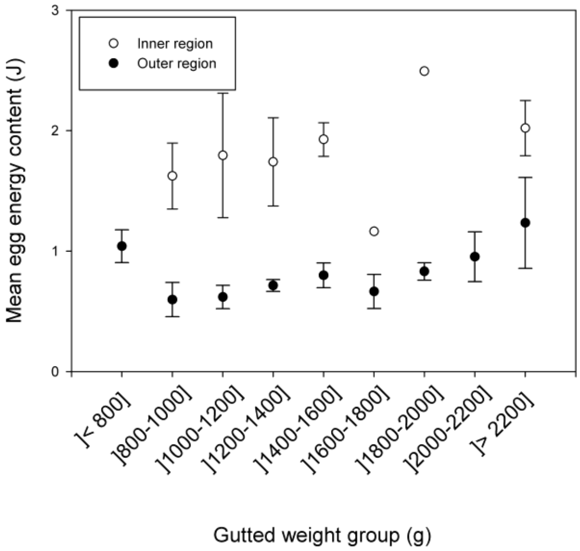
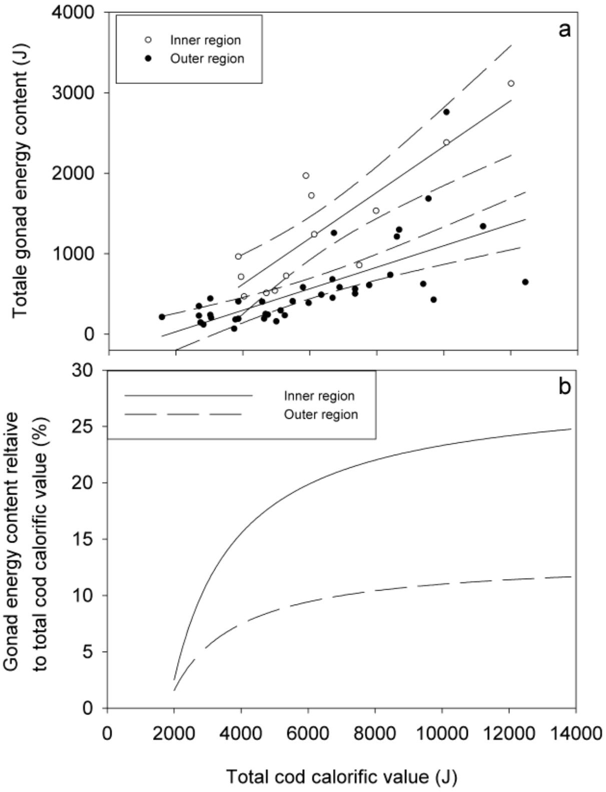


Fig. 6

a: total gonad energy content (J) of West Greenland female inshore cod (*Gadus morhua*) from the Nuuk fjord as a function of total cod somatic calorific value (J). Open circles: inner region of the Nuuk fjord. Filled circles: outer region of the Nuuk fjord. Lines represent linear regression and dotted lines are 95% confidence intervals. Y = 0.28510x -520 and Y = 0.1336x -236 for the inner (P=0.0002) and outer (P<0.0001) region respectively.

b: Total energy content of female gonads relative to total cod somatic energy content (%) as a function of female cod size in terms of energy (J). Based on linear regressions from Figure 6a



Paper VI

An Ecopath model for the Nuuk fjord, Greenland

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Unfinished manuscript

An Ecopath model for the Nuuk fjord, Greenland

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Abstract

Capelin (*Mallotus villosus*) and Atlantic cod (*Gadus morhua*) are the dominant fish species in many sub-arctic ecosystems. This is also the case in the lightly exploited Nuuk fjord, West Greenland (64˚N), but the future may include an intensified fishery on both species with subsequent ecosystem changes as a result. Here, a mass-balanced 19 compartment Ecopath model is presented for the Nuuk fjord, aiming to describe system energy flow and determine the relative importance of its key species. Additionally, three Ecosim scenarios are presented to explore the ecosystem response to different capelin fishing intensities (Low: 1.32 g C m^{-2} yr^{-1}; Medium: 4.37 g C m^{-2} yr^{-1}; High: 5.29 g C m^{-2} yr^{-1}). The system was dominated by high primary producer and capelin biomasses (7.0 g C m^{-2} yr^{-1} and 7.3 g C m^{-2} yr^{-1}, respectively). Capelin in turn constituted the main prey of higher trophic levels and was an intermediate energy node. Consistent with this, primary producers and capelin were estimated as the most important groups through trophic impact and keystoneness analysis. Total system catches were restricted to high trophic levels (mean=3.8) and required 17.5% of the primary production with zooplankton (30%) and large capelin (22%) having the highest demands. The low capelin fishing intensity scenario resulted in little system impact, but with increasing intensity noticeable declines were seen in both capelin and cod with other groups benefitting from reduced competition. Accordingly, a future fishery should be based on further knowledge on capelin stock structure and its trophic position in relation to top predators.

Introduction

The Nuuk fjord is a sub-arctic fjord system on the Greenlandic West coast covering approximately 2000 km^2. The key fish species in the system are capelin (*Mallotus villosus*) and Atlantic cod (*Gadus morhua*) which both spawn within the fjord (Smidt, 1979; Friis-Rødel and Kanneworff, 2002). Both species are present throughout Greenland, but supposedly have local genetically distinct populations in the Nuuk fjord (Sørensen and Simonsen, 1988; Storr-Paulsen *et al.*, 2004) which renders them vulnerable to over-exploitation on a local scale. The Nuuk fjord system is commercially lightly exploited and of fishes, only cod are fished beyond that of local use, but in limited amounts (2009 tonnes caught in 2009, Anonymous, 2010). However, there have been several trial fisheries for capelin in the region, and currently the cod fishery is not limited by quotas but rather by low prices, suggesting a more intense fishery if prices increase. The Nuuk fjord system has the characteristics of a wasp-waist system. This entails that capelin inhabits an intermediate trophic level and is the primary mediator of energy from lower to higher trophic levels (Cury *et al.*, 2000). Due to this key position in the ecosystem, variability in capelin biomass (of natural or anthropogenic origin) can have ecosystem impacts from both a top-down and bottom-up perspective (Arrhenius and Hansson, 1993; Vilhjalmsson, 2002). Similarly, the cascading effects of a changed cod biomass have been documented in several occasions often as a result of a population collapse following overexploitation (Frank *et al.*, 2005).

This study aims to describe the ecological interactions and carbon flow of the Nuuk fjord system in a lightly exploited state. This serves as a first attempt to join and quantify knowledge from the area and will provide insight into the importance of capelin and cod to energy flow. Such knowledge is essential for future local management on these species if they are to be fished. Additionally, studies on capelin life history traits from the region suggests a large effect of climatic changes and if such effects are to be put into an ecosystem context a more holistic approach is needed. Hence, the carbon flow of the Nuuk fjord system is quantified using the Ecopath mass balance model concept (Polovina, 1984; Christensen and Walters, 2004). This is done with special emphasis on key species capelin and cod and using the Ecosim component of the Ecopath software a future capelin fishery is modelled and its effects on the ecosystem are described.

Materials and Methods

Study site

The Nuuk fjord is located on the Greenlandic west coast (64˚18N, 51˚11W, Fig 1). The fjord has an average depth of approximately 300 m with a sill at the fjord entrance of 250 m. The tidal amplitude is 4 m ensuring a large vertical mixing. Glaciers in the inner fjord introduce a large summer run off which stabilizes the water column in early spring. Average temperature within the fjord is approximately 2˚C, with surface waters reaching 4˚C in the summer months while bottom water stays between 1-1.5˚C. Primary production peaks in July coincident with the highest PAR radiance (Jensen and Rasch, 2008, Mikkelsen et al. in prep.). For a more detailed description on fjord hydrography see Jensen and Rasch (2008).

The Ecopath model

The mass balance model was based on the Ecopath with Ecosim version 6.0 software (Christensen *et al.*, 2005; http://ecopath.org). Ecopath creates a mass balanced static snapshot of the ecosystem using two master equations. This is under the assumption that the production of a group (species or guild) equals the biomass lost to fishing, export, predation and natural mortality. This is formally expressed as:

$$P_i = Y_i + B_iM2_i + E_i + P_i(1 - EE_i) + BA_i$$

where P_i is the production of the ecological group i, which equals sum of catches (Y_i), predated biomass (B_iM2_i), net migration (E_i), other mortalities ($M0_i$, disease, old age) and biomass accumulation (BA_i) (Pauly *et al.*, 2000). MO_i is given by $M0_i = P_i(1–EE_i)$, where the ecotrophic efficiency (EE_i) is the fraction of the production of a group that is accounted for in the models, through predation, fishing and other export, or biomass accumulation. In addition to this overall mass-balance equation each individual group in the model is balanced according to: Consumption = Production + Respiration + Unassimilated food.

In addition to these basic data, the diet composition of all groups must also be entered. This is done by dividing the average yearly prey intake into the other system groups according to the share made up by each group.

Input data

All data is entered as gram carbon m^{-2} $year^{-1}$ (g C m^{-2} yr^{-1}) and conversion factors from other units can be seen in appendix A. The Nuuk fjord is represented by 19 ecological groups most of which are comprised of more than one ecologically similar species (Table 1). Additional groups could easily be implemented (e.g. bacteria and birds), but as this is the first attempt to model the area and data on some groups is non-existing, the model should to some extent be considered a minimal realistic model. However, one focus of the study was to increase understanding of the pelagic interdependencies and accordingly, pelagic species were represented with finer resolution than the benthic community. Hence, the benthic community was jointly grouped as "benthos" and due to this grouping not all included species are mentioned (Table I) but see Sejr *et al.* (2010) for a more complete species list. Although ecologically important, birds and bacteria were left out of the model as only little uncertain data are available. This may affect the model result on some levels (see discussion), but previous versions of the model that included these groups yielded models that did could not be reasonably balanced or produced unlikely results. Also, macro algae, Greenland sharks (*Somniosus microcephalus*) and certain fish species (i.e. lumpsucker (*Cyclopterus lumpus*)) are not included in the model. For the latter two no biomass estimates or other data exists locally (or globally) and for the former their habitat makes up an insignificant amount of the fjord. All input data are summarized in Table I and the estimated diet composition of all groups in Table II.

Data from the Nuuk fjord were used when possible and otherwise personal communications with local experts or literature values from similar sub-arctic systems were applied. Especially data from Disko Bay (69˚N) has been used as it is on the same coast line and represents a similar ecosystem. Additionally, the model for Sørfjord in Northern Norway by Pedersen et al. (2008) was consulted as this model represents a lightly exploited cod dominated system similar to the system addressed here. Whenever possible, the model represents the Nuuk fjord 2007 or 2008 situation to reduce inter-year variability.

For all groups the following parameters are needed to balance the model: Y_i, B_i, P/B_i, Q/B_i, EE_i and DC_{ji}. Besides catches (Y_i) and complete diet (DC_{ji}) one out of the remaining parameters can be left out as program algorithms will estimate it based on the other parameters (Christensen *et al.*, 2005). Under steady-state conditions the P/B_i parameter is equal to total mortality, Z (Allen, 1971), which was used in estimating P/B_i for cod.

Some model groups were defined as "ecological anchors" and served as fixed holding points in the model balancing process and were only changed when other options did not seem reasonable. These anchors were groups where good quality local data were available and included primary producers, cod, capelin, zooplankton and detritus and to lesser extent biomass estimates on whales, fishes, shrimp and other large zooplankton groups (see appendix A). Only cod and seals are caught commercially in the system and catch data were available for these species. All other catches are limited to that of local hunters and was considered insignificant for the model, although its extent is unknown.

Model balancing was done by focusing on the most severe problems rather than employing a top-down or bottom-up approach and was generally based on suggestions in Christensen *et al*. (2005). Hence, initially the ecotrophic efficiency (EE_i) values for the individual groups were evaluated and adjusted to fit within the 0-1 range. When these were balanced the remaining output parameters were checked (especially the growth efficiency, P/Q) and if outside a reasonable ecological range the model was modified. Diet was used as the initial balancing parameter as diet composition data is scarce for the Nuuk fjord and often represents a temporal limited snapshot of the integrated feeding behaviour. If changes here were too drastic compared to the original data or other studies other parameter changes were made; most often group biomass (Table III).

Ecosim input

The Ecosim component allows for time based dynamic simulations of changing fishing intensity on the ecosystem. It uses input from the Ecopath model and based on a set of linear and differential equations derived from the Ecopath master equation it calculates future biomasses of all groups based on a pre-set fishing scenario (Christensen *et al.*, 2005). The master equation of Ecosim is:

$$\frac{dB_i}{dt} = g_i \sum_i Q_{ji} - \sum_i Q_{ij} + I_i - (MO_i + F_i + e_i) * B_i$$

where dB_i/d_t represents the growth rate of group i during the time interval dt in terms of its biomass B_i, g_i is the net growth efficiency (production/consumption ratio), MO_i is the non-predation natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate. The key parameter, consumption rates Q_{ji}, are calculated based on the “foraging arena” concept, where B_i’s are divided into vulnerable and invulnerable components, and it is the transfer rate between these two parameters that determines if control is driven by top-down (i.e. Lotka–Volterra), bottom-up (i.e. donor-driven) or of an intermediate type (Walters *et al.*, 1997). If vulnerabilities are low an increase in predator abundance causes little change in prey abundance and vice versa. The vulnerabilities for all predator-prey interactions are pre-set prior to Ecosim model runs, and model performance is highly dependent on vulnerability settings. Time series data on abundances and fishing intensities are advisable to use in obtaining the best estimates of vulnerabilities. This is done by adjusting vulnerabilities in order to achieve congruence between observed and modelled abundances under known conditions (e.g. Griffiths *et al.*, 2010). However, no time series data are available for the Nuuk fjord except for cod catches and such calibration procedures were not possible. Hence, all vulnerabilities were set at default values (2.0) in the model assuming neither top-down or bottom-up control.

Based on the Icelandic capelin fishery in the 1990’s and coincident biomass estimates of the capelin stock (Vilhjalmsson and Carscadden, 2002) three Ecosim scenarios were set up. Current catches (e.g. cod and seals) were kept constant and only the fishing intensity on large capelin was modified. The scenarios were 1) a fishing pressure relatively identical to the Icelandic (67% of the fishable population caught – 4.37 g C m^{-2} yr^{-1}), 2) a low fishing pressure (20% - 1.32 g C m^{-2} yr^{-1}) and 3) intense (over)fishing pressure (80% - 5.29 g C m^{-2} yr^{-1}). Each scenario was allowed to run for ten years with fixed fishing intensities. For the three scenarios the relative biomass changes for cod and capelin groups as well as groups being the most affected (>50% change in biomass) are reported on graphically.

Model output

Summary statistics

The system is described in a number of summary statistics. In addition to the estimated missing ecosystem parameters (typically EE_i) I have chosen the ones most relevant in evaluating the questions posed in this study, as well as those describing the system in general.

The total system throughput represents the sum of all flows in the ecosystem and is useful in system comparisons representing flows from all consumption, respiration, export and flow to the detritus. The maturity of the system was evaluated by the ratio between system primary production and respiration with values around one indicating a mature system, values >1 indicating a young system and values <1 typical of heavily polluted systems (Odum, 1971). A further overall description of the system is presented through transfer efficiencies (%). This is the proportion of energy transferred between trophic levels and is calculated as the ratio between the export at a trophic level plus the transferred flow to the next trophic level and the total throughput on that trophic level. Furthermore, fractional trophic levels were estimated for all groups with producers having trophic level one and all other group trophic levels were equivalent to the weighted average of the consumed prey's trophic level.

Keystoneness and mixed trophic impact

To evaluate each individual group as a potential key species in the ecosystem a keystoneness index was calculated using the Ecopath routine. The routine assigns a value to each group based on its impact on other groups in relation to its own biomass. The index combines a measure of group biomass in relation to total system biomass and the mixed trophic impact which calculates the impact a change in specific group biomass has on other groups. Hence, a group with a relatively small biomass having a large ecosystem impact gets a high value (Libralato *et al.*, 2006). The mixed trophic impact also allows gives a graphical representation of how changes in different groups quantitatively affect other groups, positively or negatively. Adding to this is a flow diagram of the system, where each group is represented with relative biomasses and all interactions are scaled to strength. As the detritus biomass was relatively large in the model this group has been assigned a biomass value of 0.1 in this context to allow for distinction between other groups.

Results

Model balancing

The initial model had high EE values for especially krill, amphipods and mesozooplankton. However, simply increasing the biomass (i.e. a bottom-up approach) of these groups would lead to unrealistic estimates. Rather, the high EE values were a result of intense capelin predation pressure caused by the combination of a high biomass of capelin and a diet consisting of few prey groups. Capelin data on biomass was considered an "ecological anchor" and was not changed (Appendix A). This left capelin diet information as balancing parameter but this was also based on local information and only slight changes were made to the diet composition. Instead, the diet import was increased from 0.5 to 0.9 (for both small and large capelin). This did not completely balance the model for krill but krill biomass was based on one sampling transect in May 2007 and based on Pedersen *et al*. (2008) krill biomass was increased to 1.5 (from 0.34) to accommodate predatory demands. Similarly, the biomass of amphipods was increased (Table II).

EE for phytoplankton was initially too high and biomass was increased slightly for the group in spite of it being considered an "ecological anchor". However, calculations of biomass was based on integrated chlorophyll values, and the depth (0-150 m) may have been set too low to include all production and increasing biomass was the only approach that allowed for realistic model estimates (see discussion).

The estimated Von Bertalannfy growth parameter "k" for cod was low (0.069), even though cod growth is slow in the area (Brander, 1995). Using catch data from the region the growth equation was slightly modified (W_{inf} and W_{mat}) and "k" was re-estimated (0.091).

Other model estimates that caused an imbalance in either EE or other parameters such as gross food conversion (GE, production/consumption) where balanced by changing diet compositions for various groups. These included only minor changes and I refer to Table II for an overview of the changes made.

Model output – group level

Phytoplankton production was 125 g C m^{-2} yr^{-1} and of this 117 g C m^{-2} yr^{-1} is directly consumed by especially zooplankton and krill. Accordingly, the zooplankton groups had the highest flow to detritus (41 g C m^{-2} yr^{-1} combined for proto- and mesozooplankton) followed by phytoplankton (8 g C m^{-2} yr^{-1}). The detritus group was predated upon primarily by the benthos group (24 g C m^{-2} yr^{-1}) but detritus EE remained low (0.38) but this would increase if a bacteria group was included in the model. EE for whales was 0.0 as they accumulate biomass export it through migration and the same is partly true for seals, albeit hunting removes some biomass (0.003 g C m^{-2} yr^{-1}) giving an EE of 0.49. The only other group subject to fishing is large cod, but EE remains low for the group (0.43). EE for the small cod was only 0.05 similar to that of small capelin which were the lowest EE values except for whales. Large capelin had an EE of 0.53 whereas the other small pelagics had a higher value of 0.94.

Large pelagics had the highest trophic level (4.07, Table III) with large cod (3.85), seals (3.83) and large benthic fish (3.66) almost equally high. Large capelin had a trophic level of 2.96 and there was a large gap to lower levels such as mesozooplankton (2.16) and krill (2.15).

Mixed trophic impact and keystoneness

The mixed trophic impact quantifies the effect perturbations in a group biomass will have on other groups (Fig. 2). Phytoplankton, and to some extent other lower trophic levels, fuels the ecosystem and had pronounced positive impacts on higher trophic levels. Many groups had little impact as a result of a relatively low biomass (e.g. small pelagics). Capelin are in comparison very abundant and this is also reflected in negative impacts on prey groups and positive impacts on predators such as cod. Such direct positive/negative interactions between predator-prey connections suggest an interactive system that is susceptible to perturbations. For instance, an increase in large capelin biomass negatively affects prey but also small pelagics as a result of prey competition. All groups had negative impacts on themselves as a result of intra-group competition.

The patterns from the mixed trophic impact were also evident in the keystoneness analysis (Fig. 3). Hence, the most important group were phytoplankton followed by large capelin. This was followed by mesozooplankton and amphipods while large cod is only number eleven in keystoneness ranking. This was most likely caused by the high trophic level of cod and the relatively large dependence on a single prey item (capelin). The keystoneness index is negatively related to biomass (Libralato *et al.*, 2006), which emphasizes the high ranking of capelin and phytoplankton as their biomass is only surpassed by the benthos group. It is however noticeable that no groups have values above one indicating that no one group has a clear defining structuring role in the system.

Model output - community level

Summary statistics on the system are given in Table IV and the relative flows in Fig. 4. The system transfer efficiency (9.3%) is the geometric mean of all trophic levels and a more detailed description can be seen in Table V with efficiency being similar between detritus and primary producers. Consumption of top predator seals required 19% of primary production while zooplankton groups (30%) and large capelin (22%) had the highest single group requirements. Although low in absolute terms (0.06 g C m^{-2} yr^{-1}) total catches in the system required 17.5% of the primary production as they were limited to high trophic level species (seals and large cod, mean trophic level=3.8).

The total primary production/total respiration ratio was 0.94 and the connectance index was 0.27 (Table IV). The later is the realized links in the system in relation to the total possible number of links. These two parameters are linked as both gives an indication of ecosystem maturity as does the omnivory index which was 0.25, describing the degree of consumer specialization (0=specialist).

Ecosim scenarios

All scenarios had a large impact on certain group biomasses. The scenario equalling the Icelandic fishing intensity (4.37 g C m^{-2} yr^{-1}, Fig. 5 middle) while at the same time maintaining other fishing intensities (large cod and seal) caused a decline in all cod and capelin groups with biomasses being reduced below half of current estimates. Biomass increases were seen in small pelagics and large benthic fish which doubled; a trend consistent in all scenarios. With low capelin fishing intensity, large capelin biomass increased slightly while small capelin decreased (Fig. 5 top). Cod biomass decreased initially but seemed to rebound to initial levels at the end of the period as did the biomass of large capelin. The decrease in small capelin biomass was seen in all scenarios and is also evident when removing all fishing (not shown). Otherwise, the no-fishing scenario generally caused little changes in any groups. However, large capelin biomass increased and coincidently with the large capelin increase, the cod groups increased slightly. The scenario with high fishing intensity on large capelin (5.29 g c m^{-2} yr^{-1}) was detrimental to all cod and capelin groups with all biomasses decreasing to approximately 25% of initial estimates (Fig. 5 bottom). Benefitting from this was small pelagics with a tripled biomass.

Discussion

Parameterization and group level

The estimated parameters and subsequent model balancing only represents one possible interpretation of the data, and the model can only give as good a fit as the quality of the input data allows (Essington, 2007). However, the model does provide insight into the system, joins current knowledge and identifies areas where further data is needed to improve the model. These areas especially include high trophic level fish groups and other high levels. Hence, the “ecological anchors”, defined as high quality data in certain groups, were mostly limited to lower trophic levels with data on phytoplankton, zooplankton and capelin being the best in the model followed partly by cod. To generally improve the model, studies on ecosystem interactions such as trophic levels (e.g. isotopic analyses, Fredriksen, 2003) would allow for better estimates of model fit. Furthermore, specific studies on feeding and abundance on especially higher trophic levels would ensure better model estimates in specific groups. This also includes groups excluded from the present model, such as birds, bacteria and certain species of mammals and the grouping of benthos needs better resolution (Pedersen *et al.*, 2008). In spite of these shortcomings, the model was fairly easily balanced and estimates are within reasonable ranges and certain patterns can be deduced, especially on mid- and lower trophic levels.

Phytoplankton EE was very high for the system (0.93) also in comparison with other sub-arctic systems (e.g. Northern Norway, Pedersen *et al*. 2008, EE=0.80; Barents Sea, Blanchard *et al*., 2002, EE=0.29) and phytoplankton biomass was increased from the initial model due to too high EE value. This suggests a very effective grazing community in the system, which may also be partly true. However, phytoplankton biomass may also have been underestimated as data for this parameter are collected at a part of the fjord where the vertical mixing is very pronounced (Jensen and Rasch, 2008; J. Mortensen, pres. comm.). Here, the chlorophyll measurements where integrated to a depth of 150 meters, but this should perhaps be increased (200-250 m) thus increasing biomass and production and subsequently lowering the EE value. In general, a deficit of available resources at lower trophic levels was a problem in the initial model and the biomasses of zooplankton groups were increased but EE values are still high for these groups (Table III). The initial reason for this large demand was caused by intense capelin predation. Capelin is by far the most abundant living group in the system, and the biomass and diet estimate are among the best model estimates (Appendix A). Hence, these were kept unchanged and the only option that allowed for model balancing was increasing capelin diet import to 90% (changing other proportions relatively) as system productivity would otherwise be to low irrespective of balancing approach. Hence, the migration pattern of Greenlandic capelin reviewed by Friis-Rødel and Kanneworff (2002) is supported in this study with almost all consumption taking place outside the fjord, but nevertheless predation in the fjord is so intense that zooplankton groups EE remain high (Table III). This apparent key role of capelin with the capabilities of exerting top-down control was also supported by the mixed trophic impact and keystoneness analyses where capelin was the second most important group underlining its importance as both predator and prey. Hence, capelin appears to play a key role in the system consistent with the wasp-waist ecosystem theory (Bakun, 2006) but due to the large capelin biomass, bottom-up control does not appear to be as pronounced, which makes the system less susceptible to capelin inter-year variation. Such system redundancy maintained by high wasp-waist species abundance is also a typical wasp-waist system characteristic (Jarre, 2003). This is also reflected in the relatively low EE for large capelin (0.52) compared to other Ecopath models (e.g. 0.79, Blanchard *et al.*, 2002) and the much higher EE value of other small pelagics (EE=0.94). However, this may also partly be an artefact of capelin consumption being underestimated in the model. Hence, during capelin off shore migration they are a primary prey of minke whales (*Balaenoptera acutorostrata*) and harbour porpoise (*Phocoena phocoena*) which are common in the off shore region (Neve, 2000; Bergstrøm and Vilhjálmsson, 2006) as well as other species of seals (Ringed seals (*Phoca hispida*), Hooded seals (*Cystophora cristata*) not included in the model. Furthermore, bird predators are not included and these could consume a noticeable amount of capelin (Merkel *et al.*, 2002), although this is more likely primarily small capelin which also could explain the extremely low EE values for this group (0.05).

No data on historic capelin abundance exists, but a contributing factor in maintaining the current apparent high capelin abundance could be coincident low cod population size. Greenlandic waters have historically supported large cod populations evidenced by a large fishery (Horsted, 2000) and prey composition data (Table II) suggests that this will have had an impact on capelin through an intense predation pressure. Indeed, the importance of capelin to cod is found in many waters (Pálsson, 1997; Nielsen and Andersen, 2001) and correlations between capelin abundance and cod condition have been suggested (Rose and O'Driscoll, 2002; Hedeholm et al. Unpublished manuscript). Cod is presently the only commercially exploited fish species in the system and it had an estimated trophic level of 3.85 which is similar to other systems (range 3.7-4.4) albeit slightly lower (see studies reviewed by Pedersen *et al.*, 2008). The biomass of large cod (0.21) is high compared to heavily fished areas such as the North sea (B=0.07, Christensen, 1995) and similar to lightly exploited systems such as the Sørfjord, Norway (B=0.22, Pedersen *et al.*, 2008). Based on published Ecopath models, Tudela *et al*. (2005) categorized ecosystems as either over- or not exploited using the trophic level of the catch and the primary production required to support it. The values estimated here (Catch trophic level=3.8, Primary production required=17.5%) qualifies the Nuuk fjord ecosystem as belonging to the sustainably fished ecosystems, which is consisted with the relatively species poor and limited catch. Hence, current fisheries do not appear to be detrimental to the cod population.

Community level

The total system throughput was 545 g C m^{-2} yr^{-1} (Table IV). This is very close to other sub-arctic systems (Blanchard *et al.*, 2002; Pedersen *et al.*, 2008) indicating that the current model is accurate as well as suggesting some shared characteristics of the systems.

The transfer efficiencies declined with increasing trophic level (Table V) which is agreement with that of theoretical ecology (Odum, 1971). The mean of the individual transfer efficiencies was 9.8% and this is in good agreement with a value of 10% suggested for other marine ecosystems (Pauly and Christensen, 1995) but lower (half) than estimates from other high latitude systems (Bowering and Lilly, 1992; Pedersen *et al.*, 2008) which are often efficient short food chains (Richardson, 2008). The reason for this is probably a much lower fishing intensity in the Nuuk fjord compared to other systems, and especially a fishery at lower trophic levels would increase the transfer efficiency. Hence, in the Nuuk fjord the primary production required to support total system catches was 17.5% compared to 65.5% in the Sørfjord model in northern

Norway (Pedersen *et al.*, 2008) although the trophic level of the catch was similar (3.5 and 3.8 in Sørfjord and Nuuk, respectively). The low values also entail that a lot of dead organic material (mainly fecal pellets) flows to detritus and is subsequently re-mineralized which could also support the fairly high primary biomass and production in the system (e.g. Pedersen *et al.*, 2008).

The total primary production/total respiration ratio was 0.94 indicating a fairly mature system (Odum, 1971) consistent with a system that has not seen large perturbations through commercial catches and again parallels to the similar Sørfjord system are evident in similar ratios (1.022, Pedersen *et al.*, 2008). Other overall system descriptors, the system omnivory index (0.25) and connectance index (0.27) describe the inner linkage ecosystem structure and are expected to increase with system maturity as more links are formed. Hence, as values here are similar to values presented in studies with higher total primary production/total respiration ratios (Blanchard *et al.*, 2002; Duan *et al.*, 2009) both indexes were expected to be higher. However, model structure in this study can offer some explanation. Hence, some realized links are probably missed through poor/missing local diet data and the grouping will also have joint several links into one link, most noticeably the benthos group, and this will reduce both connectance and omnivory values.

Ecosim

In spite of the limitations imposed on the Ecosim simulations through lack of time series data and subsequently more reliable vulnerability estimates and predator consumption rates, the general patterns in the groups of most interest in this study (i.e. capelin and cod) seem valid and are based on good data. Hence, the three Ecosim scenarios resulted in some general patterns suggesting the importance of capelin, especially to cod. Hence, capelin biomass declined with increasing fishing intensity and this was coincident with a negative response of cod groups (Fig. 5). This was also supported by the increase in cod biomass coincident with that of capelin in the no-fishing scenario. Capelin prey groups krill and amphipods also responded to capelin changes, increasing in abundance when capelin declined but less than 50%. The zooplankton groups remained almost unchanged. In addition to these predator-prey responses underlining capelin importance, the results indicate that the current inshore cod fishery is not negatively affecting the cod population. However, if the current cod fishing intensity is kept constant with the introduction of a capelin fishery the cod population will likely decline, and may have difficulties rebounding if capelin is continuously fished (Rose and O'Driscoll, 2002). Such considerations are especially important as capelin cohort strength can be expected to be highly variable (Vilhjalmsson, 2002), and if the management is not accordingly flexible the potential for an overexploitation is eminent. This necessitates yearly surveys on the stock size similar to those preformed routinely in Icelandic waters.

Small pelagics benefitted from the capelin fishery in all scenarios as a result of decreased prey competition from capelin and reduced predation from small and large cod. This is in accordance with results from the mixed trophic impact analysis, where an increase in capelin biomass caused a negative development in small pelagics (Fig. 2). The large benthic fish was the last group to show any consistent change, increasing in all scenarios. This was caused by little predation on the group, with only a small degree of cannibalism (Table II). Had better data been available, groups such as seals and large cod would probably, to some extent, feed on small stages of species in this group. Additionally, there is a local fishery on especially red fish that has not been included in the study as the extent of the catches is unknown. Lastly, the catchability of most species in this group is unknown and hence the biomass estimates are associated with uncertainty and estimates are based on nearby coastal areas but if these are transferable to the fjord is unknown and these results should not overly emphasized.

Small capelin declined in biomass initially in all scenarios and then stabilized at a low level. No ecological explanation for this could be found and it is most likely a result of model parameterization. Hence, small capelin biomass is estimated based on knowledge on large capelin, and the consistent decline could well be a parameterization artefact and reflects the need to obtain further knowledge on small capelin in the system. Alternatively, the response reflects incorrect vulnerabilities in the model. These should be re-estimated but this is dependent in time series data on biomass and catches, and currently no monitoring program on fish is available.

Conclusion

The present Ecopath model combines all present knowledge on the Nuuk fjord and demonstrates that capelin is a key component of the Nuuk fjord ecosystem. It especially has the potential to top-down control main prey groups due to a high biomass. It is also important as prey to many higher trophic levels, but clear evidence of bottom-up control was not found. However, this may rest on the exclusion of certain important ecological groups, and highlights the general need for more data on especially higher trophic levels. Ecosim simulations suggest that a future fishery in capelin is possible, but must be managed from a multiple species perspective as especially cod responds to capelin biomass variability.

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Table I

Individual groups and the main taxa included in the Ecopath model for the Nuuk Fjord system.

Group number	Group name	Taxa
1	Whales	*Megaptera novaeangliae*
2	Seals	*Pagophilus groenlandica*
3	Large benthic fish	*Anarhichas* spp., *Sebastes* spp., *Reinhardtius hippoglossoides*, *Boreogadus saida*, other fish (see Pedersen and Kanneworff (1995))
4+5	Large and small cod	*Gadus morhua*
6	Large pelagics	*Salmo salar*, *Salvelinus alpines*, *Melanogrammus aeglefinus*, other fish (see Møller *et al*. (2010))
7	Small pelagics	*Myctophidae*, *Clupea harengus*, *Ammodytidae*, juvenile stages of other fishes
8+9	Large and small capelin	*Mallotus villosus*
10	Shrimps	*Pandalus borealis, Pandalus Montagui, Pandalus Propingus*
11	Krill	*Thysanoessa raschii, Thysanoessa inermis, Thysanoessa longicaudata*
12	Amphipods	*Parathemisto abyssorum, Parathemisto libulla*
13	Scyphomedusae	*Siphonophora*
14	Chaetognatha	*Sagitta elegans, Eukrohnia hamata*
15	Mesozooplankton	*Calanus* spp., *Metridia* spp., *Pseudocalanus* spp., *Onacea* spp., *Microsetella* spp.
16	Protozooplankton	Heterotrophic dinoflagellates, ciliates
17	Phytoplanton	
18	Benthos	Crabs, echinoderms, clams, mussels, polychaetes, amphipods etc.
19	Detritus	

Table II

Final diet inputs for the Nuuk fjord Ecopath model and the initial input in parentheses. Numbers represent the share of the diet (g C m^{-2} yr^{-1}) constituted by each group. All columns sum to one.

Predator/Prey	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
1: Whales																		
2: Seals																		
3: Large benthic fish			0.0729															
4: Small cod		0.005	0.00506		0.0125													
5: Large cod		0.005	0.000607															
6: Large pelagics		0.010 (0.036)																
7: Small pelagics	0.042		0.161	0.0842	0.100 (0.181)	0.040 (0.083)	0.01 (0.039)											
8: Large capelin	0.104	0.155 (0.129)	0.0194	0.632	0.577	0.44 (0.40)		0.022 (0.0)										
9: Small capelin	0.021		0.0194	0.104	0.033 (0.09)	0.17 (0.167)												
10: Shrimps		0.010	0.0239	0.011	0.09													
11: Krill	0.250	0.0617	0.195	0.011	0.028	0.009	0.29 (0.28)	0.0343 (0.171)				0.309	0.05	0.03				
12: Amphipods		0.0017	0.155	0.053	0.01	0.307	0.29 (0.28)	0.02 (0.212)		0.10		0.0206	0.05					
13: Scyphomedusae													0.05					
14: Chaetognatha						0.025						0.0515	0.03	0.02				
15: Meszooplankton			0.105			0.007	0.31 (0.30)	0.0234 (0.117)	0.02 (0.10)			0.55 (0.619)	0.50 (0.60)	0.75				
16: Protozooplankton							0.10		0.08 (0.40)	0.28	0.14	0.069 (0.0)	0.27 (0.17)	0.20	0.15	0.05		
17: Phytoplankton										0.20	0.71				0.75	0.90		
18: Benthos		0.0017	0.244	0.105	0.150 (0.102)	0.002				0.32								
19: Detritus										0.10	0.15		0.05		0.10	0.05		1.00
Import	0.583	0.750						0.900 (0.500)	0.900 (0.500)									

Table III

Summary of basic in- and output for Nuuk fjord Ecopath model. Estimated parameters are shown in bold. Parameter estimates from the balanced model is followed by the initial input/output. TL=Trophic level, B=Biomass, P/B=Production/Biomass, C/B=Consumption/Biomass, EE=Ecotrophic Efficiency, P/C=Production/Consumption, UA/C=Unassimilated/Consumption

Group name	**TL**	**B**	**P/B**	**C/B**	**EE**	**P/C**	**UA/C**
1: Whales	**3.53 (3.69)**	0.0370	0.100	4.500	**0.000**	0.022	0.200
2: Seals	**3.83 (4.34)**	0.0595	0.102	17.410	**0.494 (1.598)**	0.006	0.200
3: Large benthic fish	**3.66 (3.68)**	0.0327	0.346	2.000	**0.421**	0.173	0.200
4: Small cod	**3.92 (4.33)**	**0.1350 (0.0706)**	1.500 (1.000)	**5.368 (4.893)**	**0.051 (0.147)**	0.279 (0.204)	0.200
5: Large cod	**3.85 (4.32)**	0,2080	0.683	1.875	**0.432**	0.364	0.200
6: Large pelagics	**4.07 (4.36)**	0.3000	0.100	1.436	**0.345 (1.243)**	0.070	0.200
7: Small pelagics	**3.47 (3.50)**	0.3000	0.500 (0.265)	2.000	**0.938 (2.218)**	0.250 (0.132)	0.200
8: Large capelin	**2.96 (3.61)**	6.6160	0.630	7.830	**0.526 (0.184)**	0.080	0.200
9: Small capelin	**3.07**	**0.7300**	5.000	**31.630**	**0.046 (0.031)**	0.158	0.200
10: Shrimps	**2.84**	0.3920	2.000	13.300	**0.070 (0.065)**	0.150	0.200
11: Krill	**2.15**	1.5000 (0.3390)	2.500	15.200	**0.829 (11.614)**	0.164	0.200
12: Amphipods	**3.22 (3.23)**	0.8000 (0.4890)	2.700 (4.332)	3.474	**0.969 (5.664)**	0.777 (1.247)	0.200
13: Scyphomedusae	**3.21 (3.22)**	0.1000	2.000	23.500	**0.588 (0.588)**	0.085	0.200
14: Chaetognatha	**3.16**	0.0700 (0.0200)	3.800	19.000	**0.944 (2.321)**	0.200	0.200
15: Meszooplankton	**2.16**	0.8000 (0.6350)	8.137	59.170	**0.856 (2.188)**	0.138	0.300
16: Protozooplankton	**2.05**	0.7570	30.940	93.710	**0.782 (0.903)**	0.330	0.300
17: Phytoplankton	**1.00**	7.0000 (5.6400)	17.890		**0.931 (0.959)**		
18: Benthos	**2.00**	7.3920	0.500	3.300	**0.493 (0.477)**	0.152	0.600
19: Detritus	**1.00**	309.0000			**0.380 (0.583)**		

Table IV

Summary statistics from the Ecopath model output.

Parameter (unit)	Value
Sum of all consumption (g C m^{-2} yr^{-1})	255
Sum of all exports (g C m^{-2} yr^{-1})	60
Sum of all flows into detritus (g C m^{-2} yr^{-1})	97
Total system throughput (g C m^{-2} yr^{-1})	545
Sum of all production (g C m^{-2} yr^{-1})	174
Calculated total net primary production (g C m^{-2} yr^{-1})	125
Total primary production/total respiration	0.94
Total biomass (excluding detritus, g C m^{-2} yr^{-1})	27
System transfer efficiency (%)	9.3
Omnivory index	0.25
Connectance index	0.27

Table V

Transfer efficiencies (%) for each trophic level in the Nuuk fjord Ecopath model as well as overall efficiencies for the system.

Source	Trophic level			
	II	III	IV	V
Producer	19.6	7.6	6.3	5.2
Detritus	10.3	6.4	5.6	5.0
All flows	17.4	7.5	6.2	5.2
Transfer efficiencies (%)				
From primary producers	9.8			
From detritus	7.2			
Total	9.3			

Figure 1

The study area in the southern part of Greenland and the Nuuk fjord.

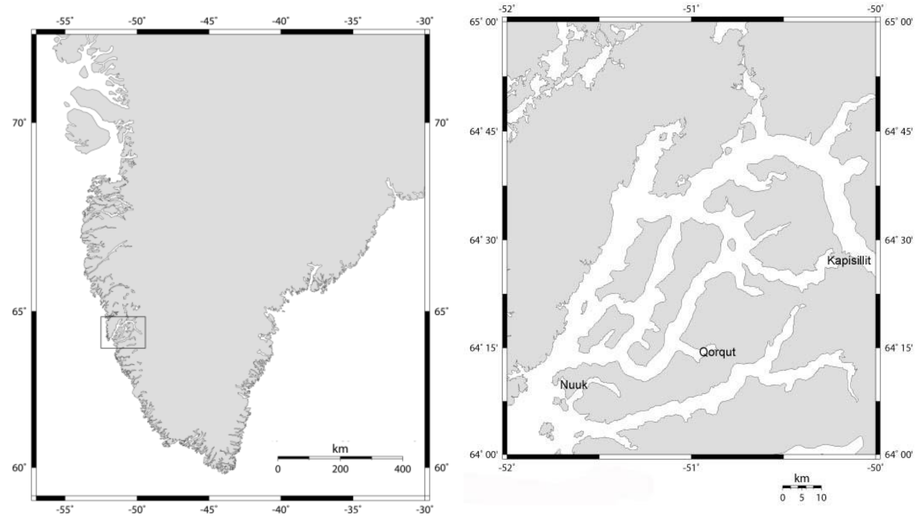


Figure 2

Mixed trophic impact of all groups in the Nuuk fjord Ecopath model. Filled circles indicate positive impacts and open circles indicate negative impacts. The circles are scaled proportional to the impacts. Note that the three last groups reefer to the fishery in the mentioned species.

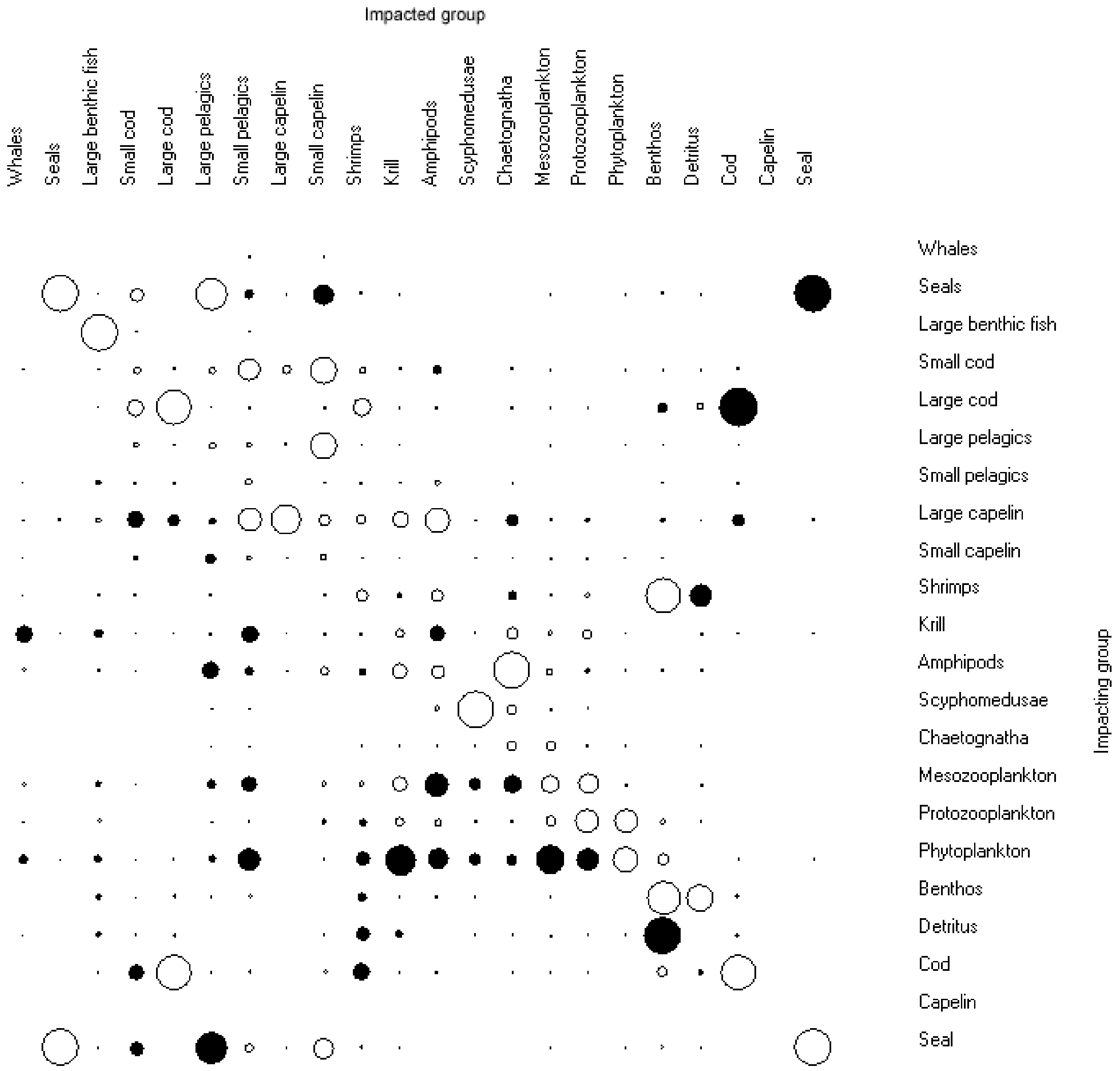


Figure 3

Keystoneness index and relative overall effect for all groups in the Nuuk fjord Ecopath model. The groups are indicated by numbers and listed in order in the legend with descending keystoneness index values.

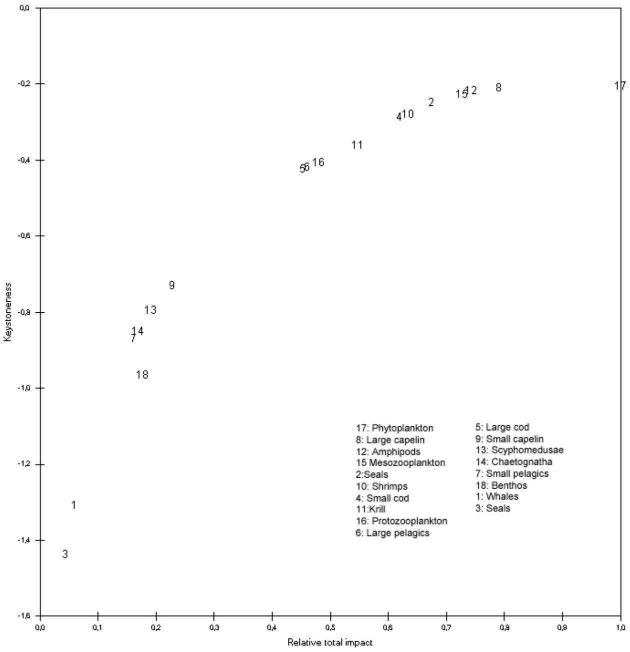


Figure 4

Flow diagram of the Nuuk fjord Ecopath model with groups vertically positioned according to trophic level. All groups are scaled relative to biomass except the detritus group which has been set 0.1 to allow for the distinction of other groups. Lines indicate the relative flow between groups.

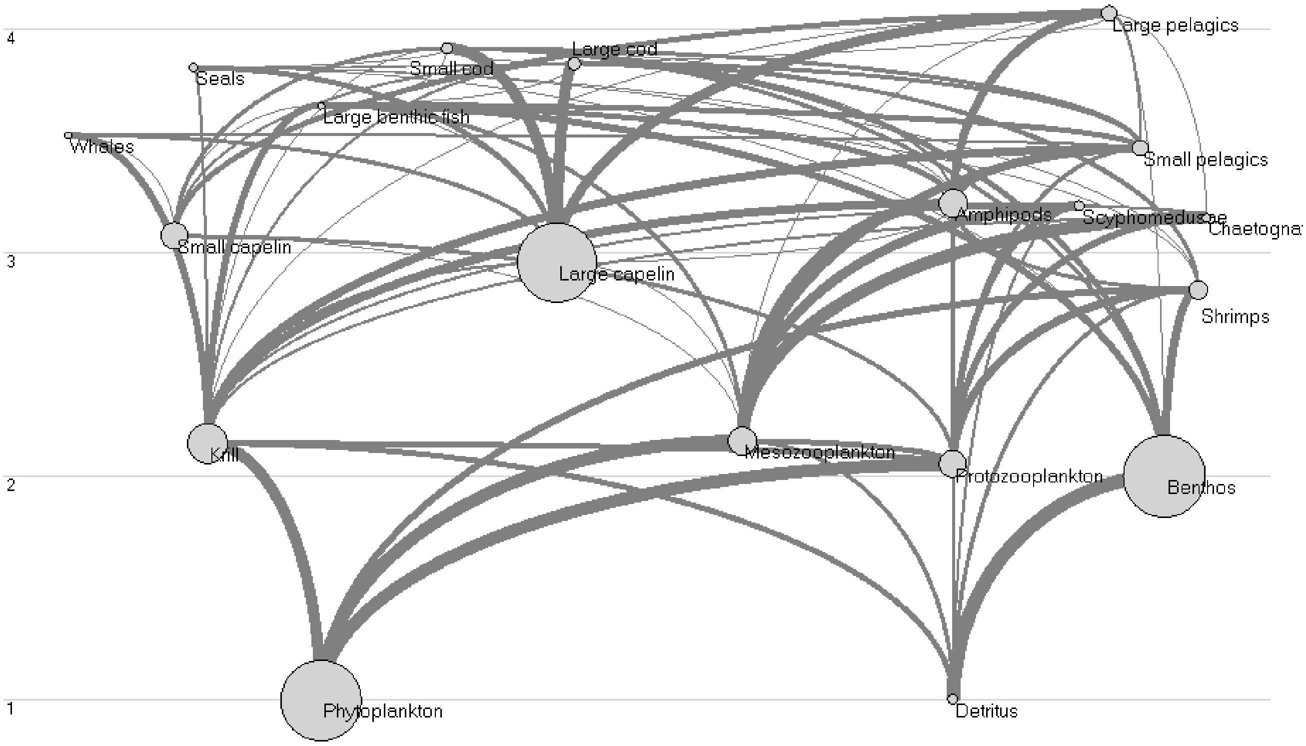
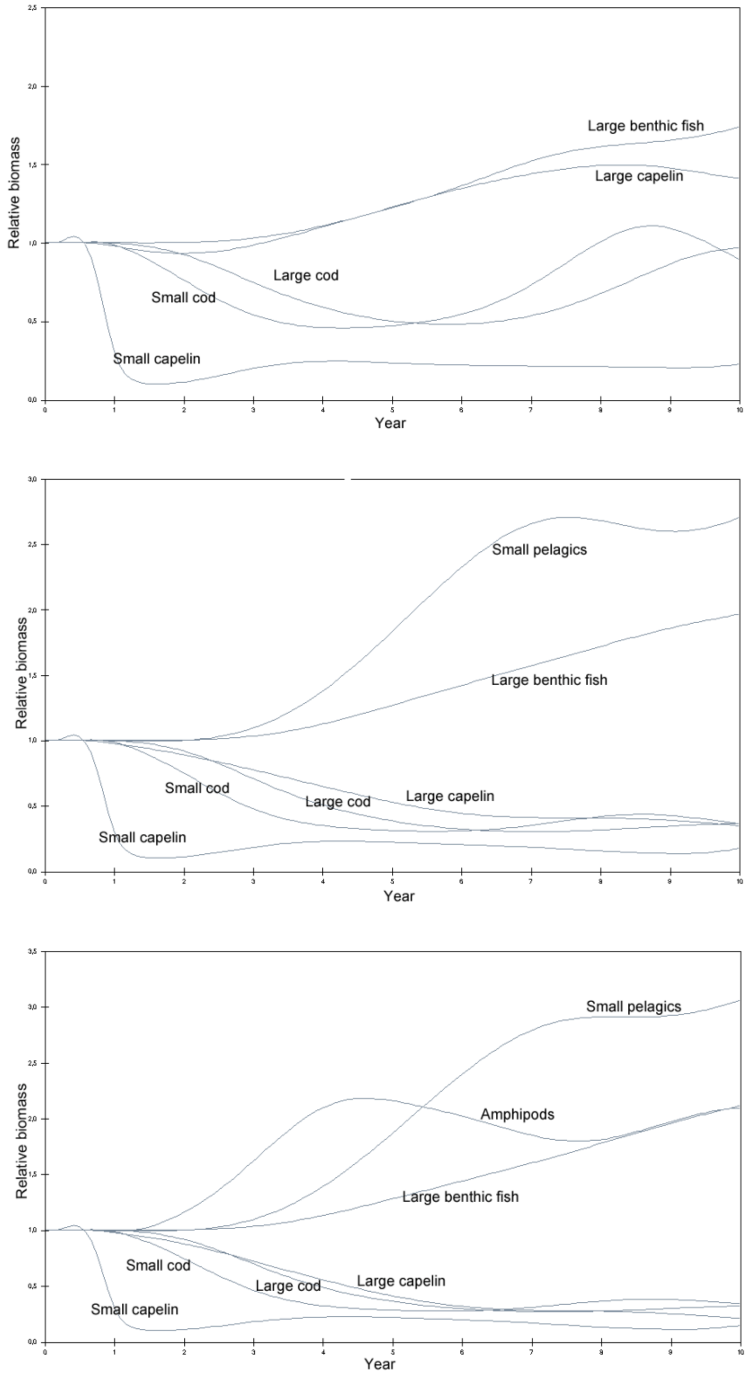


Figure 5

Results from three Ecosim scenarios showing relative biomass changes in a 10 year period in selected groups from the Nuuk fjord Ecopath model. Only capelin fishing intensity is changed between scenarios, and this is set at low (top, 1.32 g C m^{-2} yr^{-1}), Icelandic (middle, 4.37 g C m^{-2} yr^{-1}) and high (bottom, 5.29 g C m^{-2} yr^{-1}). Only cod and capelin groups and groups with relative biomass changes >0.5 are included from each scenario.



Appendix A

Detritus: This is defined as all sinking dead organic material including dead/dying phytoplankton cells and fecal pellets. Based on monthly measurements of the vertical sinking flux presented in Jensen *et al.* (2008) the mean detritus biomass is set at 309 g C m^{-2} yr^{-1}.

Benthos: This study is mainly focused on the pelagic and most benthic organisms are joined in one group. This includes invertebrates but not fish (see later). This of course groups species not necessarily ecologically similar and also entails a large fraction of within group carnivorous behaviour. However, as the benthos is not the focus of this study this does not influence conclusions. The unassimilated fraction is set at 0.6 for this group (Pedersen et al 2008). For more details on species composition of the benthos I refer to Sejr *et al.* (2010) and addition to those mentioned by Sejr *et al.* (2010) crabs are also included.

Biomass: Using data from Sejr *et al.* (2009) from the stations within the fjord to obtain a biomass of B=10.56 g*0.1 m^{-2}. Based on the species composition of the benthos presented in Sejr *et al.* (2009) and the conversion factors from Ricciardi and Bourget (1998) I apply a conversion factor of wet weight/carbon=0.07 and thus B=7.392 g C*m^{-2}.

Production and consumption: I use values suggested by Pedersen *et al.* (2008) and Bundy *et al.* (2000). Hence, P/B=0.5 and Q/B=3.3.

Diet: As no estimates are available for the Nuuk fjord, I assume that the benthic groups prey only on detritus. The likely cannibalism within the group is ignored to avoid mass balance related issues in model balancing the diet.

Primary producers:

Biomass: Using original data summarized in Mikkelsen *et al.* (2009) the biomass was calculated by integrating chlorophyll a measurements from 0-150 meters for every month. The phytoplankton community was dominated by diatoms (Mikkelsen *et al.,* 2009, Arendt *et al.*, 2010) and a C/chl.a ratio of 30 was used to calculate the carbon content. Hence, a biomass of 5.64 g C*m^{-2} was estimated.

Production: Data from Jensen *et al.* (2008) was used to calculate a mean production throughout the year. No data was present from December and January, but it is assumed that the production was the same as in February and November respectively (close to 0). Hence, a production of 88.77 g C*m^{-2}*yr^{-1} was estimated. The production of DOC by primary producers could well be important but no estimate exists for the area. Hence, the 12% suggested by Pedersen *et al.* (2008) was used here as a minimum estimate (Amon, 2004).

Thus DOC production is 12.105 g C*m^{-2}*yr^{-1} (total of 100.875 g C*m^{-2}*yr^{-1}) and the P/B ratio is 17.886 (see also Sakshaug *et al.,* 1994).

Protozooplankton:

Biomass: Data from Arendt *et al.* (2009) was used. Only data from stations GF3 and further into the fjord was used. Data was only available from May in Arendt *et al.* (2009), and data from the closely situated Disko Bay was used for comparison (Levinsen and Nielsen, 2002). In Nuuk fjord the May biomass was 0.9511 g C m^{-2} and for Disko at the same time the biomass was 0.24375 g C m^{-2}. Hence, it appears that the biomass is higher in the Nuuk fjord (the same pattern was observed for the primary production). As the May production is a factor 0.95/0.24= 3.902 higher the same is assumed to be the case for the yearly biomass. Hence, the average yearly biomass in Disko was 0.194 (ciliates and dinoflagellates combined) and accordingly the biomass in Nuuk was estimated as 3.902*0.194=0.757 g C m^{-2} yr^{-1}.

Production: The same approach as for the biomass calculations was used. Hence, I find a production for May in Nuuk of 19.06 g C m^{-2} (Arendt *et al.,* 2009) and for the whole year in Disko of 6.0 g C m^{-2} yr^{-1}. As the relationship between these two and the equivalent biomasses is nearly the same, I assume that the relationship found for biomasses also applies for production values. Hence, I estimate a production of 6.0 g C m^{-2} yr^{-1} * (0.95/0.24)=23.412 g C*m^{-2}*yr^{-1} and consequently a P/B ratio=30.94.

Consumption: From Hansen *et al.* (1997) I get a growth efficiency of 0.33. Hence, consumption = (100*production)/33 = 70.945 g C m^{-2} yr^{-1} and Q/B=93.719

Diet: These are based on data from Pedersen *et al.* (2008) as no data are available from the Nuuk fjord.

Mesozooplankton:

Biomass: As copepods constitute the vast majority of the mesozooplankton (Thor *et al.,* 2005, Mikkelsen *et al.,* 2009) I base the calculations on this group. Using data summarized in Mikkelsen *et al.* (2009) the biomasse was estimated at 4.23 mg C m^{-3}. It is assumed that the zooplankton is distributed evenly in the top 150m of the water column which gives a biomass of 4.23 mg C m^{-3} * 150m=0.635 g C m^{-2} yr^{-1}.

Production: Using Huntley *et al.* (1992) and Madsen *et al.* (2008) and data from Mikkelsen *et al.* (2009) mesozooplankton production was estimated as follows: $P=Biomass*0.0445*e^{(0.111*temp)}$, where the temperature was 2.02˚C (yearly average). Hence, I have taken the biomass and temperature for each month and calculated a mean monthly production. These monthly estimates have been averaged over the whole year, and I find that P=12.40 g C m^{-2}*yr^{-1} and consequently a P/B=12.40/0.635=19.53. However, as copepod production is limited to approximately 5 months of the year (Madsen *et al.,* 2001) a P/B ratio of 19.53*(5/12)=8.1 was estimated

Consumption: The same approach (Hansen *et al.* 1997) as used for protozooplankton is used and I find that Q=100* (12.40*(5/12)=15.65 g C*m^{-2}*yr^{-1} and Q/B=24.66.

Diet: This was based on Pedersen *et al.* (2008) and Blanchard *et al.* (2002).

Chaetognatha: These have been shown to be important in similar systems, and since data are available they were consider them separately.

Biomass: From a Greenland Institute of Natural Resources 2008 survey in the Nuuk fjord an abundance of 57 ind. m^{-2} with an average length of 16.82mm was estimated. Based on Parsons and Takahashi (1973) I get that DW=0.00097*L$^{2.365}$ and Carbon/Dry Weight=0.46 and accordingly B=0.020 g C m^{-2} yr^{-1}.

Production and consumption: Based on Pedersen *et al.* (2008) these are estimated at P/B=3.8 and Q/B=19

Diet: This is based on Brodeur and Terazaki (1999), which is in general accordance with Falkenhaug (1991 - see Pedersen *et al.,* 2008))

Scyphomedusae/hydromedusae (jellyfish):

Biomass: Based on the Greenland Institute of Natural Resources survey in May 2008 an average abundance of 240 ind.*m^{-2} with an average size of 5.71mm was estimated. From Purcell *et al.* (2003) I have that weight=0.0056*length$^{1.85}$ which gives B=33.74 g m^{-2}. From Clarke *et al.* (1992) and Larson (1986 – see Pedersen *et al.* 2008) I have that DW=0.04595*WW and C/DW=0.086 which gives a B=0.1333 g C m^{-2}. However, as this estimate is high (Pauly *et al.,* 2009) and since this is probably a seasonal peak but none the less probably close to the yearly average (cf. zooplankton data), I estimate that B=0.1.

Production: Based on Pauly *et al.* (2009) and Pedersen *et al.* (2008) I estimate that P/B=2.0

Consumption: Based on Pauly *et al.* (2009) Q/B should be fairly high for this group, but as Greenland waters are cold compared to the reviewed Q/B ratios in that study, I chose to adopt the value suggested by Pedersen *et al.* (2008), Hence Q/B=23.50.

Diet: It is difficult to find good feeding data on this group. From Zavolkin *et al.* (2008) I have a qualitative description of feeding, and this is compared to Pedersen *et al.* (2008) for an initial diet estimate.

Amphipods (pelagic):

Biomass: Based on the Greenland Institute of Natural Resources survey in May 2008 I get an average of 108.6 ind. m^{-2}. Based on Hoffer (1972), Auel and Werner (2003) and measurements of amphipods from the fjord (unpublished data) I estimate an average 4.5 mg C ind^{-1}. Hence, B=108.6*0.0045=0.4887 g C m^{-2}.

Production: As the Q/B estimate is similar to those calculated by Ikeda and Shiga (1999, see below) I adopt their production estimate of 2.117 g C*m^{-2} and consequently P/B=4.332

Consumption: Based on on Auel and Werner (2003) *Themisto libellula* eats 1.93% of their own body weight pr. day and this is most likely the most abundant species in the fjord (Hedeholm *et al*., 2010). Furthermore, it was assumed that amphipods feed mainly for 6 months of the year and then $Q=180*0.0193*0.4887=1.6977$ and $Q/B=3.474$ which is identical to Ikeda and Shiga (1999) but lower than other estimates (Auel and Werner, 2003).

Diet: Based on Marion *et al.* (2008) on *Themisto libelulla* the diet was estimated. This diet is similar to other studies (see Marion *et al.,* 2008 and references therein). Marion *et al.* (2008) also show that prey composition and the zooplankton community are highly correlated, and this was considered in the estimates.

Shrimps: These are considered separate from other groups as fairly good data are available from Greenland waters and *Pandalus borealis* is of commercial importance in the region, although no fishing is done within the fjord. Other species include *Pandalus Montagui* and *Pandalus Propingus* and others (see Nielsen and Andersen, 2001)

Biomass: Based on a yearly survey done by the Greenland Institute of Natural Resources the biomass was estimated at 4.21 t km^{-2}. These data are from outside the fjord, but it is assumed that the density is the same within the fjord, which is supported by for instance cod feeding data (Nielsen and Andersen, 2001) and findings of shrimp larvae stages in the fjord (Pedersen and Smidt, 2000, Jensen *et al.,* 2008). A Carbon/Wet Weight ratio of 0.093 was used (Rumohr *et al.*, 1987 – see Pedersen *et al.,* 2008). Hence a biomass of 0.392 g m^{-2} yr^{-1} was used.

Production: This was based on Hopkins and Nilssen (1990) and was set at $P/B=2.0$.

Consumption: This was adopted from Bundy (2001 – see Pedersen *et al.,* 2008), and from $P/Q=0.15$ I get $Q/B=13.3$.

Diet: This was based on data from Pedersen *et al.* (2008) but modified according to Hopkins *et al.* (1991).

Krill: Being a possible key species in the system krill was treated separately, and also fairly good data was available.

Biomass: Analyzing subsamples from the Greenland Institute of Natural Resources survey in May 2008 and previous knowledge from stomach analyses in cod and capelin it was confirmed that the dominating species in the Nuuk fjord is *Thysanoessa raschii*. As krill make vertical migration (Ashjian *et al.* 1998) only samples collected at night during the survey were used. Hence, a mean density of 103 ind. m^{-2} (assuming that no krill where present below 120m). The lengths from the subsample (mean 17.6mm) and conversion factors from Dalpadado and Skjoldal (1996, length to wet weight, $\log WW=3.33*\log TL-2.58$) and Parsons and Takahashi (1973, wet weight to carbon, carbon/wet weight ratio=0.089) yields a biomass estimate of 0.339 g C m^{-2} yr^{-1}.

Production: Based on Zhou *et al.* (2005) it was calculated that Z=3.45. Christensen *et al.* (1995) estimate that Z=2.43 for North Sea krill. Size distributions from catches made on the May 2008 survey indicate a mortality of 2.35. Hence, based on these it was estimated that Z=P/B=2.5.

Consumption: Jarre-Teichmann and Guenette (1996) estimate P/Q=0.16 in the Alaskan Gyre. As this is a similar environment to the cold Greenlandic waters I adopt this value, and accordingly Q/B=15.20

Diet: Falk-Petersen *et al.* (2000) have demonstrated degree of carnivore in *Thysanoesaa Raschii*, which is also in accordance with stable isotope analysis from the Nuuk fjord (Hedeholm *et al.,* 2010). This is further supported by Mauchline (1980) and Nilsen *et al.* (2008). However, the degree of carnivori is not quantified and based on Pedersen *et al.* (2008) and Nilsen *et al.* (2008) the diet for the Nuuk fjord is estimated.

Capelin: These are divided into two stanzas, which separate at 12 months of age. This age was selected based on knowledge on growth patterns for Nuuk capelin (Hedeholm *et al.*, 2010), the catch composition of a recent survey (Bergstrøm and Vilhjalmsson, 2006) and the fact that they missed the smallest capelin in the catches.

As capelin are known to make feeding and spawning migrations (e.g. Vilhjamsson 2002) the same most likely applies to Greenlandic capelin (Friis-Rødel and Kanneworff 2002), as also evidenced by offshore catches on yearly surveys conducted by the Greenland Institute of Natural Resources. It is however not known how long the capelin spend feeding in the fjord, but as capelin feeding analyses have been done within the fjord it is known that they do feed here. Initially capelin feeding import is set at 50% in both small and large capelin.

Biomass: Bergstrøm and Vilhjalmsson (2006) estimate that capelin density is 270 t nmi^{-2}. Since the fjord is 2013km^2 it was calculated that B=6.616 g C m^{-2} yr^{-1} under the assumption that the carbon/wet weight ratio=0.12 (Sakshaug *et al.,* 1994; Greenstreet, 1996).

Production: Mortality (Z) is unknown for Greenland capelin. However, from Blanchard *et al.* (2002) an estimate of mortality in adult capelin in a period of no fishing (as in Nuuk) is Z=0.63. Houde *et al.* (1989) show that for fish larvae Z=0.0256+0.0123*temp. Using temperature data from Mikkelsen *et al.* (2009) I find that Z=0.0256+0.0123*2.02=0.0504 day^{-1} and hence Z=18.413 yr^{-1}. However, as this is for the smallest life stages I assume that Z declines over the period of one year, and accordingly P/B is estimated at 10.

Consumption: Vesin *et al.* (1981) estimates that capelin on average consume 5% of their body weight per day. Similar findings have been done for capelin in Greenland (Hedeholm *et al.,* 2010). Hence, using a weighted average of data from Vein *et al.* (1981) a consumption of 4.28% was estimated. However, capelin do not feed throughout the year (Bundy *et al.,* 2000) and a feeding period of 6 months is assumed as well as a WW/C ratio of 0.12, and subsequently Q/B=781457/99772=7.83.

Diet: The feeding of large capelin is adopted from Hedeholm *et al.* (2010, submitted manuscript) who describe capelin feeding in the area using both stomach analysis and stable isotopes. The diet of small capelin is adopted from O'Driscoll *et al.* (2001) and Pedersen and Fossheim (2008).

Small pelagics: This group includes the mesopelagic fish (*Myctophidae*), herring, sandell, squids as well as younger life stages of larger fish. *Myctophidae* can be very abundant, but survey data from The Greenland Institute of Natural Resources indicate that this is not the case in Greenlandic waters, but this is to be considered in the light of a survey that primarily targets species associated with the bottom (i.e. cod, halibut and shrimp). There is no commercial fishery on any of the small pelagics.

Biomass: This is initially set at 0.3.

Production: As no fishing is done on this group it was assumed that P/B=0.265 (Bundy *et al.* 2000).

Consumption: I use an initial Q/B value of 2.0 (Bundy *et al.,* 2000 and references therein)

Diet: The diet was assumed to be similar to that of capelin, with the group also being planktivorous and of similar size (Huse 1996).

Large pelagics: These include arctic charr, salmon and non-commercial rare gadiods. The salmonids are long lived, slow growing (especially arctic charr) and salmon is only migratory in the area. Furthermore, arctic charr only feed in the fjord for 3-5 weeks each year (Kunerup 2001). Hence, the mean yearly biomass is most likely low.

Biomass: This was initially set at 0.3.

Production: The fishing pressure is low/absent on all involved species and hence P/B must be similar or close to the natural mortality. Hence, an initial estimate of P/B=0.1 was used.

Consumption: Arctic charr is the most abundant of the species in this group and very similar to salmon hence based on the empirical relationship in Christensen *et al.* (2005) it was estimated:

$\log(Q/B)=7.964 - 0.204*\log W(\inf) - 1.965*T + 0.083*A$

$W(\inf)=10000$g (personal observation)

$T=3.634$

$A=20.365^2/229.632=1.806$ (aspect ratio of tail, determined using ImageJ, Rasband 2006)

From this I obtain that Q/B=1.436. I assume this is similar for the less abundant salmon and the other species.

Diet: The diet of arctic charr is described in Kunnerup (2001) on the east coast of Greenland and by Dempson *et al.* (2002). Salmon diet is described by Jacobsen and Hansen (2001) around the Faroe Islands. Under the assumption that arctic charr is the most abundant predator in these group the diet is described. As the timing of arctic charr migration to the fjord from the surrounding streams is coincident with capelin spawning migrations to the area I also assume that the fish component of the diet is mainly capelin which is also supported by personal observations.

Cod: Cod are divided into small and large cod stanzas separating at 36 months, which corresponds to the age at which they enter the fishery. Parameter estimates are obtained by analyzing catch data (ICES 2008). No biomass estimates for younger cod exists, but can be estimated by this division into stanzas.

Biomass: Catch data from NAFO region 1D were used as these is comprised of inshore catches in the Nuuk area (ICES 2008). Using back-calculations the biomass was estimated at B=0.208 g C m^{-2} assuming M=0.2 and Carbon/wet weight ratio=0.12 (Pedersen *et al.* 2008). Other parameters used to calculate the missing values are obtained from cod caught in 2008 in the fjord (unpublished)

Production: Based on catch data from 2006 and under the assumption that all cohorts have recruited equally to the population the mortality (Z) was estimated at Z=P/B=0.683.

Consumption: This is based on the empirical relationship shown by Christensen *et al.* (2005):

log (Q/B)=5.847+0.280*log Z -0.152*log W_{inf} – 1.360 * Temp +0.062*A, where

Z=total mortslity=0.683 (from catch data – ICES 2008)

W_{inf}=30000 g (Personal observation)

Temp = 2˚C = 3.634 ((1000/Kelvin, ICES 2010, Mikkelsen *et al.* 2009)

A= 1.5336 (aspect ratio, determined using ImageJ, Rasband 2006)

This gives Q/B=1.875, and all other values are estimated by the program.

Catch: 943 tons were landed in 2006 (ICES 2008). Assuming a carbon/wet weight ratio of 0.12 landings are 0.12*943/2013=0.0562 g C^{-2} yr^{-1}.

Diet: Autumn diet is found in Nielsen and Andersen (2001) while the summer diet is found in Hedeholm *et al.* (submitted manuscript) and it was assumed that the summer diet is representative for half the yearly intake. However, only large cod (>30cm) are represented in Nielsen and Andersen (2001). Hence, the diet of small cod is based on Hedeholm *et al.* (submitted manuscript). In the calculations the capelin eggs in the diet is considered as predation on the large capelin group and the predation on juvenile crabs (especially in the smallest cod) was considered part of the benthos. The diet of the smallest cod is modified slightly according to the seasonal changes in the diet seen in the largest cod. Specifically it is believed that the small capelin will appear in the diet of the smallest cod later in the season (Personal observation).

Large benthic fish: This group includes Redfish, Greenland halibut, Polar cod, American halibut, American plaice, sculpins etc. Little data (catch or abundance) exists for other large fish species than cod, and I have chosen to pool these in a large combined group and also, the benthic and epi-benthic community is not the main focus of this study.

Biomass: Using Pedersen and Kanneworff (1995) I averaged the biomass for all groups from 1988-1992. These average are summed and the biomass for the group was 722.5942 tons within area West3 (defined in Pedersen and Kanneworff 1995) which is roughly 22131km^2 (ImageJ, Rasband, 2006). Hence, B = 766.0298/22131km^2 = 0.0346 g C m^{-2}.

Production: The P/B ratio was estimated at 0.36 (Bundy *et al.* 2000, Blanchard *et al.* 2002, Pedersen *et al.* 2008). This fairly low estimate is in good agreement with the absence of any commercial fishery on any of these species in the fjord.

Consumption: No estimates of consumption for this group exist in the Nuuk fjord. Based on Bundy *et al.* (2000) I find for redfish that Q/B=1.3. For Greenland halibut I estimate that Q/B=2.65 (Blanchard *et al.* 2002). Hence, a Q/B=2.0 is used for the entire group.

Diet: This is based on data from Bundy *et al.* (2000), Bowering and Lilly (1992), Solmundsson (2007) and was weighted according to the estimated abundances for the species.

Harp seals: Other seal are ignored as they are not abundant in the fjord and are only occasionally seen (A. Rosing-Asvid, personal communication). Based on personal communication (A. Rosing-Asvid) it is estimated that 10000 individuals pass through the Nuuk fjord system, with a mean residence time of 3 months. Accordingly, the diet import is set at 9/12=0.75.

Biomass: It was assumed that the average weight of a harp seal is 100kg (Nilssen *et al.*, 1997) and that the carbon/wet weight ratio is 0.12 (Pedersen *et al.,* 2008). Hence, the biomass was estimated as B= (10000*0.1*0.12)/2013 = 0.0596 g C m^{-2} yr^{-1}.

Production: Based on Shelton *et al.* (1997) it was assumed that the mortality of harp seals is 0.102 and hence P/B=0.102.

Consumption: Q/B was set at 17.41 based on Bundy *et al.* (2000)

Catch: 4047 seals were landed in 2006 (A. Rosing-Asvid, pers. comm.). 75% of these are younger individuals and hence the mean weight was set at 40kg (Bundy *et al.* 2000). Assuming a carbon/wet weight ratio of 0.12 (Bundy *et al.* 2000) the landings were estimated at 4047*0.12*0.04t/2013=0.003 g C m^{-2} yr^{-1}.

Diet: This was based on Kapel (1995). The prey composition was averaged over the sampled months. However, the diet is modified, such that 2% of large pelagic are included in the model, as these are otherwise un-predated causing (unrealistic) parameterization problems.

Whales: Based on Boye *et al.* (2010) it was estimated that 20 humpback whales are on average present in the Nuuk fjord during 5 months of the year. Hence, 7/12 of the diet was set as imported. Other rare whales (mink whale, harbor porpoise etc., Bergstrøm and Vilhjalmsson 2006) in the system were ignored.

Biomass: A humpback weighs on average 31 tons (Bundy *et al.* 2000) and a carbon/wet weight ratio=0.12 was assumed (Bundy *et al.* 2001). Hence, the biomass estimate was 74.4 tons which is equivalent to 0.0370 g C m^{-2} yr^{-1}**.**

Consumption: Gaskin (1982-85) estimate that humpbacks consume 3% of their own weight pr. day. Hence, Q=2.232 ton C m^{-2} day^{-1} and accordingly Q/B=(2.232*150)/74.4=4.5.

Production: This was set at P/B=0.10 based on the longevity of large whales (Bundy *et al.* 2000)

Diet: Partly based on Bundy *et al.* (2000) and Blanchard *et al.* (2002) and on observations of humpbacks feeding very near shore on capelin (T. Boye, pers. comm.)

Model balancing

Using EE values, the largest initial unbalance of the model is krill. However, EE values are also large for amphipods and mesozooplankton. All these are the result of capelin being very abundant in the system and exerting a heavy predation pressure on these groups. The biomass of capelin is considered a good estimate and so is the diet composition. Rather than increasing the prey biomasses to meet demands I chose to increase the imported diet fraction of capelin as other approaches lead to ecologically unrealistic biomasses of prey. Hence, both small and large capelin diet import is increased from 0.5 to 0.9. This did not balance this part of the model, and I believe the data on krill abundance may be too low. This is based on the limited temporal resolution of this data and krill biomass is increased to 1.5 (Pedersen *et al*. 2008). Together with the increase in capelin imported diet this balances the model with regard to mesozooplankton and krill.

The small pelagic EE was too high. The diet of major predator groups (large cod, large pelagic and cannibalism) were reduced, and the P/B ratio was increased to better reflect the production of this group in accordance with that of for instance herring.

Due to an intense predation from large capelin, the EE-value for amphipods was too high. As the diet composition of capelin is a good parameter I instead changed the biomass of amphipods which was a more uncertain estimate based on only one sample.

Chaetognatha biomass was much too low to support the consumption by amphipods and was increased to a level similar to that presented in Pedersen *et al.* (2008).

Large pelagic are only preyed upon by seals but due to large seal abundance EE was too high for this group. The diet of seals was changed with the large capelin share being increased at the expense of large pelagic.

Too balance the mesozooplankton group the diet of scyphomedusa and amphipods was changed slightly since data on their diet in the system are non-existent. Also, the biomass of mesozooplankton was increased slightly based on recent data from an ongoing study in the inner parts of the Nuuk fjord (R. Swalethorp, pers. comm.).

Growth parameters for cod were slightly modified as the growth parameter “k” was lower than can be expected for cod, even in this cold region. Additionally, juvenile cod mortality was set 1.5.

Lastly, the phytoplankton was insufficient to support feeding demands. As the biomass calculation was based on integrated chlorophyll and these are considered the least reliable of otherwise well supported primary producer data. Hence, the biomass is increased slightly to meet demands.

This balances the model with regard to EE values. However, amphipods continue to have negative respiration values. To correct this, the P/B ratio is lowered (Pedersen *et al*. 2008) and the predatory pressure of large capelin is reduced. The latter was based on personal observations of capelin feeding heavily on eggs during spawning events. If Greenlandic capelin are to some degree iteroparous these eggs could account for a significant part of capelin energy intake.